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Foraging Ecology of Gopher Tortoises (*Gopherus polyphemus*) within Boyd Hill Nature Preserve, St. Petersburg, Florida, USA

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Abstract.—**The Gopher Tortoise (*Gopherus polyphemus*) is a keystone species of Longleaf Pine (*Pinus palustris*) ecosystems and is legally protected throughout its distribution. Gopher Tortoise habitat has been reduced across the range of the species due to landscape-scale fire suppression and urbanization that have degraded habitat quality. The objective of our study was to understand the foraging ecology of an isolated population of Gopher Tortoises in a scrubby flatwoods ecosystem located in the southern portion of its distribution. We calculated Fiensinger's Proportional Similarity Index (PSI) to determine whether tortoises were generalist or specialist foragers. Based on our results, Gopher Tortoises were generalist foragers, feeding most often on multiple grass species (PSI = 0.788). We also calculated Jacob's Electivity Index (D) and Manly's alpha (α) to determine the selectivity of plant species consumed by tortoises, and these indices demonstrated that tortoises highly selected certain plant species including fruits of Hog Plum (*Ximenia americana*, D = 0.744; α = 0.121), foliage of Spurge Nettle (*Cnidoscolus stimulosus*, D = 0.821; α = 0.180) and Prickly Lettuce (*Lactuca serriola*, D = 0.772; α = 0.139). We calculated Shannon's Diversity Indices to test whether tortoises selected foraging trails that differ in diversity compared to random points within the surrounding landscape. Foraging trail plant diversity was not significantly different than the surrounding landscape plant diversity through equitability analysis of Shannon's diversity. Our results provide a better understanding of the foraging ecology of Gopher Tortoises, including their foraging selectivity.**

Key Words.—foraging selectivity; herbivory; keystone species; turtle ecology

Introduction

The Gopher Tortoise (*Gopherus polyphemus*) is considered a keystone species listed as Threatened by the U.S. Fish and Wildlife Service (USFWS) west of the Alabama River and is protected by state law throughout the rest of its range, including Florida, USA (USFWS 2020). The species ranges from southern Florida throughout the coastal plains of Alabama, Mississippi, Georgia, and southern South Carolina and southeastern Louisiana, USA (Auffenberg and Franz 1982). Tortoises spend most of their time underground in burrows that they excavate. They are specialists for habitats that depend on frequent fires, including scrub, flatwoods, and grasslands with an open canopy, sandy soils, and a low groundwater table (Ashton and Ashton 2004). Gopher Tortoises are a keystone species of the Longleaf Pine (*Pinus palustris*) ecosystem, as over 360 other species, including both vertebrates and invertebrates, use their burrows for protection, shelter, and as foraging sites (Jackson and Milstrey 1989; Rostal et al. 2014; Catano and Stout 2015; Castellón et al. 2018). Tortoise populations declined significantly in the second half of the 20th Century due primarily to habitat loss through fire suppression and human development, and thus their management has become increasingly important for conservationists (Diemer 1986; Ashton and Ashton 2008). As reptilian herbivores, Gopher Tortoise population stability depends on suitable vegetation communities (Rostal and Jones 2002).

Gopher Tortoise foraging may aid in seed dispersal and enhancing plant species diversity (Carlson et al. 2003; Birkhead et al. 2005; Richardson and Stiling 2019a,b; Hanish et al. 2020; Figueroa et al. 2021). Scientists still debate whether Gopher Tortoises are selective or generalist feeders, though some data indicate that they are in between the two foraging modes (MacDonald and Mushinsky 1988). A few studies have focused on the analysis of juvenile tortoise foraging, specifically examining foraging paths and dietary preferences (Mushinsky et al. 2003; Halstead et al. 2007). Mushinsky et al. (2003) determined that juvenile Gopher Tortoises eat a wide array of plants, including 26 plant taxa, 16 of which were positively selected. Halstead et al. (2007) determined that correlated random walk models can be used to describe juvenile Gopher Tortoise foraging paths, as tortoises leave their burrows to forage and return without significant preference of directions to turn. Gopher Tortoise foraging studies have primarily involved scat analyses, with few studies focused directly on foraging observations, particularly for adults (Mushinsky et al. 2003; Birkhead et al. 2005; Halstead et al. 2007; Ashton and Ashton 2008).

MacDonald and Mushinsky (1988) analyzed the foraging behavior of a population of Gopher Tortoises at the Ecological Research Area of the University of South Florida using both fecal matter and foraging observations. They identified 52 plant taxa from the 63 fecal samples and 68 plant taxa from 38 foraging observations. They determined, based on Feinsinger's Proportional Similarity Index and Jacob's Electivity Index, that Gopher Tortoises fall intermediately between dietary generalists and specialists. They characterized tortoises as selective foragers with respect to most plant taxa; however, for the plants that were ingested most frequently, tortoises ingested them in a random manner. Their results from a Gopher Tortoise population residing in a habitat with a highly diverse plant community demonstrate how tortoises forage when such resources are available.

At Boyd Hill Nature Preserve in St. Petersburg, Florida, Gopher Tortoises exist within the xeric upland habitats (unpubl. data). While mark/recapture studies are ongoing to study the population demographics, foraging ecology of Gopher Tortoises at this preserve remains unstudied. Most Gopher Tortoise foraging studies have focused on Sandhill habitat, Pine Rockland habitat, and Pine Savanna habitat (MacDonald and Mushinsky 1988; Mushinsky et al. 2003; Birkhead et al. 2005; Richardson and Stiling 2019a; Figueroa et al. 2021), while our study offers the first accounts of tortoises foraging in scrubby flatwoods. Previous studies have also focused on relatively pristine, intact Gopher Tortoise habitats, while our study site is within an urban nature preserve that is managed as multi-use for humans as well as species and habitat conservation. Research in Gopher Tortoise foraging ecology may help in conservation strategies by providing information about which food resources are most preferred by tortoises, and thus how to best manage plant communities in such a highly altered and managed landscape as similar conservation areas. We tested the hypothesis that Gopher Tortoises are dietary generalists overall, but we predicted that Gopher Tortoises may be selective for a few particular forage items that we have commonly observed them eating.

