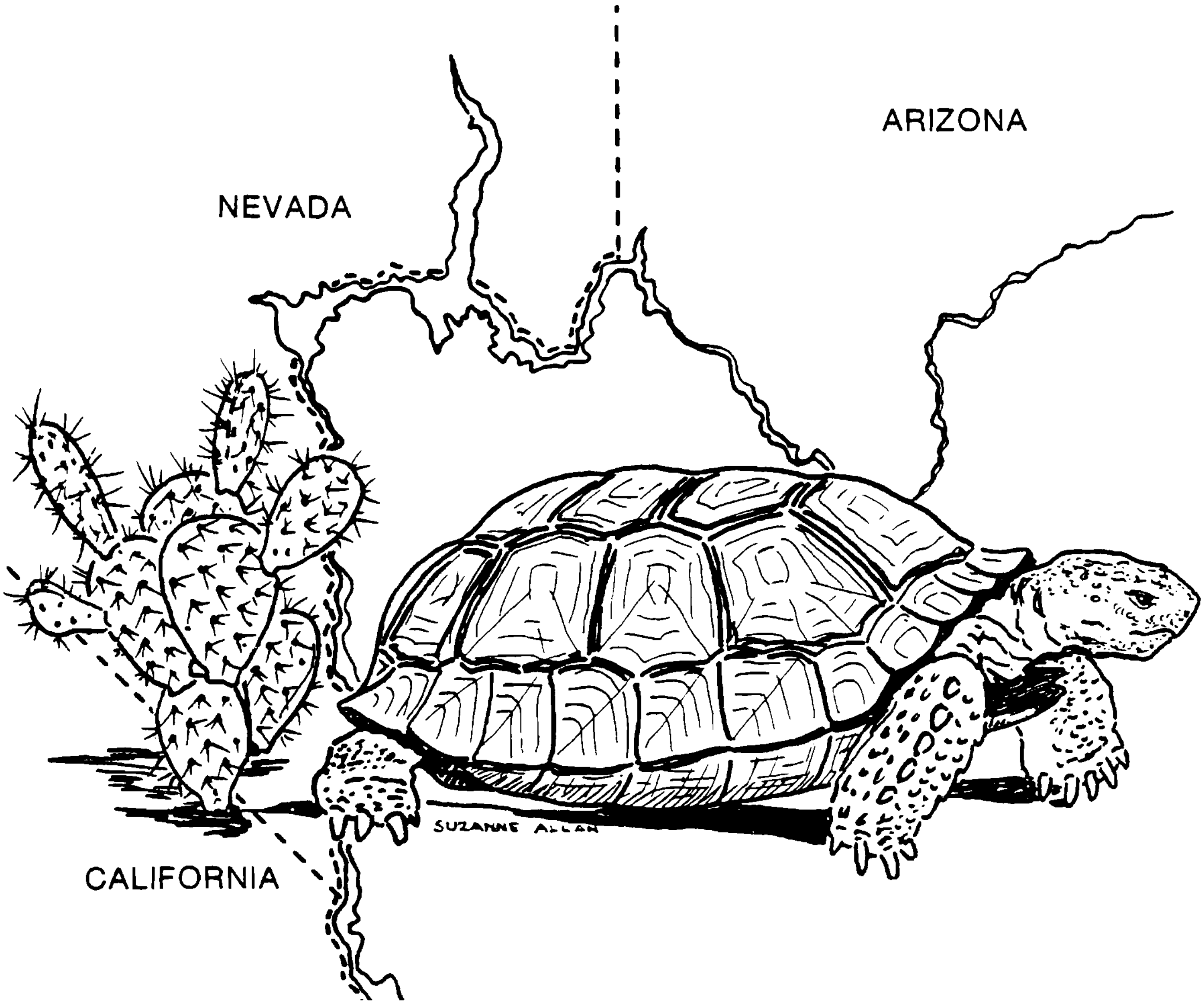
AN

ANNOTATED BIBLIOGRAPHY

OF THE

DESERT TORTOISE, *GOPHERUS AGASSIZI*



DESERT TORTOISE COUNCIL SPECIAL PUBLICATION NO. 1

AN ANNOTATED BIBLIOGRAPHY OF THE DESERT TORTOISE (*GOPHERUS AGASSIZI*)

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I. Taxonomy (Porter, 1972)

A. Class: Reptilia

B. Subclass: Anapsida

C. Order: Testudines [= Chelonia = Testudinata]

D. Suborder: Cryptodira

E. Family: Testudinidae—land tortoises

F. Subfamily: Testudininae

G. Genus: *Gopherus*

H. Species: *Gopherus agassizii* (Cooper)—sometimes spelled *Gopherus agassizi*

I. Subspecies: none

J. Common names: desert tortoise (Pope, 1939; Carr, 1952; Ernst and Barbour, 1972)

K. Original description: *Xerobates agassizii* (Cooper 1863). Proceedings of the California Academy of Sciences, 2:120. Type locality, Fort Mojave, California, USA (Cox, 1881; Stejneger and Barbour, 1943; Bogert and Oliver, 1945).

L. Synonyms

1. *Testudo agassizii*
   Cope 1875, Boulenger 1889.
2. *Gopherus agassizii*
   Stejneger 1893.
3. *Gopherus polyphemus agassizii*
   Mertens and Wermuth 1955.

M. Member of *Agassizii* complex with *Gopherus berlandieri* (Bramble, 1971; Auffenberg, 1976). One of two complexes, the other being the *Polyphemus* complex composed of *G. polyphemus* and *G. flavomarginatus*.

II. Description

A. General description—a land-dwelling turtle with a high-domed shell; prominent growth lines on carapace and plastron scutes; carapace brown or horn-colored, usually without definite pattern; plastron yellowish without a hinge; front limbs covered with large conical scales; limbs stocky and elephantine; tail short; front feet flattened for digging; broad nail-like claws; head covered with flat scales; jaw margins serrate; sharp-angled intersection of alveolar ridges of the upper jaw; laminal spurs lacking (Carr, 1952; Neill and Allen, 1957; Stebbins, 1966; Bellairs, 1970)

B. Similar species (Carr, 1952; Brame and Peerson, 1969)

1. *Gopherus flavomarginatus* = bolson tortoise
2. *Gopherus polyphemus* = gopher tortoise
3. *Gopherus berlandieri* = Texas tortoise
4. Each species is genetically isolated from the other in nature (Auffenberg, 1969)
5. *Gopherus agassizii* is more similar to *G. berlandieri* in alveolar angle, hindfoot diameter, head width and proportionate shell height (Auffenberg, 1976)
6. An additional species from Alamos, Sonora, Mexico, may be described in the future (Brame and Peerson, 1969)
    a. May be more closely related to *G. agassizii* than any other *Gopherus* species
    b. Smaller in size, with red markings on limbs

C. Distinguishing *Gopherus* species in North America (Brame and Peerson, 1969)

1. Rounded front head, interhumeral seam longer than intergular seam, single triangular axillary scale, distance from base of first claw to fourth claw equal for forefoot and hindfoot .... *G. agassizii*
2. Wedge-shaped front head, interhumeral seam same as for *G. agassizii*, often paired axillary scales, forefoot and hindfoot measurements equal as in *G. agassizii* .... *G. berlandieri*
3. Rounded head, interhumeral seam same as for *G. agassizii*, single triangular axillary scale, distance from base of first claw to third claw on forefoot equal to distance from first claw to the fourth claw on hindfoot .... *G. polyphemus*
4. Rounded front head, intergular seam longer than interhumeral seam, single rectangular axillary scale, distance between claws on feet same as for *G. polyphemus* .... *G. flavomarginatus*

D. Other distinguishing characteristics

1. Shell measurements (Bogert and Oliver, 1945)
    a. Shell length <2 X shell height .... *G. berlandieri*
    b. Shell length 2 X shell height
        1) Head relatively wide, feet relatively small .... *G. polyphemus*
        2) Head relatively narrow, feet relatively broad .... *G. agassizii*
2. Hindfoot to head width ratios (Bogert and Oliver, 1945)
    a. *Gopherus polyphemus* — .63 (.53 - .78)
    b. *Gopherus agassizii* — .98 (.85 - 1.15)
    c. *Gopherus berlandieri* — .69 (.62 - .81)

3. Plastron length/plastron width (Bogert and Oliver, 1945)
    a. *Gopherus polyphemus* — .41 (.36 - .46)
    b. *Gopherus agassizii* — .74 (.68 - .82)
    c. *Gopherus berlandieri* — .80 (.75 - .94)
4. Shell depth/plastron length (Bogert and Oliver, 1945)
    a. *Gopherus polyphemus* — .41 (.36 - .46)
    b. *Gopherus agassizii* — .43 (.40 - .46)
    c. *Gopherus berlandieri* — .48 (.45 - .57)
5. Key to species (Grant, 1960*b*)
    a. Carapace height $>50\%$ of length; nuchal scute missing or reduced in size, not reaching to line of marginals .... *G. berlandieri*
    b. Carapace height $\leqslant 45\%$ of length; prominent nuchal scute present
        1) Body widest at midbody .... *G. polyphemus*
        2) Body widest at about rear of fourth neural scute .... *G. agassizii*
6. Angle of alveolar ridges of upper jaws (Carr, 1952)
    a. *Gopherus polyphemus* $>73°$
    b. *Gopherus berlandieri* $>65°$ but $<73°$
    c. *Gopherus agassizii* $<60°$

III. Current range

A. General

1. Southwestern and southern Arizona, Sonora and Tiburon Island (Gulf of California) to northern Sinaloa, Mexico (Van Denburgh, 1922; Grant, 1936*a*; Linsdale, 1940; Bogert and Oliver, 1945; International Union for the Conservation of Nature and Natural Resources, 1970; Texas Parks and Wildlife Department, *no date*)
2. Includes most of the Mojave and Sonoran deserts including the Lower Colorado Valley of the Sonoran Desert
3. Current range suggests that the desert tortoise is a cold-sensitive species (Van Devender et al., 1976)

B. Utah

1. About 128 km^2 of the extreme southwest corner of Washington County, Utah (Coombs, 1977*b*)
2. Extreme northeast extent of the desert tortoise's range (Pope, 1939; Carr, 1952; Ernst and Barbour, 1972)
3. Extension of range (Coombs, 1977*a*, *b*)
    a. Paradise Canyon area immediately north of St. George
    b. Snow Canyon State Park
    c. Populations comprised of introduced animals

C. Nevada

1. Occurs in southern Clark County and the extreme southern portion of Nye County, the Pahrump Valley, at elevations up to 1067 m (Pope, 1939; Linsdale, 1940; Connolly and Eckert, 1969)
2. Present at the bend of the Colorado River (Stejneger, 1893)
3. Specific locations: 6.4 km south of Mesquite, near Boulder City, in Piute Valley; 16.1 km south of Searchlight (Linsdale, 1940)
4. Possibly more widely distributed than this (Linsdale, 1940)

D. California

1. Occurs in northeast Los Angeles County; eastern Kern County; southern Inyo County; Panamint and Death valleys and Shoshone area; San Bernardino, Riverside, and Imperial counties except for Coachella Valley (Camp, 1916; Grant, 1936*a*; Brattstrom, 1961; Patterson, 1976*a*)
2. Absent from low, hot Colorado Desert along Salton Basin, but recently introduced unsuccessfully to the Anza-Borrego Desert State Park (Van Denburgh, 1922; Stebbins, 1966; Leach and Fisk, 1969)
3. Urbanization and utilization (suburbs, cabins, roads, agriculture, grazing) of land by man may eliminate the desert tortoise from the upper reaches of the Mojave Desert (Bury and Marlow, 1973)
4. Specific sightings at Mecca, Riverside County; near Victorville, Barstow, Kramer in San Bernardino County; 0.8 km east of Mojave, Kern County; 4.8 km south of Palmdale, Los Angeles County; Jenson Canyon in San Gorgonio Pass, Riverside County; between Daggett and Pilot Knob; and in Leach Point Valley (Stejneger, 1893; Camp, 1916; Camp, 1917; Campbell and Evans, 1967)

E. Arizona

1. Known in 8 counties in southern and western Arizona including Yuma, Mohave, Maricopa, Pinal, Pima, Graham, and Cochise counties (Pope, 1939)
2. Specific localities include Phoenix, Florence, and Tucson areas; 12.8 km southwest of Casa Grande below Table Mountain; on road to Kit Peak Observatory; 11.0 km east of Yucca in Hualapai Mountains; Yuma and Ehrenberg area; Santa Catalina Mountains; Fort Grant; and Wilcox (Van Denburgh, 1922; Grant, 1936*a*; Pope, 1939; Kauffeld, 1943; Grant, 1946; Stebbins, 1966; Tomko, 1972)

F. Mexico

1. From Arizona—Sonora border south to below Alamos in Sinaloa and 6.1 km northeast of El Fuerte, Sinaloa (Van Denburgh, 1922; Grant, 1936*a*; Loomis and Geest, 1964; Hardy and McDiarmid, 1969)

2. Includes Tiburon Island, Gulf of California, Sonora (Stebbins, 1966; Bury et al., 1978)
3. Absent from Baja California (Bogert and Oliver, 1945)

IV. Habitat

A. Habitat types

1. Mainly Mojave and Sonoran deserts at elevations of 152.4 to 1067 m (Woodbury and Hardy, 1948*a*)
2. Restricted to suitable soil types for den construction (Woodbury and Hardy, 1948*a*; Miller and Stebbins, 1964)
3. Preference for alluvial fans, canyons, and washes (Turner and Wauer, 1963)
4. Rare on rocky hillsides with *Encelia* associations and canyon beds with *Acacia* but found in rocky foothills of Sonoran Desert where burrows have been constructed (Camp, 1916)
5. Preferred habitat in Providence Mountains region (Luckenbach, 1976)
   a. Elevations <300 up to 1000 m
   b. Sandy loam to light gravel—clay soil
   c. Area with good denning potential
   d. Small creosote bush (*Larrea divaricata*) is the dominant plant species
   e. High perennial diversity with high annual bloom potential
6. Habitat observed in Pima County, Arizona (Ortenburger and Ortenburger, 1927)
   a. Boulder strewn shelves above dry streambeds
   b. Away from mouth of canyon
7. Isla Tiburon, Gulf of California, Mexico (Bury et al., 1978)
   a. Creosote—mixed desert scrub and subtropical thorn scrub
   b. Dense scrub cover preserved because of the absence of livestock

B. Vegetation associations

1. General vegetation associations
   a. *Larrea divaricata* and *Ambrosia dumosa*; *Larrea* sp. and *Yucca brevifolia*; *Cercidium* sp., *Cassia*, *Prosopis*, and *Cereus giganteus*; *Cereus giganteus* and *Fouquieria splendens* (Ortenburger and Ortenburger, 1927; Grant, 1936a; Loomis and Geest, 1964)
   b. In Mexico, thorn scrub (Stebbins, 1966); seaside scrub and thorn brush (Auffenberg and Iverson, 1979)

2. Specific vegetation associations

   a. Rand Mountains, eastern Kern County, California (Berry, 1975a)

Larrea divaricata	creosote bush
Yucca brevifolia	Joshua tree
Ambrosia dumosa	burrobush
Acamptopappus sphaerocephalus	golden head
Hymenoclea salsola	cheesebush
Ephedra nevadensis	Nevada joint-fir
Eriogonum fasciculatum	California buckwheat
Salazaria mexicana	paperbag bush
Ceratoides lanata	winterfat
Dalea fremontii	Fremont dalea
Eriogonum inflatum	desert trumpet
Machaeranthera tortifolia	Mojave aster
Tetradymia stenolepsis	Mojave horsebrush

   plus 104 known annual species

   b. Beaver Dam Slope, Utah (Woodbury and Hardy, 1948a)

Coleogyne ramosissima	black brush
Yucca brevifolia	Joshua tree
Larrea divaricata	creosote bush
Lycium andersonii	wolf-berry
Ephedra nevadensis	Nevada joint-fir
Ambrosia dumosa	burrobush
Ceratoides lanata	winterfat
Krameria parvifolia	little-leaved ratany
Thamnosma montana	thamnosma
Salazaria mexicana	bladder-sage
Hymenoclea salsola	cheese-bush
Xanthocephalum lucidum	snakeweed
Encelia frutescens	brittlebush
Salvia dorrii	sage
Ephedra torreyana	joint-fir

   c. Arden Study Area, Las Vegas Valley, Nevada (Berry, 1977)

Ambrosia dumosa	burrobush
Larrea divaricata	creosote bush
Krameria parvifolia	little-leaved ratany
Ephedra nevadensis	Nevada joint-fir
Eriogonum fasciculatum	California buckwheat
Dalea fremontii	Fremont dalea
Yucca schidigera	Mojave yucca
Acacia greggii	catclaw

   d. Isla Tiburon, Gulf of California, Sonora, Mexico (Bury et al., 1978)

      1) 2 km west of Punta Tormenta (creosote—mixed desert scrub)

Larrea divaricata	creosote bush
Ambrosia dumosa	burrobush
Encelia farinosa	brittlebush
Bursera microphylla	elephant tree
Cordia parvifolia	cordia

2) Caracol (subtropical thorn scrub)

Ruellia californica	ruellia
Bursera microphylla	elephant tree
Bursera hindsiana	elephant tree
Olneya tesota	desert ironwood
Lysiloma divaricata	lysiloma
Fouquieria splendens	ocotillo
Cercidium microphyllum	little-leaf palo verde

e. Picacho Mountains, Pinal County, Arizona (Schwartzmann and Ohmart, 1978)

1) Of 6 vegetation types delineated, only 3 had resident tortoises

2) Vegetation type 6 had the highest perennial plant density of the 6 types and the highest number of resident tortoises

a) Vegetation type 6

Species	Percent (%) density
Eriogonum fasciculatum (California buckwheat)	64
Encelia farinosa (brittlebush)	23

b) Perennial density was 16.1 plants per 10 m^2

3) Tortoise densities may be related to perennial plant density and species composition in the Sonoran Desert

V. Paleontology

A. Range

1. Evolved in xeric southwestern United States and Mexico in Pleistocene (Bramble, 1971)
2. More extensive during late Pleistocene than now (Auffenberg, 1969; Van Devender et al., 1976; Van Devender and Moodie, 1977)
3. Desert tortoises occurred in north Chihuahuan Desert in New Mexico west to eastern California in late Pleistocene (Van Devender et al., 1976)
4. Two *Gopherus* complexes (*Polyphemus* and *Agassizii*) have been separate since Miocene (Bramble, 1971)
5. Reduction in range since end of Wisconsinian glaciation resulted in western movement of eastern edge of range (Auffenberg and Milstead, 1965)

B. Fossil localities outside current range

1. Pleistocene localities from southeast New Mexico to coastal California (Van Devender et al., 1976; Van Devender and Mead, 1978)

2. Shelter and Conkling caves, Dona Ana County, New Mexico (Brattstrom, 1961; Brattstrom, 1964)

    a. Remains from Organ Mountains

    b. Shell fragments from late Pleistocene

    c. Fragments from tortoises generally smaller in size than the present *G. agassizii*

3. Dry Cave, Eddy County, New Mexico

    a. Remains found 24.0 km west of Carlsbad on eastern flanks of Guadalupe Mountains (Van Devender et al., 1976)

    b. Easternmost location of Pleistocene forms of *G. agassizii* and oldest — ^{14}C dated at 33 590 $\pm$ 1500 B.P. (Van Devender et al., 1976; Van Devender and Moodie, 1977)

    c. Shell fragments and partial carapace from late Pleistocene (Brattstrom, 1961)

4. Robledo Cave, Dona Ana County, New Mexico (Van Devender et al., 1976)

    a. Remains from Robledo Mountains northwest of Las Cruces

    b. Two peripheral bones and right hypoplastron

    c. Possibly Pleistocene in age

5. McKittrick Asphalt Beds, McKittrick, Kern County, California (Miller, 1942)

    a. Remains of limb and shell bones from Pleistocene tortoise

    b. No difference between Pleistocene remains and Holocene phase of the desert tortoise

6. Los Angeles Basin, California (Miller, 1970)

    a. Four carapace fragments, one from a juvenile tortoise

    b. Fragments most likely belong to *Gopherus agassizii* and not *Geochelone* from Pleistocene

