9 Habitat Characteristics of North American Tortoises

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North American tortoises are distributed in semiarid and temperate deserts and coastal regions of the southern United States and Mexico (Bury and Germano 1994). The five species currently recognized each have specific habitat requirements, which they fulfill through their selection of, and interaction with, unique habitat constituents. Below, we discuss the physiographic and geological associations, perennial and annual vegetation components, shelter sites, and climatic conditions associated with the species' habitats, as well as the potential threats to their habitat.

PHYSIOGRAPHY AND GEOLOGY

Gopherus agassizii is most commonly found in valley bottoms throughout the Mojave Desert and portions of the Sonoran Desert north and west of the Colorado River (fig. 9.1). It inhabits several distinct habitat types, from alkaline areas surrounding playas, through bajadas formed by alluvial fans at middle elevations, and into rockier slopes and intermittent dunes and valleys as its distribution encroaches on mountainous areas (Bury et al. 1994, Nussear et al. 2009). The species occurs on soils where burrow construction is possible (Burge 1978, Morafka and Berry 2002), ranging from sandy to sandy loamy to gravelly (Luckenbach 1982), and in rockier soils with caves that provide cover during summer aestivation and winter dormancy (Woodbury and Hardy 1948, Bulova 1994, Nussear et al. 2007). Individuals tend to avoid areas of exposed bedrock, which impedes digging shelter and nesting sites (Bramble 1982, Bury et al. 1994) and inhibits mobility in the steep terrain typical of this soil type (Bury et al. 1994, Nussear et al. 2009).

Gopherus morafkai lives in the Sonoran Desert south and east of the Colorado River in Arizona, extending southward into Sonora and Sinaloa, Mexico (Fritts and Jennings 1994, Van Devender 2002a, Murphy et al. 2011). The species also inhabits Mojave Desert habitats in Arizona, along the transition zone of the Mojave and Sonoran Deserts (Murphy et al. 2011), although some populations may be remnant populations of *G. agassizii* isolated when river channels shifted (McLuckie et al. 1999). The distribution of *G. morafkai* spans many subdivisions within the Sonoran Desert, including the Lower Colorado River Valley and Arizona Upland, margins of semidesert grasslands in the east, and Sinaloan thornscrub and deciduous forests in the south (Brown 1994, Turner and Brown 1994, Fritts and Jennings 1994, Bury et al. 2002, Van Devender 2002b).

Within its broad distribution of habitat types, *G. morafkai* occupies a wide range of soils. The Arizona Upland consists of rocky slopes and ridges, with underlying soils formed from volcanic, metamorphic, and sedimentary rocks (Van Devender 2002b). Individuals there live on rocky slopes and bajadas and in deeply incised washes with caliche caves (fig. 9.2). Individuals generally are absent from intermountain floors (Barrett 1990, Berry et al. 2002a, Averill-Murray and Averill-Murray 2005), but occupy the entire habitat above the bajada (Averill-Murray et al. 2002b). The rocky habitat of the Arizona Upland transitions in the south to the Plains of Sonora and there, much like in the Arizona Upland, individuals inhabit rocky slopes, bajadas, and arroyos (Fritts and Jennings 1994, Van Devender 2002a).

The two species of desert tortoise are the most closely related among the five species of tortoises in North America (chapter 3), and occupy a continuum of habitats throughout the Mojave and Sonoran Deserts, ranging from valley bottoms in the Mojave Desert to uplands in the hotter and wetter Sonoran Desert. It has been hypothesized that this upward shift in elevation in the Sonoran Desert is attributable to the temperature and precipitation differences between the Mojave and Sonoran Deserts: periodic flooding, high clay and silt content in soils, and corresponding low plant diversity are typical of the valley bottoms of the Sonoran Desert, especially in the lower Colorado River Valley (Turner and Brown

