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THE FORAGING ECOLOGY OF THE JUVENILE GOPHER TORTOISE, GOPHERUSPOL YPHEMUS

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CERTIFICATE OF APPROVAL

This is to certify that the thesis of

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in the graduate degree program of
Zoology
was approved on July 2, 2001
for the Master of Science degree.

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THE FORAGING ECOLOGY OF THE JUVENILE GOPHER TORTOISE,
GOPHERUS POLYPHEMUS

by

TERRI ANNE STILSON

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
Department of Biology
College of Arts and Sciences
University of South Florida

August 2001

Co-Major Professor: Henry R. Mushinsky, Ph.D.
Co-Major Professor: Earl D. McCoy, Ph.D.

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Food plant preferences of juvenile gopher tortoises, *Gopherus polyphemus*, were investigated in a west central Florida population. The juvenile gopher tortoises were free-ranging and were located in a sandhill habitat subject to yearly prescribed burns. Diet was determined by foraging observations, in which the number of bites taken per taxon, the number of plants sampled per taxon, and the amount of each taxon available along the foraging path were recorded. Preference was determined with Manly's alpha index of preference and Jacob's D electivity index. Selected plants in the habitat were analyzed for relative nitrogen content to investigate whether preferred plants contain higher amounts of nitrogen as an indicator of protein. Risk-proneness, measured as total distance traveled during foraging and as the farthest straight-line distance from the tortoise burrow, was tested for correlations with several variables: tortoise size, tortoise size category, percent of preferred plants along the foraging path, percent of foraging event spent under cover, speed. Daily activity patterns were investigated.

Preferred plants contained significantly more nitrogen than avoided plants. Plant genera which were significantly preferred by juvenile gopher tortoises were: *Richardia*, *Chamaecriste*, *Evolvulus*, *Ruellia*, *Dyschoriste*, *Polygala*, *Crotalaria*, *Liatris*, *Hedyotis*, and "unidentified seedlings." No strong hierarchy, or degree of

preference, of preferred plants could be determined. While the group of preferred plants, in general, contained greater amounts of nitrogen than the avoided plants, some of the preferred genera contained relatively little nitrogen. These plants may provide good sources of other nutrients important for growth and shell development, such as Ca.

Speed and tortoise size category were the only variables correlated with risk-prone behavior. Larger individuals may be less vulnerable to predation, and individuals traveling farther distances may move faster to reduce exposure time. Juvenile gopher tortoises did not exhibit clear patterns in the time of day they perform specific activities, nor did they exhibit differences in the time of day of activity among seasons. They did, however, seem to follow a specific sequence of behavior regardless of when the behavior was initiated: emerge from the burrow, bask (thermoregulate), maintain the burrow, forage, re-enter burrow.

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INTRODUCTION

The gopher tortoise (*Gopherus polyphemus*) is one of four species of tortoises living in North America. Its range extends from South Carolina to Louisiana (Diemer 1992), making it the easternmost of the four species, all of which are included in the genus *Gopherus*. *Gopherus* are medium sized tortoises with long life spans (up to 60 years of age), delayed sexual maturity (Germano 1994), and fairly complex mating behaviors (Ruby and Niblick 1994).

The gopher tortoise prefers a xeric habitat with relatively little (<40%) canopy cover and loose, well-drained, sandy soil, which may be important for ease of excavation of burrows (Diemer 1995, Lovich 1995, Wilson et al. 1994). In Florida, the gopher tortoise occurs in a variety of habitats such as scrub, scrubby flatwoods, pine flatwoods, and coastal dunes (Auffenberg and Franz 1982, Diemer 1995), but is most commonly found in sandhill habitat. The vegetation of sandhill habitat is characterized by a sparse canopy of longleaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*), a ground cover consisting of grasses and herbs, and a moderate shrub layer of saw palmetto (*Serona repens*). Periodic fire maintains the patchiness of the canopy and shrub layer. An open habitat structure is important to the tortoise because it allows the tortoise's primary food plants (grasses and herbs) to

flourish, and may provide increased sunlight for maintaining higher body temperature and for enhanced development of eggs (Kwiatkowski and Connor 1995, Mushinsky and McCoy 1994).

Although all of the North American tortoises dig burrows to some extent, the gopher tortoise is one of two that digs extensive burrows (Germano 1994). Burrows provide protection from predators (for juveniles), desiccation, and temperature extremes (Wilson et al. 1994). In addition to providing refuge for the tortoise, burrows are used by a variety (over 360 species) of invertebrates and vertebrates. Some of these commensals, such as the eastern indigo snake (*Drymarchon corais couperi*) and the Florida mouse (*Peromyscus floridanus*), are federally listed species (Diemer 1995, Jackson and Milstrey 1989).

Because the habitat that the gopher tortoise prefers is located on prime land for agriculture, phosphate mining and human development, and because the gopher tortoise is consumed by humans, the species has experienced a sharp decline (estimated at 80%) in numbers during the past century (Diemer 1995). In Florida, it is a Species of Special Concern (Diemer 1992). The ramifications of the decline of the gopher tortoise may reach well beyond the decline of a single species, considering the number of commensal organisms that use its burrows. The general decline of the gopher tortoise, combined with its potential role as a keystone species in its ecosystem (Eisenberg 1983), have prompted several authors to emphasize the need for a more complete record of this reptile's biology (Diemer 1992,

Germano and Bury 1994, McCoy 1995). Among the areas considered to be lacking in knowledge is the ecology and behavior of juveniles (Germano and Bury 1994, Lovich 1995, Morafka 1994, Wilson et al. 1994).

Juvenile tortoises look like smaller versions of their adult counterparts in general morphology. They exhibit little or no external secondary sexual dimorphisms, however, and possess relatively soft shells that are somewhat more yellowish to orange in coloration than the harder shells of adults (McRae et al. 1981, Wilson et al. 1994). Juveniles experience rapid growth, most of which occurs during the summer and may correspond with increased legume availability that may provide an abundance of protein (Kwiatkowski and Connor 1995, Landers et al. 1982, McRae et al. 1981, Mushinsky et al. 1994). The shell of the gopher tortoise begins to harden as the animal approaches five to six years of age (carapace length ~81-~171 mm)(Landers et al. 1982, Mushinsky et. al 1994, Wilson et al.1994). As a tortoise matures, social interactions increase, secondary sexual characteristics begin to develop, and the growth rate begins to decline (McRae et al. 1981, Mushinsky et al. 1994, Wilson et al. 1994). One study in a central Florida population demonstrated that growth begins to diminish between 10-12 years of age (carapace length ~183-~306 mm) (Mushinsky et al. 1994). The period between hardening of the shell and sexual maturity is the subadult stage, which lasts until tortoises reach a carapace length of approximately 230-265 mm, which corresponds to a minimum documented age of nine years in the

southern part of the range and sixteen in the northern part of the range.
(Germano 1994, Mushinsky et. al 1994).

Juveniles emerge from their burrows during all seasons of the year in parts of their range, and are more active than adults during the winter (Diemer 1992, Wilson et al.1994). In a study in central Florida, juveniles were inactive (i.e., in their burrows) during 90% of all observations (Wilson et al. 1994). Juveniles tend to be less conspicuous than adults both in size and behavior, and emerge from their burrows primarily to feed and maintain their body temperatures by basking. While both adults and juveniles of this species spend a great deal of "active" (defined as time spent outside of their burrows) time basking at their burrow mouths, this behavior may be more crucial to juveniles for maintenance of body temperature because of their small size. Like adults, juvenile tortoises may use more than one burrow seasonally (Diemer 1992, McRae et al.1981, Wilson et al. 1994). The number of burrows used by juveniles aged 1 to 4 years of age (carapace length 64-130 mm) was greatest in the summer (3.6 ± 1.4) and least in the winter (1.7 ± 0.8) in a central Florida study (Wilson et al. 1994).

Inconspicuous behavior by juvenile tortoises may in part be a result of heavy predation pressure by a variety of reptilian, avian and mammalian predators (Fitzpatrick and Woolfenden 1978, Mushinsky and McCoy 1995, Wilson et al. 1994). Estimates of survivorship have been low for hatchling (0-1 years of age) tortoises through 4 years of age. No reports on survivorship of subadults are available, but their relatively harder shells and greater size

probably render them less vulnerable than their smaller counterparts (Wilson 1991).

Home ranges of radiotelemetered juveniles in North and Central Florida have been reported (Diemer 1992, Wilson et al. 1994). The mean home range of juveniles in North Florida was 0.0133 ha, while that of subadults was 0.0489 ha, adult females was 0.3073 ha, and adult males was 0.8791 ha (Diemer 1992). Although the preceding results indicate a trend of increasing home range with age class, the author recognized that there was considerable individual variation; some juveniles and subadults had larger ranges than some adults (Diemer 1992). A Central Florida study reported an annual home range of juveniles of 0.072 +/- 0.114 ha. (Wilson et al. 1994). In addition to home range sizes, reported mean distances moved between burrows are: 16.0m (Diemer 1992), 15.2m (Wilson et al. 1994), and 11.7m for juveniles aged 2-5 and 20.8m for those aged 6 (McRae et al. 1981).

Both adult and juvenile gopher tortoises ingest a variety of grasses and forbs, but are selective foragers (Garner and Landers 1981, Macdonald 1986). Juveniles may rely more heavily on forbs, and less on grasses, than adults. Adults have been documented to ingest wiregrass (*Aristida* spp.) regularly, while juveniles do so less often (Garner and Landers 1981, Macdonald 1986, Macdonald and Mushinsky 1988).

Differences between the diets of adults and juveniles may be related to juveniles' rapid growth. A fast growth rate seems important for their survival. The ability to select plants that are relatively high in protein

and other nutrients (e.g. phosphorus, calcium and magnesium) may be an important factor for achieving a fast growth rate (Avery et al. 1993, Mushinsky et al. 1994). Juveniles may select plants that provide plentiful nutrients which are relatively accessible (lower fiber content) (e.g. *Dyschoriste*, plants of the family Fabaceae), and reject items that supply bulk but have little nutritional value (e.g. *Aristida*) (Garner and Landers 1981, Macdonald 1986).

The primary objectives of my study were two. The first was to determine, through systematic observation, if juvenile gopher tortoises exhibit food preferences. The results will be compared with a similar study conducted on both juveniles and adults in the same central Florida location which focused on scat analysis and chance observation (Macdonald 1986). The second primary objective was to determine if the preferred food plants possess a higher nitrogen content (as an indicator of protein) than plants that are less preferred.

