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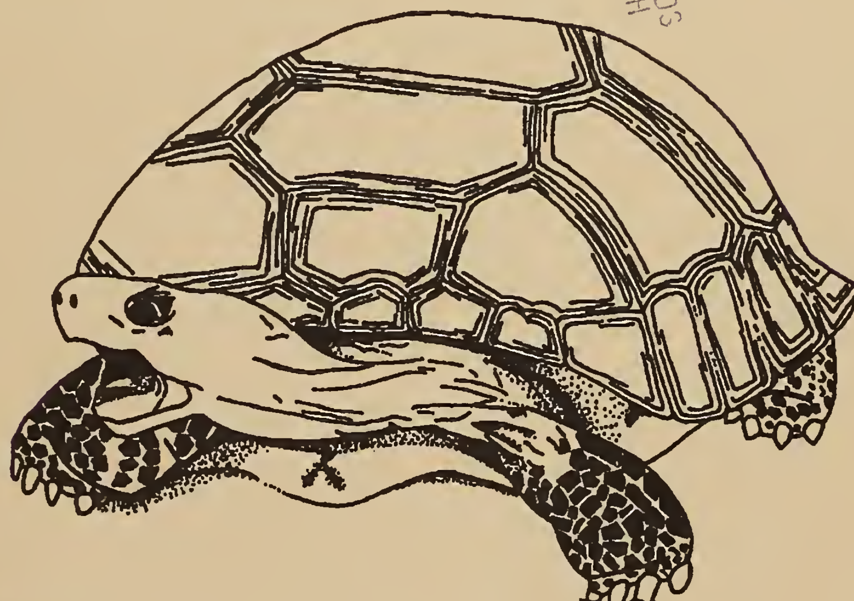
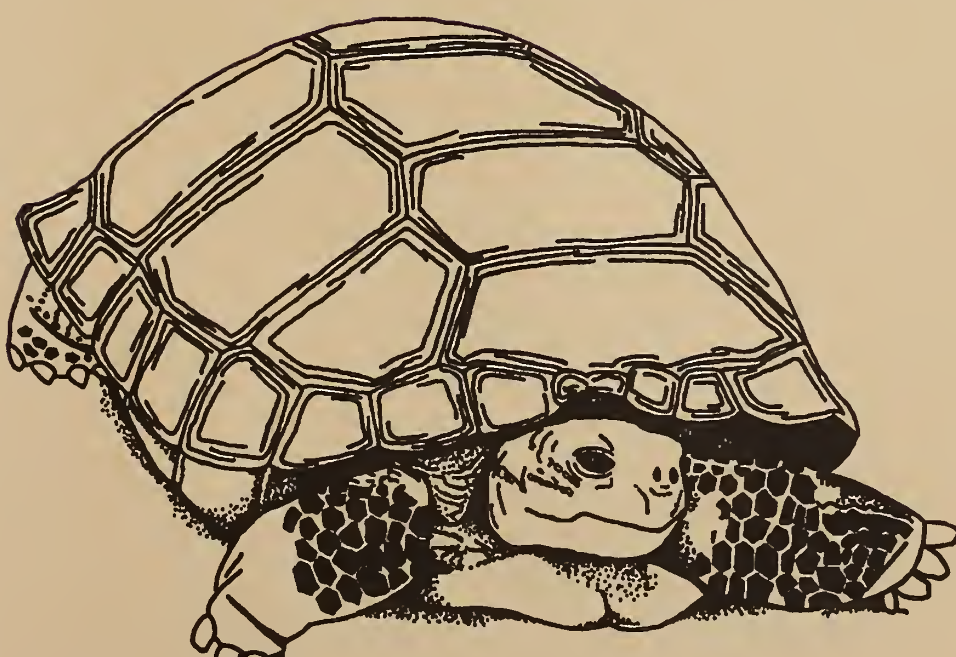
Desert Tortoise (*Gopherus agassizii*): Status-of-Knowledge Outline With References

Mark C. Grover
Lesley A. DeFalco





The Authors

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Introduction

The following document is based on literature on the desert tortoise including published books, peer-reviewed literature, government reports or memoranda, proceedings of symposia, nonpeer-reviewed journal material, and popular magazine articles. All peer-reviewed materials and any material that introduces new or unique observations on the desert tortoise is summarized in the text. Other materials, including popular magazine articles and nonpeer-reviewed materials are listed in the Bibliographies and Overview Papers and Additional Literature sections.

The format of this manuscript was created to facilitate citation of desert tortoise literature. It is the responsibility of the reader to use this manuscript with his or her own discretion (particularly with those materials not under peer review) to obtain a complete and unbiased account of desert tortoise information. It is further recommended that the user of this manuscript use it only for reference; direct citation from the summaries is discouraged.

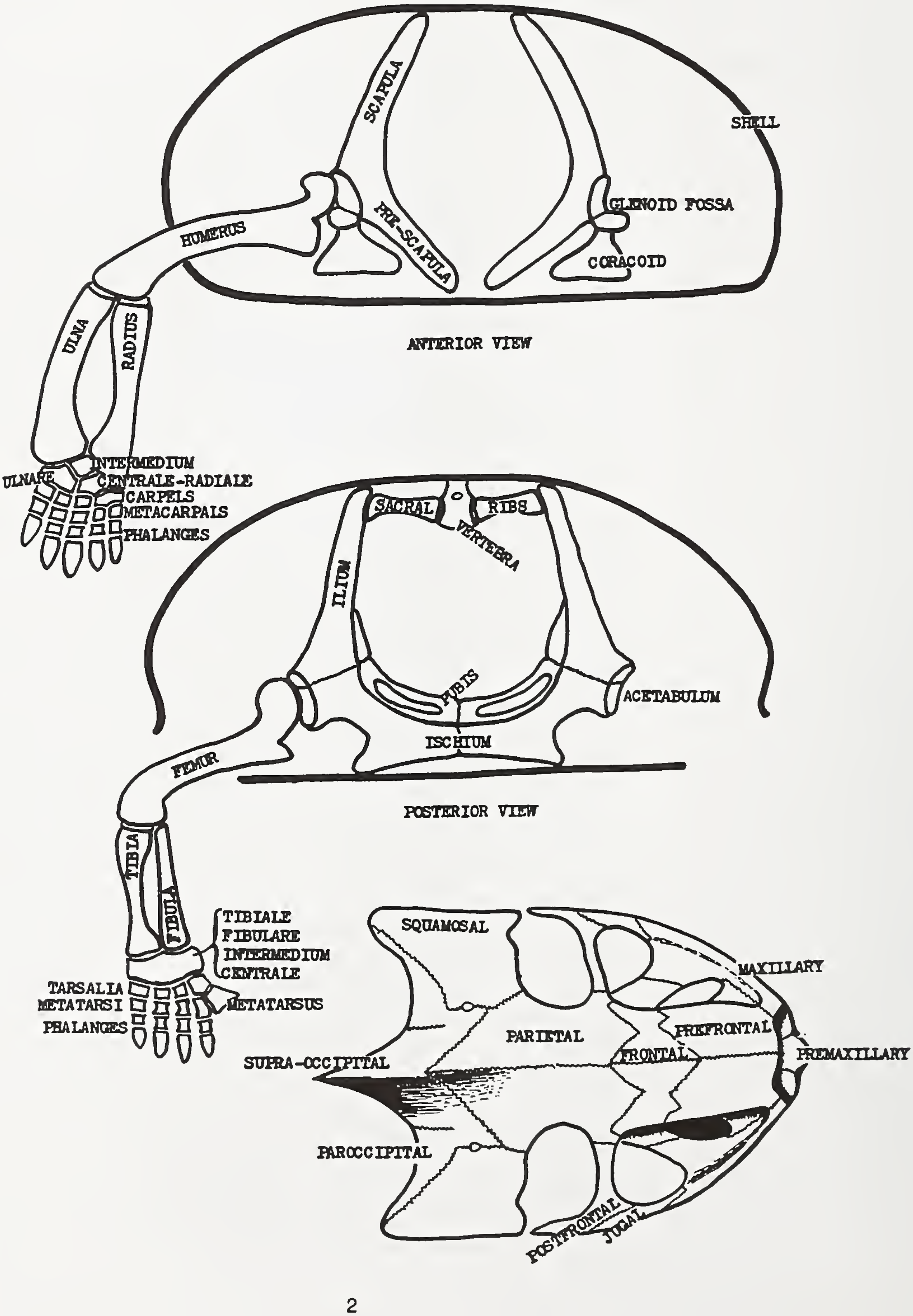
Information in this document covers materials up to and including those materials distributed and made available by 1991. The units of measure reflect the units of measure used in the source material. Scientific names also reflect those of the source material.

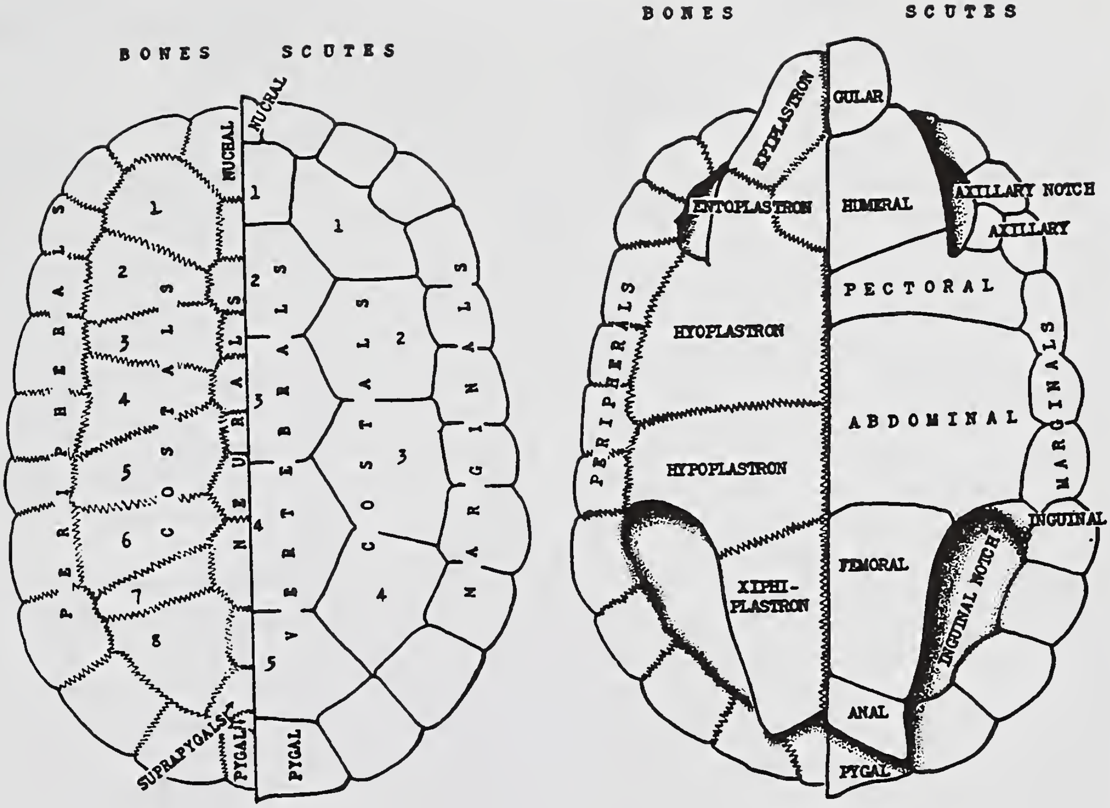
This manuscript integrates the format and material from Hohman, Ohmart, and Schwartzmann's 1980 annotated bibliography. Most of the information included in their bibliography is included here in addition to information from subsequent studies. This manuscript focuses specifically on *Gopherus agassizii*; other *Gopherus* species are included only when they were compared to *G. agassizii*. Although the nomenclature is not universally accepted, *Gopherus* was retained as the genus for the desert tortoise, largely because it is the name used in the bulk of the literature.

Existing literature encompasses the biological, ecological, and management aspects of the desert tortoise; however, the paucity of peer-reviewed literature pertaining to the desert tortoise suggests that specific aspects demand additional attention. Little research has focused on hatchling and juvenile desert tortoises exclusively. Juvenile tortoise habits, food preferences, and biological requirements have not received extensive examination. Research is also lacking on the nutritional needs of desert tortoises as well as the nutritional content of potential food plants and factors affecting their availability. To exercise practical management, knowledge regarding the factors that determine habitat quality and ecological comparisons and distinctions throughout the range of the desert tortoise are pertinent.

In addition to information on hatchling and juvenile ecology and desert tortoise nutrition, more information regarding population status is necessary. Present population densities throughout the range of the desert tortoise are generally much smaller than they have been historically. The influence of population density on social behavior and reproduction needs to be determined. Finally, mortality factors must be identified in light of recent population declines.

The following figures of a desert tortoise skeleton, skull, and shell were adapted from "Studies of the Desert Tortoise" by A. M. Woodbury and R. Hardy, Ecological Monographs, 1948, 18(2), 155, 157. Copyright 1948 by Ecological Monographs. Reprinted by permission.





Taxonomy

General taxonomy of the desert tortoise may be found in Bickham and Carr (1983), Crumly (1988), Ditmars (1907, 1933), Halliday and Alder (1987), Porter (1972), and Pritchard (1979b). The following discussion recognizes *Gopherus agassizii* at the species level and does not include general taxonomic designations, as they are more widely recognized and easily accessible in the general literature.

I. **Taxonomic classification:** *Gopherus agassizii* (Cooper); also, *Gopherus agassizi* no subspecies is formally named; however, Weinstein and Berry (1987) suggest three distinct genotypes based on shell morphometrics. Lamb and others (1989) also suggest three distinct “assemblages” based on mitochondrial DNA from samples taken at 22 localities throughout the range of the desert tortoise. The common name is desert tortoise (Carr 1952; Collins and others 1978; Ernst and Barbour 1972; Pope 1939); a less common name is western gopher tortoise (International Union for the Conservation of Nature and Natural Resources 1975).

II. **Original description:** *Xerobates agassizi*: type-locality in the “mountains of California, near Fort Mojave” (Cooper 1863). Type and collector unknown; however, Cochran (1961) records cotype as U.S. Nat. Mus. 7888: “juv. Utah Basin, Mojave River (catalog carries ‘Solado Valley, California’), J. G. Cooper, March, 1861.” (Auffenberg and Franz 1978b).

III. **Synonyms:** *Testudo agassizii* (Boulenger 1889; Cope 1875); *Gopherus agassizii* (Stejneger 1893); *Gopherus polyphemus agassizii* (Mertens 1960; Mertens and Wermuth 1955); *Scaptochelys agassizii* (Bramble

1971; 1982); *Xerobates agassizii* (Cooper 1863; Lamb and others 1989; True 1882; Weinstein and Berry 1987).

IV. **Relatedness to similar species**

A. The four species of North American tortoises have been divided into two groups (Polyphemus and Agassizii) on the basis of burrowing adaptations such as carpal structure and of cranial, cervical, and inner ear specializations (Auffenberg 1966a, 1976; Bramble 1971).

B. The Polyphemus group includes *Gopherus polyphemus* and *Gopherus flavomarginatus* (Auffenberg 1966a; Bramble 1978; Legler 1959). This group is characterized by fossorial adaptations (adaptations for digging) including a relatively wide head, a large, specially adapted inner ear with saccular otolith; short cervical vertebrae with enlarged, closely linked pre- and postzygapophyses; a specialized locking neck joint between the eighth cervical and first dorsal vertebrae; and a modified, stiff, spatulate carpus adapted for digging (Bramble 1972, 1982).

C. The Agassizii group includes *Gopherus agassizii* and *Gopherus berlandieri*. This group is more generalized with less fusion of the carpal elements and none of the fossorial adaptations mentioned above. Agassizii is considered to be the more primitive group (Auffenberg 1976; Bour and Dubois 1984; Bramble 1971, 1982, 1986).

D. *Scaptochelys* was proposed as a separate genus for the Agassizii group (Bramble 1971, 1982); however, *Xerobates* has received priority over *Scaptochelys* (see Berry 1989b). Many now accept *Xerobates* as a genus distinct from *Gopherus* (Lamb and others 1989; Weinstein and Berry 1987); others have maintained that *Xerobates* is merely a primitive *Gopherus* (Morafka 1988) or that the evidence for *G. agassizii* and *G. berlandieri* as more closely related and a separate group is weak (Crumly 1984).

Description

The physical description of *Gopherus agassizii* is included in the following discussion, beginning generally with characters of Testudinidae and then more specifically with characters of *Gopherus agassizii*.

I. **Physical description**

A. Testudinidae represents terrestrial turtles, generally with a high, arched carapace sometimes flattened dorsally. Front feet are club shaped and hind legs and feet are columnar and elephantlike. The forelegs are covered in bony scales. Toes are not independently movable and are two jointed, short, unwebbed, and have thick claws. No inframarginal scutes exist and twelve marginals appear on each side. The plastron has twelve shields and is joined by a bony bridge to the carapace. The tail is short, the top of the head is covered in scales, and the extremities are fully retractable (Blair and others 1957; Carr 1952; Pritchard 1979b).

B. *Gopherus* represents a Nearctic genus of tortoise with relatively flat forelimbs and flat, broad toenails. The carapace has steep sides and is flattened dorsally. The cervical scute is usually as wide as it is long. The caudal and cervical vertebrae are robust and short. One postcentral lamina is present. The alveolar surface of the premaxillaries has a distinct ridge parallel to the cutting edge and is elevated at the symphysis (Auffenberg and Franz 1978b; Berry 1989b; Blair and others 1957; Carr 1952).

C. *Gopherus agassizii* is generally described as having a carapace 215 to 350 mm long, oblong and high-domed; moderately flat dorsally and often flared along the lateroposterior border; serrate, especially posteriorly; scutes horn-colored or brown, often with yellowish centers; marginals not distinctly lighter than costal scutes. Usually prominent growth rings exist on both carapace and plastron. Plastron is yellow with brown on edges of laminae; in addition, the anterior projection (gular fork) projecting beyond the carapace is often deeply notched anteriorly at the midline. The bridge is well developed. Hind limbs are thick, round, stumpy and elephantlike. Front limbs are flattened and heavily scaled, with moderately sized, unfused scales. Toes are webless, with broad nail-like claws that turn inward. Front and hind feet are about equal in size. The head is small (its width is 85 to 115 percent the width of the hind foot). The alveolar ridges of the upper jaws form a sharp angle with each other; jaw margins are serrate. Iris is greenish-yellow or yellow with brown near outer edge, sometimes brown or mottled. Skin is gray, blackish-gray to black, or reddish-tan (Auffenberg and Franz 1978b; Barker 1964; Bogert 1954; Brown 1974; Carr 1952; Coombs 1977c; Ditmars 1930, 1933; Grant 1936a; Jaeger 1957; MacMahon 1985; Stebbins 1966, 1985; True 1882).

II. **Similar species:** Texas tortoise, *Gopherus berlandieri* (Agassiz); Bolson tortoise, *Gopherus flavomarginatus* (Legler); gopher tortoise, *Gopherus polyphemus* (Daudin). Proposed new species in Baja California Sur, Mexico: *Gopherus lepidocephalus*, scaly-headed tortoise (Ottley and Velazquez Solis 1989).

A. Mertens and Wermuth (1955) considered all four *Gopherus* species as a single polytypic species (Mertens and Wermuth 1955), but others considered each species as clearly distinct morphologically and geographically, and thus genetically isolated (Auffenberg 1976; Auffenberg and Franz 1978b).

B. *Gopherus agassizii* more closely resembles *G. berlandieri* than other *Gopherus* spp. in carpal elements (Auffenberg 1976), alveolar angle, hind foot diameter, head width, and proportionate shell height, as well as genetic similarity (Auffenberg 1966a, 1976; Bogert and Oliver 1945; Lamb 1987; Lamb and others 1989).

C. Keys to *Gopherus* species: Auffenberg and Franz (1978a); Blair and others (1957); Boulenger (1889); Brame and Peerson (1969); Carr (1952).

D. Other distinguishing characteristics among *Gopherus* species: shell measurements (Bogert and Oliver 1945; Grant 1960b); hindfoot-to-head width ratios (Bogert and Oliver 1945); sharp-angled intersection of alveolar ridges of upper jaws (Carr 1952); female-to-male length ratio expressed as a percent (Fitch 1981).

Morphology

Morphology of *Gopherus agassizii* is discussed with respect to adults and hatchlings. Some of the following information on adults may be applied to hatchlings, as the two growth stages share similar morphologies.

I. **Adults**

A. Shell: usually greater than half as high as it is long, may be flared posteriorly, and has a gently convex profile (Bramble 1971; Grant 1960a).

1. Carapace: a high-domed carapace allows greater space for the lungs and more efficient thermoregulation (Auffenberg 1974; Patterson 1973a).
    a. Bones: carapace includes eight neurals fused with flattened neural spines of numbers 2 to 9 of the 12 dorsal vertebrae. Carapace normally consists of 50 bones (Woodbury and Hardy 1948b). Closure of costoperipheral fontanelle is complete when the plastron reaches 200 mm in length (Patterson 1978).
    b. Scutes: include a nuchal, with 11 marginals on each side, the last pair united to form a single supracaudal plate; five vertebral or neural scutes, the last being the largest and widest; four costal scutes on each side, the first being longest and the last smallest (True 1882; Van Denburgh 1922b; Woodbury 1931).
2. Plastron
    a. Bones: plastron contains nine bones. These include a single entoplastron, two epiplastron, two hypoplastron, two hyoplastron, and two xiphiplastron (Woodbury and Hardy 1948a; Zangerl 1969). Gular scales do not overlap the entoplastron. Inguinal scale is divided to produce a smaller medial scale (Bramble 1971). Mid-ventral suture is usually asymmetrical (Grant 1944). Closure of the plastron fontanelle is complete when the plastron reaches 210 mm in length (Patterson 1978).
    b. Scutes: plastron contains six pairs of scutes. Gulars are the smallest, sometimes united and cover a narrow process of the plastron. Pectorals are very much smaller than the abdominals and possess the shortest median suture, with the exception of the anal sutures that are sometimes shorter. Abdominals are largest and have the longest median suture. Humerals are larger than femorals (Van Denburgh 1922a,b). Gular projections are present in both sexes but are more prominent and diverge more at the tips in males; they may be level or curve upward. The left gular is almost always larger than the right, especially in males (Bramble 1971; Grant 1944, 1946). The Gular shield suture was on the right side in 90 percent (331 of 366) of tortoises; median suture in 6 percent; suture on left side in 3 percent (Grant 1936a).

B. Skeleton
1. Vertebrae: includes 8 cervical vertebrae, 12 dorsal vertebrae and a varying number of caudal vertebrae (Woodbury and Hardy 1948a).
    a. Prezygapophyses have deep fossae at their bases, permitting the head to be withdrawn further into the shell (Bramble 1971).
    b. There is very little to no horizontal movement between the fourth cervical vertebra and vertebrae posterior to it (Bramble 1971).
2. Pectoral girdle
    a. Dorsal ends of girdle are attached to the first costal plates on each side of the first dorsal vertebra; ventral ends are attached to entoplastron (Woodbury and Hardy 1948a).

b. Angle of 104 degrees occurs between the two limbs of the scapula (Bramble 1971).

c. Pronounced interclavicular keel exists that functions to increase the origin of the deltoid muscles (Bramble 1971).

d. Pelvic girdle is dorsally attached to first costal plates on each side of the first vertebra: ventral oschia are anchored to xiphiplastron and ilia are attached to sacral ribs (Woodbury and Hardy 1948a).

3. Ribs: the first and second ribs are fused to costal plates. Ribs three through eight are fused with neural plates. Ribs 9 and 10 are fused to the last pair of costal plates. Sacral ribs are attached to dorsal ends of ilia (Woodbury and Hardy 1948a).

C. Limbs: forefoot has five digits, hindfoot four. Remnant of first digit is represented by a metatarsal; digits two through five have two phalanges each (Van Denburgh 1922a,b; Woodbury and Hardy 1948a). Digits are not independently movable due to shortening and flattening of articular surfaces of metacarpals and proximal phalanges (Bramble 1971). Nine carpal elements are present in the forelimbs and there is much fusion in adults (Auffenberg 1966a, 1976). Front foot is unguligrade (Auffenberg 1974).

a. Ossicles are present under the scales on the side of the foot, on the posterior surface of the thigh, and on the forearms (Auffenberg 1976).

b. The tibia shaft and the femur shaft are longer and slenderer in *G. agassizii* than in *G. polyphemus* and *G. flavomarginatus* (Bramble 1971).

c. The width of the distal end of the humerus is 38 percent of its functional length (Bramble 1971).

D. Head

1. Mouth and jaws: the serrated jaws are adapted for plant shredding (Mahmoud and Klicka 1979). *Os transiliens* (see Paleontology and Paleoecology) is also associated with plant shredding (Bramble 1971, 1974). Mucous glands are well developed (Winokur 1973).

2. Nares: well-developed posterior narial passage, analogous to a secondary palate, allows respiration during feeding. External nares are minute (Bramble 1971).

3. Eyes: protrude slightly from their orbits (Bramble 1971).

4. Chin glands (subdentary or mental glands): two glands exist beneath the bulbs of the jaws (Grant 1936a). Glands are well developed in males, especially during breeding season; however, chin glands are functional but not well developed in females (Coombs 1974; Rose and others 1969). Chin glands possess two to three external openings and a scaleless external epithelium (Rose and others 1969). Gland secretions contain triglycerides, phospholipids, free fatty acids, cholesterol, and esterase. Electrophoretic analysis of gland secretions demonstrate all *Gopherus* spp. females possess a single cathodal migrating protein band (Rose and others 1969). Function of chin glands may involve olfactory and visual cues used in courtship. Male chin gland secretions are important in sex recognition, and males respond aggressively to tortoises or objects possessing male chin gland secretions (Coombs 1974; Rose and others 1969).

E. Organs
   1. Gallbladder: located in the ventral right lobe of the liver (Pennick and others 1991).
   2. Heart: three chambered; located on the ventral midline, dorsal to the pectoral muscles and between the two hepatic lobes. The heart is dorsally flattened (Pennick and others 1991).
   3. Kidneys: appear as loosely lobulated and triangular; positioned paravertebrally at the level of the inguinal margin of the shell bridge (Pennick and others 1991).
   4. Large intestine: crosses the small intestine three times before making a sigmoid flexure to the cloaca (Woodbury and Hardy 1948a).
   5. Liver: bilobed, one lobe on each side of the pericardium. Liver-to-body mass ratio is 1.73 to 2.10 percent (Naegle 1976; Woodbury and Hardy 1948a). The right lobe is largest and covers part of the stomach and the small and large intestines (Pennick and others 1991). Liver mitochondria contain the enzymes glutamine synthetase, carbamyl phosphate synthetase-I and ornithine transcarbamylase used for amino acid catabolism (Campbell and others 1985).
   6. Lungs: sacculated and hollow with a honeycomb arrangement of the epithelium between sacculations; occurs on the ventral aspect of the carapace (Pennick and others 1991); lung volume (inches^3)- to- body-mass (oz) ratio is 0.37 (Patterson 1973a). Respiratory tract- to- body-mass ratio is 1.41 to 2.60 percent (Fowler 1976b; Naegle 1976).
   7. Urinary bladder: located in the caudal ventral coelomic cavity; extremely variable in size, ranging from a few centimeters in diameter when contracted to occupying nearly half of the coelomic volume when distended; wall of distended bladder is extremely thin (Pennick and others 1991).
   8. Genitals: females have two uteri that are joined together before entering the cloaca, giving the appearance of a united structure, but internally each uterus has its own sphincter. Males possess testes which are elongated brown bodies suspended in the posterior coelom on each side of the midline; the mesorchium separates each testis from the respective kidney, which lies behind the peritoneum against the posterior body wall (Pennick and others 1991; Woodbury and Hardy 1948a).
   9. Gross body composition of adults expressed as percent of total body mass cited by Connolly and Eckert (1969) and Naegle (1976): body water, 72.0 to 74.2 percent, and 79.6 percent; protein, 15.9 to 16.1 percent, and 17.4 percent; ash, 2.4 to 3.1 percent, and 1.0 percent; fat, 7.5 to 8.8 percent (Naegle 1976), and 1.3 to 8.8 percent (Connolly and Eckert took fat content for muscle samples only, so their estimate is low); shell, 28.0 to 34.0 percent; potassium content, 1.6 g per kg of body mass.
   10. Specific organ masses (Connolly and Eckert 1969; Naegle 1976).

II. **Hatchlings:** about the size of a silver dollar, or about 4.5 to 5 cm long, rounded, and weigh about 20.0 to 27.0 g. They appear to be immature round replicas of adults and are mustard yellow to brown in color. Edges of scutes are typically brown and the centers are dull yellow (Coombs 1977a; Grant 1936a; Jaeger 1955; Luckenbach 1982; Miller 1932, 1955).

A. Shell: hatchling has a soft pliable shell that is poorly ossified. Shell may not become completely ossified until fifth year or older, or 88.0 to 150 mm carapace length (Bury and Marlow 1973; Camp 1916; Luckenbach 1982; Miles 1953; Woodbury and Hardy 1948a). Shell skeletal structure is incomplete, and there is a large median plastral fontanelle, a peripheroplastral fontanelle on each side of the shell, and a large single fontanelle for each rib pair (Patterson 1978). Pygal and nuchal scutes are incomplete and have "M"-shaped notch until about 10 years old; gular and anal scutes are also incomplete (Coombs 1974; Stebbins 1954).

B. Plastron: dry yolk sac remains attached to umbilical area of plastron but is absorbed about two days after hatching. It is about one-third the size of the hatchling and impedes locomotion the first few hours (Grant 1936a, 1946; Luckenbach 1982; McCawley and Sheridan 1972; Miller 1932, 1955). Bend between sixth and seventh marginal scutes disappears with growth (Grant 1946). Plastron has transverse crease at the sixth and seventh marginals which smooths out with growth (Grant 1946; Miller 1932; Van Denburgh 1922b; Woodbury and Hardy 1948a).

C. Limbs: hatchling and juvenile *G. agassizii* lack laminal spurs found in *G. polyphemus* presumably used as anchors while climbing out of steep burrows (Allen 1983; Allen and Neill 1957). Nails are long and sharp in comparison to nails of adults (Miller 1932).

D. Head: a rostral head scale or egg tooth aids in breaking the egg shell, and it flattens out by two months (Grant 1936a) or by the second year (Miller 1932).

III. **Sexual dimorphism**

A. Overall size is larger in males (Fitch 1981; Graham 1979; Grant 1936a; Woodbury and Hardy 1948a).

B. Tail is longer and wider in males. The female tail is blunt and terminates at the level of the cloaca. The longer tail of the male enables the penis to penetrate the female's cloaca during copulation (Auffenberg and Franz 1978b; Grant 1936a; Patterson 1972b).

C. Gular projection is longer and upwardly curved in the male; female gular projections are short and straight (Auffenberg and Franz 1978b; Coombs 1973, 1974; Graham 1979).

D. Plastron is concave in the male (inguinal depression), especially in the femoral area, and this concavity fits over the female's convex carapace during copulation; females possess flat plastron and larger pelvic clearance from seam of anals to edge of rear marginals (Bramble 1971; Grant 1936a; Woodbury and Hardy 1948a).

E. Chin glands are larger in males, especially in the spring. The chin gland is functional but not well developed in females (Auffenberg 1977; Coombs 1974, 1977c; Rose 1970).

F. Toenails are thicker in males (Carr 1952).

G. Dermal ossicles on the thigh and hindfoot are more well developed in males (Auffenberg 1976).

H. A slightly movable posterior lobe of the plastron may exist in females (Beltz 1954).

IV. **Anomalies**

A. Scute anomalies: description of anomalous growth in scutes is found in Grant (1937). Terrestrial and semiaquatic turtles possess more scute anomalies than aquatic turtles (Zangerl and Johnson 1957).

1. Types of scute anomalies
   a. Caudal scutes: tortoises found with paired and sometimes irregularly shaped caudals (Coombs 1977c).
   b. Marginal scutes: tortoises found with 12 marginals on each side, or with 12 on one side only (Grant 1946).
   c. Gular scutes: tortoises found with gulars growing to one side (Coombs 1974) or irregularly curved and/or with extra parts (Coombs 1977c).
   d. Marginal scutes: tortoises found with 10 or 12 marginals on each side and others found with 10 or 12 on one side only (Grant 1946).
   e. Nuchal scutes: tortoises found with nuchals divided, with one part fused to first left marginal, and also found with nuchal missing altogether (Coombs 1973, 1974, 1977c; Grant 1946).
   f. Plastral scutes: tortoises found with extra plastrals (Grant 1936b).
   g. Vertebral scutes: tortoises found with two additional vertebrals; more commonly, one additional vertebral may be present or one may split to form two scutes (Coombs 1974, 1977c; Grant 1946).
2. Instances of scute anomalies
   a. From a sample of over 500 tortoises collected in California, 24 individuals possessed carapace anomalies (Grant 1946).
   b. Of 196 tortoises examined from the Beaver Dam Slope in Utah and Arizona, twice as many anomalies existed when compared to tortoises in Desert Tortoise Natural Area in California. Possible factors contributing to this high number include temperature, moisture levels, oxygen content of soil at nests, genetic inheritance, or radiation from natural sources or nuclear weapons testing (Berry 1984e; Good 1982).
   c. Most common anomalies on Beaver Dam Slope in Utah are an irregular number of marginal scutes, especially nuchal scute and gular forks. Minden (1980) found 28 percent of the tortoises had scute anomalies. The rate of occurrence in other localities is not well known. Most anomalies include too few, too many, disproportionately sized, or asymmetric scutes. Variations in marginal scutes were most common (Coombs 1977c; Dodd 1986).
   d. Good (1984) found 20.4 percent of Beaver Dam Slope tortoises surveyed had scute anomalies; there were no differences between age classes or sexes. The most common anomaly was an abnormal number of marginal scutes. In the Desert Tortoise Natural Area in California, 11.22 percent had anomalies, all but one anomaly on the carapace, but no one type was most frequent. Environmental factors and high radiation levels are possible factors contributing for the high anomaly rate at Beaver Dam Slope.

B. Pigment anomalies
1. Four albino hatchlings were found in three broods of a pair of captive desert tortoises (Dyrkacz 1981; Keasey 1979).
2. Two partial albinos were found with olive gray carapace, legs, and nails (Grant 1936a).

3. One tortoise had orange and black legs rather than gray and black legs (Grant 1936a).

C. Jaw malformations: apparently common in captives. Malocclusions have been noted as well as a thick horny growth along the rims of the mouth (Clark 1967; Heckley 1968).

D. A parietal foramen is found in 5 percent of desert tortoises (Auffenberg 1976; Crumly 1982).

V. **Regional variation in morphology**

A. Three distinct shell phenotypes are suggested by Weinstein and Berry (1987): Western Mojave Desert, Sonoran Desert, and Beaver Dam Slope types.

1. The Western Mojave Desert type is square and more boxlike than average, wider in front than in rear and relatively high-domed. The high-domed carapace may be a result of open habitats and less demanding burrowing requirements.
2. The Sonoran Desert type is more pear shaped, narrower in front than in rear and relatively low domed.
3. The Beaver Dam Slope type is low in shell height and has a shorter plastron. This shell shape may be an adaptation for constructing large burrows as well as for accommodating greater thermoregulatory requirements.

B. Shell phenotypes described by Weinstein and Berry (1987) correspond to results of mitochondrial DNA analyses, except that the Beaver Dam Slope morphology is more unique than the mitochondrial DNA analysis suggests (Lamb 1987; Lamb and others 1989).

1. The anal notch of males from the Sonoran Desert scrub is deeper than that of males in Mojave Desert and Sinaloan deciduous forest. Anal notch width of Mojave Desert males is larger than for males from Sinaloan thornscrub habitats (Jennings 1985).
2. Females from the Mojave Desert have the greatest anal notch depth; those from the Sonoran Desert have the smallest anal notch; Sinaloan thornscrub female anal notches are intermediate in size (Jennings 1985).
3. Gulars of males from Mojave Desert are the longest; Sinaloan thornscrub and Sonoran Desert males possess gulars intermediate in size; a male of Sinaloan deciduous forest possessed gulars of smallest size (Jennings 1985).
4. Front foot width of male tortoises is greater in Sonoran and Mojave Deserts than in Sinaloan thornscrub and Sinaloan deciduous forest (Jennings 1985).
5. Sonoran Desert males are flatter than Mojave Desert males; Sinaloan thornscrub males are intermediate (Jennings 1985).
6. Shell width with regard to length is greater in Mojave and Sonoran Desert tortoises than in those of Sinaloan deciduous forest tortoises; Sinaloan thornscrub tortoises are intermediate in shell size (Jennings 1985).
7. Shells are relatively wider and more depressed (Bogert and Oliver 1945).
8. Carapaces of tortoises are generally longer in the northern part of the range: carapaces at Tiburon Island, Mexico are shorter than those in Utah (Dodd 1986; Reyes Osorio and Bury 1982).