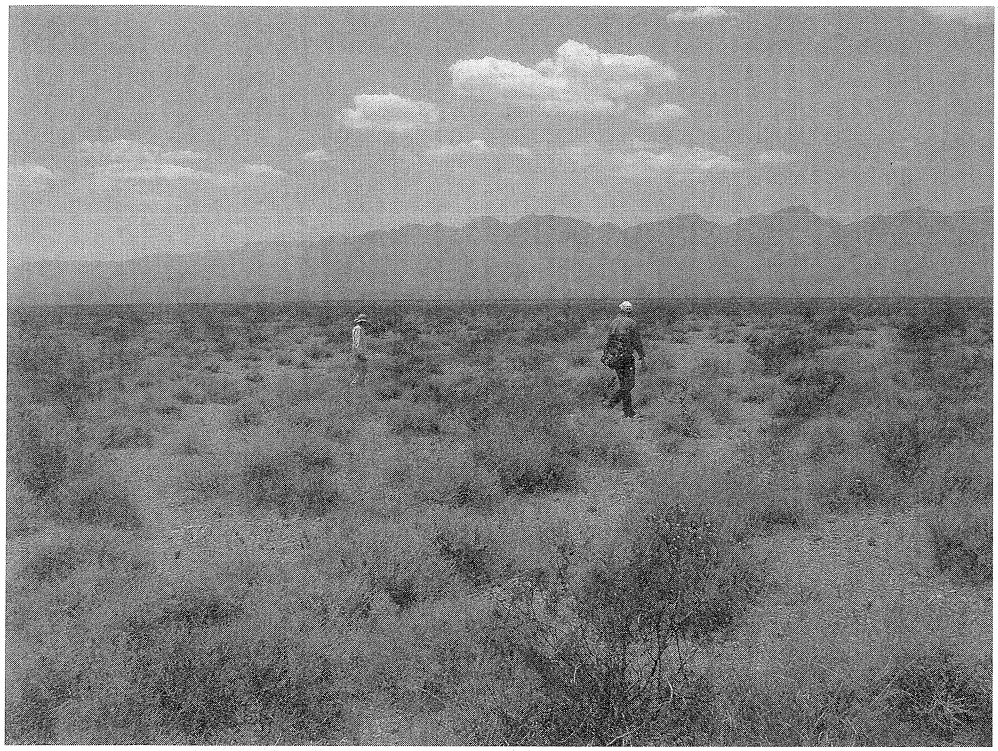

Fig. 9.1. Typical *Gopherus agassizii* Creosote scrub habitat, in the Mojave Desert, near Coyote Springs Valley, Nevada. Photo courtesy of K Nussear.

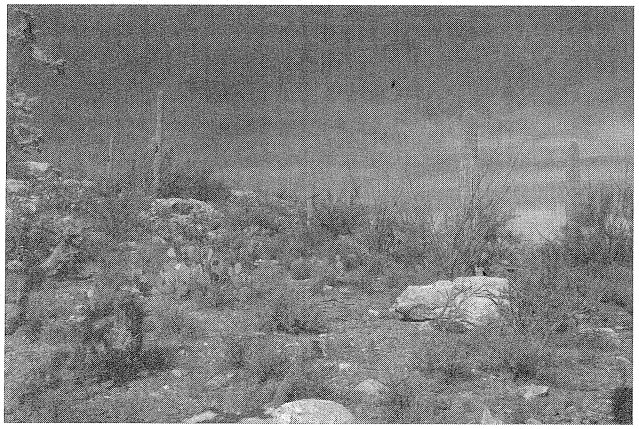

Fig. 9.2. Characteristic upland habitat of *Gopherus morafkai*, near Tuscon, Arizona. Photo courtesy of TC Esque.

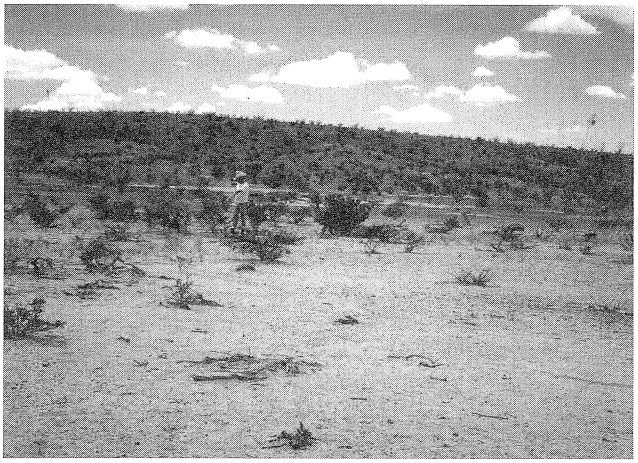

Fig. 9.3. Dave Morafka surveying *Gopherus flavomarginatus* habitat. Photo courtesy of D Biggins and B Bury.

1994, Bailey et al. 1995, Van Devender 2002a). Temperatures likely limit tortoises at higher elevations in the Mojave Desert (Luckenbach 1982).

Gopherus flavomarginatus is precinctive to an area of approximately 6000 km^2 within the Mapimian subprovince of the Chihuahuan Desert (Morafka 1982). It occupies interconnected drainages in the Bolson de Mapimi, in portions of northeastern Durango, southwestern Chihuahua, and southeastern Coahuila, Mexico (Auffenberg 1969, Morafka 1982, Aguirre 1994). The species occurs exclusively in bolsons—rolling desert valleys typically containing a playa surrounded by hillsides and mountainous areas (Bury et al. 1988; fig. 9.3). Limestone ridges surround many of these bolson lowlands, which were once pluvial lakes in the late Pleistocene and early Holocene (Morafka 1982). Individuals live and construct their burrows in areas that are predominantly sand (50–72%; Lieberman and Morafka 1988) and fine gravel, with little clay or silt (7–25%; Bramble 1982, Morafka 1982), and with high alkalinity (Morafka 1982, Adest and Aguirre 1995). Individuals generally are absent from the flat lowland areas, which flood periodically during summer rains (Bury et al. 1988), but inhabit the gently sloping sandy areas below the rocky hilltops. Individuals also are rare in areas of higher slopes, as soils change from hard compacted sand/clay composition

Fig. 9.4. Thornscrub savannas with patches of brush and cactus and scattered open grassy areas occupied by *Gopherus berlandieri* in Texas. Photo courtesy of TD Tuberville.

to desert pavement or to soils with high gravel content (i.e., 25%), which reduces their ability to burrow and limits growth of grasses and other forage species (Morafka 1982, Lieberman and Morafka 1988).

Gopherus berlandieri inhabits Tamaulipan brushlands in the plains of the Lower Rio Grande Valley (Kazmaier et al. 2001a; fig. 9.4), and prefers sandy, well-drained soils (Ernst and Lovich 2009). It occurs at elevations from sea level to 200 m elevation in southern Texas, and up to 884 m elevation in Coahuila, Mexico (Rose and Judd 1982). In coastal areas, the species is noted for its association with lomas—isolated clay or sand dunes surrounded by salt flats that may be periodically inundated with water (Auffenberg and Weaver 1969). Flats that are frequently flooded remain unvegetated, while the adjacent lomas create windbreaks that accumulate wind-blown silt. Lomas along vegetated flats are only temporarily stabilized; most of the time, however, more soil is eroding than is accumulating (Auffenberg and Weaver 1969). Lomas exhibit remarkable spatial and temporal heterogeneity, varying in size and proximity to one another. Because intervening salt flats are unsuitable for the species, lomas function as habitat islands, with populations associated with particular lomas and apparently little interchange of individuals among them (Bury and Smith 1986).

