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The Effects of Invasive Cogongrass (*Imperata cylindrica*) on the Threatened Gopher
Tortoise (*Gopherus polyphemus*)

by

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A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
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ABSTRACT

The gopher tortoise (*Gopherus polyphemus*) is critical to upland communities and considered a keystone species. A recent threat to gopher tortoise habitat is the invasive cogongrass (*Imperata cylindrica*), which spreads rapidly, eliminating native vegetation. This study consisted of three experiments to investigate the effects of the cogongrass on a population of gopher tortoises. A feeding experiment revealed that individuals readily ate native vegetation, but would not eat cogongrass. A tracking experiment showed that there was a significantly different mean angle of movement between individuals whose home ranges were outside cogongrass compared to those that overlapped cogongrass, indicating that the presence of cogongrass disrupts normal movement patterns. An orientation experiment showed that individuals outside cogongrass oriented in a direction that would take them to their home burrow, while individuals inside cogongrass showed no preferred directional orientation. Cogongrass effectively eliminates the gopher tortoises' food source and habitat, and disrupts orientation. The experiments indicate that a cogongrass infestation has the capacity to eliminate populations of gopher tortoises if its spread is not checked.

Introduction

Invasive species are a threat to worldwide biodiversity, second only to habitat loss (Allendorf and Lundquist 2003). The effects of invasion vary from none to severe. If a species doesn't pass the introduction phase, then the effect of the invasive on the community is non-existent. Species that do become invasive can have severe ecological and economical consequences. In the United States alone, an estimated 50,000 non-native species cause estimated economic losses of over 125 billion USD per year (Allendorf and Lundquist 2003). The ecological consequences include a loss of diversity, extinction of native species, as well as physical and chemical changes in the abiotic environment (Vitousek *et al.* 1996).

Adventive species must go through four stages to be considered invasive. The first is introduction, or the arrival of members of the species to a new area. Not all introduced species survive in a new environment, but if the area is not immediately unsuitable the second stage, escape and subsequent colonization or reproduction, occurs. The third stage is naturalization or establishment, where the species can maintain its population in the new area without human assistance (Di Castri 1989). The final stage is spread or invasion, in which the established population of the introduced species branches out and colonizes new areas. In the end, only about 2.5% of adventive species reach the invasion stage (Di Castri 1989).

Many species colonize new areas naturally, although humans have greatly increased the natural expansion rate of species. Non-native plant species may be introduced accidentally, via the nursery plant trade, as contaminants of agricultural seed, or as stowaways or hitchhikers on global travelers. Species are also introduced deliberately, for agricultural or biological control purposes (Primack 1998).

Any introduced species has the potential to become invasive, but some traits appear to be characteristic of successful invasives. Invasive species tend to have large geographical ranges and be more tolerant of variable physical conditions (Sakai *et al.* 2001). Often invasive animals are generalist feeders, with a broad diet (Sakai *et al.* 2001). Good invasive species have a high reproductive rate (Crawley 1986). Any species already intentionally cultivated by humans has an advantage and may escape cultivation and spread. Propagule pressure (the number of individuals introduced and the number of independent introductions) is the most important factor for predicting the establishment success of a non-native species (Allendorf and Lundquist 2003), but other factors can be critical as well, such as the presence of mutualists (Crawley 1986) or the absence of competitors and predators (Mack *et al.* 2000).

Certain characteristics of communities are associated with a higher susceptibility to invasion. Disturbed communities and those in fragmented habitat may be more susceptible to invasion, and communities with low diversity are also believed to be more open to invasion because of a lack of functional groups leaving open niches (Hobbs and Huenneke 1992, Sakai *et al.* 2001). Lower species diversity also increases the likelihood that the invaded community will lack the equivalent of the introduced species' usual predators, parasites, or competitors that normally regulate its population growth (Mack et

al. 2000). Islands have more invaders than continents, possibly because of a paucity of native island species leaving niches unoccupied (Elton 1958, Gordon 1998).

Recently the Ecological Society of America (ESA) issued recommendations for the federal government to improve the management of non-native invasive species. These include focusing prevention efforts on pathways already known to be major sources of non-natives, screening potential live imports for invasive potential before allowing entry, and improving monitoring of currently established invasives. The ESA report urges the allocation and use of emergency funding for rapid responses to newly established non-native species, when elimination is much easier to achieve. In situations where eradication is not possible, funds should be available to develop and implement “slow-the-spread” strategies (Lodge *et al.* 2006).

Currently an invasive grass, cogongrass (*Imperata cylindrica*), is spreading throughout Florida. Cogongrass has been documented in 34 of the 67 counties in Florida (Wunderlin 2000), including areas that are occupied by gopher tortoises (*Gopherus polyphemus*). The gopher tortoise is considered a keystone species, critical to upland communities, because of the numerous commensal species its burrows support (Eisenberg 1983). The gopher tortoise is listed as threatened in Mississippi and Louisiana, and west of the Tombigbee and Mobile Rivers in Alabama (USFWS 1992), and is currently a “species of special concern” within Florida (Mushinsky *et al.* 2006), although an uplisting to “threatened” status is expected once a new management plan is approved. Therefore, the cogongrass invasion has the potential to harm the gopher tortoise and its associates, and their habitats, both directly and indirectly.

The cogongrass invasion probably is encroaching on the tortoises' habitat and eliminating their food source by out-competing native vegetation. Such a direct effect on a native herbivore is unusual. Invasive non-native plants in Florida have altered habitat structure, soil erosion, water table depth, and nitrogen fixation, and have competed with native plants for light, nutrients, and water (Gordon 1998). Invasive plants have indirectly affected grassland bird densities by changing habitat structure and reducing the abundance of arthropod prey (Scheiman *et al.* 2003, Dudley and DeLoach 2004), and the development of American toad (*Bufo americanus*) tadpoles was negatively affected by the presence of the invasive wetland plant purple loosestrife (*Lythrum salicaria*) (Brown *et al.* 2006). The cogongrass invasion may be a rare example of a non-native plant directly and negatively impacting a protected native herbivore.

Objectives

This study evaluates the relationship between an expanding monoculture of cogongrass and a population of gopher tortoises in central Florida. The apparent threat of the invasive grass to this population, and, by extension, to other populations throughout the range of the gopher tortoise, is assessed by determining whether gopher tortoises consume the less-nutritious cogongrass when preferred native vegetation is no longer available, determining whether tortoises use areas of cogongrass within their potential home ranges, and comparing the navigational ability of tortoises traveling within the cogongrass to those traveling in adjacent, non-invaded habitat.

Methods

Study Species

The gopher tortoise (*Gopherus polyphemus*) is found in open-canopy areas with sandy well-drained soils in the southeastern coastal plain from the extreme south of South Carolina to southeastern Louisiana and peninsular Florida (Auffenberg and Franz 1982, Ernst *et al.* 1994). Individuals are long-lived and reach sexual maturity at various ages depending on their location, with size, rather than age, as a better predictor of maturity. Females reproduce at approximately 24 cm carapace length (CL) throughout much of the species' range (McCoy *et al.* 1995, Mushinsky *et al.* 1994). The effective rate of reproduction is approximately five hatchlings per mature female per 10 years, assuming annual egg laying (Ernst *et al.* 1994), with sometimes low hatchling success (Epperson and Heise 2003).

The gopher tortoise digs extensive burrows for shelter from the elements and predation (Douglass and Layne 1978, Mushinsky *et al.* 2006), and thus requires deep, well-drained soil for burrow construction. A gopher tortoise spends a majority of time in a burrow (Mushinsky *et al.* 2006), and most activity is conducted in a home range surrounding the burrow. Sizes of adult female home ranges vary from 0.08 to 0.56 ha, while those of adult males vary from 0.45 to 1.27 ha (Diemer 1992, McRae *et al.* 1981, Mushinsky *et al.* 2006).

Grasses (family Poaceae), especially broad-leaved grasses, are a large component of a gopher tortoise's diet, particularly during the winter when leafy forbs are unavailable (Garner and Landers 1981, MacDonald and Mushinsky 1988). Forbs, especially legumes, increase in importance as grasses become more fibrous in the summer and fall (Garner and Landers 1981). Most water is obtained from food, increasing the importance of succulents in the diet (Garner and Landers 1981), and sometimes from drinking from the burrow apron when raining (Ashton and Ashton 1991).