Materials and Methods

Study site.—Boyd Hill Nature Preserve is a 99-ha park located in Pinellas County, Florida, USA, that includes approximately 40 ha of xeric uplands classified as scrubby flatwoods (Myers and Ewel 1990) embedded in a matrix of hardwood hammock and freshwater lake shore. A Gopher Tortoise population of approximately 300 adults was estimated through a mark/recapture study from 2018–2020 within the upland system that is maintained on a fire return interval of approximately 3 y. The tortoise habitat contained modified grass fields continuously mowed by site managers and native upland habitat dominated by Saw Palmetto (*Serenoa repens*) with dispersed pine (*Pinus* spp.) and a rich native understory. As a city-owned nature preserve, Boyd Hill Nature Preserve is managed by city staff, contains multiple walking paths that divide the habitats, and is visited by hundreds of people each month, making it suitable habitat for many native species but also a highly impacted landscape. We observed tortoises feeding in a southern region of the preserve, comprising about 7 ha total, where tortoises were most abundant. The area of the preserve that we conducted our observations contained multiple crushed-shell walking paths that fragmented the habitat and a small (about 0.4 ha), open, grassy field that was highly altered, with numerous non-native plant species that were present throughout most of the region, most notably Torpedograss (*Panicum repens*). Apart from the mowed field, the site consists mostly of patches of upland native vegetation including Longleaf Pine, Slash Pine (*Pinus elliottii*), Sand Pine (*Pinus clausa*), large clumps of Saw Palmetto, Beggarticks (*Bidens alba*), and various spurges and grasses.

Foraging behavior monitoring.—From 6 July to 20 August 2020, we spotted Gopher Tortoises during the daytime hours along trails and followed them closely while observing feeding behavior to determine their foraging strategies (MacDonald and Mushinsky 1988). Gopher Tortoises at Boyd Hill Nature Preserve are highly habituated to human presence and are routinely seen mating, fighting, and foraging with people present. Therefore, we considered the human presence during foraging observations to not be disruptive of normal tortoise forage selection. We analyzed the specificity of the tortoise diet by determining if what they chose to eat differed from what was available at two scales: point availability and landscape availability. We defined point availability as all groundcover plants (i.e., plants < 10 cm off the ground) that were within a 30 × 30 cm quadrat centered on the point where a tortoise was observed actively eating. Landscape availability referred to which groundcover plants were available within a larger quadrat as determined by the foraging path of each tortoise.

We conducted foraging observations by following an individual tortoise as it foraged. We visually identified each tortoise using the mark/recapture notching system that is used within the preserve, and we did not touch the tortoises to prevent disturbance to feeding behaviors. We video recorded foraging using an iPhone (Apple Inc.,

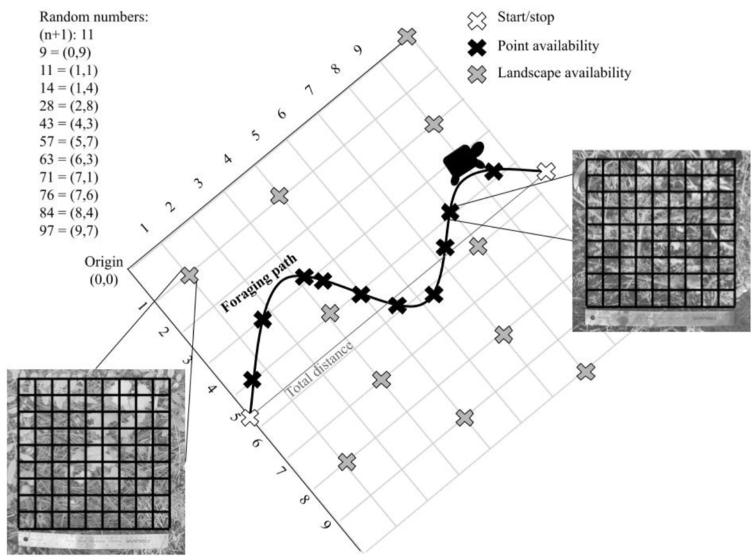

Figure 1. Study design of foraging study of Gopher Tortoises (*Gopherus polyphemus*) at Boyd Hill Nature Preserve, St. Petersburg, Florida, USA. Tortoises were followed along foraging paths, and each time they took a bite, a flag was placed, pictures were taken, and a 30 × 30 cm quadrat was affixed onto the image. Each plant at an intersecting line was identified, termed point availability. We found landscape availability Xs using an X,Y coordinate system and random numbers generated in the field.

Cupertino, California, USA), with the tortoise centered within view as well as the plants on which it was feeding. We followed tortoises from the moment they were first seen eating until they sought shelter within a burrow and were no longer visible. We counted what we defined as points as the number of times a tortoise stopped to take a bite of vegetation, and we inserted a pin flag into the ground exactly where the tortoise stopped to eat (Fig. 1). We placed flags while following the tortoise foraging after the tortoise had moved on from that particular point. After the tortoise stopped foraging, we saved recordings and took GPS location at the spot the tortoise began feeding and the spot at which it stopped feeding. We later analyzed the recordings to identify each plant species and count the number of bites a tortoise took at each point of each plant species. We frequently observed tortoises moving on the surface for non-feeding reasons, such as intraspecific social interactions. Therefore, we only considered foraging observations in our study when a tortoise was clearly stopping at a consistent interval and feeding. We did not include tortoises in our study if they were only seen walking and not feeding.

After the tortoise stopped foraging, we plotted the foraging path and took photographs with a cell phone at every point marked by the flags to determine the point availability at a subsequent time (Fig. 1). We wanted our pictures to include a 30 × 30 cm quadrat with its center at the flag. To take photographs, we placed a 30 cm ruler 15 cm away from the flag lying flat at a randomized perpendicular angle to the flag. This created the first side of a 30 × 30 cm quadrat. After removing the flag that marked the middle of the quadrat, we took a standardized digital photograph using an iPhone (Apple Inc.) with the ruler toward the bottom of the photograph, taken from a height of about 0.25 m (about knee height). We used these photos to determine point availability. We uploaded photos taken in the field into Powerpoint 2211 (Microsoft Corporation, Albuquerque, New Mexico, USA). We drew a line within Powerpoint 2211 across the ruler to create a 30 cm scaled line and made a 30 × 30 cm quadrat using this line. We created nine more identical lines to complete the box, setting up a digital grid over the photograph. Using the align tool, we distributed the lines evenly horizontally and vertically across the box to create a 10 × 10 grid (10 lines horizontally, 10 lines vertically) to create 100 points. At each point, we identified and recorded the plant species present. If no plants were present at the point, we recorded the point as litter.

