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# *Gopherus polyphemus* – Gopher Tortoise

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**Summary. – The gopher tortoise, *Gopherus polyphemus*, is the only North American land tortoise found east of the Mississippi River, where it occurs in portions of six states in the southeastern coastal plain. The gopher tortoise is a medium-sized terrestrial turtle that constructs and inhabits a distinctive burrow. Adults grow to 38.7 cm (15 in) carapace length. Distinguishing external features include short elephantine hindlimbs and shovel-like forelimbs covered with relatively thick scales. The gopher tortoise is most commonly found in upland habitats that are characterized by a deep, well-drained, sandy soil suitable for construction of their extensive burrows. The gopher tortoise digs its burrow in a relatively open site that provides sunlit areas for nesting and thermoregulation, and ample herbaceous ground vegetation for forage. Burrows of adult gopher tortoises average approximately 4.5 m in length and about 2 m in depth. A gopher tortoise may use several burrows during a year, and the number of burrows at a given site is almost always greater than the number of tortoises at that site. Sexual maturity is associated with size, not age, and individuals may become mature in 10 to 20 or more years, depending on location and habitat quality. Mating and nesting activities occur primarily from May through mid-June. Eggs are often laid just outside the burrow and hatchlings emerge from eggs between late August and October. Human activities pose the greatest threats to the survival of gopher tortoise populations. Loss of habitat to human activities can take three forms: reduction in area of suitable habitat (true displacement), degeneration of suitable habitat (abandonment of habitat), and increased fragmentation of habitat (increased isolation of populations). During the past decade or so, Upper Respiratory Tract Disease (URTD) also has been identified as a potential threat to the survival of the gopher tortoise. The State of Florida currently lists the gopher tortoise as Threatened. We consider it endangered. We propose a three-part approach to ensure a healthy future for the gopher tortoise. First, outright purchase of land known to support populations of gopher tortoises by individuals or agencies willing to conserve the species. Second, education of private land owners and public land managers about the value of active management of habitats known to support tortoise populations. Third, re-introduction of the gopher tortoise to suitable habitats on protected lands from which it has been extirpated or lands that have been restored to suitable habitat.**

**Conservation Status. – FNAI Global - G3 (Rare, Local, or Vulnerable), State - S3 (Rare, Local, or Vulnerable); ESA Federal - LT (Threatened): populations west of Mobile and Tombigbee Rivers in Alabama, Mississippi, and Louisiana, Not Listed: populations in rest of range; State - T (Threatened); CITES - Appendix II; IUCN Red List - VU (Vulnerable).**

*Species Recognition.* — The gopher tortoise, *Gopherus polyphemus*, is a medium-sized terrestrial turtle that constructs and inhabits a distinctive burrow (Fig. 25-1). Adults grow to 38.7 cm (15 in) carapace length (CL) (Timmerman and Roberts, 1994). External features that distinguish it from other turtles include short elephantine hindlimbs, shovel-like forelimbs covered with relatively thick scales, and an anterior gular projection of the plastron (Figs. 25-2, 25-3). Often, the surface of the shell is quite smooth, reflecting the abrasion it receives as the tortoise enters and exits the burrow. The carapace is oblong with the greatest width near the posterior margin of the well-developed bridge, and the greatest height is in the pelvic region. The carapace drops off abruptly posterior to the pelvic region (Ernst and Barbour, 1972). The carapace of adults varies from dark-brown to tan to grayish-black in color. In Florida, individuals from populations in coastal areas generally are darker than those from populations in central areas of the peninsula. The gular scutes of the plastron project anteriorly from below the chin. Males often have longer gular projections than females;

**Figure 25-1.** Two adult gopher tortoises, *Gopherus polyphemus*, in front of the mouth of a gopher tortoise burrow, Duval Co., Florida. Photo by Barry Mansell.

however; because both sexes use their projections during agonistic encounters, the gular projections are often broken and may not accurately reflect the sex of an individual (Mushinsky et al., 1994). Unlike the relatively smooth scutes on the carapace, plastral scutes in most individuals show concentric growth rings.

Hatchling gopher tortoises emerge from eggs at a CL of about 5 cm. Coloration of the carapace of hatchlings is yellow to yellowish-orange, but each scute has a brownish border (Fig. 25-4; Allen and Neill, 1953). The skin on the head and limbs is likewise bright yellow to yellowish-orange. The bright coloration of hatchlings darkens somewhat during the first year or two of life, but individuals less than five or six years of age typically are lighter in coloration than older individuals. Young gopher tortoises spend a considerable amount of time basking at the mouths of their burrows, and their colors blend well with the shadows on the orange-yellow sandhill soils. The gular scutes of young tortoises are less prominent than those of adults and the claws of young tortoises are relatively longer and sharper (Allen and Neill, 1953).

**Figure 25-2.** Young adult gopher tortoise, *Gopherus polyphemus*, from Alachua Co., Florida. Photo by Dick Bartlett.

**Figure 25-3.** Plastral view of adult male gopher tortoise, *Gopherus polyphemus*, from Florida, Photo by David Dennis.

**Figure 25-4.** Hatchling gopher tortoise, *Gopherus polyphemus*, from Liberty Co., Florida. Photo by Dick Bartlett.

*Taxonomic History.* — The gopher tortoise was originally named *Testudo polyphemus*, in 1802, by Daudin. In 1815, Rafinesque introduced the genus *Gopherus*, to which this species has been attributed regularly since 1893 (Smith and Smith, 1980). The extensive burrowing habits of the gopher tortoise are reflected in its common name.

## DISTRIBUTION

*Geographic Distribution.* — The gopher tortoise is the only North American tortoise found east of the Mississippi River, where it occurs in portions of six states in the southeastern coastal plain (Auffenberg and Franz, 1982). In Louisiana, populations occur in upland pine ridges in the extreme eastern Parishes of St. Tammany, Washington, and Tangipahoa. In Mississippi, populations occur in a 14-county region in the southern portion of the state. Populations exist throughout most of southern Alabama. In South Carolina, populations are restricted to river ridges in Jasper and Hampton counties. In Georgia, populations occur in a series of disjunct locations south and east of the Fall Line on the coastal plain. The state with the largest numbers of the gopher tortoise is Florida.

Gopher tortoise populations occur in all 67 Florida counties (Fig. 25-5). Throughout the state, however, many populations have become isolated and their numbers reduced greatly to small fractions of their former abundances. In the southern portion of the state, south of Lake Okeechobee, the gopher tortoise probably always occurred in relatively small isolated populations, mostly along the coastline. Scattered populations of tortoises occur in the relatively high elevation hammock islands within the northern Everglades.

*Ecological Distribution.* — The gopher tortoise is most commonly found in upland habitats that are characterized by deep, well-drained, sandy soil suitable for construction of their extensive burrows. All gopher tortoises live in burrows, usually one individual per burrow. Occasionally, two individuals may occur temporarily in one burrow, but double occupancy is rare. Individuals require open, sunny patches of habitat for feeding, nesting, and thermoregulation. The gopher tortoise is most abundant in upland habitats that are burned frequently. The notion that gopher tortoises occur in colonies, implying a social cohesion, may have been falsely created by their strong need to live in open patches. For example, high concentrations of gopher tortoises exist on many power line rights-of-way that have become surrounded by overgrown uplands that once supported the gopher tortoise. Nevertheless, the gopher tortoise is a social animal and we have only a poor understanding of its social structure.

Spatial distribution and social structuring of populations of organisms are frequently influenced by their reproductive systems. Our understanding of the ecological distribution and social structure of the gopher tortoise has changed during the past few decades. A "colony" of gopher tortoises was described as several adult females living in close proximity with one or two males, who excluded other males from interacting with the resident females (McRae et al., 1981b). The notion that a "loose or incipient harem" mating system influenced the ecological distribution and colony structure of the gopher tortoise was introduced by Douglass (1986). A colony was presumed to be occupied by a large, dominant male who was more or less surrounded by females, and those females nearest to the male experienced a greater number of courtships than females more distant from the central male. Recently, Boglioli et al. (2003) tested the ideas put forth by McRae et al. (1981b) and Douglass (1986). The setting for their research was large, contiguous populations of gopher tortoises. They concluded that distance from neighboring tortoises did not influence mating opportunities, nor did the degree of isolation of females influence the frequency of courtship or mounting by males, nor the size of the males doing the courting. The general pattern of reproduction closely resembled scramble-competition polygyny rather than harem defense polygyny. Based on our current understanding of the distribution and behavior of the gopher tortoise, there appears to be no reason to use the term "colony" to describe a local population of tortoises.

Using the broad descriptions for upland habitats found in Myers and Ewel (1990), the habitat types most often occupied by the gopher tortoise in Florida include sandhill (pine-turkey oak), sand pine scrub, xeric hammock, pine flatwoods, dry prairie, coastal grasslands and dunes, and mixed hardwood-pine communities (Landers and Speake, 1980; Auffenberg and Franz, 1982; Kushlan and Mazzotti, 1984; Diemer 1986, 1992a). The gopher tortoise is known to occupy other types of habitats occasionally, especially on islands. At some locations, for example, Sanibel Island, and Cape Sable, gopher tortoises have constructed their burrows in the shell-laden substrate. On Egmont Key, gopher tortoise burrows primarily are located around the periphery of the island among open sandy areas between the shoreline and the island interior forests.

The gopher tortoise prefers open habitats that support a wide variety of herbaceous ground cover vegetation for forage. It usually abandons densely canopied areas that lack the preferred herbaceous ground cover and frequently is forced to occupy disturbed habitats such as roadsides, fence-

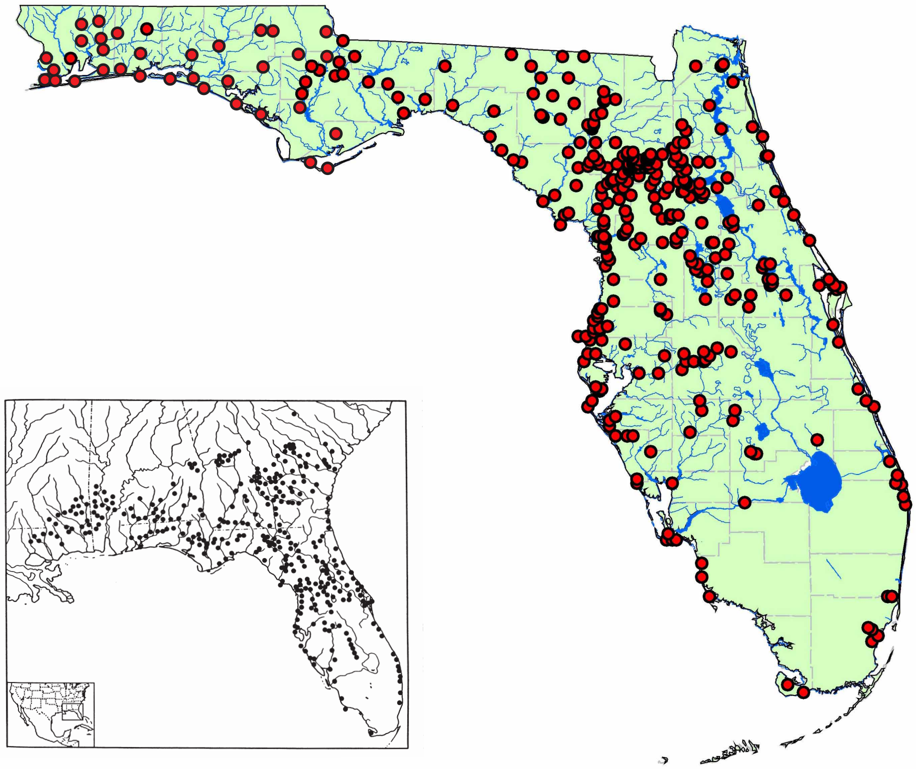

**Figure 25-5.** Available distribution records for the gopher tortoise, *Gopherus polyphemus,* from Florida. Inset: distribution records from entire range of *G. polyphemus* (from Iverson, 1992; distribution in inset map not current for Florida as presented here). Localities for the Florida panhandle were supplemented with data from the Florida Natural Areas Inventory data base for this species on 21 September 2006.

rows, old fields, and the edges of overgrown (unburned) uplands (see Diemer, 1989; Stewart et al., 1993; Breininger et al., 1994). Overgrown habitats may inhibit gopher tortoises from reaching their minimum thermal requirements for normal development and reproduction (Mushinsky and McCoy, 1994). The gopher tortoise can co-exist with resident cows in grazed pastures (Ashton, unpubl. data).