Humans are the leading cause of adult mortality in gopher tortoises (Ernst *et al.* 1994). Since the 1950s the greatest threat to the gopher tortoise has been habitat loss (Auffenberg and Franz 1982, Mushinsky *et al.* 2006). High-quality habitat for the tortoises is also prime habitat for housing development in Florida, and the human population of Florida has grown rapidly by as much as 23% per year, increasing development pressure and habitat loss (U.S. Census Bureau 2002). Auffenberg and Franz (1982) predicted a 68% decline in gopher tortoise habitat by 2000. The decline occurred even more rapidly, and by the 1990s only 4.2% and 12.3% of prime gopher tortoise scrub and sandhill habitats, respectively, remained in Florida (Mushinsky *et al.* 2006). The encroachment of the cogongrass will compound this problem of rapid habitat loss. As habitat is lost and a gopher tortoise population is compressed into small areas of high population density, the size and age structures of the population change. The large reproductive individuals emigrate, limiting the future hatching and recruitment of small individuals in that population. The remaining medium-sized individuals become stressed and stop reproducing. Although the population persists because of the longevity of the

species, the population will eventually become extinct because of the lack of reproduction and recruitment (McCoy *et al.* 1995, Mushinsky *et al.* 2006).

Cogongrass (*Imperata cylindrica*) spreads rapidly and is considered one of the ten worst weeds worldwide (Coile and Shilling 1993). Cogongrass is a fast-growing C₄ grass, able to survive in hot, dry climates. The leaves have rough serrated edges and contain silica bodies, discouraging insect herbivory (Coile and Shilling 1993).

Cogongrass is poor forage material for livestock, and has fewer nutrients than the native vegetation often ingested by the tortoises (Hubbard 1944, Kearn 1982, Garner and Landers 1981). Cogongrass in its native Asia decreased in nutrient content as it matured (Kearn 1982) and contained 3.7% crude protein, 0.5% crude fat, 8.7% crude fiber, and 10.8% nitrogen free extract (Hubbard 1944). In comparison, the tortoises' typical dietary components of *Pityopsis*, *Galactia* and *Tephrosia* contain much higher amounts: 5.4-17.2% crude protein, 2.0-4.4% fat, 19.9-35.0% crude fiber, and 46.4-57.5% nitrogen free extract (Garner and Landers 1981). The seasonally selected wiregrass (*Aristida beyrichiana*) contains 3.1-8.9% crude protein, 1.1-1.5% fat, 35.4-39.4% crude fiber, and 49.3-56.7% nitrogen free extract (Garner and Landers 1981).

Cogongrass, which can grow to more than one meter in height, was introduced to Florida and propagated for soil stabilization and forage in 1939; it rapidly expanded to cover 1000 acres in less than ten years (Shilling *et al.* 1997). Infestations along roads can expand laterally 25 to 40 centimeters per year (Willard *et al.* 1990), and swards in fire-managed sandhill spread up to 2.6 meters per year (Lippincott 1997). Cogongrass exhibits allelopathy (Coile and Shilling 1993) and is highly competitive for water (Shilling *et al.* 1997). The amount of light at ground level is significantly less in

cogongrass than in native sandhill vegetation (Lippincott 1997), indicating that cogongrass competes with native plants for light as well as water. Cogongrass grows rapidly into dense monocultures and eliminates native vegetation (Coile and Shilling 1993), and is resistant to control attempts (Shilling *et al.* 1997).

Cogongrass loses water content as it matures, decreasing from 73% moisture at 1-14 days growth to 39% at maturity (Kearl 1982). In contrast, native grasses contain 74.2-76.4% moisture at the beginning of the growing season (March through May) and 60.3-69.7% at the end (September to November), maintaining the main water source for the tortoises (Garner and Landers 1981). Dehydration may become an issue for the gopher tortoise if cogongrass eliminates the native grasses, because most of their water is obtained from food (Garner and Landers 1981).

Like the gopher tortoise, cogongrass prefers open-canopy areas, but cogongrass alters the sandhill fire regimes that maintain the open canopy areas (Hobbs and Huenneke 1992, Lippincott 2000). Because the standing mass of cogongrass is so large, the fuel load is very high, increasing fire intensity. The density of the cogongrass, or the fuel packing ratio, is also high, increasing the rate of fuel combustion. The lack of moisture content in mature cogongrass increases the probability of a fire and the length of the fire season (Brooks *et al.* 2004). The invasion of cogongrass also changes the fire type. The height of the cogongrass increases vertical fuel continuity, leading to crown fires instead of the usual surface fires (Brooks *et al.* 2004). Gopher tortoises may be killed directly by more frequent and more intense fires, and the change in fire regime will alter the plant community, lowering diversity and potentially harming the tortoise population (Lippincott 2000).

Study Site

My study was conducted at the Teneroc Fish Management Area in Polk County, Florida (28°06'00"N, 81°51'00"W). Historically composed of sandhill, pine flatwoods, and scrub habitats, the area was mined for phosphate in the 1950s. Phosphate mining is a strip mining process that severely disturbs the soil. The land was reclaimed as pasture, and in 1988, 116 gopher tortoises were relocated to a 280 hectare section of pasture (Macdonald 1996). Cogongrass was not present at the time of release, but now is encroaching on the site, already occupying about 50% of the open area as estimated by examining aerial maps (SWFWMD 2004).

To characterize the study site further, the vegetation diversity was examined to document the spread of the cogongrass. The perimeter of the cogongrass monoculture was mapped in July 2003, August 2004, July 2005, and August 2006 using a Trimble® Global Positioning System. These maps of the cogongrass monoculture were used to determine the rate of expansion across the site by using the ruler tool in ArcMap to measure the distance between consecutive years' perimeters at five randomly chosen points along each perimeter. The cogongrass expanded each year (Figure 1). From 2003 to 2004, the perimeter advanced a mean distance of 2.48m (SD=1.48), while the perimeter grew a mean distance of 1.24m (SD=0.25) between 2004 and 2005. From 2005 to 2006, the cogongrass expanded a mean distance of 1.96m (SD=1.05).

Above-ground biomass was estimated as a measure of the space cogongrass occupies. Five 10x10 centimeter areas of cogongrass were clipped at ground level, and the length of the largest blade was measured. Clippings were dried in a drying oven at approximately 60°C, with periodic weighing until the mass for each clipping was

constant. The clippings averaged 1.10m (SD=0.095) in length and had a mean dry mass of 26.42g (SD=8.9). The above-ground biomass of the cogongrass was estimated to be 26420 kg/ha based on the mean mass of the 10x10cm clippings, which is over twice the biomass of a wheat field (Thornton *et al.* 2006). The cogongrass occupies space horizontally and vertically, crowding and shading out other plants.

Cogongrass is reported to exclude other vegetation (Coile and Shilling 1993). To determine if vegetation diversity was lower in invaded areas of the site, I compared vegetation composition between locations without cogongrass and locations with cogongrass. A randomly thrown 1x1 meter quadrat was used to estimate the percent cover of each species of plant, using a field guide by Taylor (1992) for identification purposes. Dead herbaceous vegetation, bare ground, and unidentified but distinct grass species categories were also used. Six quadrats contained cogongrass, and fourteen did not, and were considered cogongrass-absent quadrats. Percent cover values were summed for each species across all quadrats within each of the two groups. An expected distribution of species in a single quadrat was calculated by averaging the percent cover of each species in the cogongrass-absent quadrats and bootstrapping 95% confidence intervals with 10000 iterations. Confidence intervals for diversity indices were bootstrapped with 10000 repeats, and the Shannon, Simpson, and Hill's N_1 and N_2 diversity indices were calculated, as well as Hill's modified evenness index, for both the cogongrass-absent group and the cogongrass-present group. Twenty-two species of plants were found in the vegetation quadrats. Twelve were identified to species, three were unidentified but distinct forb species, and seven were unidentified but distinct grass species. Species richness ranged from two to seven, with a median of four species per

quadrat. Bare ground had the highest percent cover in the cogongrass-absent quadrats. As expected, observed percent cover values fell within the 95% confidence intervals for the cogongrass-absent quadrats, and were much lower in cogongrass-present quadrats, falling outside of the confidence interval. Plant diversity and evenness decreased in the presence of cogongrass, beyond the 95% confidence interval (Table 1).

