Habitat relations of juvenile gopher tortoises and a preliminary report of Upper Respiratory Tract Disease (URTD) in gopher tortoises

by

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GENERAL INTRODUCTION

The gopher tortoise, *Gopherus polyphemus*, is one of four extant species of North American tortoises. The other three are the Bolson tortoise, *G. flavomarginatus*, desert tortoise, *Xerobates agassizii*, and Texas tortoise, *X. berlandieri*. Originally these four closely related species were members of *Gopherus* but Bramble (1982) divided them into two genera, based on neck, leg, and ear osteology. The osteological differences are presumably related to burrowing which is most developed in the gopher and Bolson tortoise and least developed in desert and Texas tortoise (Ernst and Barbour 1989).

Gopher tortoises are found along the southeastern coastal plain from extreme southern South Carolina, west to southeastern Louisiana, and south through most of Florida (Auffenberg and Franz 1982, McCoy and Mushinsky 1992). Gopher tortoises are found in xeric to mesic habitats of scrub, shrub, and forest, and from coastal areas to inland uplands (Breininger et al. 1989, Burney et al. 1987, Diemer 1986, Garner and Landers 1981, Giovanetto and Morris 1988, Lohoefener 1981, McLaughlin 1990). Tortoises occur typically on well drained sandy soils (Bramble 1982, Iverson and Etchberger 1989, Kaczor and Hartnett 1990). These friable soils are important for burrowing (Bramble 1982).

Gopher tortoises are generalist herbivores that feed mainly on grasses (Bjorndal 1987, Garner and Landers 1981, Macdonald 1986, Macdonald and Mushinsky 1988). Also important in the diet are herbaceous annuals, legumes, and the fruits of many species, especially prickly pear, *Opuntia* spp. (Jones 1992, Macdonald and Mushinsky

1988). Young tortoises may feed incidentally on insects (Macdonald and Mushinsky 1988) and there are reports of gopher tortoises feeding on carrion (Anderson and Herrington 1992, Garner and Landers 1981). Succulents are important for osmotic balance (Macdonald and Mushinsky 1988) and tortoises will opportunistically drink when standing water is available (Ashton and Ashton 1991, Medica et al. 1980).

Gopher tortoises have four defined life stages: hatchlings, juveniles, subadults, and adults. Tortoises in their first year are hatchlings. At this stage tortoises are most vulnerable to predation (Wilson 1991). Juveniles are usually less than five years old and less than 130 mm carapace length (Diemer 1992b). At this stage the shell is compressible and the tortoises are still vulnerable to predators (Landers et al. 1982). Subadults have hardened shells, but are not sexually mature (Diemer 1992b). Subadults and adults have a reduced predation risk.

Gopher tortoises have evolved to exploit habitats of physiological extremes. Temperature in tortoise habitat often exceeds upper lethal limits. Hailman et al. (1991) cited reports of desert tortoises where an individual died in 10 min at an ambient temperature of 39.4°C, and captive desert tortoises in a cage with no shade died within a day. Douglass and Layne (1978) reported that two gopher tortoises died in a cage when exposed to direct sunlight, one dying within five hours.

Temperature has been reported as the overriding factor affecting tortoise activity (Adest et al. 1988, Douglass and Layne 1978, Marlow 1984, Rose 1983, Rose and Judd 1975, Rose and Judd 1982, Voigt and Johnson 1976). Gopher tortoises use their burrows as a primary means of thermoregulation and by using many burrows they can have extensive movements during the hottest part of the day (Douglass and Layne 1978). Juvenile gopher tortoises tend to be active during the hottest parts of the day (Wilson et al. In Press) and will use urination and salivation to avoid heat stress (Douglass and Layne 1978, Rose and Judd 1982).

Gopher tortoises also must endure temperatures below their physiological optimum and sometimes below their lower lethal limit (Landers and Speake 1980). Basking is important in raising body temperatures and constitutes most above-ground activity (Morafka 1982, Nagy and Medica 1986, Rose and Judd 1975, Wilson et al. In Press). Wilson et al. (In Press) found that 80% of juvenile gopher tortoise activity during the summer was basking. Basking usually occurs on the burrow mound where the tortoise has quick access to a retreat (Wilson et al. In Press).

Tortoises must maintain a positive energy and water balance throughout the year while avoiding lethal temperature extremes. Because of the seasonality of both food and water in these habitats tortoises must be flexible in allowing physiological changes (Horne and Findeisen 1977). Most water is obtained through food or metabolically (Nagy and Medica 1986). Gopher tortoises, however, will opportunistically drink when standing water is available (Ashton and Ashton 1991, Medica et al. 1980). Afternoon rain showers can increase gopher tortoise activity (personal observation). Ashton and Ashton (1991) observed gopher tortoises at the mouths of their burrows using their forelimbs to channel flowing water to their mouths during downpours. Medica et al. (1980) found that desert tortoises constructed shallow catchment basins that held water up to six hours after rainstorms.

The burrow of the gopher tortoise is probably as important for prevention of dehydration as it is for thermoregulation. Gopher tortoises regularly migrate to more mesic and less well drained soils for winter dormancy which coincides with the dry season (Breininger et al. 1989, McRae et al. 1981). Gopher tortoises have been observed remaining in flooded burrows for extended periods during the winter (Diemer 1992a).

Tortoises must also meet nutritional needs other than energy and water. During egg development females may suffer calcium deficiencies. Marlow and Tollestrup (1982) found female desert tortoises excavating through soil to the lime layer to 'mine' calcium. They suggest this behavior is at least as complicated as seen in many ungulates. I found coquina shells in the digestive tract of a female gopher tortoise when I radiographed her to determine clutch size. This female had five eggs and presumably the coquina shells were providing her with supplemental calcium.

Tortoises are inactive for a vast majority of their time. Adult and juvenile gopher tortoises spend about 90% of their time underground (Wilson et al. In Press). Seasonal activity of gopher tortoises is affected by a north south cline (Diemer 1986). In the northern portion of their range gopher tortoises hibernate during the winter months, usually from November through February (Landers et al. 1982, Means 1982). In the southern portion of their range they may be active during any month but tend to be dormant during the winter dry season (McLaughlin 1990). Tortoises may also become inactive during hot, dry months during the summer. Gopher tortoises do not aestivate but will remain in their burrows for extended periods during hot, dry months (Douglass and Layne 1978).

There is a difference in seasonal activity patterns of male and female gopher tortoises (McRae et al. 1981). During the breeding season (March-May) males are more likely to be active than females (Douglass and Layne 1978). Males also have an increase in activity during late summer and early fall when they make longer distance movements (Diemer 1992a, McRae et al. 1981). It is possible that breeding may also be occurring during this time. Iverson (1980) noted that captive gopher tortoises will mate into November, and Tomko (1972) found a pair of copulating desert tortoises in October. Male gopher tortoises also increase the number of burrows they use during this time (McRae et al. 1981). Another reason for this increase in activity among adult males is they may be familiarizing themselves with female locations for breeding after dormancy.

Throughout the year males tend to be more active than females, out earlier in the morning and later in the day (Douglass and Layne 1978). In the Bolson tortoise adult males become active sooner in the year than females and may remain active when females are not (Aguirre et al. 1984). Douglass and Layne (1978) found male gopher tortoises are more likely to be encountered any time of the year than females. Females are most active from May through June when they are searching for nest sites. Movements and burrow use also increase at this time (personal observation). Diemer (1992a) found females were more likely to be out basking during the winter months when males were seldom above ground.

Juveniles of all four species have not been well studied (Berry and Turner 1986). Juveniles are secretive and are active only to feed and disperse (Berry and Turner 1986, Douglass 1978). Wilson et al. (In Press) found the average monthly movements of juvenile gopher tortoises greatest in summer months. McRae et al. (1981) also noted a late summer peak in movements of immature gopher tortoises. Berry and Turner (1986) found that juvenile desert tortoises have significantly higher preferred body and mean cloacal temperatures than adults, and were also active at lower ambient temperatures. Similarly, juvenile gopher tortoises are more likely to emerge from their burrows than adults during January (Diemer 1992a). These findings suggest that juvenile tortoises can sustain activity over longer seasonal and daily periods.

Gopher tortoises are reported to have unimodal and diel activity patterns depending on the time of year (Douglass and Layne 1978, Marlow 1984, Morafka 1982, Rose and Judd 1975). The general trend among adults is to restrict their activity to afternoons when ambient temperatures are at a maximum during the cooler months of winter, spring, and fall. During hot summer months they shift to a diel pattern of activity in the morning and late afternoon. Wilson et al. (In Press), however, found juvenile gopher tortoises tend to be more active during both the morning and midafternoon hours in fall and winter. They also found juveniles more active in the midafternoon hours in spring, and more active in mid and late afternoon in the summer.

The study of gopher tortoise social organization is difficult because tortoises spend little time above ground and most of this activity is basking (Douglass and Layne 1978). Intraspecific relations have been observed but primarily during the breeding season between copulating adults. There is little or no documentation of subadult and juvenile interactions, and female-female aggression has not been reported. A further complication is the apparent widespread use of chemical communication (Auffenberg 1977). Tortoises have subdentary glands which produce pheromones (Auffenberg 1977, Rose 1970) that are used in reproduction and fighting. These pheromones may be important in species and sex recognition (Auffenberg 1977), and their effect on spacing of individuals in a colony is unknown.

Gopher tortoises live in more or less discrete colonies. In areas with low population densities these colonies may be loose associations of individuals that have little contact except in the breeding season. Gopher tortoises are not necessarily territorial, there is a high degree of home range overlap within a colony (Diemer 1992a). McRae et al. (1981) found that large males had home ranges near the middle of the colony in close proximity of the females. They speculated that smaller males would be subordinate and excluded from preferred burrows and mating. Subadult males never ventured into the dominant males' home ranges. Aguirre et al. (1984) found a similar structure among Bolson tortoises, among which a small percent of the males were responsible for most of reproduction.

It may be more useful to consider tortoise colonies as having a dominance structure, rather than territoriality (Aguirre et al. 1984, Burke 1989). For the most part, resource defense has not been shown, and while male-male aggression has been well documented (Rose and Judd 1982) its context has not. Hailman et al. (1991) described the fighting behavior of males and compiled other reports of fighting but did not speculate on the significance. Fighting in males occurs throughout the year but heightens during the breeding season when chin gland secretions are greatest (Douglass 1976). Rose (1970) found that male Texas tortoises in captivity attacked models painted with chin gland secretions of other males, while females ignored the models. Fighting, therefore, is a mechanism by which males maintain their dominance status within the colony, not resource defense. Aguirre et al. (1984) found that food resources can be depleted in the center of a colony.

The geographical position of juveniles within the colony has not been identified. Chin glands do not develop before maturity and this may aid in reducing adult aggression towards juveniles. Juveniles have smaller home ranges than adults and tend to use a single burrow they dig themselves (Wilson et al. In Press). This may make them functionally isolated from others though their home ranges overlap (McRae et al. 1981).

The gopher tortoise is an important cornerstone species; their burrows are used by many other reptiles, amphibians, birds, mammals, insects, spiders, and other invertebrates (Speake 1981). Gopher tortoises also greatly affect vegetation and help maintain their habitat (Kaczor and Hartnett 1990). By burrowing, gopher tortoises bring leached nutrients closer to the surface of the soil and their burrow mounds are important colonization sites for many herbaceous plants (Kaczor and Hartnett 1990). These animals, however, are declining throughout their range because of habitat loss, degradation, and human predation (Auffenberg and Franz 1982, Diemer 1986).

The longleaf pine and wiregrass (*Pinus palustris* and *Aristida stricta*), association of the southeastern coastal plain historically was the primary habitat of the gopher tortoise (Auffenberg and Franz 1982, Kaczor and Hartnett 1990). The open park-like stands of longleaf pine have been replaced by slash pine, *Pinus elliottii*, plantations for pulp wood. These areas do not support the grass and herbaceous growth important for food. In addition, root structure changes provide a barrier to burrowing (Campbell and Christman 1982). In other areas fire suppression has allowed a successional invasion of hardwoods and shrubs that further degrade tortoise habitat (Campbell and Christman 1982, Mushinsky 1985). Gopher tortoises have also suffered from development pressure because most gopher tortoises occur in Florida where dry upland sites are preferred for construction (Diemer 1986).

Concern for declining gopher tortoise populations on Sanibel Island, Florida, prompted the Sanibel-Captiva Conservation Foundation (SCCF) to help sponsor research in cooperation with the Ding Darling Foundation (DDF), the city of Sanibel, and Iowa State University (McLaughlin 1990). This study began in 1989 and provided baseline information on demographics, morphometrics, burrow site selection, and home ranges of local populations (McLaughlin 1990).

Sanibel Island has an unusually high density of tortoises (McLaughlin 1990) which offers a unique opportunity to study juveniles. To manage for this declining species an understanding of the habitat relations of juveniles is important to provide information to increase recruitment. This study was undertaken to examine the habitat requirements of juveniles, compare their behavior with adults, and make management recommendations if juveniles have different habitat needs than adults. In addition, Upper Respiratory Tract Disease (URTD) was noted in gopher tortoises in 1989 on Sanibel Island (McLaughlin 1990). Part of this study was to begin a preliminary investigation into this disease to provide a basis for future research.

Explanation of Thesis Format

This thesis was prepared following the alternate format described in the Graduate College Thesis Manual. This thesis contains two papers suitable for submission to a journal. Following the papers there is a general summary. Literature cited in the general introduction are listed after the general summary.

PAPER I

HOME RANGE, ACTIVITY, AND HABITAT SELECTION OF JUVENILE GOPHER TORTOISES ON SANIBEL ISLAND, FLORIDA.