9. Tortoises from Mecca, Riverside County, CA, had yellow irises; tortoises from Goffs, CA, had brown irises.

C. More shell phenotypes may exist, including one from southern Sonora, Mexico (Weinstein and Berry 1987).

Genetics

Literature regarding genetics of *Gopherus agassizii* is limited. The following discussion includes genetics at the more general taxonomic levels and becomes more specific with the species *G. agassizii*.

I. **General**

A. Reptiles tested had DNA values ranging from 2.5 to 10.9 picograms. Turtles on average have higher DNA values than Squamata (such as lizards and snakes). The karyotype of turtles is very conservative (Olmo 1984).

B. Chelonoidea have primitive karyotypes of $2n = 56$. Of the three superfamilies, Trionychoidea is much different and has a primitive karyotype of $2n = 66\text{-}68$. Testudinoidea and Cryptodira are karyotypically homogeneous. All testudinoid turtles possess at least seven group A macrochromosomes. Among testudinoid families a clade that includes Staurotypidae, Platysternidae, Testudinidae, and Emydidae can be identified by the presence of a biarmed second group B macrochromosome. Platysternidae, Testudinidae, and Emydidae all primitively possess nine group A macrochromosomes. Emydidae and Testudinidae are characterized by a primitive karyotype of $2n = 52$ (Bickham and Carr 1983; Ohno 1970).

C. *Gopherus* differs from other Testudinidae in karyological details: these include a pair of acrocentric chromosomes (NA = 82) which bear secondary constrictions near the centromeres, not observed in any other chelonian (Stock 1972).

D. *G. agassizii* has a chromosome number of $2n = 52$ (Atkin and others 1965; Stock 1972).

E. Genome size is 5.8 pg/N in *G. agassizii*; it was the lowest of five Testudinidae tested (mean = 7.74 pg/N) (Atkin and others 1965; Olmo 1984).

F. Ratio of desert tortoise DNA content to human DNA content is 0.865 (Atkin and others 1965).

G. Mitochondrial DNA restriction fragments have been identified (Lamb 1986a,b, 1987; Lamb and others 1989).

H. Mitochondrial DNA genome size is 16.4 kb in *G. agassizii* (Lamb and others 1989).

II. **Regional genetic variation**

A. Starch-gel electrophoresis of 16 blood proteins and 24 proteins from heart, liver, kidney, and blood for 10 sample sites showed no fixed genetic differences between populations. Blood allozymes in two California tortoise populations also are similar (Buth 1986; Jennings 1985).

B. Mitochondrial DNA (Lamb 1986a,b, 1987, 1988; Lamb and others 1989): Restriction endonucleases used to analyze mitochondrial DNA of desert tortoises from different localities revealed distinct DNA clones and major genetic assemblages, each with distinct geographic ranges.

1. An assemblage north and west of the Colorado River included three closely related clones at specific locations: Piute Valley

and extreme southern Nevada and all California populations except Ivanpah Valley, CA, eastward through Nevada, the Arizona strip, and into southern Utah; four locales in the extreme northeastern Mojave Desert represented by the Virgin Mountains in Mojave County, AZ, the Mormon Mountains in Lincoln County, NV, Gold Butte in Clark County, NV, and Paradise Canyon in Washington County, UT (Lamb 1986a, 1987; Lamb and others 1989). The Ivanpah Valley population was also found to have a rare allele of glucose phosphate isomerase (GPI) (Jennings 1985).

2. A second assemblage is represented by one clone from west-central and southern Arizona to central Sonora, Mexico (Lamb 1986a, 1987; Lamb and others 1989).
3. A third assemblage is represented by a clone in southern Sonora (Lamb 1986a, 1987; Lamb and others 1989).
4. There was pronounced genetic divergence between eastern and western assemblages due to the historic influence of the Colorado River as a barrier to gene flow.
5. Mitochondrial DNA phylogeny supports the recognition of two genera, *Gopherus* and *Xerobates*.

C. Gene flow between isolated populations is probably low due to natural barriers and distance; effects of inbreeding are also low due to long generation times. Limited gene flow may occur along some washes between Utah, Arizona, and Nevada populations of the Beaver Dam Slope and nearby locations (Bury and others 1988a; USDI Fish and Wildlife Service 1985a).

D. The Colorado River and rainfall patterns are significant indicators of relatedness of tortoise populations. The Colorado River is probably a barrier to gene exchange. Low rainfall west of the river may have created an environmental bottleneck, as evidenced by low genetic heterozygosity values west of the Colorado River (Jennings 1985).

E. Heterozygosity values were 0.016 to 0.083 for the Mojave Desert; 0.031 to 0.146 for the Sonoran Desert, Sinaloan thornscrub, and Sinaloan deciduous forest; 0.031 for McDowell Mountains of Maricopa County, AZ and 0.016 for Beaver Dam Slope, AZ (Jennings 1985).

F. Isolated peripheral populations such as the Beaver Dam Slope and Coyote Springs populations probably have the lowest heterozygosity and greatest danger of local extinction (Bury and others 1988a).

G. Blood proteins of *G. berlandieri* demonstrate the most similarities with an Arizona population of *G. agassizii*. *Gopherus berlandieri* may have been more recently associated with *G. agassizii* of this area (Jennings 1985).

H. Mitochondrial DNA analysis suggests that *G. berlandieri* is closely related to the eastern assemblage of *G. agassizii* and probably originated from ancestral stock in north-central Sonora (Lamb and others 1989).

I. Protein profiles representative of 10 separate populations throughout the range of *G. agassizii* suggest geographic differences in genetic variability of the albumin-like protein (GP-1). Proteins of the northern (Mojave) population were polymorphic, while the southern (Sonoran) populations were monomorphic at the GP-1 locus. An east-west Mojave difference was observed: the BB genotype was isolated in populations from the eastern Mojave region of Utah and northwestern Arizona. Of the localities having the B allele at GP-1 (Kingman and Beaver Dam Slope, AZ; Lincoln Co., NV; Riverside County and San Bernardino County, CA) the Arizona and California populations were nearly identical while the Paradise Canyon, UT, samples were the most divergent (Glenn and others 1990).

J. Regarding allozyme variation, desert tortoise populations of the Kramer Hills, CA, and Chemehuevi Valley, CA, appear to be nearly identical (Rainboth and others 1989).

III. **Hybridization**

A. Female *G. agassizii* and male *G. berlandieri* successfully mated, producing two viable young (assuming females do not carry sperm for more than 1 year) (Woodbury 1952).

B. Female *G. agassizii* and male *G. polyphemus* successfully mated in captivity, producing seven eggs; one egg contained twin tortoises (Hunsaker 1968).

Paleontology and Paleoecology

Prehistoric distribution and evolution of *Gopherus agassizii* are included here. Initial dating of fossil material is presented as "years before present" due to the fact that the designation of ages changed after the late 1970's (for instance, the Miocene-Pliocene boundary was revised from 11 to 5.5 million years before present, see Morafka 1988). Materials dated after the late 1970's retain cited age classifications (Miocene, Pliocene, Pleistocene, and so forth).

I. **Evolution**

A. Tortoises probably evolved from aquatic pond turtles of the family Emydidae. Tortoise lineage began about 65 million years ago in tropical forests. Testudinidae appears in the fossil record in the Mid-Eocene. Tortoises reached their greatest abundance and diversity in the Pliocene (Auffenberg and Iverson 1979; Pritchard 1979b; Van Devender 1986).

B. Ancestors of land tortoises probably crossed the Bering land bridge to the New World. North America has an abundant fossil record of tortoises, including many giant forms weighing up to 500 lbs. North American tortoises, including the immediate ancestor of *Gopherus*, stem from a primitive Stylemydine closely related to *Hadrianus majusculus* (Auffenberg 1969, 1971; Bramble 1971; Van Devender 1986).

C. *Gopherus* is closely related to the genus *Stylemys* and may have evolved from an early member of *Stylemys* during the Late Eocene. The earliest *Gopherus* are intermediate in form between modern *Gopherus* and *Stylemys* (Auffenberg 1969, 1971; Hay 1908; Williams 1950).

D. The earliest known *Gopherus* fossils (*G. laticunea* and *G. praextons*) are from 45 million years ago, in rocks of the White River Formation in Colorado, Nebraska, Wyoming, and South Dakota (Auffenberg 1969).

E. It is speculated that modern forms of *Gopherus* are generally up to 70 percent smaller than Oligocene and Early Pleistocene forms; however, Late Pleistocene fossils from Gypsum Cave, NM, are similar in size to modern forms (Auffenberg 1962; Bramble 1971; Brattstrom 1954; Dalquest 1962).

F. During the Oligocene and Miocene up to 50 species of land tortoises, including many giant species, existed in North America. During the Pliocene the giant species became extinct throughout most of their range (Morafka and McCoy 1988), and today only four relatively small species exist in North America, all are *Gopherus* (Carr 1952).

G. Divergence of *Gopherus* groups may have occurred about 2 to 3 or 5.5 million years before present in the Middle or Late Pliocene (Lamb and others 1989) or Middle Miocene (Bramble 1981). The more conservative lineage (*Agassizii* group or proposed genus *Xerobates*) includes *G. laticunea*, from the Oligocene, *G. mohavense* from the Miocene and the recent *G. agassizii* and *G. berlandieri*. The specialized fossorial lineage (Polyphemus group or genus *Gopherus*) goes back to the Early Miocene (*G. brevisterna*) and beyond; it includes today's *G. polyphemus* and *G. flavomarginatus*, which are descendants of a Late Pliocene-Early Pleistocene radiation of giant *Gopherus* from Arizona to Texas (Bramble 1972; Preston 1979; Van Devender 1986; Weaver 1970).

H. During the Late Pleistocene, unfavorable environmental conditions separated eastern and western populations of the immediate ancestor of *G. berlandieri* and *G. agassizii*, which then differentiated to become the current species (Bramble 1971; Van Devender 1986).

I. A marine incursion, the Bouse Sea, which probably occurred around 5.5 million years ago, may have separated eastern and western *G. agassizii* populations. The region later uplifted, causing the retreat of the Bouse Sea and the formation of the Colorado River, which acted as a continued barrier between the populations (Lamb and others 1989).

J. *Gopherus agassizii* is known from a packrat midden dated at 16,000 years before present (Mead 1981).

K. Major extension of *G. agassizii* into Arizona, New Mexico, and Texas probably did not occur until the Late Pleistocene (Bramble 1981).

II. **Paedomorphosis:** adult *G. agassizii* resemble juvenile Pliocene predecessors, and trends toward paedomorphosis (juvenile features retained by adults) can be seen in the shell structure, manus, and skull (Bramble 1971).

III. **Os transiliens**

A. A sesamoid bone is found in the central raphe of the adductor mandibularis externus, which articulates in a joint capsule, with a facet formed by the quadrate and prootic bones. It increases the effective height of the trochlear process when seated on the quadrate, resulting in a more vertically directed pull of the muscle and greater upward force applied to the mandible, thus greater pressure between the masticatory surfaces of the jaws (Bramble 1974; Legler 1962; Patterson 1973b; Ray 1959).

B. Os transiliens is restricted to *Gopherus* and is present in the Oligocene in *G. laticunea*, the oldest *Gopherus* species. It is not present in closely related *Stylemys* (Bramble 1974).

C. Os transiliens is associated with a shift in diet to coarse tough vegetation associated with a habitat change to xeric and semiarid climates during the Eocene-Oligocene transition (Bramble 1974).

IV. **Prehistoric range**

A. *Gopherus*

1. *Gopherus* species ranged from Kansas south to Aguascalientes, Mexico, and from Arizona to Florida during the Pliocene. Ranges may have decreased 30 to 50 percent due to Late Pliocene-Early Pleistocene uplifts, which extirpated species from the south-central Mexican Plateau (Mooser 1972; Morafka and McCoy 1988).
2. The Pleistocene range was considerably north of the present range but shifted southward with glaciations (Auffenberg 1962).
3. Both the Agassizii and Polyphemus groups existed in the Middle Pleistocene (600,000 years ago) and had overlapping ranges in northern Mexico. Range changes occurred after the Middle Pleistocene as a result of climate shifts. The most dramatic changes occurred 30,000 years ago (Auffenberg 1969).

B. *Gopherus agassizii*

1. Known from the Pleistocene of California and New Mexico and the post-Pleistocene of Nevada. The New Mexico localities are the only ones significantly beyond the current range (Brattstrom 1954, 1961, 1964; Miller 1942; Van Devender and others 1976).
2. The southeasternmost portion of range may have overlapped the ranges of *Gopherus berlandieri*, *G. flavomarginatus*, and *Geochelone wilsoni* (Moodie and Van Devender 1979).
3. Wisconsin glaciation resulted in western movement of the eastern edge of the range (Auffenberg and Milstead 1965).

V. **Fossil sites beyond the current range**

A. Pleistocene sites occur in southeastern New Mexico and nearby Texas, and in coastal California (Moodie and Van Devender 1979; Van Devender and others 1976).

B. Four carapace fragments found, including one from a juvenile, Los Angeles Basin, CA (Miller 1970).

C. McKittrick Asphalt Beds, McKittrick, Kern County, CA. Remains recovered of limb and shell bones from Pleistocene tortoise that are identical to those of Holocene desert tortoise (Miller 1942).

D. Conkling and Shelter Caves, Dona Ana County, NM. Late Pleistocene shell fragments found from the Organ Mountains, from tortoises generally smaller than present *G. agassizii*. Fragments from Shelter Cave are generally smaller while those from Conkling Cave are similar to present *G. agassizii* (Brattstrom 1961, 1964).

E. Robledo Cave, Dona Ana County, NM. Two peripheral bones and a right hypoplastron recovered from the Robledo Mountains northwest of Las Cruces, possibly from the Pleistocene (Van Devender and others 1976).

F. Dry Cave, Eddy County, NM (Brattstrom 1961; Moodie and Van Devender 1979; Van Devender and Moodie 1977; Van Devender and others 1976):

1. Remains found 24 km west of Carlsbad on the Guadalupe Mountains; this represents the easternmost location of Pleistocene *G. agassizii*.
2. Shell fragments and partial carapace found; Late Pleistocene, radiocarbon dated at 33,590 ± 1,500 years before present; the oldest *G. agassizii* known.

VI. **Fossil sites within the current range**

A. Schuiling Cave, San Bernardino County, CA. Pleistocene remains recovered of one partial carapace and many fragments (Downs and others 1959).

B. Whipple Mountains, San Bernardino, CA (Van Devender and Mead 1978):

1. Remains radiocarbon dated at 9,980 ± 180 years before present.
2. Found at 520 m elevation; area was in or near juniper woodland at the time.

C. Manix Dry Lake, San Bernardino County, CA. Fossil coracoid fragment from the Pleistocene, similar to that of recent *G. agassizi*, but heavier; the distal and medial ends are thicker than in the modern species (Brattstrom 1961).

D. Gypsum Cave, Clark County, NV. Late Pleistocene skeletal parts similar in size to those of present day *G. agassizii* (Brattstrom 1954, 1961).

E. Four sites in Clark County, NV (Connolly and Eckert 1969):

1. Large quantities of remains recovered from 1,249.7 m to 1,432.5 m deep, including carapace, plastron, scapulae, pelvic parts, leg bones, and laminae.
2. The quantity and locations of desert tortoise remains suggest they may have been a seasonal food item for Indians.

F. Rampart Cave and vicinity, Grand Canyon, Mojave County, AZ. Late Pleistocene skeletal parts, including femur, peripheral bone, and other bone fragments and scutes (Van Devender and others 1977; Wilson 1942).

G. Welton Hills, Yuma County, AZ (Van Devender and Mead 1978):

1. Remains radiocarbon dated at 8,750 ± 320 years before present.
2. Found at 160 m elevation in an area that was in or near creosote-burrobush community at the time.

VII. **Habitat and climate**

A. During the Eocene, most, if not all, tortoises lived in tropical or subtropical regions (Brattstrom 1961).

B. Os transiliens appeared in *Gopherus* at the Eocene-Oligocene transition, associated with climate and vegetational changes; indicates a switch to coarser, more xeric plants (Bramble 1974).

C. The Oligocene was characterized by continental uplift leading to increased seasonality. Oligocene *Gopherus* were associated with humid, warm, temperate to subtropical flora and a subhumid to warm temperate climate with seasonal rainfall changes, warm winters, and hot summers. Drier areas were characterized by scrub-type forests with grasses and microphyll shrubs. The inferred burrowing habits of *Gopherus laticunea* suggest a xeric to semiarid habitat; they lived in chaparral and thornscrub regions (Bramble 1974; Bramble and Hutchison 1971; Brattstrom 1961).

D. Since small tortoises absorb heat more rapidly than larger tortoises and gigantic tortoises were still present in northern latitudes during the Oligocene and Miocene, the climate must have been warmer and less extreme than it is today (Brattstrom 1961).

E. Miocene *G. depressus* was associated with savannah, woodland, chaparral, riparian, desert scrub, and arid subtropical vegetation types (Brattstrom 1961).

F. Repeated orogenies during the Miocene may have led to the differentiation of the more specialized and fossorial *Gopherus* from the generalized *Xerobates* (Morafka 1988).

G. The Upper Pliocene saw a changing vegetation and changing climate. The tropical forest of the Eocene became restricted through the Cenozoic to its present state (Brattstrom 1961).

H. During the Pleistocene the range of *Gopherus* shifted south due to glaciation. Body size also became smaller in association with unfavorable climate conditions. Poor environmental conditions led to the split of the Agassizii group into eastern and western populations, which became *G. berlandieri* and *G. agassizii,* respectively. *G. agassizii* may have used the southern Rocky Mountain corridor as a dispersal route (Auffenberg 1962; Bramble 1971; Porter 1972).

I. Vegetation types
   1. *Gopherus agassizii* is found in the dry, subtropical, high Mojave Desert but generally not in the low Colorado Desert. In Sonora it is found in xerophytic thornscrub or chaparral. Xerophytic thornscrub probably covered most of the Mojave Desert and retreated southward as recently as 8,000 years ago. This suggests tortoises may have only recently inhabited arid desert scrub habitats (Brattstrom 1961; Jennings 1985; Van Devender and Mead 1978; Van Devender and others 1976).
   2. Fossil sites at Bishop's Cap, NM, and the nearby Hueco Mountains of Texas show the presence of *Gopherus agassizii* 11,000 to 34,000+ years before present in pinyon-juniper woodlands lacking desert species (Moodie and Van Devender 1979).
   3. Desert tortoises are able to exist in extremes of desert today due to their burrowing habit, which creates more favorable temperature and humidity (McGinnis and Voigt 1971; Pritchard 1979a; Voigt 1971; Woodbury and Hardy 1948a).

Distribution and Population Status

Present distribution of *Gopherus agassizii* is discussed based on museum records, literature records, surveys of personal sightings by professional herpetologists, federal and state monument and park rangers, and observations by high school biology teachers and their students and other amateurs (Patterson 1975). Distribution is dynamic, and additional sightings of tortoises are continually reported.

I. **General**

A. *Gopherus* spp.
   1. Genus *Gopherus* is found in the Southeastern and Southwestern United States and Northeastern, Northwestern and North-central Mexico (Auffenberg and Franz 1978a).
   2. Most *Gopherus* populations are facing serious declines. *G. flavomarginatus* has a very small distribution and is in danger of extinction; there are an estimated 10,000 adults remaining (Bury and others 1988b; Fisher and others 1969).

B. *Gopherus agassizii*
   1. *G. agassizii* is found in the Southwest desert regions including southeastern California, the southern tip of Nevada, western Arizona and the extreme southwestern corner of Utah. In Mexico it is found in most of Sonora, including Tiburon Island

in the Gulf of California, and in northwestern Sinaloa (Bogert and Cowles 1947; Carr 1952; Esque and others 1990b; Linsdale 1940; Luckenbach 1976; Patterson 1976a; Ross 1986a,b).

2. Tortoises are found in most of the Mojave and Sonoran Deserts, including the lower Colorado Valley of the Sonoran Desert. The current range indicates that *G. agassizii* is cold-sensitive (Van Devender and others 1976).

II. **Arizona**

A. Found in the Mojave and Upper Sonoran Deserts of southwestern, western, and extreme northwestern Arizona. North of the Grand Canyon, desert tortoises are found on the slopes of the Beaver Dam and Virgin Mountains and Pakoon Basin. South of the Grand Canyon they are found in patchy populations on hills and mountain slopes (Berry 1984; Burge 1980; Johnson and others 1948; Taubert and Johnson 1984).

B. Found in Cochise, Graham, Maricopa, Mojave, Pima, Pinal, and Yuma Counties (Patterson 1982; Pope 1939).

C. Specific localities include: Phoenix, Florence, and Tucson areas; 12.8 km southwest of Casa Grande below Table Mountain, Sulfur Springs Valley; northeast of Tombstone; U.S. Highway 80 near the New Mexico border; Fort Grant; Wilcox; Ragged Top Mountains; Picacho Mountains; Growler Mountains; Agua Dulce Mountains; Tortolita and Yuma and Ehrenberg areas; Dome, Mojave, Buckskin, and Whipple Mountains; Santa Catalina Mountains; Tucson Mountain State Park; Saguaro National Monument; Beaver Dam Mountains, Pakoon Basin, Hualapai Mountains, and Virgin River area (Cox 1881; Kauffeld 1943; Miller 1932; Tomko 1972; Van Denburgh 1922b; Van Denburgh and Slevin 1913).

D. Specimens collected in 1976 and 1977 suggest a range extension eastward in Cochise County: one tortoise was found 8 km north of the junction of the San Simon and Portal Roads; two others were found along U.S. Highway 80 about 1 and 2.5 km south of the Arizona-New Mexico border (Hulse and Middendorf 1979).

E. Status

1. Populations exist as scattered "islands" and densities are very low (Dodd 1982).
2. Only two sites, Little Shipp Wash and Alamo Hill, have high densities. Both high-density populations occur in isolated pockets of less than 1 square mile (Burge 1979; Schneider 1980a, 1981b).
3. In southern Arizona, six sites (5 percent of total sites with sign) had populations of greater than 300 tortoises/mi^2 (Burge 1980).
4. In the Sonoran Desert area of Arizona fewer than a dozen areas have been identified with moderate to high density populations (50 to 250 tortoises/mi^2); all island populations cover a few square miles (Berry and others 1983a,b).
5. North of the Grand Canyon populations exist in low densities, generally less than 90 tortoises/mi^2, and in patchy populations facing threats from human activity; in Mojave County the Beaver Dam Mountains, Pakoon Basin, and Virgin River area populations are 20 to 60 tortoises/mi^2. The Beaver Dam Mountain densities rarely exceed 50 tortoises/mi^2 and may be too low to

sustain viable populations. In the Hualapas and Aquarius Plateau areas half of the populations are less than 50 tortoises/mi^2 (Burge 1979, 1980; Dodd 1986; Hohman and Ohmart 1979, 1980; Sheppard 1981, 1982a,b; Sheppard and others 1983; USDI Bureau of Land Management 1981).

6. In Yuma County populations are found on small mountain ranges and occasionally in marshes where they are protected from grazing and human activities. Most populations are less than 50 tortoises/mi^2 and are probably 0 to 25 tortoises/mi^2 (Hohman and Ohmart 1979, 1980).

III. **California**

A. Tortoises are generally absent from the hot lower Colorado Desert along the Salton Basin. They are found in the Mojave Desert and uplands east of the Salton Sea including southern Inyo County; eastern Kern County; northeastern Los Angeles County; Panamint and Death Valleys; Shoshone area; Imperial, Riverside, and San Bernardino Counties, except for Coachella Valley (Camp 1916; Hill 1948; Leach and Fisk 1969; Patterson 1976a; Slevin 1934; Stebbins 1966, 1972, 1985).

B. Specific localities

1. Imperial County: Algodones Dunes; Cargo Muchacho Mountains; Chocolate Mountains and vicinity; Malpitas Wash; Paloverde Mountains; Santa Rosa Mountains; Fort Yuma; East Mesa (Dimmitt 1977; True 1882; Patterson 1982).
2. Inyo County: Dale; Death Valley; 18.5 km southeast of Lone Pine near Olancha; Black Mountains; Scotty's Canyon; 3.2 km southeast of Emigrant Junction (Miller 1932; Patterson 1982; Turner and Wauer 1963).
3. Kern County: California City and vicinity; Castle Butte; China Lake; Desert Butte; Fremont Peak area; Mojave area; 6.4 km north of Red Rock Canyon Randsburg and vicinity; northwest flanks of Red Mountain; Salt Wells Valley, China Lake Naval Weapons Center (Berry 1976; McGinnis and Voigt 1971; Miller 1932, 1955; Nicholson and others 1980b; Patterson 1982).
4. Los Angeles County: Lovejoy Buttes; Lovejoy Springs, 4.8 km south of Palmdale (Bogert 1937; Camp 1916; Dixon 1967; Miller 1932, 1955; Patterson 1982).
5. Riverside County: Chuckwalla Bench; Chuckwalla Valley; Chuckwalla Mountains; Cottonwood Mountains; Hayfield; 2.4 km south and 3.2 km east of Joshua Tree National Monument; Mecca area and near Mecca Mudhills; Orocopia Mountains; 0.8 km south of Palm Springs; Pinto Basin; Salt Creek Wash (Camp 1916; Dimmitt 1977; Jaeger 1955, 1957; Miller 1932, 1955; Patterson 1982).
6. San Bernardino County: Anderson Dry Lake and Anderson Valley; Arrowhead Junction; Barstow and vicinity; about 10 km south of Barstow in Stoddard Valley; Shadow Mountain Road, 40 km southwest of Barstow; Calico Mountains; Providence Mountains; Ivanpah area; Ivanpah Mountains; Ivanpah Valley; Chemehuevi Wash; north side of Clark Mountains, Daggett; between Daggett and Pilot Knob; Essey and vicinity; Fort Mojave and vicinity; Goffs; Hector; 1.6 km north of Hinkley; Indian Cove in Joshua Tree National Monument; 14.5 km north and 33.8 km

east of Lucerne Valley; Joshua Tree and vicinity; Kelso area; Kramer and vicinity; Leach Point Valley; Solado Valley; Turtle Mountains; 8 km northeast of Lucerne Valley; Twentynine Palms; Victorville; Wildhorse Wash; 40.2 km above Kernville (Berry 1978a; Bury and others 1977; Camp 1916; Grant 1946; Johnson and others 1948; Klauber 1932; Lee 1963; Miller and Stebbins 1964; Minnich 1977; Nicholson 1978; Patterson 1982; Stejneger 1893).

7. San Diego County: Southern end of Santa Rosa Mountains, probably introduced (Luckenbach 1982; Patterson 1982).

C. Status

1. There are four major population centers which cover a total of 6,370 mi^2: Western Mojave Desert from Fremont Valley south and east to Stoddard Valley; Ivanpah Valley in eastern Mojave Desert; Northeastern Colorado Desert from Fenner Valley south through Chemehuevi Valley; Chuckwalla Bench and Chuckwalla Valley (Berry 1979; Berry and Nicholson 1984b).
2. There are four minor population centers that have densities of 20 to 100 or more tortoises/mi^2 in Lucerne, Johnson Valley, Shadow Valley, and Kelso (Berry 1979; Dodd 1986).
3. In western Mojave Desert, highest densities, 347 to 540 tortoises/km^2, were found in the Fremont Valley and the region near the Desert Tortoise Preserve north of California City. Similar densities were found on the southern flanks of the Rand Mountains and Fremont Peak. In the eastern Mojave Desert, highest densities were in Fenner Valley, Upper Ward Valley (Camino Valley), and portions of Chemehuevi Valley (Luckenbach 1982).
4. California possessed densities of 0 to 20 tortoises/mi^2 on 84 percent of tortoise habitat. Densities of greater than 100 tortoises/mi^2 were found on only 2 to 8 percent of the habitat (Berry 1979; Dodd 1986).
5. Bureau of Land Management studies estimated densities at 165 tortoises/mi^2 in Desert Tortoise Natural Area; 88 tortoises/mi^2 in Stoddard Valley; 220 tortoises/mi^2 in Ivanpah Valley; 115 tortoises/mi^2 in Chemehuevi Valley; 250 tortoises/mi^2 at Chuckwalla Bench (Berry 1980a).
6. Fremont Valley: densities near 300 tortoises/mi^2 (Hampton 1981).
7. Ivanpah Valley: estimated 55 to 187 tortoises/mi^2 in good habitat; other estimates indicated 200 tortoises/mi^2 and 87 to 106 tortoises/km^2 (Berry 1978b; Turner and others 1982).
8. Chocolate Mountain Aerial Gunnery Range: densities of 50 to 250 tortoises/mi^2 on 5 percent of transects (Berry and others 1983a,b).
9. Pinto Basin in Joshua Tree National Monument: densities of 75 to 80 tortoises/mi^2 (Barrow 1979).
10. Barstow area: estimates were 5 to 50 tortoises/km^2 (Burge and Bradley 1976; Luckenbach 1976).
11. Estimates of tortoises in the 1970's were: 77 to 94 tortoises/km^2 at Goffs; 12 to 23 tortoises/km^2 at Chemehuevi Valley; 12 to 15 tortoises/km^2 at Fremont Peak; 77 tortoises/km^2 at Chuckwalla Bench (Berry 1978b); 58 to 77 tortoises/km^2 in Fremont Valley-Rand Mountain area of western Kern County (Berry 1977).
12. Western Mojave Desert populations have declined 89 percent since 1940, partly due to collecting and human predation.

Recently the Bureau of Land Management has found a 50 percent die-off in 6 years. At eight study plots there were declines from 20 to 30 to 70 percent over the past 6 to 8 years. The situation could be worse at areas with more disturbance (Berry 1984).

IV. **Nevada**

A. Found in Clark County, southern Nye County, and Lincoln County.

B. Specific localities

1. Clark County: Arden; 16 km south and 11 km west of Las Vegas; Big Bend of the Colorado River; near Boulder City; 10.5 km northwest of Davis Dam; Dead Mountains; near Fort Mojave; 6.4 km north of Jean; 16.1 km northwest of Las Vegas; approximately 48 km south of Las Vegas and east of Interstate 15, close to the community of Jean; 6.4 km south of Mesquite; Piute Valley; 16.1 km south of Searchlight (Burge and Bradley 1976; Esque and Duncan 1985; Klauber 1932; Linsdale 1940; Patterson 1982).
2. Lincoln County: Coyote Springs Valley, 88 km northwest of Las Vegas (Enriquez 1977; Garcia and others 1982; Patterson 1982).
3. Nye County: Frenchman Flats; Jackass Flats; Yucca Mountain; Forty-mile Canyon; Pahrump Valley; Rock Valley (Medica and others 1975, 1981; Patterson 1982; Tanner and Jorgensen 1963).

C. Status

1. Most areas in Nevada have low tortoise densities, but high densities were found in Piute Valley and Cottonwood Valley, Lake Mead National Recreation Area. Transects in 1980 showed less than 50 tortoises/mi^2 for 74.3 percent of transects and 100 to 200 tortoises/mi^2 at 6 locations representing 6.9 percent of the transects (Karl 1980; Schneider 1981a; Schneider and others 1982).
2. In Lincoln County densities of 100 tortoises/mi^2 were found in only 1 to 3 percent of total area. The remaining area had generally less than 50 tortoises/mi^2. Coyote Springs had 50 to 100 tortoises/mi^2; this may be the only viable population in the county. Nye County had an estimated 50 tortoises/mi^2; this estimate may be high, and the population may not be viable (Karl 1981a,b).
3. Transects of the Desert National Wildlife Range, Valley of Fire State Park, Blue Diamond Recreation Area, Lake Mead National Recreation Area, Piute Valley, and Goodsprings-Jean area showed most areas to be of moderate to low density. Goodsprings-Jean area population is moderate but was once high. Cottonwood Valley, Lake Mead National Recreation Area, and Piute Valley supported high-density populations (Schneider 1981a).
4. Coyote Springs density estimates were 45 to 90 tortoises/mi^2 in 25 percent of the area. Seven percent of the area has high densities; the rest, low densities (Garcia and others 1982).
5. Yucca Mountain on the Nevada Test Site supports densities of less than 20 tortoises/mi^2 (Collins and others 1983; Medica and others 1981); just west of Forty-mile Canyon, tortoise density was estimated at 90 to 100 tortoises/mi^2 (Medica and others 1981).
6. The Arden population is currently threatened due to the expansion of Las Vegas. There are serious threats to other populations from urbanization and grazing (Berry 1984; Dodd 1986; Karl 1980).

7. Data from 871 strip transects indicate that of 859 mi^2 of potential or historical habitat in southern Nevada, only 14 square miles may now support high densities of 140 to 150 tortoises/mi^2 (Berry and Burge 1984).

V. **Utah**

A. Tortoises are located in the extreme southwest corner of Washington County in small, semi-isolated to isolated or island populations of the western slopes of the Beaver Dam Mountains, Beaver Dam Wash and (isolated colonies) near St. George (Berry 1984; Coombs 1973, 1974, 1977c; Esque and others 1990a, 1991).

B. Distribution is limited to the east and north by the high elevations of the Beaver Dam, Bull Valley, and Mormon Mountains (Minden 1980).

C. Specific localities: Beaver Dam Slope area; west and northwest of Castle Cliff; northwest of Hurricane; Paradise Canyon, northwest of St. George; St. George Hills; Shivwits Indian Reservation; Snow Canyon State Park; Terry Ranch, 16.1 km west of Castle Cliff; south of the Virgin River (Coombs 1973, 1977c; Esque and others 1990a,b, 1991; USDI, Fish and Wildlife Service 1990a,b; Van Denburgh 1922b; Woodbury and Hardy 1948a,b).

D. Status

1. Beaver Dam Slope: patchy population scattered over an area of 91 mi^2. Density is generally 5 to 50 tortoises/mi^2. Surveys in 1980 found densities of 60 tortoises/mi^2 in southern Beaver Dam Slope and 16 tortoises/mi^2 in northern Beaver Dam Slope. Densities may be too low to survive more than a few decades (Minden 1980).
2. Density at the Woodbury and Hardy study site is 109 to 137 tortoises/mi^2 (Berry 1984; Minden and Keller 1981; Minden and Metzger 1981). Surveys in 1986 found densities of 13 and 18 tortoises/km^2 (Welker 1986).
3. Prior to disturbances of civilization, 2,000 tortoises may have been present on the Beaver Dam Slope. Now only 350 may exist, with only a few adult females. Collecting as pets and overgrazing are probably responsible for the decline. However, there are some indications that reproduction is occurring and the condition is improving somewhat, possibly as a result of a reduction in collection and grazing pressure (Minden 1980; Rowley 1983; Stewart 1976; USDI Bureau of Land Management 1975).
4. Estimates in 1977 of total population numbers were 350 native plus 70 introduced tortoises on Beaver Dam Slope, 150 in Paradise Canyon, and 200 in the St. George hills (Coombs 1977c, 1979).
5. Paradise Canyon covers 1.5 square miles and contains a healthy stable population of 250 tortoises with a number of reproductive females and young tortoises. It has not seen threats from grazing and appears to be expanding (Beck and Coombs 1984; Coombs 1977c; USDI, Fish and Wildlife Service 1985a).
6. St. George hills population consists of 200 tortoises in a 9-square mile area congregated in small canyons and drainages (Coombs 1976, 1977b,c; USDI Bureau of Land Management n.d.).
7. Density on the Beaver Dam Slope is five times less than it was when Woodbury and Hardy studied tortoises there; as a result of

these estimates of population densities, the desert tortoise was listed as threatened in 1980 (Coombs 1977c; Dodd 1986).

VI. **Mexico**

A. Tortoises found from the U.S. border near the Baja California Peninsula and the Arizona-Sonora border through most of Sonora, including Tiburon Island, Gulf of California and San Pedro Bay south to below Alamos; northwest Sinaloa, south as far as El Fuerte, Sinaloa in the foothills of the Sierra Madre (Auffenberg and Franz 1978a,b; Fritts and Scott 1984; Hardy and McDiarmid 1969; Loomis and Geest 1964; Smith and Taylor 1950; Van Denburgh 1922b).

B. No longer found in Baja California, although previously reported there (Auffenberg and Franz 1978a; Smith and Taylor 1950).