Feeding

To determine if the gopher tortoise will consume cogongrass, I conducted a feeding experiment in the field. I expected the tortoises to eat native vegetation readily, including wiregrass, a less-preferred native grass (Garner and Landers 1981, MacDonald and Mushinsky 1988, Mushinsky *et al.* 2003), and not to eat cogongrass at all. I conducted preliminary experiments at the Ecological Research Area of the University of South Florida. Individuals were captured in bucket traps placed outside of active burrows (Auffenberg and Franz 1982), and were also opportunistically hand-caught. Once captured, tortoises were placed in a 3x1.5m enclosure constructed of aluminum flashing. The enclosure contained either natural vegetation (including wiregrass, goldenaster [*Pityopsis graminifolia*], bahia grass [*Paspalum notatum*], and blazing star [*Liatris spp.*]) or only wiregrass. Wiregrass is ingested by gopher tortoises when it is the dominant vegetation and more preferred foods such as golden aster and *Liatris spp.* are unavailable (MacDonald and Mushinsky 1988). Five of the wiregrass feeding experiments were conducted during the winter (November-February) when tortoises are more likely to positively select wiregrass as a food source (Garner and Landers 1981). The tortoises exposed to native vegetation served as a control, determining how long it would take for a tortoise to eat in captivity, and those exposed to wiregrass only served as another

control, determining how long it would take for a tortoise to eat a less preferred food item.

At Teneroc, captured tortoises were placed in a 4x4m holding pen with natural vegetation (including wiregrass, camphorweed (*Heterotheca subaxillaris*), *Liatris spp.*, and *Galactia spp.*), or only the invasive cogongrass, which was transplanted into the pen in pots to avoid contamination and counter-sunk into the ground to mimic natural occurrence. I observed each tortoise until it began to eat, and noted the time. Some feeding trials were terminated before any vegetation was consumed because of time constraints, the approach of inclement weather, sunset, or signs of heat stress in the tortoise.

Feeding rate was calculated as the reciprocal of the time to first bite. If no vegetation was consumed, time was infinity and the feeding rate was zero. The feeding rate was graphed for each of the three types of vegetation presented to the tortoises in a box and whisker plot in SigmaStat. Because the data were not normally distributed, a nonparametric Kruskal-Wallis Test was performed and pairwise comparisons were made using a Mann Whitney U Test to determine if there was a difference in selection among the three vegetation types.

Habitat

To determine whether or not the gopher tortoises used the cogongrass as habitat, individuals were powder-tracked. I expected that the tortoises would have significantly smaller proportions of trail occurring within cogongrass compared to outside cogongrass. After trapping a gopher tortoise, a mesh bag filled with non-toxic fluorescent powder (Radiant Color®) was temporarily attached with duct tape to the posterior carapace

(Blankenship *et al.* 1998), as was a cocoon thread bobbin (Wilson 1994). I returned one to two days after release to follow the trails of powder and thread. Trails were flagged and then mapped with a Trimble® GPS. The experimental group consisted of tortoises caught at burrows within 50 meters of the cogongrass, so that the cogongrass could be considered to be within each individual's possible home range. A 50 meter radius gives an area of 0.785ha, which falls within the values of home range size for adult male gopher tortoises and is slightly larger than a female tortoise's home range (see above; Mushinsky *et al.* 2006). As a control, this experiment was repeated with tortoises whose burrows were located over 50 meters from the cogongrass. The home ranges of these tortoises most likely do not overlap the cogongrass.

To determine if either the control or the experimental groups exhibited directional movement, angle of direction from point of release (at the home burrow) to the end of the trail was measured with a protractor on maps of the mapped trails printed from ArcMap and the Rayleigh Test for uniformity was performed using Orianna software. The Watson-William Test was performed by hand following Zar (1999) to determine if there was a difference between the two groups' mean angles of movement. The original analysis would have measured trail length within each type of habitat (cogongrass-present vs. cogongrass-absent) relative to habitat availability, calculated as the percent area covered by the habitat type within a 50m radius of the tortoise's home burrow. These data would be used to determine proportional habitat use with Smith's measure of niche breadth (Krebs 1989), but control group tortoises captured 50 meters or farther from the grass mostly had east-west paths, introducing a directional bias that precluded the intended analysis of habitat use.

Orientation

To determine if the presence of cogongrass interferes with the gopher tortoises' navigational abilities, an orientation experiment was performed. Low sinuosity (index of straightness: ratio of distance true traveled to straight line displacement distance; Emlen 1969, Connor 1996), a high rate of movement, and directional movement are indicators of orientation. I expected the tortoises to become disoriented in the cogongrass and have significantly higher sinuosity values and slower, non-directed movement. A captured tortoise was displaced 30 to 50 meters from its burrow and its speed and directness of travel to another burrow were observed. Tortoise paths were flagged and mapped using a Trimble® GPS and analyzed in ArcMap. Multiple readings on each individual at different angles of displacement were attempted in order to rule out any directional bias, although some individuals (n=7) escaped into burrows before a second displacement could occur. Three of these tortoises were displaced once into habitat without cogongrass, while four were displaced once into cogongrass. Some individuals were displaced twice into habitat without cogongrass (n=9), one was displaced twice into cogongrass, and some were displaced once into habitat without cogongrass and once into the cogongrass monoculture (n=5), for a total of 22 individuals and 37 trials. The type of habitat a tortoise was released into depended on its home burrow's proximity to the cogongrass. If the home burrow was within 50 meters of the cogongrass, the tortoise was displaced into cogongrass. If the home burrow was more than 50 meters away from the cogongrass perimeter, the tortoise was displaced into non-invaded habitat.

The travel time in minutes was observed and recorded for each individual, and the true distance traveled was recorded with GPS as the paths were mapped. Straight-line

distance traveled and the distance from the cogongrass of the point of release was calculated in ArcMap with the ruler tool. Sinuosity of moving to a burrow was calculated, as well as rate of movement (true distance divided by time), rate of displacement (straight distance divided by time), and sinuosity per unit time (index of straightness divided by time).

Regressions of straight-line distance traveled onto distance from cogongrass and of actual distance traveled onto distance from cogongrass were performed using SPSS to determine if a significant relationship existed. The two slopes were compared using a t Test (Zar 1999) to determine if the latter slope was significantly larger than the former, which would indicate that tortoises placed in the cogongrass had to move farther to achieve the same displacement. One-way ANOVAs were used to compare rate of movement, rate of displacement, sinuosity, and sinuosity per unit time between the group of tortoises displaced within the cogongrass and the group displaced beyond the cogongrass to determine if the former had a more sinuous path, indicating disorientation. For sinuosity per unit time, results were also calculated with a data set created by randomly discarding one trial of individuals who were displaced during both trials outside of the cogongrass to avoid pseudoreplication.

To examine the movement patterns of the tortoises, angles of movement from point of release to the chosen burrow were calculated using printed maps of the paths and a protractor, with the cardinal direction north as 0° . In two cases, tortoises had not found a burrow after 45 minutes of movement, and the orientation experiment was terminated. In these cases, the point of recapture was used as the endpoint of the path. The Rayleigh Test for uniformity and the V Test (expected $\mu=0^\circ$) were performed to see if movement

outside of the cogongrass was directional, while movement within the cogongrass was uniform. If the distribution was bimodal, the Hodges-Ajne Test was substituted for the Rayleigh Test. Angles of movement were also calculated placing the home burrow at 0° , and the Rayleigh Test for uniformity and the V Test (expected $\mu=0^\circ$) were performed to determine if tortoises placed outside of the cogongrass tended to move towards their home burrows and tortoises placed within the cogongrass did not have a preferred direction.