ABSTRACT

The habitat relations of juvenile gopher tortoises, *Gopherus polyphemus*, differ from adult males and adult females. Juveniles had seasonal home ranges an order of magnitude smaller than adults. Adult males had the largest home ranges in the summer, but females had larger home ranges in the spring. Juveniles used one or two primary burrows throughout the year while adults used multiple burrows. Adult male burrow use increased during the summer and fall season. There were no daily modal or bimodal activity patterns for any age/sex class. Activity, however, was influenced by age/sex class and season. Overall, males were the most active and juveniles were the most inactive. Adult males and juveniles were most active in the summer, adult females in the spring. Evidence from home range and activity data suggests mating, or at least social interactions as a prelude to mating, occurred in the late summer and fall. Juveniles were the most habitat restricted; they inhabited primarily open grassy areas with reduced trees and shrubs. Adult burrow site selection was in relation to habitat availability, however, female burrows were in grassy areas with reduced trees and shrubs during the spring. All tortoises used more open areas for activity locations. Management implications of the difference in juvenile behavior and habitat selection are discussed.

INTRODUCTION

Gopher tortoises are currently declining throughout their range (Auffenberg and Franz 1982, Diemer 1986, McCoy and Mushinsky 1992, Nelson et al. 1992). This species is protected in every state it occurs, and a population in Louisiana is federally threatened. Because of their status and role as a keystone species, gopher tortoises have been well studied. Researchers have found a north-south cline in growth and maturity (Diemer 1986, Landers et al. 1982, McLaughlin 1990), sex differences in home range size (Diemer 1992, McLaughlin 1990, McRae et al. 1981), and have extensively documented food habits (Garner and Landers 1981, Macdonald 1986, Macdonald and Mushinsky 1988). In addition, social behavior is well developed in these reptiles, and their elaborate courtship and aggressive behaviors have been studied (Auffenberg 1966, Auffenberg 1977, Douglass 1976, Hailman et al. 1991, Iverson 1980, Landers et al. 1980). The overwhelming majority of research has centered on adults, and current management is based on adult information.

Juvenile gopher tortoises, however, have not been well studied. Juveniles are secretive in nature and cryptically colored which contributes to their under-representation in research (Allen and Neill 1953, Wilson 1991, Wilson et al. In Press). In many areas population densities of gopher tortoises are low, which also makes study difficult (Breininger et al. 1988, Fucigna and Nickerson 1989, Godley 1989, Wright 1982). Other researchers have noticed a low representation of juvenile tortoises in population demographics (Diemer 1992b, McLaughlin 1990). Whether the paucity of information on juveniles is due to the inability of researchers to locate them or relative to an actual demographic characteristic of the species remains uncertain.

Juvenile habitat information, however, is vital to management of this declining species. Because much of traditional gopher tortoise habitat has been transformed and degraded (Diemer 1986), understanding the habitat requirements and behavior of juveniles is necessary to manage for successful recruitment. Sanibel Island, Florida offers a unique research opportunity for two reasons. First, the tortoise habitat on Sanibel is West Indian Scrub (McLaughlin 1990), characterized by large open grassy areas and bare ground interspersed with areas of shrubs and trees. The open nature of this habitat makes tortoises more apparent. Second, Sanibel Island has tortoise colonies with high densities, possibly higher than anywhere else (McLaughlin 1990). Densities of 2.4 tortoises/ha or less have been reported in Florida and South Carolina (Breininger et al. 1988, Fucigna and Nickerson 1989, Godley 1989, Wright 1982). Kushlan and Mazzotti (1984) found a density of 11.3 tortoises/ha in a coastal population on Cape Sable, Florida. McLaughlin (1990), however, reported a mean density of 16.7 tortoises/ha on Sanibel Island, with some colonies as high as 27.5 tortoises/ha. The density of tortoises on Sanibel Island facilitates finding enough juveniles for study.

The objectives of this study were to use radio telemetry to:

1. Determine home range size of juveniles and compare with those of adult males and adult females.
2. Determine daily and seasonal activity patterns of juveniles and compare to those of adult males and adult females.

3. Determine habitat selection of juveniles and compare with that of adult males and adult females.

METHODS

Study Sites

Sanibel Island is a barrier island 1.6 kilometers off the coast of southwest Florida near Fort Myers. The island is between 26°25' and 26°30' North, 82°00' and 82°11' West. The maximum elevation of the island is 4.3 m above sea level, the mean elevation is 1-1.5 m above sea level (Cooley 1955, McLaughlin 1990). Gopher tortoises primarily inhabit the upland areas of the island. The upland habitat is West Indian Scrub with tropical and subtropical shrubs and trees within open grassy areas (McLaughlin 1990). Tortoises either occur in discrete colonies in undisturbed areas or more individually in areas divided by human development.

I selected the location of six discrete colonies to use as study sites, four having been previously described by McLaughlin (1990). All six sites had similar vegetation structure and habitat type. For a detailed description of the island's ecozones and study sites see McLaughlin (1990). The Johnston Tract was the largest study site, approximately 6.10 ha of undeveloped land along the mid island ridge. Most of this site is owned by the Sanibel-Captiva Conservation Foundation (SCCF) and has been managed for gopher tortoises. As a result, large areas have been cleared of the exotics Brazilian pepper, *Schinus* spp., and Australian pine, *Casuarina equisetifolia.* Heron's Landing is a subdivision with approximately 1.27 ha of undeveloped land at the time of this study. Heron's Landing was not managed for gopher tortoises but most of the exotic vegetation was cleared in 1988 as a prelude to housing development (McLaughlin 1990). Ding

Darling is a small portion of the J.N. "Ding" Darling National Wildlife Refuge. The tortoise colony occurs on 0.10 ha of land free of exotic vegetation, next to the visitor parking lot. West End is a 0.44 ha conservation easement near a subdivision. This area has and will be managed for gopher tortoises, and all exotic vegetation was removed during 1988 and 1989. Kinzie Island is an artificial island created by mosquito control canals. This area is a subdivision with 1.54 ha of undeveloped land largely free of exotics. Wild Lime Drive is a residential area with 0.75 ha of undeveloped land. The undeveloped lots are free of exotic vegetation, and the developed yards are landscaped in a tortoise "friendly" manner (i.e., mostly native vegetation with no barriers to tortoise movement).

Capture Methods

Tortoises were captured by hand, with pitfall traps, or with live traps. I captured all adult tortoises by hand. Juvenile pitfall traps were made by digging a hole and putting a one quart bucket at the mouth of active burrows. I covered the bucket with newspaper and spread sand on top. All pitfall traps were checked twice daily. Squirrel-sized "Hav-a-Heart" live-type traps were also used to capture juveniles. Traps were placed at the entrance of active burrows and checked twice daily.

All tortoises captured were aged, sexed, and a series of morphometric data was collected. Tortoises were aged by counting shell annuli (see Landers et al. 1982). I classified tortoises as juvenile, subadult, or adult. Juvenile status was determined by shell compressibility (Landers et al. 1982) and shell dimensions (Diemer 1992). Juveniles were five years or less and had carapace lengths below 130 mm. Subadults were not sexually mature based on shell morphology (McLaughlin 1990), were greater than 130 mm in carapace length, and did not have compressible shells. Adults were sexually mature based on shell morphometrics (McLaughlin 1990, McRae et al. 1981a). Sex could be determined for adults only. I sexed tortoises based on the presence or absence of a plastral concavity (McRae et al. 1981a), behavior (Diemer 1992b), and occasionally males extruded their penis during examination. Each tortoise was weighed and I took morphological measurements following McRae et al. (1981a). In addition all adult females captured between mid-March and mid-June were radiographed for the presence of eggs, and to determine clutch size.

Radio Telemetry

Only adult males, adult females, and juveniles were selected for radio tracking. Subadults were excluded because of lack of time and radio equipment. I radio-tracked 16 adult tortoises and 19 juveniles from January 1992 through November 1992. The number of tortoises tracked at each study site reflected the relative area of the site. Six adult males, five adult females, and ten juveniles were tracked at the Johnston Tract; one adult male, one adult female, and five juveniles at Heron's Landing; one adult male, one adult female, and one juvenile at Wild Lime Drive; one adult male and one juvenile at West End; one juvenile at Ding Darling; and one juvenile on Kinzie Island. During the study one adult male and one juvenile died of Upper Respiratory Tract Disease (URTD) at the Johnston Tract. The one juvenile tortoise on Kinzie Island was killed by a mammalian predator less than one month after its original capture. Transmitters failed on six juveniles and were not recovered. The remaining 11 juveniles and 15 adults were alive at the end of the study.

Adults were fitted with SM-1 model transmitters (AVM Instruments, Inc. Livermore, CA) which weighed approximately 15 g and had a battery life of eight months. Transmitters and antennae were affixed externally with dental acrylic. I placed the transmitter at the rear of the carapace on males, and in front on females to minimize interference with reproduction (McLaughlin 1990). For juveniles, I also used SM-1 model transmitters but with smaller batteries. Total package weight of juvenile transmitters was 2 or 6.5 g with a battery life of 30 days or 6 months respectively. Package-size depended on tortoise weight and never exceeded 10 percent of total tortoise body weight. The juvenile package differed from the adult package to minimize potential growth deformities in the carapace. The transmitter was attached to the carapace with "super glue" and dental acrylic but the glue and acrylic did not cross a carapace scute boundary. I inserted the antenna into a rubber tube also glued to the carapace. The rubber tube, however, was cut between each scute that allowed the tortoises' unrestricted growth. I tracked tortoises with a hand held, 4-element Yagi antenna and a multi-band programmable receiver (ATS, Wisconsin).

Each tortoise was located at least three times a week, but never on consecutive days so that observations would be independent (Swihart and Slade 1985). I located tortoises during one of three daily time periods as in Wilson et al. (In Press): the hottest time of the day (midafternoon, 1100-1400 hours) and midpoints between this time and the coolest times of day (midmorning, 0700-1100 hours; late afternoon, 1400-1900 hours). Tortoises were not active after dark. On each tracking day, study site and time of day to begin radio tracking were randomized.

Home Range

I mapped all tortoise locations onto aerial photographs of the island. Aerial photographs were taken in 1990 by the Florida Department of Transportation at a scale of 1" = 200'. Locations on the photographs were converted to coordinates by placing an arbitrary starting point on each photograph and measuring in mm each location from that point along an x-y axis. The scale measurements were 1 mm = 2.4 m. Home range size was calculated using the minimum convex polygon method and McPAAL software (Stuwe and Blohowiak 1985). Aguirre et al. (1984) found that the minimum convex polygon method did not overestimate home range size of the Bolson tortoise, *Gopherus flavomarginatus*. In addition, most other home range studies report minimum convex polygon (Barrett 1990, Diemer 1992a, Judd and Rose 1983, McRae et al. 1981b, Rose and Judd 1975, Wilson et al. In Press)

. Home range sizes were calculated seasonally for each age/sex class. Home ranges were analyzed seasonally because other research has shown a seasonal effect on home range size (McRae et al. 1981, Wilson et al. In Press). I used the same seasons as Wilson et al. (In Press): December through March (winter), April through May (spring), June through September (summer), and October through November (fall). These seasons are thermal periods based on average monthly temperature variations in Tampa, Florida. A tortoise's home range was included in the group analysis only if it had at least three unique locations, with a minimum of seven total locations, during that season. I also calculated overall (11 month) home range size. Overall home range size for a tortoise was included in the analysis if it met the above criteria for at least three seasons.

I compared home range size of adult males, adult females, and juveniles using a randomization test (Sokal and Rohlf 1981). Randomization testing allowed statistical inference without relying on assumptions necessary for standard methods of analysis (e.g., normality, equality of variance). I performed a one way analysis of variance (ANOVA) of age/sex class for each season. The resulting F statistic was compared with other F values calculated by randomly reassigning tortoises to other age/sex classes. I used 700 random permutations of the data for comparison. The F statistic of the original data was considered significant if the exact probability (p value) of a larger F from the randomly reassigned data was very small.

Activity

I recorded tortoise activity instantaneously for each radio location. Activity was classified into seven groups: in burrow, basking on burrow mound, basking away from burrow mound, walking, foraging, intraspecific relations (i.e., fighting, courting, mating) and opportunistically sheltering. Some of these activities were not often observed so activity was reclassified into three groups for analysis: inactive (in burrow or opportunistically sheltering), basking (on or away from burrow mound), and active (foraging, walking, or intraspecific relations). Activity was recorded with respect to time of day periods and seasons already described. I analyzed activity patterns between age/sex classes by season and time of day using a log-linear model. The CATMOD procedure of SAS (SAS Institute, Inc.) was used to select the model that best described the association in activity pattern data.

Habitat Selection

Habitat selection between age/sex groups was compared using vegetation presence/absence. I flagged all tortoise locations and returned later to sample vegetation. Vegetation was sampled with respect to the four seasons already defined. At each tortoise location I established a sampling array described by McLaughlin (1990). Each array contained 13 points centered at the tortoise location (the burrow entrance was used as the center point for burrow locations). The sampling points were the center point and points 0.5 m, 1.5 m, and 2.5 m from the center point in four directions. For each point I recorded the ground cover and all species of vegetation that overhung the point.