C. Range may extend further south than currently known into the dense vegetation of the Sinaloan deciduous forest (Fritts and Scott 1984).

D. Specific localities: 6.1 km northeast of El Fuerte on the road to Miguel Hidalgo Dam, Sinaloa; Alamos, Sonora and vicinity; 25.6 km south of Bacunora; Chollo Pinasco; Hermosillo and surrounding region; 25 km northwest of Kino Bay; Moctezuma; 3.2 km northwest of Puerto Libertad; 6.9 km south of El Norillo and 14.3 km west of Rio Yagui; 17.7 km east of San Jose de las Pimas; Sierra Seri; 16.1 km south of Sonoyta; 14.5 km west of San Javier and 113 km west of Hermosillo; Tiburon Island (Bogert and Oliver 1945; Bury and others 1978; Loomis and Geest 1964; Miller 1955; Patterson 1982; Reyes Osorio and Bury 1982; Smith and Taylor 1950; Van Denburgh 1922b); Sonora, "25 km east of Agua Caliente on road between Nuri and Esperanza" (Buskirk 1984).

E. Status

1. Forty percent of the range of the desert tortoise was in Mexico, and tortoises were widespread in Sonora and Sinaloa on bajadas (broad alluvial slopes extending from the base of a mountain range) and mountain slopes below 800 m in elevation (Bury and others 1978; Fritts and Scott 1984).
2. On Tiburon Island, the population was estimated at 28.9 to 87.3 tortoises/km^2, the highest reported density outside of California (Reyes Osorio and Bury 1982).
3. Some populations may decline due to urbanization. Overall there was no imminent danger to the species in Mexico and human-related pressures were not considered a serious threat (Fritts and Scott 1984).

Habitat

Description of habitat is well documented in the literature. Many of the distribution surveys conducted to ascertain tortoise densities also note the type of habitat occupied by tortoises. In addition, studies performed on permanent study plots also identify desert tortoise habitat. The following discussion is derived mostly from these studies with respect to habitat type, vegetative associations, and soil types.

I. **Habitat type and vegetation associations**

A. General—Mojave and Colorado-Sonoran Desert: found in creosote scrub, cactus scrub, shadscale scrub, Joshua Tree woodland, Sonoran Desert scrub, Sinaloan thornscrub, seaside scrub thornbush, and

Sinaloan deciduous forest plant communities. Creosotebush is the major plant community in well drained flats, bajadas, and upland alluvial slopes. In the Mojave Desert good habitat is found in creosote-bursage flats, basins, and bajadas. In the Sonoran Desert, steep boulder-strewn slopes often associated with paloverde communities are preferred. The greatest densities of tortoises occur in uniform creosotebush habitat with light gravel to sandy soil in Fremont Valley, CA, and Nevada tortoise habitat. The creosote community is the most stable and diversified vegetative cover, probably representing a climax community. Other habitat preferences include soil suitable for den construction, often sandy loam to light gravel or clay and caliche layers associated with washes; high production and diversity of perennials and annuals; and moderate to low elevation (Auffenberg and Iverson 1979; Brown and Lowe 1974; El-Ghonemy and others 1980; Jennings 1985; Luckenbach 1976, 1982; Patterson 1982; Schneider and others 1982; Smith and Smith 1979; Woodbury and Hardy 1948a).

B. Arizona
1. North of the Grand Canyon, desert tortoises are found in creosote scrub and Joshua tree woodland vegetation associations typical of the Mojave Desert. Some are also found in mixed blackbrush habitat. South of the Grand Canyon, tortoises are found mostly in Arizona upland communities: paloverde-cacti associations of Sonoran Desert scrub (Berry 1984d; Burge 1979).
2. Picacho Mountains tortoises inhabit the base of the mountains and associated washes to the middle and upper slopes, 540 to 719 m in elevation but only in paloverde-mixed cacti associations (Vaughan 1983, 1984a,b).
3. Pima County tortoises associated with paloverde-mixed cacti and saguaro-ocotillo cacti associations on north and northwest aspects of bajadas or steeper slopes 823 to 914 m in elevation, and near rocky streambeds in canyons (DeVos and others 1983; Ortenburger and Ortenburger 1927).
4. Tucson area: 82.8 percent of tortoise sign was found in mixed paloverde-cacti habitat; 17.2 percent was found in creosote-bursage habitat (Walchuk and DeVos 1982).
5. Virgin River-Pakoon Basin area of northern Arizona, two habitat types: desert scrub mix in washes and creosote-bursage on bajadas (Sheppard 1982a).
6. Beaver Dam Slope, Arizona: tortoises are found primarily in creosote-bursage vegetation associations (Hohman and Ohmart 1980; Sheppard 1981).

C. California
1. Tortoises are found in creosote scrub, cactus scrub, shadscale scrub, and Joshua tree woodland communities of the Mojave and Colorado Deserts. In the Colorado Desert, which is lower in elevation and hotter, tortoises are uncommon and found only in areas of creosote scrub or wash woodland associations. In the Mojave Desert, the greatest densities of tortoises occur in creosotebush habitat but are also found in moderate numbers in Joshua tree woodland and alkali scrub habitat (Dodd 1986; Luckenbach 1982).

2. Desert Tortoise Natural Area represents a lower Sonoran vegetation community dominated in the south portion by creosotebush, bursage, and goldenhead and cut by washes with saltbush. The northern portion is characterized by a creosote-saltbush community and rolling hills. The area contains a very diverse creosote scrub community and supports high tortoise densities (Campbell 1983; Good 1984; Hampton 1981).
3. Fremont Valley has very high tortoise densities supported by a uniform creosote-bursage habitat with light gravel and sandy to firm soils. Tortoises are more commonly associated with firm soils (Berry and Turner 1984; Hampton 1981; Luckenbach 1982).
4. Kramer and Kramer Hills: tortoises are found mostly in creosotebush-burrobush and creosotebush-shadscale communities. Fifty percent fewer tortoises are found in the saltbush community. When tortoises are found with saltbush, they are associated with sandy soil (Berry and Turner 1984; Luckenbach 1982; Nicholson and Humphreys 1981).
5. Goffs: favored habitat is creosote-bursage association with gravelly soil or sandy loam (Berry and Turner 1984).
6. Chemehuevi Wash: favored habitat is creosote-bursage with common plantain in sandy loam (Berry and Turner 1984).
7. Koehn Dry Lake: tortoises may be found on sand hummocks with mesquite and saltbush (Luckenbach 1982).
8. Stoddard Valley: habitat is flat desert with creosotebush communities (Medica and others 1980).
9. Providence Mountains region: favored habitat is characterized by creosotebush, high perennial diversity, and annual bloom potential, sandy loam to light gravel and clay soils with good denning potential at elevations up to 1,000 m (Luckenbach 1976).

D. Nevada
1. Tortoises are found in creosote, creosote-bursage, and creosote-blackbrush communities on bajadas and hills below 5,000 feet in areas of caliche washes (Lucas 1978, 1979; Tanner and Jorgensen 1963; Turner 1980).
2. At Yucca Mountain, on the Nevada Test Site, sign was observed between 3,200-5,240 feet elevation in creosote associations on the flats, to mixed transition and blackbrush associations on slopes (Collins and others 1983).
3. Rock Valley at the Nevada Test Site is creosote-scrub habitat, as is most of Nye County tortoise habitat (Medica and others 1980; Nagy and Medica 1986).
4. In Lincoln County, 81 percent of tortoise sign was found where creosotebush and bursage were dominant. Eleven percent of sign was found in creosotebush to blackbrush and 8 percent was found in the blackbrush communities (Karl 1981b).

E. Utah
1. Beaver Dam Slope (Washington County) is generally lower Sonoran vegetation and represents an ecotone of Sonoran, Mojave, and Great Basin flora. Joshua tree and creosote communities with a variety of annual forbes and grasses are dominant. Tortoises are found in the creosote to bursage community on the bajadas and low foothills and range up to the lower reaches of blackbrush associations.

Most tortoises are found among creosotebush and red brome at an average elevation of 2,900 feet.

2. St. George vicinity: found in highly variable terrain of Navajo sandstone north of St. George where habitats ranging from fine, red sand dunes to rocky slopes support populations of tortoises (Coffeen 1984; Coombs 1974; Esque and others 1990a, 1991; Higgins 1967; Minden 1980).

F. Mexico

1. Desert tortoises are found in areas ranging from xeric habitats near sea level to oak woodlands up to 800 m. Highest densities probably occur in Sinaloan thornscrub in southern and central Sonora. Also found in relatively moist, densely-vegetated Sinaloan deciduous forest (Fritts and Scott 1984).
2. On Tiburon Island, tortoises were found in creosotebush to mixed Desert scrub consisting of Sonoran desert scrub and Sinaloan thornscrub (Bury and others 1978; Reyes Osorio and Bury 1982).

II. **Vegetation**

A. General

1. High densities of perennial and annual flora, a high percentage of cover, and a high biomass of annual spring flora are necessary to support high densities of tortoises (Berry 1975a; Karl 1980; Luckenbach 1982; Schwartzmann and Ohmart 1978).
2. High winter-spring precipitation, reduced grazing competition, lack of surface disturbances, and long-term effects of fire positively influence forage availability, causing increased tortoise activity and increased reproduction and survival (Nagy 1973; Sheppard 1981).
3. Tortoises use creosotebush as cover for burrows and for egg laying (Sheppard 1980).

B. Specific vegetation associations

1. Arizona
   a. Picacho Mountains: Arizona upland plant community (Vaughan 1984a).
   b. Pinal County: (Schwartzmann and Ohmart 1976).
   c. Mojave County, Littlefield study plot: (Esque and others 1991; Hohman and Ohmart 1980).
2. California
   a. Western Rand Mountains (9 mi north and 6.5 mi east of California City, Kern County, CA): creosote scrub and Joshua tree woodland (Berry 1975a).
   b. Desert Tortoise Natural Area, eastern Kern County (Bickett 1980a,b).
   c. Ivanpah Valley (Turner and others 1981).
3. Nevada
   a. Tortoise density is positively correlated with creosotebush, and the upper limits of tortoise range (4,000 ft) correspond to the upper limit of the creosote community. Tortoise density is negatively correlated with dominance of blackbrush and red brome (Karl 1980, 1981a,b).
   b. Arden study site near Las Vegas: daily and seasonal behavior of tortoises monitored in creosote-bursage community (Burge 1977a; Burge and Bradley 1976).

c. Lincoln County: *Larrea tridentata* and *Ambrosia dumosa* compose the dominant shrub layer (Karl 1981b).

4. Utah
   a. Beaver Dam Slope (Coombs 1973, 1977a,b, 1979; Minden 1980; Woodbury and Hardy 1948a).
   b. City Creek study plot, north of St. George (Esque and others 1990a, 1991).
   c. St. George (Coombs 1977a,c).
   d. Paradise Canyon (Beck and Coombs 1984).
5. Mexico
   a. Tiburon Island, Gulf of California, Sonora (Bury and others 1978): 2 km west of Punta Torrenta (creosote to mixed desert scrub) and Caracol (subtropical thornscrub).

III. **Climate**

A. Desert tortoises inhabit subtropical, semiarid, and arid lands. They occupy mainly desert regions subject to long droughts, sporadic rains, poor drainage, flash floods, violent sandstorms, large temperature fluctuations, freezing winters, hot summers, sparse vegetation, and saline and alkaline soils (Auffenberg 1969; Bury and Marlow 1973).

B. The Colorado Desert is warmer than the Mojave Desert and has bimodal versus unimodal yearly rainfall, as does the Arizona Sonora Desert (Luckenbach 1982).

C. A possible trend toward increasing aridity and long-term climatic changes may be a factor in the decline of tortoise populations (Phillips and others 1984).

D. Winter temperatures in the Mojave Desert may dip below 0 °C. In the northeastern extreme of the range in Utah, temperatures may drop below –18 °C. Warmer winter temperatures in Arizona and Mexico, coupled with forage availability, may permit tortoises to be active yearround (Auffenberg 1969; Karl 1980; Minden 1980).

E. In the southern extreme of their range in Mexico, desert tortoises occupy milder and more mesic habitats than they do farther north (Fritts and Scott 1984).

F. The northern extreme of the range, Beaver Dam Slope, UT, is characterized by cool nights, daily temperature fluctuations of up to 40 °F and high temperatures exceeding 100 °F (up to 115 °F, with soil temperatures often 150 °F). Winter temperatures may drop below 0 °F. Relative humidity is 15 to 40 percent in summer and 40 to 60 percent in winter. Winds are light and generally from the southwest (Coombs 1973, 1974; Minden 1980; USDI Bureau of Land Management n.d.).

IV. **Precipitation**

A. Average precipitation in desert tortoise habitat is 12.5 cm/yr (4.9 inches/yr) and, except in areas over 200 m in elevation, evaporation is greater than precipitation. The average net water deficit is 6 to 10 cm (2.4 to 3.9 inches) per year. Rainfall is highly variable depending on the season and year (Phillips and others 1984).

B. Unimodal rainfall in winter in the western Mojave Desert is important in forage production and survival. In the eastern Sonoran and eastern Mojave Deserts, a bimodal pattern produces abundant annuals and diverse communities in both winter and summer

(Ackerman and others 1980; Phillips and others 1984; Schamberger 1985; Turner and others 1984).

C. Drought
   1. Evidence such as arroyo "cutting," the disappearance of plant species from large portions of their ranges, the decline of certain plant communities, and the spread of xerophytic species such as mesquite and tamarisk suggest a possible trend toward increasing aridity (Phillips and others 1984).
   2. A severe tortoise population crash was documented in Piute Valley, NV, during drought in areas of heavy grazing (Mortimore and Schneider 1983, 1984).

D. Tortoise population density is positively correlated with density and diversity of perennial plants and biomass of annuals, both of which are related to rainfall. Heavy rains are the trigger for growth of herbaceous perennials and annuals, and without adequate precipitation tortoises must switch to alternative food items (Beatley 1969, 1974; Sheppard 1981).

E. Winter rainfall is important to the chuckwalla, a large herbivorous desert lizard, and influences food availability that is necessary for growth and successful reproduction. There is evidence that tortoises may have similar requirements (Berry 1974c; Henen 1985, 1986; Medica and others 1975; Nagy 1972, 1973).

F. Relatively high rainfall is characteristic of preferred tortoise habitat, but precipitation can be too high and produce a negative effect by promoting a vegetative community unfavorable to tortoises. Optimum tortoise habitat is creosote scrub, which is generally found in areas with 5 to 20 cm (2 to 8 inches) of annual precipitation (Berry 1975a, 1984c; Karl 1980, 1981b; Luckenbach 1982; Schamberger 1985; Turner and others 1984).

G. High tortoise densities are known to occur in Fremont Valley, CA, which receives a minimum of 15 cm (6 inches) annual precipitation, with excellent ephemeral blooms (Luckenbach 1982).

H. Tortoise density increases where ground water is close to the surface (Luckenbach 1982).

I. In the Ivanpah Valley, CA, 6.7 cm of rain fell in the spring of 1980 and 3.2 cm fell in 1981. In 1981, tortoises were forced to shift to alternative foods such as *Opuntia* fruit (Turner and others 1984).

J. Specific precipitation measurements.
   1. Arizona
      a. Picacho Mountains: 21.8 cm (8.6 inches) of annual precipitation (bimodal), occurring mainly in late winter and late summer (Vaughan 1984a).
      b. Pinal County: 20 to 32 cm/yr (8 to 12.6 inches/yr) (Schwartzmann and Ohmart 1976).
      c. Beaver Dam Slope: average of 7.8 inches/yr (20 cm/yr), with March being the wettest month and April, May, and September the driest (Duck and Snider 1988).
   2. California
      a. Ivanpah Valley: 3.7 to 19 cm/yr (1.5 to 7.5 inches/yr) (Turner and others 1981).
      b. Desert Tortoise Natural Area, Kern County: 24.2 cm/yr (9.5 inches/yr), unimodal, (Good 1984).

3. Nevada: Arden study site, near Las Vegas: 10 cm/yr (4 inches/yr), with late fall and winter being critical periods (Burge and Bradley 1976).
4. Utah: Beaver Dam Slope: average of 24.1 cm/yr (9.5 inches/yr) of rainfall (bimodal) with peaks occurring in March and July to August. Tortoises are found at lower elevations of the mountains that receive 20 to 25.4 cm/yr (8 to 10 inches/yr). The upper boundary of tortoise distribution is the blackbrush community, which receives up to 30.5 cm/yr (12 inches/yr) (Coombs 1974; Good 1984; Minden 1980; USDI Bureau of Land Management n.d.).
5. Mexico: the slopes and hills of the Sonoran Plains area in Mexico receives 30 to 50 cm/yr of rain, 70 percent of which occurs in July through September (Brown 1982; Fritts and Scott 1984).

V. **Soil**

A. Preferred habitat contains sandy loam, light gravel to clay, or heavy gravel. The soil must be friable for burrow construction but firm enough so that burrows don't collapse (Luckenbach 1982; Schamberger 1985; Schamberger and Turner 1986; Schwartzmann and Ohmart 1978).

B. Firm soils that allow easy burrow construction promote higher tortoise densities. In habitat with both sand and firm soils in creosote communities, tortoises were more common on firm soils (Berry 1975a; Berry and Turner 1984; Wilson and Stager 1989).

C. Soil characteristics such as available water capacity, soil consistency, depth to a limiting layer, rock fragment content, soil salinity, soil temperature, and frequency of flooding may be important in identifying habitat and distribution of desert tortoises; these characteristics are easily measured in the field (Wilson and Stager 1989).

D. Specific localities and soil types

1. California
   a. Fremont Valley: predominantly sandy loams (Luckenbach 1982).
   b. North of Hinkley: soils are windblown and stabilized sand (Luckenbach 1982).
   c. Desert Tortoise Natural Area, Kern County: soil is fine-grained, loose sandy loam to coarse-grained sandy loam (Campbell 1983; Good 1984).
   d. Chocolate Mountains Aerial Gunnery Range: sandy soils (Berry and Turner 1984).
   e. Goffs: soils gravelly and loamy sand (Berry and Turner 1984).
2. Nevada
   a. Arden study site, near Las Vegas: soil is gravel with free sand, silt, and clay (Burge and Bradley 1976).
   b. Piute Valley: soil representing most tortoise burrowing and activity is sandy loam and gravelly loam to a depth of 12 inches. Lime-cemented gravelly sandy loam occurs from 12 to 19 inches (Wilson and Stager 1989).
3. Utah
   a. Beaver Dam Slope: shallow sandy loam that varies from fine to gravelly in texture (Good 1984; Minden 1980).

b. Dixie Valley, east of Beaver Dam Mountains: red Navajo Sandstone with occasional areas of overlying basalt, sand dunes, and cinder cones.

VI. **Elevation**

A. Arizona

1. South of the Grand Canyon: most tortoises are found at 915 to 1,220 m (3,000 to 4,000 ft) on granitic slopes (Berry 1984).
2. Pima County: steeper slopes from 823 to 914 m (2,700 to 3,000 ft) (DeVos and others 1983).
3. Tucson area: mostly found in paloverde communities at 823 to 914 m (2,700 to 3,000 ft) (Walchuk and DeVos 1982).
4. Beaver Dam Slope: 554 m (1,800 ft) at the Virgin River to 830 m (3,700 ft) at the Arizona-Utah border (Hohman and Ohmart 1980).

B. California

1. Ranges from below sea level at Death Valley to above 2,200 m (7,216 ft). Preferred elevation from less than 300 m (984 ft) to 1,070 m (3,500 ft) (Dodd 1986; Luckenbach 1982; Schamberger and Turner 1986).
2. Western Rand Mountains near California City: habitat is 294 to 305 m (2,900 to 3,000 ft) elevation (Berry 1975a).
3. Ivanpah Valley: 793 to 1,372 m (2,600 to 4,500 ft) elevation (Berry and Nicholson 1984b).
4. Near Chocolate Mountain Aerial Gunnery Range: 350 to 625 m (1,150 to 2,050 ft) elevation (Berry and others 1983a).

C. Nevada

1. Tortoises are found below 1,525 m (5,000 ft) and prefer 400 to 1,067 m (1,320 to 3,500 ft) elevation (Karl 1980; Lucas 1979; Ross 1986a,b; Turner 1980).
2. Lincoln County: 610 to 1,160 m (2,000 to 3,800 ft) (Karl 1981b).
3. Nye County: 732 to 1,220 m (2,400 to 4,000 ft) (Karl 1981b).
4. Yucca Mountain, Nevada Test Site: tortoise sign found at 975 to 1,598 m (3,200 to 5,240 ft) elevation (Collins and others 1983).
5. Arden study site, near Las Vegas: elevation of tortoise habitat averages 820 m (2,690 ft) (Burge and Bradley 1976).

D. Utah

1. Beaver Dam Slope: found below 1,060 m (3,500 ft); prefers 762 to 1,060 m (2,500 to 3,000 ft) and is limited by high elevation of mountains (Berry 1976; Coombs 1974, 1977a, c, 1979; Minden 1980).
2. Paradise Canyon: 975 m (3,200 ft) (Beck and Coombs 1984).
3. City Creek study plot: 975 to 1,067 m (3,200 to 3,500 ft) (Esque and others 1990a).

E. Mexico: in Sonoran and northern Sinaloa Deserts, tortoises are found from sea level to 800 m (Fritts and Scott 1984).

VII. **Terrain:** Generally sandy flats to rocky foothills. Mojave Desert habitat includes alluvial fans, washes, and canyons with soils suitable for den construction, largely on open flats or terrain with gentle slopes. Sonoran Desert habitat is usually among steep, boulder-strewn slopes (Burge 1979; Dodd 1986; Fritts 1985a; Luckenbach 1982; Turner and Wauer 1963). In the eastern Mojave Desert tortoise habitat generally consists of desert pavement with washes or washes bisecting flats (Luckenbach 1982).

A. Arizona
   1. Sonoran Desert: tortoises are found on steep, rocky slopes with extensive outcrops and boulders with gradients up to 70 percent (Burge 1979, 1980; Cole 1985; Schneider 1981a,b; Vaughan 1984a).
   2. South of the Grand Canyon: populations live mostly on hills and mountain slopes, especially among spheroidal granite rocks and large boulders that are close enough together to be inaccessible to livestock but allow tortoise movement (Berry 1984; Schneider 1980a; USDI Bureau of Land Management 1981).
   3. Pima County: tortoises are found on north and northwest aspects of bajadas and steeper slopes. In the Picacho Mountains, east-facing slopes were preferred in the winter and northwest-facing slopes in the spring. Tortoises used dens in caliche layers in the sides of washes or in crevices under rocks in the summer (DeVos and others 1983).
   4. Pinal County: alluvial basins, bajadas, and low rolling foothills, low desert, and mountains (Schwartzmann and Ohmart 1976).
   5. Tucson area: tortoise sign was found in creosote areas on 0 to 19 degree grades and in paloverde habitat on 20 to 40 degree grades (Walchuk and DeVos 1982).
   6. Virgin River and Beaver Dam Slope areas: tortoises inhabit alluvial fans and bajadas (Sheppard 1982a).

B. California
   1. Colorado Desert has high tortoise densities on southern bajadas of the Cottonwood Mountains and Chuckwalla Bench (Dimmitt 1977).
   2. Desert Tortoise Natural Area: rolling hills dominate and large open areas on gravelly hillsides are used as feeding areas (Bickett 1980a; Campbell 1983).
   3. Lucerne Valley: juvenile tortoises were associated with narrow, sandy washes adjacent to granitic boulders (Berry and Turner 1984).
   4. Goffs: bajadas with 2 percent slope and southwest aspect (Turner and others 1984).
   5. North of Hinkley: habitat is windblown and stabilized sand on top of Tertiary lava flows, bisected by washes (Luckenbach 1982).
   6. Chocolate Mountains Aerial Gunnery Range: desert pavement with interspersed washes and rolling hills (Berry and others 1983b).

C. Nevada
   1. Tortoises are found on bajadas and hills below 5,000 ft, bajadas had the highest use (Karl 1980; Lucas 1979; Turner 1980).
   2. Coyote Springs: hills and washes are favored habitat; flat gravelly and rocky areas are poor tortoise habitat due to limited burrowing potential (Garcia and others 1982).
   3. Arden study site near Las Vegas consists of an alluvial fan on 2 to 4 percent slope from the base of limestone mountains cut by large channels with exposed horizons and cavities in cemented gravel (Burge and Bradley 1976).
   4. Tortoise habitat also has areas of flat desert with sandy to gravelly soil (Linsdale 1940; Medica and others 1980).

D. Utah
   1. Beaver Dam Slope: gravelly floodplain of large alluvial fans, with limestone deposits that conglomerate gravel into a caliche layer that is used by tortoises as a ceiling for winter dens (Coombs 1974, 1977c, 1979; Minden 1980; Woodbury and Hardy 1948a).
   2. Paradise Canyon: small valley surrounded by Navajo sandstone cliffs; the valley floor is covered with sand dunes and scattered extrusions of basaltic lava flows (Beck and Coombs 1984).
   3. St. George vicinity: red Navajo sandstone with occasional areas of overlying basalt, sand dunes, and cinder cones; tortoises use sandstone shelves and large rocks for winter denning (Coombs 1974, 1977a,c; Esque and others 1990a, 1991).

E. Mexico
   1. Sonora and Sinaloa, Mexico: bajadas, mountain slopes, and peaks below 800 m elevation (Fritts and Scott 1984).

Habitat Deterioration

Detrimental effects on desert tortoise populations may involve the destruction or deterioration of habitats. The following discussion includes potential detrimental impacts most commonly discussed in the literature. The issue of livestock grazing and the desert tortoise is included here. The effects of grazing on soils and vegetation is also included: tortoises may or may not be influenced by these changes. The issue of habitat deterioration is controversial and heavily scrutinized: the following introduces the issues as they occur in the literature.

I. **Livestock grazing**

A. Effects on soil
   1. Sheet erosion and elimination of topsoil was due to reduction of perennial forage and ground cover on flatter terrain in the Picacho Mountains of Arizona. Desert tortoises are currently found almost entirely on steeper slopes that are inaccessible to cattle (Burge 1979; Vaughan 1982, 1984a).
   2. Soil erosion and compaction caused by heavy grazing has effects similar to compaction induced by vehicles (Arndt 1966; Ellison 1960; Klemmedson 1956).
   3. Infiltration rates decreased about 25 percent in areas of light to moderate grazing intensity and about 50 percent in areas of heavy grazing intensity (Gifford and Hawkins 1978).
   4. Root systems shrunk when continual grazing reduced the number of green blades for photosynthesis and energy production. As the roots decrease in volume, their ability to hold soil decreases and erosion and arroyo formation takes place (Johnson 1983).

B. Effects on vegetation
   1. Perennial grasses such as needlegrass (*Stipa speciosa*), grama grasses (*Bouteloua* spp.), and fluffgrass (*Erioneuron pulchellum*), which are common on protected areas and roadsides but absent inside fenced grazing areas, were significantly reduced in number as a result of livestock use (Berry 1984).
   2. Grazing reduced grasses and augmented unpalatable shrubs and "half shrubs." Grasses were found to be 100 percent higher in density in a desert grassland area protected from grazing for 30 years than in the surrounding grazed land (Gardner 1950, 1951).

3. New Mexico: invasion of mesquite increased in areas grazed by livestock. Grass densities increased, and total ground cover tripled in an area protected for 25 years from grazing (Potter and Krenetsky 1967).
4. Much of the western Mojave Desert has been altered from grassland to shrubland, and perennial bunch grasses have disappeared or have been severely reduced by grazing in many creosote communities. Weedy exotics, such as split grass (*Schismus arabicus*), checker fiddleneck (*Amsinckia intermedia*), filaree (*Erodium cicutarium*), and cheatgrass (*Bromus tectorum*) have been introduced by cattle and now comprise much of the annual flora in grazed areas (Berry and Nicholson 1984a).
5. Introduced exotic species such as *Erodium* have a tolerance for soil compaction and can survive heavy grazing pressure better than can native species, thus they outcompete and replace the latter in heavily grazed areas (Webb and Stielstra 1979). Exotics such as *Bromus rubens* and *Erodium cicutarium* have been correlated with low tortoise population density and low diversity of other annuals and are indicators of extensive grazing (Karl 1981a,b).
6. The replacement of native annuals and once prominent perennials such as *Muhlenbergia porteri*, which may have once been a favored food item, by exotics such as *Bromus rubens* and *Erodium cicutarium* (Coombs 1977b,c, 1979) could cause a shortage of water and nutrients and complicate electrolyte elimination. This may have resulted in protein deficiency leading to osteoporosis among Beaver Dam Slope tortoises (Jarchow and May 1987).
7. Slow recovery of vegetation from drought is exacerbated by heavy cattle grazing. In lean years with high cattle use (above 50 percent), perennial grasses are reduced, and browse, which is grazing tolerant, increases at such levels that the desert fails to recover even when given a "rest" (Hughes 1983; Johnson 1983).
8. Reduction in aboveground biomass of 60 percent under creosotebushes and a 24 to 28 percent reduction in intershrub densities of annuals resulted at the Desert Tortoise Natural Area and Rand Mountains of California due to heavy sheep grazing. Sheep trampling also caused an increase in soil strength and a 16 to 29 percent reduction in cover; the volume of goldenhead (*Acamptopappus sphaerocephalus*), a known tortoise food item, was 68 percent less (Webb and Stielstra 1979).
9. Range quality has deteriorated in the Mojave Desert due to grazing pressures. Grazing causes loss of annual biomass and shrub cover; the loss impedes reptile and rodent survival. Trampling reduces annual cover and disrupts the soil surface, causing erosion. Increases in soil strength may retard the future growth of annuals, further increasing erosion and loss of food sources (Webb and Stielstra 1979).
10. Wildlife in presettlement times probably grazed about 80 million animal unit months (AUM's) in 12 western states. Cattle currently graze 282 million AUM's (Wagner 1978).
11. Current sheep grazing levels greatly exceed the carrying capacity of the desert (Webb and Stielstra 1979).

C. Range condition on tortoise habitat
   1. All areas of the range of the desert tortoise have been, or are now being, grazed (Berry and Nicholson 1984a).
   2. Ninety percent of desert tortoise habitat was being grazed (Holing 1986).
   3. In Nevada 55 of 56 transects were rated as fair to poor in forage condition. A 1975 range survey showed 89 percent of Clark County to be in poor livestock forage condition, but grazing was reclassified from ephemeral to perennial-ephemeral. Ninety-seven percent of Piute Valley is grazed and 68 of 70 transects were rated as being in poor condition (the other two were in fair condition) (Berry and Burge 1984).
   4. Eighty-one percent of Bureau of Land Management land in the 10 Western States is rated as being in fair to poor condition due to overgrazing (Johnson 1983; Wagner 1978).
   5. Range condition has been downgraded from good to fair or, in most cases, poor over the range of the desert tortoise (Holing 1986).
   6. On the Beaver Dam Mountains, grazing has been practiced since the late 1800's, resulting in extensive habitat deterioration. In 1936, 69,470 sheep and 10,523 cattle were on the tax rolls for the area north of the Virgin River. There have been decades of sustained pressure (Sheppard 1982a,b).

D. Effects of grazing on the desert tortoise
   1. Although some contend that livestock grazing benefits the desert tortoise (Bostick 1990), many believe that heavy grazing may cause long-term, possibly irreparable damage to entire tortoise populations (Berry 1978a, 1979, 1989a; Coombs 1979; Johnson 1986; Sanchez 1973; Woodbury and Hardy 1948a). Ungrazed land was found to have twice the number of lizards and 3.7 times the biomass of comparable grazed land (Busack and Bury 1974).
   2. Livestock trample young tortoises with fragile shells, damage burrows and shrubs used for shelter, remove forage required by tortoises, and increase the overall mortality rate of tortoise populations. In late winter and spring livestock eat many of the same annuals and grasses that are the principal diet of tortoises. This may deprive tortoises of forage essential for growth, maintenance, and reproduction (Berry 1978a, 1989a).
   3. In Nevada the long-term effects of grazing, such as burrow trampling and competition for forage, are the greatest factor in decreasing tortoise densities (Karl 1981b).
   4. Livestock grazing is the biggest problem facing desert tortoises in Arizona. In many areas where populations are declining, it is the only possible cause (Johnson 1986).
   5. California tortoise populations are being hurt by livestock grazing and by possible competition with feral burros (Berry 1979; Sanchez 1977).
   6. Livestock compete directly for forage, trample vegetation, change community structure, and introduce and promote the spread of exotics. This may cause nutritional problems for tortoises by altering the normal dietary nutrients, water, and electrolyte elimination, which may affect tortoise growth, survival, and reproduction (Coombs 1979).

7. During summer and fall, tortoises—especially females—have an increased nutritional requirement for protein and calcium. Perennial grasses may be the main source for meeting these demands. If overgrazing has significantly reduced perennial grasses, tortoises may fail to meet nutritional demands (Cooper 1988).
8. Abundant spring annual forage, and perennial grasses after the annuals dry out, are essential for tortoise growth and reproduction. If juveniles emerge at a time when forage is lacking due to overgrazing, mortality may increase (USDI Bureau of Land Management 1983).
9. Females, because of their smaller home ranges and the metabolic demands of egg laying, and young tortoises are vulnerable to livestock grazing. This may explain the skewed sex ratio and absence of young tortoises in areas that have been heavily grazed, such as the Beaver Dam Slope, UT (Berry 1978a; Coombs 1973, 1977a,c; Woodbury and Hardy 1948a).
10. Tortoises have lower growth rates and possibly delayed sexual maturity when winter annuals are scarce (Berry 1978a; Medica and others 1975).
    a. If tortoise reproduction depends on adequate forage, females may have smaller clutches or be unable to lay eggs under heavy grazing pressure. This may have been the case in 1935 to 1945 when Woodbury and Hardy found mostly adults on the Beaver Dam Slope (Berry 1974c, 1978a; Coombs 1979; Woodbury and Hardy 1948a).
    b. Grazing removes vegetation allowing a greater quantity of solar radiation to be absorbed by the soil and greater transpiration of water from the soil. This alters the conditions of desert tortoise nests, which in turn may influence reproductive factors and success (Spotila and Standora 1986).
    c. Predation on tortoises probably increases under heavy livestock grazing. Tortoises on Tiburon Island, which is protected from grazing, face little predation in spite of high numbers of predators (Reyes Osorio and Bury 1982).
11. Desert tortoises need 23 lb/yr of vegetation to survive, a cow with a calf needs 10,000 lb/yr and eats more in one day than a tortoise does all year (Holing 1986).
12. Tortoises and other reptiles may not be able to tolerate interspecific competition. Sympatric reptiles are normally broadly different in food habits; tortoises may not be able to tolerate competition with cattle, which have a dietary overlap with tortoises as high as 60 percent (Bury 1982b; Hohman and Ohmart 1980).
13. Desert tortoises have food habits that are the result of thousands of years of adaptation to their environment. Grazing has brought about drastic environmental changes in 100 years (about a lifetime for a tortoise). Tortoises lack the genetic capability to adapt to these new conditions so rapidly (Coombs 1979).
14. Heavy grazing increases soil surface temperature, reduces moisture infiltration, increases evaporation and runoff, causes an overall increase in aridity, and reduces food items such as annual forbs; all of which can combine to create critically unfavorable conditions for tortoises (Sheppard 1980).