To examine the effect of the presence of cogongrass on the tortoises' ability to navigate using geotactic cues, slopes of the terrain were marked with a GPS trail labeled sloping (uphill or downhill) or level, and these trails were added to the map of tortoise trails in ArcMap. The slope of each tortoise path was determined, as well as the slope from the point of release to the home burrow. The number of tortoises moving in the same vertical direction (uphill, downhill, or level) as their burrows was compared to the number of tortoises moving in a different vertical direction as their burrows for the within-cogongrass group and the beyond-cogongrass group using a 2x2 contingency table and a G Test (Zar 1999). The sample sizes were too small for sufficient statistical power using the G Test, so a Fisher Exact Test was performed on the contingency table using SigmaStat software to determine if the proportions of individuals in each cell were different from those expected from random occurrence.

Results

Feeding

Seven of the eight tortoises exposed to native vegetation began to eat within 45 minutes. *Sabatia sp.*, *Galactia sp.*, and unidentified grasses were consumed. No feeding was observed in one individual in the native vegetation pen and the experiment was ended after 57 minutes because of signs of heat stress in the tortoise. In all eight individuals offered cogongrass, and ten of the eleven individuals exposed to wiregrass, no feeding was observed, even during the winter months. One tortoise offered wiregrass began to eat in 62 minutes. The Kruskal-Wallis Test indicated a significant difference in feeding rates among the three vegetation types ($\chi^2=20.1$, $p<0.001$, $n=28$). The Mann-Whitney U Test for cogongrass vs. wiregrass was not significant ($U=40$, $p=0.778$, $n=19$), but the feeding rates for natural vegetation were significantly smaller than those of wiregrass ($U=6$, $p<0.001$, $n=20$) and cogongrass ($U=4$, $p=0.001$, $n=17$), indicating that gopher tortoises will readily eat preferred vegetation in captivity, are reluctant to consume wiregrass but will consume it under certain circumstances, and will not eat cogongrass (Figure 2).

Habitat

The majority of trails led from the point of release to another burrow. Four of the eighteen individuals' trails were truncated because of broken thread and indiscernible powder trails. None of the tortoises' powder and thread trails entered the cogongrass

monoculture. The mean direction of movement for tortoises with home ranges overlapping the cogongrass monoculture was $\mu=221^\circ$ ($SD=93^\circ$, $n=8$), and for tortoises whose home ranges were entirely outside of the cogongrass monoculture, $\mu=53^\circ$ ($SD=78^\circ$, $n=10$) (Figure 3). Although the Rayleigh Test showed that neither group exhibited significant directionality ($z=0.564$, $p=0.584$, $n=8$, and $z=1.557$, $p=0.215$, $n=10$, respectively), the Watson-William Test revealed that the two means were significantly different from each other ($F_{(1), 1, 16}=8.476$, $p<0.02$, $n=18$), indicating that tortoises using habitat adjacent to the cogongrass move toward the southwest, away from the cogongrass (see Figure 1), and tortoises occupying a home range entirely beyond the cogongrass move northeast, or toward the cogongrass. The latter individuals may move northeast because they are bounded by the dirt road that runs along the south edge of the site.

Orientation

Only two tortoises returned to the burrow at which they were captured during the orientation experiments. The others entered different burrows, usually within 30 minutes. Two tortoises placed inside of the cogongrass walked for 73 and 61 minutes without finding a burrow, and were returned to their home burrows. Many tortoises placed inside the cogongrass found worn paths through the grass and followed them to a burrow, and many walked in circles or back and forth over the same path. Individuals often paused for up to five minutes.

True distance traveled and straight-line distance traveled were not significantly related to the distance of the initial release point from the cogongrass ($r^2=0.074$, $p=0.103$, and $r^2=0.041$, $p=0.229$, respectively, $n=36$) (Figure 4). The results of the t Test comparing the slopes of the two regressions were not significant ($t_{(2),70}=0.349$, $p>0.5$,

n=36), indicating that tortoises displaced within the cogongrass do not move a greater distance to achieve the same displacement. The rate of displacement (straight-distance traveled/time) was not significantly different between tortoises displaced outside of the cogongrass (\bar{x} =0.599, SD=0.700, n=26) and tortoises displaced into the cogongrass (\bar{x} =0.992, SD=0.660, n=26; F=2.523, p=0.121, n=37). The rate of movement (true distance traveled/time) was significantly different (F=12.472, p=0.001, n=37), with tortoises moving faster inside the cogongrass (\bar{x} =0.488, SD=0.246, n=11) than outside (\bar{x} =0.259, SD=0.146, n=26). Mean sinuosity was not significantly different between tortoises placed outside of the cogongrass (\bar{x} =2.06, SD=1.235, n=26) than those placed inside the cogongrass (\bar{x} =1.97, SD=0.487, n=11; F=0.049, p=0.826, n=37). Sinuosity per unit time was not significantly different between tortoises displaced inside the cogongrass (\bar{x} =0.139, SD=0.107, n=11) and tortoises displaced outside the cogongrass (\bar{x} =0.424, SD=0.691, n=11; F= 1.828, p=0.185, n=37). Significant differences were found when the tortoises displaced outside of the cogongrass were randomized (F=4.690, p=0.04, n=28), with a higher sinuosity per unit time outside of the cogongrass (\bar{x} =0.261, SD=0.165, n=17) than inside (\bar{x} =0.139, SD=0.107, n=11), indicating that tortoises were moving as efficiently if not more so inside the cogongrass.

The angles of movement of tortoises placed inside the cogongrass were bimodal, and randomly distributed according to the Hodges-Ajne Test (m=3, p=0.81, n=11) with a mean angle of 23° (angular deviation=0.59, n=11). Tortoises placed outside the cogongrass exhibited directional movement when the entire data set was used (z=3.459, p=0.03, n=26), with a mean vector of 38° (SD=81°, n=26), which is not significantly different from 0°, according to the V Test (u=2.066, p=0.019, n=26), but when the data

were randomized to avoid pseudoreplication, the results were no longer significant ($z=1.233$, $p=0.296$; $u=1.194$, $p=0.118$, $n=17$) (Figure 5).

The study site has variable topography. In general, the terrain slopes uphill from south to north, and begins to level off inside the cogongrass monoculture at the north end of the site. From the west to east direction, the terrain consists of a central hill with two valleys on either side. This variation in elevation may have an effect on how the gopher tortoises navigate. Eighteen of the twenty-two tortoises displaced outside of the cogongrass moved along a path with the same vertical direction (uphill, downhill, or level) as the path that would take them to their home burrow. Only six of thirteen tortoises displaced within or at the edge (less than one meter outside) of the cogongrass moved along a path with the same vertical direction as the return path to their home burrow. The results of the Fisher Exact Test on the contingency table were marginally significant ($p=0.057$, $n=35$), indicating that tortoises displaced into the cogongrass were equally likely to move uphill or downhill, regardless of which direction their burrow was, while the tortoises displaced into natural habitat were more likely than expected by chance alone to take a path with the same slope as the path that would return them to their burrow.

Discussion

The results indicate that the gopher tortoises do not consume cogongrass and do not use the cogongrass monoculture as habitat. Individual's movement patterns were affected by their proximity to the cogongrass, and individual's orientation abilities were affected by the presence of cogongrass.

Although most native vegetation was consumed readily and the native wiregrass sparingly, cogongrass was not consumed at all. Observations of tortoises consuming wiregrass, as well as the presence of wiregrass in scats, have been reported in the literature (Garner and Landers 1981, MacDonald and Mushinsky 1988, Mushinsky *et al.* 2003). As cogongrass decreases or eliminates plant diversity, it eliminates the tortoises' food sources, leaving them with a poor forage material, low in nutrients and water content.

The gopher tortoises present at the study site appear to avoid the cogongrass monoculture, rarely entering and then only along well-worn paths, some of which were created by human vehicles. Lippincott (1997) also noted active tortoise burrows inside a monoculture of cogongrass, connected to adjacent sandhill by narrow, trampled paths, usually less than ten meters in length. The tortoises' movement patterns change when their home range includes the cogongrass. Tortoises with home ranges within 50m of the edge of the cogongrass had a mean angle of movement of 221°, which corresponds to the cardinal direction southwest, whereas tortoises with home ranges beyond the cogongrass

had a mean angle of movement of 53°, or northeast. The cogongrass monoculture covers the northeast part of the field site, so tortoises with home ranges overlapping the cogongrass monoculture tend to move away from the monoculture, while other tortoises tend to move toward the monoculture. Connor's (1996) results suggested that gopher tortoises avoid areas that differ greatly from preferred open-canopy habitat, such as overgrown fire-suppressed plots. Gopher tortoises at Teneroc may also avoid the dense cogongrass because it eliminates their normal view of the horizon and landmarks, making navigation difficult.