Gopherus polyphemus is restricted to the Coastal Plain of the southeastern U.S., where it is associated with deep, well-drained sandy soils (Auffenberg and Franz 1982, USFWS 1990a). Although the relative proportions of sand, clay, and loam components may vary, these soils generally have a sandy layer extending at least 1–1.5 m deep (USFWS 1990a, Jones and Dorr 2004). Jones and Dorr (2004) found active burrows to be positively associated with sandy soils and negatively associated with loamy soils in industrial forests of Alabama and Mississippi (fig. 9.5). The probability of the species occurring in the landscape (based on presence of their burrows) decreases with increasing clay content in surface soil horizons (Baskaran et al. 2006). In the western portion of the species' range, deep sandy soils are limited, and individuals are associated with soils with higher clay content than elsewhere throughout the range (Means 1982).

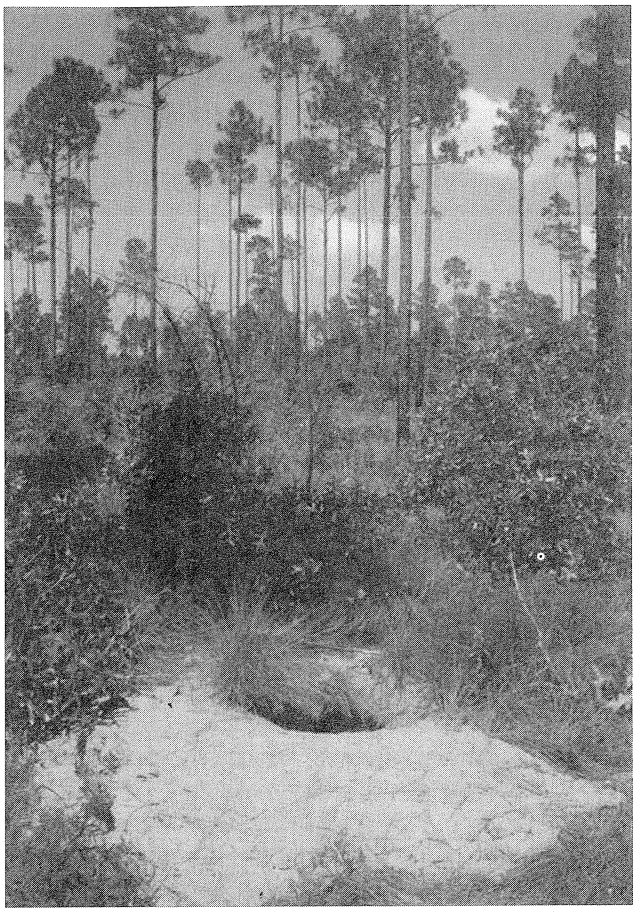

Fig. 9.5. Open canopy Longleaf pine habitat occupied by *Gopherus polyphemus*. Photo courtesy of TD Tuberville.

VEGETATION

Gopherus agassizii is found in Mojave Desert scrub vegetation with the dominant vegetation alliances of creosote/bursage (*Larrea tridentate / Ambrosia dumosa*) scrub (Turner 1994, Germano et al. 1994; fig. 9.1). Vegetation changes predictably with elevation, and at lower elevations, individuals are found in areas dominated by saltbush (*Atriplex* sp.). In upper elevations they can be found in Mojave mixed desert scrub, which frequently includes *Yucca* species (*Y. schidigera, Y. brevifolia,* and *Y. baccata*) in a diverse mix of perennial plants. With increasing elevation, the dominant vegetation transitions to blackbrush (*Coleogyne ramosissima*) and eventually piñon (*Pinus monophylla*)–juniper (*Juniperus osteosperma*) woodlands (Turner 1994), and tortoises become scarce (Schamberger and Turner 1986, Bury et al. 1994). At higher latitudes, individuals can be found at times in sage- (*Artemisia* sp.) dominated areas in the transition between the Mojave and the Great

Basin (Nussear 2004). In the Colorado Desert of California, *G. agassizii* is found in areas with incursions of plants more typically associated with Sonoran Desert scrub (e.g., ocotillo [*Fouquieria splendens*] and ironwood [*Olneya tesota*]), in washes interspersed in a *Larrea/Ambrosia*–dominated landscape, and in rockier sites with cactus-scrub vegetation (Luckenbach 1982). Individuals actively seek specific species of perennial plants for shelter (Woodbury and Hardy 1948, Luckenbach 1982, Bury et al. 1994), presumably because of their thermal characteristics (Burge 1978, Hillard 1996, Nussear 2004). In addition to creosote and bursage in the Mojave Desert, *Ephedra* sp., *Lycium andersonii,* and *Yucca* sp. also are frequently chosen (Woodbury and Hardy 1948, Burge 1978, Nussear 2004).