7. Hueco Mountains, Texas (Van Devender and Moodie, 1977) — ^{14}C dated at $>$34 000 B.P.

C. Fossil localities within current range

1. Manix Dry Lake, San Bernardino County, California. Skeletal fragments from Pleistocene (Brattstrom, 1961)

2. Gypsum Cave, Nevada (Brattstrom, 1954; Brattstrom, 1961)

    a. Late Pleistocene remains

    b. Size of skeletal parts similar to Holocene *G. agassizii*

3. Four sites in Clark County, Nevada (Connolly and Eckert, 1969)
   a. Large quantities of tortoise remains found from 1249.7 to 1432.5 m deep
   b. Include Flaharty Site, Walt's Site, R and K Site, Mule Springs Site
   c. Remains include carapace, plastron, scapulae, pelvic components, leg bones, and laminae
   d. Quantity of tortoise remains found in archaeological sites suggests that the desert tortoise may have been a seasonal food source for the Indians
   e. Ten levels were excavated, each level was 10.0 cm deep
      1) Level 1 — 34.0% of bones from *G. agassizii*
      2) Level 2 — 10.7%
      3) Level 3 — 22.2%
      4) Level 4 — 12.6%
      5) Level 5 — 6.8%
      6) Level 6 — 6.9%
      7) Level 7 — 3.2%
      8) Level 8 — 1.8%
      9) Level 9 — 0.8%
      10) Level 10 — 0.6%
4. Rampart Cave and vicinity, Grand Canyon, Mohave County, Arizona (Wilson, 1942; Van Devender et al., 1977)
   a. Late Pleistocene remains
   b. Skeletal parts include femur, peripheral bone, bone fragments and scutes
5. Schuiling Cave, San Bernardino County, California (Downs et al., 1959)
   a. Pleistocene remains of one desert tortoise
   b. Remains of one partial carapace and many fragments
6. Whipple Mountains #2, San Bernardino County, California (Van Devender and Mead, 1978)
   a. Tortoise remains ^{14}C dated to 9980 $\pm$ 180 years B.P.
   b. Remains found at an elevation of 520 m, juniper woodland present or nearby at that time
7. Wellton Hills #2, Yuma County, Arizona (Van Devender and Mead, 1978)
   a. Tortoise remains ^{14}C dated to 8750 $\pm$ 320 years B.P.
   b. Remains found at an elevation of 160 m, creosote—burrobush present or nearby at that time

D. Paedomorphosis (Bramble, 1971)

1. Adult forms of desert tortoises similar to juvenile Pliocene predecessors

2. Paedomorphic trends evident from structure of shell, manus, and skull

3. Holocene gopher tortoises up to 70% smaller than their early Pleistocene ancestors

E. Os transiliens—present in fossil tortoises since the late Eocene or early Oligocene (Bramble, 1974)

VI. Paleoecology

A. Habitat

1. Fossil locations indicative of a former arid area (Brattstrom, 1961)

2. New Mexico macrofossil plant records suggest woodland areas which included *Juniperus* sp., *Celtis reticulata*, *Pinus edulis*, *Quercus* sp., and *Prunus serotina* (Van Devender et al., 1976)

3. Fossil remains in San Bernardino, California, suggest the presence of *Juniperus* sp. nearby (Van Devender and Mead, 1978)

4. Woodland areas with mild winters and cool summers (Van Devender et al., 1976)

B. Dispersal route

1. *Gopherus* ancestors may have migrated from Asia across the Bering Land Bridge in mid-Miocene (Brattstrom, 1961; Auffenberg, 1969)

2. Climate may have been subtropical or warm temperate (Auffenberg, 1969)

3. During Pleistocene, *G. agassizii* may have used southern Rocky Mountain corridor (Porter, 1972)

VII. Morphology

A. Sexual dimorphism — *See:* X. Reproduction - B. Secondary sexual characteristics

B. Hatchlings

1. Size

a. Size of a "silver dollar" (Miles, 1953; Coombs, 1977*b*)

b. Captive tortoises

1) (Grant, 1936*a*)

Carapace length (mm)	Carapace width (mm)
36.0	39.0
41.0	37.8
48.0	42.5
44.0	36.5
44.5	36.5
$\bar{x}$ = 42.7	$\bar{x}$ = 38.4

2) (Hunsaker, 1968)

Carapace length for twins (mm)
32.0
38.0

c. Wild tortoises

1) (Miller, 1955)

Carapace length (mm)	Carapace width (mm)	Shell depth (mm)
53.0	39.0	20.4
50.0	44.0	24.4
39.9	37.5	21.2
44.7	40.5	22.3
43.7	39.8	23.8
46.9	40.6	21.7
46.8	42.8	24.3
47.2	41.0	23.8
44.2	41.2	22.8
47.9	30.5	23.3
45.2	40.3	22.5
$\bar{x}$ = 46.3	$\bar{x}$ = 40.4	$\bar{x}$ = 22.5

2) (Coombs, 1974)

Carapace length (mm)	Carapace width (mm)	Shell depth (mm)
42.0	37.0	18.0
48.0	37.0	20.0
$\bar{x}$ = 45.0	$\bar{x}$ = 37.0	$\bar{x}$ = 19.0

3) (Coombs, 1977*b*) Average size

Carapace length (mm)	Carapace width (mm)	Shell depth (mm)
40-50	30-40	15-20

4) (Burge, 1977)

Carapace length (mm)	Carapace width (mm)
45.0	41.0

2. Description

a. Dry yolk sac attached to umbilical area of plastron (Miller, 1932; Grant, 1936*a*; Grant, 1946; Miles, 1953; Miller, 1955; McCawley and Sheridan, 1972)

b. Yolk absorbed 2 days after hatching (Grant, 1936*a*; Trotter, 1973)

c. Plastron appears crumpled with a large transverse wrinkle which smooths out as the animal grows (Van Denburgh, 1922; Miller, 1932; Woodbury and Hardy, 1948*a*)

d. Bend between 6th and 7th marginal scutes, traces of fold may persist for several weeks (Grant, 1946)

e. Plastron may unroll and appear normal after 5 days (Grant, 1936*a*)

f. Nuchal and caudal plates incomplete and notched, gular and anal plates also incomplete (Woodbury and Hardy, 1948*a*; Stebbins, 1954; Coombs, 1977*b*)

g. Soft shell present, ossification poor and may not be complete until about the 5th year or 88.0 to 150.0 mm carapace length (Camp, 1916; Woodbury and Hardy, 1948*a*; Miles, 1953; Bury and Marlow, 1973)

h. Little ossification of shell at hatching (Auffenberg, 1976)

   1) Carapace—vertebrae, ribs, small areas at posterior lower corner of each of the anterior and posterior marginal scutes

   2) Plastron—more heavily ossified than carapace

i. Shell skeletal structure incomplete (Patterson, 1978)

   1) Large median plastral fontanelle

   2) Peripheroplastral fontanelle on each side of shell

   3) Large single fontanelle for each rib pair

j. Nails long, sharp (Miller, 1932; Woodbury and Hardy, 1948*a*; Coombs, 1974)

k. Rostral head scale or egg tooth aids in chipping open egg shell, flattens out by the 2nd year (Miller, 1932; Grant, 1936*a*; Anonymous, 1970)

l. Shell dimensions often wider than long (Miller, 1955)

m. Resemble miniature adults (Coombs, 1977*b*)

3. Weight (captive tortoises)

a. 23.0, 23.5, and 25.5 g for 3 tortoises at 30 days post-hatching (Grant, 1936*a*)

b. 19.7 g for one tortoise at 4 days post-hatching (Grant, 1936*a*)

c. A strong relationship exists between weight and carapace length (Jackson et al., 1978)

C. Adults

1. Size

a. Captive tortoises

1) Shell measurements in millimetres (Grant, 1936*a*)

a) Mean for 30 adult ♂♂

carapace length	283.0
carapace width	231.7
tail length	40.0
gular length	54.7

b) Mean for 30 adult ♀♀

carapace length	242.7
carapace width	198.0
tail length	22.7
gular length	41.7

2) Record size tortoises (Shaw, 1959)

a) carapace length — 359 mm ♂

b) carapace length — 369 mm ♀

b. Wild tortoises

1) Carapace length (Woodbury and Hardy, 1948*a*)

a) ♂♂: 250-350 mm

b) ♀♀: 230-365 mm

2) Carapace length, width, and shell depth in millimetres (Bogert and Oliver, 1945)

a) ♂♂:

Carapace length	Carapace width	Shell depth
228	157	95
217	140	79

b) ♀♀:

Carapace length	Carapace width	Shell depth
202	153	79
223	147	81

3) Carapace length of largest known individual: 493 mm (Jackson et al., 1980)

4) Mean carapace length for 40 adult ♂♂: 258.0 ± 2.6 mm (range 229-286 mm) (Burge, 1977)

5) Mean carapace length for 26 adult ♀♀: 225.0 ± 1.6 mm (range 215-246 mm) (Burge, 1977)

2. Description

a. Shell

1) Carapace

a) Nuchal scute, 11 marginal scutes on each side, one caudal [= supracaudal or postcentral of some authors] scute, 5 neural or vertebral scutes, 4 costal scutes on each side (Grant, 1946)

b) Fifty fused bones make up the carapace (Boynton, 1970*a*)

c) Ribs and vertebrae fused to shell (Pepper, 1963; Boynton, 1970*a*)

d) Carapace may flair posteriorly (Grant, 1960*a*)

e) Closure of costoperipheral fontanelles completed when plastron length reaches 200 mm (Patterson, 1978)

f) High vaulted shell provides greater space for lungs (Auffenberg, 1974)

2) Plastron

a) Plastron has 6 pairs of scutes with growth lines (Stebbins, 1954)

b) Nine bones make up the plastron (Boynton, 1970*a*)

c) In the female, the posterior lobe of the plastron is slightly movable due to a transverse ligamentous hinge (Beltz, 1954)

d) Gular shield suture present on right side in 331 of 366 tortoises, or 90%; 6% with median sutures; and 3% with left sutures (Grant, 1936*a*)

e) Gular projections strongly developed in both sexes; gulars of males prominent and diverge at tips (Bramble, 1971)

f) Gular scales do not overlap entoplastron (Bramble, 1971)

g) Inguinal scale divided to produce a smaller medial scale (Bramble, 1971)

h) Plastron fontanelle closure complete when plastron has reached length of 210 mm (Patterson, 1978)

3) Shell usually greater than half as high as it is long (Grant, 1960*a*)

4) Shell profile gently convex (Bramble, 1971)

b. Skeleton

1) Vertebral column

a) Twelve dorsal vertebrae, 8 cervical vertebrae, and varying numbers of caudal vertebrae present (Woodbury and Hardy, 1948*a*)

b) Deep fossae present at base of prezygapophysis to allow head to be withdrawn more fully into shell (Bramble, 1971)

c) Little or no horizontal movement possible between 4th cervical vertebra and vertebrae posterior to it (Bramble, 1971)

2) Ribs (Woodbury and Hardy, 1948*a*)

a) The 1st and 2nd rib pairs fuse with costal plates in the carapace

b) The 3rd to 8th rib pairs fuse with neural plates in the carapace

c) The 9th and 10th rib pairs fuse with the last pair of costal plates in the carapace

d) Sacral ribs attach to dorsal ends of ilia of pelvic girdle

3) Pectoral girdle and associations

a) Acute angle of 104° between two limbs of scapula (Bramble, 1971)

b) Interclavicular keel pronounced, functions to increase the origin of deltoid muscles (Bramble, 1971)

c) Dorsal ends attached to 1st costal places on each side of 1st dorsal vertebra; ventral ends attached to entoplastron (Woodbury and Hardy, 1948*a*)

4) Pelvic girdle (Woodbury and Hardy, 1948*a*)

a) Dorsal ends anchored to last costals

b) Ventrally, ischia anchored to xiphiplastron

5) Limbs

a) Shovel-like forelimbs are principal digging structures (Grant, 1960*a*)

b) Dermal armor present as ossicles under the horny scales on the sole of the foot, at the heel of the pes (Bramble, 1971) on the posterior surface of the thighs, and on the forearms (Auffenberg, 1976)

c) Tibia shaft longer and more slender than in *Gopherus polyphemus* or *G. flavomarginatus* (Bramble, 1971)

d) Femur shaft long and slender in relation to *G. polyphemus* and *G. flavomarginatus* (Bramble, 1971)

e) Width of distal end of humerus to functional length is 38% (Bramble, 1971)

f) Shortening and flattening of articular surfaces of metacarpals and proximal phalanges has eliminated digital movement (Bramble, 1971)

g) Nine carpal elements in forelimbs with evidence of much fusion in adults (Auffenberg, 1976)—probably associated with use of front limbs for digging

h) Remnant of first digit on hindfoot is represented by a metatarsal; digits 2 through 5 contain 2 phalanges each (Woodbury and Hardy, 1948*a*)

i) Front foot is unguligrade (Auffenberg, 1974)

c. Head

1) Presence of os transiliens (Bramble, 1971; Bramble, 1974)

2) Eyes protrude slightly from orbits (Bramble, 1971)

3) External nares minute (Bramble, 1971)

4) Well-developed posterior narial passage analogous to secondary palate of mammals, allows respiration to continue during prolonged feeding or mastication bouts (Bramble, 1971)

5) Serrated jaws used for plant shredding (Mahmoud and Klicka, 1979)

d. Soft tissue

1) Lungs cover anterior one-third to one-half of ventral surface of carapace (Fowler, 1976*b*)

2) Lung is a sacculated hollow structure with epithelium in a honeycombed arrangement between sacculations (Fowler, 1976*b*)

3) Liver is bilobed, one lobe on each side of the pericardium (Woodbury and Hardy, 1948*a*)

4) Large intestine is extensive (Woodbury and Hardy, 1948*a*)

5) For a 3.12 kg male tortoise with carapace length of 265.0 mm, the liver weighed 91.5 g, heart 8.0 g, kidney 20.0 g, head 67.5 g (Connolly and Eckert, 1969)

6) Bladder is bilobed and located near posterior area of carapace (Auffenberg, 1969)

7) Two uteri present in females but joined together externally (Woodbury and Hardy, 1948*a*)

e. Molecular components (Connolly and Eckert, 1969)

1) Water weight of tortoise is 79.6% of total body weight

2) Protein, fat, and ash percentages are 17.4, 1.0, and 1.3, respectively

3) Potassium content is 1.6 g per kilogram of body weight

f. Coloration

1) Ranges from a dull mustard yellow to a dark brown with the periphery of each scute somewhat darker (Miller, 1932)

2) Adults from Guaymas, Mexico, are darker than the California representatives; may be associated with environmental factors (Bogert and Oliver, 1945; Miller, 1955)

3. Weight

a. A highly variable measurement (Berry, 1974)

b. Fluctuates with food availability, egg laying, drinking of rainwater and recency of defecation (Berry, 1974)

c. Shell makes up one-third of total body weight (Fowler, 1976*b*)

d. Wild tortoises—average weights (Combs, 1977*b*)

Carapage length (mm)	Weight (g)
>250	3800
200-249	2500
140-199	1200
60-139	500
<60	<50

e. Captive tortoises—actual weights for 24 tortoises (McCawley and Sheridan, 1972)

Carapace length (mm)	Weight (g)
270	2338
280	3476
290	3745
230	1850
240	2200
235	2497
240	2120
270	3110
250	2883
240	2090
220	1900
230	2860
213	1865
270	3200
300	4425
314	5230
210	2275
248	3250
280	3880
260	3805
267	3041
254	2270
267	2724
343	5221

D. Chin glands or subdentary glands

1. Well developed in males during the spring and early summer (Rose et al., 1969; Coombs, 1974)

2. Weakly developed but functional in females (Rose et al., 1969)

3. Secretion contents—phospholipids, triglycerides, free fatty acids, cholesterol, one esterase (Rose et al., 1969)

4. Electrophoretic analysis (Rose et al., 1969)

   a. Single cathodal migrating protein band present in all *Gopherus* females but not males

   b. *Gopherus berlandieri* has 2 esterases, *G. flavomarginatus* has 4 esterases, and *G. polyphemus* has no observable esterase activity

5. Structure (Rose et al., 1969)

   a. Similar to sebaceous glands of mammals

   b. When active and enlarged, scaleless external epithelium and 2 to 3 external openings are visible

6. Function

   a. May aid in communicating the presence of an adult male desert tortoise (Coombs, 1977*a*)

   b. Shows reproductive readiness, may be olfactory and visual recognition cues for courtship (Rose et al., 1969). Experiment (Coombs, 1974; Coombs, 1977*a*):

      1) Male encounters normal female, leads to courting behavior

      2) Male encounters male with chin gland secretions, leads to fighting

      3) Male encounters male with sealed chin glands, leads to courting behavior

      4) Male encounters empty tortoise shell with chin gland secretions from a male, leads to "combat"

      5) Male encounters rock with chin gland secretions, leads to aggressive behavior

E. Special skeletal structures—os transiliens

   1. Sesamoid bone (Bramble, 1974)

   2. Unique to gopher tortoises (Bramble, 1974)

   3. Function

      a. May be an adaptation for mechanical stresses arising from specialized feeding mechanism (Bramble, 1974)

      b. Provides for a smoother, more efficient motion of the jaw musculature for more effective grinding of coarse, tough vegetation (Patterson, 1973; Bramble, 1974)

   4. Cartilaginous in young animals, ossified in adults (Patterson, 1973)

F. Eye coloration

   1. Mostly yellow iris with a brown rim (Coombs, 1977*b*)

   2. Eighty percent of tortoises examined had brassy eye coloration, 10% had brown eyes, and 10% had mottled eyes (Grant, 1936*a*)

   3. Tortoise with yellow iris found in Mecca, Riverside County, California; tortoise with brown iris found farther north of Goffs, California (Camp, 1916)

G. Shell anomalies

   1. Of 366 captive specimens examined, 19 females, 7 males, and 4 unsexed young had major scute anomalies (Grant, 1936*a*)

2. Malformed scutes

   a. Gulars

      1) Observed gulars growing to one side (Coombs, 1974)

      2) 105 of 119 tortoises had left gular larger, 6 of 119 tortoises had right gular larger (Grant, 1946)

      3) Irregularly curved or with extra parts (Coombs, 1977*b*)

   b. Caudal [= supracaudal or postcentral of most authors]

      1) Paired on 2 tortoises (Grant, 1946)

      2) Occasionally irregular in shape (Coombs, 1977*b*)

   c. Nuchal [= precentral of some authors] — divided with one part fused with the first left marginal for one tortoise (Grant, 1946; Coombs, 1977*b*)

3. Extra scutes

   a. Vertebrals [= centrals of some authors]

      1) Two additional vertebrals on one tortoise (Coombs, 1974)

      2) One extra vertebral more common, one may split forming 2 scutes (Grant, 1946; Coombs, 1977*b*)

   b. Costals [= laterals of some authors] (Grant, 1946)

      1) Three of 119 tortoises had 5 costals or 1 extra costal on one side

      2) One of 119 tortoises had 5 on both sides

   c. Marginals (Grant, 1946)

      1) Four of 119 tortoises had 12 on each side

      2) Three of 119 tortoises had 12 on one side

   d. Plastral scutes—two of 500 tortoises had extra scutes (Grant, 1936*b*)

4. Missing scutes

   a. Nuchal (Coombs, 1974)

   b. Marginals (Grant, 1946)

      1) Three of 119 tortoises had 10 on each side

      2) One of 119 tortoises had 10 on one side

H. Other anomalies

   1. Thick horny growth along upper and lower rims of mouth (Clark, 1967)

2. Coloration

   a. Legs of one male tortoise were orange and black instead of gray and black (Grant, 1936*a*)

   b. Two partial albinos found; carapace, legs, and nails were olive gray (Grant, 1936*a*)

   c. Three albino tortoises at the Arizona-Sonora Desert Museum (Keasey, 1979)

I. Growth ring formation and shedding

1. For each scute a new horny plate forms beneath its predecessor which is slightly larger in size (Boynton, 1970*a*)

2. New larger plate creates a partial or complete ring or ridge around the old plate (Woodbury and Hardy, 1948*a*)

3. Different carapace scutes have different numbers of growth rings (Coombs, 1977*b*)

4. After formation of 15-20 adult growth rings, the light brown juvenile rings near the center of the scute may be shed (Coombs, 1974; Coombs, 1977*b*)

VIII. Genetics

A. Karyology (Atkin et al., 1965)

1. Chromosome number $2N = 52$

2. DNA content of epithelial cells is 0.87 and 0.89 with human epithelial cells used as a control of 1.00

3. Genetic content slightly less than in mammals but greater than in birds

4. Based on genetic content tortoises may have a closer phylogenetic relationship to mammals than to birds

B. Hybridization

1. A female *Gopherus agassizii* and a male *G. berlandieri* successfully mated in captivity; 2 of the eggs hatched produced viable young (Woodbury, 1952)

2. A female *G. agassizii* and a male *G. polyphemus* successfully mated in captivity; 7 eggs were laid, 1 containing twin tortoises (Hunsaker, 1968)

3. In nature, *G. agassizii*, *G. polyphemus*, and *G. berlandieri* are allopatric (Carr, 1952; Stebbins, 1966; Conant, 1975)

IX. Behavior

A. Reproductive behavior — *See*: X. Reproduction

B. Defensive behavior

1. Passive resistance

a. Typical behavior exhibited by a tortoise when threatened or captured (Woodbury and Hardy, 1948*a*)

b. Animal withdraws into shell (Woodbury and Hardy, 1948*a*)

c. Knees are drawn together on front legs after head is pulled in, hind legs and tail pulled in (Coombs, 1977*a*)

2. Active resistance

a. If an attempt is made to remove a tortoise from its burrow, the animal will move toward the den interior (Woodbury and Hardy, 1948*a*)

b. The tortoise will also straighten its legs, pushing its carapace up against the den ceiling (Coombs, 1977*a*)