To determine landscape availability, we input the GPS locations where the tortoise started and stopped foraging to Google Earth 9.178.0.1 (Fig. 1, white Xs). We measured the distance of the straight-line path between these start and stop locations using the measuring tool, which we termed total distance. We recorded the total distance in meters and the compass angle of the path in degrees. To create a large quadrat based off total distance for landscape availability, we created a square that was positioned so the foraging path was directly in the middle of the quadrat. For example, if the total distance of the foraging path of the tortoise ran from north to south, we created a quadrat that had north, south, east, and west sides. We first created four lines that were exactly perpendicular to and the same length as the total distance. We positioned two of these lines to intersect the start and stop points at their midpoints, which created the north and south sides of the large quadrat. We then oriented the other two lines exactly 90 degrees and positioned them to complete the east and west sides of the large quadrat. These lines created the larger quadrat that served as the second level of availability (landscape availability). Using the add placemark tool, we marked the southwestern corner of the quadrat, and we recorded the GPS coordinates to be used later in the field. This southwestern point was the origin of the quadrat for landscape availability (i.e., corresponding to 0, 0 in an X-Y Cartesian coordinate system).

We created a large grid over the broader landscape quadrat by dividing the total distance by 10, creating 10 lines both horizontally and vertically to create 100 points (grid-point distance). After creating a larger grid using Google Earth 9.178.0.1 based on the total distance, we selected random points, we photographed plants at each random point, we affixed a 30 × 30 cm quadrat onto the image, and we identified each plant at the intersection, which we termed landscape availability. We took a series of photographs at random intersections of these lines within the grid in accordance with an X-Y Cartesian coordinate system relative to the origin established above (Fig. 1, gray Xs). We determined the intersections where the photographs were taken by a two-digit random number generator in the field. For example, if the random number was 63 (thus corresponding to 6, 3), the observer walked six grid-point distance units in the X direction and three grid-point distance units in the Y direction. The number of quadrats photographed in each foraging observation corresponded to the number of times a tortoise stopped to feed plus one (n + 1). We determined the locations in the field by walking the distance necessary in the X and Y direction, which we calculated using the grid-point distance and by using a compass, to reach the desired intersection. We analyzed the photographs taken in the field in the same way as point availability described above. We identified plants to the species level or the lowest taxonomic unit possible using a combination of field guides (Nelson 1996; Austin 1999, 2003; Nelson 2003; Wunderlin, R.P., B.F. Hansen, A.R. Franck, and F.B. Essig. 2021. Atlas of Florida Plants. University of South Florida. Available from http://florida.plantatlas.usf.edu/ [Accessed 18 March 2021]) and consultation with local naturalists who were familiar with the flora at our study site. Grasses were particularly difficult to identify when not in florescence, but we were able to confidently identify nine grasses to the species level and five grasses to the genus level.

Statistical analysis.—We performed foraging observation calculations using Excel v2211 (Microsoft Corporation). For each plant species, we totaled the number of bites taken by all tortoises across all observations for analysis. For each foraging observation, we totaled the number of identified plant species for all point availability and landscape availability for analysis. We calculated proportions of bites of each plant species eaten by tortoises compared to the total number of tortoise bites using the totals summed for the foraging observations.

To determine the feeding selectivity for each individual plant species, we calculated Jacobs' Electivity Index (D) for each plant species consumed (Jacobs 1974; Lechowicz 1982). We calculated Jacobs' D as follows:

$$D = r_i - p_i / (r_i + p_i - 2r_ip_i)$$

where r_i was the proportion of the plant species i in the diet of the tortoise summed across all foraging observations, p_i was the proportion of the plant species i available in the point availability summed across all foraging observations. In other words, r_i was the number of bites all tortoises took of species i divided by the total number of bites all tortoises took for all species, and p_i was the number of species i across all points within the 30 × 30 cm quadrats. Values of D ranged from -1 to +1, with negative values (< 0) indicating avoidance of the plant species and positive values (> 0) indicating selection of the plant species. A value of 0 indicated the tortoise was consuming the plant species in a random manner. As defined by MacDonald and Mushinsky (1988), a plant species with $D > 0.7$ was strongly selected for, D of 0.3–0.7 was moderately selected for, and $D < 0.3$ was randomly selected. Similarly, a plant species with $D < -0.7$ was strongly avoided, D of -0.7 to -0.3 was moderately avoided for, and $D > -0.3$ was randomly avoided.

To provide another measure for the selectivity of the tortoises for each plant species identified, we also calculated Manly's alpha (Chesson 1978, 1983; Gillis et al. 2020). We calculated Manly's alpha (α) for each plant species that tortoises consumed as follows:

$$\alpha = \frac{r_i / p_i}{\Sigma_{j=1}^{m} r_j / p_j}$$

where r_i was the proportion of the plant species i in the diet of the tortoise summed for all foraging observations, p_i was the proportion of the plant species i available in the point availability summed for all foraging observations, and m was the number of species of forage items totaled from those identified in the availabilities. Values of α range from 0 to +1, the sum of all α totaling 1. When $\alpha = 1/m$, the plant species was randomly consumed. If α >

$1/m$ the plant species was selected for, and if $\alpha < 1/m$ the plant species was selected against (Gillis et al. 2020).

We calculated Feinsinger's Proportional Similarity Index (PSI) to determine the degree of generalist or specialist foraging exhibited by the Gopher Tortoises (Feinsinger et al. 1981; MacDonald and Mushinsky 1988). Values of the PSI range from minimum q to +1. The minimum q is the value that represents the narrowest possible niche. A value of minimum q indicated specialist behavior while a value of +1 indicated generalist behavior. We calculated PSI as follows:

$$PSI = 1 - 0.5 \sum \left| p_i - q_i \right|$$

where p_i was the proportion of the observed plant species i compared to the total number of plant species available in the point availability and q_i was the proportion of the bites of plant species i compared to the total bites taken by all tortoises in this study.

