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

by

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

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

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

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

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

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

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

Definition of Population, Range, and Distribution

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

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

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

Material and Methods

We used several sources of information to document the distribution of the desert tortoise in the eastern Mojave Desert. The largest data set was compiled from survey transects sponsored by the Bureau of Land Management (BLM). Bureau of Land Management transects are about 9.1 m wide by about 2.4 km long and in the form of an equilateral triangle (Minden 1980; Karl 1981; Turner et al. 1985; Berry 1986a). Recorded sign were live tortoises, shells, scats, tracks, and shelter sites. Cover

and shelter included pallets (depressions that cover the shell of a tortoise), burrows (constructed underground holes about 0.5–2 m deep) and dens (2–10 m long). Although total sign on transects is used to estimate the density of tortoises (Berry 1986a), we mostly used these data to document the presence or absence of tortoises.

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

Study Area

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

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

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

Utah and Northwestern Arizona

Dixie Valley, Utah

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

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

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

To our knowledge, the first specimen of the tortoise in Utah (Van Denburgh 1922:989) was an individual "taken on the mesas south of the Shivwits Indian Reservation, about 14 miles west of Saint George, Washington County." However, no museum number was provided. Patterson (1982) reported the Shivwits record as a literature citation and one museum specimen from St. George (California Academy of Sciences [CAS] 54190, collected in July 1921). We were informed that there is only one Utah specimen (CAS 54190) from that period and it is from St. George. Possibly, Van Denburgh's report (1922) of a tortoise from Shivwits was cataloged as having been from St. George, the nearest large town. In either case, one

or two tortoises were obtained about 70 years ago in or near St. George. Also, Tanner (1927) reported tortoises near St. George, Utah. Woodbury (1931:123) recorded these localities and records from the Beaver Dam Slope and St. George where "...B. Jarvis found a juvenile freshly hatched from the egg."