Since the first general survey across the full range of the gopher tortoise by Auffenberg and Franz (1982), there has been a growing understanding of the ecological factors that influence the distribution of the gopher tortoise. For more than 20 years, biologists at the University of South Florida (USF) have studied the effects of fire periodicity on plants and animals that reside in the sandhill habitat at the University Ecological Research Area (Mushinsky and Gibson, 1991). By burning small (1–2 ha) plots of land on different frequencies, the biologists have created a mosaic of plots of land with different vegetation profiles among which the resident tortoises can choose when digging their burrows. Repeated surveys have revealed that when individuals are free to move among fragments, their movements are highly directional, and the density of tortoises increases within the most suitable patches. After 25+ years of prescribed burning, the percent of the ground surface covered by living non-woody vegetation (mostly grasses and herbaceous plants) increased among burn plots in the following order (from least to most): (1) unburned plots, (2) 7-yr plots (i.e., plots burned at 7-yr intervals), (3) 1-yr plots, (4) 5-yr plots, and (5) 2-yr plots (McCoy and Mushinsky, unpubl. data). The abundances of gopher tortoises increased in precisely the same order, as did the evenness of the size distribution of individuals (McCoy and Mushinsky, unpubl. data). In other words, gopher tortoises were least abundant in the unburned plots, where canopy coverage was high and grass and herbaceous vegetation was least common, and they were most abundant in the plots burned every two years, where canopy coverage was low and the grass and herbaceous plants were most common. In general, these results from the experimental burn plots confirmed the observations of Auffenberg and Franz (1982).

## HABITAT RELATIONS

*The Burrow.* — Regardless of the specific type of habitat, the gopher tortoise digs its burrow in a relatively open site that provides sunlit areas for nesting and thermoregulation, and ample herbaceous ground vegetation for forage (Macdonald and Mushinsky, 1988). Dimension of burrows of adult gopher tortoises average approximately 4.5 m in length and about 2 m in depth (Hansen, 1963; Diemer, 1989). Burrows have been found to be significantly shorter in clayey soils than sandy soils, which may be a result of respiratory limitations of the gopher tortoise. Decrease in $O_2$ and increase in $CO_2$ are greatest in burrows in clayey soils and are positively correlated with burrow length (Ultsch and Anderson, 1986). The high humidity within the burrow may offer the tortoise protection from desiccation (Auffenberg and Weaver, 1969; Means, 1982). Typically, a gopher tortoise burrow terminates with an end chamber at or near the level of the water table, just above the clay hardpan. Measurements of soil temperatures within burrows, taken as burrows were excavated, documented temperature gradients from the mouth of the burrow to the end chamber (Ashton, unpubl. data). From April to November, in north Florida, the end chamber temperatures were 16 to 22ºC, and from December to March the end chamber had temperatures of 5 to 12ºC. At the mouth of each burrow is a mound of subsoil. These soil mounds undergo micro-succession and contribute increased plant species diversity in the surrounding habitat (Kaczor and Hartnett, 1990). Female gopher tortoises often deposit their eggs in these deep sandy mounds immediately outside the burrow.

A gopher tortoise may use several burrows during a year, and the number of burrows at a given site is almost always greater than the number of tortoises at that site. In an attempt to estimate burrow occupancy, burrows have been classified as active, inactive, or abandoned based on their physical appearance (Auffenberg and Franz, 1982; Cox et al., 1987). "Active" burrows show signs of tortoise activity within the previous 24-hr period, such as footprints, or scrape marks in the sand at the mouth made by the plastron as the tortoises entered or exited the burrow. "Inactive" burrows show no signs of recent activity and may harbor small amounts of debris, such as leaves or grasses that have been blown into the mouth of the burrow. The roof of an inactive burrow has a distinct half-moon shape. Following heavy rains, inactive burrows may show signs of erosion. "Abandoned" burrows are those that harbor considerable vegetation near the mouth of the burrow, and in which the roof of the burrow has lost the half-moon shape. Vertically oval-shaped burrow openings typically indicate occupancy by an armadillo. Eventually, abandoned burrows fill-in with sand and debris, collapse, and disappear from the landscape.

The time of the year when assessment of burrow occupancy is made will influence the classification of a burrow. Best assessments are made during the warm summer months, when tortoises typically leave their burrow daily to forage. Estimates of burrow occupancy based on activity classes of burrows are not perfect. Of 1019 burrows classified and excavated by Witz et al. (1991), 454 active burrows yielded 341 individuals (75% occupancy), 449 inactive burrows yielded 53 individuals (12% occupancy), and 116 abandoned burrows yielded 6 individuals (5% occupancy). In another study, Ashton (unpubl. data) excavated what appeared to be abandoned burrows of adult tortoises and found that 27% of the burrows contained individuals between one and about eight years of age. Wide discrepancies in the numbers of individuals in "abandoned burrows" might suggest a need for more rigorous definitions and implementation of standards by researchers. Reliable criteria to be used to distinguish among categories of burrows have been proposed (McCoy and Mushinsky, 1992a).

The width of a burrow is related to the size (CL) of the resident tortoise (Alford, 1980; Martin and Layne, 1987; Wilson et al., 1991; Doonan and Stout, 1994; Smith, 1995). A gopher tortoise digs a burrow by alternately scooping sand from the burrow with its front legs. As it alternates the power stroke from forelimb to forelimb, it pivots from side to side to form a burrow that is wider than the width of the tortoise, but about the length of the carapace. Wilson et al. (1991) concluded that burrow width is a reliable indicator of carapace length because of the morphological components and the digging behavior used in burrow construction. It appears that the ability of a gopher tortoise to turn around in any portion of its burrow is a fortuitous by-product of its morphology and digging behavior. To assess the size of the occupant, burrow width typically is measured at a depth of 50 cm because the mouth of the burrow is frequently enlarged or eroded (Martin and Layne, 1987). Burrow widths can be used to construct a size class profile for a population study (Alford, 1980).

Most hatchlings dig their own burrows, often just a few meters away from the nest from which they emerged (Mushinsky and McCoy, unpubl. data). In fact, it is not uncommon to find groups of three to six burrows of hatchlings within a few square meters. Not all young or juvenile gopher tortoises dig their own burrows, however. Some neonates will dig a small burrow directly into the wall of a large burrow and reside in it until the following spring. Although most juvenile gopher tortoises excavate their own burrow, occasionally they can be found in an abandoned burrow of a larger individual (Ashton and Ashton, 2001).

From a human perspective, it seems an enormous task to dig a burrow that penetrates several meters into the ground, yet the gopher tortoise can dig one in a day or so in most habitats. Adult gopher tortoises may dig at a rate of 3 m per day in sandhill habitats (Ashton, unpubl. data). Perhaps it is the speed with which a gopher tortoise can dig a burrow, coupled with its strong need to reside in open sunny habitats that causes individuals to abandon existing burrows to construct new ones. For example, at a site in Alabama, Aresco and Guyer (1999a) reported that of 124 active burrows marked in 1991, only 31 (25%) were active five years later. Active burrows were abandoned at the rate of 22% per year. Surprisingly, abandoned gopher tortoise burrows seem to have about the same longevity in the clay-based soils of southern Georgia as they do in sandy soils of south Alabama (Guyer and Herman, 1997). Not surprisingly, these researchers demonstrated that the larger the burrows the longer they persist over time.

Individuals typically frequent more than one burrow as they move about their home ranges. For adult gopher tortoises, the calculated mean distance moved between burrows is $37.0 \pm 37.0$ m by females and $79.0 \pm 69.0$ m by males (Diemer, 1992c). For juvenile tortoises, the calculated mean distance moved is $16.0 \pm 17.0$ m in a north Florida population (Diemer, 1992c) and $15.2 \pm 22.8$ m in a central Florida population (Wilson et al., 1994).

Excluding moves between burrows, movements away from the burrow have been considered to be a tortoise's feeding radius. McRae et al. (1981b) reported a mean feeding radius of $7.8 \pm 4.4$ m for juvenile tortoises and $13.0 \pm 8.6$ m for adult tortoises in a Georgia population. Adults may move up to 200 m in 30 min in search of broadleaf plants (Ashton and Ashton, unpubl. data). In central Florida, Wilson et al. (1994) reported a mean feeding radius of 7.9 ± 8.6 m for juveniles. Also in central Florida, Mushinsky et al. (2003) reported that juvenile foraging forays averaged 19.4 (± 10.3) min and individuals traveled an average of 26.8 (± 41.5) m round trip from their burrows during that time.

In north Florida, Diemer (1992c) documented that, on average, adult male tortoises used 5.5 burrows and adult female tortoises used 2.7 burrows per activity season (April–December). In Georgia, tortoises were reported to use 7 and 4 burrows for males and females, respectively (McRae et al., 1981b). Average annual burrow use by juvenile tortoises ranged from 1.1 by 0–1 yrs old, 2.2 by 2 yrs old, 1.7 by 4–5 yrs old tortoises in a southern Georgia population (McRae et al., 1981b) to 4.4 burrows (1–4 yrs old) in a central Florida population (Wilson et al., 1994). Suggested reasons for differences in burrow use among populations include variation in habitat quality (i.e., canopy and ground cover), soil composition, temperature extremes at different latitudes, and number of disturbances to burrows. Although juvenile tortoises use several burrows, they reside in a primary burrow, where they may spend 75% of their time (Wilson et al., 1994). No data exist in support of a primary burrow (one in which an individual spends more than 50% of its time) for adult gopher tortoises, at least not for an extended time period. Gopher tortoises use shallow depressions, possibly as temporary resting sites, when traveling far from their burrows (Fucigna and Nickerson, 1989; Godley, 1989; Stout et al., 1989; Diemer, 1992c) and windrows, possibly for protection from cattle and machinery (Diemer, 1992c).

In north Florida, Diemer (1992b) found that the number of burrows showing signs of recent activity increased in April, peaked in July, and remained high through October. The burrow surveys showed a continuous cycle of burrow creation and abandonment. The ratio of number of captured tortoises to burrows (active and inactive) varied among sites and years; the ratio of tortoises to burrows ranged from 0.45 to 0.69. Percentages of adult individuals in the three populations studied ranged from 40–62%.

The orientation of gopher tortoise burrow often reflects man-made and natural topographic features that result in burrows being oriented in the four primary compass directions (McCoy et al., 1993). Among other things, the direction of topographic relief, the amount of tree shading, and the orientation of man-made structures such as roads, rights-of-way, and railroads all exert an influence on the orientation of the burrow.

*Activity and Home Range.* — Generally, the gopher tortoise confines its daily activities to the area immediately surrounding its burrow. The area used for routine activities by a species is the home, or activity range. Many publications provide estimates of home range size based on data collected during a small fraction of the life of a gopher tortoise. Because the gopher tortoise is a long-lived organism, and habitats change quality during the course of a life time, most individuals change the home range many times during their lives. Estimates of home range sizes will increase over time for most individuals. Home range sizes for adult female gopher tortoises range from 0.08 ha (McRae et al., 1981b) to 0.56 ha (Doonan, 1986) and adult males from 0.45 ha (McRae et al., 1981b) to 1.27 ha (Diemer, 1992c). In north Florida, Smith (1995) followed female tortoises for up to 500 days and reported home ranges that varied from 0.002 to 1.435 ha. Male home ranges have been reported to be larger than those of females in some populations (Auffenberg and Iverson, 1979; McRae et al., 1981b), but not in others (Diemer, 1992c). The home range for juveniles (1–4 yrs) varied from 0.0095 ha to 0.3576 ha in a central Florida population (Wilson et al., 1994) and from 40 $m^2$ to 0.2502 ha in a north Florida population (Diemer, 1992c). Wilson et al. (1994) found that home ranges of juveniles were largest in summer months, a pattern that is similar to that observed in adults. Home range size is a function of the quality of the habitat (Diemer, 1992c; Mushinsky and McCoy, 1994) and it decreases with an increase in the amount of herbaceous ground cover (Auffenberg and Iverson, 1979; Mushinsky and Gibson, 1991). Management of gopher tortoise habitat by controlled burning during the warm season increases the amount of herbaceous ground cover, and thus tortoises do not have to travel far from their burrows to find ample food.

*Long Distance Movements.* — Gopher tortoises make long distance movements. Using radiotelemetry, Diemer (1992c) found that among her radio-tagged animals, the longest movement made was 0.74 km by an emigrating subadult. An adult female tortoise observed by Ashton (unpubl. data) resided in two adjacent burrows for 11 months, then moved 2.1 km to a new location, where it resided for at least 9 months. Juveniles also will make relatively long distance movements, usually following some type of disturbance to the resident burrow (Diemer, 1992c; Wilson et al., 1994).

The daily and periodic movements of a gopher tortoise enable it to become very familiar with its home range, and, over the course of several decades, an individual may become familiar with a portion of its environment that is much greater than the home range it may occupy at a given point in time. It should come as no great surprise, therefore, that an individual intentionally displaced some distance from its burrow can find its way back to its home burrow. Connor (1996) observed that upon release, gopher tortoises displaced 40 to 200 m from their home burrows moved toward their home range, but several individuals displaced 200 m from their burrows demonstrated a reluctance to pass through highly overgrown habitat on their return trip, although they clearly were moving toward their home range.