Although the tortoises moved faster through the cogongrass when placed in it, the sinuosity of path was not significantly different. In fact, a tortoise's path was less sinuous if it was within the cogongrass, which may be because of a lack of obstacles to move around. In habitat without cogongrass, tortoises move around bushes and forbs that are in their path. Inside the cogongrass, there is little habitat heterogeneity, and the tortoises tended to walk along any existing pathways they encountered.

The increase in directness of path within the cogongrass may be explained by a lack of landmarks. Studies suggest that gopher tortoises orient themselves by using visual landmarks and, to a lesser extent, a sun compass (Gourley 1974, Connor 1996). Cogongrass is very dense and uniform relative to native sandhill vegetation, and may obscure the tortoises' usual landmarks while blocking any new visual cues. While inside the tall cogongrass, tortoises cannot view the horizon or the sky. Without any cues to cause them to readjust their direction, the tortoises will continue to walk in the same direction in which they started, resulting in a low sinuosity of path. Gourley (1974) found that individuals lacking visual cues continued to orient in a particular direction, but

not toward their home range. Connor (1996) found that displaced tortoises would not move into overgrown, unburned plots and instead began walking along the perimeter of the plots, resulting in low sinuosity of path.

The results indicate that gopher tortoises use geotaxis, as well as visual cues, to navigate. Geotaxis, or gravity orientation, is a response to gravitational cues (Jander 1963). Individuals can right themselves when upside down, and can sense an uphill or downhill slope. Movement uphill is negative geotaxis, and movement downhill is positive geotaxis (Murphy 1970). If an individual tortoise moves downhill as it leaves its burrow to forage, it must move uphill to return to its burrow. Other species of turtles have exhibited geotaxis: the painted turtle (*Chrysemys picta*), spiny softshell (*Apalone spinifer*), and the eastern box turtle (*Terrapene carolina*) (DeRosa and Taylor 1982), and the wood turtle (*Glyptemys insculpta*) (Tuttle and Carroll 2005). The habitat use data showed that many paths taken by tortoises were along the east-west axis. The ground slopes down from the central part of the site to the east and to the west, which supports the idea that gopher tortoises follow geotactic cues to navigate while outside of their burrows. The gopher tortoises that were released into native vegetation exhibited a tendency to orient along the same slope as the path that would return them to their home burrows. This tendency was not apparent in individuals released into the cogongrass, indicating that the tortoises' ability to navigate using geotactic cues is affected by the invasive grass. The tortoises may misinterpret the geotactic cues, possibly because of a difference in topography where the cogongrass has invaded. Another possibility why the gopher tortoises were unable to orient themselves properly inside the cogongrass is because the cogongrass obscures the view of the sky and the horizon, eliminating cues

from the sun compass as well as visual landmark cues. The exact relationship between the geotactic and visual cues used by the gopher tortoise is unknown, and warrants further research.

The cogongrass has the potential to have a negative influence on the gopher tortoise population beyond the ways investigated in this study. Gopher tortoises are dependent on fire to maintain their upland habitats as open-canopy. Cogongrass maintains a large standing biomass, altering sandhill fire regimes by increasing fine-fuel load and increasing both maximum temperature and height of fire (Lippincott 2000). Consequences of this change in disturbance regime include direct mortality of the tortoises, and a decrease in plant diversity, reducing the amount of forage material available to the tortoises. Changes in the frequency and intensity of natural disturbances, such as fire, can facilitate other invasions (Hobbs and Huenneke 1992).

A congener of the gopher tortoise, the desert tortoise (*Gopherus agassizii*), also is threatened by invasive grasses, particularly the bunchgrass *Bromus rubens* (Brooks *et al.* 2004). In the Mojave Desert non-native plants compete with native annuals, which can be 95% of the desert tortoise's diet, lowering diversity and biomass, thereby decreasing the availability of forage material (Brooks and Berry 2006). The bunchgrass also threatens to alter the fire regime in the Mojave Desert, which will have a negative effect on the native plants and animals of the region (Brooks *et al.* 2004).

As the area of their preferred scrub and sandhill habitat rapidly declines, gopher tortoises are being forced to occupy the suboptimal surrounding habitat that is being invaded by the cogongrass; the gopher tortoise in Florida will face a new threat in its natural habitat. Human disturbance has led to much relocation of gopher tortoises

throughout Florida. Over 5000 relocation permits have been issued by the Florida Fish and Wildlife Conservation Commission, and often suitable available relocation sites are lacking (Holder *et al.* 2007). Concerns about the spread of upper respiratory tract disease (URTD) and other diseases complicate the relocation process (Mushinsky *et al.* 2006). The possibility of losing local genetic variation and outbreeding depression is also a concern (Schwartz and Karl 2005); tortoises may only be relocated to sites less than 50 kilometers north or south of their native site (Holder *et al.* 2007). Often the tortoises are relocated to fragmented and/or disturbed sites such as reclaimed phosphate-mined land. Phosphate mining has disturbed more than 1180 square kilometers of Florida's 138000 square kilometers of land area (FIPR 2004), much of it in central Florida. These fragmented and disturbed habitats are more susceptible to invasion (Hobbs and Huenneke 1992, Mack *et al.* 2000), leaving many gopher tortoise populations vulnerable to cogongrass as well as other invasive species which may prove harmful. Invasive fire ants (*Solenopsis invicta*) in southern Mississippi caused 27% of gopher tortoise hatchling mortality (Epperson and Heise 2003) and have been documented to kill 70% of Florida red-bellied cooter (*Pseudemys nelsoni*) hatchlings during pipping or shortly after hatching (Allen *et al.* 2001). In fiscal year 2005-2006, federal, state, and local governments expended over nine million USD to control invasive species in Florida (DEP 2006).

Invasive species are altering communities and ecosystems throughout the world. Like the desert tortoise in the Mojave Desert, the gopher tortoise is threatened by an invasive grass. The grass is eliminating the gopher tortoises' habitat and food source, and is disrupting the tortoises' ability to navigate back to the shelter of their burrows. Cogongrass is present in much of central Florida (Wunderlin 2000), especially on the

disturbed areas of phosphate mines. Controlling the spread of the cogongrass is necessary to prevent the elimination of this population of relocated gopher tortoises and most likely many other populations throughout the species' range.

Table 1: Diversity indices calculated from quadrat vegetation sampling.

	Cogongrass-absent quadrats	Bootstrapped 95% confidence interval	Cogongrass-present quadrats
Shannon's H'	2.38	2.30-2.42	0.92
Hill's N ₁	10.76	10.00-11.26	2.50
Hill's N ₂	8.40	7.64-9.05	1.65
Simpson's 1-λ	0.88	0.87-0.89	0.40
Hill's modified evenness	0.76	0.73-0.79	0.44

Figure 1: Map of study site with cogongrass perimeters delineated. The cogongrass extends from the perimeters to the north and east.

