Habitat and Foraging-What Do Tortoises Need?

What is tortoise habitat? It is more than just a location for a tortoises' burrow (home or house). Habitat implies the physical and biological features required for the survival of the organisms that occupy that area (Table 3.1). This includes nutrients for growth, reproduction, health, and day to day interspecific and intraspecific interactions. In what habitats would you look to find gopher tortoises? Would you look in the same habitats for all of the developmental stages (egg to adult) of gopher tortoises or do they occupy different habitats? And what constitutes gopher tortoise habitat? Those habitats in which tortoises have historically and currently been most visible are the habitats with an **open canopy**. An open canopy describes areas where the overstory (the tallest dominant) trees are not so close together or thick as to close off sunlight to the ground. If you are standing in a field and look up, the percentage of the sky visible to you gives you an idea of the amount of canopy cover. In an aerial photograph, the amount of canopy cover (area covered by trees and high, dense shrubs) versus exposed ground or ground cover (area covered by herbs, low shrubs and grasses) is also easy to measure and can be used to calculate the percentage cover. An area with an open canopy provides for certain needs of the gopher tortoise but it also makes their presence more visible to human observers, this however does not necessarily mean that tortoises are not found in areas with a more closed canopy or sub-canopy, like palmetto thickets.

Table 3.1 Identifying Features of Habitat Believed Appropriate for Gopher Tortoises

OPEN CANOPY: 0% to 60% (rarely to 80%) canopy cover

SANDY SOILS: Fine grained with low clay/organic content, well-drained

LOW GROUND WATER TABLE: No less than 0.5 meter to several meters below the surface

FORAGE SPECIES PRESENT: Grasses and herbaceous forage; seasonal fruits & flowers

AGE FEATURES: The features or factors listed above are not believed to be significantly different for various developmental stages from hatchling to adult but hatchlings and juveniles have been shown to utilize thickets and protective fallen branches to feed in safety from aerial and larger predators.

Breininger et al. 1991, Cox 1987, Diemer 1986, Lohoefener 1982, Landers et al. 1981, Landers and Speake 1980

What specifically constitutes gopher tortoise habitat? It depends on whether you mean historic habitat, preferred habitat or the habitat that most gopher tortoises have available to survive in today.

Historic Habitat: Understanding the historic habitat of the gopher tortoise is meaningful because of the tendency today to rush to "restore native habitat". To do this it is necessary to understand what plant species and environmental conditions constituted the "historic native habitat" and in what context plant and animal species existed within this habitat. The historic habitat of the gopher tortoise within the southern United States, east of the Mississippi River, from the time of its appearance in the Pleistocene Epoch until today has been at times a little cooler, much drier and in warming interglacial periods with heavy rainfall even a little wetter than it is today. During the Pleistocene the glaciers that covered Canada and the northern United States made four major advances and retreats. These left a variety of tropical and subtropical climates in the south from Texas to South Carolina and south to Florida. The Florida peninsula was much wider (twice its current size) resulting from sea levels up to 133 meters (400 feet) below those of today (Miller 1998; Hulbert 2001). Very dry (xeric) conditions in the early Pleistocene habitats in Florida and across the coastal plains of southern North America resulted in an influx of western species like scrub jays that survive today in the scrub flora and fauna of Florida (Myers and Ewel 1990, Deyrup and Eisner 1993). Fossil remains of sloth, capybara and giant tortoises are evidence that some of these southern habitats were possibly a little wetter and largely warmer year-round. In a pattern repeated over and over again during the Pleistocene, the warmer interglacial periods caused flooding of land bridges and the return of the ice sheets resulted in the re-emergence of the land bridges between the North American continent and Asia to the north and South America to the south. The receding of sea level as the ice sheets formed also effectively dewatered the land as corresponding water tables dropped (Barry 1983). Thus during the long glacial periods of low sea level and cooler, drier, weather extensive grasslands and savannahs (much like the African Serengeti of today) covered the coastal plain bordering the Gulf of Mexico from Mexico and Texas to Florida.

Grazers and browsers like mammoths, bison, horses and tortoises (*Gopherus* spp.) thrived in and maintained the open nature of these habitats. Significant changes in these southern habitats (that roughly correspond to the historic range of *Gopherus*) occurred during the last glacial peak about 18,000 to 10,000 years ago and during the interglacial warming with sea level reaching current levels about 8,000 to 7,000 years ago. Pollen evidence indicates that as late as 13,000 years ago from Alabama to Florida, xeric forest conditions still dotted the landscape, covering undulating coastal plain sands and lithified marine substrates that had been previously submerged. But the Late Glacial Transition (15,000 to 10,000 years ago) was a time of profound environmental changes as the climate warmed. Temperature extremes impacted species distribution and precipitation began to increase, also resulting in expansion or reduction of the range of significant plant species and thus gopher tortoise habitat. Pollen cores (Sheelar Lake, Florida) from 14,000 years ago show a replacement of the xeric pine forest savannas with dry adapted forests dominated by oak (*Quercus*), hickory (*Carya*), Juniper (*Juniperus*) and white cedar (*Chamaecyparis*) and a herbaceous ground cover including ragweed (*Ambrosia*). As the climate continued to warm and precipitation increased and the ground water table rose, mesic (moisture moderate) species like beech (*Fagus*) became evident across the south. David Webb (in Myers and Ewell 1990) indicates that fossil evidence suggests mixed hardwood, mesic forests have persisted in Florida and the S.E. United States to a greater or lesser degree since the early Miocene (25 million years ago) and by 11,200 years ago these mesic species began to decline but not vanish, though perhaps changing the forage available to the tortoise species of that time. Xeric sandhills and scrub habitats which appeared with the buildup of coastal dune systems some 20 million years ago once again dominated the mesic forests with more xeric adapted pine, oak and herbaceous grassland species again altering the combination of forage species available to tortoises. Fire appears to have played a role in these communities as pollen cores show variation in pine pollen frequency (Watts, 1983) where fire would limit succession of hardwoods and maintain pine dominance.These changes in climate near the end of the last ice age and correspondingly in habitats also mirrored changes in vertebrate fauna. By the end of the Pleistocene large vertebrate fauna became extinct across North America. Giant tortoises that had thrived in the tropical habitats had disappeared. Vertebrates like tapirs and capybaras that were once common along the rivers and horses that grazed across the grasslands of North America had migrated across land bridges to Asia and South America, as their preferred vegetative communities continued to change. By the end of the last Ice Age winters had become colder and summers hotter creating extreme conditions in much of North America, altering habitats as plant and animal species unable to adapt became extinct and others that adapted well flourished forming new plant assemblages and altering the identity and structure of communities. In response, the tortoises had new associations of forage species available while some of the ones previously depended upon disappeared. The habitats of the southern United States, slower to be impacted by these extremes, harbored some of the last Pleistocene megafauna, roaming the same habitats as the burrowing gopher tortoise. Much of this habitat was quite xeric across the southeast. Small pockets of refugia (some of which still can be found today) were created for plant and animal species forced southward as they were repeatedly displaced by the advancing ice sheets in the north (Watts 1971). Of the tortoise species common to the southern United States, east of the Mississippi River only the Gopher tortoise remains today in plant communities not all that different from the late Pleistocene, perhaps it has been suggested, because of the protection of their burrows in these xeric forested grassland habitats dominated by grazing megafauna.

Historic Habitat: For the species of *Gopherus* including the Gopher tortoise that lived in the Pleistocene, **Historic Habitat** was open treed savannahs and extensive xeric grasslands (much like the African Serengeti of today) that covered the coastal plain bordering the Gulf of Mexico from Mexico and Texas to Florida. At times these habitats were slightly wetter and somewhat cooler but over all they were generally xeric, open, diverse and extensive.

Box 3.1

Humans entered the scene and most certainly had an impact on the plant communities that the gopher tortoise utilized as natural habitat from the post glacial to the present. The movement of humans from the north and south into the tortoises' habitat in the southeast most assuredly included the transport (actively and passively) of plant seeds and resulted in the introduction of new species and the alteration of localized plant communities. It is not pure coincidence that the list of plant species currently used as forage by gopher tortoises (Appendix 3.1) includes many species also of importance as food, medicinal and dye plants for humans and as feed for domesticated livestock as well as many naturalized “weed” species from Europe that often came uninvited as a byproduct of human trade and travels. It is an easy mistake for managers to make in believing that the plant associations with which we are currently most familiar (FLUCCS; Myers et al. 1990) are a static that represents a continued association of plant species. Botanical research (Whittaker 1958) has pointed out repeatedly that species fill roles or niches in relation to the total environment and not due to climatic factors alone. In essence, our defining of plant communities and habitats is a regional or local phenomena related to a point in time and not a universal absolute. The relationship of vegetative communities to the herbivorous species that depend upon them can be highly variable. Each plant species is free to combine and recombine with others in space and time to create and recreate associations that meet its adaptive requirements at that given time. Changes that alter factors related to the modes of distribution for plant species reproduction by seed and vegetative reproduction, micronutrient requirements related to soil composition, changing moisture regimes, temperature extremes and catastrophic events like floods, hurricanes and tornadoes and fire all can temporarily or permanently alter the plant species composition in regional or localized habitats. Within our “time of study” the concepts of climax community and succession of plant associations have meaning but over space and geologic time there are no absolutes as new variables enter the picture, like introduced species and highly adaptive exotics. We have a real problem in trying to define a “native habitat” in a modern world where plant species are brought in by modern landscape architects from all over the world and where we can plant anywhere species that have been specially bred to produce a desired flower color, species that have been genetically altered for growth, or disease or pest resistance, and species that have been bred to survive outside of their normal environmental conditions. In short, what we should try to identify and manage will be the habitats created by plant species associations that best meet the needs of the gopher tortoise or in other words the tortoises' "preferred habitats".

Preferred Habitat: In today's world where tortoise populations have been reduced to 20% of what they were in the late 1800s (Auffenberg and Franz 1982), an assessment of the natural habitats, natural plant associations and natural environmental conditions preferred by gopher tortoises is not necessarily easy to accomplish. **The definition of "natural habitat" is debatable anytime after the arrival of humans.** Both archaeological evidence and written records post Columbus indicate that trade and farming existed on a widespread basis throughout what is now the range of the gopher tortoise. Pre-Columbian trade from the northern and western parts of North America as well as from South America and the Islands of the Caribbean is indicated by the presence of a variety of trade goods as well as by the seeds and remnants of food plants. Milanich (1998) points out that the Mississippian farming cultures, after 1000 A.D. stretched from eastern Oklahoma to the coastal plain of the Carolinas and from St. Louis to Tallahassee. A farming way of life also meant villages, groups of villages (for trade) and bureaucracy to settle differences and protect local interests. Trade at its height would bring goods (and plant seeds) from across the continent and from coastal ports. Alteration of natural habitat has been on-going since the first humans and their animals and foodstuffs entered the southeastern continent. With the European discovery of the new world, colonizers brought in seed of plants with which they were more familiar, dispersed plant species of economic importance both native and non-native about, and introduced animals like cattle, hogs and goats. In 1562 engravings by Le Moyne and descriptions by De Bray provide some idea of the extent of agriculture and manipulation of habitats being carried out by the Florida Indians in the general area near what is now St. Augustine with the growing of some species of maize and fruits already being widespread. The Spanish Franciscans came to the southeastern lands called "la Florida" in 1595 and continued to have a dramatic impact on the life and habitats of the region though the early 17th century. Beyond colonization, the Spanish sought to "Europeanize" the lands they settled (Crosby 1972). Watermelon and peach were the first Old