E. Specific observations
   1. Tortoise populations in the western Mojave and Colorado Deserts were much higher with a more extensive range prior to the 1950's than in the 1970's. Lanfair Valley, CA, once supported a tortoise population, but now tortoises are rare. It was an area that received intensive cattle use and is now dominated by a vegetative community that contains mostly weedy invader perennial species (Berry 1978a).
   2. Arizona
      a. Beaver Dam Slope
         i. Seventy-three percent of the sites in Arizona had cattle present. Tortoises were restricted to steep, rocky areas inaccessible to cattle. These were the only areas with adequate forage (Burge 1980; USDI Bureau of Land Management 1981).
         ii. Tortoises used burrows under creosotebushes for overwintering egg deposits that were vulnerable to cattle (Sheppard 1980).
         iii. A dietary overlap of 60 percent was noted in April before annuals cured, and cows shifted to perennial forage. Annual grasses appeared to be a buffer for reducing competition, but only when annual densities were high (Sheppard 1981).
         iv. Forbs averaged 39 percent of cattle diet. Dietary overlap averaged 40 percent, but ranged to 60 percent in early spring. Cattle consumed huge amounts of forbs and preferred many of the same annuals that tortoises did. Competition was more intense during dry years (Hohman and Ohmart 1980).
         v. In the Grand Canyon, AZ, exotic annuals made up 85 percent of the diet of tortoises in a grazed area but only 20 percent of the diet in an ungrazed area (Hansen and others 1976).
      b. Little Ship Wash: an older population of tortoises is present in an area where transects showed that snakeweed (*Gutierrezia* sp.) and Rayless goldenrod (*Haplopappus heterophyllus*), indicators of overgrazing, have their highest densities (Schneider 1980a).
   3. California
      a. Western San Bernardino County, Kramer study plot: sheep in the western Mojave Desert used 72.5 percent of a 1 square mile plot. Ten percent of the tortoise burrows were damaged and 4 percent were destroyed; two tortoises were observed that had been trampled and trapped inside their burrows. An area grazed by sheep experienced a 45 percent reduction in annuals during the spring and summer compared to a 5 percent reduction in an area with no grazing. There were 27 percent fewer shrubs in sheep bedding areas. Exotics represented 75 percent of the cover of annual plants; sheep ate flowering annuals at the same time tortoises did, and there was a high dietary overlap between sheep and tortoises (Nicholson and Humphreys 1981).
      b. Goffs and Ivanpah Valley: cattle concentrated in washes under large shrubs where tortoises seek cover. Cattle collapsed banks, destroyed shrubs, destroyed numerous tortoise burrows, and denuded entire areas (Burge 1977b,c).

c. Desert Tortoise Natural Area
   i. Twenty-three pallets (shallow depressions in the soil) and four burrows were trampled by sheep (Marlow 1974).
   ii. Sheep were observed in 1973 entering the area by trespass a month early and grazing until almost all traces of annuals, forbes, and grasses were gone. They also trampled and uprooted shrubs and damaged tortoise burrows (Berry 1978a).
   iii. Sheep grazed in areas of high density annuals, especially under creosotebush, removing food, and destroying cover for tortoises that feed on annuals and favor creosote as cover and burrow sites (Webb and Stielstra 1979).
   iv. Eleven fresh carcasses of juvenile and small immature tortoises were found in a survey conducted in 1987 immediately after sheep were allowed onto the study plot; 10 were overturned and 1 was crushed by a sheep hoof (Berry 1989a).

4. Nevada
   a. Lincoln County: no tortoise densities above 19/km^2 occurred in areas of extensive vehicular traffic and livestock grazing; the greatest densities of cattle occurred where tortoise densities were estimated at 0/mi^2 (Karl 1980, 1981b).
   b. Piute County: a major die-off of tortoises occurred during a drought in 1981. The die-off was confined to two ephemeral-designated grazing pastures on the Crescent Peak grazing allotment (Mortimore 1984; Price 1984; Ross 1986a,b).

5. Utah
   a. Livestock grazing has negatively affected tortoises on the Beaver Dam Slope (Berry 1978a, 1984e; Coombs 1974, 1977a; Hardy 1976; Hohman and Ohmart 1980; Minden 1980; USDI Bureau of Land Management n.d.; Woodbury and Hardy 1948a).
      i. Cattle and sheep have grazed tortoise habitat since 1862. Intensity of grazing increased in the 1940's, and adult tortoises were estimated to represent 90 percent of the total tortoise population. In the early 1960's sheep grazing was discontinued, and in 1965, cattle grazing was reduced 50 percent. Data from 1973 to 1976 showed 70 percent of the tortoise population were adults. Minden (1980) reported 42 percent adults. Successful reproduction may be occurring due to decreased grazing. Minden concluded that tortoise populations would directly benefit from as much grazing reduction as was possible.
      ii. Woodbury and Hardy (1948a) reported that tortoises only had a few days in the spring to forage before sheep swept the area clean of annuals. Coombs (1974) noted that when livestock were allowed on the slope after February 28, new green vegetation was removed and tortoises had to shift their diet.
      iii. Cattle-tortoise dietary overlap on the Beaver Dam Slope was 18.6 percent during May 1977, 59.9 percent during April 1978, and 24.5 percent during May 1978 (Hohman and Ohmart 1980).
   b. Paradise Canyon: there is no present grazing pressure and an expanding and healthy tortoise population exists (Beck and Coombs 1984).

II. **Off-road vehicles (ORV's)**

A. High-intensity ORV use in the western Mojave Desert is severely damaging the habitat in many tortoise areas and may be a factor in the tortoise decline (Berry 1973a; Bury 1978; Luckenbach 1975; Stebbins 1974; USDI Fish and Wildlife Service 1990; Woodman 1983).

B. ORV's encourage problems such as tortoise collection and shooting due to greater public access (Toffoli 1980).

C. ORV's crush tortoise burrows and nests, compact soil, and inhibit plant growth (Campbell 1982).

D. Preferred tortoise habitat lacks extensive vehicular and livestock grazing. No tortoise population densities above 19/mi^2 are found in Nevada where vehicular traffic and livestock grazing are combined (Karl 1980).

E. High soil strength resulting from ORV soil compaction has been shown to limit root expansion, significantly reducing annual cover. Desert annuals were found to be very sensitive to soil compaction. Soil strength of drying, compacted (even slightly compacted) soil increased at a much greater rate than soil strength of drying, uncompacted soil. Ten to twenty passes with an ORV at 1.8 percent soil-water content resulted in soil strengths too high to measure. Soil strength exceeding 20 kg/cm^2 limits root extension. ORV's may be responsible for observed reductions in annual plant growth in the Mojave Desert (Adams and others 1981, 1982a,b).

F. It was estimated in the California desert that intensive ORV use in a 1 km^2 area impacts 3,000 animals. Moderate use was speculated to destroy 830 individual animals (Bury and others 1977).

G. Eight paired control and ORV sites showed that heavy use resulted in 19 percent fewer species of reptiles and mammals than the control sites. Off-road vehicle pit areas demonstrated 41 percent fewer reptile and mammal species when compared to the control sites. The impact extended over large areas (Bury and others 1977).

H. Desert tortoise biomass in the northeast Mojave Desert was 3.4 kg/ha in areas without ORV use and 0.5 kg/ha in areas with ORV use. Adult tortoises in the ORV area were apparently removed or killed and burrows and vegetation were destroyed (Bury 1978).

I. Noise from dune buggies and motorcycles causes animals to go deaf with little or no recovery, interferes with their detection of predators, and causes unnatural behavior, which may jeopardize their survival (Brattstrom and Bondello 1980).

J. The Frontier 500 ORV race in California expanded old tracks 103 percent, crushed and uprooted 390 shrubs per mile on each side of the road, widened the road 50 to 90 feet on each side, and passed through 12 miles of critical tortoise habitat (Burge 1983).

K. During the Parker 400 race in California, 75 percent of creosotebushes were destroyed near the pit area after the race. One racer damaged 40 to 50 percent of six creosotebushes, about 20 percent of each of four burro bushes and 60, 80, and 90 percent of three other burro bushes (*Hymenodea* sp.). Of 14 tortoise burrows found, none was damaged during the race (Woodman 1983).

L. During 1981, 710 vehicles (676 of them motorcycles) entered the Desert Tortoise Natural Area by trespassing through vandalized areas of the fence. Three tortoises outside the area were found killed after an ORV race nearby. A tortoise inside the area was killed by a sheep watering truck (Campbell 1981, 1982).

M. Five tortoises were found killed by motorcycles and other ORV's on dirt roads and trails on a 1 mi^2 study area (Garcia and others 1982).

N. ORV-free play areas have been planned at Lucerne and Johnson Valleys, CA, where ORV's otherwise might decimate tortoise populations (Hoover 1981).

III. **Urbanization and agricultural development**

A. Checkerboard land ownership patterns (which fragment tortoise range and create island populations), urban settlement, and agricultural development threaten desert tortoise survival (Berry and Nicholson 1984a; Dodd 1981; Holing 1986).

B. Urbanization is expected by the California Fish and Game Department to eliminate desert tortoises in much of California. California development schemes that result in speculation, bulldozing and road building, then inactivity, have destroyed huge tracts of desert (Bury and Marlow 1973).

C. Failure of recovery of soil and vegetation was demonstrated at a study of a ghost town in southern Nevada; soil and vegetation had not recovered after 51 years and would probably require a century to recover (Webb and Wilshire 1980).

D. Airborne pollutants in southern California may be destroying desert plants (Medders 1973); exposure to air pollution in the Las Vegas Valley may impact the desert tortoise through toxicity of smog components accumulated in forage plants (Chrostowski and Durda 1991).

E. An Arizona study found higher tortoise densities in areas protected from urbanization such as Saguaro National Monument and Tucson Mountain State Park (Walchuk and DeVos 1982).

F. Tortoise population densities increase where ground water is close to the surface. Tortoises were abundant along the Mojave River before agriculture lowered the water table (Luckenbach 1982).

G. Tortoises are known to enter alfalfa fields where they are subject to pesticides and jackrabbit poison, and to being crushed by farm machinery (Berry and Nicholson 1984a).

H. Population fragmentation may affect population structure, such as, for instance by isolating a small effective number of breeding adults (Dodd 1982). Other threats to tortoise populations include livestock grazing, off-road vehicle habitat destruction, surface mining and land development, collection, predation, disease, vandalism, and inadequately enforced regulations and laws.

I. Expanding human population has elicited the need for power transmission facilities. A problem exists when construction of these facilities occurs within desert tortoise habitat (Pearson 1986).

IV. **Roads**

A. Roads fragment tortoise habitat creating artificial, potentially nonviable island populations from a previously contiguous population (Dodd 1986; Holing 1986).

B. Preferred habitat is in areas that lack vehicular disturbance (Karl 1980).

C. Tortoise densities increase with distance from roads (Nicholson 1978). Tortoise populations were depleted 60 percent for one-half mile on each side of a 40-year-old road (Garcia and others 1982).
D. About 4,131 square miles of Bureau of Land Management critical habitat in California receives impact from roads (Fusari and others 1981).

V. **Other factors**
A. Oil and gas leasing, geothermal development, mining, utility pipeline and transmission corridors, and military maneuvers all negatively impact habitat used by tortoises (Berry and Nicholson 1984a; Toffoli 1980; Vasek and others 1975a,b).
B. Military maneuvers create localized impact and habitat destruction, and areas that previously supported tortoises now have little evidence of them (Berry and Nicholson 1984a; Nicholson and others 1980a).
C. Proposed deposition of high-level nuclear waste at Yucca Mountain, NV, may potentially impact the desert tortoise; reclamation and restoration techniques must consider the tortoise's survival (Malone 1991).
D. There may be a climatic trend toward increasing aridity and desert community shifts (Phillips and others 1984).
E. Sixty percent of the original habitat of the desert tortoise has been lost due to human activities. Ninety percent is currently grazed and 80 percent is leased for oil and gas development (Holing 1986).

Burrows and Dens

Burrows and dens are discussed in great detail in the literature. Included here are references to burrow and den structure, construction of burrows and dens, and species that share burrows and dens with tortoises (commensals).

I. **Cover sites:** four types of cover sites: den, burrow, pallet, and nonburrow (Burge 1978). One tortoise may use several burrows or pallets for shelter during the summer; winter dens are often shared by several tortoises. The ratio of burrows to winter dens on Beaver Dam Slope, UT, is 4:1 (Coombs 1973, 1974; Luckenbach 1982; Woodbury and Hardy 1948a).

II. **Summer burrows or dens**
A. Description
1. Tortoises may dig their own burrows or modify the holes of other animals, especially those of the rock squirrel (*Citellus variegatus*) and the Harris antelope ground squirrel (*Ammospermophilus harrisi*) (Bury and Marlow 1973; Lowe 1964).
2. Length varies from 0.25 to 2.4 m with tunnels sloped from 20 to 40 degrees (Berry 1975b, 1978a; Bury and others 1978; Coombs 1977a,c; Hampton 1981; Minden 1980; Ortenburger and Ortenburger 1927; Reyes Osorio and Bury 1982; Woodbury and Hardy 1940, 1948a).
3. Angle is usually downward from a horizontal surface with cool, moist soil at the bottom; burrows may extend downward 3.2 m (10 ft) or more (Bury and Marlow 1973; Duck and Snider 1988; Woodbury and Hardy 1940). Mean floor inclination is 15.0 ± 4.0 degrees for the burrows of subadults and adults and 15.5 ± 4.4 degrees for burrows used by juveniles and very young tortoises.

Burrows excavated in slopes or embankments were more horizontal than those dug on flat surfaces (Burge 1978).

4. Shape of entrance is half-moon shaped and flat on the bottom (Bury and Marlow 1973; Luckenbach 1982; Minden 1980; Stebbins 1966, 1985).
5. Size is related to the size of the tortoise (Luckenbach 1982).
6. Temperatures inside summer burrows range from 19.0 to 37.8 °C; burrow humidity is relatively high and constant, creating an environmental buffer against extreme temperature and desiccation (Brattstrom 1965; McGinnis and Voigt 1971; Voigt 1971).
7. Summer burrows are fragile and easily caved in by livestock, rodent excavations, and the elements (Burge 1977a; Coombs 1977c; Woodbury and Hardy 1948a).
8. Number of burrows increased in wet years with greater annual production, and decreased in dry years (Coombs 1977c).

B. Location
   1. Burrows often found under rocks or shrubs or in hillsides (Berry and Turner 1986; Coombs 1977a; Lowe 1964; Ortenburger and Ortenburger 1927).
   2. Burrows often found under creosotebushes. In California 58.5 percent were under creosotebushes and 21.2 percent were under bursage. In Arizona, 77.2 percent were found under creosotebushes and 21.1 percent under bursage (Berry and Turner 1984, 1986; Coombs 1977c; Duck and Snider 1988).
   3. Burrows are usually found under woody shrubs, but they are found in arroyos on Tiburon Island, Mexico, at the base of wash banks in Sonora, Mexico, and elevated from the wash bottom in Utah (Auffenberg 1969; Coombs 1977c; Crooker 1971; Reyes Osorio and Bury 1982).
   4. Use of plant species for cover is correlated with shade provided by the plant and not with species density (Burge 1978).
   5. Burrows mostly face north, northeast, east, or northwest depending on location (Burge 1978; Hampton 1981).

C. Pattern of utilization
   1. Burrows are often temporary and may only be used for a season. Of 56 burrows excavated in the summer of 1973 on the Beaver Dam Slope, 4 were used again in 1974. Thirty-two had been caved in (Coombs 1974). However, at the Arden study site in Nevada, 83 percent of burrows used in 1974 were used again in 1975 (Burge 1978).
   2. The average number of dens used by tortoises in the Picacho Mountains of Arizona was 7.6 (±0.63) during a study from April 1982 to September 1983 (Barrett 1990).
   3. In mild weather tortoises depend less on burrows and more on shallow depressions (pallets), usually constructed under a bush (Berry 1974b; Bury and Marlow 1973).
   4. Burrows are constructed when temperatures rise above 32 °C (Bury and Marlow 1973; Woodbury and Hardy 1948a).
   5. Several burrows may be used over a span of a few days, or a tortoise may return to the same burrow each night (Bury and Marlow 1973; Coombs 1974; Grant 1936a).

6. In Rock Valley, NV, burrow use was highest in the spring, ceasing in October when tortoises retreated to winter dens (Nagy and Medica 1986).
7. On the Beaver Dam Slope of Utah, burrows were abandoned in September (Coombs 1977c).
8. Arden study site, Nevada (Burge 1978).
   a. The mean density of pallets and burrows was 3.5/ha.
   b. Subadults and adults used burrows 30 to 300 cm long or greater. Thirty-eight percent used burrows 30 to 70 cm long, 32 percent used burrows 71 to 190 cm long, and 30 percent used burrows longer than 190 cm.
   c. Adults used 12 to 25 shelter sites (applies to burrows, pallets, caves, and shrub cover) per year.
   d. A burrow is usually occupied by only one tortoise at a time.
   e. Most burrows were used repeatedly; 75 percent were used by one to five other tortoises.
   f. Three to seven burrows or pallets were used each month, with 8 percent used for 1 day, 73 percent used for 2 to 15 days, and 19 percent for 16 to 46 days.
9. In Utah, the distance between burrows is 46 to 228 m (Coombs 1977c).

D. Excavation: tortoises may repair an old burrow or dig a new one. To construct a burrow, tortoises sniff the ground several times to select a location. They dig with the front legs and push soil away with the hind legs. When the burrow is about one-third of the tortoise's length, the tortoise moves in as far as possible, turns around, then walks out. Digging is then resumed and the process is repeated until the burrow is complete. Burrows about the size of an adult tortoise take 35 to 45 minutes to construct. Burrows 50 cm deep take less than 90 minutes (Hohman and Ohmart 1980).

III. **Winter dens or burrows**

A. Description

1. Length ranges from 1.5 to 10.9 m in the northern part of range. In southwestern Utah, the northernmost part of range, dens extend 2.4 to 4.5 m into the banks of washes and arroyos. Lengths of 6 to 10.9 m have been reported. On Tiburon Island in Mexico tortoises use burrows 0.03 m to less than 2 m long during winter (Berry 1975b, 1978a; Brown 1968; Bury and others 1978; Coombs 1977c; Miles 1953; Reyes Osorio and Bury 1982; Woodbury and Hardy 1948a).
2. Longer dens usually provide greater temperature stability (Brattstrom 1965).
3. In southern Nevada diurnal temperature fluctuation 2.3 m underground was less than 0.5 to 2.2 °C, and the lowest temperature was 2.2 °C in December (Burge 1978).
4. In southern Nevada temperature in a 2.3-m long den during the hibernation emergence time in March and April was usually between 12 and 14 °C (Burge 1978).
5. In southern Nevada maximum floor temperatures for the last week in July and first half of August were 30.0 to 32.8 °C 2.3 m inside the den. Daily fluctuation was 0.5 to 2.2 °C (Burge 1978).

6. Temperature and humidity were very constant at 5.3 m deep. Humidity may be as high as 40 percent (Woodbury and Hardy 1948a).
7. Winter dens may be branched and have several chambers or may be connected to other dens (Coombs 1977c; Woodbury and Hardy 1948a).
8. Den openings are half-moon shaped or semicircular (Luckenbach 1982; Stebbins 1966, 1985).
9. Beaver Dam Slope, UT: 311 dens were measured. Average width of opening was 28 cm. Average den width was 85 cm. Average thickness of soil covering the den was 68 cm, and the distance between den opening and nearest shrub was 1.89 cm (Minden 1980).
10. Some dens on the Beaver Dam Slope, UT, may be 5,000 years old (Auffenberg 1969; Pritchard 1979b).
11. In the southern part of the range, including Sonora, Mexico and southern Arizona, tortoises construct pallets or shelter burrows often just large enough to cover their carapace (Auffenberg 1969).
12. In southeastern California winter dens are usually constructed with a 45 degree slope in firmly packed sand and gravel (Camp 1916).

B. Location
1. In Utah dens are usually constructed under caliche exposures in wash banks, but are also found under large boulders and sandstone shelves (Coombs 1973, 1977c; Woodbury and Hardy 1948a).
2. In California most dens face south or southwest. Beaver Dam Slope dens open to the east or west, due to the north-south alignment of the washes. Over 50 percent face somewhat southeast (Auffenberg 1969; Berry and Turner 1984; Hohman and Ohmart 1980; Minden 1980).
3. In eastern Kern County, CA, dens are constructed with a ceiling of 0.2 to 0.3 m over the entrance, usually in the shade of a shrub (Berry 1972).
4. On Tiburon Island in Mexico, two burrows were found that had been dug into the base of woodrat middens (Bury and others 1978).
5. At Pinto Basin, Joshua Tree National Monument, CA, tortoises are known to use tunnels of kit fox (*Vulpes macrotis*) complexes (Barrow 1979).
6. Favorable locations for den sites may be a limiting factor restricting the range of the desert tortoise on the Beaver Dam Slope, UT (Coombs 1977c; Gregory 1982).

C. Pattern of use
1. Dens receive permanent use and are used year after year, but not always by the same tortoise. They are used throughout the winter and also for aestivation and shelter in the hot summer; dens are used to a lesser extent at other times of year (Berry 1972; Burge 1977a; Coombs 1977c; Hohman and Ohmart 1980; Woodbury and Hardy 1948a).
2. Dens are occupied from mid-October to mid-April on Beaver Dam Slope, UT (Woodbury and Hardy 1940, 1948a).

3. Tortoises have been observed to emerge from dens on warm days during the winter hibernation period (Woodbury and Hardy 1948b; Coombs 1977c).
4. Winter dens are often used communally; up to 17 tortoises may be found hibernating in one den (Thorpe 1957; Woodbury and Hardy 1940, 1948a).
5. Sonoran Desert tortoises use shallower dens in winter than in summer (Vaughan 1984a).

D. Excavation: see also Burrows and Dens.

1. Tortoises select excavation sites by sniffing soil then digging with the forelegs for three to four strokes. This activity is repeated until a suitable den site is found (Berry 1972).
2. The spade-like limbs are used in digging and the hind legs are used to push the soil back (Berry 1972).
3. The tortoise digs while standing, apparently bracing itself with its forefeet and hindfeet (Bramble 1978).
4. Cooperative digging has been observed where several individuals dig simultaneously or individuals dig in relays (Nichols 1953).

IV. **Commensals** (Barrow 1979; Berry 1975a; Burge 1978; Coombs 1973, 1974, 1977c; Goin and others 1978; Hohman and Ohmart 1980; Lane 1984; Luckenbach 1982; Woodbury and Hardy 1948a).

A. Mammals

Antelope ground squirrel	*Ammospermophilus leucurus*
Blacktail jackrabbit	*Lepus californicus*
Canyon mouse	*Peromyscus crinitus*
Desert cottontail	*Sylvilagus auduboni*
Desert woodrat	*Neotoma lepida*
House cat	*Felis domesticus*
Kangaroo rat	*Dipodomys merriami*
Kit fox	*Vulpes macrotis*
Pocket mouse	*Perognathus* spp.
Spotted skunk	*Spilogale gracilis*
White-footed mouse	*Peromyscus* spp.

B. Birds

Burrowing owl	*Athene cunicularia*
Gambel's quail	*Callipepla gambelii*
Poorwill	*Phalaenoptilus nuttallii*
Roadrunner	*Geococcyx californianus*

C. Reptiles

Banded gecko	*Coleonyx variegatus*
Coachwhip	*Masticophis flagellum*
Desert iguana	*Dipsosaurus dorsalis*
Desert spiny lizard	*Sceloporus magister*
Gopher snake	*Pituophis melanoleucus*
Mojave green rattlesnake	*Crotalus scutulatus*
Sidewinder	*Crotalus cerastes*
Spotted night snake	*Hypsiglena torquata*
Western rattlesnake	*Crotalus viridis*
Western whiptail	*Cnemidophorus tigris*

D. Invertebrates

Antlion larva	*Myrmeleontidae*
Blackwidow spider	*Lactrodectus mactans*

Ground beetle	*Tenebrionidae*
Roaches	*Orthoptera*
Scorpion	*Centruroides* spp.
Silverfish	*Thysanura* spp.
Tarantula	*Aphonopelma* spp.
Ticks	*Acarina, Ornithodoros parkeri*

Reproduction

Courtship, mating, and nesting behavior are well documented in the literature for both wild and captive desert tortoises. Materials included in this section include characteristics of sexual maturity, courtship, mating and egg-laying, and hatching of young.

I. **Characteristics at sexual maturity**
   A. Age at maturity
      1. Wild tortoises: 15 to 20 years, Berry 1972, 1978a; 12 to 18 years, Bury and Marlow 1973; Dodd 1986; Miller 1955; Stebbins 1974; Woodbury and Hardy 1948a.
      2. Captive tortoises: Berry 1978a; Jackson and others 1976a,b, 1978 (4 years, special diet); 12 to 13 years, Luckenbach 1982; Stewart 1973.
   B. Size at maturity generally 215 to 220 mm: Auffenberg 1965; Berry 1972, 1975b, 1978a; Burge 1977a,d; Camp 1917; Coombs 1977c; Dodd 1986; Grant 1936a; Moll 1979; Nagy and Medica 1986; Turner and others 1984; Woodbury and Hardy 1948a.
   C. Secondary sexual characteristics: see Sexual dimorphism.

II. **Breeding season:** courtship and peak breeding begins in March and April at the time of emergence from hibernation. Courtship may extend from late summer to early October. Egg laying begins May through July. Hatching usually occurs from September through October but may also occur in spring (Berry 1972, 1975b, 1978a; Grant 1936a; MacMahon 1985; Miller 1955; Nichols 1953, 1957; Patterson 1971a; Reyes Osorio and Bury 1982; Stuart 1954; Tomko 1972).

III. **Courtship and mating behavior**
   A. Species and sex recognition: see Sex recognition.
   B. Description (Auffenberg 1966b, 1977; Berry 1972, 1986b; Bickett 1980a; Black 1976; Coombs 1974; Housholder 1950; Patterson 1972b; Tomko 1972; Vaughan 1984a; Watson 1962; Woodbury and Hardy 1948a).
      1. Visual and olfactory cues are involved in species and sex recognition. After recognition the male approaches the female with his neck outstretched and begins head bobbing. The swollen subdentary glands may be everted during head bobbing. Intensity of head bobbing increases as male gets closer to female. If the female does not respond, the male may touch her head or shell or bite at her legs and shell.
      2. Usually the female moves away. The sight of a moving female is a strong visual signal and the male may follow 1 to 3 m behind the female for hours. This trailing includes low-intensity head bobbing that increases as the female walks faster.
      3. The male begins to circle the female, usually in a counter-clockwise direction. The female may try to avoid him.

4. The male decreases head bobbing and begins to bite the female on the legs, shell, and gular area and sometimes rams the female with his gular projections or raises her off the ground.
5. The biting and ramming immobilizes the female who withdraws into her shell or raises her pelvis and everts her cloaca. The withdrawal of the female causes the male to cease butting and biting and attempt to mount.
6. The male may sniff the female's cloaca before attempting to mount. Mounting is from behind or from the side and the male positions himself over the posterior part of the female's carapace with short hops on his hind feet.
7. Once in position, the male moves tail forward to copulate and begins vertical thrusting movements or pumping motion with his pygal scute striking the ground and his head extended forward.
8. During copulation the male stomps his hind feet and may paw the female's carapace with his forefeet with his head extended forward and his mouth half open. He may also emit hissing and grunting sounds.
9. The female may move her neck and head from side to side or eat during copulation.
10. Copulation continues until the female moves away and male falls off. He may attempt to copulate again.
11. Successful mating attempts involve the use of the finger-like tail tip to pull back on the undersurface of the female and hold and move her into position.
12. Mating leaves circular or oblong depressions in the sand or soil.

C. Competition for mates: in Utah two males simultaneously courted a female; the males battled, and the victor mated with the female (Coombs 1974). In southeastern California, two females were observed as they competed for the attention of a male. One female rammed the other when both were courted by the male (Bickett 1980a).

IV. **Nests and egg deposition**

A. Nest location: dug in well drained, friable, sandy soils (Coombs 1974; Ehrenfeld 1979). Nests have been found at the entrance of winter dens (Coombs 1974, 1977a; Hampton 1981); at the entrance of or just inside burrows (Berry 1974b; Hampton 1981; Roberson and others 1985; Woodbury and Hardy 1948a); and beneath shrubs (Burge 1977a; Coombs 1977c; Hampton 1981).

B. Nest construction and egg laying (Beltz 1954; Berry 1974b; Coombs 1974, 1977a; Hampton 1981; Lee 1963; Lowe 1964; Miles 1953; Miller 1932, 1955; Roberson and others 1985; Stuart 1954).

1. Females are sometimes restless prior to nest construction. They may refuse food and sniff at the ground several days before construction.
2. Female digs a broad hole with her front legs then backs in and digs with her back legs. She may urinate on the soil. Excavation may last up to two hours.
3. In captivity males have been observed helping females dig nests.
4. Before egg laying, the female holds her hind legs straight, keeping her legs in the nest.

5. The cloaca begins to swell and an egg is emitted a few seconds later. Eggs are laid one at a time. Females appear "oblivious" to surrounding activity during egg laying.
6. After egg laying, the female positions the eggs with her hind feet. The hind feet are also used to scrape dirt over the eggs and pack the dirt down.
7. After the eggs are covered, the female may release a large amount of urine over the nest, then repack the dirt.

C. Nest urination
1. Nest urination has been shown to repulse egg predators. It may also help camouflage the nest, compact the soil and soften the substrate prior to digging (Ehrenfeld 1979; Patterson 1971b).
2. Nest urination may help prevent wind or rain from exposing the eggs and may form a protective crust to keep the eggs moist (Coombs 1977c).
3. In one experiment, urine did not retard bacterial or fungal growth on eggs (Patterson 1971b).
4. Embryos do not receive any moisture from nest urination (Coombs 1977c; Ragozina and Zugman 1965).

D. Time of nesting
1. Observed naturally in late May through the middle of June in late afternoon or early evening; however, nesting may continue as late as October (Berry 1972, 1975a; Burge 1977a; Coombs 1977a,c).
2. Observed in captivity in June, July, and October in late afternoon or early evening (Booth 1958; Camp 1917; Miles 1953; Miller 1932; Nichols 1953; Stuart 1954).

E. Size of nest
1. Varies with size of tortoise and hardness of soil (Nichols 1953).
2. Specific examples of nest size in captivity: Booth 1958; Lee 1963; Miller 1932; Nichols 1953.
3. Specific examples of nest size in the wild: Berry 1972; Burge 1977a; Coombs 1977c.

F. Nest defense: observations of female tortoises defending nest from Gila monster (*Heloderma suspectum*) (Vaughan and Humphrey 1984).

G. Sperm storage: observation of a captive female laying a clutch of fertile eggs 1.5 years after isolation from males (Miller 1955).

H. Clutch size
1. Estimates: 2 to 14 eggs, 5 to 7 average (Berry 1974b, 1978a; Ernst and Barbour 1972; Grant 1936a; Miller 1955; Moll 1979); 1 to 13 eggs (Naegle 1976); 2 to 9 eggs (Stebbins 1972).
2. Specific records
   a. Wild tortoises: California (Berry 1972, 1979; Grant 1946); Rock Valley, NV (Turner and others 1987); Goffs, CA (Roberson and others 1985; Turner and others 1984, 1986); Fremont Valley, CA (Hampton 1981); Beaver Dam Slope, UT (Coombs 1974, 1977c).
   b. Captive tortoises: Booth 1958; Camp 1917; Glenn 1983; Grant 1936a; Keasey 1971; Lee 1963; Loomis and Geest 1964; Miles 1953; Miller 1955; Nichols 1953; Poorman and Poorman 1971a; Stuart 1954; Trotter 1973.

I. Clutch frequency
   1. General: zero to two clutches are laid annually (Dodd 1986; Turner and others 1986).
   2. Specific records
      a. Wild tortoises: California (Turner and others 1986); near Goffs, CA (Roberson and others 1985; Turner and others 1984); Ivanpah Valley, CA (Medica and others 1982).
      b. Captive tortoises: Miller 1955; Stuart 1954.

J. Factors influencing clutch size and frequency
   1. Size: larger females generally lay larger clutches (Hampton 1981; Turner and others 1986).
   2. Age: older females may have smaller clutches (Hohman and Ohmart 1980).
   3. Forage quality and availability may affect clutch size (Hohman and Ohmart 1980).
   4. Rainfall, and therefore forage availability, has been positively correlated with clutch frequency (Turner and others 1984, 1986).
   5. Lack of water may reduce egg production since water is utilized in egg production and nest construction (Coombs 1977c).

K. Eggs
   1. Description
      a. Shell: thick, hard, translucent, dull chalky white in color, rough in texture with pits. Shell is resistant to desiccation (Coombs 1974; Grant 1936a, 1946; MacMahon 1985; Miller 1932).
      b. Yolk: tough and pale cream-colored (Miller 1932). Egg is composed of a fluid albumin surrounding a viscid one, which surrounds a cream-colored yolk (Pope 1939).
   2. Size: eggs are about the size of a ping-pong ball and are elliptical to nearly spherical (Camp 1916, 1917; Grant 1960a; Miller 1932; Pritchard 1979a).
      a. Records of wild tortoise eggs: Berry 1975a; Burge 1977d.
      b. Records of captive tortoise eggs: Camp 1916, 1917; Grant 1936a; Miles 1953; Miller 1932; Turner and others 1981.

V. **Egg development, incubation, and hatching**

A. Egg development
   1. Procession of development after egg laying (Booth 1958)
      a. 21 days: egg contents appeared cloudy.
      b. 22 days: blood lines appeared, enlarged, and darkened.
      c. 35 days: embryo was visible and was 9.5 mm long.
      d. 37 days: movement could be detected.
      e. 66 days: embryo well developed.
      f. 82 days: hatching began.
   2. Position of fetus in egg: feet flattened and neck retracted with only part of the head projecting outward (Woodbury and Hardy 1948a).
   3. Effect of temperature on egg development: warm, favorable temperatures promote faster development (Booth 1958; Grant 1936a). However, too much heat may cause eggs to fail to hatch (Shade 1972). Captive tortoise eggs incubated failed to hatch after being incubated, except for the one farthest from the heater (Stuart 1954). Most chelonians (turtles and tortoises) show temperature-dependent sex determination, including *Gopherus*.

Temperature-dependent sex determination has not yet been investigated in *Gopherus agassizii* (Spotila and Standora 1986; Vogt and Bull 1982).

4. Effects of humidity on egg development: eggs may fail to develop if there is not enough humidity. *Gopherus agassizii* eggs can tolerate lower humidity levels then *Gopherus berlandieri* eggs (Poorman and Poorman 1971a).

B. Incubation period
   1. Wild tortoise eggs: Burge 1977d; Coombs 1974, 1977a,c; Dodd 1986; Grant 1936a; Leopold 1961; Pritchard 1979a.
   2. Captive tortoise eggs or artificially incubated eggs: Berry 1975a; Booth 1958; Grant 1936a; Hunsaker 1968; Lampkin 1966; Miles 1953; Nichols 1953, 1957; Poorman and Poorman 1971a; Shade 1972; Stuart 1954; Trotter 1973).

C. Hatching
   1. Estimated hatching from August through October with some eggs overwintering and hatching in spring (Luckenbach 1982; MacMahon 1985).
   2. Actual hatching times of wild tortoises: Berry 1972, 1975a; Burge 1977d; Coombs 1974; Naegle 1976; Roberson and others 1985.
   3. Actual hatching time of captive tortoises: Booth 1958; Grant 1936a; Miller 1955; Trotter 1973.
   4. One to three days is required for the hatchling to use its egg tooth to break through the shell (Lampkin 1966).
   5. Hatchling is born with a yolk sac one-third the size of its body, attached to the umbilical area. It impedes locomotion the first few hours but is absorbed into the body in a few days (Lampkin 1966; Luckenbach 1982).
   6. Twin tortoises (two in one egg) joined at the yolk sac have been reported (Hunsaker 1968; Young 1981).

D. Hatching success
   1. Wild tortoises
      a. Specific estimates: Burge 1977d; Roberson and others 1985; Turner and others 1984.
      b. Factors influencing hatching success: optimal temperature and moisture (Ewert 1979; Hampton 1981); egg predation by Gila monster, kit fox, or coyote (Bury and Marlow 1973; Hohman and Ohmart 1980).
   2. Captive tortoises, specific estimates: Booth 1958; Hampton 1981; Hunsaker 1968; Lee 1963; Miles 1953; Nichols 1957; Shade 1972; Trotter 1973.

E. Hatchling description: see Hatchlings.

F. Hatchling survival
   1. Of 100 hatchlings, two to five live to maturity (Holing 1986).
   2. Crucial period for survival is the first 3 to 5 years when hatchlings have soft shells and are vulnerable to predation (Grant 1936a; Jaeger 1955; Hohman and Ohmart 1980; Patterson 1971a).

Growth and Population Structure

The majority of information on the growth of the desert tortoise exists on captive tortoises; however, the following discussion also includes observations on wild populations of desert tortoises monitored during long-term studies or permanent study plots.