This study also had two secondary objectives. The first was to relate information about the foraging paths chosen by tortoises with predictions derived from foraging theory (Stephens and Krebs 1986). The specific predictions I addressed were: (1) larger individuals will forage for longer periods and travel greater distances than their smaller counterparts; (2) juvenile tortoises will forage for longer periods and travel farther if they are under the cover of low-lying shrubs for much of their foraging foray (and vice-versa); (3) juvenile tortoises will forage for longer periods and travel greater

distances when the relative abundance of preferred food types along the foraging path is low (and vice-versa); and (4) the farther juvenile tortoises move from their burrows, the faster they will move. These predictions address the amount of risk juvenile tortoises may be willing to take in order to obtain adequate, nutritious plant foods, in relation to their vulnerability to predation. Larger tortoises' shells are less soft, possibly leaving them less vulnerable than smaller individuals. They may, therefore, be more risk-prone and travel greater distances in search of preferred food plants. Similarly, tortoises (regardless of size) traveling under the cover of shrubs may be less conspicuous to avian predators and may therefore travel farther from their burrows than they would when foraging out in the open. If the path a tortoise is foraging on has a low percentage of preferred (and presumably more nutritious) plants, the tortoise may travel farther from its burrow in order to obtain adequate nutrition for growth, regardless of the size of the tortoise or the amount of shrub cover along the foraging path. Finally, a juvenile tortoise may move faster when traveling farther from its burrow to reduce exposure time.

The second secondary objective was to obtain data about the daily activity of juvenile gopher tortoises. Specifically, I wished to identify if juvenile tortoises exhibit patterns in their daily activities, such as the time of day they emerge from their burrows, the length of time they spend outside their burrows, and the time of day and length of time they spend performing

specific activities, such as foraging, thermoregulating (“basking”), and maintaining their burrows.

METHODS

Field Observations

My study was conducted on the Ecological Research Area of the University of South Florida. It is a 200ha plot located in Hillsborough County in west-central Florida, 28.05 degrees N, 82.20 degrees W. The area used in this study is xeric upland sandhill habitat with well-drained yellowish sands (Lakeland series) on a limestone base. The vegetation structure on the plot where all tortoise observations were made is maintained by prescribed burning at 1-year intervals and consists of a sparse canopy of longleaf pine (*Pinus palustris*), slash pine (*P. elliotii*), turkey oak (*Quercus laevis*) and sand live oak (*Q. geminata*). Ground vegetation includes grasses (e.g. *Aristida* spp., *Andropogon* spp.) and herbs (e.g. *Pityopsis* spp., *Aster* spp., *Liatris* spp., *Baptisia* spp.), and saw palmetto (*Serona repens*) comprises the shrub layer (Connor 1996, Wilson 1990). The area was a 0.7-hectare plot which was separated from other, less frequently burned plots, by fire lanes. A one-year burn plot was chosen for two reasons. First, because juvenile tortoises are extremely inconspicuous and both they and their burrows are difficult to locate in dense vegetation (Spangenburg 1995, Wilson 1990). The sparse canopy and shrub layer maintained by frequent fires facilitated observation.

Second, frequent fires support an abundance of grasses and forbs in sandhill habitats, perhaps providing tortoises the opportunity to exhibit more selective foraging than in less frequently burned areas. The gopher tortoises in this study area are free to move to other plots with different burn frequencies and those who remain here do so by choice.

Gopher tortoises used in this study were between the ages of two and nine years (carapace length 72-216 mm, based on a previous study of gopher tortoises at this study site) (Mushinsky et al., 1994). Age was estimated by counting plastral scute annuli (Landers et al. 1982, Mushinsky et al. 1994). This range of ages was chosen originally to detect changes in activity and behavior associated with decreasing predation pressure (shell hardening probably occurs at 5 to 6 years of age (carapace length ~81-~171), and one study indicated a significant difference between distances moved by tortoises ages 2-5 and age 6 [McRae et al. 1981]), and with the onset of sexual maturity. The majority of the tortoises included in this study are between the ages of two and six years (72-154 mm carapace length).

Tortoise burrows were located visually by walking transects between February and April, 1998. Tortoise burrows are categorized as active, inactive, and abandoned based on evidence of maintenance or activity by a tortoise (Mushinsky and McCoy 1994). Active burrows show signs of recent activity, such as footprints or marks from the plastron. Inactive burrows could potentially be used by a tortoise, but do not have obvious signs of recent activity. Abandoned burrows are often overgrown with vegetation, have a

considerable amount of litter around the mouth, or are partially caved in (Mushinsky and McCoy 1994). Both active and inactive burrows were marked with metal piping, which was driven vertically into the ground about 0.5 m to the side of the burrow. All active and inactive burrows of width 55-255 mm were marked. This range reflects the ages of tortoises selected for study. Burrow width has been demonstrated to be a reasonable predictor of resident tortoise's size (Doonan and Stout 1994, Martin and Layne 1987), and a previous study on this population of tortoises indicated that the minimum size of 3-year-olds is 59 mm carapace length, while the maximum size of 9-year-olds is 249 mm (Mushinsky et al. 1994). A total of 67 burrows was monitored over the course of this study. Burrows were surveyed weekly to assess active, inactive, or abandoned status. The activity of any tortoise observed during these surveys was recorded.

Observations of free-ranging gopher tortoises were attempted 1-3 times weekly from July 1998 through March 2000. Time and length of observations depended primarily on weather conditions and secondarily on my ability to observe and capture a gopher tortoise to bring in to the laboratory to be marked and measured. Generally, observations began between 1000 -1100 hr (preliminary studies indicated that juvenile tortoises in this location emerge from their burrows between 1100-1400 hr and I wanted to be able to observe this), and lasted until 1300-1600 hr. A few observations began later, between 1100-1300 hr, and lasted until 1300-1600 hr. Observation stations were arranged to allow more than one active burrow

to be visible to increase the chances of observing an active tortoise.

Observers seemed to be least perceptible to tortoises when the observation station was behind the burrow (opposite the direction the burrow mouth faces), and when natural visual obstructions (large branches, shrubs, etc) were present between the burrow and the observer (personal observation). If no natural visual barriers existed, "blinds" were constructed using dead palm fronds and tree branches. A portable deerstand was also used to increase the number of burrows which could be watched at one time.

During my study, I attempted to observe tortoises from all the marked burrows that were visible (some were located within shrubs and wiregrass clumps and observations of those burrows were impossible). I watched a burrow or group of burrows from an observation station until I was able to record the foraging activity of a tortoise from at least one of the burrows. Once that occurred (often after 1-4 weeks of observations), I set up a new observation station near a different burrow/group of burrows. Occasionally, I abandoned a group of burrows without having observed foraging activity if I saw very little activity over a few weeks. Also, occasionally, I returned to a previously observed group of burrows if there were several burrows in that area which were particularly active and visible (and I hadn't followed a tortoise from each of them).

All observed activities were recorded, either in writing or with a camcorder mounted on a tripod. Time of day and duration of each activity were noted. Activities recorded were:

Basking- Tortoise was sitting in front of the burrow mouth (on the apron—a mound of sand created by the burrow excavation) with very little movement

Maintaining- Tortoise was moving around the burrow apron (or just inside the burrow mouth) kicking up sand with its front legs.

Foraging- Tortoise was moving away from the burrow apron, investigating and eating plants.

Traveling- Tortoise was moving away from the burrow apron without foraging

Resting- Tortoise was sitting just inside the burrow

Entering- Tortoise was entering the burrow (without my having seen previous activity)

Switching- Tortoise was moving from one burrow to another

When a tortoise emerged fully from its burrow and began to forage, I followed it from a distance and angle that appeared to be unobtrusive to the animal, but allowed me to identify the majority of plants it ate to genus level. I did not record grasses to genus level (other than *Aristida*), but instead identified all broad-leaved grasses as Poaceae to avoid misrepresentation because of errors caused by quick and distant identification. Nomenclature followed Taylor (1992) and Wunderlin (1998). Foraging data were recorded in two ways: (1) the number of bites for each genus sampled, and (2) the

absolute number of plants per genus sampled (for example, on 3/20/00, tortoise #700 took 29 total bites from 7 *Liatris* plants). If I could not determine the identity of an adult plant with certainty, I recorded that plant as "Unknown." Most seedlings were eaten completely before I could identify them, and I placed them in the category "Seedlings." I separated adult unknown plants from unknown seedlings because seedlings of many different plants comprised a fairly significant part of the diet of the juvenile tortoises in my study (9% of all plants taken), and the nutrients of young plants may be more accessible than those of older plants (Garner and Landers 1981). Therefore, documenting ingestion of seedlings compared with their relative abundance could possibly be informative.

During field observations, a field assistant followed closely with a hand-held camcorder to allow me to identify plants the gopher tortoise ate that I may have missed during observations, and to record exact timing of activities. If a field assistant was not available, I carried the camcorder myself and recorded type and amount of plants being eaten by voice recording.

While following a gopher tortoise, I placed flagging in the ground at the location of each directional change by the animal and every 1-1.5 m along straight paths. Each individual was followed until it returned to its burrow, and just before it entered the burrow it was captured to be identified and/or brought into the laboratory to be weighed, measured and marked. Only individuals that had not been previously captured were brought into the

laboratory and weighed, marked by marginal scute notching, and measured, including: anal width, anal notch, plastron length, body width, body thickness, plastron concavity, gular projection, carapace length, and total length (McRae et al., 1981). Individuals were returned to the burrow from which they were captured within 24 hours. Individuals recaptured during the study were identified but not returned to the lab for re-measuring to reduce my interference with the study animals. Additionally, no pre-observational capturing and marking occurred in order to minimize the possibility of tortoises altering their behavior because of handling.

At the end of an observation, I retraced the foraging path (guided by flagging) and recorded all vegetation present along the path within the approximate width of the carapace length of the gopher tortoise. Each plant was counted as one encounter, with the exception of some long, low-vining plants such as *Rhynchosia* and *Shrankia* which intersected the path more than once (counted as many times as it intersected the path). The distance and direction between pairs of successive flags were then measured to construct a map of the tortoise's path and to determine the total distance it traveled and the farthest distance from the burrow that it attained.

I followed several individuals that were foraging while I was checking burrows or walking through the plot. I included that foraging and/or path information with my data only if the distance I followed them before they returned to their burrows was greater than the shortest straight-line distance from the burrow to the point where I discovered them foraging. In these

cases, I recorded the distance as the minimum distance they could have traveled.

Analysis of Plant Preference

To determine if juvenile tortoises choose food plants in a non-random fashion, two dietary preference indices were used: Manly's Alpha Index of Preference (for constant prey populations) and Jacob's D Electivity Index. Both indices were chosen because they are able to evaluate several food types at once. Jacob's D was also chosen because a similar previous study (Macdonald 1986) employed that index, and I wished to compare my results with those of that study. Manly's Alpha is derived from probability theory using the probability of encounter and capture of prey by a predator. Jacob's D is a modification of Ivlev's Electivity Index (a modification of the Forage Ratio) which attempts to make the index independent of the relative abundance of the prey (Krebs 1989).