World plants cultivated by the Native Americans and they became so widely dispersed that later naturalists believed them to be native to the southeast (Bartram 1774, Swanton 1946). Among the foods shipped to the New World for cultivation included various culinary herbs, peas, lentils, garbanzos, onions, garlic, radishes, cucumbers, melons, figs, grapes, citron, lime, lemon, orange, pear, hazelnut, pomegranate, mulberry, quince, bergamot, cardoons and olives (Garcia 1902, Connor 1925). Some grains were introduced but attempts were largely unsuccessful because cereals like wheat, oats, barley and rye require cool, moist springs and dry hot summers, conditions not common in the southeastern United States. The Spanish also introduced to La Florida species from other parts of the New World like Lima beans, papayas, squash, cassava, pineapples, chili peppers, moschata, and new varieties of corn (from Cuba and Mexico). Archeobotanical evidence suggests that by the 1690s Old World cultigens were in use by the Apalachee. Movement of Native Peoples from their lands in the northern colonies to southern and western reservations also resulted in an influx of some of these tribes (collectively called Seminoles) with their typical medicinal and food plants used in the north often being brought with them into the range of the gopher tortoise. In the late 1700s writings by naturalists like William Bartram (1774 pub.1791) and travelers like John Pope (1792) reflected the great interest in the “wild habitats” of the south and in the great potential of these habitats to be exploited. William Bartram noted the tragic loss of trees as developers completely burned and cleared land before building. Romans (1775) referred to the high relief sandy dunes and flat sandy plains covered by various species of pine as the “pine barrens” as he traveled through east and west Florida. The French government sent the “botanist to the king” Andre Michaux to the New World in 1785 to “study, collect and ship seeds, fruits and living plants from North America to France” for the purpose of reforesting the barren French countryside and adding to the royal nurseries. Michaux traveled 11 years in North America and 3 months in Florida (1787) one of only four known explorers to make observations and gather and record botanical data on the flora of Florida in the 1700s (the other three being Bernard Romans, John Bartram and William Bartram). In addition to describing habitats and plants, and shipping plants back to

France, Michaux was responsible for introducing a number of species to America and the south including the camellia (Camellia japonica), the invasive mimosa (*Albizia julibrissin*), and the Crapemyrtle (*Laegerstroemia indica*). Michaux also recorded species that are not found today in Florida or that were not currently present in the areas where he traveled, indicative again of habitat changes. Michaux's and the Bartrams' lists of species and descriptions can provide some insight into the species composition of the "natural habitats" of Florida at a time when serious development was just getting started, but also well after the introduction of numerous species by first Native Peoples and then by the Spanish, French and English colonizers.

In 1827 John Lee Williams published a map and work entitled *A View of West Florida* in which he, like Bartram, describes the peculiar animal called a Gopher which is found "in Black Jack (Oak) ridges, which are easily penetrated with its burrows". Williams also describes catching gophers by digging pits at the mouth of the burrow and then using the captured tortoise for soups and gumbos. He describes their eggs as about the size of a hen's egg but more round and he states that they are "laid in the sand and left to hatch by the heat of the sun". Williams also states that "They (gophers) feed, night and morning on the dewy herbs, near their burrows." It is from these various "descriptive snapshots" of early locations and habitat of the gopher tortoise that we can begin to select out the elements that can help define the gopher tortoise's "preferred habitat". We know that by the 1840s great herds of wild cattle, descended from the "vacos" brought over by the Spanish were roaming freely across the scrub and pine savannas of central and south Florida, perhaps in a way helping to maintain the open, savanna habitats much the same as the megafauna grazers did in the Pleistocene and after that the native bison. Summerlin, known as the Cracker King, made a fortune selling beef to the rebels and after the Civil War many other cattlemen moved in to take advantage of the wild herds across the state. The Cuban insurrection guaranteed a huge continued market for beef cattle and that the open range across Florida would be maintained, forcing even highways to stay unfenced until 1949. This open range most certainly impacted Florida's natural habitats and resulted in the continued spread of many plant seeds as well as assisted in continuing to keep these grasslands open. Some of the activities of the cattlemen were positive for keeping gopher tortoise habitat open but the purposeful influx of non-native plant species for supplemental feeding and ditching activities which altered natural water regimes still make it hard for us to now identify the gopher's once "natural preferred habitat". The authors have worked with and surveyed a number of current and former cattle ranges and found good tortoise forage diversity in areas actively grazed by cattle but not overgrazed. We have also heard many stories from the cowboys that worked the range about gopher tortoises. It was not uncommon for cowboys and later local hunters to kill the very abundant (and obviously well fed) gopher tortoises as food for their dogs.

The habitat of the gopher tortoise in the southern United States experienced continued change with the growth of "civilization". Journeys to the southeastern United States, usually departing from Charleston, South Carolina became highly popular in the post Civil War days. The growing transportation industry in the south as well as the hotels located in coastal regions, "health springs" and along transportation routes proceeded to fund a major effort in the late 1800s to bring visitors, new investors and new residents to the south and to Florida in particular, an endeavor that has not diminished to this day. Subsidized by advertisers, these companies hired writers to produce articles and guide books to enhance this development boom. One of the more popular of these guide books was the *Guide to Florida* by Rambler published in 1873 and subsequently in 1875 and 1876. Sidney Lanier produced *Florida: Its Scenery, Climate and History* in 1875 and gives details of the southward movement of the turpentine-distillers and the timber cutters, leaving scarred pines and barren lands in their wake to be followed by young oaks and then the "farmer who substitutes the civilization of corn and cotton". In 1883 Carl Webber wrote *The Eden of the South* a book directed at "tourists, invalids and those seeking a home in the orange belt, the lake region, the vegetable section and the railroad center of Florida." Researching the early writings describing the agricultural efforts, drainage activities and development of cattle ranches as well as the few early botanical lists and flora accounts throughout the south and in Florida provides the botanist with a good picture of the drastic changes the native habitats were exposed to long before serious work on the composition of these "natural habitats" ever began. Serious botanical work in the southeastern United States and Florida dates to the early 1900s with work done by J.K. Small (1913), R.M. Harper (1914), and L. Gano (1917). These works provide some species lists and habitat descriptions but are by no means complete in helping us describe what constitutes "preferred natural habitats" for the gopher tortoise. Much of the botanical work that was subsequently done was directed at agriculture, silviculture and pasture management. Pessin (1933) looked at the forest associations of the longleaf pine belt on the uplands of the Gulf Coastal Plain. The movement to improved pastures over open range fueled extensive research by Agricultural Experiment Stations during the 1940s and 1950s which continues through the present. This agricultural shift in the south to widely manipulating the natural plant associations or eliminating them in favor of specific herbage for pastures (carpet grass, grass-clover mixes, lespedeza-grass seeding mixtures with specially mixed fertilizers) drastically altered the environment of the gopher tortoise at a time when increasing development of human infrastructure was forcing the gopher tortoise into the largest segments of open space left, the agricultural lands and cattle ranges (Blaser et al. 1952). From the early 1930s gopher tortoises (as well as other wildlife) had to contend with the habitat alterations created by the increasing forest management practices that excluded natural fire, denuded lands of herbaceous competitors through use of herbicides, burning and clear cutting, and increased planting density for maximum yield. Development, intensive agriculture and silviculture and the profusion of road building that marked the period after WWII through the present has made it difficult to identify the gopher tortoises "preferred natural habitat" from the habitats it has been forced to occupy because they were the only lands available that minimally met its needs for survival.

One of the most noticeable of the gopher tortoise habitats is the sandhill or high pine association (Laessle 1958) which has been referred to as the "preferred natural habitat of gopher tortoises" by McRae et al. (1981), Franz and Auffenberg (1982) and Diemer (1986) primarily because it is easy to observe that these open, fire-maintained communities support high densities of gopher tortoises. High pine habitats, as one of the largest types of forest in the southeastern coastal plain of the United States, once stretched nearly uninterrupted from the Atlantic seaboard in Virginia to eastern Texas and south to the Gulf coast (Greene 1931 Christensen 1988). Prior to European colonization, the southeastern coastal plain was believed to have over 80 million acres in Longleaf Pine dominated habitats that now have been reduced to about 10 million acres of which only 400 acres are generally undisturbed by humans (Means and Grow 1986). Characterized by a high or rolling relief, the high pine community usually abuts the pine forests of the flat Pleistocene marine terraces with some species carrying over into those forests. These pine flatwoods and interspersed dry prairies still represent the most extensive terrestrial habitats in Florida as well as over much of the southeastern Gulf coastal plains from southern Georgia to Louisiana. These habitats are characterized by flat topography and a pine overstory with a dense shrub and herbaceous layer over nutrient-poor, acidic sandy but poorly drained soils. Together, these relatively open, pine habitats and their variations represent over 80% of the habitats associated with gopher tortoises but as Joan Berish (Diemer 1986) points out even now not enough is known about the population densities in many of the less well studied habitats. The location of the tortoise burrows only represents one aspect of the tortoises' preferred habitat and it is important to remember that the foraging area which also makes up part of the home range may not be in the same location as the burrows. The specific requirements (well-drained sandy soils, deeper ground water table) that help determine burrow location choice may not always result in good forage habitat. The suite of requirements for successful growth of tree species like longleaf pine (*Pinus palustrus*) and turkey oak (*Quercus laevis*) can be somewhat broad and the understory and herbaceous ground cover associated with this habitat can vary from the northern part of the range to the western and southern parts. The importance of the presence of herbaceous ground cover for tortoise preferred habitat is described by Auffenberg and Iverson (1979) in their study which found a positive correlation between the amount of herbaceous ground cover and the density of tortoise burrows. They found that areas with less than 35% herbaceous ground cover supported no to much fewer gopher tortoise burrows compared with areas having a herbaceous ground cover of 80% or more. Looking at it from the other side, some studies have found that tortoise burrow densities can stay high in areas with a canopy cover from 0% to as much as 80% as long as open forage areas are accessible.

Comparisons of tortoise utilization of various habitats from the 1950s through the 1980s have been reported by Auffenberg and Iverson (1979), Landers and Speake (1980), Franz and Auffenberg (1982), MacDonald (1986) and use of habitats on Federal lands from 1987-88 was surveyed by McCoy and Mushinsky (1992). Myers and Ewell (1990) have pulled together some of the most complete information from experts on the habitats in Florida (and the Southeastern United States). The authors, as well as a number of other researchers (Cox et al. 1987, Diemer 1992) have made special note of the plant communities in Florida and other parts of the range of the gopher tortoise, particularly in the context of assessing the suitability of habitat for gopher tortoise relocation or long term management of preserves for tortoises and other wildlife (Table 3.2).

Table 3.2: Habitats That May Be Suitable For the Gopher Tortoise across its Range

Habitat Names	Potential for forage species 10 = High 1 = Low	Av. Density of Gopher tortoises per acre+	Level of Suitability++ 10 = High 1 = Low
No Dominate Tree Cover			
Natural Grassland	10	5.20	10
Improved Pasture	9	3.50	8
Abandoned Pasture	10	4.21	8
Cropland (row and field)	8	.40	5
Abandoned citrus groves	9	5.00	9
Fallow Crop Land	9	3.00	7
Herbaceous rangeland	10	3.20	9
Shrub / brush rangeland	9	2.50	7
Freshwater Marsh*	7	*	5
Wet Prairie*	7	*	5
Coastal Strand – Herbaceous	8	1.83	8
Seaside Dune Scrub - Shrubby	8	4.50	8
Ephemeral (Intermittent) Ponds*	7	*	7
Disturbed (Borrow, Spoil, Fill, Roadsides)	7	.97	6
Ruderal	8	3.23	8
Has Dominate Tree Cover			
Upland Coniferous Forests			
Pine Flatwoods			
Longleaf Pine	10	5.50	9
Longleaf Pine/ Saw Palmetto	10	4.20	8
Longleaf Pine/ Gallberry	9	1.20	6
Longleaf Pine Plantation	6	1.42	6
Slash Pine/ Saw Palmetto	8	.57	6
Slash Pine / Oak / Gallberry	8	.48	5
Slash Pine Plantation – early stage (open canopy)	7	4.00	7
Slash Pine Plantation- late stage (closed canopy)	2	.10	1
Pine-Mesic Oak Hammock Longleaf/Slash/Loblolly Pines Southern Red/ Water/ Chestnut / Laurel Oaks w/ Hickory, Dogwood, Sweetgum	4	.20	3
Pine-Xeric Oak Sandhills	10	4.20	10
Longleaf Pine – Black Jack Oak	10	4.20	10
Longleaf Pine – Blue-Jack Oak	9	2.50	9
Longleaf Pine – Turkey Oak	10	4.30	10
Longleaf Pine – Sand Post Oak	9	3.80	9
Sand Pine Scrub / Rosemary	6	1.20	6
Sand Pine Plantation early stage (open canopy)	6	1.20	5
Upland Hardwood Forests			
Xeric Oak (Blueback, Blackjack, Turkey, Sand Post)	7	2.80	7
Live Oak Hammock (mesic)	5	.50	5
Sand Live Oak Hammock (xeric)	7	1.25	6