The Arizona Upland occupied by *G. morafkai* has diverse species assemblages, including palo verde (*Cercidium* sp.), ironwood, and saguaro with many shrubs (e.g., brittlebush, California buckwheat) and cacti in the understory (Turner and Brown 1994, Van Devender 2002a). Washes and arroyos emanating from the uplands frequently contain mesquite trees and lowland shrubs (e.g., *Lycium* sp.; Van Devender 2002a). The Lower Colorado River Basin has a less diverse and less dense flora as a result of high temperatures and low precipitation (Turner and Brown 1994, Van Devender 2002a). Saguaro, palo verde, and ironwood are still present but restricted to washes. The flora is dominated by creosote and bursage (Turner and Brown 1994, Van Devender 2002a), much like in the Mojave Desert (Turner 1994). In Mexico, the species inhabits densely vegetated Sinaloan thornscrub, with as many as 2,000 plants per hectare, consisting predominantly of shrubs in the north and transitioning to trees in the south (Brown 1994). Individuals are sparsely distributed on the eastern border of the species' range, and diminish quickly as habitat transitions to Madrean evergreen woodlands (Fritts and Jennings 1994).

Gopherus flavomarginatus inhabits grasslands of the Chihuahuan desert (Morafka 1982). The dominant perennial vegetation is comprised largely of sparsely distributed shrubs and small trees such as mesquite (*Prosopis* sp.), creosote, tarbush (*Flourensia cenua*), guayule (*Parthenium argentatum*), and cacti, such as pencil cholla (*Opuntia* sp.) and prickly pear (*O. rastrera*) and *Agave* sp.—all of which are used for shade (Morafka 1982, Tom 1994) or for protection of burrows (Aguirre et al. 1984). Common grasses include grama grass (*Bouteloua* sp.; Aguirre 1994, Tom 1994) and tobosa grass (*Hilaria mutica*), the latter of which can comprise up to 23% cover in tortoise-occupied areas. Although individuals are strongly associated with tobosa grass, they are not common in lowlands where tobosa grass forms a monoculture: they are more prominent in areas with a mixed community of grasses, including *Sceleropogon brevifolis, Sporoholus* sp., and *Erioneuron pulchellus* (Lieberman and Morafka 1988). Ocotillo and the euphorb *Jatropha dioica* also occur on the desert pavement slopes above the grasslands (Morafka 1982).

Gopherus berlandieri is distributed in the Tamaulipan Biotic Province and the Rio Grande Plains Ecoregion (Auffenberg and Weaver 1969, Kazmaier et al. 2001b). In coastal areas, the species occupies isolated lomas embedded in a matrix of expansive, treeless grasslands or salt flats (Auffenberg and Weaver 1969, Bury and Smith 1986). The lomas have distinct, concentric vegetation zones with characteristic plant associations—brush, *Baccharis* sp. (an aster), and grass and cactus zones (Rose and Judd 1982). Elsewhere, individuals are most commonly associated with thornscrub savannas and woodlands characterized by dense patches of brush and cactus with scattered open grassy areas (Kazmaier et al. 2001a, fig. 9.4). The species favors open scrub habitats, but will use a diversity of scrub habitats varying in cover.

Individuals of *G. berlandieri* are strongly associated with prickly pear cactus (*O. lindheimeri, O. leptocaulis*), which provides both cover and food with high water content (Rose and Judd 1982). Dominant woody species in their habitat include honey mesquite (*P. glandulosa*), huisache (*Acacia farnesiana*), lotebush (*Condalia obtusifolia*), and yucca (*Y. traculeana*) (Auffenberg and Weaver 1969). Buffalo grass (*Buchloe dactyloides*) can be prevalent on the tops of lomas, with three-awn grass (*Aristida* sp.), short grass (*Bouteloua* sp.), and sand bur (*Cenchrus* sp.) more likely around the perimeter. Lomas have few forbs, and are typically surrounded by the coarse, bunchy sacahuista grass (*Spartina alterniflora*), although glasswort (*Salicornia* spp.) and seashore saltgrass (*Distichlis spicata*) may also occur (Rose and Judd 1982, Bury and Smith 1986). Dominant woody species in thornscrub are honey mesquite, hog plum (*Colubrina texensis*), and several acacia species (*Acacia rigidula, A. berlandieri, A. schaffneri*). The most common native grasses are species of *Setaria* and *Paspalum,* hooded windmill grass (*Chloris cucullata*), hairy grama (*Bouteloua hirsuta*), and fringed signal grass (*Brachiaria ciliatissima;* Hellgren et al. 2000).

Gopherus polyphemus is best known for its association with longleaf pine (*Pinus palustris*), but the species also occurs in coastal dune, scrub, and oak hammock communities. Longleaf pine forests occur along a soil-moisture continuum ranging from xeric upland sandhills typified by smaller, scattered pines and a diverse understory of oaks and other hardwoods to more mesic pine flatwoods with large, widely spaced pines and a grassy understory and no shrubby mid-story (fig. 9.5). Dominant tree species in the overstory frequently include longleaf, loblolly (*P. taeda*), and/or slash (*P. elliottii*) pines, and turkey (*Quercus laevis*), post (*Q. stellata*), bluejack (*Q. incana*), and/or laurel (*Q. laurifolia*) oak. Hickory (*Carya* spp.) and sweet gum (*Liquidambar styraciflua*) also may be present. Blueberry (*Vaccinium arboreum, V. stamineum*), fetterbush or staggerbush (*Lyonia lucida, L. fruticosa*), gallberry (*Ilex* spp.), and wax myrtle (*Myrica cerifera*) commonly occur in the shrub understory. Saw palmetto (*Serenoa repens*) can dominate at some sites, particularly in coastal areas. The longleaf pine forest is well known for its understory diversity (Walker and Peet 1984, Peet and Allard 1993). More than 1,000 plant species have been documented at individual sites (e.g., Drew et al. 1998, Sorrie et al. 2006), although species diversity can vary as a function of local edaphic conditions, site history, and contemporary management (Kirkman et al. 2001, Brudvig and Damschen 2011). The herbaceous understory typically is comprised of a combination of grasses and forbs, including

wiregrass (*Aristida stricta, A. beyrichiana*), bluestem grasses (*Andropogon* spp.), asters, and legumes. Prickly pear cactus (*O. compressa*) is characteristic in some habitats.