At each study site random transect points were established to sample vegetation for comparison with tortoise locations (McLaughlin 1990). Transects were established at each study site beginning from a baseline established along a short side of the study site. The starting point of the first transect was randomly selected along the base line then the other transects were run parallel to the first and were 15 m apart. Points were established along each transect at 15 m intervals beginning at a randomly selected distance between zero and eight meters from the baseline. The azimuth for transects at each study site was selected at random with the caveat that it not run parallel to any major landscape feature (i.e., trial, ridge, etc.). The transect points were sampled once during each season, and the same transect points were used for each season. The number of points at each study site reflected the relative area of each study site. I established 68 points at the Johnston Tract, 32 points at Heron's Landing, 14 points at West End, and 9 points at Ding Darling. The one tortoise I was tracking at Kinzie Island died shortly after inclusion in the study so this area was not used in vegetation analysis. I could not establish transects at Wild Lime because of a landowner conflict; therefore Wild Lime locations were excluded from the analysis. The vegetation at West End was mowed after the spring season and could no longer be sampled so West End locations were also excluded from the analysis.

For analysis I converted the vegetation data into six categories: BARE (bare ground), LITTER (leaf litter ground cover), GRASS (all grasses, sedges, and rushes), HERB (all non-grass herbaceous plants), SHRUB (all shrubby plants), and TREE (all trees). For each of these six categories each location or transect point was given a value of zero through 13 reflecting how many of the 13 array points contained each category.

Locations and transect points between age classes were compared using principal components analysis PRINCOMP procedure of SAS (SAS Institute, Inc.). Principal components were obtained from the category values using both tortoise location and transect point data. Component scores were calculated for every location and transect point and scores were graphed to determine if age/sex classes had similar scores for each activity.

RESULTS

The results of morphometrics and radiographs are provided in appendices A and B. These data are presented for documentation only. For a comparison and discussion of similar data reported for gopher tortoises the reader is referred to: Alford 1980, Godley 1989, Goin and Goff 1941, Iverson 1980, Kushlan and Mazzotti 1984, Landers et al. 1980, Landers et al. 1982, Linley 1986, McLaughlin 1990, McRae et al. 1981, and Wright 1982.

Home Range

Juveniles had home ranges minimally an order of magnitude smaller than adults (Table 1). Statistical comparison was possible only for the spring and summer seasons because of insufficient data. There was a significant difference in home range size among males, females, and juveniles during the summer season (ANOVA F = 3.88, df = 2,16, p = 0.0423, probability of a larger F from randomization test = 0.0226). The average home range size for males was five times larger than females. Juvenile home range size was much smaller than that of adults. For the spring season the difference in home range size between age/sex class approached significance (one way analysis of variance F = 3.52, df = 2,11, p = 0.0659, probability of a larger F from randomization test = 0.0680). Again, juvenile home ranges were much smaller than adults, however, females had an average home range size 50% larger than males.

Comparison of the number of different burrows used by each age/sex class in each

Table 1. Comparison of seasonal home range size by age/sex class for gopher tortoises on Sanibel Island, Florida. Home ranges are in ha, n = sample size, x̄ = mean, SD = standard deviation. Differences in age/sex class approached significance (p from randomization test = 0.066) for the spring season, and were significant (p from randomization test = 0.023) for the summer season.

	Adult Males			Adult Females			Juvenile		
Season	n	x̄	SD	n	x̄	SD	n	x̄	SD
Winter	1	0.0095		0			1	0.0011	
Spring	7	0.0895	0.0613	3	0.1378	0.1031	4	0.0125	0.0205
Summer	8	0.9330	0.9570	6	0.1705	0.2245	5	0.0260	0.0345
Fall	7	0.5379	0.6093	2	0.0409	0.0550	1	0.0003	
Overall	3	1.8037	1.1360	1	0.4279		0		

season were similar to home range size comparisons (Table 2). Tortoises which used the most burrows had the largest home ranges. Males used more burrows than females during the summer when their home ranges were larger than females. Juveniles usually used only one or two primary burrows throughout the year.

Activity

Gopher tortoises spent 88% of daylight hours inactive, either in a burrow or opportunistically sheltering (Table 3). Tortoises were most active during the summer and fall seasons, and spent more time basking during the winter and spring seasons (Table 3). Overall males were the most active, juveniles the most inactive. Adults were observed basking more often than juveniles (Table 3). The selected log-linear model was significant and had a three variable interaction of activity, age/sex class, and season with the effect of time of day separate ($G^2 = 91.31$, df = 68, $p = 0.0312$). In other words tortoise activity was affected by season and age/sex class but was not affected by time of day.

The ratio of the log-linear parameter estimates to their standard error show which aspects of tortoise activity most affected the log-linear model (Table 4). Males were most likely to be basking in the fall (Table 4). Similarly, females were most likely to be inactive during the winter and males were most likely to be inactive during the spring. There is the least dissimilarity of activity between the age/sex classes during the summer season. Time of day was not involved in an interaction effect on the outcome of a tortoise activity observation but remained a factor in the model because observations were

Table 2. Comparison of seasonal burrow use by age/sex class for gopher tortoises on Sanibel Island, Florida; n = sample size, x̄ = mean number of burrows, SD = standard deviation.

	Adult Males			Adult Females			Juvenile		
Season	n	x̄	SD	n	x̄	SD	n	x̄	SD
Winter	1	2.0		0			1	1.0	
Spring	7	3.9	1.6	3	3.0	0.0	4	1.8	1.0
Summer	8	8.5	3.1	6	3.3	1.0	5	2.2	0.4
Fall	7	6.1	1.8	2	2.5	0.7	1	1.0	
Overall	3	14.7	1.5	1	7.0		0		

Table 3. Seasonal activity patterns of gopher tortoises by age/sex class. Freq. is the number of observations.

	Adult Males		Adult Females		Juveniles		Totals	
Season	Freq.	Percent	Freq.	Percent	Freq.	Percent	Freq.	Percent
Winter								
Inactive	43	68.25	36	85.71	152	87.36	231	82.80
Basking	20	31.75	5	11.90	20	11.49	45	16.13
Active	0	0.00	1	2.38	2	1.15	3	1.08
Totals	63	100.00	42	100.00	174	100.00	279	100.00
Spring								
Inactive	107	88.43	56	73.68	145	87.35	308	84.85
Basking	11	9.09	16	21.05	15	9.04	42	11.57
Active	3	2.48	4	5.26	6	3.61	13	3.58
Totals	121	100.00	76	100.00	166	100.00	363	100.00
Summer								
Inactive	201	85.17	190	94.06	239	94.84	630	91.30
Basking	19	8.05	8	3.96	2	0.79	29	4.20
Active	16	6.78	4	1.98	11	4.37	31	4.49
Totals	236	100.00	202	100.00	252	100.00	690	100.00
Fall								
Inactive	105	80.15	105	90.52	137	97.16	347	89.43
Basking	16	12.21	8	6.90	1	0.71	25	6.44
Active	10	7.63	3	2.59	3	2.13	16	4.12
Totals	131	100.00	116	100.00	141	100.00	388	100.00
Overall								
Inactive	456	82.76	387	88.76	673	91.81	1516	88.14
Basking	66	11.98	37	8.49	38	5.18	141	8.20
Active	29	5.26	12	2.75	22	3.00	63	3.66
Totals	551	100.00	436	100.00	733	100.00	1720	100.00

Table 4. Ratio of log-linear parameter estimates to their standard error for the two variables of the selected log-linear model.

Variable 1: Interaction of Age/Sex Class, Activity, and Season

Season	Activity	Adult Males	Adult Females	Juveniles
Winter	Inactive	-2.704	2.279	0.000
	Basking	-2.005	-0.271	0.000
	Active	0.000	-0.239	0.000
Spring	Inactive	4.090	-2.814	-0.505
	Basking	-0.685	0.000	0.112
	Active	-0.453	0.000	0.206
Summer	Inactive	0.000	0.055	0.000
	Basking	0.000	0.029	0.000
	Active	0.000	-0.058	0.000
Fall	Inactive	0.000	-0.947	0.000
	Basking	1.625	0.203	-0.914
	Active	-0.389	0.000	0.000

Variable 2: Time of Day

Midmorning	Midafternoon	Late Afternoon
-1.124	-7.743	10.239

most likely to occur during the late afternoon and least likely during the midafternoon (Table 4). This occurred because even though starting time of day was randomized for observations, I often was not able to locate all tortoises within that time period.

Habitat Selection

Overall I sampled 422 transect points, 157 adult male locations, 60 adult female locations and 91 juvenile locations. All age/sex classes used areas with bare ground, litter, and herbs similarly and in general proportion to available habitat (Table 5). Juveniles used areas with a lower mean value of shrubs and trees but a higher value for grass than adults and transect points. These data, however, are descriptive only, and are not adequate for statistical testing. A listing of plant species found at locations and transect points is given in Appendix C.

I retained for analysis the first three principal components derived from the entire data set of locations and transect points. The first component was a shrub, litter, and tree component (see Table 6 for component patterns). When shrubs, litter, and trees were prevalent bare ground, herbs, and grass were reduced. The second component was a tree and herb component. When trees were prevalent but shrubs reduced, herbs were prevalent. The third component, a litter component, showed when litter, grass, and herbs were present, trees and bare ground were reduced. These components accounted for 82% of the variation in vegetation structure. The remaining components did not help explain additional variation.

The first two principal component scores for transect point data alone are almost

Table 5. Mean presence of vegetation types at transect points and tortoise locations. Numbers are means ± standard deviation. Means are number of points within a sample array in which each vegetation category occurred, possible values are zero to 13.

Vegetation[a]	Transect Points	Adult Males	Adult Females	Juveniles
Bare	1.28 ± 2.40	2.08 ± 2.13	2.52 ± 2.05	2.22 ± 2.14
Litter	11.36 ± 3.01	10.67 ± 2.59	10.25 ± 2.38	10.77 ± 2.30
Herb	3.88 ± 3.11	3.51 ± 2.86	3.36 ± 2.30	5.02 ± 3.06
Grass	1.95 ± 3.20	1.82 ± 3.29	2.23 ± 3.22	3.31 ± 3.34
Shrub	7.14 ± 4.91	8.39 ± 4.36	9.05 ± 3.51	4.32 ± 4.40
Tree	4.25 ± 4.91	4.07 ± 4.36	4.18 ± 4.16	1.51 ± 2.41
Sample Size	422	114	43	82

[a] See text for explanation of vegetation categories.

Table 6. Vegetation analysis of random transect points and tortoise locations at the Johnston Tract, Ding Darling, and Heron's Landing study sites on Sanibel Island.

a. Principal component pattern for the first three components derived from the entire vegetation data set.

Vegetation[a]	Component 1	Component 2	Component 3
Shrub	0.8754	-0.4186	0.0123
Litter	0.5735	0.0649	0.6827
Tree	0.4787	0.8559	-0.1283
Herb	-0.1743	0.3552	0.5780
Bare	-0.4698	-0.0475	-0.7467
Grass	-0.6185	-0.0022	0.4628

b. Variation Explained by Each Component

Eigenvalue	30.5716	20.5405	12.4080
Proportion	0.3967	0.2666	0.1610
Cumulative	0.3967	0.6633	0.8243

[a] See text for vegetation code description.

randomly distributed (Figure 1). The first component scores are evenly divided between positive and negative values. This means the habitat overall was equally divided between areas of high shrub and tree cover and more open areas with grass and bare ground with some herbaceous plants present. The extremes in one component score are close to zero for the other component score because trees are highly positive in both components. Therefore, when there were high numbers of shrubs and trees, there were some herbaceous plants present. Conversely when grasses were high there were some herbaceous plants and trees present but no shrubs. This result suggests that presence or absence of shrubs significantly affects the presence or absence of grasses. There was a high degree of overlap of transect point scores between seasons because the relationship of each vegetation component to the others did not change seasonally.

Based on comparison of the first two principal components, juvenile burrow site selection was mostly in open, grassy areas (Figure 2). When juvenile burrows were associated with shrubs they were in areas with few trees present. Adult males and females were less restricted in burrow site selection; their burrows were found throughout the available habitat. Juvenile burrow site selection remained consistent seasonally. Adult males had burrows found throughout the habitat in all seasons. Adult female burrows were also found throughout the habitat except in spring where more of their burrows were in open, grassy areas or areas with reduced trees (Figure 3).