Ashton Biological Preserve Data and Ashton and Ashton projects data 1978-2004
Myers and Ewel 1990 Auffenberg and Franz 1982 MacDonald 1980
Cox et al. 1987 Landersand Speake 1980
DOT, 1985 FLUCCS Auffenberg and Iverson (1979)
+ approximations due to variations in data methods by different researchers
++ assumes ideal habitat management for the region of the tortoise's range
* used in drought or when seasonally dry

The problem in determining preferred habitat for the gopher tortoise as we have outlined previously is the continued and expanding presence of humans. The habitats occupied by the gopher tortoise since human expansion within its range are not necessarily the “preferred” ones but in many cases the only ones remaining that meet the tortoises’ needs. The habitats where gopher tortoises are commonly found today are dynamic and as with all habitats go through a series of changes until they reach a stable (climax) association that may remain in equilibrium for an extended period. The forces that keep these habitats in a recognizable stage (sere) include the actions of natural fire, wind and water. Humans have used management activities to replace the natural forces (megafaunal grazing and browsing and fire) that maintain these habitats. The ecosystems that we study today that support gopher tortoises share similarities with those discussed in *The Tallgrass Restoration Handbook*, and the quote by Packard and Ross (1997) is also quite applicable, “we have with us the tattered remnants of a nearly lost ancient ecosystem”. Everywhere that humans have been able to override natural ecosystems with animal husbandry and agriculture our ability to determine not only what was preferred but what will sustain populations is made more difficult. Janzen (1988) suggests that in the tropics, the remaining “wildlands are hardly more than scattered biotic debris” with remaining habitats full of the “living dead- the organisms that are living out their physiological life spans, but are no longer members of persistent populations”. Does this apply to the gopher tortoise and its remaining habitats in the southeastern United States? Most certainly it does in many places. The gopher tortoise, as primarily a generalist herbivore, within its historic range has always been tied to open vegetative associations with a diversity of herbaceous species dominated primarily by grasses and sedges. It has historically utilized grasslands, xeric woodlands, scrub, coastal strands, pine flatwoods, disturbed habitats, and ecotones of mesic woodlands. Under drought conditions tortoises would also utilize the vegetation still available in drying wetlands like marshes, lakes, and river basins. **It is important to note that these names for habitats are just that, a name given usually based on the most visible tree species and the herbaceous species composition is not usually noted in detail, primarily because it is**

highly variable. Therefore naming these habitats for the less variable tree species while efficient does not necessarily reflect the available forage species preferred by tortoises and the presence of these tree species does not guarantee that those forage species will in turn necessarily be part of the habitat composition. Gopher tortoise habitat, particularly over the last 100 years has been split into virtual "islands" of greater or lesser expanse. Depending upon the size of these islands of habitat, the tortoises within (as well as many other species) may indeed be Janzen's "living dead" if they cannot maintain the population with sufficient habitat and forage to support continued successful reproduction and recruitment.

Preferred Habitat: Habitat alterations brought about by the ever-increasing presence of humans in the same habitats as gopher tortoises has made the identification of what constitutes natural preferred habitat very difficult. One of the most noticeable of the gopher tortoise habitats is the sandhill longleaf pine – turkey oak association which has been referred to as the "preferred natural habitat of gopher tortoises" by McRae et al. (1981), Franz and Auffenberg (1982) and Diemer (1986) primarily because it is easy to observe that these open, fire-maintained communities support high densities of gopher tortoises. Joan Berish (Diemer 1986) points out even now not enough is known about the population densities in many of the less well studied habitats. **Perhaps the "preferred habitat" is the one in which the gopher tortoise can currently survive in perpetuity.**

Box 3.2

As we have presented in this quick overview of the changing botanical composition of habitats in the southeastern U.S., it is not easy and probably not possible to identify what would constitute preferred natural habitat because:

1) the data on what specific species and plant associations were present and preferred by gopher tortoises before the interference of humans are not available

2) the data are not available on what specific plant species were preferred before the introduction of the various naturalized and invasive species present today

3) the data are not available on the nature of specific plant species present for tortoises to graze on in the past and their physiology and the relationship between the herbivore and plant antiherbivory strategies

4) the data on the specific chemical nutritional needs of the gopher tortoise and how these needs can be met by specific plant species within the various habitat associations are incomplete

Ultimately, the habitats that tortoises have available to them here and now are the habitats in which they can survive. The case has been made repeatedly for restoration of habitats and in a few areas major project monies have been made available for restoration efforts even if the process and outcomes of such restoration efforts remain a questionable academic exercise. Restoration requires that we know not only the processes and intricacies of habitat and ecosystem growth and change, but also that we really know what we want to restore them to and as we have indicated above, we do not yet have the data necessary to accurately answer that question. While we fully support restoration when based on realistic goals and supported by sufficient information, for now the immediate issue is the future long term survival of the gopher tortoise in the habitats currently available that can be managed and / or (as appropriate) enhanced or restored to meet the needs of the species.

Habitat Available Now: The habitat(s) that most gopher tortoises have available to survive in today only have been studied in detail since the 1950s. The tools needed to completely understand the needs and parameters of habitat use by gopher tortoises were not really available until the technological advancements beginning in the late 1960s. The advent of radio tracking, satellite imagery, thermal imagery, radiographic equipment, GIS, video burrow scopes, sonagrams, trip cameras, remote sensing, and recording data chips has brought about new understanding of what constitutes current gopher tortoise habitat. The creation of Natural Areas Inventories and other similar efforts on local, state, national and global levels in the early 1960s and 1970s (which then took advantage of the newly available technologies) have done much to help organize, define and quantify our existing habitats (FNAI 1990). While all this information can give us clues as to what may have at one time constituted natural preferred gopher tortoise habitat it cannot yet go back in time before the alterations made by humans and identify the key factors and specific plant species that made up the gopher tortoises' preferred habitat or habitats. **Therefore we must be satisfied with identifying what constitutes currently available habitats that allow for the long term survival of the gopher tortoise.** The key here is not to get mired in the misconceptions "that we know what constitutes preferred natural habitat for gopher tortoises and that we can restore that natural habitat". We don't have the data to support either of these contentions. What we can do is identify what habitats have successfully supported gopher tortoise populations since the 1950s when some researchers started taking the data necessary for us to make those determinations. The final acceptance of fire as a necessary management tool (and restoration tool) has played a vital role in preserving and allowing for successful management of some gopher tortoise habitat.

The habitats described and analyzed as potential suitable gopher tortoise habitat (Table 3.2) share the following components (to varying extent) as identified by the authors' personal research (1970-present) and by work done by researchers including Landers 1980, Auffenberg and Franz 1982, Diemer 1986, Cox et al. 1987, Breininger et al. 1986 and 1989, McCoy et al. 2002 and Eubanks et al. 2002:

1) they contain a mixture of grasses and herbaceous plants of a quality and quantity suitable for forage and may or may not have a widely spaced tree cover and/or sub canopy of shrubby species (Hallinan 1923, Braddock 1962, Black 1965, Bramble 1974, Garner and Landers 1981, MacDonald 1986)

2) they have soils suitable for burrowing; well drained, sandy soils with a deep ground water table are usually best; soils that are somewhat shelly or contain limerock, peaty soils or even wetland soils that can be penetrated by the tortoises strong front claws and that have a water table low enough to allow even a shallow burrow (45 to 50 cm or 18 to 20 inches), may be used in less than favorable circumstances; in the case of lack of time to burrow or lack of suitable burrowing soils juvenile and adult tortoises may make use of

leaf litter and scattered logs and branches but for long term survival the habitat must provide suitable burrowing soils

3) the current range of the habitats suitable for the gopher tortoise seem to be delimited by the latitudes where current climatic conditions result in a low temperature range that does not go below that tolerated by the gopher tortoise in its burrow and that provides suitable temperatures for success in nesting habitat

4) have now or in the past had tortoises present and thus have the characteristics necessary for minimal if not optimal survival.

Other components of habitat that may impact the suitability of the habitat for long term survival of gopher tortoises utilizing that habitat include:

1) the presence of physical features (general topography, human infrastructure, water or wind erosion features) that either favor or put the gopher tortoise at a disadvantage in situations where it must compete successfully with other herbivores and where it must successfully avoid predators

2) the presence of introduced, exotic, or domesticated plants that can successfully compete with and over time limit the available forage species within the habitat

3) the presence of exotic, pet, domesticated or feral animal species that compete with or prey upon, or introduce disease or parasites to one or more of the developmental stages (egg to adult) of the gopher tortoise and over time limit the size and structure of the tortoise population

4) the presence of pollutants, toxic substances, or physical dangers like broken glass, tires, fibrous materials, metal shards, etc. in the soils of the habitat and thus creating impact on the various developmental stages of the tortoise from egg to adult

5) the presence of periodic, routine or catastrophic floods of fresh, brackish or salt water either from natural or human made causes that inundate the burrows and/or forage areas of the tortoises for extended periods of time

6) the presence of human activities like vehicles, lawn mowing, plowing, mining, ditching, building, seeding, spraying, periodic sports activities, horseback riding, off-road bicycles, motor cross or in any other ways altering the existing habitat parameters to which the tortoise has become accustomed

The variations in actual plant species composition of the major habitats available to gopher tortoises across its range are great. The presence of specific species changes with season, stage of habitat development, time of last burn, time of last catastrophic event (like hurricanes or floods), current precipitation regime (drought), levels of herbivory, human land use, presence of invasive seed source, ability of seed bank to survive and re-establish, and many other factors. For detailed habitat descriptions for all areas of the gopher tortoise range refer to more extensive botanical ecosystem works like Myers and Ewel (1990). Here we want to focus on the habitats available that have suitable potential for current and future gopher tortoise habitat (managed). It is our contention that within the next 50 years there will be no gopher tortoise populations existing outside of managed habitats throughout its range. With our current level of development, few lands outside of public or privately managed ownership will have sustainable gopher tortoise populations (see chapter 2) even in the next 20 years. **For all intents and purposes, the concept of natural habitat is thus irrelevant and rather we need to concentrate on which habitats are available to support gopher tortoise populations and which habitats can be managed and / or "restored" to a level that can support gopher tortoise populations in perpetuity. With this in mind, we need to look at the primary factors that shape and maintain the habitats that have in the past and do currently support populations of gopher tortoises; moderate to subtropical temperatures, adequate precipitation to support forage species, low ground water levels and well to moderately-drained sandy soils to support burrowing, seasonal or no standing surface**