3. Urination for possible predatory defense

a. Large amounts of urine held within the bladder may be released when the tortoise is disturbed (Coombs, 1977*a*, *b*)

b. Defensive urination more frequent in spring and fall (Coombs, 1977*a*)

c. Urination by the female on top of a tortoise nest is an effective means of repelling nest predators (Patterson, 1971*a*)

d. Amount of fluid voided ranges from 2 to 20 ml each time a tortoise is disturbed (Coombs, 1977*b*)

C. Gregarious and solitary behavior

1. Tend to be gregarious in winter

a. May be limited to tortoises in the northern part of their range (Coombs, 1977*a*)

b. Several tortoises will use one winter den for hibernating (Woodbury and Hardy, 1948a; Woodbury, 1954; Coombs, 1977*a*, *b*)

c. Up to 25 tortoises have been counted in one winter den with 10 or more tortoises in each of 20 dens (Woodbury and Hardy, 1948a)

d. Tortoises may have a loosely organized social system (Woodbury and Hardy, 1948a).

e. Large males direct behavioral interactions toward other adult males or females (Coombs, 1977*a*)

2. Fecal pellets used as a deterrent to aggregations (Patterson, 1971*c*)

   a. Experiment with 8 captive tortoises in backyard area

   b. Dominant male deposits pellets in den area where subordinate males sleep, subordinate males sleep outside the den for several nights until the pellets dry

   c. In winter, the gregarious period, fewer fecal pellets are produced; therefore there is less of a deterrent to gregarious behavior

   d. If dominant male enters winter den late, then subordinate tortoises can enter the winter hibernaculum prior to the dominant male

   e. Dominant male may be the first to exit from the winter den in spring

   f. Repellent in the fecal pellets may be due to secretions from cloacal glands

   g. Urine has no effect as a repellent

D. Righting response

1. Under normal conditions a healthy tortoise is able to right itself most of the time after being inverted (Woodbury and Hardy, 1948*a*; Ashe, 1970)

2. A tortoise can right itself from a flat surface or suspended atop a glass vessel (Ashe, 1970)

3. Description of righting reflex (Ashe, 1970; Anonymous, 1973)

   a. Head is extended dorsally toward surface along with limbs

   b. Head is used as a lever, pressure is applied until the tortoise tilts

   c. When extended foot reaches ground, the tortoise can tip over, right side up

4. Reasons for inability of tortoise to right itself — if critical thermal maximum or higher temperature has been reached (Hutchison et al., 1966) — *See*: XV. Physiology - C. Thermoregulation

E. Agonistic behavior

1. Head bobbing

    a. Initiated when 2 or more tortoises approach each other (Camp, 1916; Baerwald, 1971; Ernst and Barbour, 1972; Coombs, 1977*a*)

    b. May be used for species recognition, courtship, threat (Eglis, 1962; Coombs, 1977*a*)

    c. Occurs prior to any agonistic behavior (Camp, 1916)

2. Combat between tortoises

    a. Description (Miller, 1932; Cassel, 1945; Pepper, 1963; Switak, 1973)

        1) Usually occurs only among males (Burge, 1977; Coombs, 1977*b*)

        2) More frequent in August and September (Burge, 1977)

        3) Males recognize each other immediately, possibly by scent from chin glands (Grant, 1936*a*)

        4) Secretions from chin gland evoke agonistic behavior (Winokur, 1973; Coombs, 1974)—*See*: VII. Morphology - D. Chin glands or subdentary glands

        5) Begins with head bobs

        6) Each male draws his head in and rams or rushes toward the other male with its gular shield (Camp, 1916; Grant, 1936*a*)

        7) Ramming continues until one male tortoise retreats or one succeeds in overturning the other

        8) If a male retreats, the victor may fake a short pursuit

        9) Two large adult males observed butting and shoving each other (Berry, 1975*a*)

        10) Two subadult males observed, one was flipped over on its back (Berry, 1975*a*)

    b. Hypothesized purpose (Coombs, 1977*a*)

        1) May be for partial defense of a territory or home range

        2) May be to establish or maintain a loose and dendritic social behavior

3. Behavior of young tortoises

    a. Description

        1) Extremely belligerent, pugnacious (Grant, 1936*a*; Booth, 1958)

2) Lunge forward when touched, may open jaws and hiss (Grant, 1936*a*; Coombs, 1977*a*, *b*)

3) Occasionally attempt to bite (Coombs, 1977*a*, *b*)

4) Behavior may wane after a few days (Booth, 1958)

b. Purpose of behavior may be directed at potential predators (Coombs, 1977*a*)

F. Species recognition

1. Occurs through head bobbing (Camp, 1916; Coombs, 1977*a*)

2. Species specific

a. The head has a straight forward movement with little or no oscillations (Combs, 1977*a*)

b. Speed of head bobbing varies among the 3 gopher tortoise species in the United States (Eglis, 1962)

G. Mobility and locomotion

1. Locomotory rate and distance

a. 219.4 - 482.8 metres per hour (Woodbury and Hardy, 1948*a*)

b. As high as 0.26 metres per second for a frightened tortoise but normally .076 - .152 m per second (Coombs, 1974; Coombs, 1977*b*)

c. 6.4 to 8.0 km per day (Pope, 1939), especially if in search of water (Anonymous, 1945)

d. Hatchling normally covers 0.3 m in 25-35 seconds (Coombs, 1977*b*)

e. Average distance for trips (Burge, 1977)

1) For males, $\overline{x} = 143.0 \pm 12.0$ m (range 23.0 - 381.0 m)

2) For females, $\overline{x} = 147.0 \pm 9.0$ m (range 49.0 - 366.0 m)

f. Adults average 5.3 m per minute (range 2.0 - 7.6 m) (Burge, 1977)

g. May travel 365.8 to 1005.8 m in one day (Anonymous, 1973)

h. Over a 4-year period, 3 tortoises moved 137.2 - 274.3 m in Mojave Desert (Bogert, 1937)

i. A translocated adult female moved 2070 m (straight-line distance) over hills and washes in 15 days (Berry, 1975a)

j. Observed 8 released tortoises and their movements for up to 1 year (Crooker, 1971)

   1) November 1969 - April 1970, moved 45.6 m

   2) November 1969 - April 1970, moved 68.6 m

   3) November 1969 - April 1970, moved 45.7 m

   4) November 1969 - October 1970, moved 91.4 m

   5) November 1969 - October 1970, moved 91.4 m

   6) November 1969 - October 1970, moved 150.0 m

   7) October 1969 - October 1970, moved 68.6 m

k. Movements usually restricted to loop trips within a few hundred metres of favored burrows (Berry, 1975*a*)

2. "Tank complex" locomotion (Cassell, 1945)—a tortoise may struggle and ram against obstacles in its path instead of going around them

3. Climbing ability

   a. Able to climb steep terrain (Coombs, 1977*b*)

   b. Can reach some winter dens at the top of a steep bank (Woodbury and Hardy, 1948*a*; Boynton, 1970*a*)

4. Swimming ability

   a. Poor swimmers (Woodbury and Hardy, 1948*a*; Grant, 1960*a*)

   b. Must exert a great deal of effort to keep head above water (Woodbury and Hardy, 1948*a*)

   c. Eventually will drown (Woodbury and Hardy, 1948*a*)

   d. Captive tortoises may construct a shallow hole by a garden hose and then crawl in the pool of water formed for 30-40 minutes (Miles, 1953)

H. Feeding behavior—*See*: XII. Food and feeding behavior - D. Feeding behavior

I. Drinking behavior

1. Appear to be familiar with rock depressions that fill with water after rainstorms (Berry, 1974, Coombs, 1977*a*, *b*)

2. Drink free-standing water in rock depressions after rainstorms (Coombs 1977*a*, *b*)

3. During 2-year period, tortoises were never observed drinking free-standing water (Burge, 1977)

4. Preceding rainstorms, some tortoises have been observed digging shallow depressions in the desert floor; after rains the depressions were filled with water, but there were no observations of tortoises drinking from them (Nagy and Medica, 1977)

5. Observed thrusting head into loose earth during drinking, presumably to draw water from just below the surface (Auffenberg, 1963)

J. Sleeping behavior (Grant, 1936*a*)

1. Observed with head and neck extended from shell and resting on ground

2. Legs may also be extended from shell

K. Digging behavior

1. Nests—*See*: X. Reproduction - E. Nesting behavior

2. Dens—*See*: XVI. Burrows or dens - B. Winter burrows or dens

L. Thermoregulatory behavior—*See*: XV. Physiology - C. Thermoregulation

M. Vocalization

1. Five different recorded sounds analyzed with a sonagraph

   a. Hisses emitted (Patterson, 1976*b*)

      1) During mating (by female)

      2) When adult sleeping tortoise was grabbed

      3) During adult combat

      4) When adult was upside down

   b. Long calls emitted when adult was overturned (Patterson, 1976*b*)

   c. Pops and poinks emitted (Patterson, 1976*b*)

      1) When adult sleeping tortoise was grabbed

      2) When adult was upside down (dominant male assisted in righting the overturned tortoise)

   d. Grunts emitted (Patterson, 1976*b*)

      1) During mating (by males)

      2) When a sleeping tortoise was grabbed

      3) During combat

   e. Low cry emitted (Campbell and Evans, 1967)

      1) When resting

      2) When trying to climb out of sink

2. High thin scream emitted by a tortoise entangled in a towel in a box (Nichols, 1953)

3. Mechanism of sound production—during sound emissions gular pumping action often observed (Campbell and Evans, 1967)

4. Range

   a. 64-500 hertz, within tortoise hearing range (Patterson, 1976*b*)

   b. May contain 2 or 3 harmonics (Campbell and Evans, 1967)

5. Biological significance

   a. Unknown for low cries and grunts (Campbell and Evans, 1967)

   b. May have low information content (Patterson, 1976*b*)

      1) Long call—may elicit feeding response or fight behavior

      2) Pops and poinks—may cause flight if emitted by overturned subordinate male or may elicit dominant male assistance

N. Audition

1. Well-developed middle and inner ears (Miles, 1953)

2. Respond to ground vibration (Miles, 1953)

3. Able to hear sound of vehicle horn at distances >50 m (Coombs, 1977*a*)

O. Vision

1. Color vision

   a. Able to see color (Woodbury and Hardy, 1948a; Grant, 1960*a*; Boynton, 1970*b*; Murphy, 1973)

   b. Color range similar to man's (Miles, 1953)

   c. Tortoises in captivity have shown preference for food ite which are yellow or pink (Boynton, 1971; Olsen, 1971)

   d. May help to identify potential succulent food items from afar (Auffenberg, 1969)

2. Distance vision (Coombs, 1977*a*)—able to see man at distances >60 m

3. Depth perception (Patterson, 1971*b*)

   a. Well developed

   b. Avoid a simulated deep cliff in experiments

   c. This plus forelimb tactile sensing may be related to avoidance of falling

P. Olfaction (Eglis, 1962)

1. Well developed

2. Required more so under arid conditions than under aquatic conditions of turtles

3. Necessary; in arid environments plants are apt to give off few chemical particles

4. Behavior illustrating use of olfaction in juvenile and 3 adults (in captivity)

   a. Observed moving head into a position to make sure head was within biting range of food items

   b. Movement was a straight forward motion of head with or without tiny sideways oscillations

5. Description of "sniffing" behavior in adults (Berry, 1972)

   a. Lower head and neck to substrate

   b. Touch snout to soil and rocks

   c. Snout touched in one or more places at intervals of 1 to 3 seconds or more

   d. As tortoise walked over ground it continued to pause and sniff substrate

Q. Daily behavior patterns — activity season

1. Emerge from dens early in morning to feed (McCawley and Sheridan, 1972)

2. Move into shade of vegetation when body temperature rises (McGinnis and Voigt, 1971)

3. Seek shelter of a cool summer den as ambient and ground temperatures continue to rise (as does temperature of the tortoise) (McGinnis and Voigt, 1971)

4. May emerge in late afternoon if temperatures are cool enough (Miles, 1953; Burge, 1977; Coombs, 1977*a*)

5. Return to same summer den nightly (Grant, 1936*a*)

6. Times of daily emergence vary with the temperature (Berry, 1975*b*)

   a. March, with cool morning temperatures, 0800 to 1000 hours

   b. April, with warm morning temperatures, 0700 to 0800 and 1600 to 1900 hours

   c. May, with warmer morning temperatures, around 0700 and 1600 to 1900 hours

   d. For March to May, tortoises may be active 2 to 4 hours

e. Late May to mid-June, with hot morning temperatures, 0500 to 0700 hours

f. For July and August, rarely emerge

g. September, with cooling temperatures, become more active

7. Daily movements

a. Wild tortoises (Coombs, 1977*b*)

1) Medium size tortoise may move 152.4-365.8 m in an active day

2) Hatchlings may move 15.2-45.7 m on a warm day

3) Larger tortoises may move over 548.6 m on a single day

4) Determined largely on degree of dependence on a particular cover site as well as food availability (Auffenberg and Weaver, 1969)

b. Transplanted wild tortoises (Berry, 1972)

1) Moved 970 m in a straight line in 36 hours (July)

2) Moved 3200 m in a straight line in 4 days (October)

8. May become nocturnal in extremely hot weather (Stephens, 1914)

9. No nocturnal activity observed during summer (Coombs, 1977*b*)

R. Seasonal behavior patterns

1. Migration

a. Beaver Dam Slope, Utah (Woodbury and Hardy, 1948*a*)

1) Spend winter period of dormancy at winter den sites

2) Spend active summer period on desert flats excavating shallow burrows at base of shrubs

3) Often involves a short migration between 2 den sites

4) May be controlled by photoperiodicity and temperature (Coombs, 1977*b*)

b. Mojave Desert (Miles, 1953)

1) May spend hot summer in foothills where vegetation is more abundant

2) Cooler periods spent at lower elevations

c. Sonora, Mexico (Auffenberg, 1969)

1) Nomadic for most of year

2) Foraging largely restricted to dry arroyo bottoms

2. Following summer rains — emerge in great numbers to feed upon newly germinated annuals and drink from small collecting pools (Van Denburgh, 1922; Berry, 1972)

3. Spring emergence

   a. Generally emerge around 15 March or late February and early March (Miles, 1953; Anonymous, 1973)

   b. Northwest Mojave Desert — last 2 weeks in February to last 2 weeks in March (Berry, 1974)

   c. Beaver Dam Slope, Utah

      1) March (Woodbury and Hardy, 1940)

      2) Late March to late April (Coombs, 1977*a*)

      3) Primary trigger may be temperature and not light (Coombs, 1977*a*)

   d. Arden Study Area, Nye County, Nevada

      1) Emerged from 1 March to 20 April 1975

      2) Den temperatures of 2.3 m depth were around 15°C (Burge, 1977)

4. Active period

   a. Spring

      1) Behavior dominated by temperatures in southwest Utah (Woodbury and Hardy, 1948*a*; Coombs, 1977*a*)

      2) Short excursions from wintering dens develop into longer excursions as days become warmer (Coombs, 1977*b*)

      3) Females and young tend to remain near winter dens for most of year (Coombs, 1977*a*)

      4) Summer den construction begins in late spring when temperatures are greater than 32°C (Coombs, 1977*b*)

      5) Social interaction high (Coombs, 1977*a*)

      6) One activity period per day through May in late morning and early afternoon (southern Nevada) (Burge, 1977)

      7) Two activity periods per day, morning and, at times, late afternoon (northwest Mojave Desert, California) (Berry, 1974)

      8) Bask mostly in early spring (Burge, 1977)

      9) Some reproductive activity — *See*: X. Reproduction - C. Breeding season

      10) Feeding activity — *See*: XII. Foods and feeding behavior - C. Feeding periods

b. Summer

1) Much of time spent in summer dens (Berry, 1974*b*; Coombs, 1977*b*)

2) Two activity periods per day from May to September (southern Nevada) (Burge, 1977)

3) One activity period per day, early in morning (northwest Mojave Desert, California) (Berry, 1974)

4) Active in early morning and often in late evening, not at midday because of prohibitively high temperatures (Burge, 1977; Coombs, 1977*a*)

5) Behavior includes basking, returning to cover without further activity, traveling varying distances before returning to same cover site, or traveling to another cover site (Burge, 1977)

6) Highest activity is in July (Burge, 1977)

7) Some reproductive activity — *See*: X. Reproduction - C. Breeding season and L. Hatching time

8) Feeding activity — *See*: XII. Food and feeding behavior - C. Feeding periods

c. Estivation

1) Occurs during hottest part of summer (Coombs, 1974; Coombs, 1977*a*)

2) Often occurs in June after annuals have been consumed (Anonymous, 1973)

3) Usually conincides with drying up of annual plants used for food (Coombs, 1977*a*)

4) May be prolonged in dry years; available forage is reduced so the tortoise reduces or stops its surface activities (Coombs, 1977*a*)

5) May reduce energy expenditure significantly (Coombs, 1977*a*)

d. Late summer and fall

1) In September, when temperatures cool down, tortoises emerge from estivation to forage before heading for winter dens (Coombs, 1974)

2) By late September, tortoises are active again but at winter denning areas (Coombs, 1977*a*)

3) One activity period per day (southern Nevada) (Burge, 1977)

4) May feed on dried annuals and dirt (Anonymous, 1973)

5) Social interactions may be high (Coombs, 1977*a*)

6) Some tortoises especially juveniles did not emerge from summer dormancy and remained inside dens through winter (northwest Mojave Desert, California) (Berry, 1974)

5. Hibernation

a. Initial period

1) Generally begins around the beginning of October (Miles, 1953)

2) Northwest Mojave Desert, California — by late September or mid-October (Anonymous, 1973; Berry, 1975*b*)

3) Beaver Dam Slope, Utah — begins in early to mid-fall (Coombs, 1977*b*)

4) Arden Study Area, Nye County, Nevada (Burge, 1977)

a) Observed beginning from 20 October to 11 November

b) Five or more tortoises of both sexes were seen hibernating together

5) In Sonora, Mexico, tortoises are active for most of year (Auffenberg, 1969)

6) On Isla Tiburon tortoises were reported inactive from October to spring (Bury et al., 1978)

b. Possible causes

1) Cold temperatures and changes in atmospheric pressure (Coombs, 1977*a*)

2) Hibernate regularly in colder parts of range but not warmer areas (Auffenberg and Iverson, 1979)

c. Hibernating posture (Woodbury and Hardy, 1948*a*)

1) Head almost completely retracted into shell

2) Legs pulled part way into shell

d. Winter activity

1) May emerge to entrance of dens on warm days to feed (Coombs, 1977*a*; Auffenberg and Iverson, 1979)

2) May move to a new winter den (Woodbury and Hardy, 1948*a*)

X. Reproduction

A. Age and size at sexual maturity

1. Wild tortoises

a. 15-20 years (Woodbury and Hardy, 1948*a*)

b. 12-20 years (Miller, 1955)

c. 12-18 years (Bury and Marlow, 1973)

d. May be 20 or more years (Berry, 1972)

e. 20 years to reach reproductive maturity (Stebbins, 1974)

f. Minimum of 12 years for female tortoises (Anonymous, 1970)

g. May be 206 mm carapace length for tortoises in the Arden Study Area, Nye County, Nevada; females with carapace lengths of 206, 211, and 214 mm showed shell wear typical of older females (Burge, 1977)

h. Sexes may be differentiated at 140 mm carapace length or greater for Utah population (Coombs, 1977*b*)

i. Female with a carapace length of 203 mm laid a clutch of 4 eggs (Camp, 1917)

j. Carapace length of 230-285 mm for females and 250-300 mm for males in Utah (Woodbury and Hardy, 1948*a*)

k. 215-220 mm carapace length (Berry, 1972)

l. Female with carapace length of 220 mm laid clutch of 6 eggs (Berry, 1975*b*)

2. Captive tortoises

a. 14 or more years (Berry, 1972)

b. 12-13 years (Stewart, 1973)

c. May be as early as 3 years with continuous feeding and no hibernation period (Jackson et al., 1976)

d. Mature motile spermatozoa present in 4-year-old male tortoise (Jackson et al., 1978)

B. Secondary sexual characteristics

1. Male

a. Larger in size than the female (Grant, 1936*a*; Woodbury and Hardy, 1948*a*; Carr, 1952; Patterson, 1972*b*; Coombs, 1977*b*)

b. Longer tail and longer, more curved gulars than for females (Grant, 1936*a*; Grant, 1946; Woodbury and Hardy, 1948*a*; Coombs, 1977*b*)

c. Concave plastron and smaller pelvic clearance from seam of anals to edge of rear marginals (Grant, 1936*a*; Woodbury and Hardy, 1948*a*; Bramble, 1971; Coombs, 1977*b*)

d. Chin glands or subdentary glands well developed in spring and summer (Rose et al., 1969; Coombs, 1977*a*, *b*) — *See*: VII. Morphology - D. Chin glands or subdentary glands

e. Inguinal depression deeper and more pronounced (Woodbury and Hardy, 1948*a*; Bramble, 1971)

f. Nails more thickened (Carr, 1952)

g. Dermal ossicles are better developed on thigh and hindfoot than for females (Auffenberg, 1976)