Basking site selection was similar to burrow site selection. All juvenile basking sites had either negative first or negative second component scores, which means juveniles basked in open, grassy areas or areas with no trees (Figure 4). Adult basking sites,

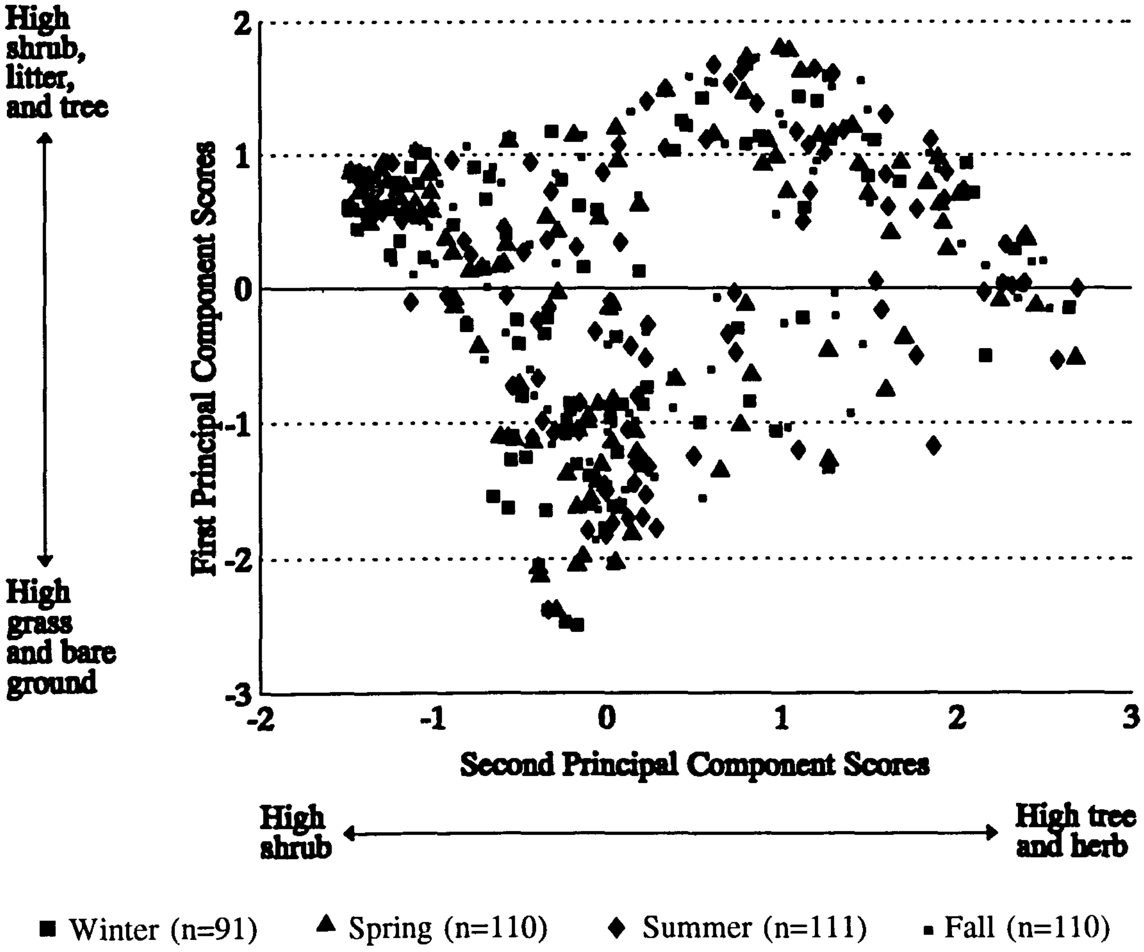

Figure 1. Results of comparison of the shrub, litter, and tree (first) principal component scores with the tree and herb (second) principal component scores for all random transect points from the Johnston Tract, Ding Darling, and Heron's Landing study sites on Sanibel Island, Florida.

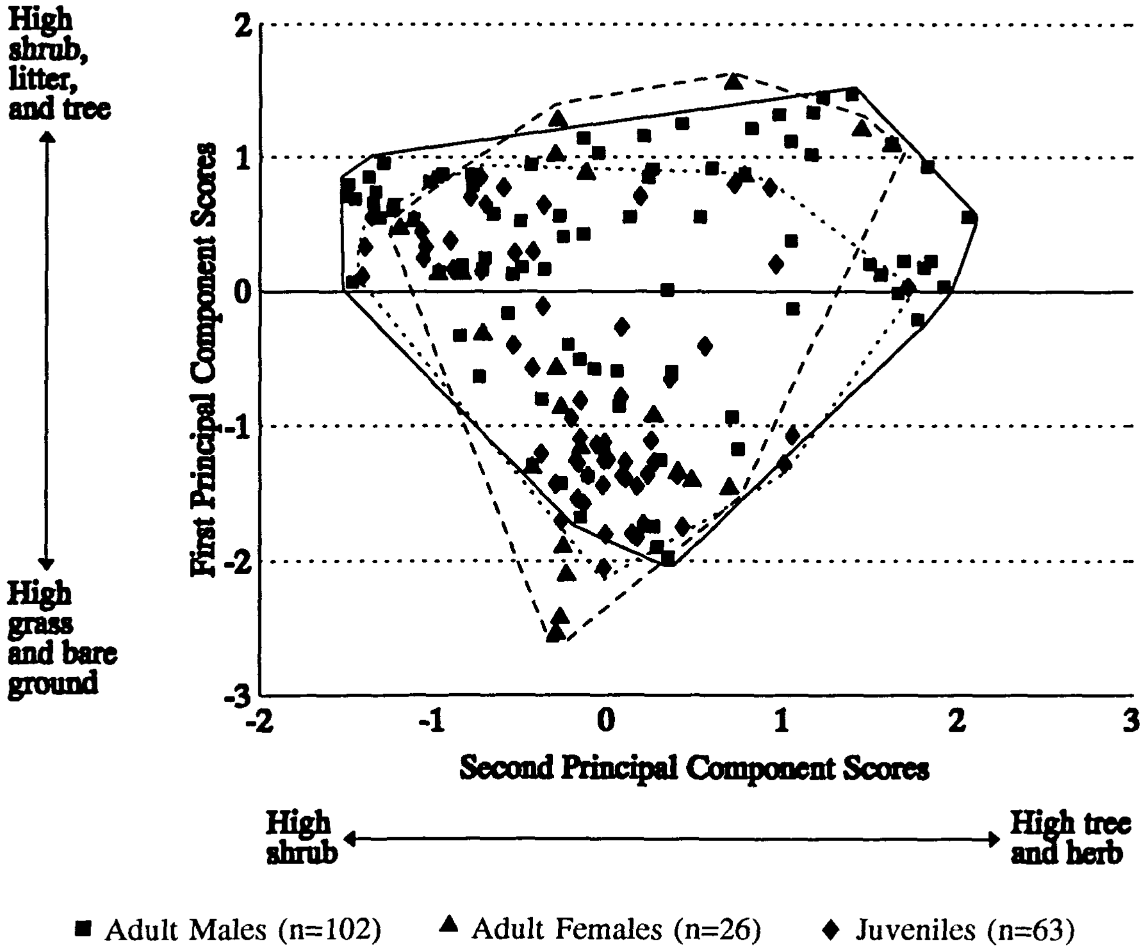

Figure 2. Results of comparison of the shrub, litter, and tree (first) principal component scores with the tree and herb (second) principal component scores of all tortoise burrow locations. Solid line bounds male scores, dashed line bounds female scores, and dotted line bounds juvenile scores.

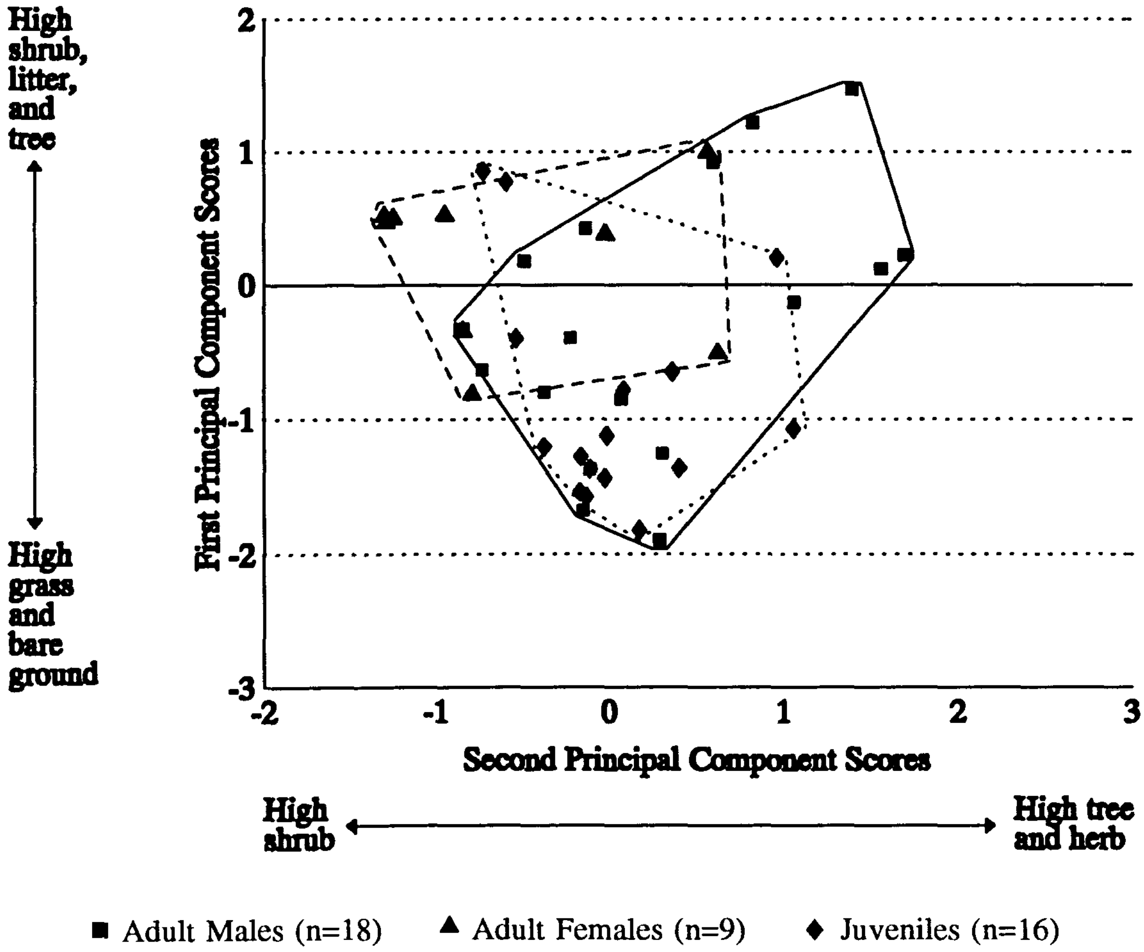

Figure 3. Results of comparison of the shrub, litter, and tree (first) principal component scores with the tree and herb (second) principal component scores of tortoise burrow locations for the spring season. Solid line bounds male scores, dashed line bounds female scores, and dotted line bounds juvenile scores.

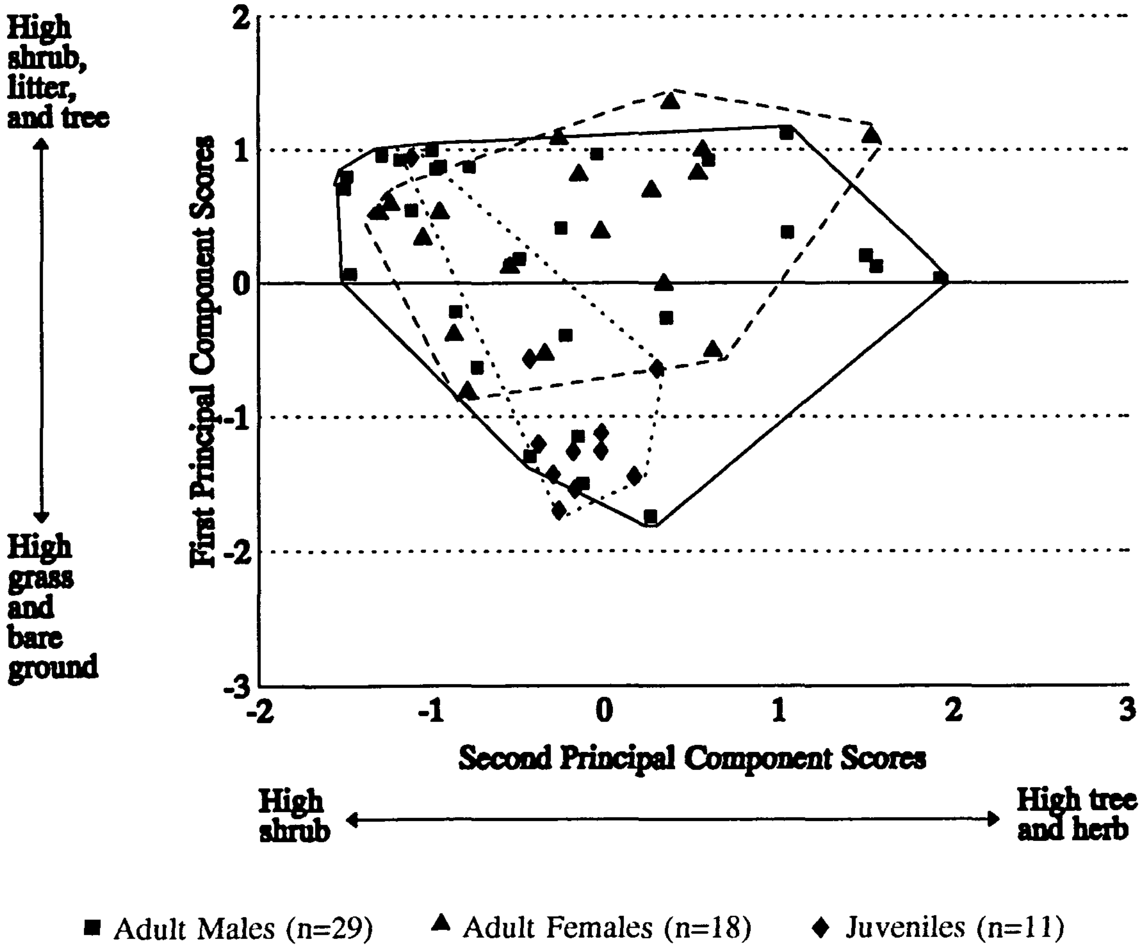

Figure 4. Results of comparison of the shrub, litter, and tree (first) principal component scores with the tree and herb (second) principal component scores of all basking sites. Solid line bounds male scores, dashed line bounds female scores, and dotted line bounds juvenile scores.

however, were distributed throughout the available habitat. I did not have enough basking sites to compare seasonal selection. Activity site scores for juveniles, females, and most males had either negative first or negative second component scores (Figure 5). Therefore, tortoises selected open, grassy areas for activity. Only males had activity locations that had positive scores for both of the first two principal components which means they were the only age/sex class that were active in areas of dense shrub and tree cover with little grass and herbaceous plants. Again, adult males occupied all the extreme points, therefore their activity site selection was the least restricted.