water and a regime that includes fire or other factors that perpetuate herbaceous forage and maintain an open to somewhat open canopy. The first thing pointed out to us when we discussed these factors with various groups of land managers was that the regional temperatures of their potential gopher tortoise habitats were not under their control and that climatic changes were not a factor they could take into account. We disagree, particularly if you are planning a preserve with an appropriate time-frame of no less than 100 years and preferably in perpetuity. The effects of regional land physiographic characteristics, surface water, and presence of heat-absorbing surfaces like roadways and concrete buildings and parking lots have been shown to produce measurable changes in microclimate and regional temperatures (Fernald et al. 1996) as well as in ground water levels and surface water. The consideration of the present plans available in regional planning and DOT offices concerning the projections for growth, development and roadway building is highly pertinent to the potential for maintaining suitable gopher tortoise habitat, particularly on lands that occupy positions subject to temperature extremes, generally at the limits of the gopher tortoise's range. Changes in temperature affect plant development rates and times of flowering and fruiting, species composition of the habitats, and quantity of tortoise forage. In addition to these more local and measurable human impacts on temperature, the long term impacts of global warming or potential for major climate change cannot be ignored in the selection of habitats to be managed for gopher tortoises and in the creation of long-term plans for those habitats (Crumpacker et al. 2001). These projections for rising sea level have implications for gopher tortoise habitat in the coastal strands and coastal lowland habitats. The effects of catastrophic hurricanes on habitat cannot be ignored and their impacts for gopher tortoise habitat can be both positive and negative as indicated in the 2001 work by Provencher et al. (*Restoration Fire and hurricanes in Longleaf Pine Sandhills*) which reminds us of the extensive opening of canopy provided over geologic time by hurricanes generally over the range of the gopher tortoise in the S.E. United States. The projections for human land use and development in regions where habitats are being maintained or managed for gopher tortoises are extremely pertinent to the water table and surface water conditions. Regional dewatering or lowering of the ground water table is a serious problem near high population centers and surface water flooding can also be a by-product of increased development. Regional water management agencies (in Florida the Water Management Districts) have had a hand in controlling surface water run-off with the goal of preventing flooding of human used lands and have worked to maintain water recharge systems to the aquifers for future human use. These actions can be positive for the maintenance of gopher tortoise habitats but in some instances they may have unforeseen long term negative affects on plant species composition, shifting the moisture regimes just enough at the right times to favor certain plant species over others. One example of gopher tortoise habitat with the long-view is the work done by Stewart et al. (1993) which looked at the dispersal of gopher tortoises within a 37 hectare preserve. The records of historic land use of the area dating back to 1936 gave the picture of the habitat as being treed with saw palmettos and then being cleared. The historic physiography of the area indicated wet prairie interspersed with dry prairie and islands of higher sand pine scrub. The habitat conditions current at the time of their study, following land clearing in the late 1930s and 1940s, were of primarily dry prairie with scrub islands surrounded by wet prairie. This study reiterates the work of Campbell and Christman (1982) that gopher tortoises use physical characteristics of their habitat rather than plant associations to select locations for burrows (Table 3.3). The results of Stewart et al. (1993) also point out how the "bigger geologic picture" plays a role in gopher tortoise habitat – as their study found that "the highest densities (of gopher tortoises) occurred in historic wet prairie associations". As climatic changes and changes in ground water conditions due to human land use alter the existing habitats, we must take a long view of what will constitute good gopher tortoise habitat, not just today but also in 50 years and 100 years and so on.

This series of photos (Plates 3.1 to 3.11) provide just a small selection of gopher tortoise habitats that can be found in the S.E. United States today. Their designations can vary according to which system of naming habitats you choose to use but we have used the names from Table 3.2 that primarily follow those of FDOT in FLUCCS (1985) and Myers and Ewel (1990).

Table 3.3: Habitat and Burrow Site Selection
The specific habitat and its plant species composition has been repeatedly found to have less influence on the selection of **burrow sites** by gopher tortoises than the physical characteristics of the habitat.

Characteristic	Selected	Not Selected
Depth of sandy soils above ground water table or impermeable clay or rock layer	Soils deep or extending no less than at least .5 m below surface	Little or no sandy soils with rock or water table at or near surface
Well-drained nature of soils	Rapid to moderate percolation rate	Slow percolation rate or saturated soils
Location of ground water table	Deep or no closer than .5m from surface	At or near surface
Seasonal patterns of surface water flow and length of inundation	Areas inundated rarely, infrequently or never	Areas inundated continually or periodically on a regular basis
Density of ground cover – without respect to species	Herbaceous ground cover very dense to moderately dense (35% to 80%)	Barren ground to sparse (less than 35%) coverage of herbaceous species
Density of shrub cover – without respect to species	Low density of shrubs or widely spaced “islands of shrubs”	High density of shrubs or continuous stands or shrubs
Density of tree cover – without respect to species	Low density of tree cover 0-60%	60-80% or greater canopy cover
Moisture level of soil at level of burrow end chamber	Moderate to saturated creating high relative humidity in end chamber	Very dry to dry with low relative humidity at end chamber

Campbell and Christman 1982, Stewart et al. 1993, Ashton and Ashton 2004

Gopher Tortoise Habitat and Forage Species

Gopher tortoises are most often found burrowing in the well-drained, sandy soils of xeric (dry) habitats, both inland and coastal but their feeding strategies are not limited to the flora of these habitats. Tortoises will feed along species rich ecotones (habitat edges) and will enter mesic habitats and even hydric habitats to feed under the proper conditions, such as drought. Tortoises are obligate herbivores (plant eaters) and the bulk of their food is in the form of grasses, herbaceous plants and seasonally, fallen flowers, fruits and leaves from trees, shrubs and vines. Gopher tortoises also are known to select and/or ingest incidentally bone, carrion, small animals, insects and other invertebrates, small stones, excrement and charcoal (Garner and Landers 1981, Auffenberg and Franz 1982, Wright 1982, MacDonald 1986, MacDonald and Mushinsky 1988, Birkhead 2001, Ashton and Ashton 2004). The nutrient requirements of gopher tortoises are not well known but are believed to be similar to ruminants, rabbits, horses and iquanas (Allen and Oftedal 2002). They forage (graze) on plant materials like cows, rabbits and deer. A diverse diet is necessary for the overall health of the gopher tortoise and any management actions, such as fencing them in a small area lacking biodiversity, can negatively impact the long term sustainability of the population. Of greatest significance in maintaining open canopy conditions for gopher tortoise forage species are fire and other methods of reducing tree species dominance and encouraging herbaceous species and grasses in the ground cover such as grazing or mowing. The recognition of the importance of fire to the continuance of gopher tortoise habitats in the southeast was slow in coming with the national push to "Stop Forest Fires" but by the late 1970s Fire Ecology was a recognized management tool in the southeastern United States. In the 1980s Walter Auffenberg and Larry Landers were just two of many herpetological researchers working with gopher tortoise habitat to emphasize the role of fire in maintaining appropriate plant community characteristics for the gopher tortoise. Fires that are too frequent present new problems by limiting the carbohydrate reserves of resprouting woody species and altering the species composition of the community (Axelrod and Irving 1978). The flowering cycles of many grasses are strongly dependent on the time and frequency of burns (Henderson et al. 1983, Abrahamson 1984). Experiments by Smith and Young (1959) validated earlier reports that spring burning of pasture grasses like little bluestem (*Andropogon scoparius*) and indiangrass (*Sorghastrum nutans*) could increase crude protein and calcium in grasses over non-burned pastures.

Fire has now been accepted as a viable management tool in rural areas but with increasing urbanization in the southeastern United States, fire is being excluded from use on smaller isolated habitats. Herbicides are often used to replace the actions of fire for the removal of hardwoods but the long term effects of these chemicals on herbivores and in particular on the gopher tortoise have not been adequately studied. A review of herbicide literature and studies on forest lands (Litt et al. 2001) reiterates the point that few studies have addressed the effects of herbicides on ground layer vegetation in xeric sandhills and flatwood ecosystems with the concensus being that more studies are desperately needed before recommending that herbicides be widely used as a substitute for burning in urban areas. Mechanical clearing and grazing by cattle can also be used to maintain open canopy and encourage forage species. In a long term study Auffenberg and Franz (1982) reported a decline of 1.5 tortoises per hectare every five years on a site left unburned for 16 years. Breininger et al. 1988 report that tortoise densities were highest in recently burned areas (0-3 years) while Auffenberg and Iverson (1979) correlated herbaceous cover in xeric habitats with gopher tortoise density.

Tortoise forage habitats require large open areas where plants can receive a lot of sunlight. Tortoises do benefit from access to forested areas where trees produce fruits or edible foliage. Tortoises will enter farm fields, gardens, flower beds and private lawns to take advantage of the tasty forage available. They also feed along ecotones (edges) where the open habitats meet marshes, swamps, forests or roadsides. In times of drought, the gradually exposed bottoms of lakes, ponds, and marshes may be the best available sources of still growing forage vegetation. Maintaining access to these areas can be vital for sustaining healthy tortoise populations in times of severe drought. The data collector must not let pre-existing bias about what or where tortoises eat affect their ability to observe and recognize tortoise foraging signs.

Box 3.3

Foraging Behavior and Forage Species

Gopher tortoises may eat a lot of one plant like grass (Bulk Foraging) near their burrow or they may walk a long way to choose (Selective Foraging) a particular part (like a flower, fruit or leaf) of a certain plant. Garner and Landers (1981) discuss changing types of forage behavior and suggest that some changes may be tied to critical physiological stresses like egg laying or recovery from hibernation. Four basic types of foraging have been identified (Table 3.4). Tortoises, particularly hatchlings, juveniles and subadults have enemies like snakes, foxes, coyotes, dogs, cats and hawks so foraging behaviors must take into account their vulnerability to predation. This may be why many of the juveniles we have followed or observed foraging stayed under cover of low fallen branches, shrubs and vines like greenbriar (*Smilax*) and blackberry (*Rubus*).

Studying Forage: What methods are used to learn more about **when, where, how and what** tortoises of all developmental stages choose to eat? Some studies have been done using the most basic methods like direct observation while others have depended upon more complex video taping, radio tracking, and computer data chips. The authors have many hundreds of hours of video taping and actual observation of tortoise foraging. Behavioral studies of foraging require lots of time and patience as well as an excellent knowledge of plant species. The quantitative methods for determining relative amount of forage consumed may include bite counts (watching how many bites are taken of each species and noting the specific parts being consumed or rejected), fecal analysis in conjunction with bite counts where what went in and what came out are looked at, and quadrat studies of what is present and how much (biomass) and what is absent after a set amount of tortoise feeding. Some studies have used total clipping of vegetation and others use a measurement like “cover class”. Video taping allows a careful study of each action taken by the tortoise in selection of food items. For example: Did the tortoise appear to “see” the plant from a distance and go to it or did it wander about sniffing and tasting until it found a suitable forage plant? How many times did the tortoise sniff the plant before tasting? Did the tortoise put the leaves down onto the ground and sniff or did it barely touch the leaves? How big a bite was taken? Was the bite repeated? If so how many times? How much did the tortoise consume at one time? Did it eat on the run or did it settle down and graze casually? How many of the same species were rejected before the tortoise chose to eat? Did the tortoise remove any plants from its mouth or reject any plant parts after smelling or tasting? In addition to the answers to these questions which can be obtained through careful observations, a researcher may use basic or sophisticated methods to analyze tortoise feces. An early fecal analysis study by the authors was the first job that Pat did for Ray. Fecal analysis often tells more about what was not digested rather than about what was ingested. In combination with observations of intake, fecal studies can be very meaningful. Microhistological and fragment analysis of feces is more accurate for even small plant parts that survive the digestive process.