We also calculated Shannon Diversity Indices (Shannon and Weiner 1963) for the point and landscape availabilities and compared them to determine if point diversity was lower than availability, which would indicate that tortoises are selecting a certain foraging path. We calculated Shannon Diversity Indices as:

$$H = -\sum_{i=1}^{s} p_i \ln(p_i)$$

where p_i was the proportion of the number of plant species compared to total number of individual plants and s was the number of plant species. We calculated Shannon Diversity Indices for point availability (H_p) and landscape availability (H_l) of each foraging observation.

We compared two availabilities by using the ratio of point availability over landscape availability. Because the point availability represents the plant species available to the tortoise while foraging, it represented the availability over the foraging path. The landscape availability, on the other hand, represented the availability if the tortoise chose a foraging path in a random direction, making it comparable to the availability of the entire habitat. If diversity was similar between the two availabilities, then tortoises randomly selected their foraging paths. If, however, the point availability diversity was significantly different from the landscape availability, this would mean that it was possible that tortoises were selecting a specific foraging path, one that was less or more diverse and therefore had more specific foraging options than the entire landscape. Comparing the diversity between point and landscape availability with Shannon Diversity Indices tested if the tortoises were choosing a specific foraging path, or if they were foraging randomly. We used the theory behind Shannon's diversity to calculate equitability, a ratio that directly compares the diversities of the point and landscape availability. By calculating the ratio between these two numbers, we were able to quantitatively determine how similar or different the diversity was between these two availabilities. Equitability (E) was calculated as:

$$E = H_p / H_l$$

We calculated equitability values for each foraging observation, and then we calculated a 95% confidence interval from the mean of the foraging observations equitability values to determine if the point availability diversity was significantly different from the landscape availability diversity. If $E = 1$, the diversities were equal between point and landscape availability. If the 95% confidence interval of the equitability value remained below 1, then the diversities of the availabilities were significantly different from each other, and the tortoises would be selecting a particular foraging path.

Results

We observed 18 adult tortoises foraging on 25 separate foraging observations. For repeated observations of the same tortoise, each observation was on a separate day. We observed 414 total points on foraging observations, ranging from three to 66 points per foraging observation, with an average (± standard error) of 17.25 ± 3.27 points per foraging observation. The foraging paths covered a total of 589.8 m, ranging from 2.0 to 76.0 m, for an average of 47.1 ± 4.0 m. The foraging videos covered 6.05 h, ranging from 4.0 to 30.2 min for each video, for an average of 13.1 ± 1.5 minutes per individual. We also observed tortoises take 4,822 bites of plants. All tortoises included in our study were adults (i.e., carapace length > 21 cm). We observed three tortoises foraging twice and one tortoise foraging three times.

We identified 58 plant taxa from foraging observations, point availability, and landscape availability (Appendix Table), 30 of which tortoises consumed. Thirteen plants were available at the point level, but not consumed by the tortoises, including foxtail grass (*Alopecurus* spp.), Carolina Ponysfoot (*Dichondra carolinensis*), lovegrass (*Eragrostis* spp.), Sand Dune Spurge (*Euphorbia cumulicola*), Bitter Melon (*Momordica charantia*), White Gaura (*Oenothera simulans*), Live Oak (*Quercus virginiana*), Winged Sumac (*Rhus copallinum*), Brownhair Snoutbean (*Rhynchosia cinerea*), Saw Palmetto, wireweed (*Sida* spp.), common smilax (*Smilax* spp.), and grapevine (*Vitis* spp.). Sixteen plants were only available at the landscape availability, and therefore were not observed being eaten by tortoises, including Rosary Pea (*Abrus precatorius*), Florida Greeneyes (*Berlandiera subacaulis*), Spurred Butterfly Pea

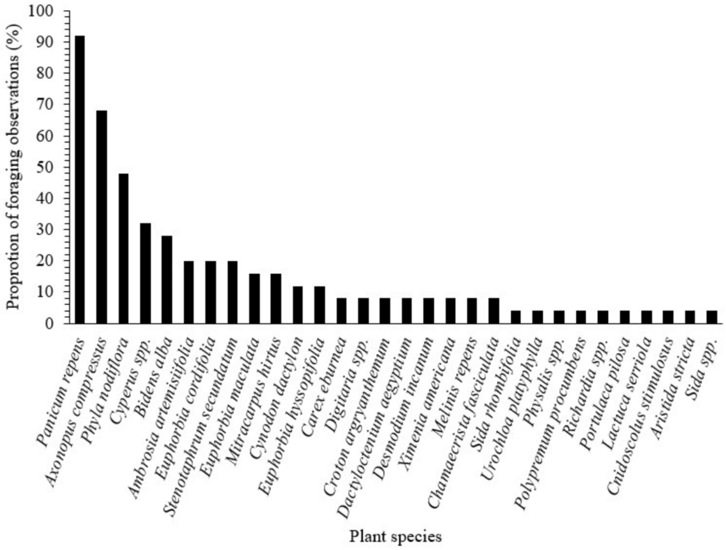

Figure 2. Proportions of foraging observations (%, n = 25) by Gopher Tortoises (*Gopherus polyphemus*) were calculated for each plant species (n = 30) at Boyd Hill Nature Preserve, St. Petersburg, Florida, USA. Common names are found in the Appendix Table.

(*Centrosema virginianum*), Showy Rattlebox (*Crotalaria spectabilis*), Dogfennel (*E. capillifolium*), Wild Poinsettia (*Euphorbia heterophylla* / *Euphorbia cyathophora*), annual mercury (*Mercurialis* spp.), woodrose (*Merremia* spp.), muhly grass (*Muhlenbergia* spp.), Switchgrass (*Panicum virgatum*), Virginia Creeper (*Parthenocissus quinquefolia*), Bracken Fern (*Pteridium aquilinum*), Laurel Oak (*Q. hemisphaerica*), Cabbage Palm (*Sabal palmetto*), skullcap (*Scutellaria* spp.), goldenrod (*Solidago* spp.), and Spanish Moss (*Tillandsia usneoides*).

Of the 30 plant taxa that tortoises consumed, the number of tortoises that ate each plant varied considerably (Fig. 2). The most consumed plants were Torpedograss, Carpet Grass (*A. compressus*), Frogfruit (*Phyla nodiflora*), nutsedge (*Cyperus* spp.), and Beggarticks. In all 25 foraging observations, tortoises consumed some sort of grass (Poaceae). Tortoises mostly consumed the leaves of all the plants, except for Hog Plum (*Ximenia americana*), of which tortoises consumed only the fleshy fruit.