I. **Size and growth rate**
   A. Adult size
      1. Captive tortoises: females 28.6 cm (n = 30), males 33.7 cm (n = 30), Grant 1936a; McCawley and Sheridan 1972.
      2. Wild tortoises: two females 202 and 223 mm, two males 217 and 228 mm, Bogert and Oliver 1945; Burge 1977d; Reyes Osorio and Bury 1982; Turner and others 1981; Van Denburgh 1922a,b; Woodbury and Hardy 1948a.
      3. Record size tortoises: 493 mm, Jackson and others 1980; Reyes Osorio and Bury 1982; 15.5 inches (393.7 mm), St. Amant n.d.; females 36.9 cm, males 35.9 cm, Shaw 1959.
   B. Adult mass
      1. Mass fluctuates with season, forage availability, state of hydration, defecation, and egg laying (Berry 1974b).
      2. Captive tortoises: McCawley and Sheridan 1972.
   C. Hatchling size
      1. About the size of a silver dollar when born (Coombs 1977c; Miles 1953).
      2. Captive hatchlings: Grant 1936a; Hunsaker 1968; Poorman and Poorman 1971a.
      3. Wild hatchlings: Andrews 1981; Burge 1977d; Coombs 1974, 1977c; Miller 1955).
   D. Growth rate: smaller tortoises grow rapidly but the growth rate slows down with age. There is a brief surge of growth as tortoises reach sexual maturity but growth decreases significantly after sexual maturity is attained (Beck and Coombs 1984; Bogert 1937; Patterson and Brattstrom 1972).
      1. Captive tortoises: Jackson and others 1976a,b, 1978; Minden 1980; Patterson and Brattstrom 1972; Tremper 1978).
      2. Wild tortoises: Beck and Coombs 1984; Berry 1975b; Bogert 1937; Coombs 1974; Germano and Joyner 1988; Hardy 1976; Medica and others 1975; Minden 1980; Nagy and Medica 1986; Turner and others 1987; Woodbury and Hardy 1948a.
      3. Based on scute annuli: Berry 1986e; Germano 1988; Medica and others 1975.
      4. Based on shell density, shell thickness, or percentage of body mass as a function of increase in carapace length (Patterson 1977, 1978).
      5. Factors influencing growth: precipitation and annual plant production (Medica and others 1975; Nagy and Medica 1986).
      6. Variation of growth rates exists throughout different parts of tortoise range (Turner and others 1987).
      7. In Southern Nevada, no growth occurs before mid-April or after the first week in July (Medica and others 1980).
      8. Males have been reported to grow faster than females as juveniles and to keep growing longer into adulthood (Andrews 1981; Woodbury and Hardy 1948a).

II. **Longevity**
      1. Captive tortoise: Bowler 1927; Conant and Hudson 1949; Glenn 1983; longer than 52 years, Jennings 1981; longer than 40 years, Miles 1953; Miller 1955; longer than 30 years, Patterson and Brattstrom 1972.

2. Wild tortoise (estimated): 50 to 100 years, Berry 1978a; longer than 50 years, Bury and Marlow 1973; Dodd 1986; Hardy 1972; Woodbury and Hardy 1948a.

III. **Age determination**

1. Using scute annuli
   a. Single growth ring may be found each year early in development (Legler 1960; Patterson and Brattstrom 1972).
   b. Relationship between age and growth rings of second right costal scute (Germano 1988).
   c. Relationship between growth rings and carapace length (Patterson 1972a), plastron length, or bone rings (Germano 1988).
   d. Problems related to age determination using scute annuli: rings may not be annual but may reflect the season and foraging patterns of each tortoise (Coombs 1973, 1977c; Miller 1932, 1955; Woodbury and Hardy 1948a); may be limited to tortoises under 25 years of age (Germano 1988); larger tortoises may lose rings due to shell wear (Patterson 1972a); many large tortoises shed juvenile rings after having acquired 15 to 20 adult rings (Coombs 1973, 1974, 1977a).
2. Using carapace length
   a. Relationship between age and carapace length (Patterson 1972a).
   b. Age classification based on carapace length (Berry 1973b, 1981).
3. Old age determination
   a. Carapace scutes become smooth, worn, and lacking growth ridges (Burge 1977d; Grant 1936a).
   b. Edge of carapace scutes become thickened, making scutes appear concave (Grant 1936a).
   c. Shell wear technique (Berry and Woodman 1984b): involves categorizing adult tortoises into seven age-wear classes. Wear is believed to be correlated with age. The shells of older and larger tortoises tend to be more worn; very old tortoises have concave carapacal scutes.

D. Age distribution and sex ratio

1. Age distribution for relatively undisturbed populations (Berry 1976).

Hatchlings	0 to 3 percent
Juveniles	5 to 10 percent
Immature	15 to 25 percent
Subadults	15 to 20 percent
Adults	45 to 60 percent

2. Sex ratio for *Gopherus agassizii* normally represented as 1:1, but ratios vary between populations (Dodd 1986). Populations studied with sex ratios heavily biased toward males are considered in poor condition (Berry 1978a).
3. Specific age distributions and sex ratios in: Arizona (Berry 1974b, 1975b, 1978a; Duck and Snider 1988; Hohman and Ohmart 1980; Vaughan 1984a); California (Barrow 1979; Berry 1974b, 1975a, 1976, 1978a,b, 1980a; Bickett 1980a; Hampton 1981; Marlow 1974; Turner and others 1984); Nevada (Berry 1978a; Burge 1977d; Burge and Bradley 1976; Esque and

Duncan 1985; Mortimore 1984); Utah (Beck and Coombs 1984; Berry 1978a; Coombs 1973, 1977a,c; Minden 1980; Minden and Keller 1981; Minden and Metzger 1981; Welker 1986; Woodbury and Hardy 1948a); Mexico (Reyes Osorio and Bury 1982).

E. Natality and mortality
   1. Rates of natality and mortality of tortoises in: Arizona (Berry 1978a; Duck and Snider 1988; Hohman and Ohmart 1978, 1980); California (Berry 1974b, 1975a; Berry and Woodman 1984a; Turner and others 1981, 1984); Nevada (Berry 1978a; Holing 1986; Mortimore 1984); and Utah (Coombs 1977c; Minden 1980; Welker 1986; Woodbury and Hardy 1948a).
   2. Desert tortoises have low reproductive potential and recruitment with high hatchling mortality (Campbell 1981).
   3. Desert tortoise populations exhibit characteristics of a K-selected species, including low birth rate, low recruitment, low mortality of individuals in older age categories, and low population turnover (Berry 1978a).
   4. Hatchling survival is typically very low (see Hatchling survival).

Physiology

Desert tortoise physiology is discussed below with respect to thermoregulation, water balance, hematology, and bone and scute regeneration.

I. **Thermoregulation**
   A. Body temperature
      1. Preferred and lethal body temperatures (Avery 1982; Berry and Turner 1984; Brattstrom 1961, 1965; Hohman and Ohmart 1980; Hutchison 1979; Hutchison and others 1966; McGinnis and Voigt 1971; Minden 1980; Naegle 1976; Voigt 1975; Woodbury and Hardy 1948a).
      2. Reptiles may have a different preferred body temperature for different activities such as mating, foraging, or digestion (Cowles and Bogert 1944; Templeton 1970).
      3. Younger and smaller tortoises select higher temperature environments and maintain higher body temperatures than older tortoises; however, older tortoises are able to maintain body temperatures within a narrower range due to greater size and insulating properties of the shell (Naegle 1976).
   B. Heating and cooling rates
      1. *Gopherus agassizii* heats and cools at equal rates under controlled conditions; however, under natural conditions, *G. agassizii* heats 3 to 10 times faster than it cools (McGinnis and Voigt 1971; Voigt 1975).
      2. Heating rates are faster than cooling rates under natural conditions (Brattstrom and Collins 1972; Spray and May 1972; Voigt 1971, 1975).
      3. Cooling rates for tortoises over 10 years old were half the heating rates. For hatchling tortoises, heating and cooling rates were nearly equal (Naegle 1976).
   C. Behavioral thermoregulation in response to high temperatures
      1. Retreat to burrows
         a. Temperatures in burrows rise slowly and remain relatively mild during high ambient temperatures (Bogert 1939; McGinnis and Voigt 1971; Schmidt-Nielsen and Bentley 1966).

b. Burrows reduce pulmocutaneous water loss (Carr 1963; Miller 1932).

2. Tortoises retreat behind vegetation and use pallets in the shade of creosotebushes to escape high soil temperature (Brattstrom and Collins 1972; Burge 1977a).
3. Activity patterns may be altered: see Daily and Seasonal Activity Patterns
   a. In spring, overnight burrows allow tortoises to have a higher temperature in the morning than would otherwise be possible (McGinnis and Voigt 1971).
   b. Activity period is shortened and emergence from burrows occurs earlier in the day as temperatures increase in the summer (Berry 1974b, 1975b; Nagy and Medica 1986).
   c. Summer nights are spent outside to possibly induce hypothermia which allows for a longer foraging period on hot mornings (Huey 1982).
   d. Tortoises occupy significantly larger dens in summer than in autumn, winter, or spring (Barrett 1985, 1990).

D. Behavioral thermoregulation in response to low temperatures
1. Retreat to winter den
   a. Hibernation occurs in winter dens where temperatures are higher than outside air, buffering the tortoise from low temperatures outside (Woodbury and Hardy 1948a).
   b. Blocking the winter den entrance with dirt and woodrat (*Neotoma* sp.) midden debris disrupts any further flow of cold air (Woodbury and Hardy 1948a).
2. Basking in the sun or lying under a bush with limbs and neck extended limply aids in thermoregulation and increases digestion (Boyer 1965).

E. Physiological and morphological thermoregulation
1. Evaporative cooling
   a. Tortoises operate under low rates of evaporative water loss (Nagy 1988).
   b. Higher rates of evaporative water loss occur in hatchlings and young tortoises (Naegle 1976).
   c. At 20 °C (61 °F) evaporative cooling accounted for 73.3 percent of heat production in hatchlings and 50.9 to 57.1 percent in older tortoises (Naegle 1976).
   d. Tortoises may salivate heavily under high temperatures near the lower limit of the lethal range (McGinnis and Voigt 1971; Schmidt-Nielsen and Bentley 1966).
2. When a weakened tortoise is overturned, urination may help cool the head (Brattstrom 1974). Turtles commonly use evaporative cooling by salivation or by urination under extreme temperatures (Naegle 1976; Riedesel and others 1971).
3. Shell
   a. Hemispheric shape and insulating properties of the shell limit thermoregulation due to a small surface to volume ratio (Bartholomew 1982).
   b. Shell protects tortoises from solar radiation, and shell temperatures are 8 to 10 °C higher than deep body temperature (Coombs 1977c; McGinnis and Voigt 1971).

c. Outer shell and extremities heat more rapidly than does the body core (Hutchison and others 1966).
d. Younger tortoises, especially hatchlings, have a rich capillary bed associated with the developing bone of the shell, which may affect heat exchange with the environment (Naegle 1976).

4. Bilobed bladder that rests against the inner surface of the carapace may be oriented when basking so that it is easily heated by the sun, thus functioning as a "hot water bottle" which may transfer heat throughout the body (Auffenberg 1969).
5. Heart rate is higher when heating than when cooling (Voigt 1971, 1975).

II. **Water balance**

A. Source of water

1. It has been suggested that land tortoises obtain all or most of their water from a succulent diet (Bogert and Cowles 1947; Cloudsley-Thompson 1971).
2. Desert tortoises have a diet high in carbohydrates for metabolic water production. Metabolic water production reported at 0.31 ml per 100 g body mass per day. This was almost as great as the reported water turnover (0.36 ml per 100 g body mass per day) (Minnich 1976; Woodbury and Hardy 1948a).
3. *Gopherus agassizii* may store lipids following late summer rains and subsequent plant growth, saving the energy for production of metabolic water during the winter and for reproduction the following spring (Henen 1985).
4. Tortoises often drink from small pools following rains. They travel directly to the pools or may even dig depressions in the soil in anticipation of rain (Berry 1974b; Coombs 1977a; Nagy and Medica 1977).
5. Some of the rainwater consumed goes to the bladder and is stored as a reserve (Barker 1964; Mertens 1960; Minnich 1971a,b, 1977).
6. Of individuals studied in Rock Valley, NV, fluctuations in available water affected plasma and urine osmolarity in spring and summer (Nagy and Medica 1977).
7. Tortoises drank water weighing 11 to 28 percent of their body mass following rains at various times of year; 58 to 93 percent of the water was retained several days after drinking (Nagy and Medica 1986).
8. Desert tortoises have been known to increase their body mass 41 to 43 percent by drinking from pools of water (Bogert and Cowles 1947; Miller 1932).
9. An average of 17 ml per 100 g of body mass is consumed after rains (Minnich 1976, 1977).

B. Source of water loss

1. Desert tortoises lose water through defecation, excretion, cutaneous evaporation, and pulmonary evaporation (Minnich 1977; Schmidt-Nielsen and Bentley 1966).
2. Cutaneous water loss represents 76 percent of total evaporative water loss, while respiratory water loss makes up 24 percent. Forty-seven percent of the evaporative loss is from the head (Mautz 1982; Schmidt-Nielsen 1969).

3. Of desert tortoises tested (mean mass = 1,770 g), an average total evaporative water loss of 2.0 $mg/cm^2/day$ was demonstrated at 23 °C ($n = 6$) and 3.8 $mg/cm^2/day$ was demonstrated at 35 °C ($n = 5$) (Schmidt-Nielsen and Bentley 1966).
4. Of desert tortoises tested, average cutaneous water loss was 1.5 $mg/cm^2/day$ at 23 °C and 2.1 $mg/cm^2/day$ at 35 °C (Schmidt-Nielsen and Bentley 1966).
5. *Gopherus agassizii* demonstrated lower evaporative water losses than did *Pseudemys scripta* and *Terrapene carolina*, turtles that normally are found in moister environments. Average cutaneous water loss for *Gopherus agassizii* was 76 percent of total water loss at 23 °C and 52 percent of total water loss at 35 °C (Schmidt-Nielsen and Bentley 1966).
6. Smaller animals demonstrated higher rates of evaporative water loss (Naegle 1976).

C. Protection from water loss
   1. Anatomical protection
      a. Egg shell is resistant to water loss (Miller 1932; Stebbins 1954).
      b. Bony shell and scales on the appendages act as a barrier to evaporative water loss (Coombs 1977c; Stebbins 1954; Tracy 1982).
      c. Small lung volume to body mass minimizes respiratory water loss (Bentley and Schmidt-Nielsen 1966).
   2. Behavioral protection (burrows as environmental refugia)
      a. Retreat to burrow in heat, thus reducing cutaneous and respiratory evaporation (Auffenberg 1969; Coombs 1977a; Woodbury and Hardy 1948a).
      b. Soil inside den is moist, humidity is relatively high, and temperature relatively cool (Woodbury and Hardy 1948a).
      c. During hibernation, water influx was 2.6 times greater than metabolic production. Tortoises must have absorbed water vapor from the high humidity air in the burrows (Nagy and Medica 1986).
   3. Physiological protection
      a. High body water content: reptiles in arid climates usually have relatively low body water content but well-hydrated desert tortoises have a higher body water content than terrestrial turtles from moister regions. This permits tortoises to extend their feeding into the summer without quickly becoming osmotically stressed from dry forage. It also reduces the effects of evaporative water loss (Brisbin 1972; Khalil and Abdel-Messeih 1962; Nagy and Medica 1977).
      b. Percent body water increases in spring and generally declines or stays constant at other times of year. Average total water volume was 73.5 ± 1.5 percent at Nye County, NV, and 67.8 percent near Barstow, CA, but has been estimated to be as high as 79.6 percent (Connolly and Eckert 1969; Minnich 1977; Nagy and Medica 1986).
      c. Urinary bladder is used to store large volumes of water (estimated at 473 ml) and nitrogenous wastes. The large volume of water increases body water content and dilution space for excess dietary salts that can't be excreted directly without

losing water. This allows tortoises to feed on dry plants without reaching toxic concentrations of ions (Minnich 1976, 1977; Nagy and Medica 1986).

   d. Wastes are precipitated in the bladder as gelatinous semi-solid urates, which can be voided with minimal water loss (Leopold 1961; Nagy and Medica 1986; Schmidt-Nielsen and Bentley 1966).
   e. Tortoises can store water and electrolytes in their bodies. In addition, they tolerate large imbalances in their water, energy and salt budgets on a daily basis while achieving balance on a yearly basis (Nagy 1988; Peterson 1990).
   f. Urinary bladder walls are extremely permeable to water, ions, and small molecules like urea. Substantial amounts of water are reabsorbed through the highly vascularized bladder membrane (Auffenberg 1969; Schmidt-Nielsen and Bentley 1966).
   g. During summer, osmotic pressure of bladder urine increased steadily until it equaled plasma osmotic pressure, indicating that as a tortoise dehydrates it reabsorbs stored water from the bladder (Minnich 1971a,b, 1976, 1977).
   h. In two Mojave Desert populations studied during drought, as long as bladder urine remained hyposmotic to plasma, plasma solute concentrations were maintained within normal, hydrated levels. Tortoises stored wastes in their bladders rather than excreting them, and bladder urine concentrations increased until iso-osmotic with plasma, after which strict homeostasis was abandoned and concentrations of both fluids increased (Peterson 1990).
   i. Bladder permeability does not change with the state of hydration, but tortoises have a sphincter muscle in the bladder neck that allows urine in the ureter to bypass the bladder and go out the cloaca, enabling tortoises to get rid of excess water (Dantzler and Schmidt-Nielsen 1964, 1966; Mahmoud and Klicka 1979).
   j. Crystalline urate deposits are sometimes formed in the bladder. These uroliths contain sodium, potassium, and ammonium, and sometimes calcium. They are eliminated with dilute urine after tortoises drink large quantities of water (Coombs 1977a; Minnich 1972; Schmidt-Nielsen and Bentley 1966).
   k. Concentrated bladder urine is dark brown with large quantities of gelatinous precipitates of urates. Well-hydrated tortoises have colorless bladder urine (Coombs 1977a; Minnich 1976, 1977).
   l. Kidney filtration rate is adapted to tolerate increases in plasma osmolality during dehydration (Dantzler 1965, 1976; Dantzler and Schmidt-Nielsen 1966).
4. Dehydration
   a. Water is lost at 0.4 ml/kg/day or 1.7 times the water intake rate. Urine is retained in the bladder during dehydration (Minnich 1976, 1977; Woodbury and Hardy 1948a).
   b. When dehydration is a threat, tortoises remain in burrows and cease feeding in order to reduce water loss and avoid toxic accumulations of dietary potassium, which cannot be adequately excreted during a state of dehydration (Minnich 1970, 1977, 1982; Nagy 1972; Nagy and Medica 1986).

c. As dehydration begins, urine osmotic concentrations gradually increase, eventually becoming iso-osmotic with plasma concentrations (Dantzler and Schmidt-Nielsen 1964, 1966; Minnich 1976, 1977; Nagy and Medica 1986).
d. Dry feces with a water content of 0.16 ml/g are voided in small amounts (Minnich 1976).
e. Tortoises are able to lose up to 30 percent of body mass and still survive without serious water stress (Minnich 1977).

5. Build-up of ions
a. Tortoises lack extrarenal salt glands and must excrete ions in precipitated urates (Minnich 1979).
b. During hibernation, water may be lost and packed cell volume and blood urea levels may rise at time of emergence (Lawrence and Jackson 1983).
c. Desert tortoises have high dietary potassium in spring (Minnich 1979; Nagy and Medica 1986).
d. Near Barstow, CA, tortoises became inactive in response to low moisture content and high potassium content of dried-out forage. However, rain fell in late summer and all tortoises became active, drank rainwater, stored it as dilute urine, voided old urine, resumed feeding, and were able to excrete their potassium load by using the dilute urine as a water reserve (Minnich 1977).
e. At Rock Valley, NV, in 1976, tortoises dehydrated slowly in the summer. During the spring, water influx rates increased from 12 to 25 ml/kg of body mass per day, bladder urine osmolarity increased from 180 to 330 mOSM, and plasma from 290 to 360 mOSM. During the summer, water influx declined to 5 ml/kg/day, bladder urine osmolarity declined from 330 to 60 mOSM and plasma from 360 to 310 mOSM. However, thundershowers in late July caused tortoises to emerge from burrows and drink. Urine became dilute and tortoises resumed feeding. Had rain not fallen, tortoises would have had a net loss in body mass in 1976 (Nagy and Medica 1977).
f. Drinking free water appears to be an essential when forage dries up. It also permits tortoises to feed on dried annuals, which would be osmotically stressful without stored bladder urine (Medica and others 1980; Minnich 1982).
g. At Rock Valley, NV, tortoises became osmotically stressed in spring while feeding on green annuals. However, after the thunderstorms came, tortoises drank rainwater, stored dilute urine, and were able to switch to a diet of dried grass. Tortoises were able to maintain water and salt homeostasis, store energy and grow only when drinking water from rain and when dried grasses were available (Nagy and Medica 1986).

III. **Metabolism**

A. Oxygen consumption

1. Tortoises have lower oxygen consumption rates than reptiles of comparable size (Bennett and Dawson 1976; Bentley 1976; Bentley and Schmidt-Nielsen 1966).
2. No correlation was found between body mass and oxygen consumption in turtles (Benedict 1932; Hutton and others 1960);

however, subsequent evidence shows younger tortoises (<500 g) have higher oxygen consumption rates (Naegle 1976; Naegle and Bradley 1974, 1975).

3. Tortoises less than 50 g consumed 125 ml O_2/h/kg of body mass (Naegle and Bradley 1974).
4. Tortoises 100 g or heavier consumed 40 ml or less O_2/h/kg of body mass (Naegle and Bradley 1974).
5. In burrows, O_2 may fall to 12 percent and CO_2 may be as high as 7 percent. This leads to moderate hypoxia (Ultsch and Anderson 1988).

B. Energy balance

1. Energy metabolism in captive tortoises was 40.5 ± 8.4 kJ/kg/day. Carbon dioxide production of tortoises was highest in spring and summer. However, metabolic rates declined in dry periods (Nagy and Medica 1986).
2. Growth in tortoises occurred only in April and July and was correlated to annual production determined by precipitation (Medica and others 1975).
3. Tortoises were in positive energy balance in 1976 in a western Mojave Desert study (Marlow 1979).
4. Tortoises in Nye County, NV, were in positive energy balance only when rainwater and dry vegetation were available (Nagy and Medica 1986).
5. Desert tortoises have large livers capable of considerable fat production; evidence suggests that lipids are stored after late summer rains and used as energy for reproduction the following spring (Henen 1985; Obst 1986).
6. Fat reserves are consumed at 0.2 to 0.4 g/day during hibernation. If fat reserves become depleted before the end of hibernation, protein tissues are broken down (Lawrence and Jackson 1983).
7. Green annuals in spring are essential for tortoises to replenish fat reserves lost during hibernation (Coombs 1976).
8. Younger tortoises have higher metabolism due to more rapid growth (Naegle 1976).

IV. **Hematology**

A. Red blood cell counts have been estimated at 550,000/mm^3 (Frair 1977) and 1.2×10^6 to $3.0 \times 10^6/mm^3$ (Rosskopf 1982).

B. White blood cell count estimated at 3×10^3 to $8 \times 10^3/mm^3$ (Rosskopf 1982).

C. Protein concentration of hemoglobin is 100 percent (Sullivan and Riggs 1967a).

D. Serum protein concentration is 2.5 percent (Frair 1964; Rosskopf 1982).

E. Hematocrit is 23 to 37 percent (Rosskopf 1982).

F. Hemoglobin pH is 7.00 (Sullivan and Riggs 1967a).

G. Oxygen properties (Sullivan and Riggs 1967c).

1. Hemoglobin demonstrated a 15 percent oxygen concentration.
2. Deoxygenated hemoglobin had an absorbency ratio of 0.702, compared to 1.000 in man, but oxygen uptake changes with pH and temperature.

H. Blood serum proteins demonstrated relatively low electrophoretic mobilities. Albumin was a normal, but minor contributor to serum proteins (Leone and Wilson 1961).

I. Hematological characters monitored in free-ranging tortoises at City Creek, UT and Littlefield, AZ (Arizona Game and Fish Department 1991b).
   1. A significant difference existed between sites in 1989 for blood urea nitrogen, total protein, albumin, and potassium.
   2. A significant difference existed between sites in 1990 for blood urea nitrogen.
   3. A significant difference existed in total protein, albumin, and calcium between years (1989 and 1990) at both sites.

J. Other blood properties (Rosskopf 1980, 1982)
   1. No blood parasites are found in any of 500 captive desert tortoises.
   2. Extremely high white blood cell counts are rare. White blood cell levels are lowest following hibernation and rise with warmer weather.
   3. Heterophils and basophils are responsive to inflammatory conditions. Heterophils increase first; basophils increase as condition becomes chronic.
   4. Lactic dehydrogenase (LDH) levels increase in many nonspecific inflammatory conditions.
   5. Increased lymphocyte counts are often seen in chronic disease.
   6. Monocytes and eosinophils are relatively rare but occasionally common. Eosinophilia occurs in cases of intestinal parasitism.

K. Differential (Rosskopf 1982)
   1. Neutrophils: 0 to 3 percent.
   2. Heterophils: 35 to 60 percent.
   3. Lymphocytes: 25 to 50 percent.
   4. Monocytes: 0 to 4 percent.
   5. Eosinophils: 0 to 4 percent.
   6. Basophils: 2 to 15 percent.

L. Blood chemistry (Rosskopf 1982)
   1. Serum glutamic-oxaloacetic transaminase (SGOT) = 10 to 100 IU/L.
   2. Blood urea nitrogen (BUN) = 1 to 30 mg/dL.
   3. Total protein = 2.2 to 5.0 g/dL.
   4. Lactic dehydrogenase (LDH) = 25 to 250 IU/L.
   5. Creatinine = 0.1 to 0.4 mg/dL.
   6. Calcium = 9.0 to 17.0 mg/dL.
   7. Glucose = 30 to 150 mg/dL.
   8. Uric acid = 2.2 to 9.2 mg/dL.
   9. Potassium = 2.2 to 4.5 mEq/L.
   10. Sodium = 130 to 157 mEq/L.
   11. For two turtle species tested, blood glucose, uric acid, inorganic sulfate, and magnesium increased under hibernating conditions. Inorganic phosphorus and sodium decreased (Hutton and Goodnight 1957).

V. **Bone and scute regeneration**
   A. If the bone of the shell is broken it is shed and replaced from beneath with new bone (Nichols 1957; Woodbury and Hardy 1948a).
   B. Repair of bone may take as long as 7 years (Stebbins 1954).
   C. A captive female's carapace injury took 3 years to heal (Miller 1932).

D. When scales were torn off, it took 3 years for the dead bone to be shed and for the scar to heal (Miller 1932).

Feeding Behavior, Diet, and Nutrition

The following section includes literature related to feeding behavior, diet, and nutrition. While more information is available on feeding behavior and tortoise food items, little information is available on the nutritive value of tortoise foods; however, current research is focusing on the nutritional needs of the desert tortoise and the nutritive value of its forage; additional literature is forthcoming.

I. **Feeding behavior**
- A. Feeding mechanism (Bramble 1973)
  1. Terrestrial turtles rely on the tongue for ingestion and manipulation of food.
  2. The mandibles make protractive and retractive movements during feeding.
  3. Structural adaptations for "lingual feeding" include a large mobile tongue; reduced hyoid apparatus; high, arched palate; serrated masticatory surfaces; and pronounced cranial flexure.
  4. The high arched palate and cranial flexure allow air to flow freely past the tongue when the tortoise's mouth is closed.
- B. Foraging behavior
  1. Desert tortoises forage by wandering from plant to plant, stopping briefly to sniff at plants or the ground (Luckenbach 1982).
  2. A tortoise sniffs selected plants before eating, and takes one to several bites before continuing to another plant (Hohman and Ohmart 1980).
  3. A tortoise seen feeding on dry Mediterranean grass (*Schismus* sp.) clipped the dead grass at ground level, then picked up the pieces and swallowed them with little chewing (Vaughan 1984a).
  4. "Climbing" behavior
     - a. A tortoise climbed into a perennial lotus (*Lotus* sp.) and foraged on the upper branches and pods while standing on hind legs (Schneider 1980a).
     - b. A tortoise was observed climbing into a range ratany (*Krameria parvifolia*) in order to access the seed pods with the forelimbs raised off the ground (Esque and others 1990a).
  5. Duration of foraging
     - a. Tortoises spent an average of 47 minutes per foraging bout during the spring activity period in 1989 at the City Creek, UT study plot. Tortoises foraged for 23 percent of the time they were observed at the City Creek study plot in 1990 and for 6.4 percent of the total time they were observed at the Littlefield, AZ study plot (Esque and others 1990a, 1991).
     - b. Tortoises observed feeding ate 13 plant species in 30 minutes. Whole plants of some species were consumed while only the flowering portions of others were consumed (Berry 1975a).
     - c. A tortoise may feed on one plant species 8 to 15 minutes, sit still for a few minutes, and then resume foraging, usually on a different species (Hohman and Ohmart 1980).
     - d. Feeding usually ranges from less than 1 minute to 30 minutes (Burge and Bradley 1976).

e. Foraging time varied from 1 to 75 minutes. On one occasion, a tortoise ate portions of 48 consecutive plants of small-flowered milkvetch (*Astragalus nuttallianus*), the preferred spring food item, in just over an hour while passing by red brome (*Bromus rubens*), cheatgrass (*Bromus tectorum*), and filaree (*Erodium cicutarium*) (Minden 1980).

6. Effects of forage condition on foraging behavior
   a. Tortoises walked 470 to 823 m/day to search for forage in a year when wildflowers were scarce. Once patches of wild flowers were located, tortoises remained there for days or weeks until the forage was eaten or dried up (Berry 1974b).
   b. Tortoises exhibited increased home range with an increase in forage biomass (Sheppard 1981).
   c. Desert tortoises cease feeding when their forage plants dry out but feed on dry vegetation after drinking rainwater (Minnich 1977, 1982; Nagy and Medica 1986).
7. Some tortoises did not feed for several weeks following emergence from hibernation (Nagy and Medica 1986).

C. Food preferences
   1. Both exotic and native annual species were selected food items (Esque and others 1991).
   2. Tortoises generally select forbs and grasses and avoid shrubs (Nagy and Medica 1986). Leaves and flowers of perennial shrubs are rarely eaten (Berry 1974b).
   3. Succulent portions of plants, such as leaves and flowers, are commonly eaten (Luckenbach 1982).
   4. Green succulent annuals are the preferred food. Often the most common foods are eaten the most (Hohman and Ohmart 1978; Minden 1980).

D. Daily feeding periods: most feeding trips are in morning, late afternoon, or immediately after rains (Barker 1964). See Behavior, Daily and seasonal activity patterns.

E. Seasonal feeding patterns
   1. Green forage is available only for 6 weeks to 3 months of the year, in spring and early summer (Berry 1978a; Luckenbach 1982).
   2. Succulent annual vegetation is not available in summer, but tortoises feed even when forage is dried up. Tortoises' ability to eat dry plants is related to their capacity to store water and to drink rainwater (Nagy and Medica 1977).
   3. Specific instances of seasonal feeding patterns
      a. Beaver Dam Slope, AZ, 1977-1978 (Hohman and Ohmart 1978, 1979, 1980).
         i. Indianwheat (*Plantago insularis*) and other annuals were used most in spring; use of perennial grasses and shrubs increased in summer when forbs were not available.
         ii. Fecal analysis indicated that forbs dominated the diet. Annual grasses received heavy use in April. Perennial grasses and shrubs were used increasingly as ambient temperature increased and green forb availability declined.
         iii. In 1979, grasses were used heavily in summer and fall. Indian ricegrass (*Oryzopsis hymenoides*) had frequencies of

utilization of 29.93 percent in July, 11.65 percent in August, and 53.54 percent in September. Galleta (*Hilaria rigida*) was consumed only in October but represented 49.75 percent of total diet (Sheppard 1981).

b. Picacho Mountains, AZ (Vaughan 1984a): forbs represented 82 percent of the dry mass of the tortoise diet in spring and 50 percent in summer; shrubs represented 31 percent of the tortoise diet in summer and 78 percent in fall. Grasses received highest use in fall, 9.56 percent of the dry mass of the tortoise diet.

c. In March through May, 1972, in California, green nutritious forage was available. After May, annual vegetation was scarce, and tortoises ate dried grasses and pieces of dried annuals (Berry 1974a,b).

d. Ivanpah Valley, CA: 1981 was a drought year; green annual plants were consumed only until mid-April. After annuals dried, tortoises subsisted on cacti and dry grasses (Medica and others 1982; Turner and others 1984).

e. Rock Valley test site, NV (Nagy and Medica 1986)
   i. In spring, annuals were eaten, including *Camissonia munzii*, *Langloisia setosissima*, and small amounts of *Bromus rubens*.
   ii. After forbs dried in mid-June, tortoises ate only *Bromus rubens* and *Oryzopsis hymenoides*, which were also dry.
   iii. In August, dry *Langloisia* sp. and dry grass were eaten.
   iv. In September, fresh green *Camissonia* sp. seedlings, green *Bromus* sp., and *Oryzopsis* sp. sprouts appeared. They were the selected food items in October.
   v. Highest feeding rates followed late summer rains when tortoises drank rainwater and consumed dried annuals.

f. Beaver Dam Slope, UT: tortoises ate *Erodium cicutarium*, *Bromus rubens*, *Muhlenbergia porteri* all year; *Plantago insularis*, *Lepidium lasiocarpum*, *Opuntia basilaris*, *Coleogyne ramosissima*, *Cryptantha micrantha*, *Eriophyllum wallacei* in spring; *Tridens pulchellus*, *Euphorbia albomarginata*, *Eriogonum inflatum*, *Eriogonum deflexum*, *Phacelia fremontii*, *Chorizanthe rigida*, *Cryptantha circumscissa*, *Krameria parvifolia* in spring and summer; *Tridens pilosus* in fall; and *Oryzopsis hymenoides* and *Hilaria rigida* in fall and winter (Coombs 1977c).

g. Beaver Dam Slope, UT: *Bromus* sp. was eaten when *Erodium cicutarium* dried up. *Bromus* sp. made up 75 percent of summer diet, but the total of *Bromus* consumed was small when compared to the amount of *Erodium cicutarium* consumed in the spring (Minden 1980).

h. Beaver Dam Slope, UT: feeding observations, April to June, 1980 to 1981 (Minden and Keller 1981).
   i. *Astragalus nuttallianus* and *Bromus rubens* consumed from April through June; *Erodium cicutarium* in May; *Plantago insularis* from April through May; *Krameria parvifolia* in June; *Opuntia basilaris* in May; *Tridens pulchellus* from May through June.
   ii. *Plantago insularis* was 71.2 percent of the diet in May but was replaced by *Astragalus nuttallianus* at the end of May.

D. Regional feeding patterns

1. Food habits may vary considerably between populations that occupy desert areas with different vegetative composition (Burge and Bradley 1976).
2. In the northern Mojave Desert, *Schismus* sp. has not been reported eaten by tortoises, yet in the eastern and central Mojave Desert it is commonly eaten, especially in the late summer months (Berry 1972, 1974a,b; Luckenbach 1982).
3. Fecal analysis found *Bromus rubens* and *Erodium cicutarium* (an exotic annual grass and an exotic forb, respectively) made up 87 percent of the diet in Utah (Hansen and others 1976).

II. **Diet**

A. Food consumed in captivity: Bermuda grass (Housholder 1950); vegetables, apples, melons, cheese, bread, clover, dry leaves, paper (Miller 1932); figs, bananas, melons, grape leaves, rose petals, snails (Nichols 1953); apples, carrots, cabbage (Miles 1953); grasses, fruits, lettuce, clover, dandelions, peach blossoms, hamburger, canned dog and cat food (Beltz 1958); insects and dried jackrabbit meat (Grant 1936a; Pope 1939).

B. Natural diet

1. Tortoises are vegetarians and eat grasses, flowers, and succulent plants (Bailey 1928; Camp 1916; Miller 1932; Woodbury and Hardy 1948a). They eat primarily succulent annuals when they are available (Berry 1973b, 1974b; Coombs 1974; Cox 1881; Minden 1980; Woodbury 1931).
2. Tortoises have been observed eating bunchgrass and alfalfa. Stomach contents included stems, leaves and roots of *Cassia armata*, *Eriogonum* sp., wild mustard, and a small *Euphorbia* sp. (Bailey 1928).
3. Flowers and vegetative portions are eaten, but flowers are preferred. Grasses are secondary food items and are probably used to maintain summer activity. In some areas late summer precipitation promotes annual grasses, which may be eaten heavily (Luckenbach 1982).
4. Species of annuals consumed generally mirror their availability, and annuals that are used most are often most common (Hohman and Ohmart 1978; Minden 1980).
5. Tortoises have been observed eating saguaro fruits (Kauffeld 1943); stalks, buds, and flowers of a beavertail cactus (*Opuntia basilaris*) (Berry 1974b); grass (Cochran and Goin 1970); grasses, cacti, and other low vegetation as well as occasional insects or dead animal matter (Brown 1968).
6. Desert tortoises commonly consume annual and perennial grasses in Arizona and Utah (Berry 1975a; Hansen and others 1976).
7. *Erodium cicutarium* is eaten when nothing else is available (Berry 1974b).
8. The diets of small tortoises are composed almost entirely of annuals (Schneider 1980a).
9. Annual grasses commonly eaten include: *Bouteloua barbata*, *Bromus rubens*, *Festuca octoflora*, and *Schismus barbatus*. Perennial grasses include: *Hilaria rigida*, *Muhlenbergia porteri*,

and *Oryzopsis hymenoides*. Shrubs receive very little use except for herbaceous types such as *Sphaeralcea ambigua* (Berry 1978a).