Both indices use the proportion of a prey taxon available to an animal, and the proportion of that taxon sampled by the animal. The proportion of a taxon available to tortoises along their foraging paths was determined by the formula:

$$(1) \text{Proportion of taxon } i \text{ available} = 100 \times \frac{\text{Number of times taxon } i \text{ was encountered}}{\text{Total number of taxa encountered (m)}} \\ (n_i \text{ or } p)$$

The proportion of a taxon in the tortoises' diets was determined using both presence/absence and number of bites taken:

$$(2) \text{Proportion of taxon } i \text{ sampled} = 100 \times \frac{\text{Number of times taxon } i \text{ was sampled}}{\text{Total number of taxa sampled}} \\ (r_i \text{ or } r)$$

$$(3) \text{Proportion of taxon } i \text{ sampled} = 100 \times \frac{\text{Number of bites of taxon } i \text{ taken}}{\text{Total number of bites taken}} \\ (r_i \text{ or } r)$$

The formula for Manly's Alpha for a plant taxon i is:

$$(4) \quad \alpha_i = [r_i/n_i] \times [1/\sum(r_j/n_j)]$$

where r (formulas 2 and 3, above) is the proportion of a plant taxon i or j sampled in the diet (i and $j = 1, 2, 3, \dots, m$) and n (formula 1, above) is the proportion of a plant taxon i or j encountered along the foraging path.

Preference for a taxon is implied if α_i for that taxon $> 1/m$, where m is the total number of food types (taxa) encountered. Avoidance is implied if $\alpha_i < 1/m$, and $\alpha_i = 1/m$ implies the taxon is being taken in a random manner.

Alpha ranges from 0 to 1. The index is normalized so that $\sum \alpha_i = 1$.

The formula for Jacob's D is:

$$(5) \quad D = \frac{[r-p]}{[r+p-2rp]}$$

where r is the proportion of a plant taxon in the diet (formulas 2 and 3, above) and p is the proportion of that taxon encountered along the foraging path (formula 1, above). A Jacob's D value for a taxon between 0 and -1 indicates avoidance for that taxon. A value between 0 and $+1$ indicates preference, and a value of 0 indicates that the animal is sampling the taxon in a random manner.

Certain individual tortoises were observed foraging on more than one occasion (see table 1 in results). I wanted to ensure that the index values would not be biased toward the preferences of these individuals, if any individual differences exist, but would instead reflect the preferences of the population that I sampled as accurately as possible. Therefore, one foraging observation was randomly selected to be included in the index calculations from each individual tortoise that was observed more than once. The indices were later recalculated using all observations to see if there were discrepancies.

The category "Unknown," which comprised 6.4% of the total diet (based on number of bites), was omitted from index calculations. The plants that I recorded as unknown were not completely eaten, I simply was not able to see and/or identify the plant from my vantage point. Therefore, I would

have counted those plants as encountered during my vegetational analysis of the foraging paths. No category “unknown” existed under “plants encountered,” so the indices would have been impossible to calculate for the “unknown” category. Because all of the “unknown” plants were sampled plants, omitting that category probably produced more conservative index values of preferred plants, if it had an effect.

Both indices were calculated based on: (1) number of plants per genus sampled (presence/absence), and (2) number of bites taken. The indices based on presence/absence were used for establishing preferred genera, and confidence limits were derived for the index values. Confidence limits for the index values were derived from resampling (without replacement) from the available plant population. The indices based on the number of bites taken were used for providing insight into whether certain preferred genera were more preferred than others by tortoises (degree of preference). I did not derive confidence limits for index values based on number of bites, only those based on presence/absence.

I attempted to determine degree of preference within the preferred group in two ways: (1) calculating Manly’s Alpha and Jacob’s D using number of bites (as stated above), and (2) making pairwise comparisons for each plant pair per date to identify consistencies in comparative amounts taken. Plants sampled by tortoises were ranked in order of the most to the least number of bites taken for each foraging event. Each plant pair was evaluated for each foraging event to see if a consistent ranking existed

across events (i.e., 95% of foraging events, tortoises ate more *Liatris* than *Elephantopus* when both were present) Only genera that occurred (either sampled or just present along the foraging path) in three or more foraging events were included in this analysis. I chose this criterion because I felt that three would be the minimum number of occurrences that would allow me to identify true patterns, if they existed.

Once preferences were established via preference indices, I conducted a Mann-Whitney U test to compare the group “preferred” with the group “avoided” for nitrogen content to see if the plants juvenile tortoises were choosing indeed contain greater amounts of protein (implied by amount of nitrogen). Index values based on presence/absence were used to establish “preference” status of each genus for this analysis, and I conducted the analysis twice: once using all genera, placed in each category as indicated by the indices, and once including only those genera whose index values were determined to be statistically significant.

Analysis of Plant Nitrogen Content

Plant specimens were collected on October 21 and October 26, 1999. Species collected were chosen because either (1) I observed them being eaten by tortoises, or (2) I did not observe them being eaten by tortoises, but they were present along many of the foraging paths. A total of 23 species was collected. For each species, I collected between one and seven specimens (some species were rare or rare at that time of year and I could

not find four representatives) for a total of 95 plants. Whole plant specimens were placed in individual labeled plastic bags and immediately brought back to the laboratory where they were dried overnight in a 60°C oven. Once dried, each plant was ground in a Wiley Mill to uniform-sized particles.

An NC2100 Soil Analyzer (CE Instruments) was used to determine percent nitrogen content of each plant specimen. The machine was calibrated and tested for leaks each time it was started, the ash trap was changed every 100 runs, and the water trap was changed every 100-150 runs, to ensure accurate readings. Atropine was used as the known standard. The Eager 200 program was used to record the output in an Excel format.

Foraging Paths

To test the predictions about the distance and time juvenile tortoises might be willing to travel from their burrows, I recorded several foraging path variables. Those variables were: total distance traveled (minimum distance if only a partial foraging event was observed), farthest point (straight-line) distance from the burrow, duration of foraging event (for complete observations only), tortoise size (carapace length)(or burrow size if the tortoise could not be captured), size category (80-99mm, 100-119mm, 120-139mm, 140-159mm), percent of preferred plants along foraging path, percent of foraging event spent under the cover of shrubs (0-25, 26-50, 51-75, 76-100), and speed (meters/minute). To test predictions addressing

factors that might affect how far a juvenile tortoise may be willing to travel from its burrow, total (or minimum) distance and the farthest point distance from the burrow were correlated with all other variables recorded using Kendall's tau and the Spearman rank correlation. Maps of foraging paths were hand-drawn from recorded distances and directions.

Activity

To address the daily activities of juvenile tortoises, I created two activity "logs": (1) point-in-time chance observations from burrow surveys, and (2) observations from watching specific burrows for several hours. Behaviors recorded were: Basking, Maintaining, Foraging, Traveling, Resting, Entering, Switching. The activity log derived from observing specific burrows (log #2) included duration of each activity. Time of occurrence was recorded for each activity. Box and whisker graphs and histograms were created to help visually identify daily and seasonal patterns in activities. The specific patterns I attempted to identify were: (1) differences in the time of day that juvenile gopher tortoises perform certain activities (ex., emerge and bask around 1100 hr, forage around 1300 hr), (2) differences among seasons in the time of day that juvenile gopher tortoises become active. Seasons were defined as: (1) March-May, (2) June-August, (3) September-November, and (4) December-February. A Kruskal-Wallis analysis of variance by ranks test was used to establish whether apparent differences were statistically significant ($P < .05$).

RESULTS

Analysis of Plant Preferences

Seventeen usable foraging events were observed. Several others were observed but I did not use them because: (1) I could not get close enough, or the tortoise was under too much cover, for me to be able to see the majority of plants it ate, (2) the tortoise detected my presence soon into its foraging foray and immediately headed back for its burrow, or (3) I discovered the tortoise toward the end of its foraging foray.

Within the 17 usable observations, 11 individual gopher tortoises were observed (Table 1). A total of 25 plant genera, plus members of the family Poaceae, were sampled by tortoises. A total of 48 plant genera, plus members of the family Poaceae, were available along the foraging paths (Appendix 1).

Table 1: Foraging Observations Used in Index Calculations

Tortoise	Date	Burrow
504	05/06/99	31
-not marked-	08/19/99	01
506	05/27/99	37
	12/09/99	37b

(continued on next page)

Table 1 (continued)

499	06/03/99	32
508	06/22/99	55
509	07/29/99	57
513	10/12/99	18
	11/09/99	18
	03/29/00	18
515	11/26/99	59
	03/29/00	59
502	03/07/00	13
	07/20/99	13
503	03/29/00	31
700	10/14/99	60
	03/20/00	60

Manly's Alpha and Jacob's D both indicated that juvenile tortoises exhibit food preferences and aversions. The "preferred" taxa found to be significant by resampling were: *Richardia*, *Chamaecriste*, *Evolvulus*, *Ruellia*, "Seedlings," *Dyschoriste*, *Polygala* (Jacob's D only), *Crotalaria*, *Liatris*, and *Hedyotis* (Jacob's D only). Of the genera sampled by juvenile tortoises, only the taxon Poaceae was determined to be significantly avoided (table 2).

Table 2: Manly's Alpha and Jacob's D Preference Index Values Based on Presence/Absence

Manly's alpha: .023 indicates neither preference nor avoidance. Greater than .023 indicates preference, less than .023 indicates avoidance. Range 0 - 1.

Jacob's D: 0 indicates neither preference nor avoidance. Greater than 0 indicates preference, less than 0 indicates avoidance. Range -1- +1.

Values determined to be significant by resampling are indicated with an asterisk.

Only genera sampled by tortoises are included in this table. All genera which were present along foraging paths but were not sampled by tortoises have the values 0 (Manly's alpha) and -1 (Jacob's D)

Genus	Manly's Alpha	Jacob's D
<i>Richardia</i>	.095*	.67*
<i>Yucca</i>	.095	.67
<i>Chamaecriste</i>	.095*	.67*
<i>Evolvulus</i>	.081*	.63*
<i>Ruellia</i>	.068*	.58*
<i>Seedling</i>	.064*	.57*
<i>Dyschoriste</i>	.062*	.57*
<i>Shrankia</i>	.057	.50
<i>Polygala</i>	.057	.5*
<i>Crotalaria</i>	.048*	.44*
<i>Liatris</i>	.039*	.41*
<i>Hedyotis</i>	.037	.33*
<i>Helianthemum</i>	.032	.25
<i>Croton</i>	.032	.25
<i>Elephantopus</i>	.031	.25
<i>Berlandiera</i>	.029	.21
<i>Dahlia</i>	.019	-.23
<i>Phoebanthus</i>	.017	-.05
<i>Balduinia</i>	.015	-.12
<i>Aster</i>	.013	-.17
<i>Poaceae</i>	.011*	-.3*
<i>Scutellaria</i>	.009	-.34

The genera *Cnidoscolus*, *Pinus*, *Eupatorium* and *Solidago* were sampled but are not represented in Table 1 because they were only present in the foraging events that were randomly omitted because they represented

multiple observations of the same tortoise/s. When the indices were recalculated including all dates, *Cnidocolus* was preferred, while *Pinus*, *Eupatorium* and *Solidago* were taken at random/slightly avoided. All other taxa remained in the same categories (“preferred,” “avoided,” and “random”).

Pairwise comparisons of the number of bites taken per genus per date (to indicate the degree of preference) did not reveal a consistent hierarchy of preferred genera. They did, however, indicate a hierarchy of two distinct groups of genera. That is, tortoises consistently took more bites of plants included in one group (*Dyschoriste*, *Richardia*, and *Liatris*) than plants included in the other group (*Polygala*, *Crotalaria*, *Ruellia*, *Elephantopus*, *Hedyotis*, and “Seedlings”) when both groups were represented along the foraging path. *Shrankia* could not be placed reliably in either group. These results indicate that juvenile tortoises in my study tend to ingest a greater amount of material from plants of the genera *Dyschoriste*, *Richardia*, and *Liatris* than from plants of the genera *Polygala*, *Crotalaria*, *Ruellia*, *Elephantopus*, *Hedyotis* and “Seedlings.”