Longleaf pine historically was widespread, constituting about 60% of the Coastal Plain. Few remnants of old-growth remain, however (<3% of historical distribution; Ware et al. 1993, Means 2006), with much having been converted to other land uses or replanted with faster-growing pine species. Where soils are suitable, *G. polyphemus* can inhabit ruderal habitats, including abandoned pastures and agricultural fields, pine plantations managed for timber production, powerline and transportation rights-of-way, military training areas, and other disturbed sites with open canopies and abundant forage (Hermann et al. 2002, Jones and Dorr 2004, Baskaran et al. 2006, Yager et al. 2007, Ashton et al. 2008).

PRECIPITATION

Global atmospheric circulation patterns result in warm, high-pressure air masses causing generally dry conditions at the latitudes where the western species of North American tortoises live. General precipitation patterns periodically are affected by the El Nino–Southern Oscillation Cycle, every seven to ten years. During positive cycling (El Niño), rainfall increases in western North America and decreases in the East, while the converse occurs during negative cycling (La Niña). In the West, mountain ranges create rain shadows that, coupled with cold marine currents, influence the North American hot deserts (Evenari 1985, Shmida 1985) occupied by the three western-most tortoise species—*Gopherus agassizii* (Mojave Desert), *G. morafkai* (Sonoran Desert), and *G. flavomarginatus* (Chihuahuan Desert) (Patterson 1982, Murphy et al. 2011, Morafka 1982). Each desert provides different opportunities for water (and consequently food; chapter 10) acquisition because of a precipitation cline overlaid on the latitudinal temperature gradient, running diagonally through all three deserts. The northwest Mojave Desert is normally dominated by winter rains from November through March. Summer storms of tropical origin move across the Mojave Desert each summer, but precipitation in the summer typically is low, increasing toward the southeast. Likewise, winter storm dominance diminishes toward the south and east. Precipitation within the distribution of *G. agassizii* ranges from 100 to 210 mm per year, with most falling as winter rain, especially in the western Mojave Desert (Germano et al. 1994, Tracy et al. 2004). Both summer and winter precipitation influence habitat suitability, with areas having winter rainfall of 50–180 mm and summer rainfall of 20–130 mm predicted to support more suitable tortoise habitat (Nussear et al. 2009).

The desert scrub habitat occupied by *G. morafkai* has low and unevenly distributed rainfall. The proportion of summer to winter rainfall is 35:70%, far greater than in the adjacent Mojave Desert (<10%; Germano et al. 1994). Average precipitation ranges from 0 to 170 mm in summer and 15 to 70 mm in winter for the Lower Colorado River Basin; 60–240 mm in summer and 40–140 mm in winter in the Arizona Upland, and 45–185 mm in summer and 20–60 mm in winter in the Plains of Sonora (Turner and Brown 1994). In each case, precipitation varies far more in summer than in winter; but summer rainfall is more reliable in the Sonoran Desert than in the Mojave Desert (Germano et al. 1994, Averill-Murray et al. 2002b). Tortoises generally are absent from areas with <100 mm of annual precipitation (Fritts and Jennings 1994). Drought can increase mortality rates and potentially decimate local populations of the desert-dwelling tortoises (Howland and Rorabaugh 2002, Averill-Murray et al. 2002b, Peterson 1994, Longshore et al. 2003). In contrast, *G. flavomarginatus* habitats receive the majority of their precipitation during summer months, as a result of tropical storms in late June through November. Annual precipitation ranges from 200 to 323 mm (Morafka and Berry 2002), and is concentrated during summer months (~70% in June through October; Morafka 1982, Adest and Aguirre 1995).

Annual rainfall is significantly higher for the two easternmost tortoise species than for the western species (fig. 9.6), because of moisture from the subtropical ridge of the Atlantic Ocean and Gulf of Mexico meeting with cooler continental air masses. These conditions create humid and subtropical environments for *G. berlandieri* and *G. polyphemus* (Rose and Judd 1982, Auffenberg and Franz 1982). Annual precipitation in *G. berlandieri* habitat averages 650–700 mm, but is seasonal and can vary dramatically from year to year. In coastal areas, nearly 70% of rainfall occurs in the "rainy season" (May–October), with peak rainfall during September–October, when a third of annual rainfall occurs (Auffenberg and Weaver 1969, Rose and Judd 1982). At the northern extent of the species' range, inland thornscrub sites have a bimodal rainfall pattern with a peak in May–June and a minor peak in September (Kazmaier et al. 2001b). Droughts are frequent, but even in drought years, relative humidity in coastal areas can average 88%, resulting in heavy dew (Auffenberg and Weaver 1969, Rose and Judd 1982).

Even though *G. polyphemus* occupies some of the most xeric sites found within its geographic range, humidity and water availability are much higher than in habitats used by its congeners (Douglass and Layne 1978), generally receiving more than ten times the precipitation of sites in the Mojave Desert, for example. Mean annual rainfall ranges from 1140–1650 mm (Minnich and Ziegler 1977). The majority of rainfall for the eastern species occurs during summer months, enhanced by tropical storms, although the northern part of the range experiences relatively even amounts of precipitation throughout the year (Germano 1994). In the humid subtropical region of south Florida, precipitation is markedly seasonal, with >60% falling during the four-month wet season (June–September; Douglass and Layne 1978).