C. Specific studies
   1. Pima County, AZ: stomach contents comprised entirely of grasses, mostly *Bouteloua aristoides* (needle grama) (Ortenburger and Ortenburger 1927).
   2. Lower Grand Canyon, AZ (Hansen and others 1976): fecal analysis.
      a. *Aristida* spp. (purple three-awn), *Sphaeralcea* spp. (globe mallow), *Tridens muticus* (slim tridens), *Bromus rubens* (foxtail brome), *Bouteloua trifida* (red grama) and *Carex* sp. (sedge) occurred as the major items consumed by tortoises.
      b. The dietary content based on studying microscope fields of ground and mounted fecal material was *Aristida* spp. 22 percent, *Sphaeralcea* spp. 21 percent, *Tridens muticus* 20 percent, *Bromus rubens* 19 percent, *Bouteloua trifida* 6 percent, and *Carex* sp. 3 percent.
   3. New Water Mountains, AZ (Hansen and others 1976): fecal analysis.
      a. *Tridens muticus*, *Muhlenbergia porteri*, *Aristida* spp., *Janusia gracilis*, and *Sphaeralcea* sp. were found in tortoise scats.
      b. Dietary content was *Tridens muticus* 50 percent, *Muhlenbergia porteri* 17 percent, *Aristida* spp. 16 percent, *Janusia gracilis* 11 percent, and *Sphaeralcea* sp. 6 percent.
   4. Little Ship Wash site, AZ (Schneider 1980a): feeding observations.
      a. *Schismus* sp. was most abundant annual and most commonly eaten species.
      b. There were eight observations of feeding on *Schismus* sp. and *Bromus* spp., five of *Plantago* sp., five of *Lotus tomentosus*, and one each of *Erodium cicutarium*, *Lotus rigidus*, and *Orthocarpus purpurescens*.
   5. Picacho Mountains, AZ: fecal analysis (Vaughan 1984a) report the percent mass and frequency of annual and perennial species in tortoise diets.
   6. Beaver Dam Slope, AZ: feeding observations and fecal analysis.
      a. *Plantago insularis*, *Erodium cicutarium*, and *Eriogonum inflatum* were the most common food items observed (Hohman and Ohmart 1979, 1980).
      b. *Plantago insularis* comprised 36 percent of the diet, *Erodium cicutarium* 18 percent, *Stylocline micropoides* 8 percent, *Astragalus* sp. 5 percent, and *Bromus rubens* 5 percent (Hohman and Ohmart 1979, 1980).
      c. *Plantago* sp. was found in every scat and was considered to be the most important food item on the Arizona slope (Hohman and Ohmart 1979, 1980).
      d. *Astragalus* sp., *Oryzopsis hymenoides*, *Hilaria rigida*, and *Krameria parvifolia* have intermittent periods of high use.
      e. Forbs made up 72 percent of the annual diet, and as much as 91 percent of the diet in May 1978 (Hohman and Ohmart 1978).
   7. Beaver Dam Slope, AZ; Littlefield study plot: feeding observations and fecal analysis (Esque and others 1990a, 1991).
      a. Over 187 hours when tortoises were observed feeding they consumed 16 different plant species: 4 annual forbs, 2 annual

grasses, 4 perennial shrubs, 3 perennial grasses, and 3 additional food items. Introduced species—*Schismus barbatus*, *Erodium cicutarium*, and *Bromus rubens*—comprised more than 75 percent of the diet consumed by tortoises observed in 1990.

   b. In the 25 fecal pellets analyzed, 22 food species were represented, including 3 annual forbs, 2 annual grasses, 8 perennials, 3 perennial grasses, and 6 additional food items, including parts of plants, unidentified plants, parts of arthropods, and rock. As demonstrated in the feeding observations, *Schismus barbatus*, *Erodium cicutarium,* and *Bromus rubens* were well-represented in the fecal samples; *Plantago patagonica* also was present.

8. Rand Mountains, Kern County, CA (Berry 1975a,b): feeding observations.
   a. From March to June the following species were consumed: *Astragalus didymocarpus*, *Erodium cicutarium*, *Amsinckia intermedia*, *Gilia* sp., *Lupinus odoratus*, *Mentzelia nitens*, *Stephanomeria exigua*, *Lasthenia chrysostoma*, *Eriogonum* sp., *Salvia columbariae*, *Camissonia* sp., *Chaenactis* sp., *Malacothrix* sp., and *Langloisia matthewsii*.
   b. Plants eaten in June were *Erodium cicutarium* and dry *Schismus barbatus*.
9. Pinto Basin, Joshua Tree National Monument, CA (Barrow 1979): plants eaten include *Lotus tomentellus*, *Gilia ochroleuca*, *Oenothera deltoides*, *Schismus barbatus*, and *Allionia ditaxis*.
10. Desert Tortoise Natural Area, eastern Kern County, CA (Bickett 1980a): feeding observations.
    a. *Lotus* sp. comprised 43 percent of the diet; *Erodium cicutarium*, 21 percent; and *Amsinckia intermedia*, 17 percent.
    b. *Lotus* sp. had low densities in most areas but was highly preferred. *Erodium* sp. was very common but often ignored.
    c. Also eaten in small amounts were *Camissonia boothii*, *Chaenactis chorizanthe*, *Malacothrix glabrata*, *Mirabilis bigelovii*, *Phacelia* sp., and *Schismus barbatus*.
11. Ivanpah Valley, CA, 1980 to 1981: fecal analysis (Medica and others 1982; Turner and others 1984).
    a. Annuals eaten included borages as well as *Camissonia* sp., *Descurainia* sp., *Lotus* sp., *Lupinus* sp., *Malacothrix* sp., *Mentzelia* sp., *Nama demissum*, and *Bromus rubens*. Grasses eaten included *Schismus barbatus*, *Hilaria rigida*, and *Stipa speciosa*. Shrubs were eaten in small amounts.
    b. During the dry year of 1981, annuals dried up by mid-April and tortoises fed extensively on cacti, which made up 87 percent of their summer diet.
    c. Cacti eaten during the drought were *Opuntia basilaris*, *O. echinocarpa,* and *Echinocactus* sp. Also eaten were *Hymenoclea salsola*, *Cryptantha* sp., dry grasses, (*Hilaria rigida*, *Festuca octoflora*), and cow dung.
    d. Cactus is apparently an important food item in dry years.
12. Arden Study Area, Nye County, NV: feeding observations (Burge and Bradley 1976).

a. Species consumed were: *Plantago insularis, Sphaeralcea ambigua, Festuca octoflora, Euphorbia albomarginata, Opuntia ramosissima, Opuntia basilaris, Gaura coccinea, Selinocarpus diffusus, Eriogonum inflatum, Mirabilis froebelii, Erodium cicutarium, Krameria parvifolia, Stephanomeria pauciflora, Echinocactus polycephalus, Allionia incarnata, Hilaria rigida,* and *Bouteloua barbata.*
b. *Plantago insularis* was the major food item with 34.3 percent total frequency of use. It was eaten while green early in season and when dry later in the season.
c. *Sphaeralcea ambigua*, an herbaceous shrub, was second in frequency of use (26.8 percent) and also was consumed throughout the year.
d. The understory received 59 percent of the use and the shrub layer received 41 percent.
e. Juvenile food preference was not known.

13. Beaver Dam Wash, UT (Hansen and others 1976): fecal analysis.
a. *Bromus rubens* (red brome), *Erodium cicutarium* (redstem filaree), and *Astragalus* sp. (vetch) were found in tortoise scats.
b. Scat content was *Bromus rubens* 64 percent, *Erodium cicutarium*, 23 percent, *Ceratoides lanata* 6 percent, and *Astragalus* sp. 4 percent.
c. Also found in scats were bird feathers, mammal hairs, reptile skin castings, and sand.
d. Scats from all three areas analyzed in Arizona and Utah contained mostly grasses; however, scats were not identified for season and probably were biased for grasses since they produce lasting scats (Luckenbach 1982).

14. Beaver Dam Slope, UT, 1936 to 1946: feeding observations (Woodbury and Hardy 1948a).
a. Grasses were dominant in diet.
b. *Hilaria* sp. was a major food item.
c. Tortoises were seen foraging on *Hilaria* sp. and *Bromus tectorum* on September 30, 1939; November 23, 1939; January 18, 1941; and October 28, 1945.
d. *Erodium cicutarium* was consumed on January 18, 1941.
e. *Muhlenbergia porteri* was also an important food item and was used all year.
f. The importance of grasses was probably overemphasized since observations were made only in late summer through winter (Luckenbach 1982).

15. Southwest Utah, 1971 to 1977.
a. *Bromus rubens* and *Erodium cicutarium* were a major part of the diet, according to direct observations (Coombs 1974, 1979).
b. Of the different kinds of plants eaten, 15 were forbs, 8 were grasses, 1 was a cactus, and 1 was a shrub (Coombs 1976, 1977c).
c. Other plant species consumed include: *Lepidium lasiocarpum, Opuntia basilaris, Bromus tectorum, Cryptantha circumscissa, C. micrantha, Eriophyllum wallacei, Oryzopsis hymenoides, Hilaria rigida, Phacelia fremontii,* and *Eriogonum deflexum.*

The flowers of *Krameria parvifolia* and *Coleogyne ramosissima* were eaten (Coombs 1979).

d. Highest availability: *Bromus rubens* and *Erodium cicutarium* (Coombs 1977c).

e. On subjective rating scale, *Muhlenbergia porteri* was rated as the most preferred food item and *Bromus rubens* the least (Coombs 1976).

f. Elsewhere, *Bromus rubens* and *Erodium cicutarium* (both exotic annuals) were eaten when nothing else was available (Coombs 1977c).

g. *Muhlenbergia porteri*, a perennial grass, stays succulent longer than annuals and may be an important late summer food item but has been reduced, along with other perennial grasses, by livestock grazing (Coombs 1974, 1976, 1977a, 1979; Woodbury and Hardy 1948a).

h. The tortoise population on the Beaver Dam Slope may consume from 2,552 to 5,104 kg of forage per year (Coombs 1979).

16. Beaver Dam Slope, UT, 1979 to 1981

a. Spring feeding observations: spring diet was 65.6 percent forbs and 21.9 percent annual grasses (Minden 1980).

b. Fecal analysis of 15 samples taken from late April to June 1980 showed that *Bromus* sp., *Plantago* sp., *Astragalus* sp., legume pods, and *Erodium* sp. received greatest use in that order (USDI Bureau of Land Management 1980a).

c. Observations and fecal analysis during spring of 1980 and 1981 showed that *Plantago insularis*, *Astragalus nuttallianus*, *Bromus rubens*, and *Erodium cicutarium* received the highest use. Frequency of utilization shifted dramatically from month to month, but the use of perennial grasses was consistently low (Minden and Keller 1981; Minden and Metzger 1981).

d. Despite seasonal shifts in food items, *Bromus rubens* is a major item in all seasons (Minden and Keller 1981; USDI Fish and Wildlife Service 1985a).

e. Feeding patterns vary from year to year, but the annuals that are most common during a given year receive the highest use (Minden 1980).

17. City Creek Study site, St. George, UT (Esque and others 1990a, 1991): feeding observations and fecal analysis.

a. Twenty-nine food items were observed being eaten during 1989; of those, 13 were annuals or biennials, 12 were perennials, and 4 were not plants. *Bromus rubens*, *Erodium cicutarium*, and *Bromus tectorum* comprised more than 80 percent of the diet. In 1990, 46 food items were consumed, of which 26 were annual forbs, 2 were annual grasses, 12 were perennial shrubs, 2 were perennial grasses, and 4 were not plants. *Bromus rubens*, *Schismus barbatus,* and *Erodium cicutarium* comprised more than 70 percent of the diet.

b. In 59 fecal pellets analyzed during 1989, 28 plant species were found; the major food items were *Bromus rubens* and *Erodium cicutarium*, which were also major items in feeding observations. In 1990, 59 fecal pellets were analyzed; 41 food items were found with the major food items being *Bromus rubens*, *Schismus barbatus,* and *Erodium cicutarium*.

III. Nutrition

A. Few forage species supply a good balance of nutrients; therefore, intake of varied forage items is important (Mayhew 1968).

B. Dietary needs

1. A desert tortoise requires about 21 kg of herbaceous forage per month (USDI Bureau of Land Management 1981).
2. Forbs are generally higher in protein, carbohydrates, fat, and calcium than annual and perennial grasses (Fowler 1976; Hohman and Ohmart 1980).
3. Forbs are nutritionally superior to browse leaves in protein, phosphorus, and digestibility (Urness and McCulloch 1973).
4. Miller (1958) and Jarchow (1984) report the nutritional content of forage species including percent protein, fat, crude fiber, carbohydrate, calcium, phosphorus, and calcium:phosphorus ratio.
5. Captive tortoises fed a standard diet grow raised carapace scutes (Jackson and others 1976a,b).

C. Regional variation in nutrition

1. The forage available to northern populations may have higher energy and lower crude fiber content than elsewhere (Jarchow 1984).
2. The most important time for tortoises in terms of nutrition is spring when tortoises require green vegetation to replenish fat reserves used during hibernation. Perennial grasses may be important in summer because they remain succulent and respond to late spring and summer rains (USDI Bureau of Land Management n.d.).
3. Tortoises have more rapid growth in years with high production of winter annuals (Medica and others 1975).
4. An improved diet can lead to increased longevity and an extension of the periods of middle and old age. The converse is also true (Fowler 1976; Rosskopf and others 1981, 1982b).
5. Reproduction may depend on adequate forage and nutrition (Berry 1978a; Coombs 1977c; Medica and others 1975).
6. Juvenile dietary preferences are generally unknown. However, young *Gopherus flavomarginatus* prefer forbs high in phosphorus and protein (Appleton 1983; Burge and Bradley 1976).
7. Malnutrition
   a. May cause many pathological processes including fatty liver infiltration, enteritis, cloacal infections, and metabolic bone disease (Jarchow 1984).
   b. Low calcium may lead to bone disease (Jarchow 1984).
   c. Respiratory disease could be a result of malnutrition (Fowler 1976).
8. Calcium requirements
   a. Adult females have higher calcium requirements. The shell and/or bones of females may be thinner and more porous due to mobilization of calcium during reproduction (Auffenberg and Iverson 1979; Zangerl 1969).
   b. Females occasionally ingest calcium-rich soil to replenish reserves lost during egg laying (Marlow and Tollestrup 1982).
   c. Flexibility of the shell is related to calcium in the diet (Ewert 1979; Patterson 1970).

d. Tortoises must have a sufficient calcium:phosphorus ratio in their forage for shell and skeletal development (Fowler 1976). A 2:1 ratio of calcium to phosphorus is required. Vitamin D and ultraviolet radiation are also important in shell formation (Murphy 1973).
e. Lack of calcium in the diet leads to poor shell formation (Rosskopf and others 1982b).

9. Potassium ion osmotic stress
   a. Natural diet is high in potassium and low in nitrogen, which is required to form urates for potassium excretion (Coombs 1977c; Minnich 1979).
   b. During late summer, nitrogen content of plants in the Mojave Desert decreases, making tortoises more susceptible to potassium buildups (Minnich 1982).
   c. Tortoises do not possess extrarenal salt glands and cannot excrete excess potassium without losing water if uric acid is not available (Dantzler and Schmidt-Nielsen 1966; Minnich 1970; Nagy 1972).
   d. Hydrated tortoises may feed preferentially on dried grasses, possibly because these plants are low in potassium (Minnich 1976, 1977, 1982; Nagy and Medica 1977).
10. Specific studies
   a. Beaver Dam Slope, AZ: 24 tortoises had indented vertebral or costal scutes (Hohman and Ohmart 1980).
   b. Rock Valley, Nevada Test Site, NV (Nagy and Medica 1986)
      i. The spring diet was osmotically stressful, and tortoises were eventually forced to stop feeding.
      ii. Rains came in summer, and tortoises drank rainwater, which allowed them to void precipitates with urine and store water.
      iii. Recently-hydrated tortoises were able to switch to a diet of dry grasses and gain mass.
      iv. The spring diet may not have provided enough nitrogen to form urates for potassium excretion.
      v. The potassium content of the spring diet was high; force-fed tortoises demonstrated an assimilation efficiency of 0.761 ± 0.045 for potassium.
   c. Beaver Dam Slope, UT (Coombs 1977b,c; Woodbury and Hardy 1948a).
      i. Perennial grasses may be an important late summer source of water and nutrients.
      ii. Perennial grasses have been severely reduced by livestock grazing and by competition with exotics.
      iii. Without perennial grasses tortoises may become dehydrated in summer, resulting in a buildup of electrolytes, especially potassium ions.
   d. Beaver Dam Slope, UT (Minden 1980)
      i. Twenty-eight percent of tortoises have concave depressions in vertebral or costal scutes.
      ii. Three tortoises out of 82 native tortoises encountered had apparent respiratory problems.

iii. Both conditions may be caused by malnutrition (Jarchow 1984; Minden 1980).

e. Beaver Dam Slope, UT (Jarchow and May 1987)

i. Central depressions in scutes, especially vertebral scutes.

ii. Osteoporosis was evident in carcasses analyzed.

iii. Six of twelve live tortoises examined demonstrated "sinking" of the carapace scutes, which may indicate osteoporosis. Since these six tortoises demonstrated scute wear not characteristic of old age, osteoporosis probably exists and is "premature and pathogenic."

iv. Physical examination failed to show any disease; the cause may be malnutrition.

v. Osteoporosis results from a diminished organic bone matrix rather than abnormal bone calcification. Malnutrition may result in insufficient protein matrix being formed.

vi. Summer diet of perennial grasses, which are now lacking, may be an important crude fiber source but they have been replaced by exotics (Jarchow and May 1987; USDI Bureau of Land Management 1983).

vii. Evidence of vitamin deficiency also was present.

viii. During summer and fall there is an increased demand for protein and calcium. Perennials may be the main source for meeting these demands, especially during years with a poor crop of spring annuals. Livestock grazing practices have been and probably still are reducing perennial grasses.

ix. *Muhlenbergia porteri* may have once been a fiber or protein source helping tortoises combat osteoporosis, but there is no solid evidence to verify this.

x. A more likely cause of malnutrition is that native annuals must compete with *Bromus* spp. and *Erodium cicutarium*, resulting in protein deficiency.

xi. *Bromus rubens*, the major summer food item, has a very low calcium content (Jarchow 1984).

xii. Rates of osteoporosis are unknown in other parts of the tortoise range (Turner 1988).

xiii. Tortoises' diets need to be analyzed for calcium, phosphorus, and boron to understand their effects on bone growth (Turner 1988).

f. Beaver Dam Slope, UT (Berry 1987)

i. Tortoise remains demonstrated evidence of bone disease; including thinning of shell, holes or a honeycomb structure in the bones, and deformed or eroded bones.

ii. Many remains were of young or middle-aged adults.

iii. Of the 73 tortoise carcasses collected from Woodbury-Hardy and Beaver Dam Slope permanent study plots, 20.6 percent were diagnosed as having bone abnormalities.

F. Osteophagia (Esque and others 1991)

1. At the City Creek, UT, study site tortoises ate bone presented to them 8 out of 11 times.
2. Tortoises persisted in eating bones and were not easily interrupted by the presence of an observer contrary to their behavior during intrusions sometimes caused during feeding observations.

G. Geophagy and lithophagy
   1. Observation of sand ingestion: frequency increases in summer and fall. Behavior may aid in digestion, and scats may serve as territorial or individual markers (Luckenbach 1982; Obst 1986; Sokol 1971).
   2. Ingestion of small stones may aid in the maceration of food (Murphy 1973).
   3. Tortoises, especially adult females, were seen mining and ingesting $CaCO_3$ deposits (Marlow and Tollestrup 1982).
   4. Tortoises sniff at the ground until they find desirable soil to eat (Bissett 1972).
   5. Tortoises sniff the ground before mining, then scrape at the soil with their forelegs until they expose the $CaCO_3$ layer (Marlow and Tollestrup 1982).
   6. Of more than 11,000 bites of food items observed in 1989 at the City Creek, UT study plot, 0.43 percent were of rock and 0.21 percent were of soil. In 1990, out of more than 31,000 bites observed, 0.12 percent were of rock; no ingestion of soil was observed. At the Littlefield, AZ study plot, out of more than 7,000 bites observed, 0.24 percent were of rock; no soil ingestion was observed (Esque and others 1990a, 1991).

H. Coprophagy
   1. Kit fox scat and the scat of other tortoises were consumed by a very young tortoise (Hohman and Ohmart 1980).
   2. Cow dung was eaten by tortoises during a drought period (Turner and others 1984).
   3. A captive desert tortoise did not eat dog feces while tortoises of other genera did (Beltz 1958).
   4. Of over 11,000 bites of food items consumed by wild tortoises in 1989 at the City Creek, UT study plot, 0.15 percent of the bites were fecal material. In 1990, out of 31,000 bites observed, 0.79 percent were fecal material. At Littlefield, AZ, in 1990, 0.10 percent of the total bites observed were of fecal material (Esque and others 1990a, 1991).

I. Other feeding behavior
   1. Captive tortoises ate calcareous materials such as concrete and egg shells (Sokol 1971).
   2. Captive female tortoises dug up and ate eggs of another female; they also ate the shells of chicken eggs (Nichols 1953).
   3. Of over 31,000 bites consumed by wild tortoises at the City Creek, UT study plot in 1990, 0.71 percent were of plant litter (Esque and others 1990a).

Scats

The literature includes descriptions of fecal material, observations of the frequency of defecation and on the use of fecal material as a marker. Most of the information presented here is from observation of both wild and captive tortoises.

I. **Description**
   A. Dark brown or black and slightly moist when fresh. About the size of a fox scat (Camp 1916).
   B. Dark brownish green and about 45 mm long and 20 mm in diameter. Made up of undigested stems of grasses (Johnson and others 1948).

C. Dimensions are 1.25 cm wide by 2.9 cm long to 1.85 cm wide by 6.6 cm long (Berry 1973b).
D. Mass of a scat averages 1.95 g (Coombs 1979).
E. Size of scat indicates size of tortoise (Luckenbach 1982).
F. Scats usually contain coarse plant fibers (Berry 1973b; Murphy 1973).
G. Scats from early spring disintegrate rapidly because they are made up of flowering stalks and other parts of succulent annuals. Summer scats last longer because they are made up of dried annuals, especially grasses (Luckenbach 1982).
H. On Beaver Dam Slope, UT, *Erodium* sp., a major food item, shows up as fine powder in scats, because of its soft nature. *Bromus rubens*, an annual grass, comprises the majority of the scat (Coombs 1974).
I. An average of 4.6 ± 1.7 foods were found in each fecal sample at three study sites in Arizona and Utah (Hansen and others 1976).
J. Scats may contain grass seeds; tortoises may disperse certain grasses (Auffenberg 1969).
K. Hot, dry desert climates may allow scats to resist deterioration from fungi, bacteria, and insects for several years (Hansen and others 1976).

II. **Frequency of defecation**
A. Tortoises fed indigestible tracers defecated them with foods about one day later (Hansen and others 1976).
B. Four captive tortoises maintained under natural conditions had a gut passage time of 20.3 ± 11.2 days (Nagy and Medica 1986).
C. During winter, defecation may be very infrequent; the large intestine is filled with grass, which may last 6 months with no noticeable breakdown (Murphy 1973).

III. **Use as markers**
A. Feces and urine may be used to mark territories and home ranges (Patterson 1971a).
B. Some scats are made entirely of sand and may serve as territorial markers (Coombs 1979; Patterson 1971a).
C. Fecal pellets of dominant males may cause subordinates to leave the area (Auffenberg and Weaver 1969; Patterson 1971a).
D. Captive desert tortoises demonstrated aversion to cloacal excretions. Fresh deposits, placed in sleeping areas, altered aggregation and sleeping behavior (Harless 1979; Nichols 1957; Patterson 1971a).

Mortality Factors

Factors related to the deaths of desert tortoises are documented in the general literature through observation and direct diagnosis by trained veterinarians. The following discussion includes verifiable causes of death (such as predation, random catastrophic events); however, potential causes of death (such as endoparasitism) are also included.

I. **Disease**
A. Conditions of disease in captive tortoises (Rosskopf and others 1981): multiple organ system involvement such as both liver and kidney diseases are found in seriously ill tortoises. Liver, heart, and kidney disease are common in desert tortoises. Systemic cancer is extremely rare.

B. Dietary factors are very important in maintaining tortoise health (Fowler 1976; Rosskopf and others 1981, 1982b).

C. Respiratory disease: see also Husbandry, Illness.

1. Symptoms include weakness, weight loss, nasal exudate, and sometimes pulmonary lesions (McCawley and Sheridan 1972; Rosskopf 1988).
2. Upper respiratory disease in desert tortoises is highly contagious in nature and exists at different levels of severity (Rosskopf 1988).
3. Desert tortoises from the wild exhibiting signs of upper respiratory tract disease (URTD) demonstrated significantly higher serum sodium, urea, SGOT (serum glutami c-oxaloacetic transaminase activity), and cholesterol, as well as significantly lower levels of hemoglobin and phosphorus when compared to healthy, free-ranging desert tortoises. There was no significant difference in serum or liver vitamin A and E between the ill and healthy tortoises. There were no significant differences between ill and healthy tortoises for lead, copper, cadmium, and selenium; however, the livers of the ill tortoises demonstrated elevated levels of mercury and iron (Jacobson and Gaskin 1990; Jacobson and others 1991).
4. The bacterium *Pasteurella* sp. was associated with respiratory lesions in captive tortoises exhibiting signs of respiratory disease; however, this microorganism has also been found to be associated with the gastrointestinal and nasal flora of healthy tortoises (Snipes and others 1980). Respiratory disease may be expressed because of stress induced from captivity (Fowler 1976; Snipes and others 1980).
5. The viral agent *Mycoplasma* sp. (and organisms similar in morphology) may be associated with respiratory disease; however, this organism has not been conclusively connected to the disease (Jacobson and Gaskin 1990; Jacobson and others 1991).
6. Viral and bacterial agents associated together may play a role in contributing to respiratory disease (Jacobson and Gaskin 1990; Jacobson and others 1991; Rosskopf 1988).
7. Differences in organ morphology between ill and healthy tortoises (Jacobson and Gaskin 1990; Jacobson and others 1991).
   a. Thyroid: one ill tortoise demonstrated a larger thyroid than those of healthy tortoises.
   b. Thymus: only 2 of 12 ill tortoises examined had thymuses that could be readily located. Thymuses of ill tortoises were smaller than those of healthy tortoises.
   c. Spleen: no differences existed between spleens of ill and healthy tortoises.
   d. Liver: granules found in the liver of ill tortoises demonstrated the presence of iron. Healthy tortoises possessed fewer of these granules.
8. Respiratory disease sometimes develops in hibernating tortoises (Clarke 1968; Rosskopf 1988).
9. Three tortoises examined on Beaver Dam Slope, UT, had mucus discharges from nasal openings suggesting respiratory disease (Minden 1980).

D. Hard urate concentrations in tortoises may block urinary channels and cause death (Frye 1972; Hunt 1957; Miller 1932, 1955).
E. Hypovitaminosis A: see Husbandry, Illness.
F. Bone disease
  1. Symptoms include decreased bone density and thinning of cortical bones (Frye 1973).
  2. Tortoises on Beaver Dam Slope, UT, may have widespread bone disease, even among young tortoises (Jarchow and May 1987).
  3. Twenty-seven percent of Beaver Dam Slope, UT, tortoises had concave depressions in vertebral and costal scutes (Minden 1980).
  4. Determination of the incidence of osteopenia and/or osteomalacia was conducted at two desert tortoise study sites: the population at the Beaver Dam Slope, UT, site was declining, possibly due to chronic malnourishment and had a history of extensive grazing; the City Creek, UT, site supported a healthy, well-nourished tortoise population; grazing has been restricted there. Shell thickness and porosity were similar between the two sites; however, the Beaver Dam Slope tortoises demonstrated a significantly greater increase in osteoid surface in relation to tortoises at City Creek. The osteoid seam width was not significantly different between tortoises of both populations. Mild bone osteomalacia was determined to be present in bone samples taken from tortoises on the Beaver Dam Slope (Arizona Game and Fish Department 1991b; Wronski and Jacobson 1990).
G. Prolapsed reproductive organs (Berry and Woodman 1984a).
H. Egg yolk peritonitis: reported for an aged captive female with several egg yolks that had ruptured in her coelomic cavity and leaked into the surrounding tissue (Rosskopf and Woerpel 1982).

II. **Parasitism**
  A. Ectoparasites
    1. Adobe tick (*Ornithodoros* spp.)
      a. *O. turicata* found in sutures between scutes or on soft skin around the neck, leg, and tail. Also commonly found at the site of an injury (Coombs 1973, 1974, 1977c; Greene 1983; Harbison 1937; Woodbury and Hardy 1948a).
      b. All specimens collected were in seams between posterior costal, vertebral, and marginal shields (Ryckman and Kohls 1962).
      c. Ticks were found to inhabit tortoise burrows (Ryckman and Kohls 1962).
      d. *Ornithodoros turicata* is not host specific (Ryckman and Kohls 1962).
      e. One male *O. parkeri* was collected from a desert tortoise on May 12, 1980 in the Tortuga Mountains of San Bernardino County, CA (Lane 1984).
    2. Trombicula mite: observed on tortoise neck and shell (Coombs 1973, 1974, 1977c).
    3. Botfly larvae found under skin on neck (Coombs 1977c).
    4. Dipteran larvae (maggots): found on injured areas of the shell and associated with navels of hatchlings (Nichols 1953; Woodbury 1952; Woodbury and Hardy 1948a).
    5. Fungi
      a. Mold or fungi may grow on tortoise's shells inside humid winter dens (Greene 1983; Woodbury and Hardy 1948a).

b. Fungi found growing on brands made in the shells of marked tortoises (Woodbury and Hardy 1948a).
c. Mildew grew on captive tortoises that soaked regularly in a water dish (Poorman 1970).
6. Red ants: may be a problem for captive tortoises. Known to bite skin around neck, sometimes causing death in young tortoises (Miles 1953).

B. Endoparasites
1. Nematodes
a. Present in intestinal tract (Jarchow and May 1987; Woodbury and Hardy 1948a).
b. Fecal flotations yielded moderate to large numbers of ova from oxyurate nematode, *Tachygonetria* sp. (Jarchow and May 1987).
c. Intestinal parasites may be important as pathogenic organisms, especially among captive tortoises (Rosskopf and others 1981).
2. Eosinophilia: common in cases of intestinal parasitism (Rosskopf 1982).
3. *Lampropedia* sp.: a bacterium associated with cellulose digestion in the gut and often eaten by nematodes, was not found in a *Gopherus agassizii* (Schad and others 1964).
4. Hemoparasites were not found in blood samples of over 500 captive tortoises and of wild tortoises (Jarchow and May 1987; Rosskopf 1982).

III. **Injury**

A. Predation
1. Injuries inflicted by predators range from scratches and holes in the carapace to scars on the appendages and missing limbs (Bailey 1928; Berry 1974b; Coombs 1974, 1977c; Grant 1946; McCawley and Sheridan 1972).
2. Predation injuries are most often found on the carapace, while other injuries are commonly found on the gular forks and plastron scutes (Hohman and Ohmart 1980).

B. Shell injuries are common on tortoises, but they usually survive them. Many individuals have old injuries (Minden 1980; Rosskopf and Woerpel 1981).

IV. **Predation**

A. Predators of adult tortoises
1. Coyote (*Canis latrans*): Berry 1974b; Berry and Woodman 1984a; Burge 1977d; Coombs 1973, 1974, 1977c; Hohman 1977; Miles 1953.
a. Seven percent of coyote scats in the Beaver Dam Mountains, AZ, contained tortoise remains (Hohman and Ohmart 1980).
b. In the Beaver Dam Mountains, UT, 1.8 percent of coyote scats contained tortoise remains (Coombs 1977a).
c. In 1978 to 1980, none of the coyote scats collected in the Beaver Dam Mountains, UT, contained tortoise remains (Minden 1980).
d. At Pinto Basin, Joshua Tree National Monument, CA, a coyote scat was found that contained tortoise scutes (Barrow 1979).

   e. Coyotes may dig tortoises out of burrows (Berry 1974b; Luckenbach 1982).
2. Kit fox (*Vulpes macrotis*): Berry 1974b; Burge 1977d; Coombs 1973, 1974, 1977b; Hohman 1977.
   a. Of kit fox scats on Beaver Dam Slope, UT, 3.2 percent contained tortoise remains (Coombs 1977a).
   b. None of kit fox scats found on the Beaver Dam Slopes in Utah and Arizona in 1978 to 1979 contained tortoise remains (Hohman and Ohmart 1980; Minden 1980).
3. A raccoon (*Procyon lotor*) attacked and injured a captive adult tortoise (Poorman and Poorman 1971b).
4. Other potential predators include: bobcat (*Lynx rufus*) (Coombs 1974; Woodbury and Hardy 1948a); Feral dog (Hohman 1977); and Golden eagle (*Aquila chrysaetos*) (Luckenbach 1982; USDI Bureau of Land Management 1990).

B. Predators of eggs and young tortoises
1. Reptiles: Gila monster (*Heloderma suspectum*) and coachwhip snake (*Masticophis flagellum*) eat tortoise eggs and young tortoises (Luckenbach 1982).
2. Birds: Common raven (*Corvus corax*), roadrunner (*Geococcyx californianus*), burrowing owl (*Athene cunicularia*), golden eagle (*Aquila chrysaetos*), red-tailed hawk (*Buteo jamaicensis*) (Berry 1985, 1986a; Berry and Woodman 1984a; Coombs 1973, 1974, 1977c; Esque and Duncan 1985; Luckenbach 1982; Thelander 1974; USDI Bureau of Land Management 1990).
3. Mammals: Coyote (*Canis latrans*), kit fox (*Vulpes macrotis*), bobcat (*Lynx rufus*), badger (*Taxidea taxus*), spotted skunk (*Spilogale putorius*), ringtail (*Bassariscus astutus*), feral dogs and feral cats (Coombs 1973, 1974, 1977c; Luckenbach 1982).

C. Signs of predation
1. Tooth marks and scratches, holes and cracks in shells, and missing or scarred appendages (Bailey 1928; Berry 1974b; Grant 1946; McCawley and Sheridan 1972).
2. Skeletal and shell parts in the scats of predators (Barrow 1979; Coombs 1973, 1977c; Woodbury and Hardy 1948a).
3. Broken and compressed remains of one-half to two-thirds of the shell (Burge 1977d).
4. Missing head and/or limbs, tooth scratch marks on shell, and young tortoises with broken shells indicated kit fox predation (Coombs 1977c).
5. Broken marginal scutes and carapace opened at the top with internal organs eaten indicated coyote predation (Coombs 1977c).

D. Specific instances of predation
1. On nest and eggs
   a. Picacho Mountains, AZ: 23 percent of nests were destroyed by predators, mostly kit foxes, coyotes, and badgers. Gila monsters uncovered a nest and consumed tortoise eggs (Vaughan 1984a; Vaughan and Humphrey 1984).
   b. Paradise Canyon, UT: a nest was excavated and four eggs were consumed by a Gila monster (Beck 1982). Three nests were found destroyed by Gila monster (Coombs 1977c).
2. On young tortoises

a. Desert Tortoise Natural Area, CA: numerous remains of small tortoises were found near fence posts by agricultural fields. They were apparently victims of the common raven (Campbell 1983).
b. Remains of skull and feet of a young tortoise were found in a raven's stomach (Miller 1932).
c. Remains of a young tortoise found in nest of a raptor (Coombs 1974).
d. Raven predation may decrease young tortoise numbers in localized areas and may contribute to the adverse effects on tortoise colonies; however, the effect of ravens on tortoise populations throughout the range is less well known (USDI Fish and Wildlife Service, National Ecology Research Center 1990).