*Temperature Relations.* — Gopher tortoises spend a limited amount of time above ground outside of their burrows, perhaps in response to physiological limitations. The gopher tortoise has been found to desiccate more rapidly when deprived of a burrow than any other member of the genus *Gopherus* (Auffenberg and Weaver, 1969). The gopher tortoise can withstand high body temperatures (Bogert and Cowles, 1947), although when heat-stressed, it will froth at the mouth and breathe rapidly. Critical thermal maximum for the gopher tortoise is 43.9ºC (Hutchinson et al., 1966). With a device positioned at the mouth of the burrow that automatically recorded activity, Auffenberg and Iverson (1979) calculated that an adult tortoise was active 9.2% of its time. An "active" tortoise is one that minimally comes to the mouth of the burrow. Juveniles have been reported to spend 90% of their time underground inside their burrows (Wilson et al., 1994). Activity away from the burrow tends to peak in the late spring and summer. For juveniles, Wilson et al. (1994) found that 80% of observed activity in fall, winter, and spring consisted of basking on the burrow mound; juveniles moved away from their burrows significantly more during the summer months. During the winter months, tortoises bask at the mouths of their burrows on warm days throughout their range (Douglass and Layne, 1978; McRae et al., 1981b; Diemer, 1992c; Wilson et al., 1994). Thus, the activities of gopher tortoises away from their burrows are limited in the winter months and increase as seasonal temperatures increase. Daily activity has been reported as unimodal in the spring and bimodal in the summer in a Georgia population (McRae et al., 1981b), and in a north Florida population (Ashton, unpubl. data). Adult tortoises may be active in the late morning and late afternoon in summer to avoid the hottest part of the day (McRae et al., 1981b). In contrast, Douglass and Layne (1978) and Wilson et al. (1994) found that juvenile tortoises were more active in the mid-afternoon and did not display a bimodal activity pattern in the summer. Activity patterns of juvenile tortoises may be influenced by the risk of predation and thermoregulatory behavior (see Wilson, 1991; Wilson et al., 1994). Mushinsky (unpubl. data) observed an adult gopher tortoise a few hours after sunset in mid-summer, but generally gopher tortoises are diurnal.

## GROWTH AND REPRODUCTION

*Growth and Maturation.* — In Georgia, Landers et al. (1982) reported rapid growth through the age of 11 yrs after which growth rates gradually decreased. In central Florida, Mushinsky et al. (1994) reported an average increase of 18.9 mm/yr for ages 1–11, after which growth slowed to approximately 3%/yr until age 20. Female gopher tortoises became sexually mature at a CL of 230–240 mm. Body size, rather than age, seems to determine sexual maturity in gopher tortoises. In southern Georgia, it may take from 19–21 yrs for females to become sexually mature (Landers et al., 1982), while in central Florida females may mature in as few as 9–11 yrs (Mushinsky et al., 1994). In part, this variation reflects the long activity season available to tortoises in central Florida. In addition to geographic location, however, local conditions also influence the number of years required to achieve sexual maturity. For example, one study of gopher tortoises in central Florida (Godley 1989) found that females attained sexual maturity in 14–16 yrs, while results of another study from the same county found that females attained sexual maturity in 9–11 yrs (Mushinsky et al., 1994). The study area occupied by the faster maturing females was a frequently burned sandhill habitat (the University of South Florida Ecological Research Area), whereas the study area with slower growth rates was a mosaic of less favorable habitats, including pine flatwoods and mixed mesic forests. Males likely mature at a smaller size than females. In both north (Diemer and Moore, 1994) and central Florida (Mushinsky et al., 1994) males apparently mature at a CL of about 180 mm. Another report (Aresco and Guyer, 1999b) underscored the relationship between body size, growth, and attainment of sexual maturity. The authors reported that the slow growth of tortoises at Conecuh National Forest in south Alabama was a response to a managed pine plantation with little ground vegetation and poor forage. Gopher tortoises at this site took about 20 yrs to become sexually mature. Gopher tortoises translocated to reclaimed phosphate mined lands in central Florida were found to be gravid at CL less than 200 mm (Small and Macdonald, 2001).

Counts of growth rings have been used to age individuals (Mushinsky et al., 1994; Aresco and Guyer, 1999b). The use of the growth rings to age individuals must be done with caution, however, because the production of "false" rings is known to occur throughout the range of the species (Ernst and Barbour, 1989). In other words, individuals may produce several rings within a single growing season, and, therefore, a ring is not necessarily an annual growth ring. Without independent methods to calibrate the production of growth rings, counts of growth rings should not be considered a reliable method to age gopher tortoises (Wilson et al., 2003). Under the best circumstances, it seems that aging gopher tortoises by counting growth rings on the plastral scutes produces reliable results on tortoises up to 12 (Mushinsky et al., 1994) or 15 (Aresco and Guyer, 1999b) yrs old. Examination of thin sections of scutes has been investigated as a means to determine the age of adult desert tortoises, *G. agassizii* (Germano and Bury, 1994).

*Sexual Dimorphism.* — The best indicator of the gender of an adult gopher tortoise is the depth of the plastral concavity (Mushinsky et al., 1994). Mature males have a distinct depression in the posterior, central portion of the plastron that facilitates mounting a female for copulation. Some mature females have a shallow plastral concavity (2–4 mm) compared to that of mature males (5–8 mm). Males often have larger integumentary glands under the chin than females (Ernst and Barbour, 1989), but the size of these glands varies seasonally. Based on numerous anatomical measurements, McRae et al. (1981a) developed a discriminate function that accurately identified the sex of adult individuals. In a similar effort, Burke et al. (1994) used a stepwise multiple regression of numerous morphological measurements to develop a non-invasive technique to determine the sex of hatchling and juvenile gopher tortoises.

*Female Reproductive Cycle.* — The ovarian cycle of female tortoises is described by Iverson (1980) and Palmer and Guillette (1988).

*Mating.* — The mating patterns of the gopher tortoise are reasonably well known. Male tortoises seek females for mating primarily from May to July, although one might observe a male following a female at any time during the summer or fall. Some observational data suggest that dominant males breed with several females (Douglass, 1976, 1986). When seeking a female, a male positions himself at the mouth of a burrow occupied by a female and displays a head bobbing behavior (Auffenberg, 1966; Wright, 1982). If the female exits her burrow, the courting male walks in a circle around her, periodically stopping and performing the head bobbing behavior. When the female approaches the courting male, he bobs his head violently, and bites her on the forelegs, head, anterior edge of the carapace and gular projection. The female then backs in a semicircle, with the male following. Eventually, the female stops and extends her rear legs. Thereafter, she rotates her body about 180 degrees, so that her posterior end is near the head of the male. The courting male will attempt to mount the female, and if unsuccessful, he will repeat the courting behavior (Auffenberg, 1966; Ernst and Barbour, 1972). The significant amount of direct head to head contact between courting adults unfortunately may serve to facilitate the spread of respiratory diseases.

A recent study examined the mating system and reproductive behaviors of a population of gopher tortoises in central Florida. Using microsatellite makers, Colson-Moon (2003) was able to determine the fathers of the offspring in clutches of eggs oviposited and incubated in the lab and determined that multiple fathers were present in 28.6% of the examined clutches. By assessing patterns of paternity, she was able to determine that the study population exhibited promiscuous mating. Paternity patterns in the study population also suggested that female size may affect the presence of multiply-sired clutches, while male size may affect the ability of a male to gain fertilizations (Moon et al., 2006).

*Nesting.* — Nesting occurs primarily from May through mid-June (Iverson, 1980; Landers et al., 1980; Wright, 1982). Females deposit white, nearly spherical, brittle-shelled eggs in a typically flask-shaped nest cavity. The cavity is excavated with the hindlimbs to a depth of about 10–15 cm. Iverson (1980) reported an average maximum egg diameter of 42–43 mm and an average wet mass of 40.9 g (also see Arata, 1958; Landers et al., 1980; Linley and Mushinsky, 1992). Note that measurements of eggs taken from radiographs of gravid females should be considered rough estimates (Linley and Mushinsky, 1994). Nests may be located in any open sunny area near the burrow of the female, but most often, nests are placed in the spoil mound (apron) immediately outside the female's burrow (e.g., Hallinan, 1923; Allen and Neill, 1951; Arata, 1958; Mount, 1975; Landers et al., 1980). In one study, 21 of 25 located nests were positioned in the apron (Butler and Hull, 1996). In contrast, during a period of three years, Smith (1995) found that fewer than 2% of the 2008 burrow aprons examined contained nests and she observed that only 2 of 18 females deposited their eggs in the apron.

*Clutch Size.* — Female tortoises lay a single annual clutch of 5 to 9 eggs (see Diemer and Moore, 1994; Butler and Hull, 1996, for summaries); however, a large female that had been translocated to reclaimed phosphate mined land in central Florida produced an exceptionally large clutch of 25 eggs (Godley, 1989). Clutch size of female gopher tortoises has been shown to increase with CL in north Florida (Diemer and Moore, 1994) and in southern Georgia (Landers et al., 1980). In a study that was conducted on gopher tortoises translocated to reclaimed phosphate-mined land in central Florida, Macdonald (1996) reported that mean clutch size of translocated individuals increased from 8.6 to 12.6 in four years. Six female tortoises that established burrows on reclaimed land (these individuals were not translocated) had clutches containing more than 13 eggs. Virtually all of the adult tortoises translocated to the reclaimed land exhibited an atypical growth spurt and were large individuals (Small and Macdonald, 2001).

*Incubation and Hatching.* — The incubation period of eggs varies latitudinally from about 80 days near the southern edge of the gopher tortoises range to 106 days farther north (Iverson, 1980; Landers et al., 1980; Butler and Hull, 1996). Most clutches of eggs hatch during August and September, but in northern Florida some may hatch as late as early October (Butler and Hull, 1996). At hatching, and from 24 to 48 hrs prior to emergence, hatchlings may exhibit a large external yolk sac (Linley and Mushinsky, 1994). The external yolk sac is absorbed as the hatchlings remain in the nest cavity prior to emergence. Just after emergence, a deep transverse groove across the plastron is visible, but it disappears two to three days after emergence as the anterior-posterior axis of the body becomes straight and the plastron flattens (Ernst and Barbour, 1972).

## POPULATION BIOLOGY

*Density.* — Densities of gopher tortoises are known to be relatively high in sandhill habitats, especially those that are frequently burned. These densities are typically based on counts of numbers of burrows per ha (see below). However, relatively high densities of gopher tortoise burrows, per se, can be misleading in areas where land is being cleared for human development. Individuals in harm's way may be forced to reside in smaller and smaller parcels of undisturbed land. The result is that one observes a relatively dense population of gopher tortoises and an illusion of a "healthy" population, based on a large number of gopher tortoise burrows per unit area. Under some circumstances, high densities of gopher tortoises have been viewed as a sign of a healthy productive population. Under current conditions, however, where human development has encroached into land occupied by the gopher tortoise or the upland habitats have become overgrown, high densities of individuals must be viewed more carefully. For example, Mushinsky and McCoy (1994) reported that apparent high densities of some gopher tortoise populations may be the result of individuals confined to either a true island or a "habitat" island. Habitat islands are patches of good quality habitat for the gopher tortoise surrounded by poor quality habitat, such as agricultural lands or urban development, and are a product of habitat fragmentation. Gopher tortoises in habitat islands are unable to move freely to new locations as the quality of the habitat degenerates. Gopher tortoises confined to these habitat fragments tend to dig many burrows creating the illusion of a large healthy population. In reality, however, the ratio of burrows to tortoises is high because individuals move and dig new burrows frequently as they search for good quality habitat. More research is needed on the effects of habitat fragmentation on the demography and social interactions of the gopher tortoise.

One significant difficulty in studying the health of populations of the gopher tortoise involves the methods used to estimate the number of individuals within a given area. Without a reliable, repeatable method to use when estimating numbers of gopher tortoises, any attempts to monitor changes in populations will be fraught with doubt. Some creative methods of directly counting individuals have been used (Cox et al., 1987), but determining population size directly by use of underground cameras or bucket trapping of burrows can be expensive and time consuming. More commonly, estimates of the number of tortoises in a population have been made on the basis of tortoise burrow surveys (Carr, 1952; Alford, 1980; Cox et al., 1987). Some years ago, researchers realized that if they could use the number of burrows to estimate the number of tortoises, then the difficulty in estimating population sizes would be greatly reduced. Auffenberg and Franz (1982) presented data on more than 100 gopher tortoise burrows in northern Florida, observed for as long as 15 years each, which indicated that an average of 38.6% of the burrows were unoccupied. Based on this relationship, a "correction factor" was suggested:

$$\textit{Number of Tortoises} = 0.614 * \textit{Number of Active Burrows}.$$

It is important to note that abandoned tortoise burrows (i.e., burrows that cannot be used again by tortoises without extensive excavation), which are often quite common, were not included in this calculation. Although Auffenberg and Franz (1982) did not suggest that their correction factor had any general application, and despite the fact that their correction factor could be shown to be unreliable in some cases (Burke, 1989; Godley, 1989; Stout et al., 1989; Breininger et al., 1991; Diemer, 1992b), the Auffenberg and Franz (1982) estimate became the standard correction for converting numbers of burrows to numbers of gopher tortoises. McCoy and Mushinsky (1992a) rigorously examined the use of this technique. They found that the "standard" correction factor overestimated the number of tortoises in 22 of the 26 populations they examined. Furthermore, they showed that environmental variables, such as habitat type, could influence the tortoise-to-burrow ratio. If the "standard" correction factor often yields estimates of numbers of tortoises that are too high, then a false complacency about the well-being of gopher tortoises could be fostered. That is, if most populations are thought to be larger than they really are, then protective measures may be implemented more slowly than needed.