2. Female

a. Smaller in size than the male (Grant, 1936*a*; Woodbury and Hardy, 1948*a*; Coombs, 1977*b*)

b. Shorter tail, less broad at the base (Grant, 1936*a*; Grant, 1946; Woodbury and Hardy, 1948*a*; Coombs, 1977*b*)

c. Gulars somewhat shorter and straight (Grant, 1936*a*; Woodbury and Hardy, 1948*a*; Coombs, 1977*b*)

d. Chin glands functional but not well developed (Rose et al., 1969; Coombs, 1977*a*, *b*) — *See*: VII. Morphology - D. Chin glands or subdentary glands

C. Breeding season

1. In captivity

a. In August (Miles, 1953)

b. June to September (Boynton, 1970*a*)

2. In wild

a. March (Coombs, 1977*b*)

b. May (Coombs, 1974)

c. July (Woodbury and Hardy, 1948*a*; Coombs, 1977*b*)

d. August (Householder, 1950)

e. Observed 9 October (Tomko, 1972)

f. In August, followed by June egg laying (Miles, 1953)

g. In spring, completed by last of April (Grant, 1936*a*)

h. Highest frequency in August and September, also observed in October (Burge, 1977)

i. Observed mating throughout the active season especially in spring and fall (Berry, 1975*b*)

D. Courtship behavior

1. Species and sex recognition — *See*: VII. Morphology - D. Chin glands or subdentary glands

2. Description (Woodbury and Hardy, 1948*a*; Householder, 1950; Watson, 1962; Berry, 1972; Patterson, 1972*b*; Tomko, 1972; Switak, 1973; Coombs, 1974; Coombs, 1977*a*, *b*)

   a. Following species and sex recognition the male approaches the female with neck outstretched and initiates head bobbing, increasing bobbing intensity

   b. Female may or may not respond

   c. If no response, the male circles the female nipping at her shell and legs

   d. Male may circle female several times

   e. Male may also bite female and raise part of her off the ground

   f. If female responds, she will remain in place, come out of her shell, and evert her cloaca

   g. Male mounts female from the rear

   h. Male exhibits pumping action with his pygal scute striking the ground and his head extended forward

   i. Male will emit a grunting sound or a hiss; he may also stamp his hindfeet

   j. Copulation continues until female moves away

   k. Female may move her neck from side to side or eat during copulation

   l. Use of tail in copulation

      1) Male uses finger-like tail tip to hold on to female

      2) Possibly tip used to steer female in straight line during male's upthrusts

3. Courtship behavior observed in wild is similar to behavior observed in captivity — wild tortoises (Tomko, 1972); captive tortoises (Householder, 1950; Nichols, 1953)

4. Five pairs of wild adult tortoises and one pair, a juvenile female (162 mm carapace length) and a subadult male (192 mm carapace length) were observed (Berry, 1975*a*)

5. Evidence of courtship and mounting can be seen in mating depressions in soil (Berry, 1972)

   a. Depression or crater 5.1 cm deep or more is created

   b. Mating depression is circular or oblong and 30.5-91.4 cm in diameter

E. Nesting behavior

1. Nest location in the wild

   a. Usually found at mouth of winter dens (Camp, 1916; Woodbury and Hardy, 1948*a*; Coombs, 1974; Coombs, 1977*a*, *b*)

   b. One deep burrow contained broken halves of 2 white hard-shelled eggs (Camp, 1916)

   c. Observed one dug in middle of group of *Ephedra nevadensis* (Burge, 1977; Coombs, 1977*b*)

   d. Occasionally inside summer den (Woodbury and Hardy, 1948*a*)

   e. Observed inside a recently dug pallet burrow (Berry, 1974)

2. Nest size

   a. Captivity

      1) 76-mm-deep hole (Miller, 1932; Boynton, 1970*a*)

      2) 254 mm deep; 203 mm diameter (Booth, 1958)

      3) 152 mm deep, 229 mm diameter at top, 178 mm diameter at bottom (Nichols, 1953)

      4) 127 mm deep, 102 mm wide, 114 mm long (Lee, 1963)

   b. In the wild

      1) 76-152 mm deep (Berry, 1972)

      2) 4-5 cm of soil covering 2 layers of eggs (Burge, 1977)

      3) Sandy area, 127-152 mm deep (Coombs, 1977*b*)

3. Nest construction and egg laying — wild tortoises (Boynton, 1970*a*; Anonymous, 1973; Berry, 1974; Coombs, 1974; Coombs, 1977*a*) — captive tortoises (Miller, 1932; Grant, 1936*a*; Miles, 1953; Stuart, 1954; Miller, 1955; Lee, 1963)

   a. Observations similar for captive and wild tortoises (Lee, 1963; Berry, 1972)

   b. Female digs a hole with her hind legs and may urinate

   c. Digging may last up to 2 hours until nest is excavated

   d. Female holds both hind legs straight and anchored in position in the nest

   e. The cloaca begins to swell and the eggs are extruded one at a time

   f. After completion of egg laying, the hindfeet are alternately used to arrange and pat down the eggs

g. Eggs are covered by scraping dirt into the hole with the hind legs, alternating with leg patting

h. When the nest is completely covered, a large amount of bladder fluid may be released over the nest and the mud patted

i. Possible reasons for urination — *See*: X. Reproduction - E. Nesting behavior - 5. Nest urination

j. Dry soil found from soil surface to nest bottom (Burge, 1977)

4. Time of nest construction and egg laying

a. In the wild

1) May (Coombs, 1977*b*)

2) Late May and early June (Anonymous, 1973)

3) 3 June (Berry, 1975*a*)

4) 11 June (Burge, 1977)

5) Possibly late May through October (Coombs, 1977*a*)

6) In late afternoon or early evening (Berry, 1972)

b. In captivity

1) June (Grant, 1936*a*; Miles, 1953)

2) 18 June (Camp, 1917)

3) 28, 29 June (Booth, 1958)

4) July (Nichols, 1953; Miles, 1955)

5) October (Miller, 1932; Miller, 1955)

6) In late afternoon or early evening (Stuart, 1954)

5. Nest urination

a. Acts as a repulsor to egg predators (Patterson, 1971*a*)

b. Helps camouflage nest (Patterson, 1971*a*)

c. Compacts soil to make nest excavation difficult (Patterson, 1971*a*)

d. Does not prevent bacterial or fungal growth (Patterson, 1971*a*)

e. May help prevent weathering from exposing eggs (Coombs, 1977*a*)

f. May form a protective crust to help prevent egg desiccation (Coombs, 1977*a*)

F. Sperm storage (apparently only the following account has been published) — possibly store sperm for up to 1.5 years; a captive female isolated from males for 1.5 years laid fertile eggs (Miller, 1955)

G. Clutch size

1. Range

a. 2 to 14 eggs (Miller, 1955; Berry, 1974)

b. 4 to 12 (Anonymous, 1973)

2. Records of clutch sizes

a. Wild tortoises

1) 3 to 7 eggs (Woodbury and Hardy, 1948*a*; Boynton, 1970*a*; International Union for the Conservation of Nature and Natural Resources, 1970)

2) 4 eggs (Berry, 1972)

3) 5 eggs (Grant, 1946)

4) 4 to 6 eggs (Coombs, 1974; Coombs, 1977*b*)

5) 6 eggs laid by female tortoise with 220 mm carapace length (Berry, 1975*a*)

b. Captive tortoises

1) 4 eggs (Camp, 1917; Nichols, 1953)

2) 5 eggs (Lee, 1963; Loomis and Geest, 1964)

3) 5 to 13 eggs (Stuart, 1954)

4) 6 eggs (Grant, 1936*a*; Trotter, 1973)

5) 7 to 12 eggs (Anonymous, 1970)

6) 8 eggs (miller, 1955)

7) 9 eggs (Miles, 1953; Nichols, 1953)

8) 10 eggs (Booth, 1958)

3. Numbers of clutches per active season — 1 clutch of 8 eggs laid, 2nd clutch laid 6 weeks later by a captive female (Miller, 1955)

4. Factors that may affect clutch size and frequency

a. Size of female — in general, smaller females produce smaller clutches (Anonymous, 1973)

b. Mature females are unlikely to produce a clutch every year in the wild (Coombs, 1977*a*)

1) May be dependent on forage availability (Anonymous, 1973)

2) Water deficit in dry years may reduce egg production. Water is needed in egg production and nest digging (Coombs, 1977*a*)

c. Desert tortoise is a *K*-selected species. It has a low natality (Berry, 1978*a*)

H. Eggs

1. Description

a. Shell is thick, hard, white, translucent, with coarse texture and pits; resistant to desiccation (Miller, 1932; Grant, 1936*a*; Grant, 1946; Coombs, 1974; Coombs, 1977*b*)

b. Shape is slightly asymmetrical from spherical (Camp, 1916; Camp, 1917; Miller, 1932; Grant, 1960*a*)

c. Tough, pale cream-colored yolk in center (Miller, 1932)

d. Fluid albumen around a viscous one (Pope, 1939)

2. Dimensions and weight

a. Wild tortoises

1) Four eggs (Burge, 1977)

a) 43.0 x 33.0 mm

b) 45.0 x 36.0 mm

c) 46.0 x 33.0 mm

d) 47.0 x 34.0 mm

2) Measurements and average weights of 6 eggs (Berry, 1975*a*)

a) 37.5 x 42.5 mm

b) 41.0 x 45.0 mm

c) 37.0 x 47.0 mm

d) 37.0 x 42.0 mm

e) 40.0 x 46.0 mm

f) 39.5 x 41.0 mm

g) Average weight 41.6 g/egg

b. Captive tortoises

1) Measurements of 2 eggs (Miller, 1932)

a) 41.6 x 36.7 x 34.9 mm

b) 48.7 x 39.6 x 38.2 mm

2) Weight and dimensions of 3 eggs (Grant, 1936*a*)

a) 27.2 g, 42.0 x 36.5 mm

b) 30.2 g, 42.0 x 37.5 x 35.7 mm

c) 27.7 g, 42.0 x 36.0 mm

3) One egg (Camp, 1917)

a) Shortest diameter 35.0 mm

b) Longest diameter 42.0 mm

4) About 25.4 to 38.1 mm in diameter (Camp, 1916; Miles, 1953)

I. Fertility rate

1. Wild tortoises — of 4 eggs laid, 2 were fertile (Burge, 1977)

2. Captive tortoises

a. Five of 5 eggs fertile (Grant, 1946)

b. Five of 6 eggs fertile (Trotter, 1973)

c. Five of 9 eggs fertile (Miles, 1953)

J. Egg development (Booth, 1958)

1. 21 days, cloudy contents

2. 22 days, blood lines seen, then expand, darken

3. 35 days, embryo discernible, 9.5 mm long

4. 37 days, embryo shows movement

5. 66 days, embryo well developed

6. 82 days, hole in shell with egg tooth protruding

7. Fully developed tortoise in egg has plastron fold between 6th and 7th marginals (Grant, 1946)

8. Position of fetus in egg is one with feet flattened, neck retracted, part of head projected out (Woodbury and Hardy, 1948*a*)

9. Rate of development of each egg per clutch varies (Grant, 1936*a*)

K. Incubation time

1. Wild tortoises

a. 105-135 days (Coombs, 1974)

b. 78-86 days for human-manipulated eggs (Berry, 1975*a*)

c. 98-101 days (Burge, 1977)

d. May be greater than 180 days as recently hatched tortoises have been seen in spring (Grant, 1936*a*; Coombs, 1977*a*, *b*)

2. Captive tortoises (incubation time varies from clutch to clutch and within a clutch)

    a. 94-102 days (Hunsaker, 1968)

    b. 98-118 days (Stuart, 1954)

    c. 83, 101, 104 days for individual eggs in one clutch (Booth, 1958)

    d. 105-120 days (Miles, 1953)

    e. 150, 270 days for 5 eggs in one clutch (Grant, 1936*a*)

    f. Sometimes greater than 120 days (Anonymous, 1970)

    g. 108-111 days (Trotter, 1973)

L. Hatching time (generally in late summer, fall, and late spring)

1. Wild tortoises

    a. 7 June to 14 September for eastern Kern County, California (Berry, 1972)

    b. 20 to 28 August for a clutch laid 3 June (Berry, 1975*a*)

    c. May (Coombs, 1974)

    d. 17, 19 September, eggs laid 11 June (Burge, 1977)

2. Captive tortoises

    a. 18 June; mid-August; 2, 15 September; 7, 8, 11 October (Grant, 1936*a*)

    b. June, October (Miller, 1955)

    c. From a clutch laid in June, 4 hatched in November and 1 the following March (Grant, 1936*a*)

    d. 18 September; 7, 10 October (Booth, 1958)

    e. 8 November through 11 November (Trotter, 1973)

3. Twinning (Hunsaker, 1968)

    a. 15 September, in captivity

    b. Junction of twins at yolk sac attachment

M. Hatching success

1. Wild tortoises (apparently only the following account has been published) — reduced success because of dessication and natural predators (Bury and Marlow, 1973)

2. Captive tortoises

   a. Of 3 eggs laid, 1 hatched (Grant, 1936*a*)

   b. Of 3 eggs laid, 0 hatched
   Of 4 eggs laid, 0 hatched
   Of 9 eggs laid, 0 hatched
   Of 6 eggs laid, 1 hatched
   Of 7 eggs laid, 0 hatched
   Of 5 eggs laid, 3 hatched
   Of 4 eggs laid, 0 hatched
   Of 4 eggs laid, 0 hatched
   Of 6 eggs laid, 0 hatched
   Of 2 eggs laid, 0 hatched
   Of 9 eggs laid, 2 hatched
   Of 5 eggs laid, 0 hatched
   Of 4 eggs laid, 0 hatched
   Of 5 eggs laid, 0 hatched
   Of 4 eggs laid, 0 hatched
   Of 3 eggs laid, 0 hatched
   Of 5 eggs laid, 0 hatched
   Of 2 eggs laid, 0 hatched
   Of 6 eggs laid, 4 hatched
   Of 4 eggs laid, 0 hatched
   Of 3 eggs laid, 0 hatched (Nichols, 1957)

   c. Of 4 eggs laid, 0 hatched (Lee, 1963)

   d. Of 6 eggs laid, 4 hatched (Trotter, 1973)

   e. Of 7 eggs laid, 7 hatched, one with twin tortoises (Hunsaker, 1968)

   f. Of 9 eggs laid, 5 hatched (Miles, 1953)

   g. Of 10 eggs laid, 5 hatched (Booth, 1958)

N. Hatchling description — *See*: VII. Morphology - B. Hatchlings

O. Parental behavior

1. Under normal conditions the female provides no care for the eggs or the new offspring (Coombs, 1974)

2. In captivity the female may crush several of her own young by walking over them and lowering her body weight on them; this has not been observed in the wild (Nichols, 1953)

P. Hatchling success — *See*: XI. Growth - G. Hatchling survival

XI. Growth

A. Growth and maturation rates

1. Growth

a. In captive tortoises

1) (Patterson and Brattstrom, 1972)

Growth period (years)	Mean (mm) carapace length	Percent increase
0	45.6	...
0-5	78.2	71.4
5-10	122.6	56.7
10-15	164.2	33.9
15-20	232.0	41.2
20-25	257.3	10.9
25-30	274.0	6.1

a) Usually more rapid for younger tortoises

b) Rate slows down as animal reaches maturity with a slight increase in years 15-20

2) Hatchling growth (Grant, 1936*a*)

Date	Carapace length (mm)
7 October	36.0
8 October	41.0
11 October	44.0
18 June	44.5
15 August	48.0

3) Growth of 6 captive tortoises (Miller, 1932)

Carapace length (mm)			
When acquired	After 1 year	After 2 years	After 3 years
85.2	92.2	98.3	...
93.3	101.4	106.6	...
108.0	...	112.5	...
106.0	...	110.5	...
46.9	70.4	...	...
44.7	46.8	58.4	74.4

b. Wild tortoises

1) Negligible growth rate for some adult wild tortoises for as long as 7 years (Woodbury and Hardy, 1948*a*; Coombs, 1974)

2) In 1 year a subadult grew from 181-193 mm carapace length (Berry, 1975*b*)

3) In 4.3 years the carapace length of a male desert tortoise increased from 206-302 mm; for a female the carapace length increased from 204-239 mm in 7 years (Woodbury and Hardy, 1948*a*)

4) Growth rate of 6 tortoises on the Beaver Dam Slope, Utah (Hardy, 1976)

Sex	Years	Growth in carapace length (mm)
Male	1945-1962	245-257
Male	1944-1966	265-271
Male	1945-1969	257-267
Male	1943-1969	260-263
Female	1944-1966	251-259
Female	1944-1969	217-218

5) Growth of tortoises in southern Nevada (Medica et al., 1975)

a) Average annual growth from 1963 to 1973 for 22 tortoises 3.3 to 10.1 years old was 9.1 mm (range 4.3 mm/yr-14.4 mm/yr

b) Growth generally restricted to April to July

c) Growth greatest following winters of high precipitation (1969 growth, carapace length)

i) One tortoise was 102 mm on 20 May and 113 mm on 29 July or an increase of 10% in 2 months

ii) One tortoise was 113 mm on 20 May and 119 mm on 18 June or an increase of 5% in 1 month

d) Growth of 3 tortoises from 1969 to 1972

i) May 1969 — 113 mm
July 1969 — 124 mm
July 1972 — 134 mm

ii) May 1969 — 107 mm
July 1969 — 120 mm
July 1970 — 130 mm
July 1971 — 134 mm

iii) May 1969 — 157 mm
July 1969 — 169 mm
July 1970 — 172 mm
July 1971 — 180 mm
July 1972 — 180 mm

2. Shell growth — strong positive correlation between shell density and carapace length (Patterson, 1978)

3. Maturation rate (Jackson et al., 1976)

   a. For male sibling captive tortoises, percent increase of carapace length over 3 years was 176, 43, 11

   b. All tortoises appear to be near sexual maturity after 3 years in captivity

   c. Length of each tortoise corresponds to length of wild tortoise after 11, 17 and 18 years

   d. In wild, sexual maturity is attained between 12 and 20 years of age (Woodbury and Hardy, 1948*a*)

   e. Four-year-old male tortoise, carapace length 236 mm, possessed mature motile spermatozoa (Jackson et al., 1978)

   f. Shell dimensions and weight increased during 4th year of growth (Jackson et al., 1978)

      1) Decrease in growth rate during the 5th year

      2) Surge in growth during 4th year associated with attainment of puberty

   g. Possible reasons for rapid maturation

      1) Captive tortoises continually have water and high quality food available

      2) Captives often do not enter winter dormancy so growth occurs year round, not just in spring ans summer

4. Factors affecting growth and maturation

   a. Food availability — best growth rates occur in years when plant production is above average (Medica et al., 1975)

   b. Food variety (Switak, 1973)

   c. Length of active season — growth usually occurs between April and July (Switak, 1973; Medica et al., 1975)

   d. Mean annual growth positively correlated with winter rainfall (October to March) (Medica et al., 1975)

B. Age determination in wild tortoises (no accurate way to determine age of a tortoise)

   1. Counting growth rings or ridges on scutes

      a. Not all rings formed may be complete (Switak, 1973)

      b. Rings are not annual in appearance (Miller, 1932; Woodbury and Hardy, 1948*a*; Boynton, 1970*a*)

      c. Juvenile scutes may be shed after 15 to 20 adult growth rings have formed (Coombs, 1974)

      d. Larger tortoises may lose rings through wear (Patterson, 1972*a*)

   2. Age based on carapace length (Medica et al., 1975)

      a. If a hatchling tortoise is 40 mm, then a 100-mm tortoise would be about 6 years old

      b. A 200-mm tortoise would grow at the same rate or be about 16 years old

   3. General classification for wild tortoises based on carapace length (Berry, 1973*b*)

      a. $>$214 mm; adult tortoise

      b. 171-214 mm; subadult

      c. 101-170 mm; juvenile

      d. 61-100 mm; young

      e. $<$61 mm; hatchling

   4. Old age determination

      a. Carapace scutes worn smooth, devoid of growth ridges (Grant, 1936*a*; Burge, 1977)

      b. Edges of carapace scutes thickened giving the appearance of scute concavity (Grant, 1936*a*)

5. Approximate age has been calculated for captive tortoises (Patterson, 1972*a*)

    a. Based on carapace length

    b. Captive tortoise with 200-mm carapace length may be 13 to 23 years old

C. Longevity

1. Captivity

    a. Two years, 9 months at the Philadelphia Zoo (Conant and Hudson, 1949)

    b. Up to 20 years when a desert climate is maintained (Miller, 1955)

    c. Some animals kept up to 26 years (Nichols, 1957)

    d. A full-grown tortoise was kept 40 years (Miles, 1953)

2. In the wild (estimates only)

    a. 60-100 years (Anonymous, 1973)

    b. 50-100 years (Woodbury and Hardy, 1948*a*; Bury and Marlow, 1973)

    c. 30-50 years (Switak, 1973)

