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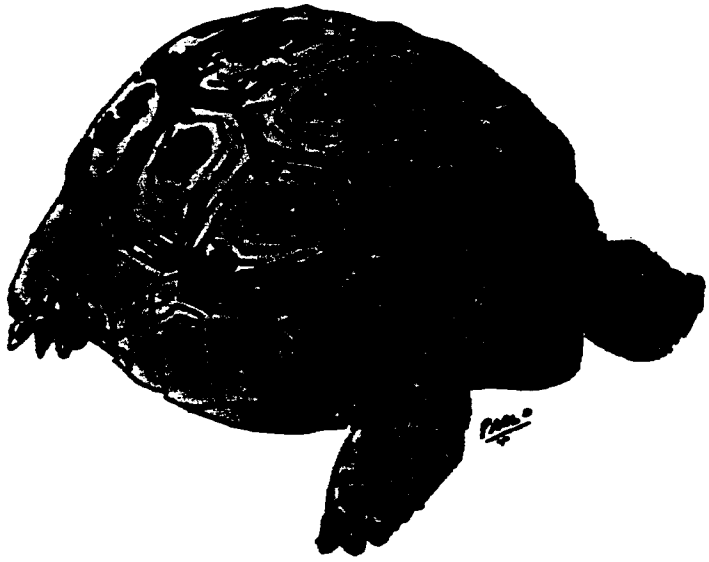

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ECOLOGY OF NORTH AMERICAN TORTOISES

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INTRODUCTION

North America has a diverse turtle fauna with 55 native species, or about 20% of the world's total, in just the United States and Canada alone (Ernst *et al.* 1994). In contrast the turtle family Testudinidae is poorly represented on the continent with only 4 species, or 10% of the world's tortoise species, including the desert tortoise (*Gopherus agassizii*), the Texas tortoise (*G. berlandieri*), the Bolson tortoise (*G. flavomarginatus*), and the gopher tortoise (*G. polyphemus*). Although members of the genus *Gopherus* appear to be well adapted to life in semi-arid and arid environments, the four species occupy a diversity of habitats ranging from deserts to pine forests and coastal areas. Box turtles (*Terrapene* sp.) are the only other North American terrestrial turtles that share some of the more xeric microhabitats occupied by the genus *Gopherus*. The fact that all four species are in need of some form of conservation action, in all or part of their range (Lovich 1994), underscores the importance of studying their ecological requirements. The purpose of this presentation is to provide a brief overview of the ecology of the genus *Gopherus* with an emphasis on comparing and contrasting the four species. Effective conservation programs can only be implemented with a clear understanding the ecological requirements and limitations of the genus.

ECOLOGY OF *GOPHERUS*

Ecogeography

The genus *Gopherus* is distributed in a disjunct pattern across the lower portion of the North American continent from about 37° N to 22° N, a distance of almost 1,400 km (Table 1). Human predation and climatic changes contributed to the fragmentation and reduction of a more continuous prehistoric distribution (Morafka 1988). The modern distribution of the genus is delineated in the east by *G. polyphemus* ranging from southern South Carolina and southern Georgia, to peninsular Florida, north of the Everglades, westward to southeastern Louisiana. Preferred habitats are characterized by well-drained, deep, sandy soils in fire-adapted plant communities including longleaf pine-wire grass associations, pine-oak forests, beach scrub and oak hammocks. The eastern limit of *G. berlandieri* starts about 580 km westward from the western edge of habitat occupied by *G. polyphemus*. *G. berlandieri* is found in southern Texas and the northern Mexican states of Coahuila, Nuevo Leon, Tamaulipas and San Luis Potosi. Habitats occupied include semidesert scrub and humid, subtropical, coastal areas, perhaps even barrier islands (Ernst *et al.* 1994). The ranges of *G. berlandieri* and *G. flavomarginatus* are separated by another hiatus of about 230 km. Although the distance from its eastern congener is short, *G. flavomarginatus* is completely isolated in remote enclosed basins in the Chihuahuan

Desert. The preferred habitat is the Tobosa grassland, characterized by the perennial grass *Hilaria mutica* (Bury *et al.* 1988).

Almost 600 km west of the basins occupied by *G. flavomarginatus*, the range of *G. agassizii* begins. The desert tortoise is widely distributed in Mojave and Sonoran desert scrub habitats in southern California, Arizona, southern Nevada and southwestern Utah. Throughout this vast area the desert tortoise inhabits desert alluvial fans, washes, canyon bottoms, and rocky hillsides in drylands having sandy or gravelly soil; it occurs to an altitude of at least 1,070 m. The range continues southward into the Mexican states of Sonora and northern Sinaloa, terminating in subtropical thornscrub habitat. In the United States, the particular habitat types utilized vary geographically, gradually changing to rocky slopes in the eastern part of the range. The spatial distribution of desert tortoises in relation to plant communities is not random. High diversity plant ecotones and communities, and possibly soil characteristics, are important features in determining tortoise densities (Ernst *et al.* 1994).