Surveys for gopher tortoises on Federal protected areas in Florida during the late 1980s yielded estimates of populations greater than 1000 individuals on Egmont Key National Wildlife Refuge (NWR), Merritt Island NWR (including Canaveral National Seashore), St. Marks NWR, and Ocala National Forest (McCoy and Mushinsky, 1988, 1991). Using Landsat Thematic Mapper imagery and Geographic Information System (GIS) technology, Cox et al. (1994) estimated that 93 conservation areas in Florida had sufficient habitat to support gopher tortoise populations greater than 200 individuals. Their estimates assumed densities of 3 tortoises/ha, which may be high for some sites. McCoy et al. (2002) provided a detailed comparative analysis of GIS and transect-survey estimates of the amount of gopher tortoise habitat and number of individuals at 44 conservation areas in Florida. Two estimates of total amount of habitat on conservation areas ≥ 20 ha in size differed by about 11%, with survey estimates larger than GIS estimates. The elimination of marginal habitats in the GIS estimates accounted for most of this difference. Two estimates of the total number of individuals on conservation areas ≥ 20 ha in size differed by about 25%. Different assumptions and methods were used to calculate numbers of individuals from GIS and survey data. The GIS method produced reasonable estimates of gopher tortoise habitat assumed to be of high quality. The authors cautioned, however, that results from GIS methods are best considered only a good first estimate. Without supporting information from transect surveys, results from GIS methods must be viewed conservatively.

## INTERSPECIFIC INTERACTIONS

*The Burrow.* — The gopher tortoise burrow provides shelter for many other upland habitat residents and provides the basis for the suggestion that the gopher tortoise is a keystone species (Eisenberg, 1983). The research needed to demonstrate that the gopher tortoise is a keystone species has yet to be done, however. Gopher tortoises excavate deep burrows which provide shelter from environmental conditions and refuge from predation for the tortoises as well as other vertebrate and invertebrate species (Hansen, 1963; Jackson and Milstrey, 1989; Lips, 1991; Witz et al., 1991). An enlarged area at the bottom of the burrow usually contains fecal matter and other organic debris, which serves as an important food source for a suite of other species (Milstrey, 1986). Many vertebrate and invertebrate species have been recorded from gopher tortoise burrows (Young and Goff, 1939; Brode, 1959; Franz, 1986), including protected species, such as the eastern indigo snake (*Drymarchon corais couperi*) and the gopher frog (*Rana capito*) (Auffenberg, 1969, 1978; Diemer, 1986). Some burrow associates have been shown to prefer burrows occupied by a gopher tortoise while others seem to prefer less active burrows (Lips, 1991). In particular, Eisenberg (1983) found that 73.7% of gopher frogs censused were found in active tortoise burrows. Witz et al. (1991) excavated 1019 burrows and found that of the vertebrate symbionts captured, only lizards were found significantly more often in active rather than in either inactive or abandoned burrows. Snakes and other potential symbionts did not seem to distinguish among active, inactive, or abandoned burrows.

As a gopher tortoise excavates its burrow, it produces a habitat disturbance by creating a mound of sand outside the mouth of the burrow that is composed of soils with a relatively low nutrient and organic content. The temperatures at the surface of the soil mounds exhibit greater diurnal fluctuations than adjacent undisturbed areas and the soil mounds are relatively cool during the periodic summer fires (Kaczor and Hartnett, 1990). Soils on the burrow mounds undergo micro-succession that contributes to increased plant species diversity in the habitat surrounding a tortoise burrow. Seedlings that emerge on the burrow mound often are consumed by the resident gopher tortoise.

*Diet and Feeding.* — As an herbivore, the gopher tortoise interacts with the plants in its environment. Gopher tortoises feed primarily on grasses and other herbaceous plants (Fig. 25-6) (Carr, 1952; Garner and Landers, 1981). Using scat analysis and foraging observations, researchers in central Florida identified 26 families of plants in 68 genera in the diet. The most common families of plants ingested were the Poaceae, Asteraceae, Fabaceae, Pinaceae, and Fagaceae (Macdonald and Mushinsky, 1988). The most common species ingested was wire grass (*Aristida beyrichiana*) (see also Wright, 1982). Young tortoises tend to ingest fewer plants of the family Poaceae and fewer plants with external defense mechanisms and more forbs, such as legumes, than adults (Garner and Landers, 1981; Macdonald and Mushinsky, 1988). The gopher tortoise tends to fall somewhere between a generalist and a specialist forager. While it does prefer some plants over others with respect to their availability in the habitat, it also tends to avoid some fairly common species (Macdonald and Mushinsky, 1988).

Juvenile gopher tortoises show dietary preferences, avoidances, and seasonal differences. At the same site where Macdonald and Mushinsky (1988) studied the foraging habits of mixed age individuals, Mushinsky et al. (2003) studied the diets of juveniles. In all, they observed individuals to ingest 26 genera of plants, of which 16 were ingested positively with respect to their availability in the environment. These 16 genera of plants were ingested more often than one would expect if plants available to gopher tortoises were ingested at random. The most abundant plant genus along the foraging pathways, *Aristida beyrichiana* (wiregrass), was selected negatively (avoided). Grasses (Poaceae) were consumed more during the cooler months than the warm weather months when many herbaceous plants were available. The rank order of plants eaten by juvenile individuals was not different from the rank order of plants eaten by mixed age gopher tortoises.

**Figure 25-6.** A gopher tortoise, *Gopherus polyphemus*, from Pinellas Co., Florida feeding on non-native grasses. Photo by Marius Moore.

Some items ingested by the gopher tortoise are unexpected. Rocks, for example, may be intentionally ingested as a source of minerals. During a study on gopher tortoise reproduction in central Florida, radiography of adult female gopher tortoises revealed that a large proportion contained rocks in their digestive tracts (Mushinsky and Wilson, unpubl. data). Insects were found in 75% of scats examined and charcoal in 67%, suggesting intentional ingestion of these items (Macdonald and Mushinsky, 1988). Details about the digestive efficiencies of the gopher tortoise have been studied by Bjorndal (1987).

In addition to obtaining water from the plants they consume, gopher tortoises drink water, at least occasionally. Similar to many other savanna-dwelling species, gopher tortoises display a specialized behavior for drinking water (Ashton and Ashton, 1991). The edge of the burrow entrance and the surrounding burrow apron functions as a collecting area for subsurface sheet flow during rain events. A gopher tortoise may respond to rainfall by positioning itself to drink water at the corner of a burrow. A gopher tortoise will drink water by projecting its nose and mouth into the surface of the sand. Individuals were observed drinking for an average of 18 seconds (Ashton and Ashton, 1991).

*Predation.* — Gopher tortoises are prey for many carnivorous species. The level of predation on gopher tortoise eggs and young individuals is high. For example, over a 2-yr period in South Carolina, 17 of 24 nests (74%) were destroyed (Wright, 1982). In Georgia, an average female is estimated to produce a successful clutch of eggs (i.e., eggs are not destroyed prior to hatching) once a decade (Landers et al., 1980). Common predators of eggs are raccoons (*Procyon lotor*), gray foxes (*Urocyon cinereoargenteus*), striped skunks (*Mephitis mephitis*), and opossums (*Didelphis virginianus*) (Hallinan, 1923; Ernst and Barbour, 1972; Douglass and Winegarner, 1977; Landers et al., 1980). Armadillos (*Dasypus novemcinctus*) dig up and destroy eggs as well. Hatchlings and juveniles, up to an age of 5–7 yrs, have relatively soft shells and are highly vulnerable to predation (Douglass, 1978; Wilson, 1991). From egg laying to one year of age, gopher tortoises in northern Florida were estimated to have a mortality rate of 94.2% (Alford, 1980). Results from a study in central Florida, which also combined mortality of eggs and hatchlings, suggested an annual mor-

**Figure 25-7.** A selection of carcasses of hatchling gopher tortoises, *Gopherus polyphemus*, observed on a single day in August 1994 on Egmont Key, Hillsborough Co., Florida. A total of 15 were observed. There are no mammalian predators on this island so it is suspected that crows were the major predators. Photo by George Heinrich.

tality rate of 92.3% (Witz et al., 1992). Wilson (1991) found that predation of juvenile tortoises, aged 1–4 yrs, was higher in October–November and April–May than any other two month interval of the year. Juvenile tortoises are known to bask at the mouths of their burrows more often in the spring and fall of the year than during the summer or winter months (Wilson et al., 1994). It appears that a juvenile tortoise, when positioned at the mouth of the burrow to thermoregulate during the cool months of the year, may be quite vulnerable to predation by avian and mammalian predators (Wilson, 1991; Fitzpatrick and Woolfenden, 1978). On Egmont Key, at the mouth of Tampa Bay, where there are no mammalian predators, crows appear to be the most important predators of hatchlings (Fig. 25-7). The shell of a dead tortoise decomposes gradually, but at a fairly predictable rate (Dodd, 1995).

*Parasites.* — The gopher tortoise and its burrow provide food and shelter for numerous parasites, some of which may be harmful to organisms other than tortoises (see Lavender and Oliver, 1996). One common external parasite of the gopher tortoise is the gopher tortoise tick, *Amblyomma tuberculatum*, which embeds into tortoise skin where it obtains a blood meal. Often, this hard tick can be found by sifting through the soils at the mouth of the gopher tortoise burrow. The gopher tortoise tick is of minor medical or economic importance, with its main host being the gopher tortoise (Milstrey, 1986). A soft tick that parasitizes the gopher tortoise, *Ornithodorus turicata americanus*, is a potential vector of African swine fever, which is a highly contagious and lethal virus of the swine, *Sus scrofa*. The swine disease has yet to be reported in the USA, but the risk of introduction is high (Milstrey, 1986).

Some concern has developed recently about a disease called heartwater. This disease, caused by the rickettsial agent *Cowdria ruminantium*, has devastated hoofed livestock in parts of Africa and has invaded into the Carribean (Deem, 1998). The disease attacks domestic livestock, such as cattle, sheep, and goats, as well as a variety of non-domestic hoofed animals. The African tortoise tick, *Amblyomma marmoreum*, is known to feed on mammals and reptiles when immature, and is known to acquire and transmit *Cowdria ruminantium* under experimental conditions (Peter et al., 2000). The tick has the potential to spread the deadly heartwater disease to domestic livestock (Allan et al., 1998). With the tremendous increase in the popularity of reptiles as pets, and the increase in international trade of reptiles, many of which are infected with ticks, there is growing concern among importing countries that a deadly disease such as heartwater could invade North America through the reptile pet trade (Burridge, 2001). Should the disease invade the southeastern U.S. and infect the gopher tortoise, it could pose another major threat to this species. One would predict a wholesale sacrifice of infected tortoises to protect livestock.

## THREATS

*Documented Threats.* — Although the gopher tortoise is taken illegally for food, the heyday of harvesting gophers for human consumption is long past. The gopher tortoise was a food source for many families during the 1930s and 1940s (Hutt, 1967; Taylor, 1982; Mickler, 1986). Its importance during the Depression was reflected in names like “Hoover Chicken” (Hutt, 1967). Recent reports of illegal harvest are sporadic and localized, but some populations may still be depleted by sustained human predation (Figs. 25-8, 25-9). The increasing proximity of human residences to gopher tortoise populations has resulted in increased predation by dogs and cats. Gopher tortoises less than about 20 cm in CL have relatively soft shells which afford them only limited protection from potential predators, such as domestic dogs. Causey and Cude (1978) described feral dog predation on tortoises in Alabama, and Hawkins and Burke (1989) described dog predation on relocated gopher tortoises in north-central Florida. In Alachua, Sumter, and Marion counties, Ashton (unpubl. data) has observed predation by coyotes (*Canis latrans*). Coyotes were observed waiting behind a

**Figure 25-8.** Pick-up truck-load of gopher tortoises, *Gopherus polyphemus*, collected illegally for the food trade. Seizure made by Florida Fish and Wildlife Conservation Commission during the early 1980s, at the truck weigh-in station on I-10 between I-75 and Tallahassee. The pullers reported that they were bringing tortoises from the peninsula to the panhandle because they had about wiped out the tortoises in a 50-mile radius from their home base in Calhoun Co., Florida. Photo from FFWC archives.

**Figure 25-9.** Recently butchered shells of the gopher tortoise, *Gopherus polyphemus*, from Sumter Co., Florida, June 1981. Separation of the carapace from the plastron along the bridge is typical of tortoises that have been butchered for human use. Photo by George Heinrich.

burrow opening for the gopher tortoise to emerge, flipping the tortoise over to prevent its retreat into the burrow, and then eating it.

Human activities pose the greatest threats to the long-term survival of the gopher tortoise in Florida. Humans and the gopher tortoise are in direct competition for limited high, dry ground. The loss of habitat to human activities can take three forms: reduction in area of suitable habitat (true displacement), degeneration of suitable habitat (abandonment of habitat), and increased fragmentation of habitat (increased isolation of populations). The direct influences of humans on the gopher tortoise are manifested through development of upland habitats for urban, agricultural, or mineral recovery uses. The gopher tortoise cannot live in most subdivisions, mall parking lots, agriculturally developed land, and most reclaimed phosphate-mined land. As significant as the direct influences of humans on the gopher tortoise may be, the indirect influences also are great. Suppression of natural fires and the reluctance of the general public to support controlled fires have contributed greatly to a general decline in the quality of most gopher tortoise habitat. The upland habitats occupied by the gopher tortoise are normally dynamic. If fire is excluded from sandhill habitat for just a few decades the quality of the habitat for the gopher tortoise and other members of upland ecosystems decline dramatically. Frequent warm-season burns promote healthy sand hill habitats (Mushinsky and Gibson, 1991).