Table 3.4: Types of Foraging Activities

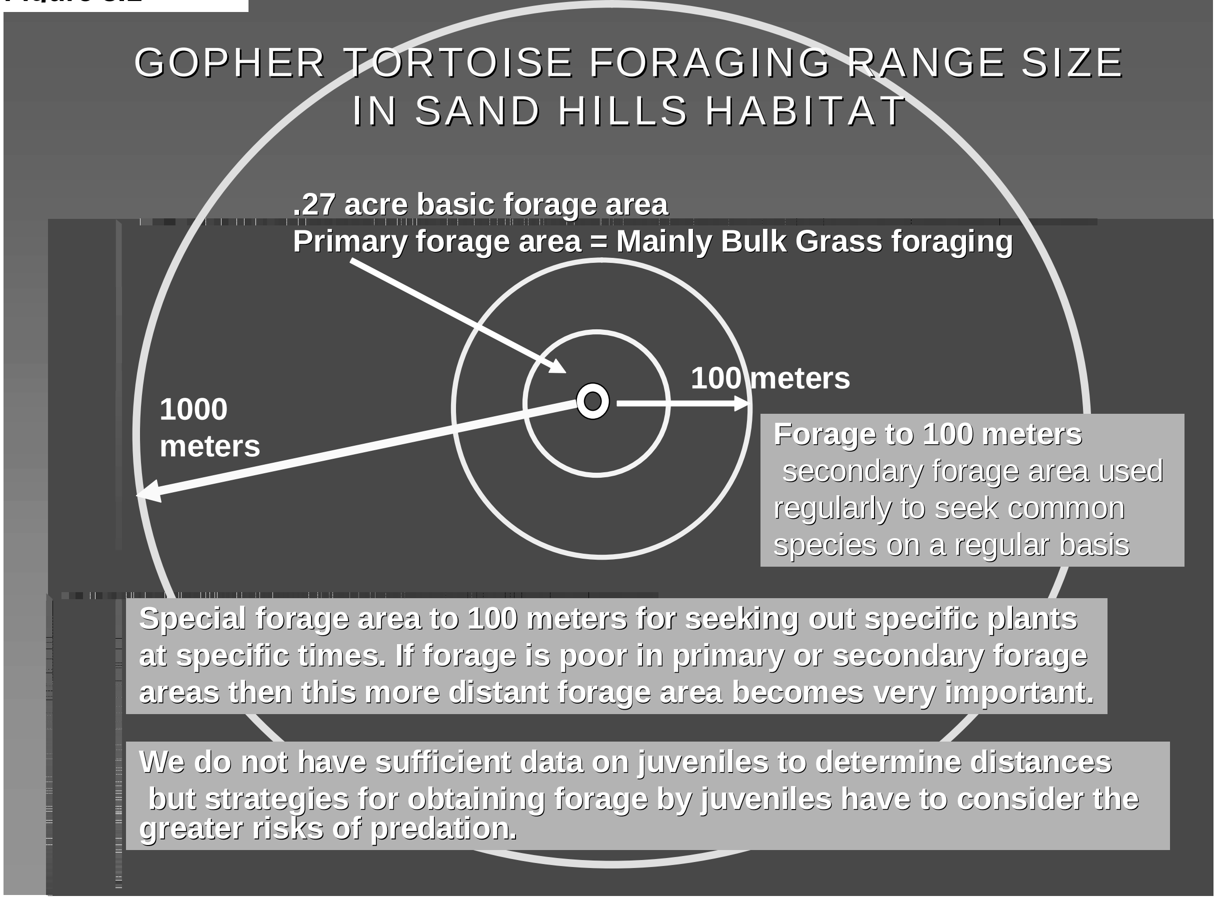
	FORAGING ACTIVITY	MANAGEMENT
BULK FORAGING **Primarily Grass foraging**	Grass probably makes up 70-80% of total intake by volume and feeding on grasses takes up about 30% of the total time spent on forage. Grass foraging is seasonal – grasses are best when actively growing. Winter forage is needed in southern regions.	**Grass management is the top priority in maintaining healthy long term forage. Biomass, diversity and nutrient content are important factors to monitor.**
SEASONAL SELECTIVE FORAGING **More Broadleaf Foraging**	Various parts of forage species are selected seasonally and according to life cycle (flowering or fruiting). Foraging of this type takes up about 40% of the time spent on foraging and represents 10-20% of intake. Broad leafed grasses and herbaceous species make up the bulk of this foraging (which can include shoots, stems, leaves, fruits and even roots).	**Maintaining diversity, nutrient content and sufficient biomass of seasonal forage is the second most important priority for management of a preserve for tortoise forage.**
PERIODICALLY AVAILABLE RESOURCE FORAGING	Tortoises will travel more than 2000 meters to forage on specific flowers, berries, foliage, fruit, planted garden species and deer food plots. Takes 15-25% of the foraging time and represents about 10% of total intake.	**Maintaining diversity, nutrient content, and biomass as well as accessible paths to periodic forage resources - like fruiting trees or shrubs or wetland edges is an important goal.**
HIGHLY SELECTIVE FORAGING	Tortoises will seek out specific plants and specific parts to eat. They use smell extensively and will pass over many plants of the same species until they find what they are seeking. Plants can be within the "home range" or well beyond it. Represents less than 10% of intake and probably less than 10% of foraging time**.**	**Maintaining diversity, nutrient content, and biomass of more distant selected species and accessible paths to these forage resources selected and utilized on occasion as needed is also an important management goal.**

As we have observed feeding in all age groups of tortoise we have found the behavior of wild individuals to vary greatly. In some habitats and in some seasons, we followed and observed feeding for extended periods without great response from the tortoises. In pine flatwoods during October and November we found tortoises actively searching among fallen pine needles for fallen grape leaves, remnant fruits, and various herbaceous species including poison ivy. During these feeding episodes, the tortoises took in mouthfuls of pine needles in the process of acquiring various other food items. They did not make any effort to remove the pine needles from their mouths but the feces we collected and analyzed showed the pine needles passed virtually undigested while the grape and poison ivy leaves and fruits taken in were largely digested. Plant cell walls are not digestible by vertebrates without the help of cellulolytic microflora. Studies have shown that like many herbivores, gopher tortoises maintain a microflora in their digestive tract to breakdown the cell wall (cellulose, lignin) parts of their diet, making more nutrients and energy available to the tortoise (Bjorndal, 1987). We also followed tortoises in open pastures with grazing cattle during mid-summer temperatures and found them also to be moderately tolerant of being observed and photographed as they spent considerable time feeding on grasses and then traveled over 1000 meters to select specific herbaceous species. The tortoises in sandhills that we followed in early spring were the least tolerant to being observed and rather than continuing to eat, they headed rapidly for the nearest burrow. Adult tortoises in remnant habitats in neighborhoods were also surprisingly tolerant of being observed while foraging, of course if they were not tolerant they might not find enough time suitable for foraging with so much on-going normal human activity. On Ashton Biological Preserve we have wild tortoises with regular feeding trails throughout the sandhills habitat that are tolerant of being watched, including one large female that regularly leaves feces samples on our front cement porch, after she feeds on our flower beds as well as on her favorite patches of *Richardia* (Mexican Clover) and *Diodia* (Poor Joe).

Tortoises can get too hot (43.9 degrees Celsius is the survival limit) or too cold and foraging behavior is generally secondary to thermoregulatory behavior. Tortoises change the time of day and the length of time they come out of their burrow to forage in response to temperature and other perceived dangers. Unless you know when and where to look for a tortoise feeding you might never see anything but their tracks or the grass or leaves bitten off as evidence of their foraging. They generally forage for 20 minutes to 2 hours at a time. Tortoises forage at different times in different seasons and in different parts of their range. They begin to forage when the temperature is warm enough but not too hot. In the hottest months they may come out in early morning, at mid-day and/or later in the evening. We have observed tortoises feeding from just before sunset to after dark in the summer and they have also been found out wandering in pre-dawn hours during the hottest months. In cool months they may only come out during the heat of mid-day. When foraging in very hot weather they have been observed retreating into the shade to cool down and then re-emerging to continue feeding or searching for forage. Along the coast, gopher tortoises have been observed walking into the water, remaining for a period of time and re-emerging and then moving back to the vegetation edge to forage. This behavior of walking into water during the heat of the day and re-emerging to continue foraging has also been observed at pond and lake edges. It is assumed that they are using the water as a means of temperature reduction. In some regions, tortoises are known to stay in their burrow for an extended time ranging from several days to weeks during very cold, very hot or very dry periods. Tortoises have been found to gorge themselves on fruits like palmetto berries or fill their guts with fallen foliage just prior to their burrow "retreats".

Tortoises have been documented traveling long distances (to 3.3 km or 2 miles) from their usual home range to feed on seasonal vegetation (flowers, fruits, seeds). Auffenberg and Iverson (1979) found that home range size for gopher tortoises increased as the percent ground cover of herbaceous plants decreased; an indication that tortoises have to move farther to find food in areas with fewer herbaceous plants. Joan (Diemer) Berish (1992) found a dispersing subadult moved 0.74 km (0.44 miles). Data from Ashton Biological Preserve recaptures of adult tortoises have shown movements of 3.3 km (2 miles) from the burrow to a feeding area with legumes. A gopher tortoise's home range is generally defined (McRae 1980) as including 2 primary components: 1) the daily activity area immediately around the burrow where they regularly feed and carry out thermoregulatory and other activities, and 2) the larger annual activity range which includes the long distance treks to obtain tasty seasonal foods and/or males long distance visits to female burrows for mating purposes (Figure 3.1).

Figure 3.1



On a daily basis, tortoises usually engage in feeding behaviors in the immediate region of their burrow and/or pod. In pastures or areas where burrows are located within dense grasses, the tortoises may actually create a visible “clipped or farmed” area around their burrow where they graze regularly (Plate 3.12). This grazed grass will actually produce more proteins as it re-grows the leafy material it lost to grazing. Thus the tortoise gains forage with more protein than the surrounding grasses which as they age put their energy towards reproductive structures and contain fewer proteins. Many botanical studies confirm that different parts of plants produce different chemicals (some aromatic and discernable by smell) at different times of day, in different seasons or under different conditions such as when injured. Tortoises have been observed sniffing and actually crushing the plant part into the ground at the same time- perhaps releasing aromatic compounds as the cells are ruptured that the tortoise can detect by smell.

The question we still cannot answer is – “What is the relationship between the selection of a plant part at a particular time and the nutritional needs of the tortoise?”. Little work on gopher tortoise nutritional details has been done in comparison to that available on the Desert Tortoises. Some work has been done in pure botanical physiology that gives us clues to the life (phenological) stages and chemical processes of some of the forage species. A lot of work has been done on species which are of interest for livestock forage and we have that for comparison as well. All herbivorous animal species feeding in the diverse habitats of the southeastern United States, containing native and introduced plant species must contend with the need to obtain required nutrients from the plant material while also not utilizing too much energy or losing too much water or gaining too much of various toxic components. Plant toxins common in the plant species of gopher tortoise habitats include tannins, phytates, oxalates, alkaloids, terpenoids and excesses of minerals such as calcium, sodium or potassium (Table 3.5). In spite of the presence of many chemicals of varying amounts and in different forms, gopher tortoises appear to be able to detect and select the appropriate parts to ingest at the appropriate times to prevent harmful effects. It is important to remember that much of our information on these plants and their chemical effects come from research on livestock and mammals rather than on gopher tortoises directly. Little information is available on toxicity of particular plant species to tortoises and many observers, including the authors have witnessed tortoises being highly selective in plant part and species choices. Tortoises are frequently observed feeding on species that are toxic to humans and many mammals, and those individual tortoises have been observed or recaptured days to years later with no evidence of having been harmed (Table 3.6). Of a greater problem to tortoises than toxins is the delicate balance they need to maintain of minerals, particularly those obtained as salts like calcium, potassium and sodium. Calcium and sodium can be deposited in bone but abnormally severe excesses have caused death, particularly in juvenile tortoises (Ashton and Ashton personal experience). Tortoises have been observed feeding on excrement of other species and excrement is known to often concentrate high levels of minerals, some desireable and some not for the tortoise (Esque et al. 1991).

Table 3.5: Potentially Toxic Plant Components in Forage Species

Potential Toxin	Action
Tannins, tannic acid	Interferes with protein digestion and uptake; often found in oak acorns and leaves, and leaves of other hardwoods
Phytates	Interferes with mineral uptake
Oxylates, oxalic acid	Interferes with mineral uptake, crystallizes; found in *Oxalis spp.*
Alkaloids	Neurologic dysfunction; found in many different kinds of plants
Terpenoids	Neurologic dysfunction; found in many different kinds of plants
Excess Calcium	Critical imbalances, interferes with trace element (like zinc) uptake
Excess Potassium	Potassium (K) cannot be stored and if not excreted excess is toxic. Excreted in urine.
Excess Sodium	Interferes with critical mineral balance; excreted or stored

Kingsbury 1964
Hardin and Arena 1974
Bently 1976
Minnich 1979
Rosenthal and Janzen 1979
Nagy and Medica 1986
Westbrooks and Preacher 1986
Gibbons et al. 1990
Allen and Oftedal 1994
Oftedal et al. 1995
Peterson 1996
Everest et al. 1996
Nellis 1997
Van Devender 2002

Tortoises, like other turtles (sea turtles excepted) do not have salt excretion glands and must depend upon other means to control levels of potassium. Uric acid is produced during protein metabolism and is expelled as a semisolid urate precipitate formed with excess ions of ammonium, potassium and sodium (Minnich 1979). This method requires less water though small amounts of urea are also produced when dehydration or fasting requires it to help offset the osmotic tendency to pull more water into the bladder. Studies by Oftedal et al. (1994) suggest that increased levels of potassium intake can result in loss of normally retained nitrogen (needed for growth), particularly in times of drought. All of these factors bring into question, what chemicals the tortoises are able to detect and on what basis tortoises are selecting or rejecting certain food items. Because food items do not contain just one nutrient or mineral but are rather a chemical cocktail including substances needed as well as chemicals that may be in excess, researchers have created various trials in attempts to determine how selections are made by tortoises.