TEMPERATURE

North American tortoise habitats range from hot deserts to subtropical regions. Tortoises are notably absent from the colder temperate regions in the United States, appearing to

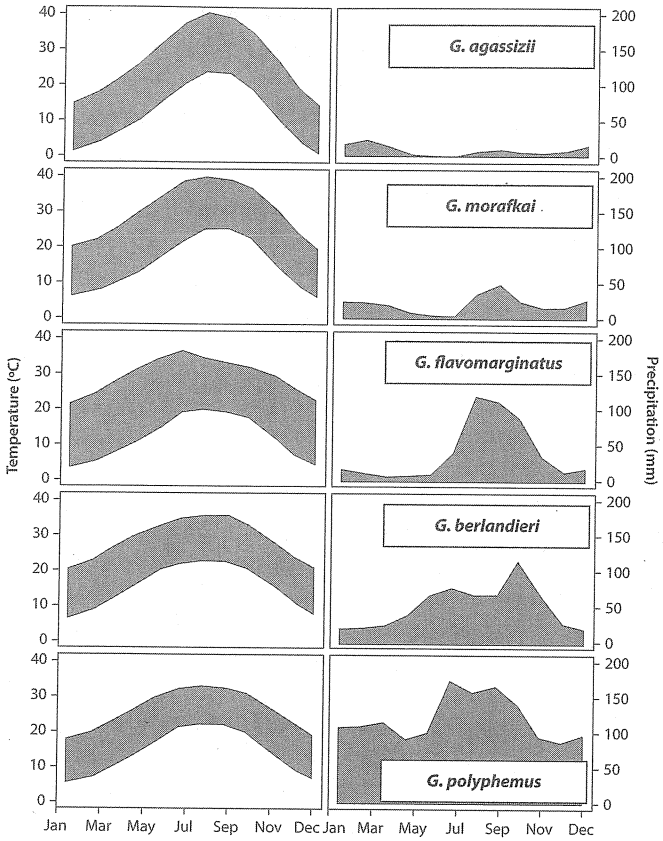

Fig. 9.6. Average high and low monthly temperatures (*left*) and precipitation (*right*) for localities within habitats for the five species of tortoises in North America. Data for *Gopherus agassizii* were compiled from 30 year normals of Inyokern, California; Baker, California; Twenty-Nine Palms, California; Las Vegas, Nevada; and St. George, Utah. Data for *G. morafkai* were for Needles, California; Phoenix, Arizona; Tuscon, Arizona; Ajo, Arizona; and Hermosillo, Mexico. Climate for *G. flavomarginatus* was represented by three locations in Mexico: Minas Nuevas, Sonora; Ciudad Delicias, Chihuahua; and Ciudad Jimenez, Chihuahua. Stations contributing to the climate data for *G. berlandieri* included Brownsville, Crystal City, and Del Rio in Texas and Sabinas, Coahuila; Monterrey, Nuevo León; and Ciudad Victoria, Tamaulipas, in Mexico. Climate data for *G. polyphemus* were taken from Yemassee, South Carolina; Hialeah, Florida; Tampa, Florida; Gainesville, Florida; Albany, Georgia; Atmore, Alabama; Hattiesburg, Mississippi; and Baton Rouge, Louisiana. All data for U.S. cities were acquired from www.weather.com, and data for Mexico were acquired from www.weatherbase.com.

be more limited by the presence of cold than hot temperatures. The combinations of precipitation and temperature that define their habitats vary greatly among the five species (fig. 9.6). In the western deserts, tortoises inhabit some of the hottest areas, with distributions largely limited by cold temperature extremes in the Mojave Desert (although the mechanism is not well understood). High temperatures may restrict tortoises to upland habitats in the Sonoran and Sinaloan Deserts, although in southern regions they may also be excluded from the lowlands due to the potential for flooding.

Temperature extremes in the Mojave and Sonoran Deserts are broad, with mean annual high and low temperatures for each ranging from –2 to 43°C (Germano et al. 1994). Preferred temperatures for *Gopherus agassizii* (20–38°C; McGinnis and Voigt 1971, Zimmerman et al. 1994) and *G. morafkai* (20–45°C; Averill-Murray et al. 2002a) are bracketed closely by these temperatures; however, the temperature experienced by the individuals (operative temperatures) are much greater. Operative temperatures are influenced by air temperature, solar radiation, and other inputs (Porter and Gates 1969, Tracy 1982) and for tortoises in deserts are estimated to be as high as 55–60°C. Tortoises avoid extreme temperatures by retreating to burrows (Zimmerman et al. 1994). Favorable operative temperatures for *G. agassizii* generally are available during midday in spring, in mornings and evenings during summer months, and again during the midday in fall (Zimmerman et al. 1994, Hillard 1996). Although summers typically are hot in the Sonoran Desert, seasonal monsoonal events stimulate activity as tortoises respond to the resulting increased forage availability (Averill-Murray et al. 2002a). *Gopherus agassizii* has the northernmost distribution of the North American tortoises, and its northern limit is associated with the boundary between the Mojave (hot) and the Great Basin (temperate) Deserts. Despite ample precipitation in the eastern Sonoran Desert, extended periods of cold and freezing temperatures exclude most of the Sonoran Desert perennial plant species and likely limit the distribution of *G. morafkai*, as well (Van Devender 2002a). The habitat of *G. flavomarginatus* is considered warm-temperate to subtropical (Lieberman and Morafka 1988), with annual temperatures typically averaging 20–35°C; however, in extreme years winter temperatures can fall as low as –7°C and summer temperatures can reach 39°C (Morafka 1982).