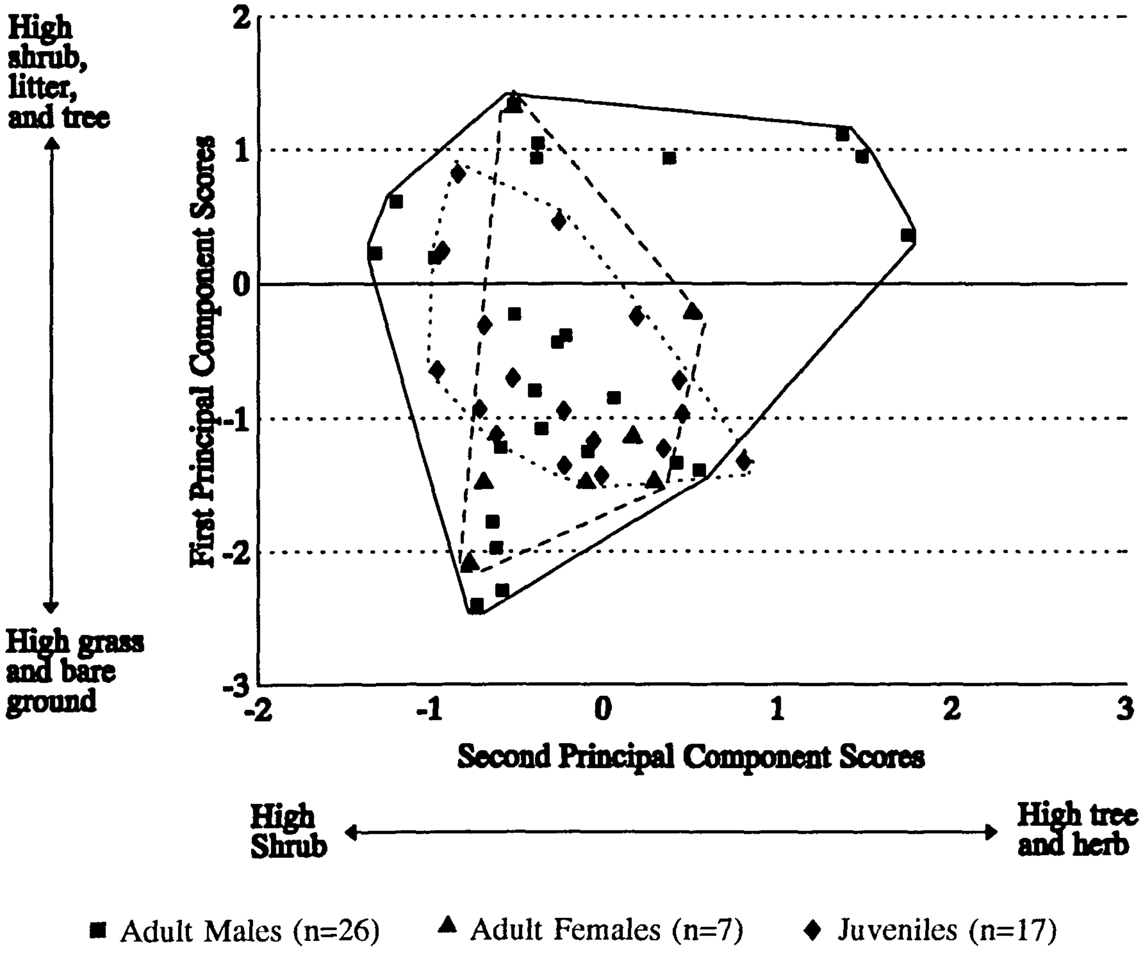

Figure 5. Results of comparison of the shrub, litter, and tree (first) principal component scores with the tree and herb (second) principal component scores of all activity sites. Solid line bounds male scores, dashed line bounds female scores, and dotted line bounds juvenile scores.

DISCUSSION

I found juveniles had much smaller home ranges than adults which is not surprising because juveniles have a smaller body mass with a lower forage quantity requirement, and have less locomotor ability than adults. Juveniles also have little or no social interactions with subadults and adults (McRae et al. 1981b). Juvenile home range is a foraging range only (Wilson et al. In Press). My estimates of juvenile home ranges are comparable to those found by Wilson et al. (In Press) and Diemer (1992a) who both used minimum convex polygon. Wilson et al. (In Press) tracked 12 to 18 juveniles over the course of a year in central Florida, Diemer (1992a) tracked seven juveniles each for at least a year in northern Florida.

Wilson et al. (In Press) and Diemer (1992a) found an average yearly home range size of 0.072 ha and 0.013 ha respectively. Estimates from these two studies were not significantly different (Wilson et al. In Press) and my estimates for spring and summer, 0.013 and 0.026 respectively, fall between those of Diemer (1992a) and Wilson et al. (In Press). If I had been able to determine yearly home range size it probably would have been closer to Wilson's et al. (In Press) study. The added locations from the winter and fall seasons would make my estimates of yearly home range size larger than my findings for spring and summer home ranges alone.

Juvenile home range sizes on Sanibel exhibited considerable individual variation like that found in other studies (Wilson et al. In Press, Diemer 1992a). Sanibel estimates for individual seasonal home ranges were from 0.0003 to 0.0866 ha (standard deviation =

0.027). Wilson et al. (In Press) and Diemer (1992a) found individual home ranges from 0.0095 to 0.3576 ha (standard deviation = 0.011) and 0.0004 to 0.2502 ha (standard deviation 0.089) respectively. Wilson's et al. (In Press) seasonal home ranges were from 0.0001 to 0.3534 (standard deviation not available). This variation may be due to microhabitat differences from one tortoise location to another. Gopher tortoises will increase their home range size in response to reduced forage (Diemer 1986, Diemer 1992a, McRae et al. 1981b).

Diemer (1992a) did not analyze home ranges seasonally, but Wilson et al. (In Press) found juvenile summer home ranges to be significantly larger than any other season. Wilson et al. (In Press) calculated summer home ranges at 0.036 ha which is comparable to my estimate of 0.026 ha. I also found spring home ranges to be smaller than summer (0.013 ha), but not to the degree of Wilson's et al. (In Press) finding (0.005 ha). This suggests that a similar seasonal effect on home range size may exist for juveniles on Sanibel Island. Summer is the most active season for juveniles and they are probably increasing their range to maximize forage intake (McRae et al. 1981b). Growth of juvenile tortoises is also greatest during this time (Landers et al. 1982). Summer is also the longest season on Sanibel, which may allow tortoises to cover more ground.

Burrow use reflected home range size. Juveniles used only one or two primary burrows throughout the year. Wilson et al. (In Press) reported that juveniles used a mean of 4.4 ± 2.4 burrows, but primary burrows accounted for 75% of burrow use. In Diemer's (1992a) study juveniles used 2.6 ± 1.3 burrows. By using only a few burrows of their own construction, juveniles reduce their interaction with conspecifics (McRae et al.

1981b). This may allow juveniles which would otherwise be low on a hierarchal social scale to coexist spatially with adults. In this study, juvenile home ranges always at least partially overlapped with adults.

Overall home range size of adult males from this study, 1.80 ± 1.14 ha, is consistent with McLaughlin's (1990) findings of 1.052 ± 0.271 ha for Sanibel Island tortoises. Other estimates of adult male home ranges, using minimum convex polygon method, are 0.879 ha for a north Florida population (Diemer 1992a), and 0.47 ± 0.51 for tortoises in southern Georgia (McRae et al. 1981b). These findings are similar, but there is variation between studies. Diemer (1992a) attributed differences in home range size between studies to differences in study duration and habitat type. Sanibel Island habitats are much different from upland areas in other studies, there is no little or no wiregrass on Sanibel and trees are predominately sub-tropical species (McLaughlin 1990). In addition, because of the sub-tropical climate on Sanibel, tortoises are active for a greater portion of the year than northern populations. McLaughlin (1990) also suggested that home range size calculations on Sanibel are affected by the high degree of disturbance from human development.

I was unable to estimate overall home range size of adult females because of insufficient data. Studies have shown, however, that females from Sanibel Island and south Georgia have significantly smaller yearly home ranges than males (McLaughlin 1990, McRae et al. 1981b). For the spring season, however, I found female home ranges to be as large as male home ranges. Females are gravid at this time and maximum movements of females occur in spring when they are seeking nesting sites (Diemer 1992a).

Other studies have reported that mating in gopher tortoises occurs during the spring (Iverson 1980, Landers et al. 1980). Vitellogenesis began in September and continued until the following nesting season (Iverson 1980), but according to McRae et al. (1981b) females are not receptive after June. Inferential data from this study, however, suggest mating on Sanibel Island may be occurring later in the summer and early fall. If mating occurs in the spring, males should have a larger home range because they are actively seeking females and challenging other males (Diemer 1986, Iverson 1980, McRae et al. 1981b). I never observed mating attempts, but males did increase their home range size and burrow use during the summer and early fall. In addition, the only male-male aggression I observed occurred in the fall. Diemer (1992a) also found long distance movements by males occurring primarily in late July and August which coincides with the late summer/fall period of active spermatogenesis. Courtship behavior by males has been observed through fall (Landers et al. 1980). Despite these findings there are no reports of mating occurring in the late summer or fall. Consequently males, instead of mating, may use the late summer and fall to maintain and establish dominance and determine conspecific locations before the relatively dormant winter season. This behavior would help facilitate mating during the following spring.

Sanibel tortoises did not exhibit the daily modal or bimodal activity pattern reported for gopher tortoises (Douglass and Layne 1978, McRae et al. 1981b, Wilson et al. In Press), and other North American tortoises (Marlow 1984, Morafka 1982, Nagy and Medica 1986, Rose and Judd 1975). Sanibel tortoises were no more likely to be active at one time during daylight hours than any other. The lack of a daily activity pattern may relate to climate effects of the position of Sanibel Island in the Gulf of Mexico. Although daily temperatures are high, the island is not subject to wide daily fluctuations. Tortoises were sometimes observed near the mouths of their burrows following afternoon rain storms. These animals have been reported opportunistically drinking when standing water is present or during rain events (Ashton and Ashton 1991, Medica et al. 1980).

Overall, juveniles were less active than adults. Juveniles spent 92% of the daylight hours inactive compared to 89% for females and 83% for males. Juvenile activity met their physiological requirements for growth while minimizing predation risk and social interactions. Juveniles were most active during the summer which is similar to Wilson's et al. (In Press) findings. Juveniles achieve their fastest growth rate during the summer, a time when forage is most available (Landers et al. 1980). Unlike adults, juveniles spent little time basking. Wilson et al. (In Press) reported this also, and interpreted it as predation avoidance. During the winter and spring, however, juveniles did increase their time spent basking which may allow them to be active over a greater portion of the year (Berry and Turner 1986, Diemer 1992a).

Active juveniles were always foraging. I never found a juvenile involved in intraspecific interactions, nor ever sharing a burrow. Juveniles were much more secretive than were adults, and were more likely than adults to freeze or seek out a burrow when approached. This behavior of juveniles is probably for predator avoidance, but also will reduce their social interactions. McRae et al. (1981b) reported that immature tortoises, when placed in the middle of the colony, would move to the periphery to avoid adults. Juvenile home ranges on Sanibel were located within adult home ranges, but juvenile behavior may make them functionally separate from adults.

Overall males were more active than females or juveniles, a result which agrees with other studies (Aguirre et al. 1984, Douglass and Layne 1978) and with the observations that males were the most likely to be involved in intraspecific relations. Female activity was highest in the spring, the time when egg laying occurs. Males, however, were the least active age/sex class during the spring. Male activity increased in the summer and fall. This further suggests that mating, or establishing dominance as a prelude to mating, may be occurring later in the year on Sanibel Island.

The vegetation analysis did not yield strong, conclusive results. The first two principal components from all the sampled vegetation points only accounted for 66% of the variation in the vegetation structure. These data, however, do show some trends and suggest areas of future research. Juveniles were the most habitat restricted; their burrow and activity locations being primarily in open, grassy areas. High tree and shrub presence exclude juveniles because trees and shrubs shade out grasses and herbaceous food plants. Juveniles, with their smaller home ranges and limited movement, are not tolerant of areas with limited food resources. In addition, areas with heavy shrub cover may preclude juveniles because they are unable to move through thick branches.

Juveniles might be expected to use shrubby areas for protection from predators. Juvenile burrows, however, are cryptic even in open areas. There is no conspicuous burrow mound and juveniles spend little time basking in front of their burrows, presumably to minimize predation (Wilson 1991). The coloration of juvenile shells makes them cryptic even in open grassy areas (Landers et al. 1982, McRae et al. 1981b, Wilson

1991).

Adults were often observed in burrows under heavy shrubs, particularly Brazilian pepper. This shrub does not appear to significantly impede the movements of adults and although it may not be quality habitat, adults can use areas with this invasive exotic. Although adults tolerate a wider variety of habitats than juveniles, for at least some life processes (i.e., nesting and foraging) they need open grassy areas with herbaceous plants. The density and movements of tortoises are related to herbaceous biomass; reduced herbaceous biomass means reduced forage, and tortoises will increase their home range and movements to compensate (Diemer 1986).