Table 3.6: Tortoise Forage Species and Toxicity
Toxicity to tortoises is untested and largely unknown or speculative; this table refers to toxicity to livestock or humans of plants also used as forage by tortoises.

Plant Family	Genus and species	Common name	Part(s) eaten by tortoises	Toxicity to livestock or humans
Anacardiaceae	Schinus terebinthifolius	Brazilian pepper	Leaves, berries	Produces allelopathic chemicals; fruits contain phenol cardanol and terpenes - phellandrene
Anacardiaceae	Toxicodendron radicans	Poison ivy	Leaves	Urushiol converted to quinine which binds to proteins in the animal skin
Araceae	Epipremnum aureum	Pothos	Leaves	Calcium oxalate needles
Apocynaceae	Catharanthus roseus	Periwinkle	Leaves, flowers	Alkaloids and glycosides
Commelinaceae	Tradescantia pallida Tradescantia spathacea	Purple Queen Oyster lily	Leaves Leaves	Oxalate Crystals Irritating sap
Euphorbiaceae	Euphorbia cyathophora	Wild poinsettia	Leaves, Sepals, Flowers	Irritant latex with proteolytic enzymes
Euphorbiaceae	Phyllanthus spp.	Phyllanthus	Leaves, stem, flowers, fruits	Leaves have Alkaloids and dhurrin -cyanogenic glycoside, carboxylic acid; phyllanthin in the bark
Leguminosae / Fabaceae	Crotalaria spectabilis	Crolalaria / rattle box	Leaves, flowers	Pyrrolizidine alkaloid monocrotaline, and spectabiline
Leguminosae / Fabaceae	Erythrina corallodendrum E. herbaceae	Coral Bean Cherokee Bean	Leaves, flowers Leaves, flowers	Toxic curare-like alkaloids
Leguminosae / Fabaceae	Melilotus spp.	Sweet clover	Leaves, flowers, fruits	Mold in dried hay can convert coumarin into dicoumarin resulting in hemorrhage
Phytolaccaceae	Phytolacca americana	Pokeweed	Leaves, fruit	Alkaloid phytolaccin
Poaceae	Sorghum bicolor Sorghum halepense	Sudan grass Johnson grass	Leaves, seeds Leaves, seeds	Cyanogenic glycoside dhurrin, releases hydrocyanic acid upon consumption; also nitrate poisoning
Solanaceae	Solanum americanum	Black nightshade	Leaves, fruits	Glycoalkaloids including solanine
Verbenaceae	Lantana camara	Lantana	Leaves, flowers, fruits	Belladonna alkaloids; lantadene and pentacycllic triterpenes
Dennstardtiaceae	Pteridium aquilinum	Bracken fern	Young shoots, leaves	Enzyme Thiaminase

Kingsbury 1964
Hardin and Arena 1974
Bently 1976
Minnich 1979
Rosenthal and Janzen 1979
Nagy and Medica 1986
Westbrooks and Preacher 1986
Gibbons et al. 1990
Allen and Oftedal 1994
Oftedal et al. 1995
Peterson 1996
Everest et al. 1996
Nellis 1997
Van Devender 2002

Lora Smith, Joan (Diemer) Berish, L. MacDonald, Henry Mushinsky, Earl McCoy and the authors among others have various experiences observing selective feeding and presenting plant materials to gopher tortoises. It is clear that selection of specific species and specific parts of plants is made at times using both the sense of smell and sight. Parts of species that are selected and consumed in one situation have been noted to be rejected at other times. Cut parts of plants that are normally foraged in the wild have been rejected, perhaps in part due to the production of antiherbivory chemicals. Non-food items of the correct color (bright magenta or bright yellow) are often tasted even when smell and or texture do not confirm edibility. A piece of 2 inch wide bright yellow plastic “caution” tape was personally witnessed by one author in the process of being excreted by a tortoise. Non food items of an inappropriate color smeared with edible material from a preferred food like the pawpaw (Asimina spp.) were also tasted apparently based on smell. Much more work on forage selection needs to be done specific to the gopher tortoise. Work by Oftedal and others on the desert tortoise, particularly with regard to the potassium excretion potential index (PEP) of particular plant species is useful but there are notable differences in the desert conditions and species adaptations. A positive PEP index indicates there are more water and nitrogen present in the food item than needed for the excretion of the excess potassium. A negative PEP index indicates there is not enough water and nitrogen in the food to excrete the potassium contained. Data from van Devender and Schwalbe (2000) gives their calculated PEP for selected plants from desert habitats. While none of these species are commonly listed as gopher tortoise forage within its range, the genera are shared, though there is great variation of PEP as calculated within a species (based on stage and plant parts sampled) and over time based on environmental conditions. Research by van Devender (2002) indicates that desert tortoises have been shown to seek out high PEP plants in wet years, suggesting that PEP may have some predictive value for highly selective foraging behavior, but this index does not take into account possible other deterrents or attractants like toxic compounds or scarce minerals. Families and genera from which the gopher tortoise feeds regularly for which PEP was calculated for the desert tortoise are found in table 3.7. We still do not know what drives tortoise choice of food though the need for energy, nutrients, and chemicals necessary for various metabolic functions is always assumed to be the driving force. Animal nutritionists make the assumption that at the cellular level, all animals require much the same slate of nutrients (Allen and Oftedal 1994). They assume that nutrient needs are similar and that differences that do exist are a result of the differences in specific metabolic functions and in digestive anatomy and function. Tortoises are assumed to have the same basic needs as most vertebrate herbivores. The diet choices of herbivores are often guided by digestive capacity parameters including: intake, digestibility and time of passage through the digestive system (Sibley 1981). Studies of tortoise digestion suggest that a high fiber diet encourages high intake rates with a shortened transit time and that low quality diets were compensated for by increasing foraging time and by increasing intake. Since high fiber diets require a longer resident time of the digesta for breakdown Dean-Bradley et al. (1995) suggest that some fiber or selective particulates may be retained in the hindgut for further fermentation. We do know that any natural plant species eaten by humans usually will be eaten by tortoises.

Table 3.7: Selected Gopher Tortoise and Desert Tortoise Forage Species and PEP

Family and Genera	Gopher tortoise forage species	Desert tortoise forage species	PEP (g/kg DM) of Desert Tortoise species	Season when sample for PEP was taken
Brassicaceae Lepidium	L. virginicum	L. lasiocarpum	19.1	Early Spring
Cactaceae Opuntia	O. humifusa O. stricta	O. basilaris O. ramosissima	22.4 12.2	Late Spring Late Spring
Euphorbiaceae Euphorbia	E. exserta E. floridana E. inundata	E. albomarginata E. micromera	14.2 15.9	Spring Late Summer
Fabaceae Astralagus	A. obcordatus A. villosus	A. didymocarpus A. layneae	24.6 22.2	Early Spring Early Spring
Onagraceae Oenothera	O. biennis O. speciosa O. laciniata O. humifusa	O. deltoides	19.1	Early Spring
Plantaginaceae Plantago	P. aristata P. lanceolata P. major P. virginica	P. ovata P. patagonica	13.9 15.3	Late Winter Late Winter
Poaceae Aristida Sporobolis	A. stricta S. junceus	A. adscensionis S. flexuosus	13.6 5.7	Fall Fall

Adapted from Wunderlin 1998 van Devender 2002

Tortoises living near occupied areas will enter gardens, lawns or landscaped sections and consume a variety of plant parts, occasionally leaving real evidence of their feast. Tortoise choice of plant species in the wild shows great diversity, seasonality and specificity of selection of parts. A study in 1981 by Garner and Landers found that grasses and certain species of Cyperaceae (sedges) and Asteraceae (asters and sunflowers) were the primary food items selected in their study area in Georgia throughout the active season there (late Spring-early Fall) and they found legumes were extensively foraged as well. They also found that the use of wire grass (*Aristida*) was very seasonal, being highest in the early spring and late fall when other species were unavailable. The foraging on wiregrass dropped sharply when other species of broad leafed grasses and herbaceous species became available in late spring and summer. Mushinsky et al. (2003) indicates that in a study of juvenile foraging, *Aristida* was negatively selected (in comparison with its abundance on the site). That study also noted that juveniles minimized the time spent foraging; probably a response to the potential for predation and that time spent foraging was not directly correlational to the biomass of available forage. It is interesting that while this and other studies confirm the high selectivity of species exhibited by all age classes, Mushinsky, Stilson and McCoy's study did not find nitrogen content to be correlated with that selectivity, at least for juveniles. The role played by mineral and chemical content of plant species as an indicator of forage selection is still unclear. Critical periods for obtaining specific nutritional needs such as when females are producing eggs or when males are traveling extensively to find females and mate correspond to seasonal availability of forage production in different regions of the gopher tortoise range. In warmer, wetter areas of central to south Florida, tortoises have been found to feed almost year-round and the probability of two periods of reproduction rather than just one as in the northern areas has been suggested. Tortoises also forage selectively for species high in fats and complex carbohydrates prior to "hibernation" during periods of extreme cold or extreme drought. Recovery of tortoises from burrows during such periods as part of relocation activities has revealed the presence of palmetto (*Serenoa*) seeds, grape (*Vitis*) leaves, oak (*Quercus*) leaves, blueberry (*Vaccinium*) leaves, and pine (*Pinus*) needles in their feces. There are studies that have looked at seasonal feeding in various parts of the gopher tortoise's range and in general we see feeding strategies closely tied to the natural plant cycles. Food choices and frequency of feeding have definitely been affected in areas where presence of exotics, changing climatic conditions or presence of out-of-season plants due to agricultural or landscape maintenance have made forage available when it would not have been under normal circumstances.

Understanding Forage Plant Terminology

Woody vs. Herbaceous: Woody plants are those that usually produce a visible thick outer bark and have xylem tissues where lignin is deposited to produce "wood". Trees, shrubs, woody vines and some low ground covers are woody plants. Woody plant species can supply fallen leaves and fruits for tortoises, and some may provide tender shoots when seeds sprout. Herbaceous plant species are those that are non-woody and though their stems may be quite stout, they often are flexible without a woody support.

Perennials vs. Ephemerals (Annuals and Biennials): Perennial plants continue to grow as long as conditions are right. In adverse conditions they die back to the roots and then re-grow when the proper environmental conditions return. They can die back due to normal seasonal changes, drought, fire, extreme hot or cold temperatures, grazing or artificial clearing, or due to catastrophic events like floods or hurricanes. Annuals are plants that complete their entire life cycle in one season, usually in less than 1 year and then survive adverse conditions as seeds until the next growing season. Biennials usually mature in one season and reproduce and die the next growing season. Tortoises feed on species of all three types. Perennials are easier to manage than annuals and biennials. The seed source and/or bank for the ephemeral species needs to be protected in order to maintain those forage species within the habitat. A given genus may have some members that are perennial and some that are ephemeral.