The two eastern tortoise species experience a more hospitable climate with respect to temperatures than the western species (fig. 9.6). *Gopherus berlandieri* occurs where summers are hot and winters short and mild (Kazmaier et al. 2001c, 2001d). Mean temperatures are relatively warm in all seasons, peaking in July when mean air temperatures are 28.7–30.4°C (Auffenberg and Weaver 1969, Kazmaier et al. 2001d). Like tortoises in the desert regions, *G. berlandieri* experiences temperatures that are sufficiently high to induce bimodal activity (morning and afternoon), which is more pronounced in the warmer months of June and July than in the cooler months of November and April (Auffenberg and Weaver 1969). Mean temperatures where the species occurs are 12.5–15.4°C in the coldest month (January), with an average daily minimum of 10.5°C. The distribution of *G. polyphemus* has a relatively narrow range of average daily temperatures (5–17°C in winter and 20–32°C in summer; fig. 9.6). Individuals are most active from March to April through October to November (Eubanks et al. 2003, Yager et al. 2007), with activity becoming bimodal

during the hot summer months. Winter temperatures drive a brief period of overwintering (Douglass and Layne 1978). Although individuals may be active above ground in any month of the year, winter activity is more likely in the southern portion of their range. Even at the northernmost portion of the species' range, however, individuals may occasionally emerge to bask on warmer winter days (DeGregorio et al. 2012).

SHELTER

The burrow is a key feature of the habitat for all species of *Gopherus,* and is used to avoid temperature extremes both in summer and winter, and to provide protection from predators (Woodbury and Hardy 1948, Zimmerman et al. 1994, Nussear et al. 2007; chapter 9.4). Burrows are of such importance that friability of the soil can limit tortoise occurrence: in some areas, soils are too sandy to support burrows, and in other areas, soils are too rocky, or consist of exposed or shallow bedrock in which burrows cannot be constructed (Burge 1978, Averill-Murray 2002a). Tortoises, however, are quite adaptable, and individuals of some species take advantage of naturally occurring caves, rock crevices, or other shelter sites. For example, in the northern extent of the species' range, individuals of *G. agassizii* living in sandy soils use naturally occurring caves to provide needed shelter during winter hibernation (Woodbury and Hardy 1948, Nussear et al. 2007), and also use dens formed by erosion in the gravel layers within washes, especially in habitats with a shallow caliche layer beneath the soil (Woodbury and Hardy 1948, Germano et al. 1994). Individuals of *G. morafkai,* which live on rocky hillsides, also use caves under large rocks or boulders and caliche dens, and both desert tortoise species opportunistically use pack rat middens (Woodbury and Hardy 1948; Barrett 1990; Averill-Murray et al. 2002a, 2002b; Van Devender 2002b; Riedle et al. 2008). Individuals of *G. flavomarginatus* use burrows of other species, such as rodents, if available; but, unlike desert tortoises, are not known to use rock shelters (Lieberman and Morafka 1988, Tom 1994).

Some tortoise species are more closely tied to their burrows than others. For example, both *G. polyphemus* and *G. flavomarginatus* exhibit strong affinity to burrows. Individuals typically have one or two primary burrows which they occupy during periods of daily and seasonal inactivity (Aguirre et al. 1984). Both species dig extensive burrows extending 6 m to 10 m in length, with a depth of 2 m below the surface (Auffenberg 1969, Morafka 1982, Aguirre et al. 1984, Witz et al. 1991, Aguirre 1994, Smith et al. 2005). Burrows are reused among years (Guyer and Hermann 1997), but individuals of *G. polyphemus* can have high abandonment rates in disturbed habitats (22% per year; Aresco and Guyer 1999a). Interestingly, burrows of *G. polyphemus* in mesic habitats can be subject to winter flooding, but individuals usually continue to occupy them, and have even been observed submerged in water (Means 1982, Diemer 1992a). Individuals of *G. flavomarginatus* also can withstand periodic short-term flooding of burrows, but areas subject to extended periods of flooding are not inhabited (Lieberman and Morafka 1988).

THREATS TO HABITAT

Most threats to tortoise habitat generally can be attributed directly to anthropogenic influences, including habitat loss and fragmentation as a result of the establishment of urbanized areas and their associated infrastructure, agriculture, and the proliferation of paved and unpaved roads. Roads, in addition to causing direct mortality and injury to animals, impede movements of individuals among populations and facilitate the spread of invasive plants (Auffenberg and Weaver 1969, Bury and Smith 1986, USFWS 1994a, Howland and Rorabaugh 2002, USFWS 2011b). Effects of habitat loss and fragmentation are most pronounced for *Gopherus polyphemus,* which has been relegated to small, fragmented populations throughout much of its range (McCoy et al. 2007). Although many tortoises are successfully translocated after being displaced by development and other losses of habitat (e.g., Drake et al. 2012; Nussear et al. 2012; Tuberville et al. 2005, 2008), the net loss of suitable habitat continues to reduce the number of extant viable populations. In *G. flavomarginatus* habitat, the added threat of human predation on tortoises for consumption and export to the pet trade has depleted individuals from large areas, isolating populations and impeding gene flow (Morafka 1982, Bury et al. 1988, Lieberman and Morafka 1988, Aguirre 1994). For many *Gopherus* species, military installations represent some of the largest tracts of intact natural communities (Wilson et al. 1997), but increased training demands and/or increased training intensity could result in detrimental consequences for tortoise populations and their habitats.