Conversion of native upland habitats to housing developments, commercial centers, landfills, citrus groves, thickly planted pine monocultures, phosphate and heavy metals mines, and sand extraction pits constitutes the most significant threat to gopher tortoise populations (Landers and Garner, 1981; Auffenberg and Franz, 1982; Diemer, 1986, 1987a; Mushinsky and McCoy, 1996). Suppression of natural fires and limitations of controlled fires, however, cause a rapid decline in habitat quality even in protected areas. Many areas that appear to be suitable gopher tortoise habitat, for example, longleaf pine (*Pinus palustris*)— turkey oak (*Quercus laevis*) sand ridges, actually support low tortoise densities because of increased canopy closure, shrub density, and accumulated ground litter which results from a lack of fire (Diemer, 1987a). Prescribed burning in such areas would reduce the woody component, increase herbaceous ground cover, and foster nutritious tortoise forage plants such as legumes (Landers, 1980; Landers and Speake, 1980; Mushinsky and Gibson, 1991). If all of the publicly owned lands that could support populations of the gopher tortoise were burned frequently and routinely, then we would be increasing greatly the opportunity to expand existing and already protected gopher tortoise populations. Generally, managers of Florida State Parks and other protected lands have insufficient funds and lack the personnel to implement the rigorous burn program necessary to maintain or grow the resident gopher tortoise population.

A comprehensive study of about 50 Florida populations of gopher tortoises (McCoy and Mushinsky, 1988) found several trends resulting from the loss of habitat for the species. Populations residing on sites that had experienced severe area reduction (greater than 25% reduction over the past 20 years), or occurred on sites with greater than 50% tree canopy, or occurred on sites of small size (< 2 ha), tended to have demographic profiles that suggest little recruitment of individuals into the population and abandonment of the site by larger, mature individuals. In contrast, tortoise populations on sites where area reduction was limited or absent, or sites with less than 50% tree canopy, or relatively large sites (> 2 ha), tended to have a high proportion of large, mature individuals and evidence of recruitment of young into the population (McCoy and Mushinsky, 1988).

Comparisons of tortoise populations on true islands and in habitat fragments on the mainland suggested that tortoises are affected similarly by the small size and isolation of the two kinds of areas (McCoy and Mushinsky, 1988; Mushinsky and McCoy, 1994). Both island and mainland tortoise populations show a direct correlation between the number of active and inactive burrows and the area of habitat. Density of burrows, however, decreased as area increased on the mainland, but density of burrows was not related to area on the islands. Also, on the mainland, the ratio of inactive to active burrows (a measure of the tendency of individuals to construct new burrows) increased with area of habitat, and burrow density increased with increasing herbaceous vegetation, but neither of these relations could be demonstrated on islands. Collectively, these findings suggest that tortoises have a greater choice of habitats on the mainland than on islands. Gopher tortoises on islands are confined and may be forced to live in less than ideal conditions. The implications of these findings are profound for tortoises living in small, fragmented “habitat islands” on the mainland. In time, perhaps a few decades, as the quality of their habitat island is degraded, mature adults may be forced to abandon a site in search of better habitat quality. Individuals that may be forced to abandon isolated patches of habitat in areas surrounded by human dwellings seem doomed to perish. Prior the work of Mushinsky and McCoy (1994), the observation of large numbers of active and inactive gopher tortoise burrows in a confined area would likely have been viewed as indicators of a "healthy" population; however, these findings suggest just the opposite. Rather than a signal of a healthy population, large numbers of active and inactive gopher tortoise burrows, relative to the actual number of tortoises, may signal a stressed population (see also Stewart et al., 1993).

Fragmentation of upland habitats by roads and highways increases the opportunity for gopher tortoises to be killed by automobiles. Mortality on highways affects gopher tortoise populations (Landers and Garner, 1981; Lohoefener, 1982; Diemer, 1987a). Landers and Buckner (1981) cited vehicular traffic as the greatest mortality factor on their study area in rural Georgia. Diemer (1987a) observed seven road killed gopher tortoises on a single July day along the southbound lane of the Florida Turnpike; three of the dead tortoises occurred in a 5-km stretch near Orlando. During a 21-month examination of road-killed wildlife, the gopher tortoise was the third most frequently killed species along 19.3 km of highway north of Orlando; the number of tortoises killed (18) was exceeded only by the numbers of opossums (65) and raccoons (47) (J. Roof, unpubl. data). One can only wonder just how many gopher tortoises are killed by automobiles annually in Florida, although some quick calculations suggests that the number could reach into the thousands. The rate at which gopher tortoises are killed on highways is greater in urban than rural areas for two reasons. The heavy automobile traffic in urban areas increases the likelihood of death for any tortoise on a highway, and the more or less continuous sprawl of urban areas increases the likelihood of displacing tortoises which causes them to venture onto highways in search of new habitat.

To appreciate fully the consequences of habitat loss, we need to review some facts about the upland habitats that may support gopher tortoises. Gopher tortoises are most frequently associated with xeric uplands, especially sandhill and scrub habitats (Auffenberg and Franz, 1982; Garner and Landers, 1981; Diemer, 1986). Because these habitats have been (and still are) in high demand for urban development and other human activities, their rate of destruction is alarming. In the 1960s, scrub habitat covered approximately 1.03 million acres of Florida (Davis, 1967). But only 422,000 acres remained by 1990 (Kautz, 1993; Kautz et al., 1993), and much of that has been developed or cleared for agriculture during the 1990s. In the 1960s, sandhill habitat occupied about 6.9 million acres in Florida (Davis, 1967), but less than 851,000 acres remained by 1990 (Kautz et al., 1993), and it also has undergone further reduction during the past decade. A conservative estimate is that less than 20% of the xeric upland habitat that existed in the 1960s remained in 2000. If the rate of loss of gopher tortoise habitat is indicative of the rate of loss of the gopher tortoise, then we estimate at least an 80% decline in the gopher tortoise in Florida since the 1960s. The decline is likely greater, however, because as humans have developed the xeric lands, they also have altered the burn cycles of the surrounding undeveloped uplands, which translates into habitat degradation for the gopher tortoise.

No other southeastern state rivals Florida in the magnitude of urban development (Diemer, 1987b). According to the Florida Chamber of Commerce, the population of Florida is expected to grow at a minimal rate of 2% per year through the year 2010. Continuous urbanization is predicted on both coastal ridges and along Interstate Highway 4 between Tampa and Daytona Beach (Fernald, 1981). Remaining unprotected scrub and flatwoods habitats on the extreme southeastern and southwestern coasts will disappear unless they are protected from development in the immediate future. Similarly, very rapid habitat loss and tortoise population fragmentation are occurring near Orlando and on the Brooksville Ridge. Even opportunities for habitat restoration and subsequent re-introduction of gopher tortoises will diminish as former orange groves in central and south Florida are converted to housing developments. In summary, the future of the gopher tortoise is threatened by tremendous growth of the human population, which causes expanded use of upland habitats, increases fragmentation of existing parcels of land, increases the likelihood of road kills, and decreases the opportunity for the proper management of the fire-dependent habitats (McCoy et al., 2006).

During the past decade or so, upper respiratory tract disease (URTD) has also been identified as a potential threat to the gopher tortoise (Brown et al., 2002). We may never know if humans had any role, direct or indirect, in causing and/or spreading the disease in the gopher tortoise. Many biologists suspect that URTD has a long history as a gopher tortoise disease and that we have recently discovered the disease because more biologists are now studying the species. It is possible that URTD was introduced to the gopher tortoise by humans through the pet trade, although the widespread nature of the disease does not support this notion. Furthermore, one of the organisms known to cause URTD is the same organism that causes the disease in the desert tortoise (Brown et al., 1994, 1999), suggesting that the disease has a long evolutionary history. Perhaps the tremendous amount of development of uplands and fragmentation of formerly large populations of gopher tortoises during the past several decades have increased levels of stress and thereby lowered the resistance of the gopher tortoise to the pathogens that cause URTD. Perhaps a more virulent form of the pathogen has evolved. Although we may never know the origin of URTD, we can investigate how humans today may be affecting the spread and severity of this disease.

Although much attention and research have been directed toward increasing our understanding of clinical aspects of URTD, virtually nothing is known about the ecology of the disease. In particular, fragmenting formerly large populations of the gopher tortoise into numerous small isolated ones may exacerbate the effects of the disease. Gopher tortoises in small isolated populations likely have increased contact with their neighbors, thereby increasing the potential to spread the disease and the probability that many individuals within the small isolated population will be exposed to the disease. In effect, the detrimental aspects of the disease may be intensified in small populations simply because of the small numbers of individuals that may survive the disease. A small population, especially a population of long-lived organisms with a slow rate of reproduction, is less likely to recover from a population crash than a large population. Additionally, prescribed burning often becomes more difficult in habitats surrounded by development, and the resulting habitat degradation may also be a source of physiological stress because food resources are depleted. Disturbance from humans and dogs can also increase in fragmented habitats. Unfortunately, our ability to determine what role these "stresses" might play in URTD transmission and spread currently suffers from an inadequate understanding of exactly how such factors negatively affect gopher tortoise populations (Berish et al., 2000; McCoy et al., 2005).

Upper respiratory tract disease has been observed in both captive and wild gopher tortoises in Florida (Beyer, 1993; Epperson, 1997; McLaughlin, 1997; Smith et al., 1998; Berish et al., 2000; McLaughlin et al., 2000; Gates et al., 2002; Seigel et al., 2003). *Mycoplasma agassizii* is known to be a causal agent of URTD in both the gopher tortoise (Brown et al., 1999) and the desert tortoise (Schumacher et al., 1993; Brown et al., 1994). Recently, other *Mycoplasma* species and possible strains have been isolated from the nasal passages of wild gopher tortoises (Berish et al., 2000; Brown et al., 2001, 2003). Early in the disease cycle, clinical signs may be difficult to ascertain (e.g., a slight swelling of the eyelids). Later in the disease cycle, clinical signs of URTD can include nasal discharge, ocular discharge, swollen eyelids, conjunctivitis, eyes recessed into the orbits, and dullness to the skin and scutes (Fig. 25- 10) (Jacobson et al., 1991; Schumacher et al., 1993; Brown et al., 1994; McLaughlin, 1997); however, some infected individuals may remain asymptomatic (McLaughlin et al., 2000). This disease is highly contagious and is transmitted by close contact between tortoises (McLaughlin, 1997), as during courtship or male combat. Clinical signs may appear within 1–2 wks post-exposure, but it takes 6–8 wks for an exposed gopher tortoise to develop a detectable immune response (McLaughlin, 1997). Because mycoplasmas (bacteria lacking cell walls) can be difficult to culture, a blood test has been developed to detect antibodies to *M. agassizii* in desert tortoises (Schumacher et al., 1993) and has been refined for use in gopher tortoises. This test is currently the most effective, rapid, and inexpensive way to detect exposure to this pathogen (Schumacher et al., 1997). However, the test indicates only whether a gopher tortoise has been exposed to the pathogen and cannot distinguish between asymptomatic carriers (which may pose a threat to healthy animals) and tortoises which have cleared the pathogen and are no longer infected (Brown et al., 1994; Schumacher et al., 1997). Consequently, a polymerase chain reaction (PCR) test was developed to detect actual presence of *Mycoplasma* in gopher tortoise nasal secretions (Brown et al., 1995).

**Figure 25-10.** Close-up of head of gopher tortoise, *Gopherus polyphemus*, from Duval Co., Florida, showing nasal discharge and palpebral edema (swollen eyelids), common symptoms of Upper Respiratory Tract Disease (URTD). Photo by Lori Wendland.

Exposure to URTD may not necessarily confer immunity on an individual; in fact, some data suggest gopher tortoises exposed a second time may become ill more quickly than when initially exposed (McLaughlin, 1997). The studies regarding second exposure were conducted under laboratory conditions, however, and more field research is needed to determine if post-exposure immunity occurs in wild tortoise populations. Based upon some recent findings from captive tortoises in zoos, seropositive individuals may be able to lead apparently healthy lives for many years. In captivity, transfer of antibodies from females to their offspring has been documented in both gopher tortoises (McLaughlin, 1997) and desert tortoises (Schumacher et al., 1999).

Mortality correlated with URTD has been high in some desert tortoise populations (Jacobson et al., 1991, 1995; Berry, 1997), but little is known about the effect of the disease on gopher tortoise populations (Berish et al., 2000; McLaughlin et al., 2000; Brown et al., 2003). Symptomatic gopher tortoises have been found with some regularity on Sanibel Island in Lee County (McLaughlin, 1990; Beyer, 1993), and at least one Sanibel Island population appears to have experienced a 25–50% reduction in breeding age adults (McLaughlin, 1997; McLaughlin et al., 2000). This barrier island has a history of gopher tortoise releases, primarily animals used in tortoise races during the 1970s (Dietlein and Smith, 1979). Numerous dead gopher tortoises have been found at a state preserve, a water management district landholding, a federal facility, and two mitigation parks (Gates et al., 2002; Seigel et al., 2003; M. Allen, *pers. comm.*; B. Blihovde, *pers. comm.*; M. Barnwell, *pers. comm.*). We cannot assume that gopher tortoises residing on public lands are safe from diseases or other threats.