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

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

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

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

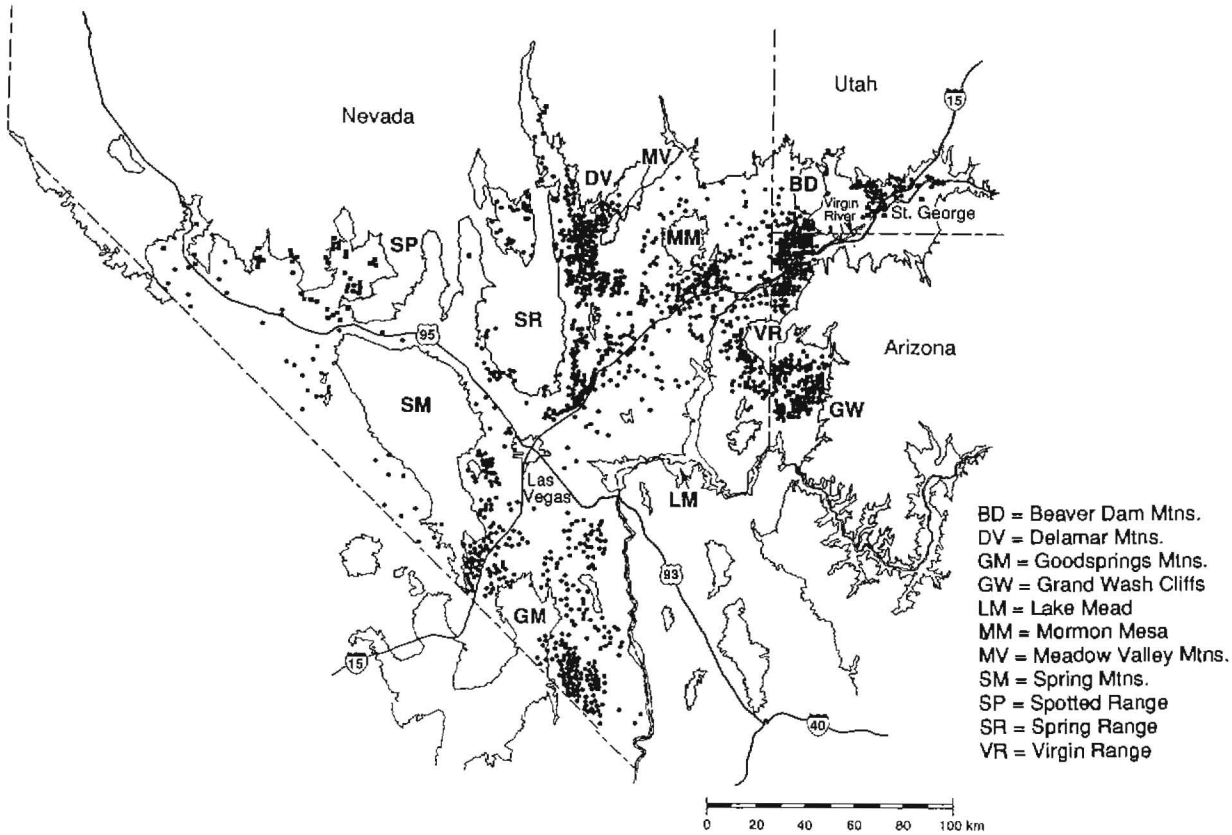

Fig. 1. Distribution of the desert tortoise (*Gopherus agassizii*) in Nevada, northwestern Arizona, and southwestern Utah. *Solid circles* indicate records of one or more signs at transects by the Bureau of Land Management; and *solid squares* are our observations or those of colleagues. *Irregular lines*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

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

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

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

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

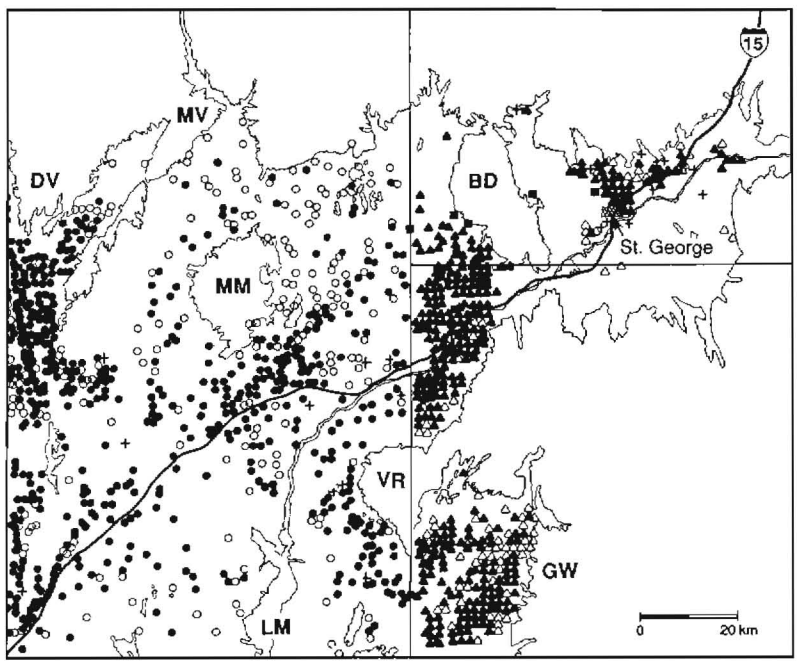

Fig. 2. Occurrence of the desert tortoise (*Gopherus agassizii*) in the northeastern portion of its range. *Solid symbols* are sites with tortoises or their sign; *open symbols* indicate that no tortoises and no sign were observed. *Circles* indicate transects based on records at the Bureau of Land Management,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

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

North St. George, Utah

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

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

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

Beaver Dam Slope and Vicinity, Utah and Arizona

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

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

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

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

washes with coarse sand and gravel (Hohman and Ohmart 1978).