From the summed number of bites that all tortoises took, we determined proportions of consumed plants. Torpedograss and Carpet Grass comprised 57.1% of the total number of bites (Fig. 3). Sixteen plant taxa comprised 93.7% of the total number of bites. Of these 16 plant species, 10 are native and six are non-native to

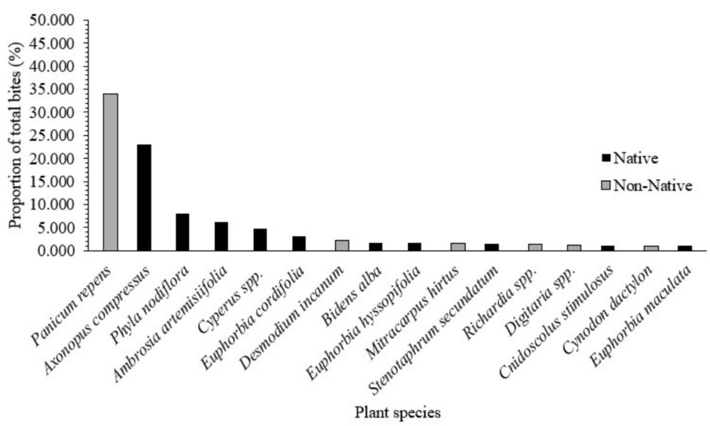

Figure 3. Plant consumption by Gopher Tortoises (*Gopherus polyphemus*) at Boyd Hill Nature Preserve, St. Petersburg, Florida, USA, was measured as proportion of total bites (%, n = 4,822) of each plant species for all tortoise foraging observations, distinguished between native and non-native plants. The following plant species (not shown) made up less than 1% of the total: Crowfoot Grass (*Dactyloctenium aegyptium*); Natal Grass (*Melinis repens*); wireweed (*Sida* spp.); Hog Plum (*Ximenia americana*); Bristle-leaf Sedge (*Carex eburnea*); Pink Purslane (*Portulaca pilosa*); Arrowleaf Sida (*Sida rhombifolia*); Broadleaf Signalgrass (*Urochloa platyphylla*); Wiregrass (*Aristida stricta*); Silver Croton (*Croton argryanthemum*); Prickly Lettuce (*Lactuca serriola*); groundcherry (*Physalis* spp.); Partridge Pea (*Chamaecrista fasciculata*); and Juniperleaf (*Polypremum procumbens*). Common names of other plants can be found in the Appendix Table.

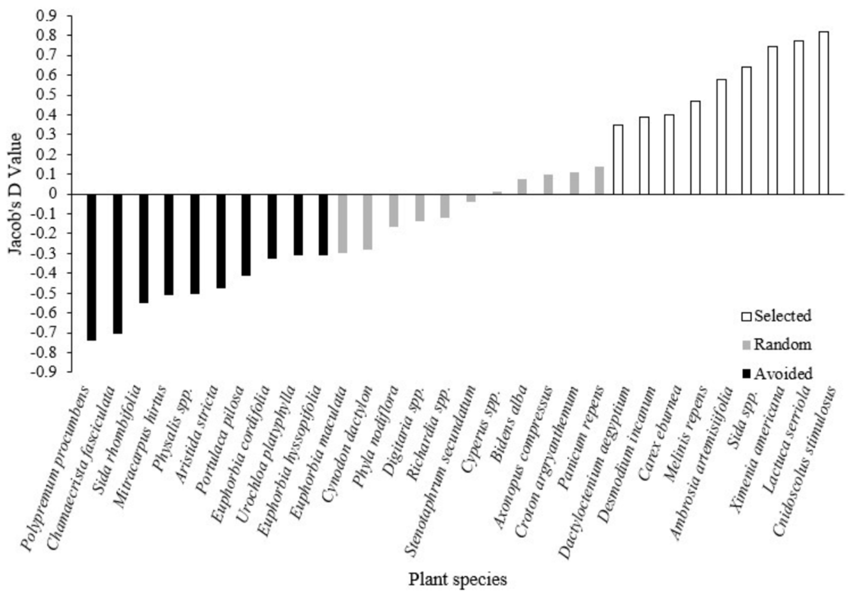

Figure 4. Jacob's Electivity Index *D* values were calculated for each plant species based on observations of Gopher Tortoise (*Gopherus polyphemus*) foraging at Boyd Hill Nature Preserve, St. Petersburg, Florida, USA. Values range from -1 to +1, negative numbers indicating avoidance, and positive numbers indicating selection. Common names of plants can be found in the Appendix Table.

Florida. Torpedograss, the most frequently consumed plant species (34.1% of all bites), is non-native. The next plants within the top five most frequently consumed are all native: Carpet Grass (23.0%), Frogfruit (7.9%), Common Ragweed (6.2%), and nutsedge (4.3%).

Using reference values defined by MacDonald and Mushinsky (1988), Gopher Tortoises selected Spurge Nettle (D = 0.821), Prickly Lettuce (D = 0.771), Hog Plum (D = 0.744), wireweed (D = 0.641), Common Ragweed (D = 0.580), Natal Grass (*Melinis repens*, D = 0.469), Bristle-leaf Sedge (*Carex eburnea,* D = 0.401), Creeping Beggarweed (*Desmodium incanum,* D = 0.387), and Crowfoot Grass (*Dactyloctenium aegyptium,* D = 0.348) according to Jacob's D. We also calculated Manly's α for each plant consumed by tortoises (Fig. 4, Table 1). The critical value 1/m for our study was 0.033, and nine plants produced Manly's α values greater than the critical value. Gopher Tortoises selected Spurge Nettle (α = 0.180), Prickly Lettuce (α = 0.139), Hog Plum (α = 0.121), wireweed (α = 0.081), Common Ragweed (α = 0.064), Natal Grass (α = 0.049), Bristle-leaf Sedge (α = 0.042), Creeping Beggarweed (α = 0.040), and Crowfoot Grass (α = 0.037). These are the same nine plants that also produced Jacob's D values greater than the 0.3 threshold, indicating selection. Neither statistical measure considered the two plant species that tortoises consumed most frequently, Torpedograss and Carpet Grass, as having been selected.