Blood samples have been collected at various sites around the Southeast to determine exposure to the *Mycoplasma* that causes this disease. Seropositive (i.e., exposed), wild gopher tortoises have been found in several locations in Georgia and Mississippi (Smith et al., 1998; R. Birkhead, *pers. comm.*; D. Rostal, unpubl. data; D. Epperson, unpubl. data), and in more than a third of Florida's 67 counties (Beyer, 1993; Epperson, 1997; McLaughlin, 1997; Smith et al., 1998; Berish et al., 2000; McLaughlin et al., 2000; Seigel et al., 2003). On Sanibel Island, 85% of tortoises tested were seropositive for exposure to the pathogen. Exposure to the disease has been detected on numerous public lands in Florida (Epperson, 1997; Smith et al., 1998; Berish et al., 2000; Seigel et al., 2003; McCoy et al., 2005). As available habitat on private lands is converted to development, the health of tortoise populations on public lands becomes more important. Data are needed regarding URTD-related effects on mortality in tortoise populations. Although seropositive tortoises have been found at the previously noted sites with tortoise die-offs, the mortality has not yet been linked directly to URTD. Several recent (McCoy et al., 2005) and ongoing studies are investigating the effects of URTD on gopher tortoise populations; results of these studies should help elucidate anthropogenic and habitat-related influences.

Many areas of uncertainty remain regarding URTD. The disease, like many other diseases, has the potential to influence survival and reproduction of individual tortoises but definitive data are lacking (Brown et al., 2003). More research is warranted to rule out transmission between female and offspring, and transmission from contact with burrows of infected tortoises; current thought is that these types of transmission are either minimal or unlikely (Brown et al., 2003).

A tendency exists for humans to use resources to combat diseases in sick individuals that might be better used to protect healthy ones. We already know that upland habitats available to the gopher tortoise in Florida have long been under siege and the threat imposed by loss of habitat is going to increase in the future. We know also that land managers in Florida are strapped for funds to manage public lands properly, yet we know that lack of management of gopher tortoise habitat for just a few decades can have a strong negative effect on the population that may take centuries to overcome. A wise use of all resources aimed at protecting and increasing current gopher tortoise populations for future generations seems prudent. The purchase, protection, and proper management of upland habitats for the gopher tortoise are the most direct means to insure the future of the species.

*Potential Threats.* — A great deal of uncertainty exists regarding the future of the gopher tortoise in Florida. Much of our present uncertainty is the same as that expressed by Auffenberg and Franz (1982), when they completed the first systematic gopher tortoise surveys throughout the state between 1959 and 1975. They warned about a rapid rate of extirpation of the gopher tortoise in certain portions of its range, sometimes caused by human consumption (Taylor, 1982; Diemer, 1986), but mostly caused by human disturbance of one sort or another. Auffenberg and Franz (1982) predicted a near total loss of gopher tortoise habitat in Florida by the year 2025. If humans continue to move into and develop the state as they have for the past 25 years, then it seems likely that their prediction will be accurate, except for those gopher tortoises that reside on protected areas. Of course, without proper management, populations on protected areas will also eventually perish (McCoy et al., 2005).

A major contributor to the survival of local populations will continue to be proper management of the habitat. In the absence of fire for only a few decades, good quality gopher tortoise habitat can become too overgrown to support the grasses and herbaceous vegetation needed as food. Gopher tortoises abandon overgrown habitat. When an individual in an overgrown patch of habitat attempts to move, there often exists no alternative suitable habitat to which they can move without crossing roads. The large number of tortoises killed by vehicles on roads likely reflects the increased frequency with which gopher tortoise are forced to move in search of good quality habitat.

The general decline in habitat quality may be accelerated by the invasion of non-native plants into upland habitats. Previously we emphasized the dependence of the gopher tortoise on relatively open land where grasses and herbaceous plants can thrive, however, an aggressive, invasive grass exists that may cause displacement of gopher tortoise populations. Cogon grass (*Imperata cylindrica*), an Asian invasive exotic, is a serious problem on rangelands, pastures, roadsides, and reclaimed phosphate mines (Shilling et al., 1997). It can form a continuous monospecific ground cover that is hostile to the gopher tortoise. With half-inch wide leaves that can grow to a meter in length, and a fibrous root system composed of branched rhizomes, Cogon grass can form monospecific expanses of dense ground cover that will eliminate all other vegetation. Such a dense ground cover could force a population of gopher tortoises to abandon their habitat in search of better quality land. Cogon grass is particularly aggressive in disturbed areas, such as roadsides or reclaimed phosphate mined land.

## STATUS

In 1987, the U.S. Fish and Wildlife Service gave formal Threatened status to gopher tortoise populations that occur to the west of the Mobile and Tombigbee Rivers in Alabama, Mississippi, and Louisiana (Wilson et al., 1997). The total area occupied by the threatened western populations is about 148,000 ha (USFWS, 1987). In five of the six states in which the gopher tortoise occurs, it has some form of state protection. In Mississippi, the species is listed as Endangered; and in Alabama it is a Protected Nongame Species. In Georgia the species is listed as Threatened, and in South Carolina, as Endangered. In Louisiana the gopher tortoise is not protected by state laws, rather, it is Federally protected. Populations residing in Washington, northern Mobile, and southeastern Choctaw counties in Alabama also are afforded Federal protection.

The legal status of the gopher tortoise in Florida was previously ambiguous; the Florida Committee on Rare and Endangered Plants and Animals (FCREPA) listed it as a threatened species (McDiarmid, 1978; Moler, 1992), however, the gopher tortoise was listed as a Species of Special

Concern by FFWC in 1979, but very recently in 2006 uplisted it to Threatened (see below).

Threatened species, according to FCREPA, are "species that are likely to become endangered in the state within the foreseeable future if current trends continue" (Moler, 1992). Endangered species, on the other hand, are "species whose numbers have already declined to such a critically low level or whose habitats have been so seriously reduced or degraded that without active assistance their survival in Florida is questionable" (Moler, 1992). When a threatened species turns into an endangered species, therefore, is simply a matter of expert opinion. We suggest that the uncertain numbers of protected individuals; the increasing difficulty in managing the habitats of protected individuals; the possibility that remaining populations may be devastated by a variety of threats, and the relatively poor ability of long-lived, slowly-reproducing species to recover any of the threats means that the gopher tortoise already is endangered in much of Florida. If we wish to maintain the gopher tortoise's historical distribution in all 67 counties and its significant ecological role in enhancing Florida's biodiversity, then the degree of endangerment of the gopher tortoise in each of these counties must be assessed, and quickly.

As we were making final preparations for the publication of this chapter, the Florida Fish and Wildlife Commission (FFWC) adopted Florida Administrative Code 68A 1.004 and 68A 27 and implemented new standards for listing species (see *Guidelines for Using IUCN Red List Categories and Criteria*, March 2004). A species may be listed if it meets one of several criteria for threatened or endangered status. One aspect of the protocol places emphasis on population trends during the past three generations, nearly 100 yrs for the gopher tortoise. The *Gopher Tortoise Biological Status Report* recommended that the gopher tortoise be listed as a Threatened species because evidence exists that the number of individuals in the Florida population has declined by more than 50% in three generations. As a result, in 2006 the FFWC listed the gopher tortoise as Threatened in the State of Florida and changed regulations regarding testing individuals for URTD.

## CONSERVATION OPTIONS AND SOLUTIONS

We believe that a three-part approach is needed to ensure a healthy future for the gopher tortoise. First, the most certain long-term conservation method is the outright purchase of land known to support populations of gopher tortoises by individuals or agencies willing to conserve them. Second, education of private land owners and public land managers about the value of active management of habitats known to support tortoise populations is needed to promote the health of existing gopher tortoise populations. State and local governments should be encouraged to adopt specific legislation to establish conservation easements and tax incentives to encourage landowners to maintain gopher tortoise habitat. Third, re-introduction (defined as the movement of individuals to replenish an area once inhabited by the species) of the gopher tortoise to suitable habitats on lands from which it has been extirpated or lands that have been restored to suitable habitats. This effort is needed to extend the species' ever-diminishing distribution.

A better understanding of the ecology of infectious diseases would be beneficial to any re-introduction program for the gopher tortoise. Likewise, a comprehensive understanding of the social structure of gopher tortoise populations would facilitate proper re-introductions. We know gopher tortoises interact with one another often, especially during the spring and fall breeding seasons, yet we can only guess about the influence of human intervention on the social structure of populations.

Public ownership of upland habitats known to support gopher tortoise populations is the most direct method of protection. Roughly 18.7% of the terrestrial area of Florida lies in conservation land (Cox, 1992). Exactly how many of these publicly held protected areas can support the gopher tortoise, and more importantly, how much of this land actually supports gopher tortoises today, are open questions. During the past decade or so we have witnessed the expansion of several Florida state parks that support populations of gopher tortoises. During more recent years, however, we have witnessed a decline in the resident gopher tortoise populations and a decline in active management practices at most state parks because of inadequate resources to execute controlled burns, and inadequate funds to support the parks properly (McCoy and Mushinsky, 1992b; McCoy et al., 2005; McCoy et al., 2006).

Recommendations for specific management procedures for gopher tortoises have been made by Landers and Speake (1980) for Georgia, Wright (1982) for South Carolina, Lohefener and Lohmeier (1984) for Louisiana, Mississippi, and Alabama, and Auffenberg and Franz (1982), Diemer (1986), and Diemer-Berish (1994) for Florida. Conservation measures include habitat management, establishment of preserves, protection from over-harvest, and public education (Landers, 1980; Diemer, 1986; Diemer-Berish, 1994).

Several counties in Florida have established local programs to purchase environmentally sensitive lands for public ownership. For example, Hillsborough County in central Florida has had an Environmental Land Acquisition and Protection Program (ELAPP) in place for most of the 1990s. By 1999, the Hillsborough County ELAPP had purchased about 35,000 acres of environmentally sensitive land. Soil surveys (Rob Heath unpubl. data) allow us to evaluate what proportion of that land might support the gopher tortoise. About 55% of the land was characterized as having mesic soils (typical of pine flatwoods and dry prairies which support relatively low densities of tortoises) and 10% was xeric soils (typical of sandhill and scrub habitats, which support relatively high densities of tortoises). It appears that although the gopher tortoise has benefited from the purchase of environmentally sensitive lands in Hillsborough Co., only a relatively small fraction of the purchased land supports them in relatively high densities.

Threats to the gopher tortoise, such as disease, harvesting, and habitat degradation, may have long-lasting consequences for the local tortoise population. Gopher tortoise populations in the panhandle of Florida likely are still recovering from the great harvest of adults for human food during and after the Depression. While it is appealing to attempt to protect nests and hatchlings from predation, human or otherwise, the fragile demography of the gopher tortoise is best served by protecting individuals that have already survived to adulthood. Because the gopher tortoise is long-lived, and eggs, hatchlings, and juveniles are vulnerable to predators, conservation efforts aimed at protecting adults likely will provide the greatest benefits for future populations of the gopher tortoise.

As is true for any species at risk, providing an opportunity and a forum for the education of individuals who own and/or manage their habitats potentially can have a great benefit. For example, as a result of gopher tortoise surveys on about a dozen state parks, McCoy and Mushinsky (1991) were able to make specific suggestions to improve the quality of the habitat for the gopher tortoise at each of those sites. Such efforts to work with land managers should not be limited to those who manage public lands, however. At present, many private land owners seem to be unaware of the land management practices needed to maintain healthy populations of gopher tortoises. Perhaps future state and locally funded programs might consider making such public education a high priority.

Efforts to educate the citizens of Florida need to reach out beyond traditional educational outlets. The Florida Fish and Wildlife Conservation Commission (FFWC) produced and distributed a poster depicting the protected status of the gopher tortoise when legal hunting for the tortoise was banned. Such posters are needed and valuable and additional posters that inform the public about the plight of the species might be considered in the future. Furthermore, a poster designed to inform the public about URTD might function to decrease the spread of the disease if people are discouraged from releasing "rescued" individuals into public lands. The public should be alerted to the potential damage that can be accidentally thrust upon a healthy tortoise population by moving individuals from sick to healthy populations or by releasing sick individuals into a population. Humans with good intentions but naive about URTD and other diseases could impart devastating affects on a tortoise population by "rescuing" a single sick tortoise and releasing it into another population. Brochures outlining habitat management techniques, and slide series/videos on gopher tortoise conservation are educational tools that should be developed and distributed throughout the species' range. Educational efforts on behalf of the gopher tortoise should emphasize that xeric habitats, as well as wetlands, have aesthetic and biological value (Diemer, 1986).

Proactive management of upland habitats not only increases available gopher tortoise forage and nesting sites (Landers and Speake, 1980), but also affects growth rates and age to sexual maturity (Mushinsky et al., 1994). Healthy populations of the gopher tortoise are found most frequently in upland habitats with a grassy and herbaceous laden ground cover (Auffenberg and Franz, 1982; McCoy and Mushinsky, 1988). A proactive management plan for the remaining large parcels of land that support the gopher tortoise will benefit not only the resident tortoises but also the humans that reside nearby. The extensive wildfires following the wide-spread droughts experienced in Florida in the late 1990s and early 2000s have taught us the extreme dangers associated with poor land management practices. The upland habitats of Florida are fire dependent ecosystems. They accumulate fuel quickly and burn at a high frequency. If humans act to suppress fire, as we have done for most of the 1900s, then natural fires become catastrophic and extremely destructive. Frequent controlled burns of uplands benefit the wildlife that resides in the uplands and the humans that live nearby (Mushinsky and Gibson, 1991).