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

Northwestern Arizona and Nevada

Virgin Mountains, Arizona

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

Pakoon Basin and Gold Butte, Arizona and Nevada

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

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

Nevada

Statewide Records

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

Mormon Mountains and Vicinity

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

The Meadow Valley Mountains separate tortoises in Meadow Valley to the east from the Coyote Springs Valley to the west. We have found tortoises in the Meadow Valley on lower bajadas and flats,

where there are gravelly, sandy loams with low slopes (3–5%). Tortoises have not been reported in adjacent playas (old lake beds) and tall mountain ranges, where no surveys have been conducted.

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

Coyote Springs and Pahranagat Valleys

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

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

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

Desert National Wildlife Refuge and Vicinity

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

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

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

Nellis Air Force Base

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

Few records existed in this region until an extensive survey was conducted over 1,181 km^2 from December 1991 to May 1992 (Revegetation Innovations, unpublished data). Tortoise signs were recorded at 110 of 431 transects, in all major vegetation associations, and from valley bottoms to

upper slopes (Table 1). Tortoise sign was only absent in dry playas. Surveys were mostly in winter, which reduced the likelihood of locating tortoise sign. Still, tortoises seem to be widespread and in low density on the Nellis Air Force Base.

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

Nevada Test Site and Vicinity

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

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

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

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

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

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

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

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

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

Discussion

Comparison of Occurrences and Estimated Densities

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

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

Dixie Valley Tortoises: Native or Introduced?

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

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

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

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

Most reptiles in the eastern Mojave Desert, including the banded gecko (*Coleonyx variegatus*),

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

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

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

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

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

Beaver Dam Slope of Utah, Arizona, and Nevada

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

Limitation of Distribution

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

Habitat Use

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

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

cactus gardens, rocky slopes, and steep terrain, are seldom surveyed.

Cover

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

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

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

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

Elevational Limits

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

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

Threats to Tortoises

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

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

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

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

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

Protection of Small and Isolated Populations

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

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

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

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

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

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

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

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

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Cited Literature

Auffenberg, W. 1969. Tortoise behavior and survival. Biological Science Study Curriculum, Patterns of Life Series. Rand McNally and Co., Chicago, Ill. 38 pp.

Beck, D., and E. Coombs. 1987. The current status of the Paradise Canyon, Utah, desert tortoise population. Proceedings of the Desert Tortoise Council 1984:43–50.

Berry, K. H. 1986a. Desert tortoise (*Gopherus agassizii*) research in California. Herpetologica 42:62–67.

Berry, K. H. 1986b. Desert tortoise (*Gopherus agassizii*) relocation: implications of social behavior and movements. Herpetologica 42:113–125.

Berry, K. H. 1989. *Gopherus agassizii*: desert tortoise. Pages 5–7 in I. A. Swingland and M. W. Klemens, editors. The conservation biology of tortoises. International Union for Conservation of Nature and Natural Resources Species Survival Commission, Occasional Paper 5.

Burge, B. L., and W. G. Bradley. 1976. Population density, structure and feeding habits of the desert tortoise, *Gopherus agassizi*, in a low desert study area in southern Nevada. Proceedings of the Desert Tortoise Council 1976:51–74.

Bury, R. B., T. C. Esque, and P. S. Corn. 1994. Conservation of desert tortoises (*Gopherus agassizii*): genetics and protection of isolated populations. Proceedings of the Desert Tortoise Council 1987–1991:59–66.

Coffeen, M. C. 1990. State report, Utah—1985. Proceedings of the Desert Tortoise Council 1986:20–28.

Collins, E., T. P. O'Farrell, and M. L. Sauls. 1986. Survey for desert tortoise on the possible site of a high-level nuclear waste repository, Nevada Test Site. Proceedings of the Desert Tortoise Council 1983:19–26.

Coombs, E. M. 1977. Status of the desert tortoise, *Gopherus agassizii*, in the state of Utah. Proceedings of the Desert Tortoise Council 1977:95–101.

Corn, P. S. 1994. Recent trends of desert tortoise populations in the Mojave Desert. Pages 85–93 *in* R. B. Bury and D. J. Germano, editors. Biology of North American tortoises. National Biological Survey, Fish and Wildlife Research 13.