--- 2003 --- 2004 --- 2005 --- 2006

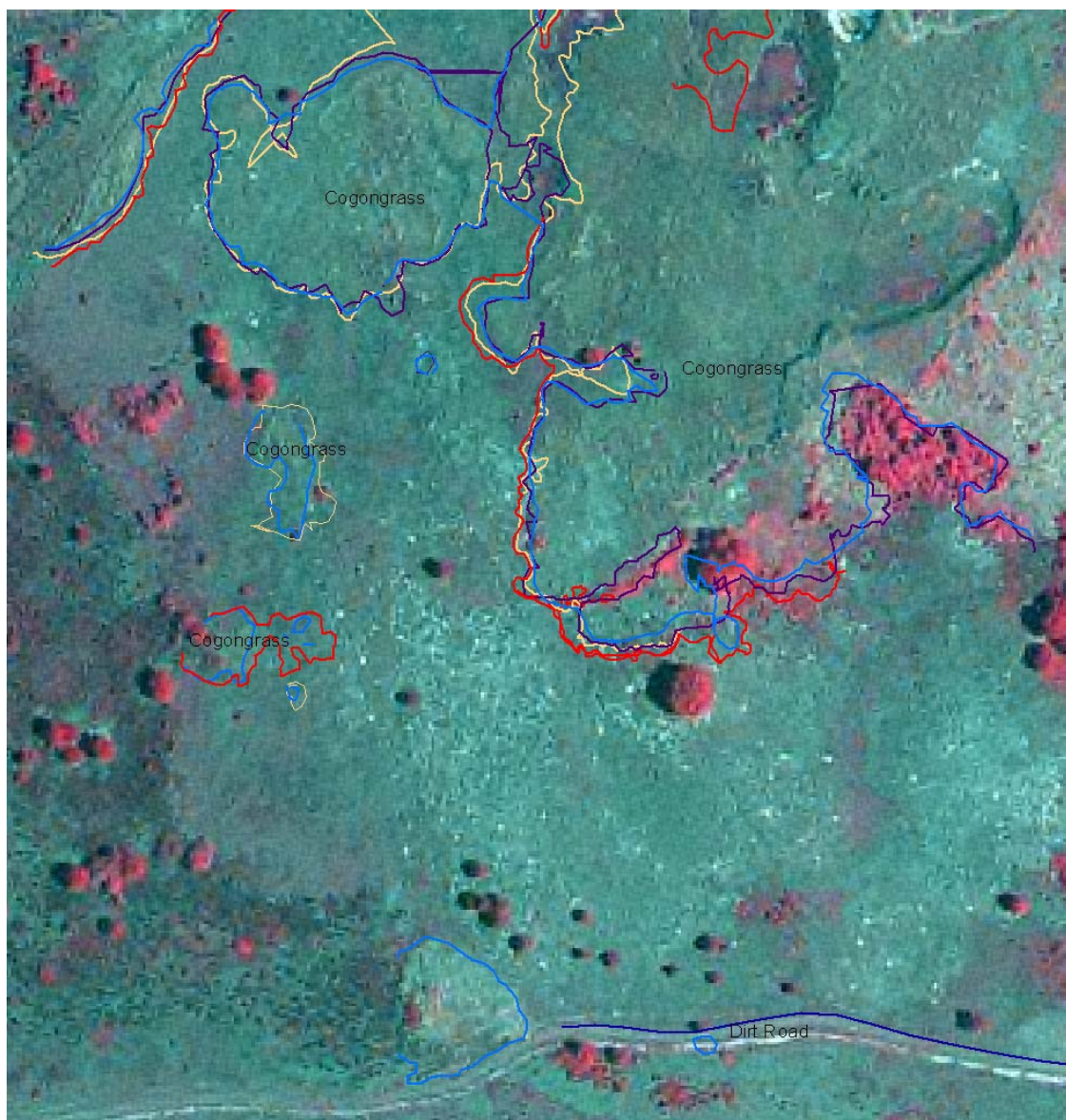


Figure 2: Reciprocal rates of feeding on three types of vegetation.

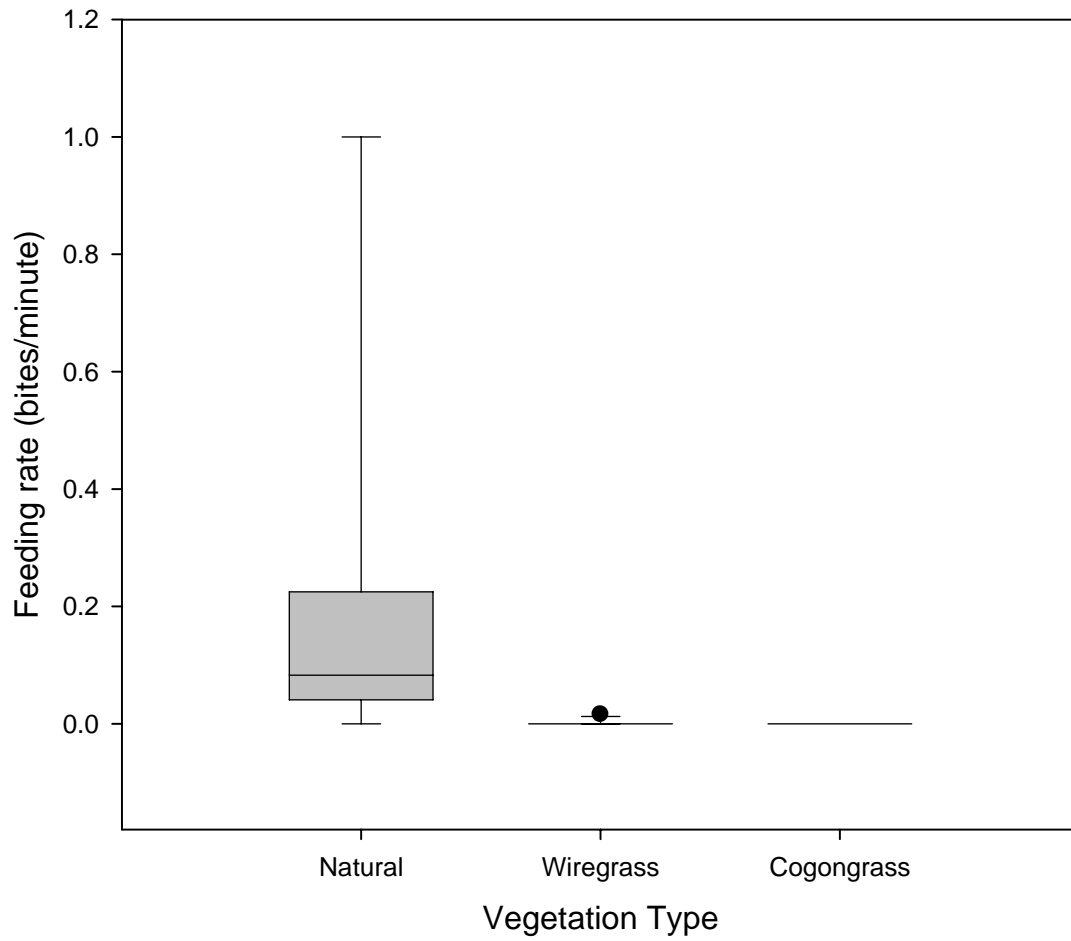


Figure 3: Angles of movement and mean vectors of tortoise paths. (A) Tortoise's home range includes the cogongrass. (B) Tortoise's home range is entirely outside of the cogongrass. North=0°.