The vegetation analysis was based on species' presence/absence; however, gopher tortoises are midway between specialist and generalist herbivores (Macdonald and Mushinsky 1988) and vegetation structure may be even more important. For example, it may not be the species in the herbaceous layer that is important, but the density of the herbaceous layer. Future research on juvenile habitat requirements should concentrate more on vegetation structure such as the percent cover of shrub and tree layer and vegetation density at all levels. Two Habitat Suitability Index (HSI) models for gopher tortoises were presented by Cox et al. (1987); both included some vegetation structure. The first includes percent canopy closure and percent herbaceous cover but does not account for shrub cover. In this study, shrub cover was an important determinant of juvenile habitat selection. The second includes pine canopy cover, oak canopy cover, and percent non-*Aristida* (wiregrass) herbaceous cover. No pine, oak, or wiregrass, however, occur in tortoise habitat on Sanibel, and Mclaughlin (1990) found these models were not suitable for Sanibel. Any new HSI should account for juvenile habitat requirements and should include vegetation structure of tree and shrub layers for wider applicability.

Habitat loss and degradation are cited as the main reasons for declining gopher tortoise populations (e.g., Auffenberg and Franz 1982, Diemer 1992). Changes in habitat probably affect recruitment more than directly affecting adults. Changes in habitat are often accompanied by woody invasion with a greater canopy closure and an increase in shrub density (Auffenberg and Franz 1982, Landers and Speake 1980, Lohoefener 1981). The resultant change in vegetation structure shades out grasses and herbaceous plants and excludes juveniles. As habitat characteristics are changed, juveniles also suffer more because they are more restricted in movements, have less access to food, and are more susceptible to predation then adults.

Management Implications

Relocation is a common conservation tool for tortoises and its pros and cons have been well debated (Berry 1986, Burke 1989, Burke 1991, Dodd and Seigel 1991, Fucigna and Nickerson 1989, Gibbons 1986, Godley 1989, Lohoefener and Lohmeier 1986). Results from this study, however, identify other areas for consideration. When moving tortoises, the social structure of the colony being moved as well as the colony already at the relocation site need to be considered. In general, tortoises should not be moved into an area with an existing colony. When new tortoises are added to a colony, the dominance structure and spatial arrangement of the resident tortoises will be disrupted. This may upset the existing social structure and induce stress on the population. In addition, Upper Respiratory Tract Disease (URTD) has been documented in many areas of Florida and possibly in South Carolina (Beyer 1993). This highly contagious disease will be further spread by relocations.

The timing of relocations should take tortoise behavior into account. Tortoises should be moved at the beginning of the rainy season, that is, in early summer. This will help to ensure a good food supply at the recipient site and will minimize nutritional stress. Having an adequate food supply at the recipient site may also help reduce the possibility that tortoises will move away in search of a better area. Females should be established at the recipient site before males. The presence of resident females will help keep males from wandering once they are moved. Juveniles should be moved last so they can establish their burrows in relation to adult burrows. This will allow juveniles to minimize social contact with conspecifics but hopefully they will also stay in the same area. Moving tortoises in early summer will also allow the tortoises to become familiar with their surroundings and the locations of conspecifics before the mating season. This will better ensure a successful mating season in the year following relocation.

The traditional habitat of gopher tortoises was the longleaf pine/wiregrass association of the southeastern coastal plain (Auffenberg and Franz 1982, Lohoefener 1981). This habitat was characterized by open park-like stands of longleaf pine and a grass-dominated herbaceous layer. Habitat management for gopher tortoises should try to emulate this structure. Gopher tortoises are midway between specialist and generalist herbivores (Macdonald and Mushinsky 1988) and vegetation composition is not as important as vegetation structure.

The vegetation presence/absence data from this study can be converted to percent cover. This is a crude estimate of percent cover because it is the percent of sampling points in each array where at least one member of a vegetation category occurred (see Table 5 for data). Therefore, juveniles used areas with 25% grass (3.31 of 13), 33% shrubs (4.32 of 13), and 12% trees (1.51 of 13). When managing for gopher tortoises these values should be limits for each vegetation category. Native grass cover should be a minimum of 25% because grasses were only present in the habitat at 15% (1.95 of 13), but juveniles were using areas with 25% grass cover. This suggests that juveniles might use areas with even higher grass cover if they are available. Conversely, shrub cover should be a maximum of 33% because shrubs were present in the habitat at 55% (7.41 of 13), but juveniles were using areas with only 33% shrub cover. The same is true for tree cover; trees were present at 33% (4.25 of 13) in the habitat, but juveniles used areas with only 12% cover. Therefore, 12% should be the maximum cover managed for because juveniles selected areas with lower tree cover than what was available. Adults were not as restricted in habitat use so these limits will also benefit their management.

Spatial organization of vegetation is also important. Because larger open areas will allow for greater herbaceous diversity, shrubs and trees should be placed in clumps within a larger mosaic of grassy areas. Islands of trees and shrubs will also be important in creating larger areas of thermal cover. Exotics should be removed from sites. Management should encourage native grasses but also a variety of native herbs. In areas of low tortoise density a mosaic of natural disturbances similar to burrow mounds can be artificially created which will help herbaceous plants. Kaczor and Hartnett (1990) found that tortoise mounds were important colonization sites for many herbs. This has been shown in other grasslands by the action of burrowing mammals (Grant et al. 1980, Hobbs and Mooney 1985, Huntly and Inouye 1988, Peart 1988). Mowing and prescribed burns will also encourage herbaceous growth and limit the encroachment of trees and shrubs (Marshall and Stout 1990).

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PAPER II

PREVALENCE, AND DISTRIBUTION OF UPPER RESPIRATORY TRACT DISEASE (URTD) IN FLORIDA GOPHER TORTOISES

ABSTRACT

Exposure to *Mycoplasma agassizii* and Upper Respiratory Tract Disease (URTD) in free-ranging gopher tortoises was documented using a culture technique and an enzyme-linked immunosorbent assay (ELISA) developed for desert tortoises. Exposure to *M. agassizii* on Sanibel Island, Florida, was ubiquitous; no colonies or isolated areas were located free of this pathogen. On Sanibel Island 84.9% of tortoises tested were exposed to *M. agassizii*, and 30.3% of tortoises evaluated were clinically ill with URTD. Adults were significantly more likely than immatures to be exposed to *M. agassizii* and have clinical signs of URTD. Limited testing has confirmed exposure to *M. agassizii* in free-ranging gopher tortoises at six locations in three Florida counties. Free-ranging clinically ill tortoises have been documented at six locations in five Florida counties.

INTRODUCTION

Upper Respiratory Tract Disease (URTD) was first described in desert tortoises (*Xerobates agassizii*) in 1988 (Jacobson et al. 1991). URTD is characterized in early stages as a rhinitis with intermittent mucous discharge from the nostrils, mouth and eyes. As the disease progresses it may debilitate the tortoise leading to dehydration and emaciation. In rare cases sub-shell hemorrhaging may occur because of the disease or secondary infection. Death may occur directly or indirectly from secondary infection, starvation or dehydration (for a complete description of URTD pathology in desert tortoises see Brown et al. 1992, Jacobson et al. 1991). URTD is believed to be responsible for a reduction in desert tortoise density at the Desert Tortoise Natural Area (DTNA) from 200 per square mile to less than 20 per square mile in two years.

In 1991, a new species of Mycoplasma, *Mycoplasma agassizii*, (proposed species novum) was isolated from clinically ill desert tortoises (Mary Brown, pers. comm.). *M. agassizii* has been verified through transmission studies as the etiologic agent of URTD (Brown et al. unpubl. data). This mycoplasma is highly communicable between tortoises by direct contact, or indirectly by feeding on the same plants or inhabiting the same burrows (Mary Brown, pers. comm.). An enzyme-linked immunosorbent assay (ELISA) has been developed at the University of Florida to determine exposure to *M. agassizii* in desert tortoises (Schumacher et al. 1993).

In 1989, gopher tortoises (*Gopherus polyphemus*) on Sanibel Island, Florida, were described with clinical signs of URTD (McLaughlin 1990). Although not verified, this was the first report of URTD occurring in a free-ranging *Gopherus* species. Before this, URTD had not been substantiated in gopher tortoises although anecdotal reports from other parts of Florida did exist (Joan Diemer, pers. comm.). Based upon this occurrence, the objectives of this preliminary study were to:

1. Use culture and ELISA techniques developed for the desert tortoise to determine if URTD in gopher tortoises is caused by *M. agassizii*.
2. Determine the prevalence of URTD in gopher tortoises on Sanibel Island.
3. Document exposure to and distribution of *M. agassizii* and URTD in gopher tortoises off Sanibel Island.

METHODS

Study Area

Sanibel Island is a barrier island 1.6 kilometers off the coast of southwest Florida near Fort Myers, Lee County. The island is between 26°25' and 26°30' North, 82°00' and 82°11' West. The maximum elevation of the island is 4.3 m above sea level, the mean elevation is 1-1.5 m above sea level (Cooley 1955, McLaughlin 1990). Gopher tortoises primarily inhabit the upland areas of the island. The upland habitat is West Indian scrub with tropical and subtropical shrubs and trees within open grassy areas (McLaughlin 1990). Tortoises either occur in discrete colonies in undisturbed areas or more individually in areas divided by human development.

In addition to Sanibel Island, tortoises were sampled on Captiva, North Captiva, and Cayo Costa Islands. These barrier islands run in a line north of Sanibel. Captiva Island is connected by a bridge to Sanibel, North Captiva and Cayo Costa Islands can be reached only by boat. Habitat on all islands is similar to that on Sanibel but with less human development.

Additional tortoises were sampled in Lee County on the mainland. Sample sites were the future Caloosahatchee Regional State Park, along State Road 78 just south of Alva, Koreshan State Historical Site in Estero, and Pelican Landing Westinghouse development in Estero. These areas were characterized by slash pine (*Pinus elliottii*) and saw palmetto (*Serenoa repens*). In addition, incidental captive and free-range tortoises were sampled from around Florida.

Six clinically ill gopher tortoises from Sanibel Island were cultured for the presence of *M. agassizii*. Culturing was done by researchers from the University of Florida. All six tortoises were from the same colony and consisted of two juveniles, two adult females, and two adult males. The tortoises were held at Care and Rehabilitation of Wildlife (CROW) on Sanibel Island where they were given food and water. Cultures were taken using nasal washes following the procedure described in Jacobson et al. (1991).

Tortoises sampled were caught by hand in the field (in a few cases tortoises were trapped with live traps or pitfalls as part of another study). I took a series of morphometric measurements and body weights and determined the sex and relative age for each tortoise. Criteria for aging and sexing followed Diemer (1992b), Landers et al. (1982), and McRae et al. (1981a). I gave each tortoise a unique identification number using a marginal scute drilling technique modified from Cagle (1939). All equipment was rinsed with 95% isopropyl alcohol between uses.

A total of 311 blood samples were taken from 132 Sanibel tortoises and 29 tortoises from the other areas. Blood was drawn from an occipital sinus (n=210), forelimb vein (n=91), lateral head vein (n=5), shoulder vein (n=3), or heart (n=2). One cc of blood per kilogram of body weight, never exceeding two cc, was taken per tortoise. The same tortoise was not sampled again for at least two weeks. I used 3cc syringes with 22 gauge needles or 1cc syringes with 25 gauge needles depending on the size of the tortoise. Occasionally the needles were heparinized to prevent clotting. Blood was immediately transferred to 3cc Lithium Heparin vacutainers and kept on cool packs until it was brought to the laboratory.

All blood samples were centrifuged on Sanibel Island and the serum drawn off. Serum was frozen until shipment to the University of Florida for testing. Samples were sent by overnight mail in cool packs. Serum samples were frozen at the University of Florida until testing.

An enzyme-linked immunosorbent assay (ELISA) developed for desert tortoises was used to detect *M. agassizii*-specific antibodies in gopher tortoises (see Schumacher et al. 1993 for a complete description of the ELISA). Each serum sample was assayed at 1:2 and 1:10 dilutions. These dilutions were converted to ratios of the raw sample scores to the mean of negative controls. The negative control was a plasma sample taken from a known healthy animal and run with each batch of serum samples. Development of cutoff values for positive exposure to *M. agassizii* follows Kao et al. (1993). Twenty-three healthy tortoises from Sanibel were used to determine ratio cutoff values. I selected these tortoises because they had no history of clinical illness and had low ratio values. The means of these negative controls plus three standard deviations were used to determine cutoff values for exposure to *Mycoplasma agassizii.* The 2x sample dilution can give false negatives (Kao et al. 1993); therefore, we only used the 10x dilution to determine exposure.

The disease condition of each tortoise was evaluated based on its clinical history and serum results. Tortoises were evaluated as unexposed if they had no clinical history of URTD and all serum results were negative. I evaluated tortoises as exposed-healthy if they had only a single positive serum result and did not show clinical signs of URTD. If they had multiple serum results, they were also evaluated as exposed-healthy if subsequent results did not exceed 3SD (of negative controls) of their first serum result. Tortoises were evaluated as clinically ill if they had positive serum results and showed clinical signs of URTD. Tortoises not showing clinical signs were also evaluated as ill if they had multiple positive serum results and subsequent results had at least a 3xSD (of negative controls) increase from their first serum result.

RESULTS

M. agassizii was successfully cultured from only one juvenile gopher tortoise. The mycoplasma was not found in the other five tortoises, but this is not surprising because the culturing technique is delicate and can be contaminated by other organisms that mask the mycoplasma. In addition, these tortoises were cultured on Sanibel, and the media had to be packed in dry ice and transported to the University of Florida.

A total of 40 tortoises evaluated (24.8%) had clinical signs of URTD. Signs varied in severity from minor mucous discharge from nares and eyes to heavy mucous exudate in the nares, eyes, and mouth. In advanced cases tortoises exhibited extreme lethargy, emaciation, and dehydration. In one extreme case I found massive sub-plastral hemorrhaging while preforming a necropsy on a tortoise that had died of URTD. Tortoises with URTD did not always exhibit clinical signs, some days ill tortoises appeared healthy.