D. Age distribution

1. Beaver Dam Slope, Utah, 1936-1946 (Woodbury and Hardy, 1948*a*)

    a. Few young tortoises found

    b. Immature tortoises may make up $<5\%$ of the population

    c. Adults make up 90% of the population

    d. Subadults, 9%

    e. Juveniles, 1%

    f. High percentage of adults in a population may be characteristic of an old population

2. Beaver Dam Slope, Utah, 1972-1974 (Coombs, 1977*b*) — High percentage of adults

    a. 28.2% old adults — carapace length >250 mm

    b. 43.7% adults — carapace length 200-249 mm

c. 18.3% young adults — carapace length 140-199 mm

d. 8.5% juveniles — carapace length 60-139 mm

e. 1.4% hatchlings — carapace length <60 mm

3. Paradise Canyon, Utah, 1972-1974 (Coombs, 1977*b*)

   a. More than one third were juveniles and hatchling tortoises

      1) 15.5% old adults — carapace length >250 mm

      2) 26.5% adults — carapace length 200-249 mm

      3) 19.9% young adults — carapace length 140-199 mm

      4) 27.7% juveniles — carapace length 60-139 mm

      5) 10% hatchlings — carapace length <60 mm

   b. High percentage of younger animals may be characteristic of a population newer than that on the Beaver Dam Slope

4. Salt Wells Valley, California (Berry, 1974)

   a. Adults, 58% — carapace length >214 mm

   b. Subadults, 17% — carapace length 171-214 mm

   c. Juveniles, 19% — carapace length 101-170 mm

   d. Hatchlings and small tortoises, 6% — carapace length <100 mm

5. Desert Tortoise Natural Area, eastern Kern County, California (Berry, 1974; Berry, 1975*b*)

   a. Adults, 42%

   b. Subadults, 14%

   c. Juveniles, 33%

   d. Small tortoises, 10%

   e. Hatchlings, 2%

6. Arden Study Area, Nye County, Nevada, 1975 (Burge and Bradley, 1976)

   a. Adults, 50% of marked population

   b. Adults, 55%

   c. Subadults, 17%

   d. Juveniles, 18%

   e. Young tortoises, 10%

   f. Hatchlings, 1%

7. Ivanpah Valley Study Plot, San Bernardino County, California, 30 March to 6 June 1977 (Berry, 1978*b*)

   a. Adults, 43%

   b. Subadults, 18%

   c. Juveniles, 34%

   d. Very young tortoises, 3%

   e. Hatchlings, 2%

8. Goffs Study Plot, San Bernardino County, California, 1 April to 11 June 1977 (Berry, 1978*b*)

   a. Adults, 47%

   b. Subadults, 29%

   c. Juveniles, 20%

   d. Very young tortoises and hatchlings, $<$ 5%

9. Chemehuevi Valley Study Plot, San Bernardino County, California, 15 April to 21 May 1977 (Berry, 1978*b*)

   a. Adults, 33.3%

   b. Subadults, 36.4%

   c. Juveniles, 24.2%

   d. Very young tortoises, 0.0%

   e. Hatchlings, 6.2%

10. Fremont Peak Study Plots, San Bernardino County, California, 31 March to 12 June 1977 (Berry, 1978*b*)

   a. Adults, 34%

   b. Subadults, 16%

   c. Juveniles, 48%

   d. Very young tortoises, 2%

   e. Hatchlings, 0.0%

11. Chuckwalla Bench Study Plot, Riverside County, California, 25 April to 31 May 1977 (Berry, 1978*b*)

   a. Adults, 49.2%

   b. Subadults, 22.5%

   c. Juveniles, 25.8%

d. Very young tortoises, 2.5%

e. Hatchlings, 0.0%

12. Picacho Mountains, Pinal County, Arizona, 1976-1978 (Berry, 1978*a*)

a. Adults, 69%

b. Subadults, 27%

c. Juveniles, 4%

d. Young tortoises, 0.0%

e. Hatchlings, 0.0%

E. Sex ratios (sex can be determined for mature tortoises only)

1. Populations with sex ratios heavily biased in favor of males are in poor condition (Berry, 1978*a*)

2. Beaver Dam Slope, Utah, 1936-1946 (Woodbury and Hardy, 1948*a*)

a. Of 318 marked adult animals, 204 were females and 114 were males

b. 66 ♂♂:100 ♀♀

c. 36% males and 64% females

3. Beaver Dam Slope, Utah, 1972-1974 (Coombs, 1977*a*, *b*)

a. Of 350 adult animals marked, 245 were males

b. 71.7% males and 28.3% females, or 253 ♂♂:100 ♀♀

c. Reversal in the sex ratio from 1945

d. Reduced number of tortoises plus a high ratio of males to females lowers the probability of male-female encounters

e. Reason for high ratio of males to females may be due to past selective collecting by man for female tortoises

4. Paradise Canyon, Utah, 1972-1974 (Coombs, 1977*a*, *b*)

a. 30% males and 70% females, or 43 ♂♂:100 ♀♀

b. Of 103 marked adult animals, 32 were males and 71 were females

5. Salt Wells Valley, California (Berry, 1974)

a. Ratio of 39 ♂♂:100 ♀♀ for adults and subadults

b. Ratio of 47 ♂♂:100 ♀♀ for adults only

6. Desert Tortoise Natural Area, eastern Kern County, California (Berry, 1974) — ratio of 87 ♂♂:100 ♀♀

7. Arden Study Area, Nye County, Nevada, 1975

    a. Ratio of 136 ♂♂:100 ♀♀ for subadults and adults (Burge and Bradley, 1976)

    b. Of 67 adults 40 were males and 27 were females (Burge, 1977)

8. Ivanpah Valley Study Plot, San Bernardino County, California, 30 March to 6 June 1977 (Berry, 1978*b*) — ratio of 70 ♂♂:100 ♀♀ for adult and subadult tortoises

9. Goffs Study Plot, San Bernardino County, California, 1 April to 11 June 1977 (Berry, 1978*b*) — ratio of 120 ♂♂:100 ♀♀ for adult and subadult tortoises

10. Chemehuevi Valley Study Plot, San Bernardino County, California, 15 April to 21 May 1977 (Berry, 1978*b*) — ratio of 77 ♂♂:100 ♀♀ for adult and subadult tortoises

11. Fremont Peak Study Plots, San Bernardino County, California, 31 March to 12 June 1977 (Berry, 1978*b*) — ratio of 175 ♂♂:100 ♀♀ for adult and subadult tortoises

12. Chuckwalla Bench Study Plot, Riverside County, California, 25 April to 31 May 1977 (Berry, 1978*b*) — ratio of 100 ♂♂:100 ♀♀ for adult and subadult tortoises

F. Population growth rate

1. Beaver Dam Slope, Utah, 1936-1946 (Woodbury and Hardy, 1948*a*)

    a. Natality of 1.57%

    b. Mortality higher

    c. Net effect equals population decline

2. Beaver Dam Slope, Utah, 1972-1974 (Coombs, 1977*b*)

    a. Minimum known natality, 1.74%

    b. Minimum known mortality, 4.57%

    c. Probable mortality rate of 8.9%

    d. This population has a negative annual growth rate, resulting in a decline

3. Paradise Canyon, Utah, 1972-1974 (Coombs, 1977*b*)

    a. 5.6% annual natality

    b. 1.1% annual mortality

    c. Annual increase of 4.5%

4. Beaver Dam Slope, Arizona, 1977-1978 (Hohman and Ohmart, 1978)

   a. Mortality may be as high as 20%

   b. Natality is much lower

   c. Result is negative annual growth rate for population

5. Picacho Mountain, Pinal County, Arizona (Berry, 1978*a*) — possible mortality of <2%

6. In natural undisturbed situations desert tortoise populations exhibit characteristics of *K*-selected species (Berry, 1978a)

   a. Low birth rate

   b. Low recruitment

   c. Low mortality in the older age categories

   d. Low population turnover

G. Hatchling survival in wild tortoise populations (apparently only the following accounts have been published)

1. Less than 1 to 3% of all hatchlings survive to maturity (Anonymous, 1973)

2. Hatchlings are more vulnerable to predation because of their soft shells (Grant, 1936*a*)

XII. Food and feeding behavior

A. Food taken in captivity: insects, dried jackrabbit meat (Pope, 1939); hamburger, canned dog and cat food (Beltz, 1958); grasses, fruits, buds, flowers, lettuce, bananas, clover, dandelions (Boynton, 1971); vegetables, cheese, bread (Miller, 1932); figs, peaches, melons, rose petals, radishes, snails (Nichols, 1953); apples, carrots, cabbage (Grant, 1936*a*; Miles, 1953)

B. Natural diet

1. General diet

   a. Sight observations

      1) Herbivorous (Camp, 1916; Miller, 1932)

      2) Green herbs, flowers (Woodbury and Hardy, 1948a)

      3) Succulent vegetation when available (Cox, 1881; Woodbury, 1931)

      4) *Hilaria* sp. (galleta grass) and *Bromus tectorum* (cheat grass), leaves and blossoms of annuals (Boynton, 1971; Olsen, 1971)

5) Grasses, cacti, blossoms of composites (Ernst and Barbour, 1972)

6) Annual wildflowers and grasses in California (Berry, 1973*a*; Berry, 1974)

7) Grasses, cactus, other low vegetation, occasionally insects and dead animal matter (Brown, 1968)

8) Annual and perennial grasses especially in Utah and Arizona (Berry, 1975*b*)

9) *Erodium cicutarium* used when nothing else is available (Berry, 1974)

10) Leaves and flowers of perennial shrubs are usually not taken (Berry, 1974)

b. Scat analysis

1) Minimum of 52% of tortoise diet is made up of grasses (Hansen et al., 1976)

2) Total diet composed of grasses, sedges, forbs, and shrubs (Hansen et al., 1976)

2. Food consumed — specific studies

a. Beaver Dam Slope, Utah, 1936–1946 — sight observations (Woodbury and Hardy, 1948*a*)

1) Grasses make up largest bulk of diet

2) *Hilaria* sp. and *Bromus tectorum* taken on 30 September 1939, 23 November 1939, 18 January 1941, and 28 October 1945

3) *Erodium cicutarium* (filaree) consumed on 18 January 1941

4) *Hilaria* sp. is chief food source

5) *Muhlenbergia porteri* (bush muhly) also an important part of diet and can be utilized year round

6) Observed reduction of perennial grasses possibly due to overgrazing

b. Pima County, Arizona — stomach analysis. Only grasses found in stomach, mostly *Bouteloua aristidoides* (needle grama) (Ortenburger and Ortenburger, 1927)

c. Lower Grand Canyon — scat analysis (Hansen et al., 1976)

1) *Bromus rubens* (foxtail brome), *Sphaeralcea* sp. (globemallow), *Tridens muticus* (slim tridens), *Aristida* sp. (three awn)

2) *Bromus rubens* made up 19%, *Tridens muticus* 20%, and *Aristida* sp. 22%

d. New water Mountains, Arizona — scat analysis (Hansen et al., 1976)

   1) *Aristida* sp., *Tridens muticus*, *Muhlenbergia porteri*, *Janusia gracilis* (slender janusia)

   2) *Tridens muticus* made up 50% of diet

e. Beaver Dam Wash, Utah — scat analysis (Hansen et al., 1976)

   1) *Bromus rubens*, *Erodium cicutarium*, *Ceratoides lanata* (winterfat)

   2) *Bromus rubens* made up 4% of the analyzed parts

f. Southwest Utah — sight observations and scat analysis (Coombs, 1977*b*)

   1) Winter food — *Erodium cicutarium*, *Bromus rubens*, *Bromus tectorum*

   2) Summer food — *Muhlenbergia porteri*

   3) Major part of diet during year is *Erodium cicutarium*, *Bromus rubens*, *Euphorbia albomarginata* (rattlesnake weed), *Erioneuron pulchellum* (fluff grass), *Muhlenbergia porteri*

   4) Of over 24 species eaten, 8 were grasses, 15 were forbs, 1 a cactus, 1 a shrub

   5) Other species consumed — *Cryptantha circumscissa* (Western forget-me-not), *Opuntia basilaris* (beavertail cactus), *Chorizanthe rigida* (rigid spiny-herb), *Chorizanthe brevicornu* (brittle spine-flower), *Eriogonum inflatum* (desert trumpet), *Erioneuron pilosum* (fluff grass)

   6) Availability of plants consumed (most to least) — *Bromus rubens*, *Erodium cicutarium*, *Euphorbia albomarginata*, *Muhlenbergia porteri*, *Bromus tectorum*

   7) Highest preference — *Muhlenbergia porteri*, but low availability

   8) Highest availability — *Bromus rubens* and *Erodium cicutarium*

   9) *Bromus rubens* has the lowest preference rate

   10) Observed consumption of plant species (most to least) — *Erodium cicutarium*, *Bromus rubens*, *Muhlenbergia porteri*, *Cryptantha circumscissa*, *Bromus tectorum*, *Eriogonum inflatum*

   11) Plants used by tortoises in Utah:

       Eriogonum inflatum
       Erodium cicutarium
       Euphorbia albomarginata
       Opuntia basilaris
       Bromus tectorum
       Erioneuron pulchellum
       Bromus rubens

Lepidium lasiocarpum (pepper-grass)
Muhlenbergia porteri
Chorizanthe rigida
Eriophyllum wallacei (wooly-daisy)
Cryptantha micrantha (purple-rooted forget-me-not)
Coleogyne ramosissima (black-brush)
Plantago insularis (plantain)
Cryptantha circumscissa
Phacelia fremontii (Fremont phacelia)
Eriogonum deflexum (skeleton weed)
Krameria parvifolia (little-leaved ratany)
Aristida sp.
Sporobolus sp. (dropseed)
Stipa sp. (needlegrass)
Acacia sp. (acacia)
Artemisia sp. (sagebrush)
Astragalus sp. (locoweed)
Atriplex sp. (saltbush)
Ephedra sp. (Mormon tea)
Erioneuron pilosum
Oryzopsis hymenoides (Indian rice grass)
Hilaria rigida (big galleta)
Larrea divaricata (creosote bush)
Leptodactylon sp. (prickly gilia)
Potentilla sp. (rock five-finger)
Sphaeralcea sp.
Mirabilis sp. (four-o'clock)
Kochia sp. (red molly)

g. Arden Study Area, Nye County, Nevada — sight observations (Burge and Bradley, 1976)

1) 17 species consumed:

Plantego insularis
Sphaeralcea ambigua
Festuca octoflora (six weeks fescue)
Euphorbia albomarginata
Opuntia ramosissima (pencil cactus)
Opuntia basilaris
Gaura coccinea (gaura)
Selinocarpus diffusus (desert sign-fruit)
Eriogonum inflatum
Mirabilis froebelii (giant four o'clock)
Erodium cicutarium
Krameria parvifolia
Stephanomeria pauciflora (desert straw, stick weed or wire lettuce)
Echinocactus polycephalus (nigger heads)
Allionia incarnata (windmills)
Hilaria rigida
Bouteloua barbata (six-weeks grama

2) *Plantago insularis* (plantain) major food item with 34% frequency of use

3) *Sphaeralcea ambigua* (desert mallow) second major food item with 27% frequency of use

h. Rand Mountains, Kern County, California — sight observations (Berry, 1975*a*, *b*)

1) Plants consumed March to June:

Astragalus didymocarpus (dwarf locoweed)
Erodium cicutarium
Amsinckia intermedia (common fiddleneck)
Lupinus odoratus (royal desert lupine)
Mentzelia nitens (Venus blazing star)
Stephanomeria exigua (annual mitra)
Gilia sp. (gilia)
Lasthenia chrysostoma (goldfields)
Salvia columbariae (chia)
Eriogonum sp. (buckwheat)
Camissonia sp. (primrose)
Chaenactis sp. (pincushion)
Malacothrix sp. (dandelion)
Langloisia matthewsii (desert calico)

2) Plants consumed in June:

Erodium cicutarium, dried *Schismus barbatus*

C. Feeding periods

1. Daily (McCawley and Sheridan, 1972)

a. During the morning and possibly late afternoon throughout the spring, summer, and early fall

b. Increase in duration during the cooler periods of the active season

2. Seasonally (Berry, 1975*b*)

a. In spring and early summer, feed on succulent plants for 6 weeks to 3.5 months

b. In late summer and early fall, feed on dried annuals

D. Feeding behavior

1. Duration of bouts varies from <1 minute to 30 minutes (Burge, 1977)

2. Description

a. Selective, walk about sniffing various plants taking one to several bites per plant before moving on (Coombs, 1977*a*)

b. May stay and browse at leisure on perennials if ambient temperatures are not extreme (Coombs, 1977a)

c. Fallen fragments from a plant are usually not consumed (Burge, 1977)

d. Little mastication occurs other than biting the food and swallowing it (Burge, 1977)

e. Consume leaves, stems, flowers, often the entire plant (Berry, 1975*a*)

3. Often feed along roadsides where annuals are more abundant (Coombs, 1977*a*, *b*)

4. Sonora, Mexico (Auffenberg, 1969) — foraging largely restricted to bottoms of dry arroyos

E. Nutrition

1. Grasses, forbs, and browse consumed by tortoises in the wild are more nutritious than vegetables and fruits eaten in captivity (Fowler, 1976*a*)

2. A sufficient calcium content and calcium:potassium ratio are necessary for shell and skeletal development (Fowler, 1976*a*)

3. A 2:1 ratio of calcium to phosphorus is needed (Murphy, 1973)

4. For proper bone and shell growth the relationship between ultra-violet radiation, vitamin D synthesis and calcium-phosphorus ratio is extremely important (Murphy, 1973)

5. Iodine deficiencies will lead to goiters (Murphy, 1973)

F. Gastroliths — deliberately swallow small stones for the purpose of macerating food (Murphy, 1973)

G. Food utilization (Boynton, 1970*a*)

1. Source of metabolic water

2. Carbohydrates in plant material converted to fats and stored for winter

II. Scats

A. Description

1. Dark brown or black and slightly moist when fresh (Camp, 1916)

2. Vary in size from 1.25 cm width by 2.9 cm length to 1.85 cm width by 6.6 cm length (Berry, 1973*b*)

3. About the size of a fox scat (Camp, 1916)

4. Coarse plant fibers contained in scats (Woodbury and Hardy, 1948*a*; Berry, 1973*b*; Murphy, 1973)

5. Dry in nature, H_2O content 0.6 ml/g (Minnich, 1976)

B. Frequency of defecation

1. During spring and summer the ingestion to defecation can take only one day when temperatures are favorable (Hansen et al., 1976)

2. In winter there are long periods without defecation; the large intestine is filled with grass stems which undergo no noticeable breakdown for as long as 6 months (Murphy, 1973)

C. Decay — with high temperatures and low humidity, the scats may escape fungal, insect, and bacterial attack for several years (Hansen et al., 1976)

D. Utilization (Patterson, 1971*c*; Coombs, 1977*a*)

1. Tortoises may mark their home ranges with scats

2. May mark their dens or burrows with scats

E. Geophagy (Sokol, 1971)

1. Scats composed entirely of soil have been observed

2. May be a means of maintaining intestinal flora

3. May be a method of obtaining scats to be used as scent markers for home ranges (Berry, 1978a)

F. Lithophagy

1. Observed scats composed of a large percentage of rocks (Sokol, 1971)

2. May be a means of obtaining supplementary calcium or other minerals (Sokol, 1971)

3. May be a method of producing scats to be used as scent markers for home ranges (Berry, 1978*a*)

XIV. Tracks

A. Description

1. Parallel rows of rounded dents (Stebbins, 1966)

2. Direction of travel indicated by toe marks; pressure ridges at end of each mark (Stebbins, 1954)

B. Reading tracks (Berry, 1973*b*)

1. Indicate traveling, courtship behavior, mating, aggressive encounters, feeding, predator encounters

2. Only clearly visible on aeolian sand

XV. Physiology

A. Hematology

1. Protein concentration of hemoglobin is 100% (Sullivan and Riggs, 1967*a*)

2. pH of 7.00 (Sullivan and Riggs, 1967*a*)

3. Oxygen properties (Sullivan and Riggs, 1967*c*)

a. 15% concentration

b. Absorbancy ratio for deoxygenated hemoglobin is 0.702 as compared to 1.0 in man

c. Oxygen uptake subject to changes in pH and temperature

4. Electrophoretic properties (Sullivan and Riggs, 1967*b*)

B. Oxygen consumption (Naegle and Bradley, 1974)

1. Individuals weighing <50 g consumed 125 ml of O_2 per hour per kg of body weight

2. Individuals weighing 100 g consumed 40 ml of O_2 per hour per kg of body weight

3. Individuals weighing >100 g showed a slight but regular and progressive decrease in O_2 consumption in relation to the increase in body weight

C. Thermoregulation

1. Recorded body temperatures of tortoises

a. Critical thermal maximum 39.5°C (Brattstrom, 1961; Brattstrom, 1965)

1) Locomotory activity becomes disorganized and animal loses ability to escape, eventually leading to death