Manly’s Alpha and Jacob’s D derived from the number of bites taken were also examined to indicate the degree of preference within the preferred group of plants (Table 3).

Table 3: Manly's Alpha and Jacob's D Preference Index Values Based on Number of Bites Taken

Manly's alpha: .023 indicates neither preference nor avoidance. Greater than .023 indicates preference, less than .023 indicates avoidance. Range 0 - 1.

Jacob's D: 0 indicates neither preference nor avoidance. Greater than 0 indicates preference, less than 0 indicates avoidance. Range -1- +1.

Genus	Alpha	Jacob's D
Shrankia	.194	.85
Chamaecriste	.128	.77
Crotalaria	.109	.75
Richardia	.105	.73
Dyschoriste	.070	.66
Ruellia	.071	.64
Evolvulus	.055	.53
Croton	.043	.43
Polygala	.038	.40
Hedyotis	.037	.38
Elephantopus	.031	.31
Liatris	.027	.27
Berlandiera	.023	.15
Yucca	.013	-.14
Phoebanthus	.012	-.19
Balduinia	.011	-.20
Seedling	.011	-.23
Poaceae	.009	-.34
Aster	.005	-.51
Helianthemum	.005	-.53
Dahlia	.002	-.83
Scutellaria	.001	-.86

The indices take into account an approximate estimate of availability, while the pairwise comparisons do not. Neither takes into account the size of plants, which determines the amount of a plant that can be ingested. The index values did not support the groupings suggested by pairwise comparisons (Table 4).

Table 4: Comparison of the Degree of Preference of the preferred genera as indicated by preference indices based on number of bites taken and by pairwise comparisons of the number of bites taken per genus per date.

The numbers (1) and (2) indicate whether they belonged to the first group (1) or the second group (2) in the pairwise comparisons.

Genera are listed in decreasing order of preference as indicated by the preference indices based on number of bites. Members of group 1 were taken in greater amounts than group 2.

Indices	Pairwise Comparisons
<i>Shrankia</i>	N/A
<i>Crotalaria</i>	2
<i>Richardia</i>	1
<i>Dyschoriste</i>	1
<i>Ruellia</i>	2
<i>Polygala</i>	2
<i>Hedyotis</i>	2
<i>Elephantopus</i>	2
<i>Liatris</i>	1
"Seedlings"	2

The preference indices based on presence/absence and based on the number of bites taken generally agreed about which taxa were preferred, which were being sampled randomly and which were avoided, with a few exceptions. Both *Yucca* and "Seedlings" were indicated as preferred by presence/absence and random/avoided by number of bites. *Liatris* was indicated as highly preferred by presence/absence but was closer to random (though still preferred) by number of bites. Table 5 compares Jacob's D values of genera sampled based on presence absence with those based on number of bites taken. Both are presented in descending order, to

emphasize where genera fall within categories, not compare exact index values per genus.

Table 5: Comparison of Jacob's D values based on presence/absence and number of bites. 0 indicates neither preference nor avoidance. Greater than 0 indicates preference, less than 0 indicates avoidance. Range -1- +1.

Presence/Absence		# of Bites Taken	
Genus	Jacob's D	Genus	Jacob's D
<i>Richardia</i>	.67*	<i>Shrankia</i>	.85
<i>Yucca</i>	.67	<i>Chamaecriste</i>	.77
<i>Chamaecriste</i>	.67*	<i>Crotalaria</i>	.75
<i>Evolvulus</i>	.63*	<i>Richardia</i>	.73
<i>Ruellia</i>	.58*	<i>Dyschoriste</i>	.66
<i>Seedling</i>	.57*	<i>Ruellia</i>	.64
<i>Dyschoriste</i>	.57*	<i>Evolvulus</i>	.53
<i>Shrankia</i>	.50	<i>Croton</i>	.43
<i>Polygala</i>	.5*	<i>Polygala</i>	.40
<i>Crotalaria</i>	.44*	<i>Hedyotis</i>	.38
<i>Liatris</i>	.41*	<i>Elephantopus</i>	.31
<i>Hedyotis</i>	.33*	<i>Liatris</i>	.27
<i>Helianthemum</i>	.25	<i>Berlandiera</i>	.15
<i>Croton</i>	.25	<i>Yucca</i>	-.14
<i>Elephantopus</i>	.25	<i>Phoebanthus</i>	-.19
<i>Berlandiera</i>	.21	<i>Balduinia</i>	-.20
<i>Dahlia</i>	-.23	<i>Seedling</i>	-.23
<i>Phoebanthus</i>	-.05	<i>Poaceae</i>	-.34
<i>Balduinia</i>	-.12	<i>Aster</i>	-.51
<i>Aster</i>	-.17	<i>Helianthemum</i>	-.53
<i>Poaceae</i>	-.3*	<i>Dahlia</i>	-.83
<i>Scutellaria</i>	-.34	<i>Scutellaria</i>	-.86

Liatris, members of *Poaceae*, and *Dyschoriste* were the top three taxa taken by the tortoises in my study, both in terms of times taken and in terms of total bites taken (*Poaceae* was not included in the pairwise comparisons examining degree of preference because this taxon was found to be avoided with respect to its abundance). *Aristida* was the most abundant plant along

foraging paths, followed by broad-leaved Poaceae, *Liatris*, and then *Dyschoriste*. *Dyschoriste*, however, was approximately half as abundant as *Liatris*, one-third as abundant as Poaceae, and one-sixth as abundant as *Aristida*, whereas it was taken more often than Poaceae, and two-thirds as often as *Liatris*. Tortoises took over three-fourths as many bites of *Dyschoriste* than both Poaceae and *Liatris*. These differences in amounts taken vs. availability are reflected by the index values, with *Dyschoriste* consistently more preferred than *Liatris*, and Poaceae avoided with respect to its availability. Table 6 lists the top four most available taxa and the top 3 most sampled taxa.

Table 6: Availability vs. Usage of the Top Four Most Abundant Taxa, Including the Top Three Most Sampled Taxa

Taxon	Times Taken		Bites Taken		Times Encountered	
	Total	Percent	Total	Percent	Total	Percent
<i>Aristida</i>	0	0%	0	0%	396	29%
Poaceae	34	12%	369	15%	231	17%
<i>Liatris</i>	64	22%	411	17%	136	10%
<i>Dyschoriste</i>	44	15%	325	13%	61	4%

Analysis of Plant Nitrogen Content

The nitrogen content between the avoided plants and the preferred plants was found to be significantly different (Mann-Whitney U Test $P < 0.001$). Groups were compared using all plants analyzed and also using only those whose index values were significant via resampling. The difference in N content was significant at $P < .001$ in both cases. Table 7

lists the average percent nitrogen content of all genera analyzed, and reveals the general trend of increasing nitrogen content in the preferred plants over the avoided plants.

Table 7: Average Nitrogen Content of Genera Analyzed

* An asterisk (*) indicates that the index value was shown to be significant by resampling. Unless otherwise noted, an asterisk indicates that both Manly's alpha and Jacob's D values were significant.

Genus	n	Avg. %N	S.D. %N	Preferred or Avoided
<i>Aristida</i>	4	0.84	.17	Avoided*
<i>Pityopsis</i>	4	1.25	.08	Avoided
<i>Phoebanthus</i>	1	1.30	--	Avoided
<i>Scutellaria</i>	4	1.33	.39	Avoided
<i>Carphephorus</i>	4	1.58	.39	Avoided
<i>Aster</i>	4	1.59	.06	Avoided
<i>Stillingia</i>	4	1.60	.33	Avoided
Poaceae	7	1.62	.43	Avoided*
<i>Eriogonum</i>	5	1.80	.53	Avoided
<i>Balduinia</i>	4	1.98	.22	Avoided
<i>Rhynchosia</i>	3	2.04	.22	Avoided
<i>Tephrosia</i>	4	2.46	.21	Avoided
<i>Hedyotis</i>	4	1.22	.27	Preferred * (Jacob's D only)
<i>Richardia</i>	1	1.43	--	Preferred *
<i>Elephantopus</i>	4	1.65	.21	Preferred
<i>Ruellia</i>	4	1.83	.21	Preferred *
<i>Dyschoriste</i>	4	1.95	.21	Preferred *
<i>Evolvulus</i>	1	2.19	--	Preferred *
<i>Croton</i>	3	2.25	.30	Preferred
<i>Liatris</i>	5	2.29	.21	Preferred *
<i>Crotalaria</i>	7	2.31	.59	Preferred *
<i>Cnidoscolus</i>	4	2.36	.48	Preferred
<i>Polygala</i>	4	2.59	.83	Preferred * (Jacob's D only)
<i>Shrankia</i>	5	3.25	.50	Preferred

Foraging Paths

A total of 25 foraging paths was obtained from observing foraging

events. Of those 25, 14 were complete observations, where I was able to observe the tortoise from the time it emerged from its burrow to the time it returned; and 11 were partial observations, where the tortoise was already outside of its burrow when I detected it. Recall that both (1) total (or minimum) distance traveled by tortoises during foraging and (2) the farthest distance from the burrow tortoises attained during foraging, were tested for correlations with the following variables: duration of foraging event, tortoise size, size category, percent of preferred plants along foraging path, percent of foraging event spent under the cover of shrubs, and speed. Of all path variable pairs tested for correlations, only the following were significant (all were significant at $P < .01$ except total distance traveled and tortoise size category, which was significant at $P < .05$):

Total (or minimum) distance traveled and: Duration of foraging event

Tortoise size category

Speed

Farthest distance from the burrow and: Duration of foraging event

Speed

The juvenile tortoises in my study traveled an average of 13.5m round-trip (S.D. 10.1), and reached a mean of 5.7m (S.D. 4.2) as the farthest distance away from their burrows while foraging. See Appendix 3 for sample

foraging path maps.

Activity

I was able to observe active gopher tortoises from observation stations on 60% of the days that observations were attempted (53/89), for a total of 98 observations. Of those, during only 34 did the tortoise move far enough away from the burrow that I was able to capture and mark or identify the tortoise. I was able to observe active tortoises during burrow surveys on 68% of the days that I surveyed the burrows for signs of activity (46/68), for a total of 75 observations. Of those, I was only able to capture the tortoise to mark or identify it 5 times (Table 8).

Table 8: Observations of All Marked/Identified Tortoises

“Foraging” followed by an asterisk (*) indicates that those foraging observations were complete and were included in preference index calculations.