3. On adults
    a. Coyote tooth scratches seen on tortoise shell (Bailey 1928).
    b. Coyotes observed digging tortoises out of dens (Berry 1974b).
    c. Coyotes observed attacking, carrying, and eating a tortoise (Berry 1972; 1974b).
    d. On the Beaver Dam Slope, UT, 1.8 percent of coyote scats had tortoise remains in them; 3.2 percent of the kit fox scats contained tortoise remains (Coombs 1977c).
    e. Shells of adults were fractured, possibly by coyotes that dropped the tortoises on rocks (Berry 1972; Burge 1977d).
    f. A bobcat was observed killing a tortoise (Woodbury and Hardy 1948a).
    g. Four tortoises had limbs chewed off by predators (Coombs 1977c).

E. Predation rates
1. Predation is the highest cause of death among Beaver Dam Slope, UT, juveniles (Jarchow and May 1987).
2. Juvenile tortoises may be the major prey item of common ravens near Kramer, CA (Woodman and Juarez [In press]).
3. Thirteen of 65 shells found on the Beaver Dam Slope, UT, showed signs of predation (Coombs 1974).
4. Predation was thought to be responsible for 2.42 percent of the mortality on the Beaver Dam Slope, UT (Coombs 1977c).
5. Predation accounted for 3 percent of mortality on the Beaver Dam Slope, UT, but 11 percent of tortoises studied there showed signs of attempted predation (Minden 1980).
6. Of the 100 tortoise remains collected on the Beaver Dam Slope, UT, between 1982 and 1986, the remains of four individuals showed signs of predation or scavenging (Berry 1987).
7. Seventy-one percent of adult carcasses recovered (10 out of 14) and 77 percent of hatchling carcasses through subadult size classes (10 of 13) on the Beaver Dam Slope, AZ, showed signs of predation or scavenging (Duck and Snider 1988).
8. Tortoises on the Beaver Dam Slope in Utah and Arizona may have an unusually high incidence of osteoporosis resulting from malnutrition. This may make them particularly vulnerable to predation (Jarchow and May 1987).
9. Woodbury and Hardy reported that predation on tortoises increased in 1945 and 1946 when the numbers of rabbits and rodents were low (Woodbury and Hardy 1948a).

10. Of 48 marked tortoises, 13 were killed between February 1972 and February 1973. The predation rate was 20 to 28 percent but had previously been 5 percent. The increase was attributed to low winter rainfall and the resulting drop in rodent and rabbit populations (Berry 1973b, 1975b).
11. On Tiburon Island, Mexico, predation on tortoises was low in spite of a large coyote population. The lack of predation may be a result of large rodent populations and cover that has not been diminished by livestock grazing (Reyes Osorio and Bury 1982).

V. **Human-related mortality**: see also Habitat deterioration.
   A. Tortoise populations are declining due to livestock grazing, collecting, vandalism, urbanization, land management patterns, agriculture, roads, and recreation (Berry and Nicholson 1984a).
   B. Habitat destruction is the most serious threat to desert tortoises; the major cause of tortoise mortality is human activity (Auffenberg 1969; Luckenbach 1982).
   C. Sixty percent of the tortoise habitat in the western Mojave Desert has been lost to human use (Holing 1986).
   D. Urban development increases the mortality of nearby tortoise populations through collection, road kills, vandalism, and predation by domestic animals (Campbell 1981).
   E. Areas of human activity correspond to areas of low tortoise density (Berry and Nicholson 1984a).
   F. Human predation
      1. Historically used as food by many Indian tribes including Piutes, Pima, Hopi, and Seri (Bogert 1933; Connolly and Eckert 1969; Felger and Moser 1976; Felger and others 1981; Miles 1953; Stejneger 1893; White and Stevens 1980).
      2. Burned desert tortoise bones have been found in Late Pleistocene deposits at Shelter Cave, NM. Tortoises may have been a food source for Indians (Brattstrom 1961; Van Devender and others 1976).
      3. Prospectors and white settlers also killed desert tortoises for food (Miller 1932; Stephens 1914).
      4. Mexican traders carried live desert tortoises as a fresh meat source. Tortoises were also hunted by Mexican fishermen (Felger and others 1981).
      5. Of 635 carcasses collected between 1976 and 1982 in the California deserts, 91 demonstrated evidence of gunshots (Berry 1986d).
      6. Evidence of gunshot in tortoise carcasses can be seen in conchoidal fractures, a characteristic pattern left by the bullet as it passes through the bone (Berry 1986d).
      7. Of desert tortoise carcasses at study sites in California, 14.3 percent showed evidence of gunshots. Of the carcasses in the western Mojave Desert exclusively, 20.7 percent of tortoise carcasses had been shot. The figures may be even higher in areas with more human disturbances (Berry 1986d).
      8. Average mortality in undisturbed populations is 2 percent. In western Mojave, mortality is 6.2 percent. Gunshot death may be a major factor in this high mortality (Berry 1986d).
      9. Ten percent of Arizona shell remains from the Littlefield study plot had gunshot wounds.

10. At the Desert Tortoise Natural Area in California, hunters are usually indiscriminate in firearms use. A study found desert tortoises, eagles, hawks, and owls were killed by hunters (Campbell 1981, 1982).
11. Many tortoises have been found shot at California sites; including the Desert Tortoise Natural Area, Fremont Valley, Fremont Peak, Kramer Hills, Stoddard Valley, Lucerne Valley, and Chuckwalla Bench. Gunshot deaths are also common at Piute Valley, NV (Garcia and others 1982).
12. One individual bragged of putting 47 desert tortoises in a line and shooting them (Bury and Marlow 1973).
13. Eight tortoises were found shot on a 3.2 km stretch of unpaved road near California City, CA (Bury and Marlow 1973).
14. Tortoises are commonly used for target practice and shot repeatedly (Bury and Marlow 1973; Olsen 1971).
15. The shell of an adult male with numerous bullet holes was found several hundred meters away from a trail (Berry 1975a).
16. Many turtles, including desert tortoises, are often run over on the road, sometimes intentionally (Kahn 1970; Ragsdale 1939).
17. Some people apparently go out of their way to run over tortoises with automobiles (Hamilton 1944).
18. Roads and use by off-road vehicles increase tortoise mortality: see Habitat deterioration, Off-road vehicles, and Roads.
19. Road kills often affect the young and most sensitive portion of desert tortoise populations (Fusari and others 1980, 1981).

G. Collection

1. Desert tortoises are slow moving, nonaggressive, and diurnal, making them vulnerable to collection (Jaeger 1961; Luckenbach 1982).
2. On the Beaver Dam Slopes in Utah and Arizona, heavy collection for pet trade took place until the 1970's when Interstate 15 was completed and traffic was diverted from Highway 91 (Coombs 1973, 1977c; Sheppard 1982a).
3. All dens along Castle Cliff in Utah were inactive because all the tortoises in the area were collected for the pet trade (Coombs 1977c).
4. Utah Hill service station on Highway 91 paid children to collect tortoises and sold them to passing motorists (Coombs 1973, 1977c).
5. Railroad workers used to collect tortoises from the Beaver Dam Slope and sell them to passengers (Luckenbach 1982).
6. The skewed sex ratio, in favor of males, on the Beaver Dam Slope is probably due to collection. Mortality does not differ between sexes, but females remain close to dens and are more vulnerable to collection (Coombs 1973, 1974; Hohman and Ohmart 1980; Minden 1980).
7. Turtles, especially tortoises, are popular pets in California. Pet tortoise populations in metropolitan areas of California probably exceed wild populations in the Mojave Desert (Cowan 1972; Luckenbach 1982; St. Amant 1979).
8. In May 1935, a man collected 200 tortoises for sale to tourists in San Bernardino County, CA. In October, 100 more were collected (Grant 1936a).

9. In 1970, a man was caught in California with 185 tortoises in his possession. He had already shipped 105 tortoises to pet stores in Utah (Bury and Marlow 1973).
10. Tortoises have also been collected for entertainment purposes such as turtle races. At least in one instance, the tortoises were later released where they were captured (Delaney 1969).
11. Of desert tortoises in California about 9,000 to 10,000 are legal captives (St. Amant and Hoover 1978).

H. Livestock grazing: Negative influence has resulted in range deterioration. Most Bureau of Land Management land has declined from good to fair or poor range condition (Holing 1986). See Habitat deterioration, Livestock grazing.

VI. **Environmental factors**

A. Tortoises may occasionally be unable to right themselves when overturned. If this occurs, they may overheat or dehydrate, or they may suffocate due to the pressure of the internal organs on the lungs (Berry and Woodman 1984a; Coombs 1973, 1974).
B. Drought has been implicated in reduced reproduction and even in dramatic increases in mortality (Mortimore 1984).
C. Long-term climatic change may be a factor in declining populations, and there may be a trend toward increasing aridity (Phillips and others 1984).
D. Grass fires may occasionally kill tortoises (Berry and Nicholson 1984a; Woodbury and Hardy 1948a).
E. Flash floods may occasionally kill tortoises; several dead tortoises were observed in Fenner Valley and Fremont Valley, CA, after flash flooding (Luckenbach 1982).

VII. **Estimating the years since death by examining carcasses** (Berry 1973b; Woodman and Berry 1984).

A. Less than 1 year: scutes adhere tightly to the bone.
B. One to two years: scutes lightened in color, growth rings begin to peel.
C. Two to five years: scutes fall from bone, bone falls apart.
D. Aging methods may not apply across the range of the desert tortoise due to different environments (Minden 1980).

VIII. **Other causes**

A. Some tortoises have drowned in guzzlers constructed to provide water for gallinaceous birds in Utah (Coombs 1974).
B. Tortoises may fall into exploration pits and be unable to escape (Berry 1975a).
C. Human settlement may attract tortoise predators such as ravens (Campbell 1983).
D. Water projects such as the central Arizona Project may drown major tortoise populations (Vaughan 1983).
E. Establishment of electric generating facilities may impact desert tortoise habitat (Stevens 1976).
F. Radioactive fallout from atomic weapons testing in Nevada may have damaged tortoise populations in Utah, Arizona, and Nevada. Bones of tortoises on the Beaver Dam Slope have unusually high levels of radioactive elements, including plutonium. Scute anomalies here are much more common than in other areas studied. Radiation may have played a role in this and other factors affecting

tortoise survival (Dodd 1986; Good 1982, 1984; Singh and others 1984; USDI Bureau of Land Management 1980b).

G. Multiple factors such as overgrazing, collection, and possible radioactive fallout may have reduced the Beaver Dam Slope, UT, population from about 2,000 to 350 native tortoises (Bolwahnn 1982; Coombs 1977b).

H. Habitat destruction through urban expansion, livestock grazing, and other human activities appears to be the greatest threat to desert tortoise survival (Auffenberg 1969; Berry and Nicholson 1984a).

Behavior

Behaviors of the desert tortoise are well documented throughout the literature. The following discussion includes normal daily behavior (such as drinking, agonistic behavior, and locomotion) as well as courtship and nest defense behaviors. This section also includes sensory perception of desert tortoises (such as audition, vision, olfaction).

I. **Courtship behavior:** see Reproduction, Courtship and Mating Behavior.

II. **Sex and species discrimination**

A. Visual signals (Auffenberg 1965, 1969; Berry 1986b; Camp 1916).

1. Adult males respond to the presence of another tortoise with vertical head movements.
2. Identical head movements are made if the other tortoise is a male of the same species. This serves to distinguish between males of the same species and other turtles.
3. If head movements are not reciprocated, the male approaches to identify cloacal scent, which is also species specific.
4. Speed of head bobbing is species specific and varies among species of *Gopherus* (Eglis 1962).

B. Olfactory signals

1. Cloacal scent: may serve to identify females of the same species (Auffenberg 1965).
2. Chin glands serve as both olfactory and visual recognition signals during courtship and combat and are used in sex discrimination. Enlarged scales on the median edge of the forelimbs are rubbed on the chin glands to spread their scent (Auffenberg 1977; Coombs 1974; Weaver 1970).
3. Chin glands are used by male *Gopherus agassizii* in sex recognition (Coombs 1974, 1977c): see Morphology, Adults.
   a. Male encounters with other males with normal chin gland secretions leads to combat.
   b. Male encounters with normal females lead to courtship behavior.
   c. Male encounters with males with taped chin glands may lead to courtship behavior.
   d. Male encounters with empty tortoise shells and rocks covered with male chin gland excretions lead to aggressive behavior.
4. Head movements are exaggerated movements of basic motor pattern associated with olfaction (Auffenberg 1965).

III. **Social behavior**

A. Social behavior may be an important factor in tortoise survival. Declining population densities may have altered social structures;

without enough individuals to form a normal social structure, the ability to breed may decline (Coombs 1974).

B. Visual cues, such as head bobbing, are of great importance in species and sex recognition. Also important are the two subdentary (chin) glands, which produce fatty acid in the form of a creamy white fluid. The chin glands serve as a visual and olfactory means of differentiating the sexes and are important in social behavior (Auffenberg 1966b; Coombs 1974; Eglis 1962): see also Behavior, Sex and Species discrimination.

C. *Gopherus* species head bob with the neck extended; the head is bobbed vertically. Head bobbing occurs when tortoises smell objects, meet other tortoises, and when they engage in combat and courtship (Weaver 1970).

D. Males approach other tortoises more often than do females and also do more head bobbing (Bury and Wolfheim 1979).

E. Vocalization may also be important in social behavior. There are specific vocal patterns for different situations and for tortoises of different ages (Patterson 1976b).

F. Gregarious behavior
   1. Most noticeable in the northern part of range where several tortoises share a winter den for hibernation (Coombs 1973, 1977a,c; Woodbury 1954; Woodbury and Hardy 1948a).
   2. Up to 17 tortoises were found in one winter den. Ten or more tortoises were found in 20 different dens (Woodbury and Hardy 1948a).
   3. At the Desert Tortoise Natural Area, CA, five male-female pairs were observed sharing burrows and three pairs were observed together outside burrows (Bickett 1980a).
   4. Cooperative digging has been observed among captive tortoises (Nichols 1953; Thorpe 1957).

G. Dominance hierarchies
   1. Agonistic behavior and dominance hierarchies may determine opportunities to breed and access to food, mineral licks, and cover (Berry 1986b; Douglass 1976).
   2. Tortoise hierarchies are related to age and size and influence subtle behavior, such as the order of entry into burrows or dens (Brattstrom 1974).
   3. Well-structured hierarchies seen in captive tortoises may be the result of high densities that do not occur under natural conditions (Bickett 1980a).

H. Territorial behavior
   1. Desert tortoise territories seem to be loosely protected and are marked with scats and possibly urine (Patterson 1971a; Woodbury and Hardy 1948a).
   2. Tortoises find fecal pellets aversive, possibly due to secretions from cloacal scent glands (Patterson 1971a).
   3. When male fecal deposits were placed in denning areas, subordinate males would not aggregate or sleep near the den until the pellets were dry (Harless 1979; Patterson 1971a).
   4. A captive tortoise urinated inside sleeping quarters and other tortoises refused to sleep there until it was cleaned (Nichols 1957).
   5. In the winter, fewer fecal pellets are produced, permitting more gregarious behavior (Patterson 1971a).

6. Larger males enter communal winter dens later than smaller males. This may allow smaller tortoises to enter communal dens without being driven away by aversive cloacal odors from large dominant males (Harless 1979; Patterson 1971a).
7. Dominant males may also be the first to leave winter dens in the spring (Patterson 1971a).

IV. **Defensive behavior**

A. Defense of nests

1. Female tortoises urinate on the nest during construction. The urine may repulse egg predators through taste or smell and may camouflage the nest (Auffenberg 1965; Patterson 1971b).
2. Fresher urine was more likely to inhibit predation (Patterson 1971b).
3. Females have been observed to attack Gila monsters (*Heloderma suspectum*), which try to raid nests and eat the eggs. A female, with its mouth wide open and neck extended, pursued a Gila monster. Bites were exchanged, and the Gila monster fled. The scenario was repeated several times (Vaughan 1984a; Vaughan and Humphrey 1984).

B. Defense by hatchlings

1. Hatchlings are by nature aggressive and pugnacious. Aggressive behavior may be the young tortoises' only means of defense against predators (Booth 1958; Coombs 1977c).
2. Young tortoises may lunge forward, open their jaws, and hiss when touched (Coombs 1977a,c; Grant 1936a).
3. Occasionally young tortoises may bite (Coombs 1977a,c).

C. Typical defensive behavior of adult tortoises involves passive resistance. Tortoises withdraw into their shell, bring their armored forelimbs together to protect the head after it is drawn into the shell, and pull the hind limbs and tail in (Coombs 1973, 1977c; Woodbury and Hardy 1948a).

D. When attempts are made to remove a tortoise from its den, the tortoises will move further into the den, straighten its legs, and push its carapace against the ceiling, thus wedging itself inside (Coombs 1973, 1977c; Woodbury and Hardy 1948a).

E. Urination

1. Tortoises may void large quantities of urine when handled or disturbed (Bailey 1928; Coombs 1973, 1977a,c).
2. The amount of fluid voided ranges from 2 to 20 ml (Coombs 1977c).
3. Females and young tortoises are more inclined to urinate when handled than are males (Coombs 1974).
4. Tortoises may also urinate when overturned, in part to deter predators (Coombs 1974).
5. Urine apparently has a taste or smell that is repulsive to predators (Patterson 1971b).
6. Defensive urination is more common in spring and fall when water is more abundant (Coombs 1977c).

V. **Agonistic behavior**

A. Head bobbing generally precedes agonistic behavior (Coombs 1977a).

B. Fighting is common among males but infrequent among females. There is very little aggression between sexes (Burge 1977d; Bury and Wolfheim 1979; Nichols 1953.

C. Three instances of female-female agonistic behavior were observed at the City Creek, UT, study plot in 1989 (Esque and others 1990a).
   1. A larger female was the aggressor in each instance.
   2. One of the confrontations occurred in the spring near a wintering den.
   3. Two of the confrontations occurred in areas where tortoises were frequently observed foraging and mating.
D. Female-male agonistic behavior was observed on one occasion when an adult female confronted a subadult male at a wintering den (Esque and others 1990a).
E. Males may recognize each other immediately, probably due to reciprocated head bobbing and chin gland scent, which tends to evoke agonistic behavior (Auffenberg 1965, 1969; Coombs 1974; Grant 1936a; Winokur 1973).
F. All age classes and both sexes exhibit agonistic behavior to some degree; however, combat is minimized because male tortoises usually avoid each other (Berry 1986b).
G. Agonistic behavior may be used to establish dominance-subordinance relationships; to defend burrows, territory, or home range; or to compete for breeding opportunities (Coombs 1977a; Douglass 1976).
H. Combat was more frequent in August and September (Burge 1977a).
I. Agonistic encounters may begin at the burrow, last 5 to 25 minutes, cover 20 to 60 m, and end with the subordinate traveling 25 to 40 m away, then withdrawing into his shell. The dominant tortoise returns to the burrow (Berry 1986b; Bickett 1980a; Burge 1977a).
J. When two males meet, they begin head bobbing and separate a short distance. The males stand as high as possible and make short charges at each other with their heads partially withdrawn into their shells. The combat involves ramming and butting with the gular projections, head bobbing, and biting. The gular projections and often the head and front legs are used to try to flip the opponent over. The combat continues until a tortoise is flipped on its back or it retreats (Baerwald 1971; Camp 1916; Carpenter and Ferguson 1977; Cassell 1945; Grant 1936a).
K. Specific observation: during combat between two males, one tortoise used his gular forks to flip the other over 11 times. The prone tortoise was sometimes flipped upright again by his opponent. Whenever he managed to right himself or was flipped upright, his legs and head were bitten by the dominant tortoise. The dominant tortoise continued head bobbing throughout the combat. Both tortoises panted heavily and emitted short, high-pitched sounds. The fight ended with the subordinate upside-down and withdrawn into his shell. The dominant male quickly moved to his den (Vaughan 1984a).
L. Desert tortoises may also show aggressive behavior when defending nests. Females are known to attack Gila monsters raiding their nests by quickly advancing to the entrance of the burrow and wedging themselves in the opening to discourage the Gila monster from entering (Barrett and Humphrey 1986; Esque and others 1990a; Vaughan and Humphrey 1984).
M. Captive females may be aggressive before egg laying (Nichols 1953).

VI. **Feeding behavior:** see Feeding behavior, diet and nutrition.

VII. **Drinking behavior**

A. When drinking, a tortoise immerses its lower jaw in the water and allows water to enter the mouth passively. When its mouth is full, the tortoise closes its jaws and forces the water into the esophagus with its throat muscles. The process is repeated several times (Mahmoud and Klicka 1979).

B. Captive tortoises have been known to drink constantly for half of an hour (Cochran 1952), increasing their body mass by up to 45 percent (Miller 1932).

C. Desert tortoises have been observed to thrust their head into loose earth to drink water just below the surface (Auffenberg 1963).

D. Tortoises frequently drink from puddles and water in rock depressions after a rain (Bailey 1928; Coombs 1977a,c).

E. Desert tortoises appear to have the ability to sense oncoming rain and congregate at catchment basins prior to or at the onset of rainfall. They travel in a straight line to these locations and appear to be familiar with them (Berry 1974b; Medica and others 1980).

F. Tortoises anticipated rain and dug shallow basins in the soil before rain began (Nagy and Medica 1977, 1986).

G. In southern Nevada, 10 of 11 tortoises emerged from their burrows during the rain. Some constructed shallow basins in the soil, which caused rainwater to pool. Others walked straight to preexisting basins to drink (Nagy and Medica 1986).

H. Tortoises emerged from burrows to dig depressions prior to rainstorms in temperatures as cool as 2.8 °C (Medica and others 1980; Minnich 1982).

VIII. **Sleeping behavior:** Tortoises sleep with head and neck extended and resting on the ground. The legs may also be extended from the shell (Grant 1936a).

IX. **Digging behavior:** see Burrows and Dens.

X. **Thermoregulatory behavior:** see Physiology, Thermoregulation.

XI. **Audition**

A. Many turtle species are sensitive to airborne sounds, especially those below 1,000 cycles per second (Campbell 1967; Wever and Vernon 1956).

B. Desert tortoises respond to ground vibrations (Miles 1953).

C. Middle and inner ears are well developed (Miles 1953).

D. Tortoises responded to the sound of a vehicle horn at distances greater than 50 m (Coombs 1977a).

XII. **Olfaction**

A. Smell may possibly be the desert tortoise's strongest sense; it is important in feeding (Obst 1986).

B. Well-developed olfaction may be necessary in arid environments where plants give off few chemical particles (Eglis 1962).

C. Olfactory cues are used during courtship and other social interactions, pheromones are produced by the cloaca and chin glands. *Gopherus polyphemus* uses a scale on the forelimb to spread the scent of the chin gland during courtship (Auffenberg 1966b, 1969; Berry 1986b; Manton 1979; Weaver 1970).

D. Fecal pellets and urine are probably important olfactory territorial markers (Auffenberg 1977; Patterson 1971a,b).

E. During olfaction, the head is lowered to the substrate or object being investigated so that the snout makes contact (Berry 1972).
F. Desert tortoises may touch the snout to the substrate every 1 to 3 seconds. When traveling, they may pause occasionally to sniff the ground (Berry 1972).

XII. **Vision**

A. Turtles have a high degree of color discrimination and can detect very subtle differences in the red spectrum. Their color sensitivity even extends into part of the infrared portion of the spectrum (Obst 1986).
B. The eye of *Gopherus agassizii* is modified for vision in air. All of the receptor cells are cones (Campbell 1969; Walls 1942).
C. *Gopherus* species are attracted to the colors of their food items. Captive desert tortoises preferred pink or yellow when fed food items representing those colors. Texas tortoises prefer green food items when succulent vegetation is available in the spring, and red when opuntia fruit ripens in late summer (Auffenberg 1969; Mahmoud and Klicka 1979; Olsen 1971).
D. *Gopherus agassizii* has good color vision with a color range that is probably similar to that of humans. Vision is important in finding foods from afar (Miles 1953; Murphy 1973; Obst 1986).
E. Distance vision: a tortoise spotted and reacted to a human over 60 m away (Coombs 1974, 1977c).
F. Depth perception in *Gopherus* spp. is well developed. Depth perception plus a forelimb tactile sense may help tortoises keep from falling (Patterson 1971c).

XIII. **Vocalization**

A. Desert tortoise vocalizations differ under different circumstances; some sounds have been described as moans, whistles, hisses, grunts, pops, hips, whoops, faint mews, and high, thin screams (Campbell 1967).
B. Vocalization is species specific and may be important in individual recognition and behavior. Vocalization is especially common during mating and combat, but also has been reported during foraging (Auffenberg 1977; Grant 1936a; Nichols 1953; Van Denburgh 1922b).
C. Complexity and frequency of vocalization increases with age (Patterson 1971d, 1976b).
D. Sound characteristics of tortoise vocalizations.
    a. Sixty-four to 500 hertz: tortoises probably hear well for sound below 1,000 hertz (Campbell 1967; Patterson 1976b).
    b. Most sounds exhibited two or three harmonics (Campbell and Evans 1967).
    c. Calls were 5 to 15 dB above the ambient sound, which was 75 to 87 dB (Campbell and Evans 1967).
    d. Fundamental frequency varies at least an octave (Campbell and Evans 1967).
E. Specific vocalizations and their context
    1. Hisses (Patterson 1976b).
        a. During mating (sound emitted by female).
        b. During combat.
        c. When a adult was turned upside-down.

    d. When a sleeping tortoise was grabbed.
2. Grunts (Patterson 1976b).
    a. During mating (sound emitted by males).
    b. During combat.
    c. When a sleeping tortoise was grabbed.
3. Pops and poinks (Patterson 1976b).
    a. When tortoise was upside-down: call caused dominant male to assist in righting tortoise.
    b. When a sleeping tortoise was grabbed.
4. "Low piteous cry": a gular pumping action was observed and the mouth was kept closed (Campbell and Evans 1967).
    a. While trying to climb out of a sink.
    b. When tortoises were trying to right themselves.
    c. While tortoises were resting.
5. Long "drawn out moan" (Campbell and Evans 1967; Patterson 1976b).
6. "High thin scream": could be an alarm call (Nichols 1953).
    a. When a tortoise was caught in a towel in a box.
    b. When a tortoise was pinned in a sink.
    c. When a tortoise was turned upside-down.
7. Whistling: sound made when screen door was locked and tortoise could not push it open (Campbell 1927).

F. Significance
    a. A short "poink" emitted by an overturned subordinant male may cause the dominant male to retreat or to help turn the subordinant male upright (Auffenberg 1977; Brattstrom 1974; Patterson 1971d, 1976b).
    b. A long, drawn-out call may elicit a feeding response or fighting behavior (Patterson 1976b).
    c. Vocalizations may aid in individual recognition and seem to be most important when made to an unfamiliar tortoise (Berry 1986b).

XIV. **Righting reflex**

A. Healthy tortoises are normally able to right themselves after being turned over on their back (Ashe 1970; Woodbury and Hardy 1948a).

B. All of 14 tortoises overturned were able to right themselves (Coombs 1974).

C. Desert tortoises can right themselves on a flat surface (Ashe 1970).

D. Description of righting reflex (Ashe 1970; Carpenter and Ferguson 1977).
1. One foreleg is extended into the air and the other is used to paw at the ground.
2. Head and limbs are extended toward the ground.
3. Head is used as a lever to apply pressure to tilt the tortoise.
4. When the extended foot reaches the ground, the tortoise is able to right itself.
5. If a tortoise is overturned and cannot right itself, it may die from suffocation or congestion of blood in the lungs due to pressure of the internal organs against the thin, flat lungs (Coombs 1974; Jaeger 1950).
6. May be unable to right itself if at critically high temperatures (Hutchison and others 1966).

XV. Locomotion

A. Mechanics: *Gopherus* spp. walk mainly on the claws of their front feet, but the hind feet are placed flat on the ground with toes directed forward and slightly outward. As the body pivots forward during limb retraction, the heel of the hind foot swings medially so that the toes point outward. By the end of the contraction, the hind foot is far forward. After retraction the hind leg is pushed back and fully extended, lifted off the ground and brought forward again (Ditmars 1907; Walker 1973, 1979).

B. Rate
   1. 219.4 to 482.8 m/hr (Woodbury and Hardy 1948a).
   2. 6.1 m/min (Leopold 1961).
   3. 0.13 to 0.30 mi/hr (Leviton 1970).
   4. Adults average 5.3 m/min (range 2.0 to 7.6 m/min) (Burge 1977d).
   5. Hatchlings travel 0.3 m in 25 to 35 s (Coombs 1977c).
   6. Up to 0.26 m/s when frightened. Under normal conditions, 0.76 to 0.152 m/s (Coombs 1977c).
   7. Speed depends on type of activity and difficulty of terrain (Coombs 1977c).
   8. Young tortoises traveled 15 to 45 m on a warm day, and a larger tortoise traveled more than 548 m on a single day; tortoises typically travel 150 to 457 m per day depending on temperature (Smith 1978).
   9. Actual rate of travel has been found to be 20 ft/min (Pope 1939).

C. Distance
   1. Averages 437 to 656 m or more per day. Adult male travelled more than 1,441 m in spring. Hatchlings or juveniles generally travel less than 50 m per day (Berry 1974b; Coombs 1977c).
   2. Average distance for trips in Nevada study was 143.0 ± 12.0 m for males (range 23.0 to 381.0 m) and 147.0 ± 9.0 m (range 49.0 to 366.0 m) for females (Burge 1977d).
   3. Movements are usually restricted to loops within a few hundred meters of burrows (Berry 1975a).
   4. Released captives moved just a short distance away from release site in the course of a year (Crooker 1971).
   5. Over a 4-year period, two tortoises were found close to the original capture site; one was found not more than 200 yd away, and later 150 yd away; another tortoise was found 300 yd from the original capture site (Bogert 1937).

D. Tortoises may ram objects in their path rather than go around them (Cassell 1945).

E. Climbing ability
   1. Can climb steep terrain and reach winter dens near the top of steep banks (Coombs 1977a; Woodbury and Hardy 1948a).
   2. Tortoises typically inhabit steep, rocky slopes in Arizona. Tortoises were seen dropping off rock shelves, sliding through narrow crevices, and even climbing into a *Lotus* sp. forb to forage in its upper branches (Schneider 1980a).

F. Swimming ability
   1. Gopher tortoises (*Gopherus polyphemus*) float high in the water and are good swimmers. They have been seen swimming across channels over 18 m wide (Brode 1959; Patterson 1973a).

2. Desert tortoises are poor swimmers (Grant 1960a; Woodbury and Hardy 1948a).
3. Desert tortoises will eventually drown if forced to swim. They have been found drowned in bird guzzlers (Coombs 1977c; Woodbury and Hardy 1948a).

XVI. **Orientation**

A. Desert tortoises appear to have good orientation abilities and are able to find their way back to burrows each night. They also remember the locations of mineral licks and drinking sites and will travel to them in a straight line (Berry 1974b, 1986b; Grant 1936a).

B. Orientation probably involves visual, chemical, and tactile cues that are learned and remembered (Auffenberg 1969).

C. Desert tortoises may use a time-compensated solar compass to establish contact with landmarks. The landmarks themselves may be used for precise information (Gourley 1979; Vaughan 1984a).

XVII. **Learning**

A. Reptiles perform well in learning experiments at optimum temperatures and are able to learn mazes and similar tasks rapidly (Brattstrom 1974; Burghardt 1977).

B. Reptiles exhibit learned behavior in homing, territorial boundaries, food preference, and dominance relations (Burghardt 1977).

C. Desert tortoises exhibit learned behavior and are able to learn and remember specific locations (Berry 1986b): see Behavior, Drinking behavior, and Orientation.

XVIII. **Daily and seasonal activity patterns**

A. Daily activity patterns.
1. During cooler months daily activity is unimodal; tortoises are active at midday. During hot periods activity becomes bimodal, and tortoises are active in morning and late afternoon (Auffenberg and Iverson 1979).
2. When temperatures become too high tortoises seek shade beneath vegetation. As ambient and ground temperatures continue to rise, tortoises take shelter in summer burrows (McGinnis and Voigt 1971).
3. During favorable temperatures when food is abundant, tortoises are active much of the day and possibly at night (Dodd 1986; Jaeger 1922).
4. In hot months of the summer, desert tortoises are active mainly early in the morning and emerge from dens as early as 5 a.m. (Berry 1975a; Hohman and Ohmart 1980; McCawley and Sheridan 1972).
5. Tortoises are diurnal and return to summer dens each night; however, rainstorms or hot weather may trigger nocturnal activity (Stephens 1914; Grant 1936a; Luckenbach 1982).
6. Of tortoises captured, 38.6 percent were walking or standing, 19.0 percent were basking, 23.1 percent were inside, exiting or entering burrows, 14.0 percent were feeding, and 1.9 percent were interacting with other tortoises or animals (Berry and Turner 1984).

B. Daily movements: see Behavior, Locomotion

C. Seasonal activity patterns

1. Tortoises are active when green succulent vegetation is available; peak activity corresponds with annual blooms (Berry 1978a; Luckenbach 1982).
2. Peak activity is in late spring in northern parts of range and early fall in the south. Activity corresponds with peak rainfall; dry parts of year are spent in estivation (Jennings 1985; Minnich 1977).
3. Mexican and southern Arizona populations may be active year round in response to mild winters and year-round forage availability (Auffenberg 1969; Weaver 1970).
4. On Tiburon Island in Mexico, tortoises are most active during the cool fall season (Bury and others 1978; Reyes Osorio and Bury 1982).
5. In southern Nevada individual tortoises were in hibernation 151 days of the year and in estivation 30 days of the year. They were active 15 of the 61 days in spring and 30 of the 120 days of summer and fall. Only 29 hours or 0.3 percent of the year was spent feeding (Nagy and Medica 1986).
6. Tortoises in Kern County, CA were actively foraging 0.89 of the daily activity-time budget in early May and 0.12 of the total daily time budget; late June demonstrated foraging 0.97 of the daily activity-time budget but only 0.04 of the daily time budget. Over the year, tortoises spent 0.015 of the annual time budget actively foraging (Marlow 1979, 1982).
7. Tortoises in the northern part of range are occasionally active in the winter in response to warm temperatures (Coombs 1977c; Sheppard 1980).
8. After nesting, females spend more time underground than males. In August 1973, a study found 80 percent of males were active, but females were largely inactive and underground (Luckenbach 1982).
9. Midday dormancy took 33 percent of the daily time budget at the peak of midday dormancy in late June (Marlow 1982).
10. Beaver Dam Slope, UT.
    a. Tortoises were most active in spring. Tortoises emerged from winter dens between 9 and 10 a.m., returning late in afternoon when temperatures began to exceed 90 °F. Many tortoises left winter dens and dug holes at foraging areas for shelter during the summer. Tortoises returned to winter dens in September (Coombs 1974).
    b. Peak activity was in early June; by late June tortoises spent most of their time in summer burrows. Highest activity is at 70 to 79 °F (Minden 1980).
    c. Time spent foraging (days foraging/month) was lowest in January, February, November, and December and greatest in April, May, June, August, and September (Coombs 1977c).
11. Tortoises are active for a maximum of 7 out of 10 days (Huey 1982).
12. Migration: described as yearly movements over short distances between hibernacula (winter dens) and feeding areas. It may be controlled by seasonal rhythms, including temperature and photoperiod (Coombs 1977a; Gourley 1979).

a. Beaver Dam Slope, UT: winter is spent hibernating in winter dens in arroyo banks. In early spring tortoises forage near the mouths of winter dens. During late spring and summer they migrated to grassy flats to forage, and construct summer burrows beneath shrubs. They returned to winter dens in September (Cochran and Goin 1970; Minden 1980; Woodbury and Hardy 1948a).
b. Sonora, Mexico: tortoises may be nomadic most of the year (Auffenberg 1969).

13. Activity patterns probably depend on ambient and substrate temperatures (Bickett 1980a; Gregory 1982).

D. Spring emergence from winter dens
1. Generally occurs in late February or early March (Gates 1957; Miles 1953).
2. Northwest Mojave Desert, CA: mid-February to late March (Berry 1974b).
3. Arden study site, NV: March 1 to April 20 (Burge 1977d).
4. Beaver Dam Slope, UT: March to late April (Coombs 1977a; Woodbury and Hardy 1940, 1948a).
5. Spring activity includes basking, foraging, social interaction and reproduction. Activity is unimodal when temperatures are cool (Berry 1974b; Burge 1977d; Coombs 1977a).
6. Females and juveniles stay near the winter dens for much of the active period; males venture further from dens as temperatures increase (Coombs 1977a,c).