In north Florida, a private gopher tortoise management area has been developed by Ray Ashton (Ashton et al., 1994). The goal of the management area is to establish and maintain optimal habitats for gopher tortoises, burrowing owls (*Athene cunicularia* ), and American kestrels (*Falco sparverius*). Three gopher tortoise preserves, totaling about 60 ha, have been created. Each preserve is surrounded by fencing, above and below the ground, to insure the integrity of the designated preserve sites. These preserves have not been in place for a sufficiently long time period to draw any meaningful conclusions about their success or future; however, the outlook is promising. The concept of a multiple species approach to on-site mitigation for non-competitive species is one that should appeal to developers and conservation biologists alike, and has great promise for these taxa.

Because the gopher tortoise is long-lived, it is important that biologists and land managers think about long-term survival as they plan for the future of this species. At any point in time, apparent differences between suitable, marginal, and poor quality gopher tortoise habitats may be temporary or misleading, and may cause some small or partially overgrown areas to be dismissed too quickly as unworthy of conservation effort. It is important to view habitat quality for the gopher tortoise as a dynamic gradient, based on a cycle of fire, hurricanes, or other land-altering events. Area reduction and habitat degradation are two of the greatest threats to the future of tortoise populations: as each of these threats becomes greater, the probability of extirpation increases. In combination, the effects of area reduction and habitat degradation are likely to increase local extirpation probability in a synergistic fashion. Hence, while tortoises on large areas of land are in need of continuous monitoring, tortoises on small areas are likely to be in need of continuous management as well. Future research priorities aimed at improving methods for managing small areas should include the delineation of the consequences of gopher tortoise translocation (defined as the deliberate and mediated movement of wild individuals into an existing population of conspecifics) on the existing populations at recipient sites. Future research priorities also should include derivation of methods that increase the likelihood that translocated and re-introduced tortoises establish residency at recipient sites.

Gopher tortoises can be maintained on relatively small managed parcels of land for a few decades or so (Landers and Speake, 1980), but large parcels (up to several hundred hectares) would reduce the population effects of emigration and certain sources of mortality. Areas as small as of 10–25 ha of favorable, actively managed habitat should be set aside for populations occupying lands slated for development (Cox et al., 1987). McCoy and Mushinsky (1988) surveyed a wide variety of sites for the gopher tortoise, including some of the largest federal lands in Florida and numerous relatively small parcels with small and unprotected populations of tortoises. They recognized the importance of protecting, if possible, large areas (tens to hundreds of hectares) of gopher tortoise habitat, but also recognized the value of the numerous small isolated populations that exist throughout the range of the tortoise. McCoy and Mushinsky (1988) pointed out four themes to be considered regarding the protection of gopher tortoises: (1) the gopher tortoise functions as a "keystone species" (Campbell and Christman, 1982; Eisenberg, 1983; Jackson and Milstrey, 1989), and therefore merits special consideration in ranking conservation priorities; (2) fragmentation of gopher tortoise populations will continue to increase, and relatively-large tracts of habitat will rapidly become rare; (3) conservation of large areas of gopher tortoise habitat is not without risk; and (4) conceiving of fragmented gopher tortoise populations as metapopulations suggests alternate conservation strategies.

The conservation of "large" areas of land has the potential to create false security about the future of resident tortoises. Because of the lack of a coordinated effort to catalog known populations of the gopher tortoise in Florida, the number of large areas, with reasonably large populations of tortoises, can only be approximated (e.g., Cox et al., 1994; McCoy et al., 2002; B. Stys, unpubl. data). We do know that development patterns throughout peninsular Florida are such that it is not practical to set aside even 10 ha of land in many places. Furthermore, continuous habitat management is essential to maintain the gopher tortoise, especially on relatively small isolated habitat patches. Yet, large areas with many resident gopher tortoises typically have not been managed with the gopher tortoise in mind (McCoy and Mushinsky, 1992b). Populations of tortoises on isolated parcels of land are vulnerable to stochastic disturbances that may have profound effects on their well-being, effects which are exacerbated if the areas are not properly managed. The sensitivity of gopher tortoise demographic factors in general, may make tortoise populations even more vulnerable to extirpation from disturbance events than other long-lived vertebrates. McCoy and Mushinsky (1988) believed it unwise to place full emphasis upon the single large area notion of conservation. Rather, they proposed that greater emphasis be placed upon alternate conservation strategies for the gopher tortoise in Florida. Whenever feasible, large areas of land should be secured, with the stipulation that rigorous management practices be employed to monitor continuously the demographic health of the resident population. In parallel with the securing of large areas, however, large numbers of small areas also should be secured. Such small areas allow "banking" of genetic diversity, as well as of individuals, for decades or perhaps longer. Management practices tailored to these small areas might even be able to perpetuate the populations for tens of decades or longer. Ultimately, however, large, properly managed preserves will be necessary to insure the future of the gopher tortoise in Florida.

While biologists recognize the value of preserving large parcels of land for the future well-being of the gopher tortoise, the literature is not clear about how large is large enough. Researchers have assumed that the smallest population that can maintain itself consists of about 50 adult individuals (this number is derived from genetic considerations). Cox et al. (1987) suggested that, to maintain 50 adult individuals, an area of 10–20 ha was required. Their estimate was based on inclusion of about 80 burrows and the average distance an individual travels within its home range. Eubanks et al. (2002) expanded the minimum area estimates to maintain 50 adult gopher tortoises. Based on a year-long study of home ranges of individuals tracked with radiotelemetry, they estimated the minimum area needed to maintain 50 adult tortoises was from 25–81 ha. Had the researchers not tracked individuals and based their calculations on burrow density alone, the minimum area to maintain 50 adults would have been 19–41 ha.

Other researchers used a different approach and logic to determine the minimum area needed to sustain a population of the gopher tortoise. Based on data from 19 populations for which the actual area inhabited by gopher tortoises was determined, McCoy and Mushinsky (unpubl. data) observed that tortoise densities tended to plateau at about 100 ha, and typically included about 500 burrows on large parcels of land. In parcels of land less than 100 ha, tortoise densities tend to be relatively high, suggesting that they are crowded by artificial boundaries and not free to move about as they would if the boundaries did not exist. Therefrore, 100 ha was considered to be the minimum area needed to maintain a population of gopher tortoises in the current setting. Additional security for the resident population can be gained by providing a buffer zone around the perimeter of the 100 ha.

In 2001, the Florida Fish and Wildlife Conservation Commission sponsored a population viability assessment for the gopher tortoise in Florida (Conservation Breeding Specialist Group, 2001). Population Viability Analysis (PVA) was conducted based on estimates of age specific mortality and fecundity rates. Spatial analysis was based on real and potential gopher tortoise habitat using GIS technology. Much of the data used for the PVA were estimated with high levels of uncertainty. Nevertheless, demographic sensitivity analysis indicated that mortality rates of juveniles (up to one year of age) and adult females were the primary drivers of overall growth dynamics in populations of the gopher tortoise. Research efforts and broad management actions should be directed preferentially at these aspects of the species' life history.

Very little information is available regarding the capacity of the gopher tortoise to recover following a major decline in population numbers. The severely depressed densities of gopher tortoises in the panhandle of Florida, reflecting heavy human predation many decades ago, suggest that the recovery process is a slow one, as one might predict based on the general life history of the species. Using population models, Cox (1989) estimated minimum population sizes needed for a re-introduction of tortoises to an unoccupied site. He suggested that the persistence of small populations was longer for mixed populations consisting of subadults and adults than those of composed strictly of adults.

The details of any habitat management program aimed at maintaining or increasing the number of gopher tortoises present in an area must be site specific; however, the goal should be to produce a mosaic of vegetation density by altering the frequency and timing of controlled burns (Mushinsky and Gibson, 1991; Diemer-Berish, 1994). A multi-aged forest is desirable, ranging from treeless areas with high diversities and abundances of grasses and herbaceous plants, to areas with tree canopies that cover about 30–50% of the area. Summer burning mimics the natural fire cycle, promotes flowering of annual herbaceous plants, and facilitates the production of seeds by many of the grasses. Sandhill habitat responds well to summer burns on a 2–7 yr periodicity (Mushinsky, 1985; Mushinsky and Gibson, 1991). Pine flatwoods also should be subjected to summer burns on a 2–5 yr cycle to encourage the production of the plants used as forage by gopher tortoises. Sand pine scrub habitat burns less frequently, perhaps every 15–50 yrs. A highly overgrown site may be first burned during the winter months to reduce the risk of a very hot fire and to thin the canopy prior to implementing a cycle of summer burns which promote vegetative regrowth.

Management needs of gopher tortoises in disturbed habitats such as pastures, old fields, and power lines have been poorly studied. Gopher tortoises seem to be attracted to powerline and pipeline rights-of-way where there is no tree canopy and grass cover is dense compared to surrounding overgrown habitats. The attraction is an illusion—gopher tortoises accumulate in open areas when the surrounding lands are not burned and are overgrown. Gopher tortoise densities in these disturbed habitats typically exceed those of surrounding natural areas (Auffenberg and Franz, 1982). Research on densities and foraging behavior of gopher tortoises in pasture land preserves currently is being conducted, and preliminary findings indicate an average tortoise density of 2 tortoises/acre in improved pasture (Ashton et al., 1994). In managed grassland preserves, tortoises exhibited higher rates of recruitment and population growth after five years than rates described for some natural habitats (Ashton et al., 1994). Site-specific plans will be needed for tortoises in disturbed habitats and may include prescribed fire, mechanical shrub removal, and/or mowing.

Longleaf pine is the preferred pine species for planting in commercial pine stands on most well-drained sites (an exception is the Ocala Scrub in central Florida, for which the sand pine, *Pinus clausa*, is the preferred species). Sand pine should not be planted on former sandhill sites. The dense growth form of this species allows little or no sunlight to reach the forest floor, thereby reducing potential tortoise forage (Landers and Buckner, 1981). Thinning of trees should be undertaken to keep the canopy sufficiently open to allow sunlight to penetrate. Minimally disruptive site preparation (e.g., single drum chopping) is favored over more intensive methods such as bedding or root-raking. Previous studies have demonstrated that gopher tortoises can dig out following chopping treatment on deep, sandy soils (Landers and Buckner, 1981; Diemer and Moler, 1982). Recommended fire frequencies and seasons for pine plantations are similar to those on sandhill. A 1–2 yr interval is recommended if only winter fires are feasible.

We have discussed in detail two of the three issues associated with contemporary changes to the habitats typically occupied by the gopher tortoise, those of area reduction and habitat degeneration. The third component, habitat fragmentation, is a product of the problem caused by area reduction. As formerly large populations of gopher tortoises are forced to live on smaller and smaller parcels of land, the distance between neighboring populations increases, and the probability of successful exchange of individuals between populations diminishes. The steps needed to counteract the inevitable isolation of gopher tortoise populations created by fragmentation of upland habitats are not known at this time. In fact, our knowledge base is not sufficient to allow us to sort out the separate, but interactive, effects of area reduction and habitat fragmentation with any degree of certainty. Clearly, small populations are more vulnerable to extirpation than large populations. The added consequence of isolation by fragmentation will likely increase the probability that small populations will go extinct.

To evaluate the efficacy of the various management methods that may be used, gopher tortoise populations should be monitored periodically. Monitoring the status of the species statewide is an enormous undertaking. Remote sensing (e.g., Landsat/GIS data) appears to have the most potential for long-term large-scale monitoring of gopher tortoise habitat status. Monitoring of small populations may be warranted as well. Gopher tortoise translocation sites (see below), for example, should be surveyed 3–5 yrs post-movement. Possible methods include bucket-trapping gopher tortoises (accurate but labor-intensive), video camera surveys of burrows (limited to large burrows because of the large size of the camera relative to the size of the burrows), and burrow surveys (Cox et al., 1987). Because of time and labor constraints, burrow surveys are the most commonly used methods of surveying gopher tortoise populations.

Burrow surveys must be done carefully to be accurate. In particular, we know that not all burrows are occupied by a tortoise, and we know that an average tortoise will use several burrows during one activity season (McRae et al., 1981b). Nevertheless, if done with proper care, a researcher can estimate the number of gopher tortoises in various size classes based solely on their burrows, without ever encountering a gopher tortoise. To estimate numbers of tortoises in a given area based upon counts of burrows, the burrows are counted and classified as active, inactive, or abandoned to reflect the perceived time since a tortoise last occupied the burrow (McCoy and Mushinsky, 1992a). To evaluate the size distribution of the gopher tortoises in a population, the diameter of each burrow is measured. The burrow count data are multiplied by a correction factor. Unless site-specific correction factors are determined (see Cox et al., 1987), correction factors of 0.6 for disturbed sites, 0.5 for sandhill, and 0.4 for scrub and flatwoods are probably more accurate than using 0.614 for all habitat types. McCoy and Mushinsky (1992a) reported that the linear regression of log number of tortoises on log number of active burrows was the best predictor of number of gopher tortoises for the sites they studied. Witz et al. (1991) found young tortoises in a few burrows that appeared abandoned. If such behavior by young tortoises is widespread, then most current methods to survey gopher tortoises may underestimate the numbers of gopher tortoises. The cryptic nature of young gopher tortoises, their small size, and their propensity to place burrows near other structures on the ground all contribute to the difficulty of attaining an accurate estimate of young tortoises in a population.