Monocot Grasses vs. Dicot Herbs: The botanical terms monocot (monocotyledon) and dicot (dicotyledon) refer to the number of "seed leaves" or cotyledons that first emerge from the embryonic seed as it germinates. Other characteristics that separate monocots from dicots are the arrangement of vessels (xylem and phloem) in the stem and of veins in the leaves. In monocots the vessels are scattered throughout the stem tissue and the veins in the leaves are parallel. In dicots the xylem forms toward the inside of the stem and the phloem towards the outside creating a ring of vascular tissue with old dead xylem on the inside of the stem.

Grasses vs. Forbs: In range management terminology, grasses (annuals and perennials) are usually separated from other herbaceous plants and the term forb is used to describe the growth form of all nongrass herbs (and some low woody plants and vines) eaten by livestock. Many papers written on gopher tortoise foraging have also used this forbs classification when referencing tortoise forage.

Succulents vs. Nonsucculents: Plants with the ability to store water in the tissues of the stems (cacti and euphorbias) and/or leaves (agaves, yuccas, and portulacas) are considered to be succulents. Plants that are not adapted to store noticeable or excessive amounts of water are nonsucculents.

Box 3.4

Seasonal plant cycles or phases include:

1) A germination phase where seeds sprout and growth begins into a world of dangers for the new young plant. Many species pump their young embryonic tissues full of nasty tasting or irritating chemicals to discourage herbivory at this stage. Gopher tortoises have been observed specifically selecting very tiny *Ambrosia* (ragweed), *Eupatorium* (dogfennel), *Elephantopus* (Elephant's foot), *Gnapthalium* (rabbit tobacco), *Cnidoscolus* (treadsoftly), and *Oenothera* (evening primrose) that were emerging on the sandy areas around the burrow mouths. These young plants were consumed in their entirety, roots and all. The chemicals poured into the young tissues of these species were obviously acceptable or desirable to the gopher tortoise. Annuals and biennials go through this stage every year as new ephemeral plants germinate from last year's seed. Biennials in their second year and perennials sprout new tender growth from last years roots or stems. Tender stems and young leaves of grape vines (*Vitis*), poison ivy (*Toxicodendron*) and Greenbrier (*Smilax*) are sought out and eaten. Eating these shoots often forces the plant to continue to produce new shoots that are also available to be eaten.

2. A young growth stage where proteins are increasing in tissues as new plant growth is added. For most species the active and often rapid growing phase brings in a lot of minerals and nutrients from the soil and much effort is put into production of leaf and stem structures, particularly those involved in photosynthetic activities. Grazing can revitalize the forbs or herbaceous species' efforts at production of the lost leafy materials, increasing the production of proteins and carbohydrates again. Over grazed plants may produce antiherbivory compounds or may proceed to reproductive tissue development at a size considerably less than usual to ensure that they are able to reproduce. It is this growth phase or plant stage that provides most of the bulk of gopher tortoise forage. The grazing of the tortoise as mentioned can re-set the growth cycle of the grasses or herbaceous species. New growth is also encouraged by the fresh nutrient rich soils from the ground water table brought up by the tortoise from where its burrow ends and spread by wind and movements of the tortoise out over the forage plants near its burrow. This acts like a kind of fertilizer and can re-stimulate active growth as well as providing an open sandy area for new seeds to take root. In this seasonal growth phase woody species often use their increased structural strength not only to reach the sunlight but also to grow out of the reach of some herbivores, like tortoises. Their woody bark is also a protection against herbivory. Adult gopher tortoises have been observed literally walking over or pushing over woody-stemmed plants to reach tender new leaves (and later the flowers and fruits).

3. A maturing stage finds plant species putting their energies towards production of reproductive structures. The energy of the plant photosynthetic parts and from the plant's storage cells is now converted into the production of reproductive tissues – flowering. Tortoises have shown preference for some flowers, in particular red hibiscus and yellow dandelion flowers. They have been observed gorging on these. Tortoises have also been observed feeding on the sweet-smelling saw palmetto (*Serenoa repens*) flowers and the multitude of insects that are also present on the flowers. Many flowers are designed to attract pollinators and while the intent is to achieve fertilization of the eggs without loss of the physical flower and ovary, the presence of sweet and nourishing nectars may encourage consumption by tortoises. On the other hand, some flowers for obvious reasons at this stage in addition to producing nectar, also produce antiherbivory chemicals in the petals or sepals. Torotises have been observed specifically smelling and rejecting or even pushing certain flowers out of the mouth. In particular the flowers of certain Euphorbia species that are normally eaten, were rejected when the flowers first opened yet older flowers were consumed entirely.

4. A reproductive stage is where the flowering parts have produced the colors, shapes, nectar or fragrances necessary to result in successful fertilization and the seeds are being produced within their ripening fruits or shells. Fallen flower petals following fertilization are often snatched up by gopher tortoises, particularly those of *Hibiscus*. The reproductive parts themselves appear to produce antiherbivory chemicals at the time of fertilization. Tortoises have been observed specifically avoiding or knocking off the plant the ovaries of flowers that are apparently finished being fertilized and where the ovaries are in the process of ripening. This has occurred during selective foraging but during rapid bulk foraging, tortoises have been observed consuming all parts of the plant including the developing seed heads or ripening ovaries.

5. The ripe fruit or fully developed seed stage of most ephemeral species marks the end of its active photosynthesis and water and mineral up-take. At this stage tortoises have been seen eagerly eating all parts of the plant, particularly where the species' dispersal strategies can benefit from consumption by the tortoise. At this stage many plant species break carbohydrates down into sugars and other compounds attractive to potential seed dispersers. Tortoises have been observed eating leaves, stems and fruits (blueberries) of *Vaccinium myrsinites* and *V. darrowii* in an almost bulk feeding fashion. They consumed mouthfuls of plant material as an effective way of getting the most fruits without the tiny berries falling off into the soil. The later feces produced by these same tortoises were full of woody stems and undigested leaves and tiny blueberry seeds. Perennial plants and grasses also may slow or stop their production of chlorophyll and fresh leafy and stem materials at this stage. They may send carbohydrates and sugars to storage organs (tubers, roots, underground stems) and the photosynthetic organs (leaves and/or stems) may turn brown and fall off the plant. Some species become dormant for a period after this reproductive stage.

6. The Dormancy or Senescence stages represent the end of the life cycle of ephemeral species and a resting stage of perennial species. Tortoises have been observed feeding on brown, dried, senescent plant materials. Dried grasses including seed heads, and dried, fallen tree leaves often are consumed in late fall through early spring as they represent the bulk of the biomass available to tortoises, particularly in the northern parts of the range and in the drier or droughty areas. Succulents that retain their moisture in stems or leaves through the driest seasons may represent important food items while other species are dormant or senescent.

Gopher tortoises are structurally designed for foraging on items found both on the ground and to about 15-30 cm above the ground (depending upon the size of the tortoise), using their senses of sight and smell to locate and identify food items and then using their serrated, sharp beak-like mandibles and strong, flexible tongue to maneuver the food into their mouth and down the esophagus. Biting motions are evident with some food items before swallowing though many items are swallowed whole (Photo 3.13). Milk pea (*Galactia* spp. – Photo 3.14), a herbaceous trailing legume is often ripped from the ground, roots and all, with a lifting motion of the head and then pulled into the mouth slowly like spaghetti as the tortoise continues walking. Tortoises have also been observed clipping off parts of leaves or flowers of both woody and herbaceous species and then consuming these clipped-off parts from the ground.

Olfactory cues are known to be used during courtship, to identify and respond to pheremones produced by the cloaca and chin (mental) glands. *G. polyphemus* is known to use a scale on its forelimb to spread the scent of the chin gland during courtship. They have also been observed pushing leaves broken off from a plant into the ground and then lowering their nostrils and apparently “sniffing”, followed by either eating the leaf or moving on to other forage species. These points strongly support the concept that smell and/or taste senses are very strong and utilized to allow very discrete selection of plant parts and plants over the season. Non-flowering plants like ferns, lichens and mosses are also consumed by choice at varying times, both when they are green and also when they are dried. Gopher tortoises have been observed using a variety of strategies to obtain food items that are above their usual reach including simply walking over the main plant stem to push the flowers, leaves or fruits down to a level they can reach. Tortoises have been observed climbing into the middle of sturdy woody vegetation and/or propping and balancing on hind legs to reach fruits or leaves that were too high. Tortoises have been observed selectively clipping off flowers of Treadsoftly (*Cnidoscolus stimulosus)* allowing them to fall to the ground and then consuming the leaves and stem but not eating the flowers. On two separate days, a tortoise was observed traveling to a series of blue Porterweed (*Stachytarpheta jamaicensis*) shrubs which were not within sight of each other. At each plant the tortoise selectively ate from several stems the flowers and a few smaller leaves before moving on to find another plant. Species of plants that this tortoise had eaten with relish the day before were totally ignored as the tortoise passed them by to reach the Porterweed. Sniffing various plants and tasting parts of plants and then moving on was frequently observed foraging behavior. Tortoises are less discriminating and most “voracious” when they are BULK FORAGING – feeding on grasses and incidentally taking in fallen leaves, lichens, dried materials, fruits and seeds. Mouthful after mouthful is rapidly chomped with fewer to none of the incidents of sniffing or looking or tasting behaviors being exhibited.

Table 3.8: Factors that Affect Tortoise's Ability to Acquire Forage

Plant Biochemistry	Species Availability	Ability of Tortoise to Find the Resource
Changes By Growth Stage	Seasonality	Ability To Smell Or See The Plant On The Landscape
Changes Daily And Changes Seasonally	Weather Conditions (such as Drought)	Size Of The Plant Vs. Size Of Tortoise
Changes Due To Weather Conditions	Microclimate Of The Soils, Water Table, Shade/Sun	Relative Location To Burrow(S)
Changes With Health Of The Plant; Infections Cause Changes	Elimination Of Species Due To Herbivory Or Disease	Relative Abundance Of The Plant On The Landscape.
Changes In Various Parts Of The Plant	Time From Last Fire	Memory Of The Tortoise
Changes Caused By Herbivory	Botanical Time Table Within The Species	Biophysical Need Of The Tortoise - Stimulating Craving

Gopher tortoises have been stimulated into following or moving towards non-food objects colored bright buttercup yellow (common color for edible Asteraceae flowers) or bright crimson to maroon (common color for ripe *Opuntia* fruits). Smell and memory also appear to play an important role in foraging behavior. Tortoises have been observed traveling from 1,000 meters (.62 miles) to 3.2 km (2 miles) to feed on deer feeding plots or ripe orchard fruits on neighboring properties. The same tortoises have been recorded doing this repeatedly over several years (1997-2005), even when there was no logical explanation for how they would know a deer plot had been put in or that an orchard had ripe, fallen fruit. It is assumed that smell plays a role, but the prior locations of some of the tortoises before they were found at the feed plot or in the orchard had been up-wind and at an average distance of .4 km (.25 miles).

All of this information on feeding behavior has implications for management actions which are discussed further in Chapters 5 and 10. Factors that can impact decisions on habitat management relate to the distance tortoises travel to reach seasonal forage, the times of high seasonal availability of certain nutrients, and the relationship of density and quality of herbaceous cover to size of tortoise's home range and rate of growth and development. The importance of availability of high quality forage and the tortoise selectivity for high quality species has been suggested as a means of accelerating growth rate (and potential for survival) in chelonians (Okamoto 2002). Studies have documented the increase of mass by individuals having higher quality and diversity of forage available versus those living in habitats with forage of a lesser quality (Barboza 1995). Management decisions will require we understand and know how to manipulate factors important for healthy and efficient feeding by tortoises. For example, if sight and smell are important cues for tortoises to locate food resources then any interference would be detrimental to the health of the population being managed. While hard data is limited, we can speculate that strong overpowering odors coming into a preserve would have a detrimental affect on tortoises using their sense of smell to locate distant food resources. Management choices might include limiting the placement of facilities on or around the preserve that could generate repeated overpowering smells. Barriers that impair vision (like walls) are also likely to prevent movement of tortoises and both of these issues are pertinent to managing any potential barriers that could prevent tortoises from reaching potentially important seasonal food resources.