Tortoise #	Date	Burrow #	Carapace Length(mm)	Behavior
496	07/14/98	N/A	97	Traveling
497	09/28/98	43	76	Foraging
498	10/02/98	28	72	Foraging
499	10/13/98	27	82	Foraging
	06/03/99	32	104	Foraging*
500	10/16/98	N/A	113	Traveling
501	11/23/98	17	89	Foraging
502	03/23/99	13	114	Foraging

(continued on next page)

Table 8 (continued)

	07/15/99	13		Foraging
	07/20/99	13	137	Maintaining/Foraging*
	07/22/99	13/13b		Foraging/Switching/Maintaining
	09/17/99	13		Entering
	03/07/00	13		Foraging*
	03/20/00	13		Foraging
503	04/12/99	24	109	Maintaining/Traveling/Entering
	08/17/99	52		Foraging
	03/29/99	31		Foraging*
504	04/20/99	31	124	Entering
	05/06/99	31		Foraging*
505	05/11/99	53b/53d	139	Traveling/Switching
506	05/27/99	37	89	Foraging*
	12/09/99	37b	132	Basking/Foraging*
507	06/03/99	48b	86	Basking/Maintaining/Foraging
508	06/22/99	55	88	Foraging*
509	07/29/99	57	97	Basking/Foraging*
510	09/17/99	50	128	Foraging
700	08/03/99	58	98	Foraging
	08/05/99	58		Entering/Basking/Foraging
	10/14/99	60		Basking/Foraging*
	03/20/00	60		Foraging*
	03/29/00	60		Basking/Foraging
512	11/12/99	24	123	Foraging
513	10/12/99	18	119	Basking/Foraging*
	11/09/99	18		Basking/Foraging*
	03/29/00	18		Foraging
514	11/19/99	61	127	Maintaining/Basking/Foraging
515	11/26/99	59	154	Foraging*
	03/29/00	59		Basking/Foraging*

The only field days when I consistently did not see activity or at least evidence of activity (based on the condition of the burrows) were on cold, overcast/rainy days. Tortoises were active when the weather was cold but sunny, and often when the weather was overcast but warm. I did not remain in the field when heavy rain occurred.

During observations of specific burrows, basking was the most common activity observed, followed by maintenance behavior, and then foraging. Generally, tortoises emerged from their burrows and basked on the apron for a period of between 10-30 minutes (mean 23.5 min., S.D. 27.6 min., range 1-171 minutes). After basking, they usually performed some burrow maintenance for a few minutes (mean 12 min., S.D. 20.7 min., range .08-95 minutes), and then re-entered their burrows. They usually re-emerged from their burrows several minutes later and repeated the process of basking, maintenance, and re-entry. Often, a tortoise would repeat this pattern three or more times over the course of a few hours. Usually I observed a tortoise emerging from its burrow to forage only after several bouts of basking, maintenance, and re-entry. Only once did I see a tortoise emerge from its burrow and begin foraging without basking first. Foraging typically lasted for between 15-20 minutes (mean 16.7 min., S.D. 10.7 min., range 2-50 min.).

The mean and range of starting times for all three of these behaviors was similar:

<u>Behavior</u>	<u>Mean Starting Time</u>	<u>Range of Starting Times</u>
Basking	1307	1020-1605
Maintenance	1254	1100-1522
Foraging	1312	1050-1519

No significant differences of starting times of activity could be detected among the four seasons (March-May, June-August, September-November, December-February). These results indicate that the juvenile tortoises in my study initiated activity within a range of times (during the times that I was observing). They did, however, typically exhibit a predictable sequence of behaviors once they emerged from their burrows: bask, maintain burrow, forage.

During burrow surveys, most of the activity I observed was “entering” or “resting.” Tortoises generally detected my approaching so I could not determine if they had been basking, maintaining their burrows, or beginning/returning from a foraging event. I did observe those activities during surveys on several occasions, however.

The tortoises I was able to identify and observe more than once in my study used an average of 1.75 burrows (S.D. .71, range 1-3). The most burrows I observed any one tortoise utilize was three (Table 8, above). Most of the multiple burrows used by one tortoise were within 7.62 m of each

other. The only exception was tortoise #503, who I observed in three separate burrows. Burrows 52 (found there 08/17/99) and 31 (found there 03/29/00) were within 7.62 m. of one another, but burrow 24 (found there 04/12/99) was well beyond that distance from both burrows 52 and 31.

DISCUSSION

Food preferences and Plant Nitrogen Content

Juvenile gopher tortoises in central Florida appear to be selective foragers. They choose plants with a relatively high nitrogen content. Other foraging studies on juveniles and adults of both gopher tortoises and desert tortoises (*Gopherus agassizii*) have indicated that both species are selective foragers (Garner and Landers 1981, Jennings and Fontenot 1992, MacDonald 1986, Spangenberg 1995).

Overall, the preference indices, based both upon presence/absence (times taken) and number of bites taken, agreed with one another and reflected what I expected based on my observations. For example, individual plants of the genera *Crotalaria*, *Richardia*, and *Ruellia* were entirely or almost entirely consumed almost every time they were encountered. In contrast, plants of the taxa *Liatris*, *Elephantopus*, and *Poaceae* were taken often but typically just a leaf or two at a time. These taxa were respectively deemed “preferred,” “random,” and “avoided” by the indices based on both criteria (with the exception of *Liatris*, see below).

Some other interesting examples of the indices, based on both criteria (presence/absence and number of bites taken), agreeing and reflecting what

I observed are the genera *Dyschoriste*, *Evolvulus*, and *Cnidoscolus*, which were all indicated as highly preferred by the indices based on both criteria. Whenever a tortoise sampled a plant from these three genera, it ate the entire plant.

Dyschoriste was fairly abundant along foraging paths (recall, the fourth most abundant taxon), and was present throughout most of the year. These were small plants, from about 3 to 13 cm. in height and sparsely branched, if at all. *Evolvulus* was only present on the plot during my study for a short time and even then, it was rare in the habitat. The plants encountered by the tortoises I observed were large, about 23 cm. long (creeping) and branched. *Evolvulus* was only present during two usable foraging observations, but I observed two other juvenile tortoises on separate occasions encounter *Evolvulus* plants and eat the entire plant each time. *Cnidoscolus* plants were also rare along foraging paths, although they appeared to be more abundant in the habitat in general. The plants encountered by tortoises ranged in size from about 5 cm. high unbranched to about 15 cm. high, with 2-4 branches. *Cnidoscolus* was only present in one foraging observation. I also observed, however, two other tortoises in incomplete foraging observations eat several entire *Cnidoscolus* plants.

On some occasions the indices, based on presence/absence vs. number of bites taken, disagreed, or did not reflect my observations. For example, both indices indicated a high degree of preference for *Yucca* when based on presence/absence. *Yucca* was only present once along the

foraging paths, and the tortoise in question investigated the plant then sampled one bite and moved on. The indices derived from number of bites taken place *Yucca* in the “avoided” category, which is probably more accurate.

An example of a genus in which the indices, based on presence/absence vs. number of bites taken, disagreed somewhat but still reflected my observations is *Liatris*. Based on presence/absence, the preference indices indicated that *Liatris* was preferred, while the indices based on the number of bites taken indicated that *Liatris* was being taken more at random (with a slight preference). Most tortoises would take at least one leaf from many of the *Liatris* plants they passed, but rarely stopped and ate more than a few leaves from one plant, like they did from plants of most of the other preferred genera. *Liatris* was the third most abundant genus along foraging paths. Indeed, *Liatris* was so abundant along foraging paths that tortoises probably were sampling this genus in proportion to its availability. Most tortoises would pluck a leaf or two from this plant, then pluck a leaf or two from the next plant as they went along. Even though juvenile tortoises may have been sampling *Liatris* in proportion to its availability (in terms of bites taken), I think that the higher index values based on presence/absence reflect the important role *Liatris* probably played in the diets of the tortoises in this study.

In contrast with *Liatris*, *Polygala* was relatively rare along foraging paths but was usually taken when encountered. Most of these plants were

quite small, 10-16 cm high with few if any branches and sparse leaves, so tortoises simply could not take many bites from these plants. For this taxon, the index values based on presence/absence—which indicate strong preference—better reflect what I observed than the values based on number of bites—which indicate only slight preference.

Again, overall both Manly's alpha index of preference and Jacob's D electivity index did a good job of reflecting what I observed about the choices tortoises seemed to be making. Because of examples like *Yucca*, *Liatris*, and *Polygala*, I think it was worthy to calculate these indices based on two different criteria (presence/absence and number of bites taken). Doing so may have helped to create a more complete and accurate picture of the choices made by the tortoises in my study.

I was not able to detect a strong hierarchy among the plants that were preferred. The one-year prescribed burn regime on this plot maintains a very open canopy and supports a variety forbs and grasses. Tortoises in this study probably obtained the most complete nutrition by sampling a variety of different plants that offer different nutritional benefits.

Two previous studies specifically addressed foraging, preference and nutrition of gopher tortoises (both adult and juvenile). The first study was conducted in SE Georgia in an area also subject to a one-year burn regime, and investigated overall diet based on scat analysis, stomach content analysis and chance observations (Garner and Landers 1981). Juveniles and adults were included. No preference indices were calculated. Thirteen

genera (plus members of Poaceae) which made up the major portion of the diet were analyzed for their nutritional content.

The second study was conducted in the same research area as my study, but included several additional plots which were subject to varying burn schedules (1-year, 2-year, 3-year, 5-year, 7-year, and control) (Macdonald 1986). This previous study investigated food preference based on scat analysis and chance foraging observations. Juveniles and adult gopher tortoises were included. Macdonald (1986) conducted a Kolmogorov-Smirnov test of frequency distributions to determine if scat composition reflected what was ingested by tortoises during foraging events. No difference could be detected. Plant availability was determined by conducting vegetational analyses along randomly chosen transects in early summer and again in autumn, and Jacob's D electivity index was applied to determine preference. Nutritional analyses of plants were not conducted.

These two previous studies share four similar results with my present study. First, both previous studies found that forbs were an important component of the gopher tortoises' diets. Some forbs which were eaten by tortoises in all three studies include *Dyschoriste*, *Richardia*, and *Shrankia*. In both previous studies, juvenile tortoises relied less on Poaceae than did adult tortoises.

Second, both studies revealed that, although juveniles relied less on Poaceae (which contains relatively little protein and other nutrients and a relatively high crude fiber content [Garner and Landers 1981]) than adults,

this family of plants still constituted a substantial part of their diets. The same is true in my study. The Jacob's D preference index in both my study and that conducted by Macdonald (1986) revealed, however, that Poaceae was not a highly preferred taxon. In my study, it was slightly avoided (juvenile tortoises foraged on grasses less than one would expect based on the abundance of grasses in the habitat) (see Table 9). Jacob's D values in Macdonald's study revealed that Poaceae was taken at random in autumn and was slightly preferred in summer. Because both juveniles and adults were included in this analysis, and because Macdonald (1986) found that juveniles took significantly less Poaceae than adults, however, it would be safe to assume that juveniles in that study were ingesting slightly less Poaceae than one would expect based on its abundance.