The Feinsinger's Proportionality Index, used to determine if tortoises were selective or generalist feeders based on our observations, was PSI = 0.788, which indicated tortoises in our study were relatively generalist feeders. Mean equitability for all foraging observations was $E = 0.927 \pm 0.315$. We calculated the 95% confidence interval to be 0.804–1.051. Because the upper bound of the 95% confidence interval was greater than 1.0, we concluded that the diversity of point and landscape availability were not significantly different from each other, indicating that plant diversity on foraging paths is not significantly different than what is available at the landscape scale.

Discussion

Based on our findings, we reject the hypothesis that Boyd Hill Nature Preserve Gopher Tortoises are dietary specialists and found support for the hypothesis that they are generalists. Within this pattern however, we found that tortoises have preferences for a few plant taxa. Yet, these plants are not the most frequently consumed. The tortoises ate a relatively wide diversity of plant species, but a high proportion of their diet was Torpedograss and Carpet Grass, which were also common throughout both foraging paths and landscape availability. Tortoises especially ingested Torpedograss, a non-native invasive plant species; six of the 16 most common species ingested by tortoises were non-native.

The fact that tortoises frequently ingested non-native species has important implications for the management of Gopher Tortoise habitat. Scientists have conducted few studies to estimate the preference of food items ingested by Gopher Tortoises, but some have analyzed these qualities for the closely related Mojave Desert Tortoise, *G. agassizii.* Tortoises can select high quality

Table 1. Manly's *a* and Jacob's *D* were calculated and compared for each plant species, with total number of bites by Gopher Tortoises (*Gopherus polyphemus*) at Boyd Hill Nature Preserve (St. Petersburg, Florida, USA) included for each species. Bolded values indicate positive or negative selection.

Plant Species	Manly's	Jacob's	Number of Bites
Torpedograss *(Panicum repens)*	0.0217	0.1393	1642
Carpet Grass (*Axonopus compressus*)	0.0210	0.0997	1110
Frogfruit (*Phyla nodiflora*)	0.0132	-0.1673	383
Common Ragweed (*Ambrosia artemisiifolia*)	**0.0642**	**0.5795**	298
Nutsedge (*Cyperus* spp.)	0.0183	0.0118	230
Roundleaf Spurge (*Euphorbia cordifolia*)	0.0094	-0.3267	155
Creeping Beggarweed (*Desmodium incanum*)	**0.0400**	**0.3871**	109
Beggarticks (*Bidens alba*)	0.0209	0.0777	80
Hyssopleaf Spurge (*Euphorbia hyssopifolia*)	0.0096	**-0.3092**	78
Tropical Girdlepod (*Mitracarpus hirtus*)	0.0060	**-0.5089**	77
St. Augustine Grass (*Stenotaphrum secundatum*)	0.0166	-0.0398	73
Mexican clover (*Richardia* spp.)	0.0142	-0.1173	70
Crabgrass (*Digitaria* spp.)	0.0137	-0.1358	60
Stinging Nettle (*Cnidoscolus stimulosus*)	**0.1799**	**0.8206**	54
Bermuda Grass (*Cynodon dactylon*)	0.0102	-0.2782	50
Spotted Spurge (*Euphorbia maculata*)	0.0098	-0.2976	50
Crowfoot Grass (*Dactyloctenium aegyptium*)	**0.0368**	**0.3476**	48
Natal Grass (*Melinis repens*)	**0.0493**	**0.4698**	45
Wireweed (*Sida* spp.)	**0.0812**	**0.6409**	45
Hog Plum (*Ximenia americana*)	**0.1213**	**0.7444**	42
Bristleleaf Sedge (*Carex eburnea*)	**0.0418**	**0.4012**	27
Pink Purslane (*Portulaca pilosa*)	0.0075	**-0.4151**	26
Arrowleaf Sida (*Sida rhombifolia*)	0.0052	**-0.5508**	21
Broadleaf Signalgrass (*Urochloa platyphylla*)	0.0094	-0.3101	12
Wiregrass (*Aristida stricta*)	0.0064	**-0.4765**	12
Silver Croton (*Croton argryanthemum*)	0.0223	0.1089	9
Prickly Lettuce (*Lactuca serriola*)	**0.1386**	**0.7715**	8
Groundcherry (*Physalis* spp.)	0.0059	**-0.5044**	3
Partridge Pea (*Chamaecrista fasciculata*)	0.0031	**-0.7031**	3
Juniperleaf (*Polypremum procumbens*)	0.0027	**-0.7414**	2

food items that accelerate their growth and allow them to be more successful in terms of both survival and reproductive capacity (Hazard et al. 2010). Hazard et al. (2010) studied juvenile desert tortoises, but they still found that when tortoises foraged on more forbs or herbaceous plants other than grasses, they obtained more minerals. When desert tortoises foraged on grass, they lost phosphorus, which Hazard et al. (2010) hypothesized decreased their growth. Barboza (1995) analyzed foraging of adult desert tortoises, and they seemed to prefer forbs over grass. Barboza (1995) discovered that intakes and retention of nitrogen and potassium were greater from the forbs, calcium was more available in forbs but was not absorbed as much as in grass, magnesium was lost from forbs, and sodium was lost for both forbs and grass. Therefore, they concluded that diversity and abundance of both forbs and grasses were necessary for tortoises to obtain necessary nutrients. In our study, tortoises ate mostly leaves and grasses, but we also observed multiple tortoises eat the fruit of Hog Plum. The tortoises consumed only the fruit of this species, and because Hog Plum was deemed selected by Jacob's *D* and Manly's α, we hypothesize that the tortoises are selecting this species for the nutritional benefit of the fruits.

While all observed tortoises consumed grasses, Jacob's *D* and Manly's α indicated that only Natal Grass and Crowfoot Grass were selected grass species.

Torpedograss, Carpet Grass, Bermuda Grass (*Cynodon dactylon*), Broadleaf Signalgrass (*Urochloa platyphylla*), crabgrass (*Digitaria* spp.), St. Augustine Grass (*Stenotaphrum secundatum*), and Wiregrass (*Aristida stricta*) were all grass species that were consumed by tortoises but not selected for. Overall, it appeared that tortoises foraged heavily on highly available plant species, but they did so in a random manner and were not selecting for those plants. Then, they highly selected plant species that were not as widely available, like the fruits of Hog Plum and all parts of Spurge Nettle, so when these were present, tortoises would very likely consume them. MacDonald and Mushinsky (1988) reported a similar foraging pattern.