Behavior

Most members of the genus generally construct deep burrows for protection from heat, cold, and predators (Table 1). Burrows of *G. agassizii* can be up to 10 m long while those of *G. polyphemus* may reach 14.5 m. In contrast, *G. berlandieri* rarely constructs burrows but instead constructs a shallow "pallet" or scrape on the surface, normally near the base of a shrub or clump of grass. Surface activity of all species is governed largely by temperature and the availability of food (Ernst *et al.* 1994).

Aggressive interactions and territoriality are displayed by *G. agassizii* and *G. polyphemus*. Both species use head-bobbing as a visual display when confronted by another tortoise. The gular extension of the males is used to ram, hook and sometimes overturn another male. The fights rarely cause any physical harm, but if a tortoise is overturned and cannot right itself it will die. Although not known to be territorial, males of *G. berlandieri* will fight with each other during the breeding season (Weaver 1970). Combat involves biting and ramming. Resident *G. polyphemus* do not necessarily dominate when an intruder is introduced into experimental enclosures (Weaver 1970).

Feeding Ecology

All *Gopherus* are herbivorous, feeding mainly on forbs and grasses, often selectively. The most important foods for *G. agassizii* are desert annuals that often have life spans of less than 30 days and are generally available only from April to June. Since food quality decreases dramatically after June, tortoises must harvest enough energy during the brief feeding period to carry them through summer estivation, winter hibernation and the next reproductive cycle. Cacti and other food plants may be important in dry years. *G. berlandieri* prefers the stems, fruits and flowers of *Opuntia* cactus, but grasses and a variety of forbs are also eaten. Grasses and forbs constitute the majority of the diet in *G. flavomarginatus* (Aguirre *et al.* 1978) and *G. polyphemus* (Ernst *et al.* 1994).

Reproduction

Most species of *Gopherus* have relatively late maturation. *G. agassizii*, *G. polyphemus* (Ernst *et al.* 1994), and *G. flavomarginatus* (Legler and Webb 1961) typically take 10-20 years to reach sexual maturity while maturity in *G. berlandieri* (the smallest species) is reached in 3-5 years (Rose and Judd 1982). Typical clutch sizes and clutch frequencies are summarized in Table 1.

Demography

Like all turtles, the demographic structure of tortoise populations is a reflection of low and variable annual nest success, high adult survivorship, and long life spans (Lovich 1994). Due to the difficulty of locating juvenile *Gopherus* virtually nothing is known of this stage of their life history. Juveniles are poorly represented in all population samples. This could be due to their rarity, their cryptic nature or both. Sex ratios vary widely within and among species of *Gopherus* as does sexual size dimorphism (Table 1). The only life table for the genus is that of Turner *et al.* (1987) for *G. agassizii*.

The Functional Role of Tortoises in the Ecosystem

Tortoises of the genus *Gopherus* play important roles in the ecosystem. Some populations achieve high biomass and may be significant primary consumers. Their burrows provide homes for many commensals including invertebrates, mammals, reptiles and amphibians (Luckenbach 1982, Lago 1991, Witz and Wilson 1991). Activities including burrowing, mound building and grazing by *G. polyphemus* promotes environmental heterogeneity resulting in increased rates of microsuccession and higher plant diversity (Kaczor and Hartnett 1990). Some (perhaps all) species facilitate plant dispersal. The seeds of *Opuntia* that pass through the digestive tract of *G. berlandieri* have enhanced germination rates relative to those that do not (Rose and Judd 1982).

Table 1. Ecological and physical attributes of the genus *Gopherus*. Various references were consulted including Morafka (1982), Aguirre *et al.* (1984), Iverson (1982, 1991), Bury *et al.* (1988), Gibbons and Lovich (1990), Iverson *et al.* (1993), Ernst *et al.* (1994), and references cited therein.

Attribute	Species			
	G. agassizii	*G. berlandieri*	*G. flavomarginatus*	*G. polyphemus*
Ecotype	Mojave/Sonoran desert scrub - Sinaloan thorn scrub	Tamaulipian Biotic Province (desert to coastal)	Chihuahuan Desert	Longleaf pine/wire grass
Latitudinal distribution	37° N - 26° N (11°, ≈ 1300 km)	29° N - 22° N (7°, ≈ 770 km)	28° N - 26° N (2°, ≈ 230 km)	33.5° N - 27° N (6.5°, ≈ 800 km)
Longitudinal distribution	118° W - 108° W (10°, ≈ 900 km)	101° W - 96° W (5°, ≈ 470 km)	104.5° W - 103° W (1.5°, ≈ 170 km)	90° W - 80° W (10°, ≈ 950 km)
Max. body size	to 37 cm	to 22.8 cm	40 cm + ?	to 40 cm
Sexual size dimorphism	males larger	males larger	females larger	females ≥
Sex ratio	female biased	male biased	female biased	variable
Biomass/density	0.19-2.05 kg/ha	54.5 kg/ha	10 tortoises/km^2	220 kg/ha
Annualized adult survivorship	0.883	?	?	0.89
Clutch size	4.5	2.6	6	5.2
Clutch frequency	3	1	3	1
Egg mass	38.9 g	26.9	?	40.9
Clutch mass	175.2 g	69.94	?	212.7
Burrower	yes	no	yes	yes
Territorial behavior	yes	no	no	yes

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