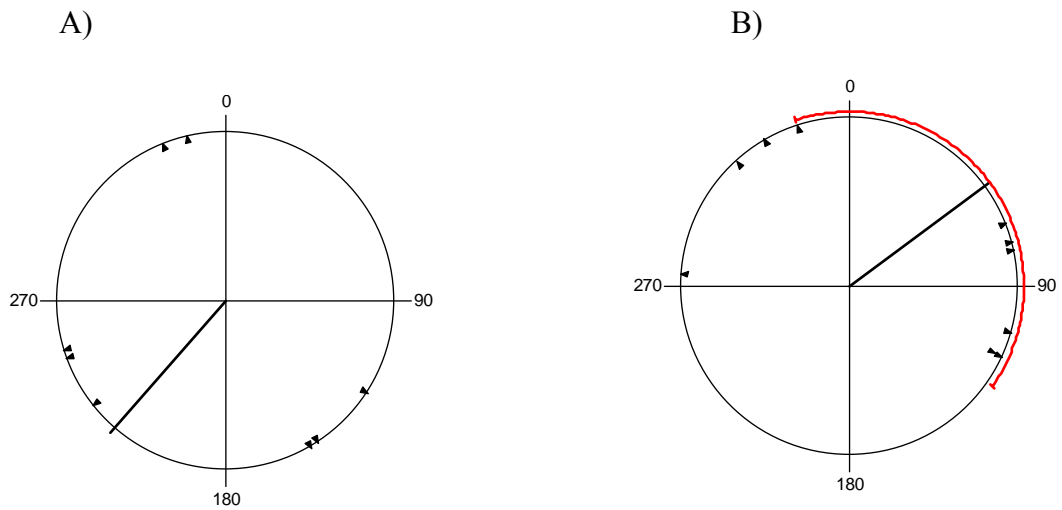
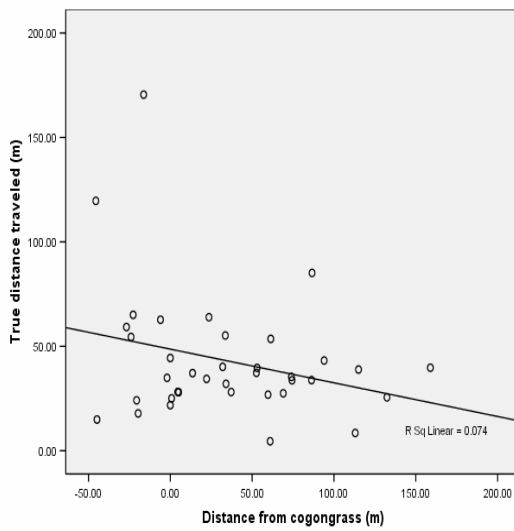
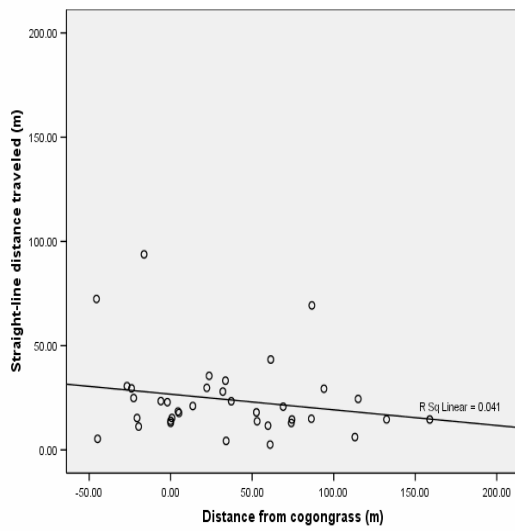


Figure 4: Regressions of distance traveled onto distance from the cogongrass. A) Regression of true distance traveled onto distance of point of release from the cogongrass monoculture. B) Regression of straight-line distance traveled onto distance of point of release from the cogongrass monoculture.



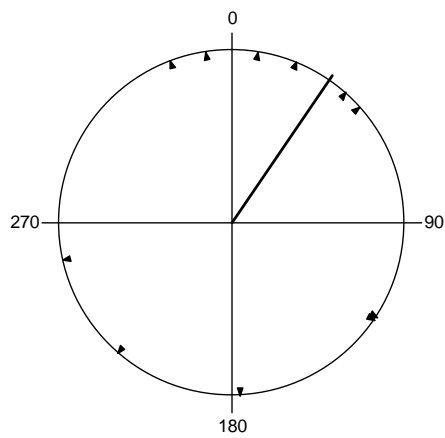
A)



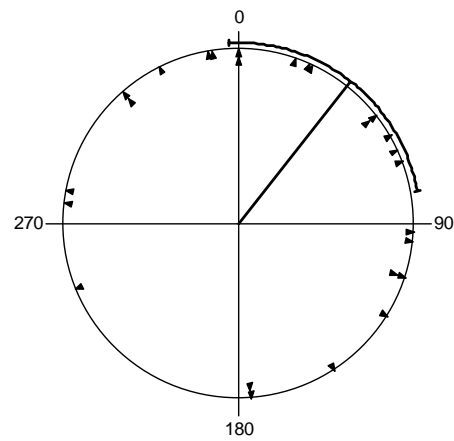
B)

Figure 5: Angles of movement and mean vectors of displaced tortoises. A) Tortoises displaced into the cogongrass. B) Tortoises displaced outside or at the edge of the cogongrass. North=0°.

A)



B)



References

- Allen, C.R., E.A. Forsys, K.G. Rice, and D.P. Wojcik. 2001. Effects of fire ants (Hymenoptera: Formicidae) on hatchling turtles and prevalence of fire ants on sea turtle nesting beaches in Florida. *Florida Entomologist* 84:250-253.
- Allendorf, F.W., and L.L. Lundquist. 2003. Introduction: population biology, evolution, and control of invasive species. *Conservation Biology* 17:24-30.
- Ashton, R.E., and K.J. Ashton. 1991. *Gopherus polyphemus* (gopher tortoise), drinking behavior. *Herpetological Review* 22:55-56.
- Auffenberg, W., and R. Franz. 1982. The status and distribution of the gopher tortoise (*Gopherus polyphemus*). In: R.B. Bury, ed. *North American Tortoises: Conservation and Ecology*. U.S. Fish and Wildlife Survey, Wildlife Research Report 12, pp. 95-126.
- Blankenship, E.L., T.W. Bryan, and S.P. Jacobsen. 1998. A method for tracking tortoises using fluorescent powder. *Herpetological Review* 21:88-89.
- Breining, D.R., P.A. Schmalzer, and C.R. Hinkle. 1994. Gopher tortoise (*Gopherus polyphemus*) densities in coastal scrub and slash pine flatwoods in Florida. *Journal of Herpetology* 28:60-65.
- Brooks, M.L., C.M. D'Antonio, D.M. Richardson, J.B. Grace, J.E. Keeley, J.M. DiTomaso, R.J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54:677-688.

- Brooks, M.L., and K.H. Berry. 2006. Dominance and environmental correlates of alien annual plants in the Mojave Desert, USA. *Journal of Arid Environments* 67:100-124.
- Brown, C.J., B. Blossey, J.C. Maerz, and S.J. Joule. 2006. Invasive plant and experimental venue affect tadpole performance. *Biological Invasions* 8:327-338.
- Coile, N.C. and D.G. Shilling. 1993. Cogongrass, *Imperata cylindrica* (L.) Beauv.: a good grass gone bad! Florida Department of Agricultural and Consumer Services, Botany Circular Number 28.
- Connor, K.M. 1996. Homing behavior and orientation in the gopher tortoise, *Gopherus polyphemus*. M.S. Thesis, University of South Florida, Tampa, FL.
- Crawley, M.J. 1986. The population biology of invaders. *Philosophical Transactions of the Royal Society of London B* 314:711-731.
- Department of Environmental Protection. 2006. DEP Upland Plant Management Program. Website accessed February 7, 2007.
<<http://www.dep.state.fl.us/lands/invaspec/2ndlevpgs/uplandsplntman.htm>>
- DeRosa, C.T., and D.H. Taylor. 1982. A comparison of compass orientation mechanisms in three turtles (*Trionyx spinifer*, *Chrysemys picta* and *Terrapene carolina*). *Copeia* 1982:394-399.
- Di Castri, F. 1989. History of biological invasions with special emphasis on the Old World. In: J.A. Drake, ed. *Biological Invasions: a Global Perspective*. Wiley & Sons, Cichester, United Kingdom, pp. 31-60.
- Diemer, J.E. 1992. Demography of the tortoise *Gopherus polyphemus* in northern Florida. *Journal of Herpetology* 26:281-289.

- Douglass, J.F. 1976. The mating system of the gopher tortoise, *Gopherus polyphemus*, in southern Florida. M.S. Thesis, University of South Florida, Tampa, FL.
- Douglass, J.F., and C.E. Winegarner. 1977. Predators of eggs and young of the gopher tortoise, *Gopherus polyphemus* (Reptilia, Testudines, Testudinidae) in southern Florida. *Journal of Herpetology* 11:236-238.
- Douglass, J.F., and J.N. Layne. 1978. Activity and thermoregulation of the gopher tortoise (*Gopherus polyphemus*) in southern Florida. *Herpetologica* 34:359-374.
- Dudley, T.L., and C.J. DeLoach. 2004. Saltcedar (*Tamarix spp.*), endangered species, and biological weed control—can they mix? *Weed Technology* 18:1542-1551.
- Eisenberg, J. 1983. The gopher tortoise as a keystone species. Proceedings of the 4th Annual Meeting of the Gopher Tortoise Council, Valdosta State College, Valdosta, GA.
- Elton, C.S. 1958. *The ecology of invasions by animals and plants*. Wiley, New York, NY.
- Emlen, S.T. 1969. Homing ability and orientation in the painted turtle *Chrysemys picta marginata*. *Behaviour* 33:58-76.
- Epperson, D.M., and C.D. Heise. 2003. Nesting and hatchling ecology of gopher tortoises (*Gopherus polyphemus*) in southern Mississippi. *Journal of Herpetology* 37:315-324.
- Ernst, C.H., R.W. Barbour, and J.E. Lovich. 1994. *Gopherus polyphemus* (Daudin, 1802). In: C.H. Ernst, ed. *Turtles of the United States and Canada*. Smithsonian Institution Press, Washington, DC, pp. 466-478.