Dodd, K. C., Jr. 1986. Desert and gopher tortoises: perspectives on conservation approaches. Pages 54–72 *in* D. R. Jackson and R. J. Bryant, editors. The gopher tortoise and its community. Proceedings of the Fifth Annual Meeting of the Gopher Tortoise Council.

Dodd, K. C., Jr., and R. A. Seigel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? Herpetologica 47:336–350.

Fritts, T. H., and R. D. Jennings. 1994. Distribution, habitat use, and status of the desert tortoise in Mexico. Pages 49–56 *in* R. B. Bury and D. J. Germano, editors. Biology of North American tortoises. National Biological Survey, Fish and Wildlife Research 13.

Fusari, M., D. Beck, K. H. Berry, M. Coffeen, J. Diemer, and J. A. St. Amant. 1987. A panel discussion of relocation and related issues and implications for management of the desert tortoise. Proceedings of the Desert Tortoise Council 1984:136–146.

Germano, D. J. 1993. Shell morphology of North American tortoises. American Midland Naturalist 129:319–335.

Germano, D. J. 1994. Comparative life histories of North American tortoises. Pages 175–185 *in* R. B. Bury and D. J. Germano, editors. Biology of North American tortoises. National Biological Survey, Fish and Wildlife Research 13.

Germano, D. J., R. B. Bury, T. C. Esque, T. H. Fritts, and P. A. Medica. 1994. Range and habitats of the desert tortoise. Pages 73–84 *in* R. B. Bury and D. J. Germano, editors. Biology of North American tortoises. National Biological Survey, Fish and Wildlife Research 13.

Germano, D. J., and M. A. Joyner. 1988. Changes in a desert tortoise (*Gopherus agassizii*) population after a period of high mortality. Pages 190–199 *in* R. C. Szaro, K. E. Severson, and D. R. Patton, editors. Management of amphibians, reptiles, and small mammals in North America. U.S. Forest Service, General Technical Report RM-166.

Gilpin, M. E., and M. E. Soule. 1986. Minimum viable populations: processes of species extinction. Pages 19–34 *in* M. E. Soule, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Mass.

Glenn, J. L., R. C. Straight, and J. W. Sykes. 1990. A plasma protein marker for population genetic studies of the desert tortoise (*Xerobates agassizii*). Great Basin Naturalist 50:1–8.

Hardy, R. 1945. The influence of types of soil upon the local distribution of some mammals in southwestern Utah. Ecological Monographs 15:71–108.

Hohman, J. P., and R. D. Ohmart. 1978. Historical range use of the Beaver Dam Slope, Arizona, and its possible effects on a desert tortoise population. Proceedings of the Desert Tortoise Council 1978:116–125.

Jennings, R. D. 1985. Biochemical variation of the desert tortoise, *Gopherus agassizii*. M.S. thesis, University of New Mexico. 70 pp.

Karl, A. 1981. The distribution and relative densities of the desert tortoise, *Gopherus agassizi*, in Lincoln and Nye counties, Nevada. Proceedings of the Desert Tortoise Council 1981:76–92.

Lamb, T., J. C. Avise, and J. W. Gibbons. 1989. Phylogenetic patterns in mitochondrial DNA of the desert tortoise (*Xerobates agassizii*), and evolutionary relationships among the North American gopher tortoises. Evolution 43:76–87.

Linsdale, J. M. 1940. Amphibians and reptiles of Nevada. Proceedings of the American Academy of Arts and Sciences 73, 8:197–257.

Luckenbach, R. A. 1982. Ecology and management of the desert tortoise (*Gopherus agassizii*) in California. Pages 1–37 *in* R. B. Bury, editor. North American tortoises: conservation and ecology. U.S. Fish and Wildlife Service, Wildlife Research Report 12.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. Harper and Row, New York. 269 pp.

Mayr, E. 1970. Populations, species, and evolution. Belknap Press, Cambridge, Mass. 453 pp.