Comparing our study with that of MacDonald and Mushinsky (1988), tortoises at Boyd Hill Nature Preserve are exposed to a slightly less species-rich plant community (58 plant taxa observed), with fewer consumable plant species than at the Ecological Research Area of the University of South Florida (USF; 68 plant taxa). This is also evident in the fact that MacDonald and Mushinsky (1988) found a much greater number of ingested plant taxa than those found in our study: 52 taxa ingested compared to 30 taxa ingested in our study. Overall, the Ecological Research Area of USF had greater plant richness and diversity, and more native plant species compared to our study site (Fig. 5).

MacDonald and Mushinsky (1988) determined that their tortoises fell halfway between a generalist and a specialist forager based on their PSI value (0.566), while our study found tortoises to be more generalized foragers based on the same measure (0.7884). Our result is important because few studies have found Gopher Tortoises to clearly fall on one side of the generalist vs. specialist diet spectrum. Our study contributes to understanding of tortoise foraging strategies and how habitat quality might affect tortoise foraging behavior. Because fewer plant species are available at our study site, the lower plant diversity may not afford tortoises the opportunity to be dietary specialists. Like MacDonald and Mushinsky (1988) describe, tortoises randomly chose or avoided plants that were common in the landscape and consumed them the most frequently, but they highly selected for a few species.

Gopher Tortoises have been reported to eat grasses, including Bluestem Grass (*Andropogon* spp.), panicgrass (*Dichanthelium* spp.), and bahiagrass (*Paspalum* spp.) by MacDonald and Mushinsky (1988), but we did not observe tortoises consuming these at Boyd Hill Nature Preserve during our study. Other species found in both studies can be compared directly. Tortoises frequently ingested Wiregrass at the USF Ecological Research Area (MacDonald and Mushinsky 1988), yet the Jacob's *D* value produced a negative number, showing random selection of the plant species (*D* = -0.27). Tortoises

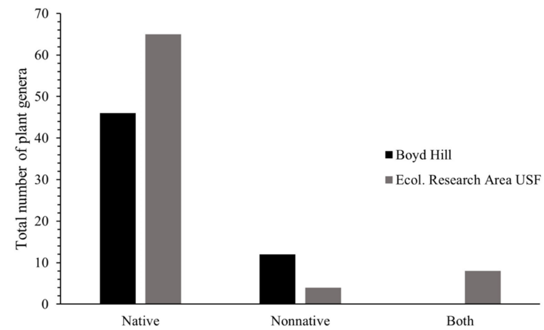

Figure 5. Total number of plant genera found at Boyd Hill Nature Preserve, St. Petersburg, Florida, USA, and the Ecological Research Area of University of South Florida (USF), USA, were divided into categories. The term Both refers to plants identified at the genus level that included both native and nonnative species (MacDonald and Mushinsky 1988).

in our study did not consume Wiregrass as frequently and the Jacob's *D* value (*D* = -0.476) showed negative selection or avoidance. While the tortoises at the Ecological Research Area also commonly ate milk peas (*Galactia* spp.), pines (*Pinus* spp.), and Live Oak as indicated by presence in scats (MacDonald and Mushinsky 1988), we did not observe tortoises in our study consuming these species even though they were present throughout our study site. Despite the leaves being found in scats, MacDonald and Mushinsky (1988) only had one instance of oak ingestion and no pine ingested within foraging observations.

Both our study and that of MacDonald and Mushinsky (1988) found that tortoises selected for Spurge Nettle. In our study, both the Jacob's *D* value and the Manly's α indicated that tortoises selected for Spurge Nettle. The Jacob's *D* was slightly higher than what MacDonald and Mushinsky (1988) found (*D* = 0.65). Hog Plum and Prickly Lettuce also had high Jacob's *D* values in our study, indicating strong selection for these species. MacDonald and Mushinsky (1988) did not report a similar finding for Hog Plum and Prickly Lettuce, with no report of Hog Plum and a report of < 1.0% composition in tortoise scat for Prickly Lettuce. MacDonald and Mushinsky (1988) found the highest Jacob's *D* value for Mexican clover (*Richardia* spp.; *D* = 0.92), a common plant also present at Boyd Hill Nature Preserve. Although Mexican clover was consumed by tortoises in our study as the 12th most frequently consumed species, based on its Jacob's *D* value (*D* = -0.117), it was randomly consumed by tortoises.

Management implications.—Based on our results, habitat management can have direct impacts on Gopher Tortoise foraging ecology. Habitat conservation usually encourages the preservation of native plant species and the removal of non-natives. The most-consumed plant species by the tortoises, Torpedograss, was randomly consumed and is a non-native grass. Given that Gopher Tortoises use hind-gut fermentation (Goessling et al. 2018), tortoises randomly consuming large amounts of Torpedograss grass are likely doing so simply to fill their gastrointestinal tract with large amounts of cellulose fiber of relatively poor nutritive quality. A majority (10 of 16) of the most consumed plants were native, suggesting that tortoises still prefer native plants to non-natives. Gopher Tortoise habitat managers should attempt to eliminate non-native species and preserve native species, particularly grasses. The most preferred plant species are all open-canopy fire-adapted native plants. Increased prescribed fire and management for canopy openness will facilitate those species. Overall, Gopher Tortoise habitat must include a variety of plant species with rich diversity to ensure survivorship of the tortoises (MacDonald and Mushinsky 1988; Mushinsky et al. 2003).

The diversity comparisons of our study showed that tortoises forage on paths that are not significantly different than plant diversity within a broader landscape. In our study, tortoises were not choosing a specific foraging path, contrary to our original hypotheses. Further studies may test our hypothesis by considering more in depth the differences in the plant species between the foraging paths of tortoises and what is available in the surrounding habitat.