In the western U.S., where some of the fastest-growing human populations in the country are located (U.S. Census Bureau 2010), livestock grazing has occurred in tortoise habitat for many years and directly and indirectly affects tortoises and their habitats. Effects of grazing include reduction and alteration of native vegetation and changes in soil nutrients and soil structure, which may take decades to recover (Morafka 1982, Lieberman and Morafka 1988, USFWS 2011b). *Gopherus berlandieri* appears to be somewhat more tolerant than the desert tortoises to grazing. Some managed grazing techniques may even be beneficial, particularly if they promote establishment of *Opuntia* patches (Auffenberg and Weaver 1969, Rose and Judd 1982). Even for this disturbance-tolerant tortoise species, however, overgrazing can significantly alter habitat structure by favoring shorter grass species and by contributing to brush encroachment. In response to encroachment, many managers have implemented "range improvement" techniques to control woody vegetation, such as "chaining," roller chopping, and root plowing (Kazmaier et al. 2001a, 2001c), all of which are extremely detrimental to *G. berlandieri* (Rose and Judd 1982). Furthermore, the benefits of these techniques to livestock grazing are short-lived, as these habitats become shrubbier and less diverse following brush removal (Kazmaier

et al. 2001a). Fire has been suggested as a potential technique to control woody vegetation and create grassy openings on lomas, but its effectiveness is unknown (Bury and Smith 1986).

With increasing invasions of exotic grasses in western U.S. deserts, wildfires are becoming more common in desert tortoise habitats. For example, the grasses *Bromus madritensis* and *Pennisetum ciliare* can be in high densities in intershrub spaces (12–20% cover), connecting an otherwise sparsely vegetated shrub habitat with fine fuels (Brown and Minnich 1986, Brooks 1999, Esque et al. 2002, Van Devender 2002a). This situation has artificially increased fire frequency and intensity in the Mojave and Sonoran Deserts (Brown and Minnich 1986, Brooks and Esque 2002, Esque et al. 2002). For instance, fire destroyed 36,000 acres of critical habitat for *G. agassizii* in southern Nevada in 2005. Unlike ecosystems inhabited by the *G. polyphemus,* the Mojave and Sonoran Desert ecosystems have not evolved with fire, and thus wildfires have the potential to alter habitat drastically. After each fire, the prominence of exotic grasses typically increases, creating a dynamic in which native vegetation is replaced by exotic grasses, which in turn increases fire risk (Brown and Minnich 1986, D'Antonio and Vitousek 1992). Changes in habitat may be realized not only in a reduction of annual forage species, but also loss of cover sites, as fire causes mortality of many perennial species that provide shade resources for tortoises (Esque et al. 2002). In contrast to the desert species, fire suppression presents a threat for the *G. polyphemus.* For this species, prescribed fire is important for maintaining the open canopy conditions. Fire not only suppresses the hardwood mid-story, but also is critical for germination of many groundcover species. Thus, frequent application of fire shapes the habitat structure and contributes to the incredible plant diversity of longleaf pine communities (Walker and Peet 1984, Van Lear et al. 2005). In the face of encroaching development, however, it becomes increasingly difficult to implement prescribed fire, even in protected areas. Without fire, habitat once suitable for *G. polyphemus* can quickly become unsuitable, resulting in high rates of burrow abandonment (Aresco and Guyer 1999a). Sites with a long history of fire suppression will require multiple fire applications to be restored (Yager et al. 2007, Ashton et al. 2008). Alternative methods for controlling hardwoods, such as mechanical removal and herbicide application, are being used on some sites, but their effectiveness in promoting desired habitat conditions has not been thoroughly evaluated.

Alternative energy is a new threat to tortoises, especially in the western U.S., with approximately 70 projects being proposed at the time of this writing, and a combined 10,000 km^2 of habitat potentially affected. In combination with other disturbances, these developments will result in further loss and fragmentation of habitat. Desert tortoise populations exist as metapopulations, and gene flow and the possibility of demographic rescue depends on the ability of individuals to migrate among habitat patches (Hanski 1991, Averill-Murray et al. 2002b, Edwards et al. 2004a). With each additional loss and fragmentation of habitat, this capability is diminished and ultimately negatively influences the potential for continued survival of these species.

CONCLUSIONS

We have described habitat for the North American tortoise species, using vital constituents of the landscape that bound the factors that provide or constrain their opportunity to acquire resources and persist. These factors include the physiography and geography of the landscape, and the associated vegetation, precipitation regimes, and environmental temperatures that promote the well-being of tortoise populations. Collectively, these factors represent important components of habitat interacting with the needs of tortoises, ranging from suitable temperatures for activity and egg incubation, to substrates that facilitate their ability to dig burrows and find shelter, to the availability of sufficient rainfall to provide needed forage and water. The perennial vegetation associated with each of the species provides shelter from the typically warm environments they inhabit, and these associations also have specific soils, temperatures, and precipitation regimes that drive their distributions. The combinations of these habitat attributes not only have shaped the distributions of tortoises over time, but perhaps even the distinctions among species as they adapted to local habitats. Sadly, many of these habitats are threatened by human development, and thus North American tortoises, like most tortoises around the world, face many threats to their persistence, and require conservation efforts to ensure their continued presence.

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