Mitigation requirements of the State of Florida for gopher tortoises on development sites have evolved over the last decade or so. Many upland sites, however, are developed without prior review by wildlife agencies, and inequities in review and permitting requirements allow the unmitigated destruction of both tortoise habitat and tortoises (Diemer, 1989). Current mitigation options in Florida include the following: (a) avoidance of individual burrows during development, (b) habitat protection on- or off-site (usually an area equal to 15–25% of the occupied tortoise habitat being affected), and (c) translocation or re-introduction of tortoises to suitable habitat. In response to the wide-spread occurrence of URTD, a fraction of the gopher tortoise population to be relocated must be tested and found to be seronegative before a permit to move tortoises is issued. The habitat protection option may be fulfilled by contributing to a mitigation banking fund an amount sufficient to buy the requisite acreage in an existing or proposed mitigation park. As of July 2005, nine mitigation banks provided about 10,000 acres of protected land. A developer also may purchase an appropriate amount of land adjacent to public lands and then donate the parcel to the public landowner. Finally, a developer may protect an appropriate-sized area on-site in perpetuity (generally ± 10 ha). About 10,000 acres have been preserved on-site or on land provided by developers for protection of the gopher tortoise. On-site preserves, like other habitat set-asides, require approved habitat management plans. In some cases, on-site preserves incorporate pastures, golf course roughs, and retention areas. Although long-term management can be a challenge, these preserves have high educational value and provide scattered habitat for other upland listed species, such as the southeastern American kestrel, Florida scrub jay, gopher frog, Florida pine snake, and Florida burrowing owl.

Gopher tortoise translocation is controversial, labor-intensive, and time consuming, but the future of the species may depend upon perfecting translocation practices and procedures. Biological concerns include contamination of locally adapted gene pools, disease or parasite transmission, social structure disruption, and dispersal-related mortality (Diemer, 1989). Unfortunately, the rate of loss of uplands is so great that time does not permit the proper assessment of the potential concerns associated with translocation. If, as seems to be the case, the State adopts the policy of “no tortoise left behind” as recently suggested by McCoy et al. (2006), then finding suitable, secure recipient sites will become increasingly difficult with continued development. Such a policy has the effect of forcing the public to deal with the issue of whether gopher tortoise conservation is sufficiently important to slow development of unaltered upland habitats. From 1989 to July 2005, more than 60,000 gopher tortoise have been translocated to make way for development (FFWC, unpubl. data), but untold numbers have been entombed in their burrows under the provisions of “take” permits.

Two additional serious problems associated with moving tortoises have become increasingly apparent: the potential spread of disease and the lack of long-term protection and management of recipient sites. Although under review at the time of writing this chapter, current practices of testing a portion of a group of tortoises to be moved have proved to be inadequate and often with inconclusive results. Many healthy individuals have been killed because some in the groups to be moved tested positive for exposure to a disease such as URTD. Gopher tortoises showing clinical symptoms of any disease should not be translocated anywhere. The potential for disease transmission can be minimized or eliminated by moving tortoises only to sites without resident tortoises. The problem of long-term recipient site security can be addressed by moving tortoises only to previously established translocation sites, public lands, or private lands protected in perpetuity by conservation easements.

As increasing numbers of gopher tortoises are injured by vehicles or dogs; wildlife rehabilitation centers and veterinarians are treating more of these tortoises. Some individuals can be successfully treated and released, but many are of unknown origin, have been held in captivity with other tortoises, and/or have sustained injuries that prevent their release. A list of schools, nature centers, and private individuals willing to accommodate non-releasable gopher tortoises should be compiled. The State of Florida has developed a gopher tortoise adoption program, similar to that which has been developed in Arizona and Nevada for the desert tortoise.

Restocking (defined as the adding of individuals to an already existing population of conspecifics) is a conservation measure that differs from translocation in both intent and technique. The goal of restocking is to enhance severely depleted populations. The goal of translocation, on the other hand, typically is to salvage individuals displaced by development. [Note that if the goal of re-introduction is to replace an extirpated population, rather than to "dump" excess individuals, then it is closely related to restocking.] Restocking efforts must employ the best available source (genetically, socially, and geographically) of individuals for restocking. Translocation efforts may try to find "suitable" recipient sites, but the urgency of most translocation efforts often forces individuals to be placed in less-than-ideal situations. Possible restocking and re-introduction sites for the gopher tortoise include protected lands where they have been overharvested (e.g., Eglin Air Force Base in the Florida panhandle), reclaimed mining lands, abandoned orange groves and pastures, restored former pine plantations, and other "created" tortoise habitats (e.g., areas where the water table has been lowered by drainage) (Diemer, 1989). A list of potential restocking and re-introduction sites in Florida was compiled by FFWC (Berish, 1995). All of these sites should have habitat management commitments, and those on private lands should be secured by conservation easements or other binding agreements. Re-introduction of all ages of gopher tortoises to sites they formerly occupied has been tried in Florida, but the fate of most of these tortoises is unknown (Diemer, 1986). In southern Georgia, about 40% of the tortoises re-introduced into an area remained in that area for three years after their release (Landers and Buckner, 1981). In north Florida, about 30% of re-introduced tortoises were recaptured five years after their release (Diemer, 1987b). Clearly, these studies, and others (e.g., Godley, 1989; Macdonald, 1996), suggest that most tortoises quickly abandon sites to which they have been re-introduced. Relocation (including re-introduction, translocation, and restocking) is not an exact science, and until the methods for efficient and successful relocation are developed, only experienced, well-trained individuals with well-conceived plans should be permitted to make any relocation attempts.

At this time, it is hard to know if a unified conservation strategy for the gopher tortoise exists in Florida, and if one does exist, just what that strategy might be. Collection of the gopher tortoise was banned in 1988, and the use of live gopher tortoises for tortoise racing was abandoned in 1989. Recently, a few gopher tortoise reserves have been established. Furthermore, beneficial habitat management practices have been instituted at many public land holdings, illegal harvest has been reduced, and stronger legislation to protect uplands has been introduced in some parts of Florida. Despite these measures, the gopher tortoise continues to decline in distribution and numbers. Existing populations of gopher tortoises are increasingly fragmented and isolated on smaller and smaller parcels of land. Although it is still often encountered in Florida, the gopher tortoise is much less broadly distributed and much less numerous than before the dramatic influx of humans following World War II. Using GIS methods, Cox et al. (1994) estimated that 93 conservation areas with sufficient habitat of at least 68 ha (170 acres) supporting populations of at least 200 individuals existed in Florida. They concluded (Cox et al., 1994), "that the current system of conservation areas in Florida provides the *minimum level* (emphasis ours) of habitat protection required to maintain gopher tortoises." More recently, B. Stys (unpubl. data) used GIS methods to estimate that 140 conservation areas have at least 68 ha of gopher tortoise habitat. In fact, she noted that these 140 conservation areas contained more than 500 individual patches of suitable habitat of at least 68 ha. Ground-truthing of about 40 of the conservation areas identified by GIS has revealed that a proportion of the apparently suitable habitat actually is unoccupied and that areas not considered as suitable habitat actually are occupied (McCoy et al., 2002). Whether or not the current system of conservation areas in Florida provides the minimum level of habitat protection required to maintain gopher tortoises, therefore, is not clear. Furthermore, as development continues to creep ever closer to areas currently occupied by tortoises, our ability to manage them via prescribed burning diminishes, and habitat suitability will be reduced (McCoy and Mushinsky, 1992b; Mushinsky and McCoy, 1994; McCoy et al., 2006).

In spite of the legal protection afforded the gopher tortoise, and efforts by the Florida Fish and Wildlife Conservation Commission (Cox et al., 1987) to establish guidelines aimed at conserving gopher tortoise habitat, the question remains as to what can be done to insure the future viability of the gopher tortoise throughout Florida. How much protected habitat is needed to ensure the long-term persistence of gopher tortoises in Florida? The future of the gopher tortoise, like all other wildlife, is not simply a biological or scientific issue. Individuals, including land owners, developers, legislators and, in fact, all the inhabitants of Florida must make a conscientious decision to value wildlife and their habitats more than they value the things that displace or destroy wildlife and wildlife habitats. Biologists may be able to make a stronger argument for the protection of tortoises than for other species because of the many other species that are at least partially dependent upon tortoise burrows for their survival. Clearly, the presence of the gopher tortoise in the State of Florida enhances the biodiversity of the State. In other words, providing protection for the gopher tortoise and its habitats simultaneously provides protection for dozens, or even hundreds, of other upland habitat species. Biologically based arguments, however, may not be sufficiently strong to sway public opinion; much depends upon the context in which the arguments are made. For example, during the Depression, when tortoises were an important part of the diets of many Floridians, it would have been impossible to protect them.

Our existing laws and regulations need to be reviewed and re-evaluated in light of the tremendous growth in the human population during the past 50 years. Under the current Florida Endangered Species Act, agricultural interests in the State are exempt from many of the regulations that apply to most non-agriculture landowners or individuals wishing to develop natural habitat. "Incidental take" (killing) of the gopher tortoise by altering the habitat in a way that makes it unsuitable for the gopher tortoise is permissible in a variety of circumstances. Under current regulations farmers and silviculturists may elect to use "best management practices," to clear gopher tortoise habitat and, as a consequence, kill tortoises and other protected species. A permit from the Florida Fish and Wildlife Conservation Commission is not required if natural habitat is converted to farmland, plantation, or citrus grove. Converting ranch land into row crop fields also can be done without a permit.

A specific recent example illustrates the effect of silvicultural "best management practices" on the gopher tortoise. In western Alachua County, near the Ashton Biological Preserve, 2000 acres of longleaf pine-turkey habitat was converted to tree farm in the first two months of 2000. Aerial spraying of herbicides (eliminating most tortoise broadleaf food plant species), clearing, and deep plowing were used to prepare the land to become a tree farm. Prior to the clearing, the density of gopher tortoises was about 0.8 tortoises per acre (Ashton, unpubl. data). Given that density of gopher tortoises, 200 acres would have supported about 160 tortoises. A survey of about 200 acres of the cleared land was conducted in April 2000, and only two gopher tortoise burrows were observed (Ashton, unpubl. data).

Existing Federal and State of Florida tax laws regulating agricultural profit requirements and laws regulating tax exemptions on land used for agricultural purposes contribute to the loss of habitats used by the gopher tortoise. Furthermore, when the owners of natural habitats convert them to plantations, State regulations require planting 400–600 trees/acre if the owners wish to maintain their agricultural tax exemptions on that land. Dense, single-species tree plantations create a canopy that virtually eliminates many native species of plants and animals, including the gopher tortoise.

Under current regulations, a land owner may elect to use "best management practices" to convert his/her land to farmland, obtain an agricultural tax exemption, and then sell the property to a developer. Because the land was dedicated to agricultural use, it can quickly be developed. While an intermediate, and perhaps expensive, step has been inserted into a chain of events and it may take decades to complete, the outcome for the gopher tortoise is high mortality and loss of habitat.

In contrast to the kinds of regulations that promote habitat loss, there are incentives, in the form of "conservation easements," that reward land owners for maintaining gopher tortoise habitat. Although regulations for tax exemptions on conservation easements are in place, they are not widely used. A conservation easement removes the right of the landowner to develop the land within the easement. An easement may be perpetual or it may exist for ten years. Currently, conservation easements are used most frequently by Water Management Districts to protect the state's wetlands; they are less often used to conserve upland habitats. Agencies may pay a high percentage of the value of the property for a permanent easement. If agencies could match the tax exemptions granted to land owners who elect to convert their land to farms, plantations, or groves, then land owners may be more willing to establish conservation easements on portions of their land not dedicated to agriculture.

The use of "best management practices" is not limited to privately owned lands; they are applied to public lands as well. Frequently, the Florida Department of Forestry is established as the land manager for Conservation and Recreation Lands (CARL) and State Forests. In 1999, The Department of Agriculture and Consumer Affairs notified regional offices to increase revenues generated from tree harvests and to plan for increased tree productivity in future management plans. Among the practices now employed, at least at some state forests, is the elimination of natural pineland habitats by conversion to intense silviculture (400–800 trees/acre). Furthermore, burning and other land management practices are conducted, not to sustain or increase tortoise habitat, but rather to maximize the yield of timber. These current trends do not bode well for the future of gopher tortoises that reside on these publicly owned lands.

In conclusion, there appears to be much room to improve the protection of this species on both public and private lands within the State of Florida. To establish a meaningful plan to protect the tortoise into the 22nd Century will require the full participation of all those who can influence the future of the gopher tortoise and its habitats. Perhaps in response to the existing uncertainty about the future of the gopher tortoise, McCoy et al. (2006) have called for the State of Florida to adopt a "no tortoise left behind" policy. The authors recognized that implementation of such policy would require significant changes to current operating procedures and create considerable problems for developers.

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