Because our study was limited temporally, future studies should include data across the entire year for these foraging animals, as well as over multiple years, as both tortoise foraging and plant developmental stages may vary seasonally or yearly. For example, tortoises in our study were not observed to consume common smilax, although during the spring vegetation flush, tortoises have been observed to consume this plant intensively when the apical shoots are softer and palatable (pers. obs.). Plants vary in their flowering and fruiting phenology, which also likely affect palatability to herbivores, as well as the availability of seeds that tortoises could disperse throughout their habitat (Carlson et al. 2003; Birkhead et al. 2005; Figueroa et al. 2021). Tortoises themselves may exhibit different foraging patterns depending on the season as well, such as during vitellogenesis when females are producing yoked follicles. Therefore, more data are needed on each season to better understand the overall foraging pattern of Gopher Tortoises at our study site.

Conclusions.—Gopher Tortoises at Boyd Hill Nature Preserve exhibited strong generalist foraging behaviors, with a bulk of tortoise diet being food items like grasses that were commonly available in the surrounding landscape, but with a few tortoises selecting particular forage items when they were available. Boyd Hill Nature Preserve was presumed to represent lower quality habitat for tortoise foraging compared to sites in other similar studies (MacDonald and Mushinsky 1988), and the tortoises did show preferences that varied from those studies, selecting or avoiding different forage items. While previous studies showed tortoise foraging patterns when tortoises have access to more diverse resources, our study demonstrates the common foraging patterns seen in a less diverse habitat. For Gopher Tortoises, a highly urbanized, isolated habitat like our study site is becoming the norm due to human development and habitat fragmentation. Our study provides evidence for the benefits of increasing fire and reducing non-native plant species, which ultimately will increase diversity in the plant communities available for the tortoises. For this reptilian herbivore, it is better to give tortoises the chance to be specialist by providing a plethora of foraging options, rather than forcing them to be foraging generalists due to low plant richness.

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Appendix Table 1. Plant species were found in Gopher Tortoise (*Gopherus polyphemus*) foraging observations, point availability, and landscape availability (n = 58) at Boyd Hill Nature Preserve (St. Petersburg, Florida, USA). Bolded plant species indicate those found in all three scenarios (n = 28).

Species	Eaten by tortoise	Point availability	Landscape Availability
Rosary Pea (*Abrus precatorius*)			X
Foxtail grass (*Alopecurus* spp.)		X	
Common Ragweed (*Ambrosia artemisiifolia*)	X	X	X
Wiregrass (*Aristida stricta*)	X	X	X
Carpet Grass (*Axonopus compressus*)	X	X	X
Florida Greeneyes (*Berlandiera subacaulis*)			X
Beggarticks (*Bidens alba*)	X	X	X
Bristleleaf Sedge (*Carex eburnea*)	X	X	X
Spurred Butterfly Pea (*Centrosema virginianum*)			X
Partridge Pea (*Chamaecrista fasciculata*)	X	X	X
Stinging Nettle (*Cnidoscolus stimulosus*)	X	X	X
Showy Rattlebox (*Crotalaria spectabilis*)			X
Silver Croton (*Croton argryanthemum*)	X	X	X
Bermuda Grass (*Cynodon dactylon*)	X	X	X
Nutsedge (*Cyperus* spp.)	X	X	X
Crowfoot Grass (*Dactyloctenium aegyptium*)	X	X	X
Creeping Beggarweed (*Desmodium incanum*)	X	X	X
Carolina Ponysfoot (*Dichondra carolinensis*)		X	
Crabgrass (*Digitaria* spp.)	X	X	X
Lovegrass (*Eragrostis* spp.)		X	X
Dogfennel (*Eupatorium capillifolium*)			X
Roundleaf Spurge (*Euphorbia cordifolia*)	X	X	X
Sand Dune Spurge (*Euphorbia cumulicola*)		X	X
Wild Poinsettia (*Euphorbia cyathophora / Euphorbia heterophylla*)			X
Hyssopleaf Spurge (*Euphorbia hyssopifolia*)	X	X	X
Spotted Spurge (*Euphorbia maculata*)	X	X	X
Prickly Lettuce (*Lactuca serriola*)	X	X	
Natal Grass (*Melinis repens*)	X	X	X
Annual mercury (*Mercurialis* spp.)			X
Morning glory (*Merremia* spp.)			X
Tropical Girdlepod (*Mitracarpus hirtus*)	X	X	X
Bitter Melon (*Momordica charantia*)		X	X
Muhly grass (*Muhlenbergia* spp.)			X
White Gaura (*Oenothera simulans*)		X	X
Torpedograss (*Panicum repens*)	X	X	X
Switchgrass (*Panicum virgatum*)			X
Virginia Creeper (*Parthenocissus quinquefolia*)			X
Frogfruit (*Phyla nodiflora*)	X	X	X
Groundcherry (*Physalis* spp.)	X	X	X

Appendix Table 1 (continued). Plant species were found in Gopher Tortoise (*Gopherus polyphemus*) foraging observations, point availability, and landscape availability (n = 58) at Boyd Hill Nature Preserve (St. Petersburg, Florida, USA). Bolded plant species indicate those found in all three scenarios (n = 28).

Species	Eaten by tortoise	Point availability	Landscape Availability
Juniperleaf (*Polypremum procumbens*)	X	X	X
Pink Purslane (*Portulaca pilosa*)	X	X	X
Bracken Fern (*Pteridium aquilinum*)			X
Laurel Oak (*Quercus hemisphaerica*)			X
Live Oak (*Quercus virginiana*)		X	X
Winged Sumac (*Rhus copallinum*)		X	X
Brownhair Snoutbean (*Rhynchosia cinerea*)		X	X
Mexican clover (*Richardia* spp.)	X	X	X
Cabbage Palm (*Sabal palmetto*)			X
Skullcap (*Scutellaria* spp.)			X
Saw Palmetto (*Serenoa repens*)		X	X
Arrowleaf Sida (*Sida rhombifolia*)	X	X	
Wireweed (*Sida* spp.)		X	X
Common smilax (*Smilax* spp.)		X	X
Goldenrod (*Solidago* spp.)			X
St. Augustine Grass (*Stenotaphrum secundatum*)	X	X	X
Spanish Moss (*Tillandsia usneoides*)			X
Broadleaf Signalgrass (*Urochloa platyphylla*)	X	X	
Grapevine (*Vitis* spp.)		X	X
Hog Plum (*Ximenia americana*)	X	X	X