- Florida Institute for Phosphate Research. 2004. Florida's Phosphate Deposits. Website accessed February 7, 2007. <<http://www1.fipr.state.fl.us/phosphateprimer/>>
- Garner, J.A., and J.L. Landers. 1981. Foods and habitat of the gopher tortoise in southwestern Georgia. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 35:120-134.
- Gordon, D.R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. *Ecological Applications* 8:975-989.
- Hobbs, R.J., and L.F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6:324-337.
- Holder, G., M. Allen, J. Berish, M. Hinkle, A. Kropp, R. McCann, A. Williams, and M. Yuan. 2007. *Draft gopher tortoise management plan*. Florida Fish and Wildlife Conservation Commission, Tallahassee, FL.
- Hubbard, C.E. 1944. *Imperata cylindrica*: taxonomy, distribution, economic significance and control. Imperial Agricultural Bureau Joint Publication No. 7. Imperial Forestry Bureau, Oxford, UK.
- Jander, R. 1963. Insect orientation. *Annual Review of Entomology* 8:95-114.
- Kaczor, S.A., and D.C. Hartnett. 1989. Gopher tortoise (*Gopherus polyphemus*) effects on soils and vegetation in a Florida sandhill community. *American Midland Naturalist* 123:100-111.
- Kearl, L.C. 1982. *Nutrient requirements of ruminants in developing countries*. Utah State University, Logan, UT.
- Krebs, C.J. 1989. *Ecological Methodology*. Harper & Row Publishers, New York, NY.

- Layne, J.M. and R.J. Jackson. 1994. Burrow use by the Florida mouse (*Podomys floridanus*) in south-central Florida. *American Midland Naturalist* 13:17-23.
- Lippincott, C.L. 1997. Ecological consequences of *Imperata cylindrica* (cogongrass) invasion in Florida sandhill. Ph.D. Dissertation, University of Florida, Gainesville, FL.
- Lippincott, C.L. 2000. Effects of *Imperata cylindrica* (L.) Beauv. (Cogongrass) invasion on fire regime in Florida sandhill (USA). *Natural Areas Journal* 20:140-149.
- Lodge, D.M., S. Williams, H.J. MacIsaac, K.R. Hayes, B. Leung, S. Reichard, R.N. Mack, P.B. Moyle, M. Smith, D.A. Andow, J.T. Carlton, and A. McMichael. 2006. Biological invasions: recommendations for U.S. policy and management. *Ecological Applications* 16:2035-2054.
- Macdonald, L. A. 1996. Reintroduction of the gopher tortoise (*Gopherus polyphemus*) to reclaimed phosphate land. Florida Institute of Phosphate Research, Publication Number 03-105-126.
- Macdonald, L. A., and H. R. Mushinsky. 1988. Foraging ecology of the gopher tortoise, *Gopherus polyphemus*, in a sandhill habitat. *Herpetologica* 44:345-353.
- Mack, R.N., D. Simberloff, W.M. Lonsdale, H. Evans, M. Clout, and F.A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689-710.
- McCoy, E.D., H.R. Mushinsky, and D.S. Wilson. 1995. Demography of *Gopherus polyphemus* (Daudin) in relation to size of available habitat. Nongame Wildlife Program Project Report, Project GFC-86-013.

- McRae, W.A., J.L. Landers, and J.A. Garner. 1981. Movement patterns and home range of the gopher tortoise. *American Midland Naturalist* 106:165-179.
- Murphy, G.G. 1970. Orientation of adult and hatchling red-eared turtles, *Pseudemys scripta elegans*. Ph.D. Dissertation, Mississippi State University, State College, MS.
- Mushinsky, H.R., D.S. Wilson, and E.D. McCoy. 1994. Growth and sexual dimorphism of *Gopherus polyphemus* in central Florida. *Herpetologica* 50:119-128.
- Mushinsky, H.R., T.A. Stilson, and E.D. McCoy. 2003. Diet and dietary preference of the juvenile gopher tortoise (*Gopherus polyphemus*). *Herpetologica* 59:475-483.
- Mushinsky, H.R., E.D. McCoy, J.E. Berish, R.E. Ashton, Jr., and D.S. Wilson. 2006. The Gopher Tortoise, *Gopherus polyphemus*. In: P. Meylan, ed. *The Turtles of Florida*. Chelonian Research Monographs 3:350-375.
- Primack, R.B. 1998. *Essentials of Conservation Biology* (2nd ed.). Sinauer Associates, Sunderland, MA.
- Sakai, A.K., F.W. Allendorf, J.S. Holt, D.M. Lodge, J. Molofsky, K.A. With, S. Baughman, R.J. Cabin, J.E. Cohen, N.C. Ellstrand, D.E. McCauley, P. O'Neil, I.M. Parker, J.N. Thompson, and S.G. Weller. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* 32:305-332.
- Scheiman, D.M., E.K. Bollinger, and D.H. Johnson. 2003. Effects of leafy spurge infestation on grassland birds. *Journal of Wildlife Management* 67:115-121.
- Schwartz, T.S., and S.A. Karl. 2005. Population and conservation genetics of the gopher tortoise (*Gopherus polyphemus*). *Conservation Genetics* 6:917-928.

- Shilling, D.G., T.A. Bewick, J.F. Gaffney, S.K. McDonald, C.A. Chase, and E.R.R.L. Johnson. 1997. Ecology, physiology, and management of cogongrass (*Imperata cylindrica*). Florida Institute of Phosphate Research, Project Number 93-03-107.
- Southwest Florida Water Management District. 2004. Q3316NE. Southwest Florida Water Management District Digital Orthophotos. Website accessed April 4, 2006. <<http://ftp.swfwmd.state.fl.us/pub/gisdata/Imagery/2004CIR/>>
- Taylor, W.K. 1992. *The Guide to Florida Wildflowers*. Taylor Publishing Company, Dallas, TX.
- Thorstead, M.D., J. Weiner, and J.E. Olesen. 2006. Above- and below-ground competition between intercropped winter wheat *Triticum aestivum* and white clover *Trifolium repens*. *Journal of Applied Ecology* 43:237-245.
- Tuttle, S.E., and D.M. Carroll. 2005. Movements and behavior of hatchling wood turtles (*Glyptemys insculpta*). *Northeastern Naturalist* 12:331-348.
- U.S. Census Bureau. 2002. State Population Projections. Website accessed December 14, 2004. <<http://www.census.gov/population/projections/state/stpjpop.txt>>
- U.S. Fish and Wildlife Service. 1992. *Endangered and Threatened Species of the Southeastern United States (The Red Book), Volume 2*. USFWS Southeast Region, Atlanta, GA.
- Vitousek, P.M., C.M. D'Antonio, L.L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* 84:468-478.
- Willard, T.R., D.W. Hall, D.G. Shilling, J.A. Lewis, and W.L. Currey. 1990. Cogon grass distribution on Florida highway rights-of-way. *Weed Technology* 4:658-660.

- Wilson, D.S. 1991. Estimates of survival for juvenile gopher tortoises, *Gopherus polyphemus*. *Journal of Herpetology* 25:376-379.
- Wilson, D.S. 1994. Tracking small animals with thread bobbins. *Herpetological Review* 25:13-14.
- Witz, B.W., D.S. Wilson, and M.D. Palmer. 1991. Distribution of *Gopherus polyphemus* and its vertebrate symbionts in three burrow categories. *American Midland Naturalist* 126:152-158.
- Wunderlin, R.P. 2000. *Atlas of Florida Vascular Plants*. Institute for Systematic Botany, Tampa, FL.
- Zar, J.H. 1999. *Biostatistical Analysis, Fourth Edition*. Prentice-Hall, Inc., New Jersey.