2) An example would be loss of righting response (Hutchison et al., 1966)

b. Lethal maximum 43.0°C (Brattstrom, 1961)

c. Maximum voluntary temperature or temperature at which an animal retreats to shade or underground retreats, 37-38°C (Brattstrom, 1965; Brattstrom and Collins, 1972)

d. Minimum voluntary temperature or lowest temperature voluntarily tolerated by the animal, usually the lowest body temperature of an active individual, 15°C (Woodbury and Hardy, 1948*a*; Brattstrom, 1965; Brattstrom and Collins, 1972)

e. Temperature of active tortoises 19.0 to 37.8°C (Brattstrom 1965)

f. Mean activity temperature, 30.6°C (Brattstrom, 1965; Brattstrom and Collins, 1972)

g. Preferred body temperature was 26.7 to 29.4°C (Woodbury and Hardy, 1948*a*)

h. Preferred body temperature in late May, eastern Kern County, California, 32.3 $\pm$ 3.2°C, range 20.8 to 38.0°C (McGinnis and Voigt, 1971)

i. Preferred body temperature in eastern Kern County, California, in mid-July, 34.7 $\pm$ 2.7°C, range 27.5 to 38.3°C (McGinnis and Voigt, 1971)

j. Preferred or optimum temperature is the narrow range at which reptiles are found carrying on their normal activities (Brattstrom, 1965)

k. Smaller tortoises appear to have higher preferred body temperatures than larger tortoises (Burge, 1977)

2. Heating and cooling rates

a. Cooling rates are slower than the heating rates (Brattstrom and Collins, 1972; Voigt, 1975)

b. Young tortoises heat up and cool off at about the same rate (Burge, 1977)

c. With increasing body size, the heating rate decreases but remains greater than the cooling rate (Burge, 1977)

3. Thermoregulation in summer

a. Behavioral methods of temperature regulation

1) Denning

a) Retreat to cooler summer dens to escape from high ambient and ground temperatures (Woodbury and Hardy, 1948*a*)

b) Body heat is dissipated across the surface of legs and neck resulting in a decline in deep body temperature after retreating (McGinnis and Voigt, 1971)

c) Temperature in den rises very slowly during the day (McGinnis and Voigt, 1971)

d) Retreating to den also may reduce water loss from evaporation through skin and lungs (Miller, 1932)

2) Vegetation cover — may utilize shade of nearby shrubs to escape from high surface temperature (Brattstrom and Collins, 1972; Burge, 1977)

3) Time spent abroad

a) Shorter daily activity period as daily summer temperatures increase (Berry, 1975*b*)

b) Emergence from summer dens occurs earlier as daily summer temperatures increase (Berry, 1974)

c) Summer dens give a higher initial activity temperature when used before morning foraging in spring than if tortoises had remained abroad all night (McGinnis and Voigt, 1971)

d) Summer dens used less frequently as an evening retreat in July; this results in a lower initial activity temperature than occurred earlier in the season and provides for longer forage time, a longer warm-up time which may be desirable since vegetation is usually sparse and dry during this time (McGinnis and Voigt, 1971)

e) *See*: IX. Behavior — Q. Daily behavior patterns

b. Morphological and physiological methods of temperature regulation

1) Shell

a) Protects tortoise from solar radiation; acts as a buffer (Coombs, 1977*b*)

b) Shell temperature is 8-10°C higher than the deep body temperature (McGinnis and Voigt, 1971)

c) Outer shell, head and limbs heat more rapidly than body core (Hutchison et al., 1966)

d) Tortoise removed from a burrow in late May and held in sun, after 15 minutes the deep body temperature had reached near critical thermal maximum (McGinnis and Voigt, 1971)

e) *See*: XV. Physiology — C. Thermoregulation - 1. Recorded body temperatures of tortoises

2) Evaporative cooling — tortoise produced copious amounts of saliva which foamed from the mouth and spread down the neck when deep body temperature reached the lower limit of lethal range, 39.5°C (McGinnis and Voigt, 1971)

4. Thermoregulation in winter

   a. Behavioral methods of temperature regulation (Woodbury and Hardy, 1948*a*) — dens

      1) Retreat to deep winter dens in fall and remain there through winter to escape extreme cold temperatures in southwest Utah

      2) Time lag between severity of the cold air outside reaching the innermost part of the den

      3) Tortoises have been known to partially block their winter dens with dirt or debris from woodrat (*Neotoma*) nests, this may slow down cold air intrusion from outside to the den interior

   b. Morphological and physiological method of temperature regulation (Auffenberg, 1969) — bladder

      1) Located laterally just under the inner surface of the posterior part of the carapace

      2) May function as a "hot water bottle"

      3) By basking in the sun the fluid in the bladder is heated

      4) Stored bladder heat may be transferred to other body parts by radiant energy

D. Water balance

1. Sources of water

   a. Small pools after infrequent rains

      1) Two tortoises increased their body weight by 41% and 43% by drinking (Miller, 1932)

      2) Average amount of water consumed when available is 17 ml per 100 g body weight (Minnich, 1976)

   b. Succulent food (Bogert and Cowles, 1947; Woodbury and Hardy, 1948*a*; Switak, 1973)

   c. Metabolic (Minnich, 1976)

      1) Diet of forbs and grasses, is high in carbohydrates (Woodbury and Hardy, 1948*a*)

      2) Metabolic water intake for 16 July to 12 August 1970 was 0.27 ml per 100 g per day (Minnich, 1976)

   d. Water balance, controlled by quality of available forage (Nagy and Medica, 1977)

2. Storage of water — a large urinary bladder for storage of water and nitrogenous wastes, urea and uric acid (Cox, 1881; Switak, 1973; Minnich, 1977); approximately 473 ml (Minnich, 1977)

3. Sources of water loss

   a. Defecation

   b. Evaporative water loss

      1) Major avenue in the desert tortoise (Schmidt-Nielsen and Bentley, 1966)

      2) Less than from tortoises in mesic regions (Schmidt-Nielsen and Bentley, 1966)

   c. Respiratory water loss

   d. Tortoises can lose up to 30% body weight and still survive without undue water stress (Minnich, 1977)

   e. Excretion — *See*: XV. Physiology — D. Water balance - 4. Water loss reduction

4. Water loss reduction

   a. Behavioral methods — summer dens

      1) Reduces evaporation from respiration and external body surfaces by escaping heat (Miller, 1932; Woodbury and Hardy, 1948*a*; Burge, 1977; Coombs, 1977*b*)

      2) Soil inside den is moist and relative humidity is higher than outside (Woodbury and Hardy, 1948*a*)

   b. Anatomical methods

      1) Egg — shell impervious to H_2O loss (Miller, 1932)

      2) Adults and young possess horny scales on appendages which help conserve body moisture (Boynton, 1970*a*)

      3) Horny protective shell may act in a similar manner to help conserve body moisture (Coombs, 1977*b*)

   c. Physiological methods

      1) Uric acid and urea are excreted in approximately equal portions (Dantzler and Schmidt-Nielsen, 1966)

      2) Uric acid is less toxic than urea and can be voided using less H_2O (Miller, 1932; Schmidt-Nielsen and Bentley, 1966; Boynton, 1970*a*)

      3) Urine is retained in bladder and consists of urates stored in a noncrystalline precipitated state (Woodbury and Hardy, 1948*a*; Minnich, 1976)

      4) Urates precipitate allowing water and ions to be resorbed through the bladder (Dantzler and Schmidt-Nielsen, 1966; Schmidt-Nielsen and Bentley, 1966)

      5) During hibernation or for long periods of inactivity even though no urination is occurring water loss must be minimized (Baze and Horne, 1970)

6) Crystalline urate bladder deposits sometimes formed (Schmidt-Nielsen and Bentley, 1966)

   a) Pellets or uroliths contain sodium, potassium, ammonium, and have a high pH (Minnich, 1972)

   b) Bladder may also have calcium deposits (Fowler, 1976*b*)

   c) Drinking causes elimination of these bladder uroliths with urine (Coombs, 1977*a*)

7) Urine color varies from dark brown with solid gray matter to a clear fluid (Coombs, 1977*b*)

8) Tortoise lacks secretory ability to remove excess sodium chloride from body (Schmidt-Nielsen, 1964)

   a) Inject hypertonic solution of sodium chloride and metacholine to stimulate secretory gland activity

   b) No secretions observed comparable to marine turtles

9) Dehydration reduction mechanisms

   a) Water loss of 0.4 ml per 1000 g per day or 1.7 X the H_2O intake rate (Minnich, 1976)

   b) Urine retained in bladder (Woodbury and Hardy, 1948*a*; Minnich, 1976; Minnich, 1977)

   c) Osmotic concentrations of plasma are elevated to equal those of bladder urine (Dantzler and Schmidt-Nielsen, 1966; Minnich, 1976)

   d) Blood-urea concentration increases up to 200 moles per litre (Baze and Horne, 1970)

   e) Helps reduce evaporative water loss by increasing the osmotic concentration of the blood

   f) Small amounts of dry feces (water content 0.16 ml per gram are voided (Minnich, 1976)

E. Bone and scute regeneration

1. If underlying bone is exposed or broken on the shell, it is shed, replaced from beneath by a new piece of bone (Woodbury and Hardy, 1948*a*; Nichols, 1953; Stebbins, 1954; Boynton, 1970*a*)

2. Slow repair

   a. May take as long as 7 years in some cases (Stebbins, 1954)

   b. Scales on gular forks torn off, took 3 years for dead bone to be sloughed off and for cornified material to cover scar (Miller, 1932)

   c. A female with a carapace injury in captivity took 2 years to heal (Miller, 1932)

XVI. Burrows or dens

A. Summer burrows or dens

1. Characteristics

a. Length 1.0-1.6 m or more (Woodbury and Hardy, 1940; Woodbury and Hardy, 1948a; Switak, 1973; Coombs, 1977*a*, *b*)

b. May extend more than 3.2 m underground (Bury and Marlow, 1973)

c. Angle down somewhat from the horizontal, soil at bottom is cool and moist (Woodbury and Hardy, 1940; Woodbury and Hardy, 1948*a*; Boynton, 1970*a*)

d. Temperatures of summer dens range from 19.0 to 37.8°C (Brattstrom, 1965)

e. More numerous than winter dens (Coombs, 1974)

f. Entrance is half-moon shaped, flat on bottom (Stebbins, 1966; Bury and Marlow, 1973)

g. Tortoises dig their own dens or modify initial excavations of other animals particularly the rock squirrel (*Spermophilus variegatus*) and Harris antelope squirrel (*Ammospermophilus harrisii*) (Lowe, 1964; Bury and Marlow, 1973)

h. Temporary, may not be used in subsequent years (Woodbury and Hardy, 1948a; Berry, 1974; Coombs, 1977*a*)

1) Of 56 burrows used in summer 1973, only 4 were used in summer 1974 (Coombs, 1974)

2) 32 of 56 1973 summer burrows caved in (Coombs, 1974)

3) Often summer burrows are easily caved in by sheep and cattle, weathering, and rodent activity (Woodbury and Hardy, 1948*a*; Coombs, 1977*b*)

i. Numbers were higher in wet years and fewer in dry years (Coombs, 1977*b*)

j. Two types used by tortoises in Rand Mountains, California (Berry, 1975*b*)

1) Pallet

2) Multiple use 0.9-1.2 m deep

k. In Pima County, Arizona, burrows were just deep enough to shade the tortoise (Ortenburger and Ortenburger, 1927)

l. On Isla Tiburon, Mexico, the lack of wear on protuberant spurs and scales suggests that burrowing habits may be little developed here (Bury et al., 1978)

m. Mean floor inclination below horizontal was 15.0° $\pm$ 4.0° ($\pm$ 1 *S*) for burrows used by subadults and adult tortoises (Burge, 1978)

n. Mean floor inclination below horizontal was 15.5° $\pm$ 4.4° ($\pm$ 1 *S*) for burrows used by very young and juvenile tortoises (Burge, 1978)

o. Cover sites excavated in embankments were more horizontal than those dug on a flat surface (Burge, 1978)

2. Location

a. Often under rocks or in hillsides (Ortenburger and Ortenburger, 1927; Lowe, 1964; Coombs, 1977*a*)

b. Under bushes, especially under creosote bush (Coombs, 1977*a*)

c. Also numerous along wash banks, either at the base (as in Sonora, Mexico) (Auffenberg, 1969), or elevated from the wash bottom (as in the more northern part of their range) (Crooker, 1971; Coombs, 1977*a*)

d. Distance between burrows was 46.0-228.0 m in Utah (Coombs, 1977*b*)

e. Orientation of most cover site openings was east, northeast, or north possibly to reduce length of time sun's rays would shine directly into cover site (Burge, 1978)

f. Relative use of plant species for cover sites was correlated to shade-giving properties of the plant and not species density (Burge, 1978)

1) *Acacia greggii* — density: 0.9, relative use as cover site: 37.7

2) *Ambrosia dumosa* — density: 56.7, relative use as cover site: 0.3

3. Pattern of utilization

a. Repaired or dug using forefeet in early part of summer (Johnson et al., 1948; Woodbury and Hardy, 1948*a*; McCawley and Sheridan, 1972)

b. During mild weather a shallow burrow is dug or a shallow depression is made under a bush; also referred to as a pallet (Bury and Marlow, 1973; Berry, 1974; Berry, 1975*b*)

c. In hot weather when temperatures rise above 32°C deep burrows are constructed (Woodbury and Hardy, 1948*a*; Bury and Marlow, 1973)

d. Several burrows may be used in the course of a few days or the animal may return to the same burrow each night (Grant, 1936*a*; Bury and Marlow, 1973; Coombs, 1974)

e. Abandoned in September to return to winter dens in Utah (Coombs, 1977*b*)

f. Arden Study Area, Nye County, Nevada (Burge, 1978)

1) Mean density of 3.5/hectare for repeatedly used pallets and burrows

2) Subadult and adult tortoises used burrows with lengths ranging from 30 to >300 cm

3)

Length of burrow (cm)	Percent of use
30 to 70	38
>190	30

4) Adults may use from 12 to 25 cover sites per year with most used repeatedly

5) Burrows usually occupied by 1 tortoise at a time

6) 75% of burrows utilized by 1 to 5 other tortoises

7) Used 3 to 7 cover sites per month with 8% used for 1 day, 73% for 2 to 15 days, and 19% used for 16 to 46 days

8) 83% of burrows used in 1974 were used again in 1975

4. Excavation — *See*: XVI. Burrows and dens - B. Winter burrows and dens - 5. Excavation

B. Winter burrows or dens

1. Characteristics — northern range of desert tortoise

a. Length, 1.5 m to as long as 10.9 m (Woodbury and Hardy, 1948*a*; Miles, 1953; Woodbury, 1954; Bellairs, 1970; Boynton, 1970*a*; Berry, 1975*b*; Coombs, 1977*b*)

1) Long dens usually provide greater temperature stability, 10.0-12.5°C (Brattstrom, 1965)

2) Little fluctuation in temperature and humidity at a depth of 5.3 m (Woodbury and Hardy, 1948*a*)

3) Depth of 2.3 m, less than 0.5-2.2°C for diurnal temperature fluctuations (Burge, 1977)

4) Temperature extreme in burrows at 2.3 m depth was 7.2°C in December (Burge, 1977)

5) Temperatures in hibernating den at 2.3 m usually remain between 12°C and 14°C (Burge, 1978)

6) Maximum floor temperatures at 2.3 m inside den for last week in July and first half of August were 30.0-32.8°C with a daily fluctuation of 0.5-2.2°C (Burge, 1978)

b. Half-moon shaped or semicircular opening (Stebbins, 1966; Switak, 1973; Coombs, 1977*b*)

c. May be branched, have several chambers, or may connect with other winter dens (Woodbury and Hardy, 1948*a*; Nichols, 1953; Coombs, 1977*b*)

d. Some excavations in southwest Utah may be 5000 years old (Auffenberg, 1969)

2. Characteristics — southern range of desert tortoises

a. Sonora, Mexico, and southern Arizona (Auffenberg, 1969)

1) Construct pallets or shallow burrows

2) Often just cover the length of carapace

3) In parts of Sonora, Mexico, tortoises may not hibernate

b. Isla Tiburon, Mexico (Bury et al., 1978)

1) Shallow burrows used as winter retreats

2) 0.3-1.0 cm in length

3. Location

a. Often constructed under caliche and rocky outcrops in desert wash banks (Woodbury and Hardy, 1948*a*; Coombs, 1977*b*)

b. May be under large boulders and sandstone shelves (Coombs, 1977*b*)

c. Suitable locations may be a limiting factor in determining the distribution of the desert tortoise on the Beaver Dam Slope, Utah (Coombs, 1977*b*)

d. In eastern Kern County, California, dens are constructed on the shady side of shrubs with soil depths of 0.2 to 0.3 m covering entrances (Berry, 1972)

e. Den dug with a 12° to 45° slope (Camp, 1916)

f. Constructed in rather firmly packed sand and gravel (Camp, 1916)

g. On Isla Tiburon, Mexico, burrows frequently are dug into the base of woodrat middens rather than into gravelly soil (Bury et al., 1978)

4. Pattern of utilization

a. Permanent, may be used year after year, mainly in winter but may be used throughout the year (Woodbury and Hardy, 1948*a*; Burge, 1977; Coombs, 1977*b*)

b. May not be used by the same tortoise year after year (Woodbury and Hardy, 1948*a*)

c. May be shared with other tortoises (Boynton, 1970*a*)

d. Up to 25 hibernating tortoises have been found in one den (Woodbury and Hardy, 1948*a*)

e. Occupied from mid-October to mid-April on the Beaver Dam Slope, Utah (Woodbury and Hardy, 1940; Woodbury and Hardy, 1948*a*)

f. Infrequently left on warm days (Woodbury and Hardy, 1948*b*; Coombs, 1977*a*)

g. Used most often during summer and winter (Berry, 1972; Berry, 1974; Berry, 1978a)

5. Excavation

a. Use front legs

b. Description in eastern Kern County, California (Berry, 1972)

1) Tortoise sniffs soil then digs with forelegs for 3 to 4 strokes

2) Sniffing activity performed several times at various locations until a suitable den site is selected

3) Forelimbs used and soil kicked back with hindlimbs

4) Forelimbs adapted for digging (Auffenberg, 1969)

a) Feet and forelimbs flattened with immovable digits and flattened claws

b) Wrists largely immovable because of sheet-like ligaments

c) Resulting structure is like a small spade

5) Digs while standing and appears to brace body with forefeet and hindfeet (Bramble, 1978)

6. Other cover types — nonburrow cover or shade, shrub bases (Burge, 1977)

C. Commensal animals

1. Mammals

a. Rodents — packrats (*Neotoma lepida*) (Woodbury and Hardy, 1948a; Coombs, 1977*b*; Burge, 1978), kangaroo rat (*Dipodomys merriami*), white-footed mouse (*Peromyscus* sp.), antelope ground squirrel (*Ammospermophilus leucurus*) (Burge, 1978)

b. Lagomorphs — desert cottontail (*Sylvilagus audubonii*), California jackrabbit (*Lepus californicus*) (Woodbury and Hardy, 1948*a*)

c. Carnivores — kit fox (*Vulpes macrotus*) (Coombs, 1974; Coombs, 1977*b*), house cat (*Felis domesticus*) (Burge, 1978)

2. Birds — Burrowing Owl (*Athene cunicularia*) (Berry, 1975*b*; Burge, 1978), Roadrunner (*Geococcyx californianus*) (Woodbury and Hardy, 1948*a*), Gambel Quail (*Lophortyx gambelii*) (Coombs, 1974)

3. Reptiles

   a. Lizards — banded gecko (*Coleonyx variegatus*), desert spiny lizard (*Sceloporus magister*) (Coombs, 1977*b*)

   b. Snakes — spotted night snake (*Hypsiglena torquata*), sidewinder (*Crotalus cerastes*), Great Basin rattlesnake (*Crotalus viridis*) (Woodbury and Hardy, 1948*a*), Mojave rattlesnake (*Crotalus scutulatus*) (Coombs, 1974; Coombs, 1977*b*), coachwhip (*Masticophis flagellum*) (Burge, 1978)

4. Invertebrates — ant-lion larvae (Myrmeleontidae), beetle larvae (Tenebrionidae), spiders, silverfish, cockroaches, scorpions, other insects (Woodbury and Hardy, 1948*a*; Coombs, 1977*b*), black widow spiders (*Latrodectus mactans*), silverfish (Lepismatidae) (Burge, 1978)

5. Animal remains

   a. Mammals — spotted skunk (*Spilogale gracilis*), desert cottontail, California jackrabbit, packrat (Woodbury and Hardy, 1948*a*)

   b. Reptiles — gopher snake (*Pituophis melanoleucus*) (Woodbury and Hardy, 1948*a*)

6. Commensal interaction — evidence of woodrats gnawing on the shell of live tortoises (Burge, 1977)

XVII. Spatial relations

A. Home range

1. General (Berry, 1973*b*)

   a. Often dependent on size or age and sex of tortoise

   b. Younger animals have smaller home ranges than adults

   c. Males have larger home ranges than females

   d. May rarely move more than 3.2 km from their hatching spot during their lives (Auffenberg and Iverson, 1979)