Medica, P. A., R. B. Bury, and R. A. Luckenbach. 1980. Drinking and construction of water catchments by the desert tortoise, *Gopherus agassizii*, in the Mojave Desert. Herpetologica 36:301–304.

Minden, R. L. 1980. An investigation of the desert tortoise (*Gopherus agassizii*) on the Beaver Dam slope, Washington County, Utah. Utah State Division of Wildlife Resources, Publication 80–21. 43 pp.

Minden, R. L., and S. M. Keller. 1981. Population analysis of the desert tortoise (*Gopherus agassizii*) on the Beaver Dam Slope, Washington County, Utah. Utah State Division of Wildlife Resources, Publication Number 81–14. 49 pp.

Oldemeyer, J. L. 1994. Livestock grazing and the desert tortoise in the Mojave Desert. Pages 95–103 *in* R. B. Bury and D. J. Germano, editors. Biology of North American tortoises. National Biological Survey, Fish and Wildlife Research 13.

Patterson, R. 1982. Distribution of the desert tortoise (*Gopherus agassizii*). Pages 51–55 *in* R. B. Bury, editor. North American tortoises: conservation and ecology. U.S. Fish and Wildlife Service, Wildlife Research Report 12.

Rainboth, W. J., D. G. Buth, and F. B. Turner. 1989. Allozyme variation in Mojave populations of the desert tortoise, *Gopherus agassizii*. Copeia 1989:115–123.

Reyes Osorio, S., and R. B. Bury. 1982. Ecology and status of the desert tortoise (*Gopherus agassizii*) on Tiburon Island, Sonora. Pages 39–49 *in* R. B. Bury, editor. North American tortoises: conservation and ecology. U.S. Fish and Wildlife Service, Wildlife Research Report 12.

Rowlands, P., H. Johnson, E. Ritter, and A. Endo. 1982. The Mojave Desert. Pages 103–162 *in* G. L. Bender, editor. Reference handbook on the deserts of North America. Greenwood Press, Westport, Conn.

Schneider, P. B., R. J. Turner, and K. E. Bohuski. 1985. Distribution and relative density of desert tortoises

at six selected sites in southern Nevada. Proceedings of the Desert Tortoise Council 1982:36–50.

Schonewald-Cox, C. M., S. M. Chambers, F. MacBryde, and L. Thomas, editors. 1983. Genetics and conservation: a reference for managing wild animals and plant communities. Benjamin/Cummings, Menlo Park, Calif. 722 pp.

Sheppard, G. P. 1980. Status of the Arizona Beaver Dam Slope population of desert tortoises. Proceedings of the Desert Tortoise Council 1980:23–32.

Tanner, V. M. 1927. Distributional list of the amphibians and reptiles of Utah. Copeia 163:54–58.

Tanner, W. W., and D. C. Jorgensen. 1963. Reptiles of the Nevada Test Site. Brigham Young University Science Bulletin, Biological Series 3:1–31.

Turner, F. B., P. A. Medica, and R. B. Bury. 1987. Age–size relationship of desert tortoises (*Gopherus agassizii*) in southern Nevada. Copeia 1987:974–979.

Turner, F. B., C. G. Thelander, D. C. Pearson, and B. L. Burge. 1985. An evaluation of the transect technique for estimating desert tortoise density at a prospective power plant site in Ivanpah Valley, California. Proceedings of the Desert Tortoise Council 1982:134–153.

U.S. Fish and Wildlife Service. 1993. Proposed determination of critical habitat for the Mojave population of the desert tortoise: proposed rule. Federal Register 58:45748–768.

Van Denburgh, J. D. 1922. The reptiles of western North America. Occasional Papers, California Academy of Sciences 1–1028.

Woodbury, A. M. 1931. A descriptive catalog of the reptiles of Utah. University of Utah Biological Series. Bulletin 21 1(4):1–129.

Woodbury, A. M., and R. Hardy. 1948. Studies of the desert tortoise, *Gopherus agassizii*. Ecological Monographs 18:145–200.

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