Third, Garner and Landers (1981) found that juveniles relied more heavily on plants with relatively high protein content, which mirrors my finding that juvenile tortoises prefer plants with relatively higher nitrogen content. I did not assess the content of any other nutrient or a plant's digestibility, as did Garner and Landers (1981). They found that gopher tortoises, particularly juveniles, also seem to choose plants with low crude fiber content. Some plant taxa that were evaluated for nutrient/fiber content by Garner and Landers (1981) were also sampled by tortoises in my study. Indeed, the plant taxa that were preferred (*Chamaecrista*, *Dyschoriste*, *Shrankia*, *Richardia*) by the tortoises in my study contained lower amounts of crude fiber than those which were avoided (*Clitoria*, *Poaceae*, *Tephrosia*).

Studies on juvenile slider turtles (*Trachemys scripta*) and juvenile green turtles (*Chelonia mydas*) suggest that diets high in protein with relatively little fiber are associated with rapid growth rates, while diets with reduced protein and/or increased fiber content are associated with slowed growth rates (Avery et al. 1993). Gopher tortoises and green turtles are both capable of maintaining cellulolytic gut microflora, and may rely on the activity of these microflora to make available the energy (and bound nutrients) from the fibrous portion of their diets (cellulose, hemicellulose, and lignin) (Bjorndal 1987). However, it seems that, given the choice, juvenile gopher tortoises will choose plants containing reduced amounts of fiber (Garner and Landers 1981).

Fourth, all three studies (Macdonald 1986, Garner and Landers 1981, my present study) revealed frequent ingestion of the genera *Dyschoriste* and *Richardia*, which contained comparatively less nitrogen than other preferred plants in my analysis. These genera were consistently indicated as highly preferred by the preference indices in my study. Macdonald (1986) found *Richardia* to be highly preferred based on a Jacob's D analysis (*Dyschoriste* was not included in the analysis) (see Table 9). Garner and Landers' (1981) study also revealed that these genera contained only median levels of protein, but that they contained relatively little fiber (indicating high digestibility) and comparatively high amounts of other nutrients analyzed. In particular, *Dyschoriste* had one of the highest amounts of both Calcium and Magnesium of all plants analyzed. *Richardia* had relatively high amounts of

Potassium, Phosphorus, and Calcium (Garner and Landers, 1981). It seems that the apparent heavy reliance by gopher tortoises on these two genera, which do not contain extraordinarily high amounts of protein, underscores the importance of gopher tortoises sampling a variety of plants to fulfill their complete nutritional requirements.

Research on the desert tortoise (*Gopherus agassizii*) has yielded similar findings. A study examining the nutrient requirements of the desert tortoise suggested that this close relative of the gopher tortoise depends upon the availability of a variety of forage types to maintain long-term nutrient balances (Barboza 1995). Another study examining foraging of juvenile desert tortoises suggested that individuals that had a wider variety of forage plants available experienced a greater percentage increase in weight and size than those with a more restricted variety of available forage during the same time period (Spangenberg, 1999).

Three distinct differences also exist between these two previous studies on gopher tortoise foraging and my present study. First, both Garner and Landers (1981) and Macdonald (1986) observed or detected ingestion of *Tephrosia*. Garner and Landers (1981) found that, "...(*Shrankia microphylla*) and hoary pea (*Tephrosia* spp.) were...the most important legumes in the spring." Macdonald (1986) calculated a Jacob's D value for *Galactia-Tephrosia* (they were combined in that study) of 0.44 in early summer and 0.33 in autumn, both values indicating moderate preference. Not only did I never observe a tortoise sample plants of this genus, which were present

along several foraging paths throughout the year, but on a few occasions I observed tortoises examine plants of this genus (touching them with their nostrils), and then reject them. *Tephrosia* had relatively high nitrogen content in my study, and contained a high amount of protein in Garner and Landers' (1981) study. *Tephrosia* contained one of the highest amounts of crude fiber of all forbs analyzed in the Garner and Landers (1981) study, which could to some degree explain why the gopher tortoises in my study were avoiding that genus. Perhaps gopher tortoises are foraging optimally, foregoing plants whose abundant nutrients are more bound when plants with more readily available nutrients are plentiful in the habitat.

Second, *Liatris* was the most common genus eaten by the tortoises in my study, both in terms of the number of plants sampled (times taken) and the number of bites taken. *Liatris* did not seem to play a major role in the diets of the tortoises in Macdonald's (1986) study, accounting for less than 1% of the total scat composition, and 4.7% of foraging observations. The foraging observations may be more comparable with my study. However, *Liatris* only composed 2.8% (early summer) and 4.4% (autumn) of plant availability in the habitat in Macdonald's (1986) study, while in my study *Liatris* was the third most abundant taxon along foraging paths at 10%. Macdonald (1986) did not calculate a Jacob's D value for this genus; perhaps if she had, a preference for this genus would have been revealed.

Third, both previous studies observed and detected non-plant items in the diets of gopher tortoises. Non-plant items included mushrooms, carrion,

scat, shells, insects, and rocks. The only non-plant item I observed a tortoise eat was a white rock that it appeared to “gnaw” on for a few minutes, but did not ingest. I suspect that insects which were on plants being eaten were probably ingested.

One area which revealed both similarities and differences between my study and that of Macdonald (1986) was the preference index, Jacob’s D. Only 12 taxa were analyzed by both Macdonald (1986) and me. Macdonald’s (1986) study included both juveniles and adults, and the Jacob’s D values were derived from information from both. For the most part our analyses are in agreement (Table 9), at least in terms of the general categories to which the taxa belong (“preferred,” “random,” “avoided”).

Missing from the two previous studies was a more exact representation of the food choices each tortoise had along its foraging path. Similarly, my study lacked a representation of all vegetation available to the tortoises on the entire research plot. It would be interesting to investigate whether the vegetation along tortoises’ foraging paths was representative of the vegetational composition of the entire plot, or if tortoises are choosing their burrow locations and/or foraging paths in patches which contain a high percent of preferred plants.

Table 9: Jacob's D values of taxa analyzed in both this study and in Macdonald's (1986) study (both based on presence/absence)

Genera in bold are those that were not included in my index calculations for statistical comparisons because they were only present in foraging events which were randomly omitted. Values shown are those calculated including all foraging events.

Genus	Macdonald (1986)		Stilson (2001)
	Jacob's D: Early Summer	Jacob's D: Autumn	Jacob's D
<i>Richardia</i>	1.00	0.85	0.67
<i>Pinus</i>	0.95	1.00	0.23
<i>Cnidoscolus</i>	0.53	0.88	0.52
Poaceae	0.33	0.00	-0.30
<i>Hedyotis</i>	0.00	1.00	0.33
<i>Aristida</i>	-0.06	-0.26	-1.00
<i>Eriogonum</i>	-0.22	-1.00	-1.00
<i>Pityopsis</i>	-0.46	-0.59	-1.00
<i>Eupatorium</i>	-0.74	-0.48	-0.23
<i>Helianthemum</i>	-0.78	0.00	0.25
<i>Phoebanthus</i>	-1.00	-1.00	-0.05
<i>Solidago</i>	-1.00	-1.00	-0.09

Foraging paths

The predictions about foraging paths which were supported by my data were that (1) larger individuals travel greater distances during foraging events (in total distance, not necessarily the farthest point distance from their burrows), and (2) juvenile tortoises move faster when they travel farther, both in total distance traveled and the farthest point from their burrows. I would expect those variables to be interrelated: larger individuals, that may be willing (or may need) to travel greater distances would probably move faster just because they are larger. Tortoise size was not correlated with speed, however. Also, the range of tortoise sizes in this study was quite limited.

Even the large individuals in my study were small enough that they were probably still quite vulnerable to predation. I doubt that the range of tortoise sizes in this study would allow me to identify differences in risk-proneness based upon size differences, if they exist. In addition, one study conducted in central Florida addressing the home range of both adult and juvenile tortoises found that, within the group of tortoises size 71-153 mm carapace length, there was an overall trend for larger individuals to travel farther, but she also reported that individual variation existed, with some small individuals traveling further than some of their much larger counterparts (Diemer 1992). This finding may help to explain why size category, but not actual tortoise size, was correlated with distance traveled in my study.

The availability of preferred food plants was not correlated with risk-prone behavior, measured as total distance traveled and farthest straight-line distance reached from the burrow. Foraging and movement studies of gopher tortoises (*Gopherus polyphemus*), desert tortoises (*G. agassizii*), and bolson tortoises (*G. flavomarginatus*) have indicated that activity and movement decrease during times when available forage diminishes (Aguirre et al. 1984, Diemer 1992, Jennings 1993). The tortoises in my study did not seem to be adjusting the distances they traveled during foraging (either positively or negatively) based on the relative availability of suitable forage.

Activity

Juvenile tortoises in my study were active during all seasons, although I observed the least activity in January and February, 2000. These results are consistent with a previous study that addressed activity and survival of 0-4 year old tortoises in the same research area (Wilson 1994). The previous study calculated the average distance juveniles moved away from their burrows as 7.97 ± 8.56 m. (Wilson 1994). The juvenile tortoises in my study traveled an average of 13.51 ± 10.14 m round-trip. The average farthest distance from the burrow that the tortoises in my study reached was 5.73 ± 4.24 m. Wilson's (1994) results were based on locating radio-telemetered individuals. Of my results, the farthest distance from the burrow is probably the more comparable measure, and it seems that the juvenile tortoises I studied did not venture as far from the burrows as did those studied by Wilson (1994). Several factors could possibly account for the observed differences: (1) the tortoises in my study could have been aware of my presence, (2) I only followed tortoises who were foraging, whereas Wilson (1994) could have discovered tortoises who were searching for new areas to establish burrow/s, (3) if Wilson's (1994) study included areas which were burned less frequently than mine, juvenile tortoises may have had to travel farther to find adequate forage.

The juvenile gopher tortoises in Wilson's (1994) study used an average of 4 ± 2.2 burrows per year, much greater than the number of burrows I detected tortoises using. The tortoises in Wilson's (1994) study

were fitted with radiotransmitters, so were able to be located while they were in their burrows. Wilson (1994) may have been able to detect more multiple-burrow use than I was able to do.

Juvenile tortoises in my study seemed to be quite active, based on my direct observations of activity and on the indirect evidence of burrow appearance. I suspect that many of the times I was not able to detect any activity, the tortoises were aware of my presence. Observing tortoises at their burrows was difficult. The sand of the burrow aprons often matched the color of the tortoises' carapaces fairly well, and the patterns created by shadows from the sparse trees falling onto the burrow aprons would often create the illusion that a tortoise was present on the apron. In order to be sure, I would first check with binoculars and if I still couldn't tell, I would change position at the risk of startling a basking tortoise and alerting it to my presence, which happened several times. Because the tortoises moved so slowly onto their burrow aprons to bask (and then often didn't move again for up to an hour), it was very difficult for me to simply rely on detecting movement to identify when they emerged. This crypticity on the burrow apron may be a valuable defense against predation for basking tortoises (but see Wilson 1994).