2. Beaver Dam Slope, Utah, 1936-1946 (Woodbury and Hardy, 1948*a*)

   a. From 4-40 hectares with a mean of 20 hectares

b. Individual overlap

c. Two types (Auffenberg, 1969)

1) Large, warm weather range on desert flats

2) Much smaller, cool weather range near winter dens

d. Annual movement usually does not exceed 3.2 km (Auffenberg, 1969)

3. Beaver Dam Slope, Utah, 1972-1974 (Coombs, 1977*a*, *b*)

a. Vary with area, size and age of the animal

b. Two types of home ranges — annual and total home range (multi-annual area)

c. Usually linear or triangular

d. Mean annual is 0.8 hectare (range 0.2-1.0 hectares)

e. Smaller in younger tortoises; often $<$50 m radius from hatching site or winter den

f. Usually smaller in dry years than in wet years

g. Few tortoises found more than 0.48 km from winter denning sites (Coombs, 1974)

4. Arden Study Area, Nye County, Nevada (Burge, 1977)

a. Usually largest when green forage available

b. Smallest when cool temperatures support little activity

c. Sizes change during the active season

d. Mean home range over 1 active season

1) Adult males, 26 hectares (range 20-38 hectares)

2) Adult females, 19 hectares (range 11.3-27.0 hectares)

3) Juveniles, 5.7 $\pm$ 1.5 hectares (range 0.5 - 13.0 hectares)

e. Overlap

5. Rand Mountains, California (Berry, 1975*b*)

a. Ranges from 38.8-76.9 hectares for males

b. Ranges from 7.7-45.5 hectares for females

B. Identification of home range

1. May be marked by scat distribution (Coombs, 1977*a*, *b*)

2. Strong familiarity; trips between cover sites made in straight lines (Burge, 1977)

3. Transplanted wild tortoises (Berry, 1975*b*)

    a. Excavate a burrow

    b. Make small loop trips from burrow until familiar with local area

    c. Move burrow 50 to 100 m away and initiate more loop trips

C. Population size and density

1. Density estimates

    a. Not common in any location (Woodbury and Hardy, 1948*a*; Anonymous, 1970)

    b. General rapid decline in past 70 years (Anonymous, 1973)

    c. Beaver Dam Slope, Utah, 1936-1946 (Woodbury and Hardy, 1948*a*)

        1) Estimate one tortoise per 1.6 hectares or 62 per km^2

        2) Based on number of winter dens and amount of food available

    d. Beaver Dam Slope, Utah, 1972-1974 (Coombs, 1977*a*, *b*) — estimate 250-350, down from 2000 reported in 1948; one per 9.6 hectares

    e. Possible reasons for decline

        1) Human collection (Woodbury and Hardy, 1948*a*; Coombs, 1977*a*)

        2) Overgrazing of livestock (Woodbury and Hardy, 1948*a*; Coombs, 1977*a*, *b*)

            a) Changes in plant densities

            b) Plant introductions

            c) Reduced perennial grass densities (Coombs, 1977*b*)

        3) Road and water development (Coombs, 1977*a*, *b*)

    f. Area north of St. George, Utah, 1972-1974 (Coombs, 1977*b*)

        1) Paradise Canyon, estimate 66 tortoises per 1.0 km^2 for a 2.6 km^2 area

        2) St. George Hills, estimate 8.6 tortoises per 1.0 km^2 for a 23.4 km^2 area

    g. Salt Wells Valley, California (Berry, 1974*b*)

        1) Estimate 3.5 tortoises per km^2

2) Population appears to be stable and at or near carrying capacity

h. Desert Tortoise Natural Area, eastern Kern County, California (Berry, 1974)

1) 103 marked in 2.59 km^2 area

2) Estimate 58-78 per km^2

3) Has highest known tortoise densities (Berry, 1975*a*)

i. Arden Study Area, Nye County, Nevada, 1975 (Burge and Bradley, 1976) — 119 marked in 292 hectares to yield an estimated 44.3 per km^2, based on 5 methods for estimating density

j. Ivanpah Valley Study Plot, San Bernardino County, California, 30 March to 6 June 1977 (Berry, 1978*b*)

1) 151 tortoises were marked in 2.59 km^2 area

2) Estimate 87-106 tortoises per km^2

k. Goffs Study Plot, San Bernardino County, California, 1 April to 11 June 1977 (Berry, 1978*b*)

1) 148 tortoises were marked in 2.59 km^2 area

2) Estimate 77-94 tortoises per km^2

l. Chemehuevi Valley Study Plot, San Bernardino County, California, 15 April to 21 May 1977 (Berry, 1978*b*)

1) 33 tortoises were marked in 2.59 km^2 area

2) Estimate 12 to 23 tortoises per km^2

m. Fremont Peak Study Plots, San Bernardino County, California, 31 March to 12 June 1977 (Berry, 1978*b*)

1) 50 tortoises were marked in 5.18 km^2 area

2) Estimate 12 to 15 tortoises per km^2

n. Chuckwalla Bench Study Plot, Riverside County, California, 25 April to 31 May 1977 (Berry, 1978*b*)

1) 120 tortoises were marked in 2.59 km^2 area

2) Estimate 77 tortoises per km^2

XVIII. Mortality factors

A. Disease

1. Inflammation of skin about head, affects eyes (Miller, 1932)

2. Concretions within urinary bladder (Miller, 1932; Miller, 1955; Hunt, 1957; Frye, 1972)

3. Respiratory infections

   a. Symptoms

      1) Nasal exudate, general depression, weakness, weight loss (McCawley and Sheridan, 1972)

      2) May or may not have pulmonary lesions (Fowler, 1976*b*)

   b. Respiratory diseases (Fowler, 1976*b*)

      1) Pneumonia

      2) 22 species of bacteria found in lungs of 6 tortoises

      3) Healthy tortoises had sterile lungs

   c. Treatment — 0.5 to 1.0 cm^3 penicillin depending on tortoise size (Crooker, 1971)

4. Metabolic bone disease — decreased bone density with thinning of cortical bones (Fowler, 1976*b*)

5. Stress

   a. Possible causes (Fowler, 1976*a*)

      1) Temperature extremes

      2) Improper humidity

      3) Inability to burrow

      4) Photoperiod differences

      5) Malnutrition

      6) Increased cortisol production, can lead to adrenal gland failure and death

   b. Symptoms — similar to respiratory infection (Fowler, 1976*a*)

      1) Also leucopenia

      2) Poor wound healing

      3) Interference with immune responses

      4) Refusal of food

      5) Increased aggression

      6) Failure to exhibit normal reproductive responses

6. Hypovitaminosis A (Fowler, 1976*a*)

   a. Usually seen in captive tortoises

   b. Symptoms similar to respiratory disease infection

7. Healthy tortoise maintains an intestinal microflora of 26 species of bacteria including: *Corynebacterium* sp., *Staphlococcus epidermidis*, *Micrococcus* sp., *Pasteurella haemolytica*-like, *Pasteurella ureae*-like, *Pasteurella* sp., *Acinetobacter*, *Escherichia coli*, *Citrobacter intermedius*, *Citrobacter*-like sp., *Proteus mirabilis* (Fowler, 1976*b*)

B. Fire and flood

1. Occasionally fires will kill tortoises (Woodbury and Hardy, 1948*a*)

2. Occasionally tortoises die in flash floods (Woodbury and Hardy, 1948*a*; Coombs, 1974)

C. Parasites

1. Ectoparasites

a. Adobe tick (*Ornithodorus turicata*) (Murphy, 1973)

1) Attached to shell sutures, soft skin around neck, legs, and tail, and where bone is exposed because of injury (Grant, 1936*a*; Harbinson, 1937; Woodbury and Hardy, 1948*a*; Coombs, 1974; Coombs, 1977*b*)

2) May be found in tortoise burrows (Ryckman and Kohls, 1962)

3) Not host specific (Ryckman and Kohls, 1962)

4) Heavy infestation near end of a hot, dry summer (Ryckman and Kohls, 1962)

b. Red ants (Miles, 1953)

1) More of a problem for captive tortoises (Miles, 1953)

2) Bite the skin about the neck, sometimes causing death in young tortoises (Miles, 1953)

c. Mold — observed growing on shell brands (Woodbury and Hardy, 1948*a*)

d. *Trombicula* mites — located on tortoise's shell (Coombs, 1974; Coombs, 1977*b*)

e. Bot fly larvae — under neck skin (Coombs, 1977*b*)

2. Endoparasites

a. *Lampropedia* sp.

1) A bacterium in the gut where cellulose digestion occurs (Pope, 1939)

2) Not reported in *Gopherus agassizii* (Schad et al., 1964)

b. Nematodes — intestinal (Woodbury and Hardy, 1948*a*)

D. Egg predators

1. Gila monster (*Heloderma suspectum*) — raided 75% of tortoise nests in Paradise Canyon, Utah (Coombs, 1977*b*)

2. Kit fox (*Vulpes macrotus*) — dug up one nest in Paradise Canyon, Utah (Coombs, 1977*b*)

3. High rate (Bury and Marlow, 1973)

E. Predators

1. Possible predators of adult tortoises

   a. Coyote (observed) and kit fox (Berry, 1974)

   b. Bobcat (*Lynx rufus*) (observed) (Woodbury and Hardy, 1948*a*)

   c. Coyote, bobcat, fox (Coombs, 1977*b*)

   d. Coyote, kit fox, and possibly domestic dog (*Canis familiaris*) (Burge, 1977)

   e. Coyote, wildcats (Miles, 1953)

   f. Man — *See*: XVIII. Mortality factors - F. Human-caused mortality

2. Possible predators of young tortoises

   a. Ringtail (*Bassariscus astutus*), Roadrunner, Common Raven (*Corvus corax*), kit fox, coyote, bobcat, skunk (Coombs, 1974; Coombs, 1977*b*)

   b. Golden Eagle (*Aquila chrysaetos*) (Thelander, 1974)

   c. Roadrunner, Common Raven, Burrowing Owl (*Athene cunicularia*), gopher snake (*Pituophis melanoleucus*), glossy snake (*Arizona elegans*), spotted skunk, badger (*Taxidea taxus*), kit fox, Mojave rattlesnake (*Crotalus scutulatus*) (Anonymous, 1973)

3. Predation signs

   a. Tooth scratches, cracks, and holes in shells (Bailey, 1928; Grant, 1946; Berry, 1974; Coombs, 1977*b*)

   b. Skeletal and shell remains in predator scats (Woodbury and Hardy, 1948*a*; Coombs, 1977*b*)

   c. Missing or chewed appendages (McCawley and Sheridan, 1972)

   d. Fractured and compressed remains of two-thirds to one-half of shell (Burge, 1977)

4. Specific examples of predation

   a. Coyote tooth scratches on shell (Bailey, 1928)

   b. Remains of skull and feet of young tortoise in droppings of Raven (Miller, 1932)

   c. Observations of coyotes digging tortoises out of dens through den ceiling (Berry, 1974)

   d. Observation of coyote attacking, carrying, and eating a tortoise (Berry, 1972; Berry, 1974)

   e. Remains of young tortoise found in raptor nest (Coombs, 1974)

   f. Missing front leg chewed by predator (Coombs, 1974)

   g. Bobcat observed killing a tortoise (Woodbury and Hardy, 1948*a*)

   h. Coyote scats containing tortoise material (Woodbury and Hardy, 1948*a*)

   i. Tortoise parts found in 1.8% of coyote and kit fox scats (Coombs, 1977*b*)

   j. Two transplanted tortoises died from attacks by domestic dogs (Berry, 1975*a*)

   k. Depressed fractures of adult shells possibly caused by being dropped on a rock by coyotes (Berry, 1972; Burge, 1977)

   l. Possible signs of kit fox predation (Coombs, 1977*b*)

      1) Head and one or more limbs missing

      2) Light scars from teeth sliding over shell

      3) Shells broken in young tortoises

   m. Possible signs of coyote predation (Coombs, 1977*b*)

      1) Marginal scutes broken, especially near rear limb area

      2) Carapace often open in top portion and internal organs consumed

5. Predation rates

   a. 2.42% of mortality of tortoises on Beaver Dam Slope, Utah, attributed to predation (Coombs, 1977*b*)

   b. Kit fox predation is higher at lower elevations in southwest Utah (Coombs, 1977*b*)

   c. Coyote predation is higher at higher elevations in southwest Utah (Coombs, 1977*b*)

d. As rodent population decreases, the predation potential toward tortoises may increase (Woodbury and Hardy, 1948*a*)

e. Mortality increased from 5% prior to 1972 to 20-28% in 1973 because of canid predation in Rand Mountains, Kern County, California (Berry, 1975*b*)

F. Human-caused mortality

1. Roads

a. Direct effects

1) Tortoises killed by automobiles and trucks (Woodbury and Hardy, 1948*a*; Miles, 1953; Anonymous, 1973; Berry, 1973*b*; Bury and Marlow, 1973; Switak, 1973; Coombs, 1974; Coombs, 1977*b*)

2) Increase in number of roads in the desert has led to an increase in the number of tortoises run over (Leach and Fisk, 1969)

3) In 1932, two of 6 tortoises seen near a road had been run over (Klauber, 1932)

4) More than one dozen tortoises were crushed by vehicles during spring 1973 (Berry, 1975*a*)

5) Some people derive pleasure from running over tortoises to hear them pop (Hamilton, 1944)

b. Indirect effects (Nicholson, 1978)

1) Paved roads and vehicular traffic have a detrimental effect upon tortoise populations within about 1 km of a road

2) Tortoise sign increases with increasing distance from unpaved and paved roads

3) Tortoise sign increases eightfold from a distance of about 90 m to 1600 m from roads

4) A gradual, nearly linear increase in tortoise sign occurs at increasing distances from old paved roads

5) A sharp increase in tortoise sign occurs at increasing distances from new paved roads especially between 91.4 m and 365.6 m

2. Wanton killing — used as target practice

a. Eight found on a 3.2 km stretch of unpaved road north of California City, California (Bury and Marlow, 1973)

b. One tortoise had been shot with five .22-caliber slugs (Boynton, 1971)

c. Shell of an adult male found with many bullet holes several hundred metres off of a trail (Berry, 1975*a*)

d. Bullet-riddled carcasses seen on many unpaved roads (Bury and Marlow, 1973)

e. Use young tortoises for skeet shooting (Bury and Marlow, 1973)

f. Tortoises (47) lined up and killed with shotgun blasts (Bury and Marlow, 1973)

g. Tortoise shell full of bullet holes (Olsen, 1971)

h. Used for target practice (Switak, 1973)

3. Habitat destruction

a. Development of land for subdivisions and agriculture (Anonymous, 1973; Bury and Marlow, 1973)

1) Mojave River Basin and Antelope Valley (Leach and Fisk, 1969)

2) Changes plant densities (Coombs, 1977*a*)

3) Introduces invader species (Coombs, 1977*a*)

b. Off-road vehicles (ORV)

1) Cause cave-ins of tortoise dens, nests (Anonymous, 1973; Luckenbach, 1975; Bury et al., 1977)

2) Expose roots of plants and crush annual and perennial wildflowers needed for forage and cover from solar radiation (Anonymous, 1973; Bury and Marlow, 1973; Stebbins, 1974; Luckenbach, 1975; Bury et al., 1977)

3) Destroy cover (Anonymous, 1973; Berry, 1973a; Bury and Marlow, 1973; Luckenbach, 1975)

4) Run over tortoises (Bury et al., 1977)

5) Increase in tortoise vandalism, shootings, crushed animals, carried off as pets (Bury and Marlow, 1973)

6) Mechanical disturbance upsets (Bury et al., 1977)

a) Water storage, penetration capacities, thermal structure of soil, and germination strategies of seeds

b) Results in reduction of spring annuals which means reduction in forage and seeds

7) Continual use of area even at low intensity results in (Bury et al., 1977)

a) Reduced recruitment into the population

b) Loss of tortoises through death and removal

c) Loss of the removed animals' reproductive potential in the wild population

8) Comparison of an ORV-used area with an unused area (Bury, 1978)

   a) Used area had tortoise biomass of 0.5 kg/ha

   b) Unused area had tortoise biomass of 3.4 kg/ha

9) Effects on habitat in Dove Springs area, California (Stebbins, 1974)

   a) 388 hectares heavily damaged

   b) 220 hectares denuded

   c) Loss of food and denning sites for tortoises

10) Two motorcycle races, one with 700 motorcycles, one with 300 motorcycles went through the Rand Study Area, Kern County, California, in April 1973 (Berry, 1975*a*)

c. Overgrazing

1) May cause introduction of annuals which may not be acceptable tortoise forage (may not be nutritionally comparable to native forage) (Anonymous, 1973; Berry, 1973*b*; Berry, 1978*a*; Coombs, 1974; Coombs, 1977*b*; Hohman and Ohmart, 1978)

2) Decreases native perennials which are needed for food and shelter (Berry, 1973*b*; Berry, 1978*a*)

3) Collapses den sites (Woodbury and Hardy, 1948*a*; Berry, 1973*b*; Berry, 1978*a*)

4) Tramples small tortoises (Berry, 1978*a*)

5) Tramples forage (Hansen et al., 1976; Berry, 1978*a*)

6) Competition for food

   a) Cattle (Hansen et al., 1976)

      i) Diet of cattle is 49% grasses (scat analysis)

      ii) Diet of tortoises is at least 52% grasses (scat analysis)

   b) Sheep

      i) Sheep strip annual plants from desert (Bury and Marlow, 1973)

      ii) Diet of tortoises is mainly annual wildflowers and grasses in California (Berry, 1973*a*; Berry, 1974) and annual and perennial grasses in Utah and Arizona (Berry, 1975*b*)

   c) In late winter and spring, livestock eat many of the same winter annuals and grasses that form the principal diet of tortoises (Berry, 1978a)

   d) Possible competition from burros (Anonymous, 1973)

7) Habitat may be changing faster than animals can adapt to it (Berry, 1978*a*)

8) Indirect effects (Berry, 1978*a*)

   a) Reduction of food supply could slow growth rates and increase time needed to attain sexual maturity

   b) The number and size of clutches produced per female could be reduced if reproduction is dependent on adequate diet

   c) With reproduction suppressed recruitment is reduced

   d) Reduction in food supply may stress a reproducing female because of the heavy metabolic demands of egg laying — the result could be fewer females than males

   e) Greatest detrimental effect from overgrazing would be experienced by:

      i) Animals with small home ranges (very young tortoises)

      ii) Animals with fragile shells (very young tortoises)

      iii) Animals with high energy commitments (reproductive females)

d. Mining (Berry, 1975*a*)

   1) Tortoises fall into exploration pits and cannot escape

   2) Die of exposure, starvation or dehydration

e. Recovery of land (Vasek et al., 1975)

   1) Optimistic estimates of 30 to 40 years (following pipeline construction) — creosote bush scrub community, Lucerne Valley of California

   2) After 33 years disturbance effects still evident (powerline construction) — creosote bush scrub community, Lucerne Valley of California

   3) Invasion of pioneer shrubs constituted zero to 85% of shrub cover of sample plots

   4) Enhancement of vegetation at road edge (powerline road)

G. Other causes

1. Drown — in Utah tortoises have drowned in gallinaceous bird guzzlers (Coombs, 1974)

2. Occasionally overturned tortoises are unable to right themselves (Coombs, 1974)

   a. Overheating can occur quickly

   b. Suffocation may occur because of pressure on lungs

H. Aging time since death (Berry, 1973*b*)

1. Less than one year — scutes adhere tightly to bony skeleton

2. 1 to 2 years — scutes lighten in color, growth rings begin to peel

3. 2 to 5 years — scutes fall from bone, bone falls apart

XIX. Economic value

A. Food

1. Late Pleistocene bones of *Gopherus agassizii* in Shelter Cave, New Mexico, had been burned; possibly used as a food source by Indians (Brattstrom, 1961; Van Devender et al., 1976)

2. Eaten by prospectors (Miller, 1932)

3. Mexican traders carried them alive as a fresh source of meat and water (Pepper, 1963)

4. Some white settlers also consumed tortoise meat (Stephens, 1914)

5. Eaten by Indians in southern Nevada (Connolly and Eckert, 1969)

6. Pah-Ute (Paiute) Indians near the Great Bend of the Colorado River ate tortoises until the 1860s (Stejneger, 1893)

7. Desert Indians used tortoises as a staple food along with snakes and chuckwallas (*Sauromalus obesus*) (Miles, 1953)

8. Regular food item for Seri Indians of Isla Tiburon, Mexico (Felger and Moser, 1976)

B. Shell

1. Cultural value to aboriginal tribes (Pepper, 1963)

2. Used for implements in turquoise mines (Pepper, 1963)

3. Carapace used as a cooking vessel by Indians (Bailey, 1928; Grant, 1936*a*)

C. Pets

1. Exploited for sale

a. In 1970, one man was arrested for collecting and selling hundreds of desert tortoises (Murphy, 1973)

b. In San Bernardino County, California, in May 1935, 200 tortoises had been collected to be sold; in October there were 100 more collected (Grant, 1936*a*)

c. Utah Hill service station along U.S. Highway 91 paid children to collect desert tortoises, the station then sold the tortoises to passing motorists (Coombs, 1977*b*)

d. In 1970, 105 tortoises were shipped to Utah, 185 were already there (Bury and Marlow, 1973)