E. Summer activity
1. Most of the time is spent in summer burrows (Berry 1974b; Coombs 1977c).
2. In the Mojave Desert, CA, activity is unimodal and restricted to early morning (Berry 1974b).
3. In southern Nevada, activity is bimodal from May to September with peak activity in July (Burge l977a).
4. At Beaver Dam Slope, UT, tortoise activity is bimodal with tortoises active in early morning and late evening (Coombs 1977c).
5. Summer activity is bimodal, or sometimes restricted to early morning, and includes foraging, traveling, basking, and some reproduction (Berry 1974b; Burge 1977d).
6. Estivation occurs in the hottest and driest period of the summer and usually takes place after annual forage plants have dried up. Estivation reduces energy expenditure and dehydration and may be prolonged during drought (Coombs 1977a; Nagy and Medica 1986).

F. Late summer and fall activity
1. Tortoises increase activity and foraging when summer temperatures become less extreme and when they are preparing for hibernation (Coombs 1974).
2. Activity becomes unimodal again during summer and fall (Burge 1977d).
3. On Beaver Dam Slope, UT, tortoises return to winter den areas later in the season (Coombs 1977c).
4. Hatchlings may emerge and social interactions may increase during late summer and fall (Coombs 1977a; Luckenbach 1982).

G. Hibernation
1. Time of hibernation
   a. Mojave Desert, CA: between late September and mid-October (Berry 1975b).
   b. Southern Nevada: October 20 to November 11 (Burge 1977d).
   c. Beaver Dam Slope, UT: early to midautumn or about the second week of October (Coombs 1977c; Woodbury and Hardy 1948a).
   d. Tiburon Island, Mexico: October (Bury and others 1978).
   e. Sonora, Mexico: may be active most or all of the year (Auffenberg 1969).
   f. Beaver Dam Slope, UT, congregated in mid-September to enter hibernation in communal dens (Woodbury and Hardy 1948a).
2. Tortoises may emerge briefly on warm days to forage or move to a new den (Auffenberg and Iverson 1979; Woodbury and Hardy 1948a).
3. Tortoises enter hibernation later and emerge earlier in warmer climates and may not hibernate at all in the warmest parts of their range (Auffenberg 1969; Voigt 1971).
4. Hatchlings either dig a burrow or find an existing burrow and enter dormancy shortly after hatching (Luckenbach 1982).
5. Hibernating position: head is almost completely retracted and legs retracted partly into the shell (Woodbury and Hardy 1948a).
6. Cold temperatures and changes in atmospheric pressure may trigger hibernation. Captive tortoises may or may not hibernate when kept at constant temperatures (Clarke 1968; Coombs 1977a; Gregory 1982).

XIX. **Spatial relations**

A. Home range
1. Defined as the activity area where tortoises forage, travel, and burrow (Bury 1982a).
2. Depends on age, size, and sex of the tortoise and the availability of forage (Berry 1973b).
3. Variation in home range.
   a. During years with more precipitation and abundant forage tortoises demonstrate larger home ranges (Coombs 1974; Vaughan 1984a).
   b. Adults demonstrate larger home ranges than young tortoises (Berry 1978a).
   c. Males have larger home ranges than females (Berry 1973b).
   d. Home range for five tortoises did not vary significantly from that of nine females during a study in the Picacho Mountains of Arizona (Barrett 1985, 1990).
   e. During their entire lives tortoises rarely move more than 3.5 km from the nest where they hatched (Auffenberg and Iverson 1979).
   f. Home range size was not correlated with maximum carapace length or the number of observations in the Picacho Mountains of Arizona (Barrett 1990).
4. Specific home ranges (home range determination varies among studies).
   a. Beaver Dam Slope, AZ (Hohman and Ohmart 1980).

b. Beaver Dam Slope, AZ, Littlefield Study Plot, mean home range for 1990 was 3.663 ha (n = 10) (Esque and others 1991).
c. Picacho, AZ (Vaughan 1984a).
d. Picacho Mountains, AZ, mean home range from 1982 to 1983 was 19.07 ± 4.63 ha (n = 14) (Barrett 1985, 1990).
e. Ivanpah Valley, CA (Turner and others 1982).
f. Western Mojave Desert, CA (Marlow 1974).
g. Arden, NV (Burge 1977d).
h. Beaver Dam Slope, UT (Coombs 1974; Minden 1980; Woodbury and Hardy 1948a).
i. City Creek study plot, UT, mean home range for 1989 was 7.88 ha and for 1990 was 12.079 ha (n = 10 for each year) (Esque and others 1990a, 1991).
j. Paradise Canyon, UT (Coombs 1977c).

5. Only tortoises that use summer burrows instead of pallets have well-developed home ranges (Auffenberg and Iverson 1979; Auffenberg and Weaver 1969).
6. Tortoises on Beaver Dam Slope, UT, have two home ranges, a large one corresponding to warm weather forage areas on desert flats and a smaller one near winter dens (Auffenberg 1969).
7. Home ranges in the Beaver Dam Slope are usually linear or triangular and very rarely extend more than 0.48 km from winter den areas (Coombs 1974, 1977a,c).
8. Home ranges of individual tortoises usually overlap (Burge 1977d; Woodbury and Hardy 1948a).
9. Home ranges may be marked with scat (Coombs 1977a,c; Patterson 1971a).

Management

The management and maintenance of desert tortoise populations depends upon the cooperation of government agencies, universities, and community planners. Some recommendations have been addressed for the management of the desert tortoise on public lands (Spang and others 1988). The following discussion details the management of the desert tortoise with consideration for methods of monitoring and management.

I. **Population estimation** (Turner and Berry 1984)
   A. Line transects
      1. Berry (1978b)
         a. Length is 2.4 km, density may be varied.
         b. All tortoise sign is recorded.
         c. Yields information on relative abundance of tortoises in a relatively small amount of time.
      2. Berry and Nicholson (1984b)
         a. Length is 2.4 km.
         b. Width is 10 yd (9.14 m).
         c. Count burrows, scats, tracks, and live and dead tortoises.
         d. Estimate population numbers based on known population of other areas that have been surveyed.
         e. Corrected sign [CS] = 0.3 (TC) + 1.69, where TC = live tortoise count.
      3. Turner and others (1982)
         a. Three belt transects 9 m wide and 805 m (0.5 mi) long arranged to form an equilateral triangle.

b. Convert sign counts to density estimates based on known density elsewhere.

B. Quadrat and grid system (Bury and Luckenbach 1977)
   1. Used to accurately determine population characteristics while taking into consideration the effects of regional variations in environmental conditions.
   2. Use 25 to 100 ha quadrat subdivided into 1 ha sections.
   3. Search method involves walking along one edge, then criss-crossing along parallel lines 5 m apart so that every part of the grid is viewed from two angles.
   4. Record tortoise sign and related information within each section on a map and in field notes.
   5. Mark and record information on all tortoises located.
   6. Quadrats can be used for long-term monitoring of populations.
   7. Information on tortoise habitat, vegetation, topography, burrows, spatial distribution, and population density is recorded.
   8. Shell measurements, body mass, age and sex composition, and other characteristics of the population are also recorded.

C. Permanent study plots (Berry 1978b, 1984a)
   1. Size is 2.59 square kilometers (1 square mile).
   2. An effort is made to mark all tortoises in the study plot within a 30-day period in the spring.
   3. Tortoise sign is recorded.
   4. Information on population density, sex ratios, age class structure, size of tortoises, burrow habits and feeding habits is acquired.

D. Mark and recapture estimation
   1. Lincoln index $N = Mn/m$: where N is total population, M is number marked and released, n is total capture, and m is number of marked recaptured (Graham 1979).
   2. Schnabel formula

   $$\frac{P = Sm\,(u + r)}{Sm}$$

   where S represents Sigma; P = population estimate; m = number captured, marked and released; r = number captured each day; and u = number of unmarked captured each day (Graham 1979).
   3. Comparison of Lincoln Index, Schnabel Method, and Stratified Lincoln Index (Schneider 1980b).

E. Transects at Ivanpah Valley, CA, yielded four equations (Turner and others 1982).
   1. $b = 0.14m + 0.7$
   2. $m = 3.5b + 7.70$
   3. $m = 1.7TCS + 3.98$
   4. $TCS = 0.36m + 1.7$

   Where b = burrow sign, m = tortoises marked, TCS = total corrected sign.

F. Based on 113 strip transects in and adjacent to Chocolate Mountain Aerial Gunnery Range, CA (Berry and others 1983b); $D = 7.09CS + 19.33$, where CS = corrected sign and D = density. Tortoise sign was represented by burrows, scats, live tortoises, shells, tracks, courtship rings (depressions left in the sand after copulation), and drinking sites.

G. Tortoise tracks are commonly used as sign; they have the appearance of parallel rows of rounded dents and are usually seen only in sand. Tracks can indicate direction of travel, courtship and aggression, mating, feeding, and encounters with predators (Berry 1973b; Stebbins 1954, 1966, 1985).
H. Problems with surveys: tortoise sign must be calibrated with sign counts of areas with known tortoise densities; however, sign frequency varies with season, environmental conditions, and vegetation types, making accurate estimates difficult (Berry 1986c; Fritts 1985a; Fritts and Scott 1984; Luckenbach 1982). Juvenile tortoises are under represented in surveys (Berry and Turner 1984). Methods may not be reliable on variable terrains, such as steep slopes in Arizona (Burge 1980). A 60-day survey of 1 square mile may significantly underestimate tortoise densities and the proportion of small tortoises in a population (Shields 1980).

II. **Marking**

A. Scute marking

1. Scute branding (Plummer 1979; Woodbury and Hardy 1948a) is a long-term marking method, but branding too deep may lead to parasitism by adobe ticks and mold; in some cases regeneration may obscure the brand.
2. Paint on the posterior carapace usually wears off in 1 to 2 years due to weathering and abrasion (McCawley and Sheridan 1972; Woodbury 1953; Woodbury and Hardy 1948a).
3. Engraving marks in the carapace (Cowan 1972).
4. Notching marginal scutes with a triangular file, then filing with a square-edged file or marking with a hacksaw. A permanent mark occurs if shell is well ossified (Bury and Luckenbach 1977; Coombs 1973, 1974; Woodbury 1953).
5. Drilling holes through marginal scutes (Crooker 1971; Plummer 1979).
6. Drilling holes through marginal scutes and wiring on metal identification tags (Crooker 1971; McCawley and Sheridan 1972).
7. Drilling holes through posterior marginal scutes and attaching a pair of color-coded plastic beads for identification (Galbraith and Brooks 1984).

B. Radio telemetry

1. Burge (1977d)
   a. Radio-transmitter package consists of a battery pack, transmitter, and 30-cm wire antennae.
   b. The package's mass is 191 g, with a battery mass of 120 g.
   c. Attached to fifth vertebral scute with contact cement and fiberglass woven tape.
2. Schwartzmann and Ohmart (1977)
   a. Transmitter with lithium sulfate battery, antenna system of helical wire, and copper ground plate.
   b. Multichannel receiver with four-element yagi directional antenna.
   c. Transmitter and battery attached to carapace of adult tortoise with epoxy, on either side of the nuchal scute. Ground plate attached to right marginal scutes; antenna attached to left marginals, pygals, and vertebrals.

III. **Recapture**

A. Out of 79 marked tortoises, 25 were recaptured over a 4-year period on the Beaver Dam Slope, UT (Coombs 1977a).

B. At Paradise Canyon, UT, 72 marked tortoises were recaptured 91 times (Coombs 1977a).

C. In southern Nevada, 126 tortoises were marked and released; they were recaptured 696 times; this total does not include radio relocations for tortoises with radio transmitters (Burge and Bradley 1976).

D. In Pinal County, AZ, out of 11 tortoises, 11 tortoises with radio transmitters were recaptured over a 3-year period (Schwartzmann and Ohmart 1977).

E. At Ivanpah Valley, CA, 75, of 84 tortoises with transmitters were recaptured (Berry 1983; Medica and Lyons 1982).

F. Removal from burrows (Medica and others 1986).

1. Traditional method is to use hook or stick in attempt to pull tortoises out.
2. Dramatic increase in recapture success obtained by tapping on the carapace of the tortoise three to four times with a long stick.
3. If burrow is too long or crooked, researchers can strike the roof, floor or burrow entrance, then move away from the burrow.
4. The tortoise will turn in burrow and emerge within a brief time.
5. Eighty-two percent of the tortoises tapped in Ivanpah Valley, CA, emerged from their burrows.

IV. **Conservation**

A. Conservation organizations

1. The Nature Conservancy has worked with the Bureau of Land Management to increase protected habitat for the desert tortoise, especially on the Desert Tortoise Natural Area in California, which now contains 2,773 acres.
2. Desert Tortoise Council, Desert Tortoise Preserve Committee (Berry 1989b; Forgey 1977, 1982; Radtkey 1978; Stockton 1978, 1980, 1981, 1983, 1984a,b; Turner 1986).
   a. The Desert Tortoise Council was formed in 1976 to establish the Desert Tortoise Natural Area in California.
   b. The primary goal is to preserve natural area for protection of desert tortoise habitat. Other goals include educating the public and raising funds for fencing and for purchasing private land.
   c. The Desert Tortoise Natural Area was set up to preserve prime habitat of the Fremont-Stoddard tortoise population and is closed to off-road vehicles and grazing.
3. Tort-group (Nevada): primary goals are protection of free-living tortoises and their habitat, and responsible care of captive tortoises (Davis 1984).
4. San Diego Turtle and Tortoise Society (Herpetological Review 1986): emphasis is conservation and preservation of declining populations.
5. The Defenders of Wildlife, National Resource Defense Council, and Environmental Defense Fund have petitioned the U.S. Fish and Wildlife Service to list the desert tortoise as an endangered species (Turner 1986).

6. The Bureau of Land Management currently manages most of the desert tortoise habitat and has been required, following lawsuits by environmental groups and congressional orders, to address the deterioration of public lands and analyze alternative grazing levels and land-use practices. However, most tortoise habitat on Bureau of Land Management land is still grazed, and desert tortoise populations continue to decline (Edelson 1983; Foreman and others 1986).

V. **Management programs and recommendations**

A. Preserves

1. California (Berry 1989b)
   a. Desert Tortoise Research Natural Area: see Management, Conservation, Desert Tortoise Council, Desert Tortoise Preserve Committee.
   b. Chuckwalla Bench Area of Critical Environmental Concern.
2. Utah
   a. In 1979 the Bureau of Land Management fenced an area on the Beaver Dam Slope to protect vegetation, tortoises, and other wildlife. In 1983, the fenced area was reduced to about 1,230 ha due to grazing interests. The area is fenced and closed to grazing. Vehicles are restricted to roads, drilling is not allowed in sensitive areas and no surface-disturbing activity is allowed from April to September (Douglas 1980; Good 1982; Rowley 1977, 1981; U.S. Department of the Interior, Fish and Wildlife Service 1985a).
   b. A natural area has been proposed for Paradise Canyon (Beck 1984; Good 1982).

B. Captive release and transplant programs

1. "Insufficient information is available for *G. agassizii* in any of the movement categories at this time and intensive research efforts must be undertaken before relocation programs with predictable results can be established" (Gibbons 1986).
2. Captive tortoises released into the wild generally have poor survival (St. Amant and Hoover 1978).
3. Tortoises from captive release programs face problems such as vulnerability to predation, inability to forage in the wild, difficulty in finding suitable shelter, lack of familiarity with the area where they are released, and their attempts to return to their accustomed home. When nonnative tortoises are introduced, they may also hurt wild populations by introducing maladapted genes, competing with wild tortoises for forage, disrupting social structures, and introducing new diseases and parasites (Boynton 1970; Bury and others [In press]; Dodd and Seigel 1991).
4. Specific releases
   a. California Fish and Game authorized the California Turtle and Tortoise Clubs to relocate 30 to 35 tortoises from California City to the Lancaster area (Herpetological Review 1971).
   b. Anza-Borrego Desert State Park, CA (Cowan 1972).
      i. Three groups of captive tortoises were released in the Upper Fish Creek area in 1971 and 1972.
      ii. Seven live tortoises and three carcasses were seen several months later.

c. California Fish and Game released 66 captive tortoises on the Colorado Desert, CA, between Indio and Desert Center. After 336 days, eight were recovered, five of which were dead (Crooker 1971).
d. Thirty-three desert tortoises in a California Fish and Game rehabilitation program were released in June 1977. Survival was 64 to 76 percent the following year. A second group was released a year later with survival estimated at 89 percent (Cook and others 1978; Weber and others 1979).
e. A minimum of 145 tortoises were released between June 1973 and 1981 on the Beaver Dam Slope, UT. Most were adults from various regions (Minden and Keller 1981). Seventeen were recaptured in 1980 and 1981 (Minden and Metzger 1981).
f. Twenty-four percent of tortoises on the Beaver Dam Slope, UT, are released captives of unknown genetic origin (Dodd 1986).
g. The 0.4-ha Tin Can Enclosure on the Beaver Dam Slope, UT, provides an area with natural winter den sites and habitat for rehabilitation of captive tortoises before they are released in the wild. Tortoises from the enclosure were transplanted to Castle Cliff Wash (Coombs 1974, 1977c).
h. Pet owners commonly release tortoises into the wild. In California 26,500 captive tortoise permits have been issued as of 1984. The actual captive population is much greater. Many pets, including other *Gopherus* species, have been released in the wild (BLM News Beat 1973; Brode 1984).
i. The California Fish and Game Department operated a rehabilitation program for captive tortoises turned in by the public. Healthy tortoises were kept at "half-way houses;" very adaptable tortoises were released into the wild after 2 years of rehabilitation and screening. Release sites were areas with reduced populations capable of supporting larger numbers (Cook and others 1978; St. Amant and Hoover 1978).
j. California Department of Transportation transplant program (Berry 1975a,b).
   i. Tortoises from a highway corridor were transplanted.
   ii. Tortoises were transplanted to areas where tortoises naturally occur or had lived in the recent past.
   iii. Habitat closely matched original habitat.
   iv. Area must have a minimum radius of 7 to 10 km and have tortoise populations below carrying capacity.
   v. All tortoises were relocated in the same general area to minimize mixing gene pools.

5. "Rehabilitation" of captive tortoises increases chances of successful introduction to the wild (Cook and others 1978; Weber and others 1979).
6. Tortoises should be released as close to their source population as possible and should be tested to determine their genetic origin (Weinstein and Berry 1987).
7. Relocation sites should consider specific vegetational, topographic, and edaphic (related to soils) habitats utilized by the parental populations (Baxter 1988).

8. Best success rate may be obtained by relocating wild tortoises to areas with depleted populations. A population at Big Wash on the Beaver Dam Mountains, UT, is in danger of extinction, and transplants from areas such as Paradise Canyon or Welcome Wash may be beneficial (Beck and Coombs 1984; Smith 1978).
9. Breeding efforts may be enhanced through the use of oxytocin to induce oviposition and obtain viable eggs. A tortoise was observed digging a nest 0.5 to 3 hours after an oxytocin injection (Ewert and Legler 1978).
10. Survival is enhanced if tortoises are released during early afternoon at the time of normal spring emergence (Cook and others 1978).

C. Habitat management
1. Management must recognize that off-road vehicles have widespread impact and are irresponsible for negative effects of desert wildlife (Bury and others 1977).
2. Roads
    a. Place low fences along freeways and roads (Bury and Marlow 1973).
    b. Establish road signs to alert motorists to the presence of tortoises (Bury and Marlow 1973).
    c. Fences along roads should be 40 to 50 cm high and interspersed with culverts to allow tortoises to cross the road safely. Tortoises eventually become familiar with culverts (Fusari 1981, 1982; Fusari and others 1981).
    d. Fencing results in restoration of critical habitat area near roads and minimizes road deaths (Fusari and others 1981).
3. Grazing: see also Habitat deterioration, Livestock grazing.
    a. Ninety-two percent of Bureau of Land Management lands in the Western States are grazed. Most land is in poor to fair range condition. In 1978 the Federal government spent $12,000,000 more on grazing land lease programs than it made from grazing fees. However, the Southwest deserts are very fragile and unproductive; and Bureau of Land Management land in the Southwest produced only 0.7 percent of the nation's beef. Public interest would probably be better served by considering more ecological returns over such unprofitable economic returns (Handwars 1980; Hughes 1983; Johnson 1983; Rice and others 1979; U.S. Department of the Interior, Bureau of Land Management 1978; Wagner 1978).
    b. The Bureau of Land Management must manage for annuals and perennial grasses rather than browse species (Coombs 1979).
    c. Grazing systems: ephemeral use is most common in the desert but is very damaging because tortoise growth and reproduction depends on years of above average annual forage; rest rotation systems ignore fluctuating desert environment; continued use is devastating to tortoises for obvious reasons. Must develop new types of grazing systems with the objective of maintaining tortoise populations (Medica and others 1975).
    d. Grazing programs on tortoise habitat must take into account the diet of tortoises, the condition of specific populations, the

amount of forage to be allotted to tortoises by season, the amount of forage needed for reproduction, mortality caused by livestock grazing, effects of livestock on tortoise behavior, and effects of livestock grazing on vegetation (Medica and others 1975).

e. Good management programs should monitor season of use, hold livestock utilization levels below 50 percent in all areas, and permit flexibility in the number of grazing animals to prevent overgrazing in periods of low precipitation (Hughes 1983).

f. Trespass grazing should be eliminated and some areas should be left ungrazed year after year (Nicholson and Humphreys 1981).

g. Current provisions that allow extended grazing at times of abundant annual forage must be eliminated, since tortoises depend on above average years for growth (USDI Fish and Wildlife Service 1985a).

h. Specific recommendations

    i. Little Ship Wash Site, AZ: close areas with high density tortoise populations to livestock grazing. Economic impact on lessees would be slight (Schneider 1980a).

    ii. Beaver Dam Slope, AZ: grazing should be rotational, with less than 50 percent utilization. All cattle should be removed by March or removed altogether (Hohman and Ohmart 1980).

    iii. Beaver Dam Slope, UT: use rest rotation to maintain spring annual growth; reduce number of livestock, and locate watering sites away from areas with high density tortoise populations. Enclosures should be constructed to protect certain areas (Coombs 1977c; Smith 1978).

    iv. Cattle must be main emphasis of management of the Beaver Dam Slope, and it may be that only the complete elimination of grazing will be effective in restoring the vegetation and habitat necessary to sustain a viable tortoise population (Coombs 1977b; Johnson 1983; Smith 1978).

D. Habitat modeling

1. A model implements a habitat suitability index to evaluate elevation, soil types, denning potential, vegetation, rainfall, species diversity of perennial plants, and biomass of annual plants. Habitat suitability is defined using the lowest value of all variables as a limiting factor. Management is designed to improve that variable (Schamberger 1985; Schamberger and Turner 1986).

2. By simulating environmental conditions such as soil, vegetative composition, and elevation, and including conditions such as drought and grazing, a computer model may be generated to aid in management of the desert tortoise (Wilson and Stager 1989).

E. Predator control

1. Troublesome kit foxes should be trapped and transported elsewhere (Coombs 1977a; Smith 1978).

2. Tortoises are more vulnerable to predators when forage, cover, and nutrition are lacking. The best way to reduce losses to predators is to improve range conditions (Reyes Osorio and Bury 1982).

F. Use as indicator species

1. Management of the ecosystem should focus on the desert tortoise (Dodd 1986).
2. Desert tortoises are sensitive to environmental changes and are excellent indicators of the health of desert ecosystems (Holing 1986).
3. The desert tortoise is a keystone species and has great influence on the environment and other animals, especially those that use its burrows (Dodd 1986).

G. Possible endangered status
1. Listing as an endangered species would allow better law enforcement and designation of critical habitat areas (Holing 1986).
2. The public has been hostile toward efforts to list the tortoise as an endangered species in Utah due to perceived conflicts with local grazing interests (Dodd 1980, 1981).

H. General recommendations
1. Luckenbach (1982)
    a. Prohibit or restrict off-road vehicle use in areas of high tortoise abundance.
    b. Investigate impacts of grazing.
    c. Coordinate efforts of various agencies across the entire geographic range, including Mexico.
    d. Give legal protection to habitat.
2. Sheppard (1981)
    a. Fence protected areas.
    b. Adjust grazing systems.
    c. Place livestock watering facilities 2 miles or more from critical areas.
3. Fritts (1985a,b)
    a. Develop better techniques to survey and study juvenile tortoises.
    b. Obtain better knowledge of tortoise reproduction.
    c. Learn more about habitat quality and ecological comparisons over the entire geographic range of the tortoise.
    d. Document effects of livestock grazing on the ability of tortoises to meet their nutritional requirements.
4. Dodd (1986)
    a. Set aside large tracts of undisturbed habitat with a buffer zone to counter the edge effects as land is fragmented by development.
    b. Must realize that tortoise studies today may be of artificial systems resulting from much reduced populations. Although much is unknown, management cannot be postponed until all data are in. The status of the desert tortoise requires immediate action.
5. Most general land management plans fail to adequately recognize tortoise needs. Habitat preservation must be emphasized, or public lands will be dominated by livestock grazers and well-organized recreational concerns such as off-road vehicle groups, resulting in continued deterioration (Berry 1980b; Edelson 1983).

Legal Status

The legal status of the desert tortoise is included with respect to the listing of the species and the rules and regulations governing the protection of the desert tortoise.

I. **International**: Appendix II of the International Convention of Trade and Endangered Species of Wild Fauna and Flora lists *Gopherus agassizii* and requires permits for its export (Dodd 1986).

II. **Mexico**: A permit is required to capture and export desert tortoises (Bury and Marlow 1973).

III. **United States**

- A. *Gopherus agassizii* is protected to some degree in all four states that it occupies (Berry 1979).
- B. The U.S. Fish and Wildlife Service first reviewed the status of the desert tortoise in 1978 (USDI Fish and Wildlife Service 1978).
- C. On August 14, 1980, the U.S. Fish and Wildlife Service listed the Beaver Dam Slope, UT, population of desert tortoises as threatened and designated 90 km^2 of critical habitat (Dodd 1980, 1981; Minden 1980).
- D. The U.S. Fish and Wildlife Service listed the desert tortoise under emergency rule and protected the tortoise for 240 days effective from August 4, 1989 through April 2, 1990. This ruling protected the desert tortoise throughout its range in the Mojave Desert. The concurrent status of the Beaver Dam Slope population as threatened with critical habitat in 1980 did not change at this time (USDI Fish and Wildlife Service 1989).
- E. There was much opposition to the listing and critical habitat proposal by local grazing and special interest groups. An aide from Senator Hatch's office threatened the existence of the Federal endangered species program if the desert tortoise was not removed from the threatened species list (Dodd 1981; USDI Bureau of Land Management 1980b).
- F. In September 1985, the Defenders of Wildlife, Natural Resource Defense Council, and the Environmental Defense Fund petitioned the U.S. Fish and Wildlife Service to list the desert tortoise as endangered under the Endangered Species Act of 1973, and cited evidence in Kristin Berry's report on the status of the desert tortoise in the United States. The Fish and Wildlife Service responded to the proposal by stating that the endangered status was warranted but more urgent listing proposals precluded it. Pressure from grazing interests and lack of funds and staff may have prevented the listing (Berry 1984; Dodd 1986; Holing 1986; USDI Fish and Wildlife Service 1985b).
- G. National parks, national monuments, and State parks are the only areas where tortoises receive complete protection (Dodd 1986).

III. **Status by State**

- A. Arizona: "Desert tortoises held legally prior to January 1, 1988, may be possessed, transported, and propagated. Possession limit is one desert tortoise per person. Progeny of lawfully held desert tortoises may, for twenty-four months from date of birth, be held in captivity in excess of the stated limit. Before or upon reaching twenty-four months of age, such progeny must be disposed of by gift to another person or as directed by the Department" (Arizona Game and Fish Department 1991a).

B. California
   1. In 1939 the sale of the desert tortoise in California was forbidden (Grant 1946).
   2. California Fish and Game Commission Code 5000-5003 has protected *Gopherus* sp. from shooting, vandalism, and transport (Berry 1986d; Bury and Stewart 1973).
   3. "It is unlawful to sell, purchase, harm, take, possess, or transport any tortoise (*Gopherus*) or parts thereof, or to shoot any projectile at a tortoise (*Gopherus*)" (Bury and Marlow 1973; Bury and Stewart 1973).
   4. Tortoises may be collected with a special permit for scientific, zoological, and educational purposes (Bury and Stewart 1973).
   5. Violations are punishable with a $1,000 fine and/or 1 year in jail for each offense (Bury and Marlow 1973).
   6. Legally possessed tortoises must be tagged (St. Amant 1976).
   7. It is unlawful to remove desert tortoises from their natural habitat (Crooker 1971).
   8. It is unlawful to display native reptiles in any place of business where pets or other animals are sold (Brode 1983).

C. Nevada
   1. Nevada Statute 503-600: "It shall be unlawful to catch or kill the desert tortoise or terrestrial turtle in the State of Nevada" (Bury and Marlow 1973; Leach and Fisk 1969).
   2. Nevada Revised Statute 501-379 was amended to protect all wildlife species. Sale, trade, or barter of any wildlife species or parts thereof is prohibited. Possession of desert tortoises is also prohibited (Mortimore 1983).
   3. Collection of desert tortoises is illegal and punishable by fines up to $500 and/or jail terms up to 6 months (Nevada Department of Wildlife n.d.).

D. Utah
   1. Placed on protected wildlife list in Utah in 1971 (Coombs 1977a,c, 1979; Day 1979).
   2. The Beaver Dam Slope population was recommended for endangered status in 1977; currently the population is listed as threatened (Dodd 1978, 1979; Holing 1986; Minden 1980; USDI Fish and Wildlife Service 1985b).
   3. Utah Wildlife Resources Code Section 23-12-2, subsection 27, and Section 23-13-3 make it unlawful to kill, capture, or possess desert tortoises, except for research purposes by permit (Berry 1984).
   4. State regulations prohibit commercial activity, disturbance of dens, export and trade, possession, purchase, or selling of any reptile (Berry 1984).

Husbandry

Material discussing general care in raising desert tortoises is included here with respect to environmental conditions, diet, and health care, as well as material discussing care in rearing young tortoises.

I. **General husbandry**

A. Provide shade and a shallow pan of water for soaking and drinking in the summer (Tremper 1978).

B. Temperature, humidity, light, nutrition, and housing are important factors when maintaining healthy herds of captive tortoises (Flanagan 1986).
C. Diet recommended: 40 percent raw spinach leaves, 5 percent chopped apple, and 5 percent grated carrot or tomato with tricalcium phosphate mixed in (Tremper 1978).
D. A twice daily diet of chopped avocados, tomatoes, and lettuce plus grazing access to grass, clover, *Dichondra*, dandelion leaves and flowers supplemented with vitamins, cod liver oil, squash, and hibiscus flowers resulted in rapid growth of hatchlings and young tortoises (Jackson and others 1976a).
E. The best diet for providing nutritional requirements is a combination of alfalfa, hay, Bermuda grass, and natural forage (Jarchow 1984).
F. Starving tortoises were given antibiotics, vitamin supplements, and dextro-saline solution twice daily. Liquid food, such as apple juice and vegetable juice, was administered until succulent food was taken (Bissett 1972; Ewing 1973).

II. **Incubation of eggs** (Trotter 1973)
A. Eggs must remain in the same position at all times.
B. Temperature must be controlled.
C. Humidity must be kept constant.
D. Eggs must be kept in darkness.
E. Incubator used was styrofoam ice box with 3 inches of water on the bottom in which a 25-watt aquarium heater rests. A rack for eggs was constructed out of hardware cloth and placed above water about halfway up the chest.

III. **Rearing of hatchlings** (International Turtle and Tortoise Society Journal 1970)
A. Feeding
1. Begin feeding before the yolk sac is absorbed.
2. Offer hatchlings fresh food several times each day and provide fresh water with vitamins in it.
3. Provide bone meal twice weekly and add vitamin supplements to food.
4. Suggested foods are finely chopped tomatoes, melons, lettuce, and bananas.
B. Hatchlings may be kept in a glass terrarium with a light above as a heat source and an upside-down box with a small opening for cover (International Turtle and Tortoise Society Journal 1970).
C. The terrarium should be placed in sunlight and kept between 27 °C and 29.5 °C (International Turtle and Tortoise Society Journal 1970).
D. Inorganic substrates may lead to 100 percent hatchling mortality within 18 months. Litter-green is recommended as substrate (Tremper 1978).

IV. **Illness**
A. Hypovitaminosis A (Burke 1970)
1. Usually results from a lack of dietary vitamin A or from gastrointestinal disease.
2. Symptoms include swelling of eyelids, swelling of eye lids and/or nictating membrane, lack of appetite, excess oral mucous, secondary bacterial infections, diarrhea, and breathing through the mouth.

3. Treatment is intramuscular injection of 5,000 I.U. of vitamin A palmitate per 0.46 kg of body mass. Treatment of secondary infections includes broad spectrum antibiotic ophthalmic ointment four times daily. Give one to five drops of cod liver oil daily to prevent future occurrences.

B. Hypothyroidism (Frye and Dutra 1974)
   1. Occurs due to diet of goitrogenic vegetables, brussel sprouts, cabbage, and kale.
   2. Can be prevented through a well-balanced natural diet or by adding trace minerals to diet.
   3. Symptoms are lethargy, lack of appetite, fibrous goiter, and myxedema of subcutaneous tissue.
   4. Treatment is oral administration of sodium iodide.

C. Respiratory disease: see also Mortality factors, Disease
   1. The respiratory tract of tortoises suffering from respiratory infections harbors opportunistic bacteria (Fowler 1976; Jacobson and Gaskin 1990; Jacobson and others 1991; Rosskopf 1988).
   2. Speculation exists regarding the contagiousness of the respiratory disease: some believe that it may not be a contagious disease and may result from decreased resistance that allows common bacteria to gain a foothold (Fowler 1976); others believe the disease is highly contagious (Rosskopf 1988).
   3. Resistance to disease may be decreased by stress caused by temperature and humidity extremes, photoperiod differences, and lack of burrowing opportunities associated with captivity, and by malnutrition (Fowler 1976).
   4. Nutritional status is an important stress factor; captive tortoises often have inadequate nutrition. Energy, vitamin A, protein, calcium, and phosphorus are especially important and are usually lacking in captive diet (Fowler 1976).
   5. Iceberg lettuce, a common captive tortoise food, contains 1.2 percent protein and 2.5 percent carbohydrates. Forbs commonly found in tortoise natural diet are 9.36 percent protein and 38.8 percent carbohydrates (Fowler 1976).
   6. For tortoises exhibiting symptoms of upper respiratory disease, treatment includes antibiotics, nasal flushes and nasal drops for less severe cases, and fluid therapy, immune-stimulant drugs and anti-viral drugs for more complicated cases. Tortoises demonstrating symptoms of upper respiratory disease should be immediately isolated from asymptomatic tortoises (Rosskopf 1988).

D. Pharyngeal abscess (Harper and others 1982): a 6-year-old tortoise in poor nutritional condition and which had been maintained in captivity since a hatchling possessed a herpesvirus-like agent associated with a lesion upon necropsy.

E. Paraphimosis (Rosskopf and others 1982a): inflammatory swelling of the protruded penis which prevents its return to its normal position inside the cloaca. Administration of tranquilizer is the most thorough method of treatment since it is possible to completely reduce the swollen organ without pain and the organ can be replaced in its proper place in the cloaca.

F. Testicular interstitial cell tumor was found in a desert tortoise with a history and signs of chronic respiratory distress and anorexia; this case was unusual because testicular tumors have rarely been reported in reptiles (Frye and others 1988).

V. **Treatment of anomalies and injuries**
   A. Treatment of broken shell: may be repaired using epoxy (Frye 1973); by drilling holes in broken bone and wiring together with surgical wire (Rosskopf and Woerpel 1981); by using gauze and rope to apply pressure (Bissett 1971).
   B. Sources of information on specific treatments.
      1. Methods of abdominal surgery (Rosskopf and others 1983).
      2. Treatment of a hatchling tortoise with an indented plastron (Bissett 1973).
      3. Surgical repair of a thick horny growth along the rims of the mouth (Clark 1967).
      4. Surgical removal of a cystic calculus (Frye 1972).
      5. Anesthesia and anesthetics (Dantzler and Schmidt-Nielsen 1966; Frye 1972; Maxwell 1989).

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Provides an overview of extant desert tortoise literature, summarizing literature on taxonomy, morphology, genetics, and paleontology and paleoecology of the desert tortoise, as well as its general ecology. Literature on desert tortoise ecology encompasses distribution and habitat, burrows and dens, reproduction, growth, physiology, feeding and nutrition, mortality factors, and behavior. Information on habitat deterioration, management of tortoises, their legal status and tortoise husbandry is also included.

The manuscript is a complete overview of existing literature, including peer-reviewed literature and other literature. Information was compiled from materials available in 1991.

Keywords: bibliographies; reference works; endangered species; taxonomy; morphology; genetics; ecology; paleontology

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