Prevalence

Tortoises from off Sanibel Island were sampled only for verification and distribution of URTD. Only 29 off island tortoises were tested, some specifically because they were thought to be ill, therefore, these tortoises were not used in analyses. Of these tortoises, 37.9% were sero-positive (n=11), four of which also had clinical signs of URTD.

Of Sanibel tortoises tested, 84.9% were sero-positive for exposure to *M. agassizii*. There was a significant age effect on exposure to *M. agassizii* (X^2=25.312, df=2, p<.001).

Immature gopher tortoises were less likely to be exposed than adult males and adult females (Table 1). I evaluated 30.3% of Sanibel tortoises as clinically ill; 90% of these tortoises had clinical signs of URTD (36 of 40 tortoises). There was also a significant age/sex effect on URTD evaluation (X^2=29.924, df=4, p<.001). Adult males were more likely to be ill than adult females and adults were much more likely to be ill than immatures (Table 2).

Distribution

Exposure to *M. agassizii* and URTD was ubiquitous on Sanibel Island. All large discrete colonies of gopher tortoises on Sanibel Island had high exposure to *M. agassizii* and clinically ill tortoises (Figure 1). Seventeen tortoises were tested that were not associated with colonies, mostly from residential areas. Of these tortoises, 13 had been exposed and two were clinically ill with URTD. Three tortoises were tested from the J.N. "Ding" Darling National Wildlife Refuge that also were not associated with colonies; all three were exposed to *M. agassizii.* I was unable to locate any colony or area on Sanibel Island unexposed to *M. agassizii* despite efforts to locate such areas.

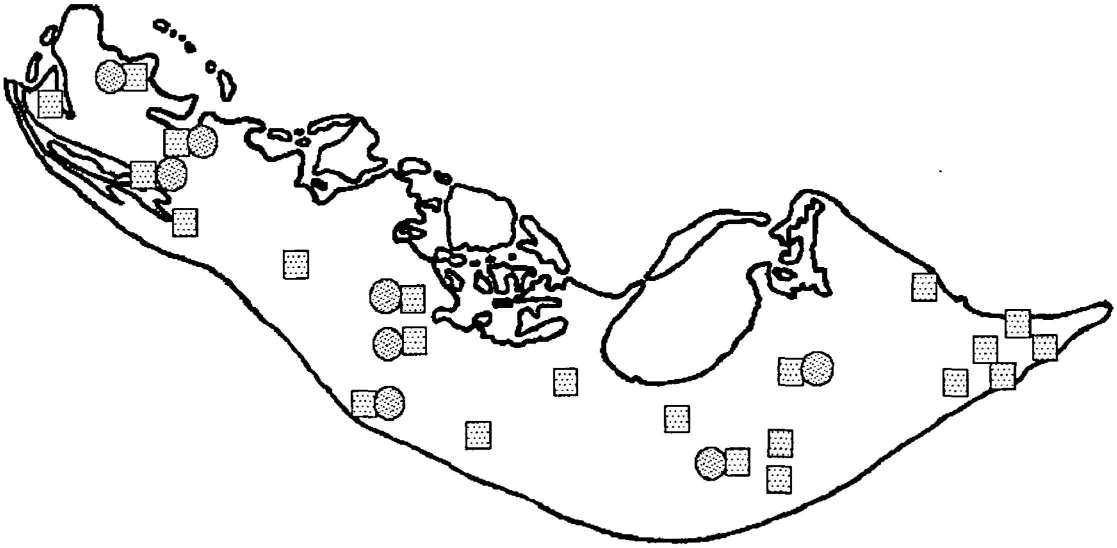
Free-ranging gopher tortoises that tested positive for exposure to *M. agassizii* in this study were from: 1) Sanibel Island, Lee County; 2) North Captiva Island, Lee County; 3) Pelican Landing, Westinghouse development, Estero, Lee County; 4) Koreshan State Historical Site, Estero, Lee County; 5) Emerald Bay development, Collier County; and 6) Florida Atlantic University (FAU), Fort Lauderdale, Broward County; (Figure 2). Captive gopher tortoises tested positive for exposure to *M. agassizii* at: 1) Lee County

Table 1. Serum sample ELISA results indicating exposure to *M. agassizii* of tortoises on Sanibel Island.

Result	Adult Male	Adult Female	Immature	Total
Negative				
n	2	2	16	20
%	5.9	3.6	38.1	15.1
Positive				
n	32	54	26	112
%	94.2	96.4	61.9	84.9
Total				
n	34	56	42	132
%	25.8	42.4	31.8	100.00

Table 2. Clinical health evaluation of URTD of tortoises on Sanibel Island.

Evaluation	Adult Male	Adult Female	Immature	Total
Unexposed				
n	2	2	15	19
%	5.9	3.6	35.7	14.4
Exposed				
n	16	34	23	73
%	47.1	60.7	54.8	55.3
Ill				
n	16	20	4	40
%	47.1	35.7	9.5	30.3
Total				
n	34	56	42	132
%	25.76	42.42	31.82	100.00



▦ Sero-positive tortoises occurring in a colony or individually

● Clinically ill tortoises occurring in a colony or individually

Figure 1: Distribution of colonies or individuals affected by URTD on Sanibel Island, Florida.

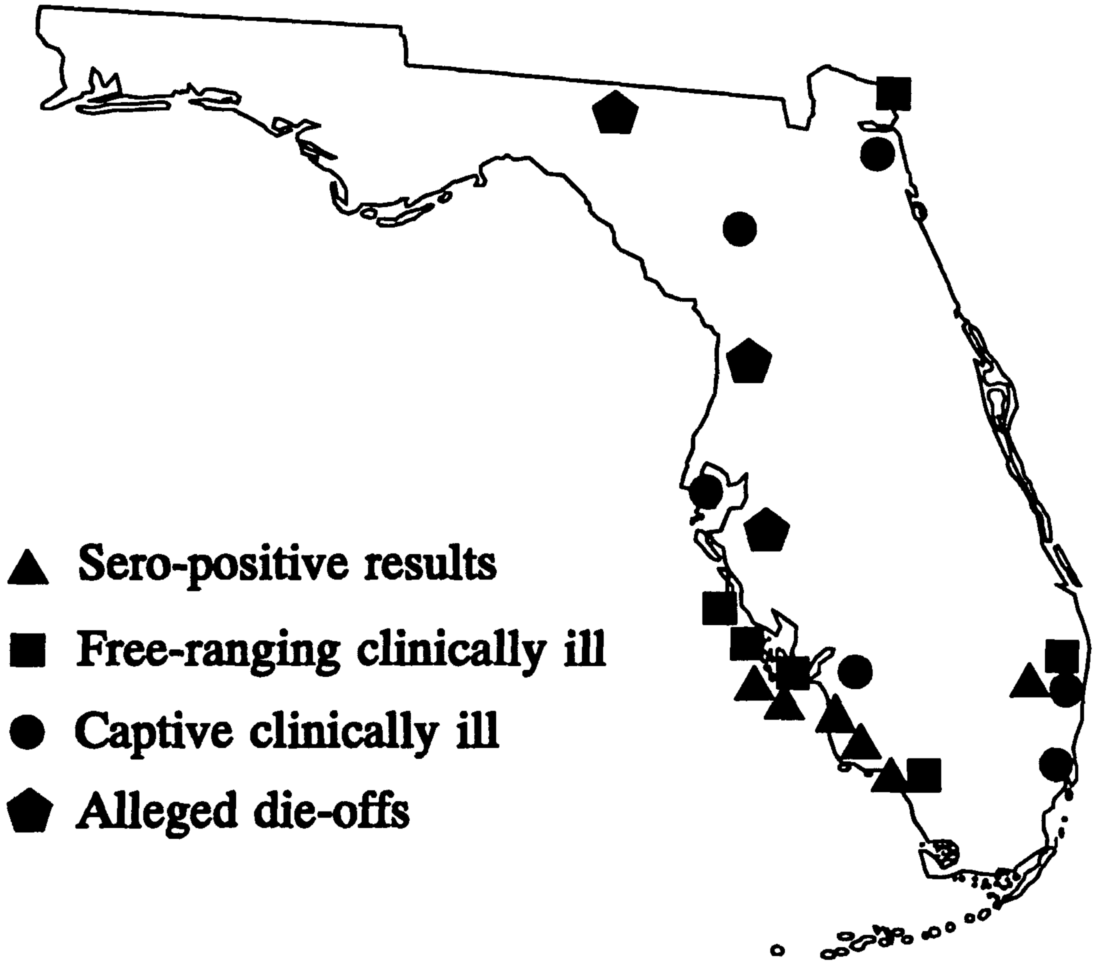


Figure 2. Known distribution of *M. agassizii* and URTD in Florida., see text for location descriptions.

Nature Center, Fort Myers, Lee County, original locations unknown; and 2) CROW, Sanibel Island, Lee County, originally from near State Road 80 near Labelle, Lee County, and Cape Coral, Lee County (Figure 2).

The present study and other research (Jacobson unpubl. data, Joan Diemer pers. comm.) documented free-ranging gopher tortoises with clinical signs of URTD on 1) Sanibel Island, Lee County; 2) Gasparilla Island, Lee County; 3) Little Gasparilla Island, Charlotte County; 4) Emerald Bay development, Collier County; 5) FAU, Fort Lauderdale, Broward County; and 6) Summer Beach development, Nassau County (Figure 2). Symptomatic captive tortoises have been seen in 1) Jacksonville, Duval County; 2) Miami educational facility, Dade County; 3) Fort Lauderdale, Broward County; 4) Moccasin Lake Nature Center, Pinellas County; 5) Gainesville, Alachua County; and 6) Lee County Nature Center, Lee County (Figure 2). In addition there have been reports of alleged gopher tortoise die-offs from 1) Highway 255, north of Day, Madison County; 2) Withacoochee State Forest, Citrus County; and 3) Little Manatee River State Park, Hillsborough County (Joan Diemer pers. comm.).

DISCUSSION

The existence of URTD in free-ranging gopher tortoises has been confirmed primarily from Sanibel Island, but also from other areas of Florida. Results from this preliminary study suggest clinical signs of URTD are similar in gopher tortoises and desert tortoises. Adults are at a higher risk of exposure to *M. agassizii* and developing URTD because of their larger home range sizes and more frequent social encounters (Beyer 1993, Diemer 1992a, McLaughlin 1990, McRae et al. 1981b). Adult males travel extensively during the breeding season visiting female burrows and fighting other males to attain dominance within the colony. Both adult males and adult females use many burrows throughout the year (Beyer 1993), and when these burrows are vacant other tortoises will use them. Juveniles are at a lower risk even when they occur within affected colonies because of their secretive lifestyle and minimal social interactions (Beyer 1993, Wilson et al. In Press). Juveniles primarily use one or two burrows they dig themselves and avoid contact with conspecifics.

The prognosis of gopher tortoises exposed to *M. agassizii* is yet unknown; however, the potential for drastic population reductions similar to those seen in desert tortoises may exist. Within the eleven months of this study, 16% (8 of 56) of tortoises evaluated from one Sanibel Island colony died directly from URTD or indirectly from secondary infections they were unable to fight off in their weakened state. This figure is probably conservative because tortoises may have died in their burrows and were not found.

Sanibel Island, however, may not be a good predictor of how gopher tortoise populations elsewhere will respond to URTD because of the history and density of tortoises on the Island. There is no documentation on the origin of gopher tortoises on Sanibel Island, however, the native population was augmented in 1978 by the release of 108 tortoises from the Edison Festival of Light annual gopher tortoise races (Dietlein and Smith 1979). Before 1978, gopher tortoises were collected from throughout their range for tortoise races in Fort Myers. After 1978, the races were prohibited, and the tortoises from the last race were released on Sanibel Island. No documentation exists on the origin of each tortoise, but most were not from southwest Florida and approximately 30 came from south Georgia (Dietlein and Smith 1979). In addition, illegal dumping on Sanibel from around southwest Florida probably has occurred and still occurs because the island is thought of as a wildlife sanctuary (Erick Lindblad pers. comm.).

Sanibel Island has been heavily developed, and tortoise habitat has been lost (McLaughlin 1990). Tortoises on development sites have been relocated into smaller areas with less available habitat. As a result the density of gopher tortoises on Sanibel is artificially high. The history and density of tortoises may have been responsible for both the introduction of *M. agassizii* and creation of favorable predisposing factors for the development and spread of URTD.

As tortoises are condensed into smaller areas of lower habitat quality, stresses will increase. Nutritional stress increases with greater competition for a reduced food base. Social stresses may also increase. Research has shown a high level of social organization in North American tortoises (Aguirre et al. 1984, Auffenberg 1977, Berry 1986, Burke

1989, McRae et al. 1981). Tortoises are not territorial but instead develop a dominance hierarchy that determines which males will be responsible for most of the breeding. In addition, adult males have extended movements and burrow use in the late summer and fall which allows them to familiarize themselves with the location of conspecifics before the breeding season (Beyer 1993). As tortoises are moved, these social bonds are broken and new ones must be established which can induce stress on the entire colony. These stresses may be potential predisposing factors affecting the severity and spread of URTD (Jacobson et al. 1991, Fowler 1980).

Although the situation on Sanibel may be unique (dense, mixed genetic tortoise population), it is a model for what can occur elsewhere. Florida is becoming increasingly developed and current management practices are to relocate tortoises from development sites into smaller set aside areas that may or may not have tortoises already there. As a result, similar predisposing factors are being created, and exposure to *M. agassizii* has now been documented throughout Florida.