Diversity of Gopher Tortoise Forage

Tortoises have been noted as feeding on plant species from 83 plant families and 376 genera. Depending upon the area and on the expertise of the botanist doing the survey, gopher tortoises have been recorded as feeding or potentially feeding on 400-500 species within a general habitat and potentially some 1103 species over the entire range. Not all of these species are of equal importance in the gopher tortoise diet and not all of them are available to the same tortoises at one location. These numbers relate to the overall species utilization across the gopher tortoise's range and include exotic and naturalized and common pasture and agricultural species. The listing of forage species is always a work in progress as observations and studies continue. These figures do not include genera or species of mosses or fungi due to lack of available data. Tortoises have been widely reported as feeding on fungi and personal observations revealed tortoises eating in entirety a variety of mushrooms following rains. Work on gopher tortoise feeding by MacDonald and Mushinsky (1988) found that 50% or more of plants ingested and found in scats belonged to Asteraceae, Euphorbiaceae, Fabaceae, Fagaceae, Pinaceae and Poaceae. Forage observations revealed that 50% of species selected were from the Poaceae and Asteraceae. Studies that include direct observation often have similar results with some variation by season and specific habitat. In some areas the reliance on Asteraceae may be overshadowed by greater biomass availability of Amaranthaceae, Ericaceae, Onagraceae, or Polygonaceae species. Table 3.9 gives a list of 45 important plant families that contain members that are frequently foraged upon by gopher tortoises. Tortoises are opportunistic in their use of agricultural, garden, landscape, introduced and "weedy" species. Often these species are representatives of a family already commonly used as forage by gopher tortoises and most likely share identifiable characteristics with native species that are familiar to the tortoises. In times of stress or drought tortoises may feed on species not normally selected either because the plants are now more available (such as wetland plants that are more accessible as marshes or ponds dry up) or due to desperation because they are the only species available. These "marginal species" taken only in times of stress are not generally included in Table 3.9 or Table 3.10 because they do not represent typical tortoise forage that would be managed on a regular basis as part of tortoise habitat. This does not mean that wetlands are unimportant for inclusion in tortoise preserves or as part of long-term management plans.

Table 3.9: Some Important Tortoise Forage Families and Genera

(in alphabetical order, not necessarily in order of importance as forage)

Scientific Name of Family	Common Name of Family	Some Genera used as Forage*	Importance Level**
1. Acanthaceae	Acanthus	Ruellia, Dyschoriste, Elytraria, Stenandrium	BL
2. Agavaceae	Agave	Polianthes, Nolina, Yucca, Sansevieria	S
3. Amaranthaceae	Amaranth	Amaranthus, Iresine, Froelichia, Alternanthera, Blutaparon, Gomphrena	S
4. Anacardiaceae	Sumac	Schinus, Rhus, Mangifera, Toxicodendron	S
5. Annonaceae	Custard Apple	Asimina, Annona,	S
6. Apiaceae	Carrot	Apium, Daucus, Eryngium, Hydrocotyle, Centella, Ptilimnium	V
7. Arecaceae	Palm	Serenoa, Sabal	V
8. Asteraceae	Aster or Daisy	Ambrosia, Artemisia, Krigia, Lactuca, Hieracium, Helenium, Solidago, Bidens, Conyza, Aster, Gnaphalium, Liatris, Carphephorus, chrysopsis, Coreopsis, Cirsium, Eupatorium, Emilia, Erechtites, Elephantopus, Helianthus, Heterotheca, Hieracium, Hypochaeris	V
9. Brassicaceae	Mustard	Lepidium, Brassica, Raphanus, Descurainia, Capsella, Draba, Polanisia, Warea	S
10. Blechnaceae	Midsorus Fern	Belchnum, Woodwardia	V
11. Boraginaceae	Borage	Heliotropium, Lithospermum, Myosotis, Onosmodium,	BL
12. Buddlejaceae	Butterflybush	Polypremum	S
13. Cactaceae	Cactus	Opuntia, Cereus, Hylocereus	V
14. Chenopodiaceae	Goosefoot	Atriplex, Chenopodium, Salicornia, Salsola,	S
15. Chrysobalanaceae	Coco Plum	Chrysobalanus, Licania	S
16. Clusiaceae	Mangosteen	Hypericum	V
17. Commelinaceae	Spiderwort	Commelina, Cuthbertia, Murdannia, Tradescantia	S
18. Convolvulaceae	Morningglory	Cuscuta, Dichondra, Stylisma, Convolvulus, Ipomoea, Evolvulus	B
19. Cucurbitaceae	Gourd	Coccinia, Cucurbita, Melothria, Momordica	S
20. Cyperaceae	Sedge	Bulbostylis, Cyperus, Fimbristylis, Kyllinga, Rhynchospora, Scleria	V
21. Dennstaedtiaceae	Fern	Pteridium	V
22. Dioscoreaceae	Yam	Dioscorea	S
23. Ericaceae	Heath	Vaccinium, Gaylussacia	S
24. Euphorbiaceae	Spurge	Acalypha, Chamaesyce,	S

		Cnidoscolus, Croton, Euphorbia, Phyllanthus, Stillingia	
25. Fabaceae	Pea	Acacia, Aeschynomene, Amphicarpaea, Apios, Arachis, Astragalus, Baptisia, Canavalia, Cassia, Centrosema, Chamaecrista, Chapmannia, Clitoria, Crotalaria, Dalea, Desmodium, Galactia, Indigofera, Lespedeza, Lupinus, Macroptilium, Medicago, Melilotus, Mimosa, Phaseolus, Pisum, Pueraria, Rhynchosia, Senna, Stylosanthes, Tephrosia, Trifolium, Vicia, Vigna, Zornia	V
26. Fagaceae	Beech	Quercus	S
27. Malavaceae	Mallow	Abutilon, Alcea, Hibiscus, Malva, Modiola, Sida	S
28. Melastomataceae	Meadowbeauty	Rhexia	S
29. Moraceae	Mulberry	Morus	S
30. Onagraceae	Primrose	Gaura, Oenothera, Ludwigia	S
31. Oxalidaceae	Woodsorrel	Oxalis	S
32. Passifloraceae	Passionflower	Passiflora	S
33. Plantaginaceae	Plantain	Plantago	S
34. Poaceae	Grass	Amphicarpum, Andropogon, Axonopus, Bouteloua, Bromus, Cenchrus, Chloris, Cynodon, Dactylis, Digitaria, Dichanthelium, Echinochloa, Eragostis, Eremochloa, Eustachys, Muhlenbergia, Panicum, Paspalum, Poa, Schizachyrium, Setaria, Stenotaphrum, Sporobolus, Tridens	V
35. Polygonaceae	Buckwheat	Antigonon, Coccoloba, Eriogonum, Polygonella, Polygonum, Rumex	S
36. Portulacaceae	Purselane	Portulaca	V
37. Rosaceae	Rose	Agrimony, Amelanchier, Crataegus, Eriobotrya, Photinia, Potentilla, Prunus, Rubus	V
38. Rubiaceae	Madder	Diodia, Ernodea, Galium, Hedyotis, Richardia, Spermacoce	V
39. Scrophulariaceae	Figwort	Agalinis, Aureolaria, Buchnera, Gratiola, Linaria, Penstemon, Seymeria, Verbascum, Veronica	S
40. Smilacaceae	Smilax	Smilax	S
41. Solanaceae	Nightshade	Solanum, Lycopersicon, Petunia, Physalis,	S
42. Turneraceae	Turnera	Piriqueta	BL

43. Verbenaceae	Vervain	Stachytarpheta, Lantana, Lippia, Phyla, Stylodon, Verbena, Callicarpa	S
44. Violaceae	Violet	Viola	BL
45. Vitaceae	Grape	Ampleopsis, Cissus, Parthenocissus, Vitis	S

* if a family or genera is not listed it does not mean that it is never used as forage, it simply means it does not appear in the data we have of most important forage genera over most of the range.

** General Level is for the group (Family) as a whole and does not apply to specific species or locations: Very Important most of the year (V), Secondary or Seasonal Importance (S), Biomass low (BL) so available amount limits importance even though often specifically sought out and selected but this designation should still be considered as an important component of appropriate forage habitat.

In keeping with our idea that gopher tortoise habitat today is that habitat which can sustain the tortoise in perpetuity, the same rationale applies to forage species. Those species which are being consumed successfully by healthy tortoises in healthy populations should be considered suitable forage species whether or not they are native. Now, whether these species are a desirable addition to a habitat is another story. We have noted on many occasions tortoises leaving a preserve or more “natural habitat” to feed on lawns, in orchards or gardens, golf courses, or on landscaped or weedy roadsides and road islands. Often these feeding excursions would result in the tortoises bringing new seed back to the preserve (in feces), sometimes of invasive or undesirable species. Yet many of the species they were feeding upon provided important nutrients as well as considerable biomass in the form of seasonal fruits or expansive lawns. In a preserve is it worth the cost (in money and potential harm from herbicides) to remove all “non-native” species? This is a question that is destined to be debated but even that will be an “academic” exercise in many cases where the resources are simply not available to provide an end result of total eradication of all non-native (assuming we can really identify what constitutes native and non-native) species. In some habitats we may find that gopher tortoises, as well as other herbivores, may be feeding successfully on species which have become a “naturalized” part of the habitat. We need to focus on which species tortoises are eating and on which of these species are providing the needed nutritional requirements for the tortoise populations to remain healthy and reproduce successfully. In an effort to assist managers in identifying what species can be foraged upon by gopher tortoises we have searched the literature, asked many researchers and referred to our own field notes and data to produce this comprehensive list (Appendix 3.1) of the species that have been reported as forage species. The designations given for the importance level of a plant species as forage are very dependent upon the overall plant associations in a particular area and the general overall climate. In other words, a species present in the southern and northern parts of the range may have different importance levels for the specific area based on their abundance and seasonal growth in that location. Appendix 3.1 gives a general picture for the mid-part of the range corresponding mostly to central to north Florida, the Florida panhandle and southern Georgia. The more tropical to subtropical areas of south Florida and the coastal areas often have severe limitations and specialized species that may or may not be included in Appendix 3.1. Species that are in more stressed habitats or at the extent of their range may have a different importance level for such situations. The importance levels we have assigned for the examples in Appendix 3.1 are based on the following criteria:

VH = Very High level of usage and importance as forage. These are species that are very highly selected and foraged by gopher tortoises. Within the appropriate temperature ranges, in the proper soils and with the appropriate levels of moisture they produce sufficient biomass to be very important to the tortoise as a component of overall forage usually year round or in multiple seasons. Within a given plant association these species represent a very important component of the available forage.

H = High level of usage and importance as forage. These are species that like those in the VH level are highly selected and foraged by gopher tortoises. They may not be as abundant or as robust in a given plant association or habitat and that generally represents the distinction between very high and high important levels of usage as forage. These species are generally available year round or in more than one season though the seasonal production of the parts generally foraged may also limit their overall importance.

M = Moderate level of usage as forage. These are species that may be highly selected for or specifically sought out and foraged but only in one season or the plant may be of such limited biomass that the overall importance is not as high. This does not negate the importance of the plant in the overall association of forage species. Plants that are selected for even on an irregular basis may provide important micronutrients or chemicals which we are not yet able to identify.

L = Low level of usage as forage does not mean no usage. Low level forage species are important for forage; they just represent a lower level of importance in comparison to the other species. Usually low level forage is limited by having a very low level of biomass productivity or by being very seasonal in production of the parts that are eaten. Low level species are not unimportant! There are some species that get a low level rating for other reasons.

Plants like some of the introduced peas (Kudzu), yams (air potato) and morningglories (Ipomoea) that are heartily eaten by tortoises but that also tend to cover and ultimately reduce availability of other more important forage species are given an “L” rating in importance to the overall forage in some habitats. The ultimate affects of such species are detrimental to the overall forage and they should not be encouraged in managed tortoise habitats even though they may be utilized as important forage in old field habitats or other unmanaged natural areas. These invasive species can produce a large amount of biomass and are fairly nutritious but they cannot support tortoise populations for the long-term in absence of a diversity of grasses and other herbaceous species.