2. Taken as souvenirs or pets

a. Removal by man in southern Nevada (Burge, 1977)

b. In Utah many have been collected (Woodbury and Hardy, 1948*a*; Coombs, 1977*a*)

c. Sheepherders in Utah collected them as well as university staff studying flora and fauna in southwest Utah (Coombs, 1977*b*)

d. Thousands of desert tortoises are pets in backyards in southern California (Cowan, 1972)

e. Thousands more are believed to be in captivity in other locations (Bury and Marlow, 1973)

f. There are 9000 to 10 000 known legally possessed tortoises in California and at least this many more in captivity in California being held without permits (St. Amant and Hoover, 1978)

D. Entertainment (Delaney, 1969)

1. Desert tortoises were collected for the Joshua Tree, California, annual turtle races which are held in early May

2. Tortoises are released after the races at the locations where they were found

XX. Management

A. General survey and census techniques

1. Line transects (Berry, 1978*b*)

a. Method

1) Length is 2.4 km

2) Transect density may be varied

3) All tortoise sign seen and related information is recorded

b. Results

1) An area may be sampled rapidly for the presence of tortoises

2) Information on the relative abundance of tortoises is obtained

2. Quadrat and grid location system (Bury et al., 1977)

a. Standardized censusing technique needed to accurately determine and compare effects of different environmental regimes on population characteristics

b. Method

1) Delineate a permanent grid of 25-100 1-hectare quadrats

2) Systematically search each 1-hectare quadrat of the grid

3) Record all tortoise sign seen and related information within each quadrat on a map and in field notes

4) Mark all new tortoises found

5) Search quadrats several times during tortoise active season

6) Quadrats may be useful for long-term monitoring of population characteristics

c. Results

1) Number of tortoises seen, shell measurements, weights

2) Tortoise habitat including vegetation, topography, burrows and pallets

3) Spatial distribution, age and sex composition, and density

3. Permanent study plots (Berry, 1978*b*)

a. Method

1) Permanent plot size of 2.59 km^2 is established

2) An intensive attempt is made to mark all tortoises within the plot within a 30-day period in spring

3) All tortoise sign seen and relevant data are recorded

b. Results

1) Age class structure and sex ratio, shell measurements, weights, and density

2) Utilization of burrows, feeding habits

B. Marking methods

1. Scute branding

   a. Long-term marking method (Woodbury and Hardy, 1948*a*; McCawley and Sheridan, 1972)

   b. Problems (Woodbury and Hardy, 1948*a*)

      1) Too deep a brand results in area for ticks to parasitize a desert tortoise and for mold to grow

      2) Too deep a brand also initiates regrowth

      3) Too shallow a brand will not give a long-term mark

2. Painting on carapace (McCawley and Sheridan, 1972)

   a. Short-term marking method

   b. Usually wears off after 1 to 2 years (Woodbury and Hardy, 1948*a*; Woodbury, 1953)

3. Drilling small holes in the marginal scutes and underlying bone in various combinations (Crooker, 1971)

4. Carving marks in the carapace for identification (Woodbury, 1953; Cowan, 1972) — distinct after 10 to 15 years

5. Notching marginal scutes down to bone (Woodbury, 1953; Coombs, 1974)

   a. Permanent if made after the shell is well ossified

   b. Cover notches with yellow acrylic polymer emulsion to make notching pattern more visible (Burge, 1977)

6. Metal identification tags attached to carapace

   a. Hole is drilled through marginal scute and tag is attached by a metal wire through the scute hole (McCawley and Sheridan, 1972)

   b. Problems

      1) Mutilation of tags can occur through chewing by predators (McCawley and Sheridan, 1972)

      2) After 1 year, tags show signs of wear and breaking (Crooker, 1971)

7. Radio transmitters

   a. (Burge, 1977)

      1) Battery pack, transmitter and 30-cm wire antenna carried by tortoise

      2) Transmitter weight = 191 g

3) Large batteries weighed 120 g and had a 6-month life span

4) Equipment attached to carapace with contact cement and fiberglass woven tape

5) Unit covered with clear silicone rubber and then desert soil while silicone rubber was still wet

6) Transmitters placed on the 5th vertebral scute

b. (Schwartzmann and Ohmart, 1977)

1) Transmitter system

a) 26-g transmitter (35 x 27 x 10 mm, 40-g or 85-g lithium sulfate battery, transmitting antenna system of helical wire and ground plane

b) Battery life

i) 12 months for 40-g battery

ii) 36 months for 85-g battery

2) Receiver system

a) Multichannel receiver

b) 4-element yagi directional antenna

3) Attachment to carapace for adult tortoise only (carapace length $>$214 mm)

a) Use fast-setting epoxy

b) Final epoxy coat mixed with colored compound to resemble natural scute coloration

4) Location of equipment

a) Epoxy transmitter and battery on either side of nuchal scute

b) Ground plane attached to right marginals; antenna attached to left marginals, pygal, vertebrals

5) Removal

a) File notch in epoxy to scute material

b) Carefully pry off epoxy with screwdriver

8. Identifying numbers written on anterior and posterior marginals (Burge, 1977)

9. Identify tortoises by making rubbings of carapace (Berry, 1974)

C. Recapture success

1. Of 11 tortoises equipped with transmitters, 11 were captured over a 3-year period in Pinal County, Arizona (Schwartzmann and Ohmart, 1977)

2. 25 of 79 marked tortoises retrieved over a 4-year period on the Beaver Dam Slope, Utah, were recaptures (Coombs, 1977*b*)

3. 72 marked tortoises with 91 recaptures in Paradise Canyon, Utah (Coombs, 1977*b*)

4. 119 marked animals, 563 recaptures in southern Nevada (Burge and Bradley, 1976)

D. Management programs

1. Preserves — desert tortoise preserve (Forgey, 1976; Forgey, 1977)

   a. North of California City in Kern County, California

   b. On slopes of western Rand Mountains and adjacent Fremont Valley

   c. Preserve closed to all ORVs in 1973

   d. Sheep grazing halted in January 1976

   e. Working with The Nature Conservancy to purchase selected parcels of land

   f. Future plans include completion of fencing of the preserve to exclude ORVs (Forgey, 1977)

   g. Has perhaps one of the highest densities of desert tortoises in the Southwest

2. Introductions and reintroductions

   a. Anza-Borrego Desert State Park (Cowan, 1972)

      1) During 1971-1972 three groups of captive tortoises released in area of Upper Fish Creek

      2) 65 tortoises engraved with identification numbers, weighed, and measured

      3) After 18 months, none was seen

   b. California Fish and Game in Colorado Desert (Crooker, 1971)

      1) 66 captive tortoises were released south of Interstate Highway 10 between Indio and Desert Center

      2) Tortoises not native to the area of release

      3) All were measured, tagged, treated for disease and released

      4) After 336 days, 8 of the 66 tortoises were recovered; 5 were dead

      5) Releasing tortoises directly to desert was unsatisfactory because of low survival (St. Amant and Hoover, 1978)

c. Tin Can Enclosure, Beaver Dam Slope, Utah (Coombs, 1974)

   1) 0.4 hectare of fenced land which confines tortoises within it

   2) Natural winter den sites within wash banks are included

   3) Used to rehabilitate captive tortoises so they may be released into the wild

d. Castle Cliff Wash, Utah (Coombs, 1977*b*)

   1) Captive tortoises placed in Tin Can Enclosure on Beaver Dam Slope, Utah

   2) After a time they were transplanted to Castle Cliff Wash

3. Special management programs (current)

   a. California — Rehabilitation Program for Captive Tortoises (Cook et al., 1978; St. Amant and Hoover, 1978)

      1) Operated by California Fish and Game Department

      2) Captive tortoises turned in by public

      3) Screened for general health at Chino Fish and Wildlife Base

      4) Healthy adaptable tortoises sent to Quarterway House at Palm Desert for 1 year

         a) Tortoises are provided with water, burrows and native vegetation

         b) Human contact is limited

      5) Healthy adaptable tortoises from Quarterway House are sent to Halfway House at Fort Soda for 1 year (provided with a natural environment)

      6) After 2 years in the rehabilitation program only those tortoises which are healthy and adaptable are released into the wild

      7) All sick and nonadaptable tortoises are sent to adoption committees

      8) Reintroduction sites

         a) Area must have potential for supporting tortoise populations

         b) Area must have a population that is reduced in numbers

         c) Area must have little human activity

   b. Results of rehabilitation program (Cook et al., 1978)

      1) 1 year after release 72 to 79% of rehabilitated tortoises survived

2) Most of the deaths occurred within 2 weeks of release

3) Cause of death was believed to be hyperthermia — tortoises were unable to find suitable protection from sun

4) Evidence of displacement of released tortoises by native tortoises

5) 7 of 11 animals gained weight and 2 lost weight

6) Recommendations

a) Release rehabilitated tortoises at time of normal emergence from hibernation in spring

b) Release tortoises in early afternoon

c. California permit system (St. Amant, 1977)

1) Permits issued to persons who possess tortoises hatched in captivity

2) Permits issued to persons who possess captive tortoises which cannot be released into the wild again

3) Permit system is to deter tortoise collecting from wild populations while allowing persons to keep legally acquired captive tortoises

d. Utah

1) Letters of appreciation are sent to those persons who have turned in their captive tortoises to the state's wildlife department (Coombs, 1974)

2) Some of the animals were then placed in Tin Can Enclosure — *See*: XX. Management — C. Management programs - 2. Introductions and reintroductions

3) Establishment of 2 management areas, one west of Highway 91, one east of Highway 91 (Rowley, 1977)

a) West area managed for multiple use

b) East area managed for multiple use except for the proposed Research Natural Area

e. Transplant program for wild tortoises, California Department of Transportation (Berry, 1975*a*, *b*)

1) Tortoises removed from a highway corridor and transplanted

2) Choice of transplant site

a) Area where tortoises now occur or lived in recent past

b) Area must have minimum radius of 7 to 10 km

c) Habitat of area must match closely that of transplant's habitat

d) Tortoise population at relocation site must be below carrying capacity

e) Relocate all transplants in same general area of desert to lessen gene pool mixing — *See*: XX. Management — E. Other management aids and problems

4. Special management programs (proposed)

   a. Utah (Rowley, 1977)

      1) Total area of proposed Research Natural Area would be about 1600 hectares

      2) Would include Tin Can Enclosure area

      3) Grazing would be eliminated

      4) Area would be fenced

      5) Vehicle use would be restricted to designated roads

      6) No mineral activity would be allowed

   b. Southwest — increasing publicity on the declining numbers of tortoises (St. Amant, 1976)

E. Other management aids and problems

1. Problems — tortoise relocations

   a. Releasing captive tortoises (Boynton, 1970*b*)

      1) Animals not acquainted with release site

      2) Must seek out shelter from weather, predators, must find food

      3) This exposure results in increasing mortality hazards

   b. Gene pool mixing (Berry, 1973*b*; Bury and Marlow, 1973; Berry, 1975*b*; St. Amant and Hoover, 1978)

      1) Releasing captive tortoises in areas other than where their local populations occur

      2) Causes genetic mixing of populations of different regions, which is detrimental to natural biological phenomena

   c. Increased social interactions (Berry, 1975*b*)

      1) Releasing tortoises into a new population results in increased densities, perhaps beyond carrying capacity

      2) Home ranges may be disrupted

d. Introduction of diseases by captive tortoises, particularly those foreign to wild populations (St. Amant and Hoover, 1978)

2. Aids

a. Grazing

1) May be useful in scattering and trampling of seeds of annuals (Coombs, 1977*b*)

2) May increase production of annuals which are the main food source for tortoises (Coombs, 1977*b*)

b. Burning — burn out winter dens which are clogged with packrat nests (Coombs, 1977*b*)

c. Grazing management of poor rangelands

1) Omit grazing until perennial densities increase (Coombs, 1977*b*)

2) 50-year study (Blydenstein et al., 1957, cited by Busack and Bury, 1974) — grazed and ungrazed areas had same species composition occurring in about the same order of abundance but density greatly increased when protected from grazing in the Sonoran Desert

3) 30-year study (Gardner, 1950, cited by Busack and Bury, 1974)

a) With protection from grazing, grass density was 110% higher than in grazed areas

b) Grazing alters vegetational biomass

4) Use rest rotation to maintain spring annual growth for tortoises (Coombs, 1977*b*)

5) Reduce the number of grazing animals on the rangeland (Coombs, 1977*b*)

6) Locate watering sites for livestock away from high density tortoise population sites (Coombs, 1977*b*)

7) Create grazing exclosures to restrict livestock grazing from certain areas (Coombs, 1977*b*)

d. Predator control (Coombs, 1977*b*)

XXI. Legal status

A. International

1. Listed on Appendix II of the International Convention of Trade in Endangered Species of Wild Fauna and Flora

2. An export permit is required to send a desert tortoise out of the United States

B. Federal

1. Department of the Interior currently is reviewing the status of Utah population for possible listing as an endangered population

2. Department of the Interior is also reviewing status of species throughout its range

C. California

1. Currently protected (Bury and Marlow 1973)

   a. "Fish and Game Code 5000-5002 — 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*)."

   b. May be collected with a permit for scientific, zoological, and educational purposes only (Bury and Stewart, 1973)

   c. $1,000 fine and/or 1 year in jail for each offense

   d. Official state reptile (Anonymous, 1973; Bury and Stewart, 1973; Switak, 1973)

   e. Ban on possession and transport of all *Gopherus* species (Bury and Stewart, 1973)

   f. Illegal to remove from its natural habitat (Crooker, 1971)

2. History

   a. In 1939 the sale of the desert tortoise was forbidden (Grant, 1946)

   b. In 1961 partially protected, still unlawful to sell, harm, or take a desert tortoise (Bury and Stewart, 1973)

D. Arizona

1. "Commission Order T-43 — Possession limit on live horned lizards or live desert tortoises is one of each species and neither of these may be killed...reptiles may not be purchased, sold, offered for sale, or bartered and may not be imported or exported from the State unless authorized by the Commission" (Leach and Fisk, 1969)

2. Statute enforced by the Arizona Game Commission (Bury and Marlow, 1973)

E. Nevada (Leach and Fisk, 1969)

1. "503-600 — Catching, killing desert tortoise, terrestrial turtle unlawful. It shall be unlawful to catch or kill the desert tortoise or terrestrial turtle in the State of Nevada"

2. Nevada has no legal allowance for tortoises already in captivity before the Nevada law was passed

F. Utah

1. Wildlife resources code of Utah — Section 23-12-2, subsection 27 lists the desert tortoise as protected wildlife. Section 23-13-3 states that "it shall be unlawful for any person to take any protected wildlife or for any person to permit his dog to take protected wildlife except as provided by this code or the rules and regulations of the wildlife board or board of big game control."

2. Placed on the protected wildlife list in 1971 (Coombs, 1977*a*, *b*)

3. Voted to recommend endangered population status for the Utah desert tortoise at the federal level (Dodd, 1978)

4. Maximum fine for violation of law is $500 (Bury and Marlow, 1973)

G. Mexico — a special permit is needed to capture and export the desert tortoise (Bury and Marlow, 1973)

XXII. Husbandry

A. Rearing hatchlings

1. Feeding (Anonymous, 1970)

a. Initiate feeding before yolk sac is absorbed

b. Good to add multiple vitamin supplements to food and give bone meal twice per week

c. Offer hatchling fresh food several times daily

d. Provide fresh water with vitamins in it

e. Appropriate foods are finely chopped tomatoes, melons, lettuce, bananas

f. Chopped raw or cooked vegetables and fruits, grasses and flowers, ground raw meat or canned dog food (Clarke, 1968)

2. Environment (Anonymous, 1970)

a. Keep hatchling in a glass terrarium with a light at top for heat control

b. Provide cover or a "den" for the animal, an upside down box with a small entrance

c. Keep temperature between 27° and 29.5°C

d. Place in sunlight but protect from cats, birds, dogs, and other potential predators

e. Do not wash off hatchling's mucus coat, let it dry

B. Hatchling illnesses (Anonymous, 1970)

1. Illnesses caused by improper feeding

2. Illness caused by lack of natural sunlight

3. Respiratory ailments

4. Dry skin

a. Treatment is to rub cod liver oil or baby oil on the affected spot

b. Increase humidity

C. Adult illnesses

1. Eye infections (Burke, 1970)

a. Usually caused from decreased dietary intake of Vitamin A or disease in the gastrointestinal tract

b. Symptoms

1) Swelling of lids

2) Protrusion of nictitating membrane

3) Swelling of gland of nictitating membrane

4) Secondary bacterial infections

5) Lack of appetite

6) Diarrhea

7) Excessive oral mucus

8) Mouth breathing

9) Harshness of expiratory sounds

c. Treatment consists of intramuscular injection of 5000 I.U. of Vitamin A palmitate per 0.46 kg of whole body weight, 1 to 5 drops daily of cod liver oil administered orally for small to medium size specimens, and a broad spectrum antibiotic opthalmic ointment administered 4 times daily (Neomycin or Polymyxin B)

2. Hypothyroidism (Frye and Dutra, 1974)

   a. Caused by ingestion of goitrogenic vegetables, cabbage, kale, and brussel sprouts

   b. Symptoms include anorexia, lethargy, fibrous goiter, and myxedema of subcutaneous tissue

   c. Prevention consists of providing a well balanced natural diet for the desert tortoise and adding supplements of trace minerals to an artificial diet

   d. For treatment give sodium iodide (NaI) orally or parenterally

3. Most diseases of captive tortoises are caused by a combination of malnutrition and other stresses (Fowler, 1976*a*)

   a. Vegetables and fruits do not supply sufficient protein or energy for daily requirements

   b. Iceberg lettuce contains 1.2% protein and 2.5% carbohydrates

   c. Average percent of protein and carbohydrates for forbs is 9.36 and 38.8, respectively

D. Anomalies and their repair

1. Thick horny growth along upper and lower rims of mouth (Clark, 1967)

   a. Altered by surgical procedure

   b. Use Striker Cast Cutter® to trim away excess growth at top front portion

   c. Hole drilled in left and right lower part and pinned

   d. Cast drill cuts of material above pinned part

   e. Wire passed through 2 holes so jaw would not split

   f. File down any new growth seen

2. Repair of broken shell — epoxy method (Frye, 1973)

   a. Bathe exposed surface in Ringer's solution to which crystalline penicillin and dihydrostreptomycin have been added

   b. Remove all detritus and loose fragments

   c. Swab surface with Providone® iodine solution

   d. Gently fit shell fractures together beginning at the periphery and working to the center

e. Mix rapid polymerizing epoxy resin and apply with short strips of fiberglass cloth overlaid with more resin

f. Resin hardens quickly, several batches must be mixed

g. Inject 50 mg ampicillin trihydrate for 3 days

h. Epoxy does not irritate tissue it contacts

i. Care was taken to confine epoxy to shell surface

j. Heat during polymerization reached 45°C but this is rapidly dissipated when thin layers of epoxy are applied

3. Repair of broken shell — pressure method (Bissett, 1971)

   a. Bleeding stopped with boiled and cooled boric acid and water solution

   b. Area cleaned and 3% Aureomycin applied

   c. Area covered with gauze and tape creating little pressure

   d. Placed in box on heating pad

   e. After 3 days, dressing removed, area cleaned with boric acid solution and area covered with Aureomycin ointment, gauzed and taped securely applying slight pressure to carapace crack

   f. Tortoise ate clover with bone meal sprinkled on it, drank water, and eliminated

   g. Bandages changed after 1 week with more pressure applied to crack

   h. Crack healed after 4 months, bone knitted but cracks still evident in scutes

4. Repair of indented plastron of hatchling tortoise (Bissett, 1973)

   a. After 3 months the plastron had not unrolled; it was highly indented

   b. Tortoise had not eaten during the 3-month period

   c. Orally fed V-8® juice and Avitron® vitamins with a blunt syringe

   d. Given shallow warm water to drink

   e. Kept in a terrarium at 32°C

   f. X-rayed and no damage to internal organs evident

   g. After 2 weeks began eating

h. After 3½ weeks of feeding, plastron began to drop and egg sac fell off

5. Anesthesia — Lidocaine® used effectively in 2% solution as local analgesia (Dantzler and Schmidt-Nielsen, 1966)

E. General husbandry

1. In summer (Anonymous, 1972)

a. Provide ample shade

b. Shallow pan of water

2. For nonfeeding tortoises (Bissett, 1972)

a. Administer Avitron® and V-8® vegetable juice orally with a blunt syringe several times a day

b. Alternate with apple juice

c. Place in yard under fruit box to provide sun and shade when air temperature is moderate

d. Provide water

e. After several days try feeding clover and lettuce

f. After a few more days the animal is usually eating on its own

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