Suggestions for Further Research and Recommendations

Some authors have pointed out the need for a more complete record of the biology of the gopher tortoise, and have identified the ecology of juveniles

as particularly lacking (Germano and Bury 1994). Given the sharp decline in numbers of this species, and the continuing destruction of their habitat, a complete understanding of its biology and the factors that affect survival may be crucial for ensuring that this species will endure. Gopher tortoises on this study site have some of the fastest growth and maturation rates of any tortoise populations studied in its entire range (Mushinsky 1994). The wealth of forbs and grasses supported by frequent prescribed burns (between 1 and 7 years in different plots) combined with the warm, subtropical climate of this region may contribute to the rapid growth of individuals in this population (Mushinsky et. al 1994). In addition, some authors have suggested that superior habitat can support higher densities of tortoises (Diemer 1992, Mushinsky et. al 1994). Understanding the plant preferences and nutrient requirements of juvenile tortoises may help us to explore, adopt and experiment with land management practices that could allow relatively dense, healthy populations to thrive in the few remaining pockets of suitable habitat.

A worthy follow-up to this study might be to examine if juvenile tortoise burrows are predictably located in areas where preferred plants are relatively abundant. This certainly seemed to be the case in my study area, based on personal observation. I did not attempt to quantify this observation. If this were the case, how do burning practices affect the quality and quantity of the preferred plants of juveniles? "Frequent" burning tends to open the canopy and support a diverse forb understory (Garner and Landers 1981,

Mushinsky et. al 1994), but what frequency maintains optimum foraging opportunities for juvenile tortoises?

The area my study was conducted in has plots with different burn frequencies, separated by fire lanes. The burn frequencies are: 1-year, 2-year, 5-year, 7-year, and control (no burning). Juveniles seemed to be more densely populated in the 1- and 2-year burn plots (they would also be much easier to spot in those plots as they are more open). Adults seemed to be more densely populated in the 5- and 7-year plots (pers. obs.). If this were the case, perhaps land that is set aside for tortoise habitat would benefit by being subjected to a variety of burn regimes in different, adjacent areas, to support a diverse age structure of recruits and breeding adults.

Understanding the plant preferences and nutrient requirements of juvenile gopher tortoises could help to establish guidelines for conducting vegetational surveys on land slated/set aside for gopher tortoise relocation/preservation. Such surveys could specifically attempt to quantify the presence of plants known to be preferred by juvenile tortoises, and address whether those plants were present in adequate abundance to (1) support a population of a given density, and (2) allow juvenile tortoises to remain as close to their burrows as possible while foraging, to reduce predation pressure. In addition, they could assess whether an adequate variety of preferred plant genera was available, which I suspect is important for juvenile gopher tortoises to meet their complete nutritional requirements for optimum growth and condition. If the amount or variety of preferred

plants was suspected to be deficient, land managers could adopt practices to promote the growth of these plants, such as planting native preferred species, removing competing non-natives, and prescribed burning.

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APPENDICES

Appendix 1: Plants taken, bites taken, and plants available by date. Italisized dates are those that were omitted because they represent multiple observations of the same individual tortoise. Totals were adjusted to reflect the omitted dates when calculating preference indices.

TIMES TAKEN

Tortoise	504	506	499	508	502	509	—	513	700	513	515	506	502	700	503	515	513	
Date	5/6/99	5/27/99	6/3/99	6/22/99	7/20/99	7/29/99	8/19/99	10/12/99	10/14/99	11/9/99	11/26/99	12/9/99	3/7/00	3/20/00	3/29/00	3/29/00	3/29/00	TOTAL
Genus																		
<i>Chamaecriste</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Liatris</i>	5	2	7	0	3	6	6	5	2	0	0	0	0	7	5	9	7	64
<i>Seedling</i>	4	5	4	0	3	1	0	0	0	0	0	0	4	0	4	1	1	27
<i>Helianthemum</i>	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	5
<i>Hedyotis</i>	1	0	1	2	1	0	0	0	0	0	2	1	1	0	2	1	1	13
<i>Phoebanthus</i>	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Elephantopus</i>	5	1	0	0	2	2	0	0	0	0	2	1	0	2	0	0	0	15
<i>Dyschoriste</i>	1	5	1	0	6	3	1	4	0	5	1	0	0	1	7	0	9	44
<i>Ruellia</i>	0	1	7	0	2	1	0	1	0	1	0	0	0	3	0	0	2	18
<i>Evolvulus</i>	0	0	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	6
<i>Balduinia</i>	0	0	0	1	0	0	0	0	0	0	0	0	2	0	2	0	0	5
<i>Shrankia</i>	0	0	1	0	2	0	0	0	1	0	0	0	0	0	0	0	0	4
<i>Aster</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2
<i>Polygala</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	1	4
<i>Scutellaria</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Berlandiera</i>	0	0	0	2	0	0	0	0	0	0	0	0	1	0	2	0	0	5
<i>Richardia</i>	0	0	0	1	0	0	3	0	0	0	0	0	8	0	1	0	0	13
<i>Crotalaria</i>	0	0	0	0	0	2	0	3	0	2	3	1	0	0	1	0	0	12
<i>Dahlia</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Yucca</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Poaceae</i>	2	0	0	0	0	0	0	10	2	0	3	13	0	0	3	1	0	34
<i>Cnidoscolus</i>	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	6
<i>Pinus seedling</i>	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3

Appendix 1 (continued)

TIMES TAKEN (continued)

[illegible]

Appendix 1 (continued)

BITES TAKEN

Tortoise	504	506	499	508	502	509	—	513	700	513	515	506	502	700	503	515	513	
Date	5/6/99	5/27/99	6/3/99	6/22/99	7/20/99	7/29/99	8/19/99	10/12/99	10/14/99	11/9/99	11/26/99	12/9/99	3/7/00	3/20/00	3/29/00	3/29/00	3/29/00	TOTAL
Genus																		
<i>Chamaecriste</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	10
<i>Liatris</i>	11	2	4	0	17	25	66	64	16	0	0	0	0	29	20	69	88	411
<i>Seedling</i>	5	5	4	0	6	2	0	0	0	0	0	0	12	0	4	2	0	40
<i>Helianthemum</i>	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	10
<i>Hedyotis</i>	7	0	5	14	15	0	0	0	0	0	10	11	6	0	15	33	5	121
<i>Phoebanthus</i>	5	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
<i>Elephantopus</i>	30	3	0	0	14	17	0	0	0	0	26	13	0	15	18	0	0	136
<i>Dyschoriste</i>	0	21	5	0	84	22	15	30	0	41	15	0	0	7	47	0	38	325
<i>Ruellia</i>	0	8	49	0	9	15	0	16	0	45	0	0	0	20	0	0	29	191
<i>Evolvulus</i>	0	0	10	20	0	0	0	0	0	0	0	0	0	0	0	0	0	30
<i>Balduinia</i>	0	0	0	3	0	0	0	0	0	0	0	0	63	0	14	0	0	80
<i>Shrankia</i>	0	0	16	0	60	0	0	0	23	0	0	0	0	0	0	0	0	99
<i>Aster</i>	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	20	0	23
<i>Polygala</i>	0	0	4	0	0	0	0	0	0	0	0	0	0	0	8	0	4	16
<i>Scutellaria</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Berlandiera</i>	0	0	0	2	0	0	0	0	0	0	0	0	18	0	21	0	0	41
<i>Richardia</i>	0	0	0	5	0	0	18	0	0	0	0	0	134	0	18	0	0	175
<i>Crotalaria</i>	0	0	0	0	0	44	0	10	0	8	43	27	0	0	10	0	0	142
<i>Dahlia</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Yucca</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Poaceae</i>	10	0	0	0	0	0	0	37	22	0	47	205	0	0	0	48	0	369
<i>Cnidoscolus</i>	0	0	0	0	0	0	0	0	0	0	0	0	98	0	0	0	0	98
<i>Pinus seedling</i>	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	20
<i>Croton</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	10

Appendix 1 (continued)

BITES TAKEN (continued)

Tortoise	504	506	499	508	502	509	—	513	700	513	515	506	502	700	503	515	513	
Date	5/6/99	5/27/99	6/3/99	6/22/99	7/20/99	7/29/99	8/19/99	10/12/99	10/14/99	11/9/99	11/26/99	12/9/99	3/7/00	3/20/00	3/29/00	3/29/00	3/29/00	TOTAL
Genus																		
<i>Carphephorus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tephrosia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gnaphalium</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pityopsis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tillandsia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Solidago</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		21	21
<i>Persimmon</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Polypremum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Stylosanthes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Clitoria</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Seronoa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Plantago</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eriogonum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Stillingia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rhynchosia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cyperus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Quercus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aristida</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eupatorium</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	87	0	87
<i>Physalis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Asimina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Baptisia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 1 (continued)

		TIMES ENCOUNTERED																		
Tortoise		504	506	499	508	502	509	—	513	700	513	515	506	502	700	503	515	513		
Date		5/6/99	5/27/99	6/3/99	6/22/99	7/20/99	7/29/99	8/19/99	10/12/99	10/14/99	11/9/99	11/26/99	12/9/99	3/7/00	3/20/00	3/29/00	3/29/00	3/29/00	TOTAL	
Genus																				
99	<i>Chamaecriste</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	
	<i>Liatris</i>	14	5	10	0	24	17	8	6	2	0	0	0	5	9	19	10	7	136	
	Seedling	4	6	2	0	10	1	0	0	0	0	0	0	4	0	8	1	1	37	
	<i>Helianthemum</i>	3	0	0	0	0	0	0	0	0	0	0	2	0	0	9	8	0	22	
	<i>Hedyotis</i>	1	1	1	2	1	0	2	0	0	0	12	1	4	0	3	2	2	32	
	<i>Phoebanthus</i>	3	5	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	11	
	<i>Elephantopus</i>	9	9	0	0	2	12	4	0	0	0	5	2	0	2	0	0	1	46	
	<i>Dyschoriste</i>	3	5	2	1	7	4	3	5	0	2	2	0	2	1	13	0	11	61	
	<i>Ruellia</i>	0	2	10	0	2	0	0	1	0	1	0	0	0	4	2	0	2	24	
	<i>Evolvulus</i>	0	0	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	7	
	<i>Balduinia</i>	0	8	0	1	0	0	0	0	0	0	0	0	30	0	10	0	0	49	
	<i>Shrankia</i>	1	0	1	1	2	0	0	0	0	1	0	0	0	0	0	0	0	6	
	<i>Aster</i>	0	0	4	0	0	1	0	0	0	0	2	0	0	0	0	1	0	8	
	<i>Polygala</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0	3	0	1	6	
	<i>Scutellaria</i>	4	0	1	1	3	1	0	0	0	0	0	0	0	0	0	0	1	11	
	<i>Berlandiera</i>	1	0	0	7	0	0	0	0	0	0	0	0	12	0	5	0	0	25	
	<i>Richardia</i>	0	0	0	2	0	0	3	0	0	0	0	0	11	0	0	0	0	16	
	<i>Crotalaria</i>	0	0	1	0	0	6	0	4	0	2	4	1	0	0	3	0	2	23	
	<i>Dahlia</i>	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	
	<i>Yucca</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	
	Poaceae	35	8	27	9	11	20	5	20	3	4	10	20	17	2	9	7	24	231	
	<i>Cnidoscolus</i>	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	9	
	<i>Pinus seedling</i>	1	2	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	9	
	<i>Croton</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	4	

Appendix 1 (continued)

TIMES ENCOUNTERED (continued)