This research was done to determine if techniques developed for desert tortoises could be used with gopher tortoises. The study was not specifically designed to investigate URTD in gopher tortoises; however, the findings have management implications and identify areas for future research. Long term management of gopher tortoises will depend on identifying areas and populations not exposed to *M. agassizii*. These populations may become important for brood stock in repopulating areas where gopher tortoises have been eliminated by URTD. In addition, current relocation policies for gopher tortoises must be evaluated. Exposed tortoises must be identified to prevent their being moved into areas that may be free of *M. agassizii*.

Future research is needed to determine the course of the disease in gopher tortoises from exposure to long term disposition. A few tortoises had clinical signs of URTD in 1989 but appeared healthy in 1992. Whether they have successfully fought off URTD or are in remission, however, is not known. All of these tortoises had positive serum results in 1992 and can probably still transmit *M. agassizii*. Whether or not tortoises can naturally become free of *M. agassizii* once affected is not known. The ELISA test only identifies tortoises that have been exposed to *M. agassizii*; it does not provide an evaluation of the disease condition of a tortoise. In addition, the ELISA test does not identify tortoises that are active carriers and can transmit *M. agassizii* to other tortoises. A new test is being developed at the University of Florida that will provide information on the disease condition of a tortoise, and will be easier to administer and cost less. This test will facilitate future research and will help prevent the destruction of tortoises with clinical signs, but have ailments other than URTD.

Gopher tortoises are currently protected by state laws wherever they occur. A subpopulation in Louisiana is federally listed as threatened. In Florida, the gopher tortoise is a species of special concern. Gopher tortoise populations are declining, therefore, caution should be exercised before euthanasia policies are developed for affected colonies. In addition, any proposed status changes for the gopher tortoise, whether state or federal, should consider the potential future impacts of URTD.

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GENERAL SUMMARY

Juvenile gopher tortoises have smaller home ranges than adults. Juveniles restrict their burrow use to one or two primary burrows throughout the year. Adult males had larger home ranges than females during the summer, but females had larger home ranges during the spring. Home ranges in other seasons could not be analyzed because of insufficient data. Both adult males and females used many burrows in all seasons, and males increased burrow use during summer and fall. Home range size and burrow use shows mating, or related activity, may occur later in the year than what has been reported.

There was no time of day affect on tortoise activity. Activity, however, was affected by age/sex class and season. Adult females were most active in the spring, adult males and juveniles were most active in the summer. Overall, males were the most active and juveniles were the least active. Juveniles did not have intraspecific contact even though their home ranges overlapped with adults.

Juveniles were the most habitat restricted. Juveniles were more often found in open, grassy areas with reduced tree and shrub cover. Adults used habitat more in relation to what was available for burrow locations, but females used open, grassy areas, or areas with reduced tree cover for burrow locations in the spring. All tortoises used more open areas for activity locations but adults were not as restricted to these areas as were juveniles.

Upper Respiratory Tract Disease (URTD) is ubiquitous on Sanibel Island. Of tortoises tested, 85% had been exposed to *M. agassizii,* the known etiologic agent of

URTD. Juveniles were least likely to be exposed because of their smaller home ranges and reduced social contact. Exposure to *M. agassizii* and URTD have been confirmed in other areas of Florida and unconfirmed in South Carolina.

The management implications of juvenile habitat relations and URTD are discussed. Management recommendations are included.

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APPENDIX A: MORPHOLOGICAL CHARACTERISTICS BY AGE/SEX CLASS OF GOPHER TORTOISES ON SANIBEL ISLAND, FLORIDA

Shell dimensions and weights of tortoises from Sanibel Island, Lee County, Florida. Variables are: TL = total length; CL = carapace length; PL = plastron length; W = width; TH = thickness; AN = length of anal notch opening; AT = anal scute thickness; AW = width between tips of anal scutes; PC = plastron concavity; WT = weight. All linear dimensions are in mm, weights are in g.

	Hatchlings			Juveniles			Subadults			Adult Females			Adult Males		
Var	n	x̄	SD	n	x̄	SD	n	x̄	SD	n	x̄	SD	n	x̄	SD
TL	4	55.8	1.6	24	109.7	26.0	31	218.9	60.4	72	324.8	26.6	39	311.4	23.8
CL	4	55.2	1.2	24	106.8	24.8	31	209.0	56.3	72	308.9	24.6	39	293.7	23.7
PL	4	52.2	2.4	24	105.7	27.8	31	208.1	57.5	72	305.1	25.1	39	293.4	22.6
W	4	46.7	1.9	24	81.7	16.4	31	150.5	39.4	72	223.1	25.1	39	208.2	16.2
TH	4	26.8	1.6	24	46.9	9.7	31	89.0	24.1	72	129.8	17.7	39	126.4	10.3
AN	2	8.3	0.5	23	12.2	4.2	31	28.0	8.2	72	52.9	46.9	38	39.2	4.4
AT	1	0.9		19	1.7	0.7	31	6.1	3.4	72	10.1	2.3	38	11.2	2.2
AW	2	7.7	0.3	23	14.6	4.0	30	38.0	13.0	71	56.1	6.5	38	64.7	13.7
PC	1	0.0		19	0.3	0.7	27	4.5	4.0	66	4.6	2.4	38	15.8	4.9
WT	3	35.3	1.2	23	237.1	145.2	31	1804.2	1225.7	72	5238.9	1310.5	37	4487.8	1035.0

APPENDIX B: CLUTCH SIZES DETERMINED FROM RADIOGRAPHS OF GOPHER TORTOISES ON SANIBEL ISLAND, FLORIDA

Clutch size of gopher tortoises from Sanibel Island, Florida. Data from 1989 is from McLaughlin (1990). Overall clutch size is combined data from this study and McLaughlin (1990). Only clutches determined from radiographs are included.

		Clutch Size			
Year	n	Minimum	Maximum	Mean	SD
1989	16	1	16	6.94	3.97
1991	17	3	17	7.71	3.84
Overall	33	1	17	7.33	3.86

APPENDIX C: PLANT SPECIES FOUND AT THREE STUDY SITES ON SANIBEL ISLAND, FLORIDA

Numbers of plants recorded at random transect points and tortoise locations from three study sites on Sanibel Island, Florida. JTT = Johnston Tract transect points; JTL = Johnston Tract tortoise locations; HLT = Heron's Landing transect points; HLL = Heron's Landing tortoise locations; DDT = Ding Darling transect points; DDL = Ding Darling tortoise locations.

Common Name	Scientific Name	JTT	JTL	HLT	HLL	DDT	DDL
Grasses and Sedges							
Crow foot grass	*Dactyloctenium aegyptium*	2	6	3		1	
Finger grass	*Digitaria* spp.	35	46	37	42	3	6
Foxtail grass	*Setaria* spp.	10	12	5	7	2	1
Miscellaneous grass		52	83	22	25	9	3
Hairy grama grass	*Bouteloua hirsuta*		3				
Hurricane grass	*Fimbristylis* spp.				1		
Miscellaneous rush	*Juncus* spp.	1					
Muhly grass	*Muhlenbergia capilliformis*	13	10	21	28		
Nut grass	*Scleria* spp.	1	1	1	1		
Panic grass	*Panicum* spp.	9	27				
Saw grass	*Cladium jamaicensis*	1					
Sand spur	*Cenchrus* spp.	2	7	7	5		1
Miscellaneous sedge	*Carex* spp.	29	21	7	18	11	3
Sea oats	*Uniola paniculata*			3	19		
Cultivated grass			1	11	2		
Spartina	*Spartina* spp.						
Saint augustine grass	*Stenotaphrum* spp.	14	19	9	1	1	

Common Name	Scientific Name	JTT	JTL	HLT	HLL	DDT	DDL
White bracted sedge	*Dichromena latifolia*	6	3				
Wire grass	*Aristida* spp.		3				
Herbs							
Alligator weed	*Alternanthera philoxeroides*	8	22	4	6		
Bed straw	*Galium obtusum*	1		1			
Bed straw	*Galium hispidulum*	15	14	9	10		
Blueheart	*Buchnera americana*			1			
Butterfly pea	*Centrosema virginiana*	3	4	1			
Camphor weed	*Pluchea rosea*	5	2			1	
Capraria	*Capraria biflora*	5	8	3	2	3	
Cassia	*Cassia* spp.	1					
Cape weed	*Lippia nodiflora*	1		1		1	
Cow pea	*Vigna* spp.	7	8	3			
Coin vine	*Dalbergia ecastophyllum*			19			
Crownbeard	*Verbesina virginia*	12	22			3	3
Daisey fleabane	*Erigeron quercifolius*	1		2			
Dodder	*Cuscuta campestris*	1	11	24	24	2	
Dog fennel	*Eupatorium capillifolium*	35	16	2	5	3	
Dollar-weed	*Rynchosia* spp.	1					
Gopher apple	*Licania michauxii*	80	81				
Golden aster	*Pityopsis* spp.	2					
Goldenrod	*Solidago* spp.	1					
Ground cherry	*Physalis elliotti*	2	10			5	4
Ipomoea	*Ipomoea* spp.	1		7	5	7	1

Common Name	Scientific Name	JTT	JTL	HLT	HLL	DDT	DDL
Kalanchoe	*Kalanchoe* spp.	3	7				
Lemon grass		13	7				
Late flowering bone set	*Eupatorium serotinum*	5	1			3	
Marsh pink	*Sabatia campanulata*		1				
Miscellaneous composite		1	1				
Miscellaneous euphorbaceae						1	1
Miscellaneous herb		3	4	1	2		
Milk pea	*Galactia* spp.	3	3				
Miscellaneous legume		5				3	1
Mother-in-law's tongue	*Sanseviera quianenesis*	10	16				
Miscellaneous rubiaceae		7					
Periwinkle	*Vinca* spp.		8				
Pigweed	*Chenopodium album*	5					
Poor man's vetch	*Mentzelia* spp.	37	3			6	
Poison ivy	*Toxicodendron radicans*	1	41	75	5		
Rabbit bells	*Crotalaria* spp.	8	5		39	2	
Rabbit foot fern	*Polypodium* spp.	9	7				
Rattlebox	*Crotalaria* spp.	29	21				
Ragweed	*Ambrosia* spp.		32	19	36		
Pimpernell	*Samolus* spp.					1	
Scorpian's tail	*Heliotropium* spp.		5	3			
Semaphore eupatorium	*Eupatorium mikanioides*			1			
Sida	*Sida* spp.		7	10	14		1
Smilax	*Smilax* spp.	13	22	5	5	3	
Snowberry	*Chiococca alba*	4	22	6	3	1	
Spanish needle	*Bidens pilosa*	29	64	50	49	3	5
Spurge	*Chamaesyce hypericifolia*	1	6	2	1	11	

Common Name	Scientific Name	JTT	JTL	HLT	HLL	DDT	DDL
Tillandsia	*Tillandsia* spp.	1	5	17	16		
Trailing wild bean	*Strophostyles* spp.		9				5
Virginia creeper	*Parthenocissus quinquefolia*	34	34	1	5		
Wild coffee	*Psychotria* spp.	50	27	6	5	7	
Wild hemp	*Mikania cordifolia*	8	1			6	
Wild poinsettia	*Poinsettia* spp.					5	
Wild sensitive plant	*Chamaecrista* spp.			3	1	1	
Yellowtop	*Flaveria linearis*	8	1	3			
Shrubs							
Agave	*Agave* spp.	33	60	3	2		
Brazilian pepper	*Schinus terebinthifolius*	217	217	42	19	11	1
Buckthorn	*Bumelia* spp.	10	9				
Coral bean	*Erythrina herbacea*					3	
Golden creeper	*Ernodea littoralis*		3	29	40		
Gray nickerbean	*Caesalpinia crista*		3	4	1		
Guava	*Psidium guajava*		1				
Joewood	*Jacquinia keyensis*			4	3	3	
Lantana	*Lantana* spp.	37	82	3	7		1
Leather fern	*Acrostichum danaeaefolium*	11	3			4	
Mahoe	*Hibiscus tiliaceus*					3	
Myrsine	*Myrsine quianensis*	56	50	40	15	4	2
Night blooming cereus	*Cereus* spp.		4				
Necklace pod	*Sophora tomentosa*		3	7			
Papaya	*Carica papaya*		2				

Common Name	Scientific Name	JTT	JTL	HLT	HLL	DDT	DDL
Prickly pear cactus	*Opuntia* spp.		11	3			
Salt bush	*Baccharis* spp.	21	23			6	
Spanish bayonet	*Yucca aloifolia*	16	18	10	5		
Varnish leaf	*Dodonaea viscosa*	4					
Wax myrtle	*Myrica cerifera*	104	57	12	18		
White indigo berry	*Randia aculeata*	33	54	12	4	9	1
Wild lime	*Zanthoxylum fagara*	21	16			5	1
Wild olive	*Forestiera segregata*	65	80	54	37	7	1
Trees							
Australian pine	*Casuarina equisetifolium*	10	2	4	1		
Buttonwood	*Conocarpus erecta*			32	3	7	
Ear-leafed acacia	*Acacia* spp.	4					
Exotic related to stopper	*Eugenia* spp.		4				
Gumbo limbo	*Bursera simaruba*	9	15	1		11	3
Leadwood	*Leucaena leucocephala*	4	3				
Red mangrove	*Rhizophora mangle*			11	12		
Sabal palm	*Sabal palmetto*	137	141	26	42	15	
Sea grape	*Coccoloba uvifera*	7	22	76		6	3
Strangler fig	*Ficus aurea*	4	4			8	1
Tamarind	*Lysiloma bahamense*					3	
White mangrove	*Laguncularia racemosa*			9			
White stopper	*Eugenia axillaris*	6	5			7	