Tortoise	504	506	499	508	502	509	---	513	700	513	515	506	502	700	503	515	513	
Date	5/6/99	5/27/99	6/3/99	6/22/99	7/20/99	7/29/99	8/19/99	10/12/99	10/14/99	11/9/99	11/26/99	12/9/99	3/7/00	3/20/00	3/29/00	3/29/00	3/29/00	TOTAL
Genus																		
<i>Carphephorus</i>	0	4	3	0	0	0	0	0	0	0	0	1	7	0	4	3	0	22
<i>Tephrosia</i>	6	3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	10
<i>Gnaphalium</i>	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	6
<i>Pityopsis</i>	0	0	0	0	0	1	1	0	0	0	0	4	0	0	0	0	0	6
<i>Tillandsia</i>	6	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	9
<i>Solidago</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2	4
<i>Persimmon</i>	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	2
<i>Polypremum</i>	2	0	0	0	0	0	1	0	0	0	0	0	2	0	0	1	0	6
<i>Stylosanthes</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Clitoria</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Seronoa</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Plantago</i>	0	0	0	0	3	0	1	1	1	1	0	0	2	1	0	0	3	13
<i>Eriogonum</i>	5	1	5	0	0	1	0	0	0	0	0	0	2	0	1	2	0	17
<i>Stillingia</i>	1	2	3	0	0	1	0	0	0	0	0	0	0	0	0	1	0	8
<i>Rhynchosia</i>	3	2	1	0	2	0	0	0	0	0	0	0	0	0	1	0	0	9
<i>Cyperus</i>	2	2	0	1	0	4	0	0	0	0	0	0	0	0	0	0	0	9
<i>Quercus</i>	4	1	0	2	6	5	6	8	1	1	1	9	4	0	0	0	1	49
<i>Aristida</i>	33	33	38	19	39	40	11	2	7	3	26	40	35	10	35	14	6	391
<i>Eupatorium</i>	0	11	0	0	3	0	0	0	0	0	0	0	0	0	0	4	0	18
<i>Physalis</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Asimina</i>	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3
<i>Baptisia</i>	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2

Appendix 2: Families and species (if identified) of genera sampled by juvenile gopher tortoises

ACANTHACEAE

Dyschoriste oblongifolia

Ruellia carolinensis

AGAVACEAE

Yucca filamentosa

ASTERACEAE

Aster tortifolius

Balduinia angustifolia

Berlandiera subacaulus

Elephantopus elatus

Eupatorium capillifolium

Liatris gracilis

Liatris tenuifolia

Phoebanthus grandiflora

Solidago fistulosa

Solidago stricta

CISTACEAE

Helianthemum corymbosum

CONVOLVULACEAE

Evolvulus sericeus

EUPHORBIACEAE

Cnidoscolus stimulosus

Croton linearis

FABACEAE

Chamaecrista fasciculata

Crotalaria rotundifolia

Dalia pinnata

Shrankia microphylla

Appendix 2 (continued)

LAMIACEAE

Scutellaria arenicola

PINACEAE

Pinus elliottii and/or *palustris*

POACEAE

Andropogon spp.

Aristida stricta

Dicanthelium spp.

Paspalum spp.

POLYGALACEAE

Polygala grandiflora

RUBIACEAE

Hedyotis procumbens

Richardia brasiliensis

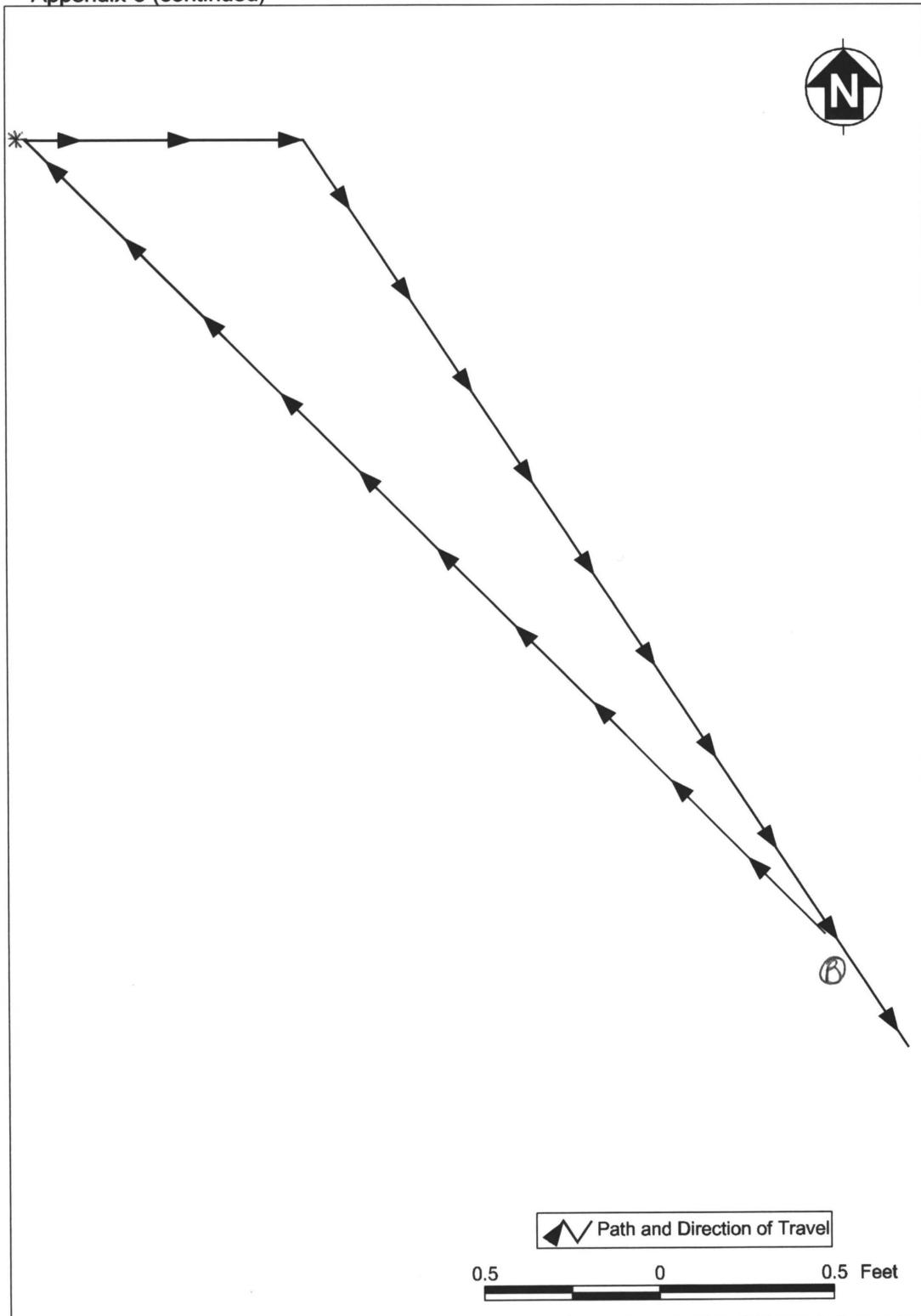
Richardia scabra

Appendix 3: Sample Foraging Path Maps

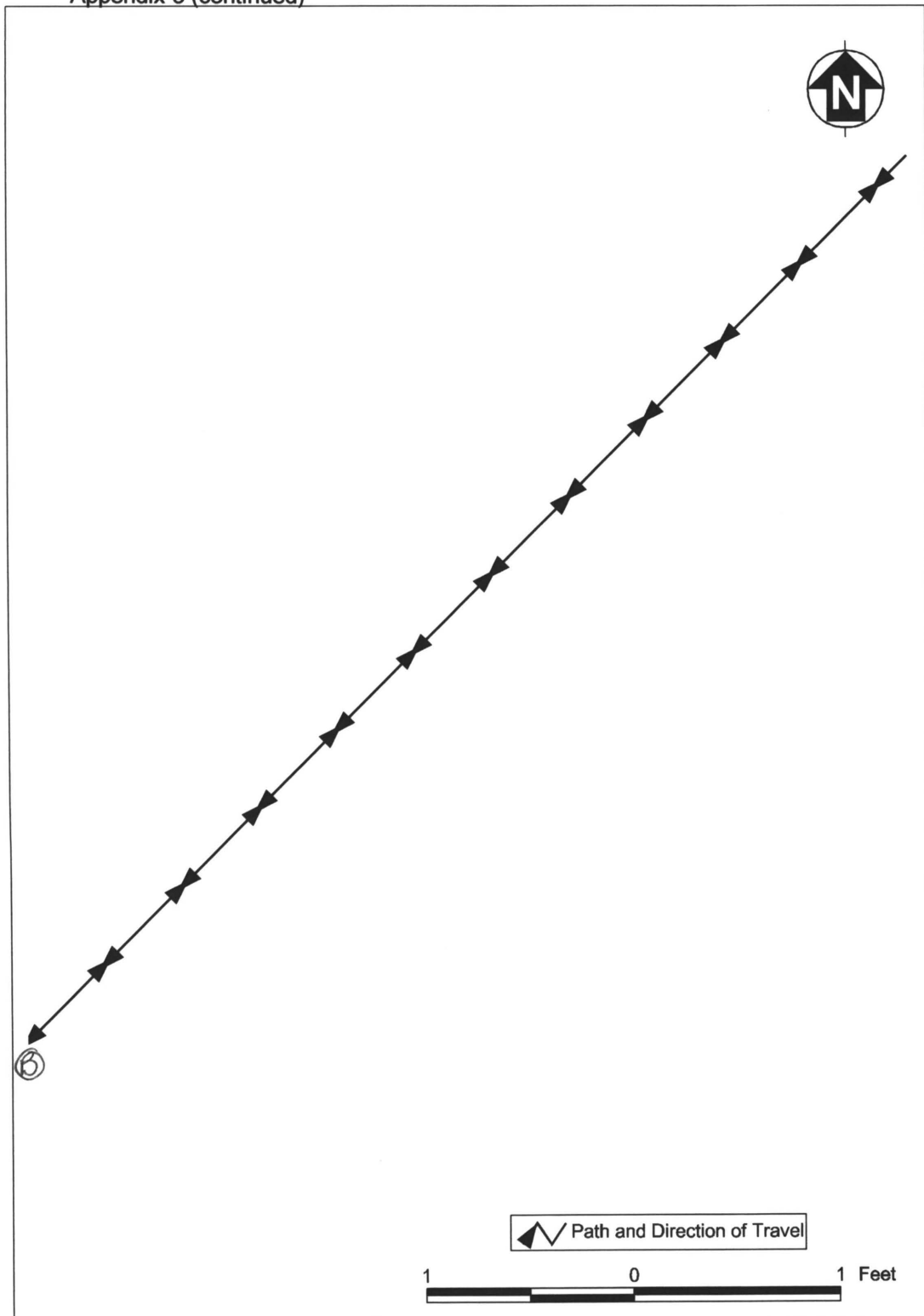
An asterisk (*) Indicates the point along the path where the tortoise was first sighted if the foraging observation was incomplete.

The location of the burrow is indicated by (B)

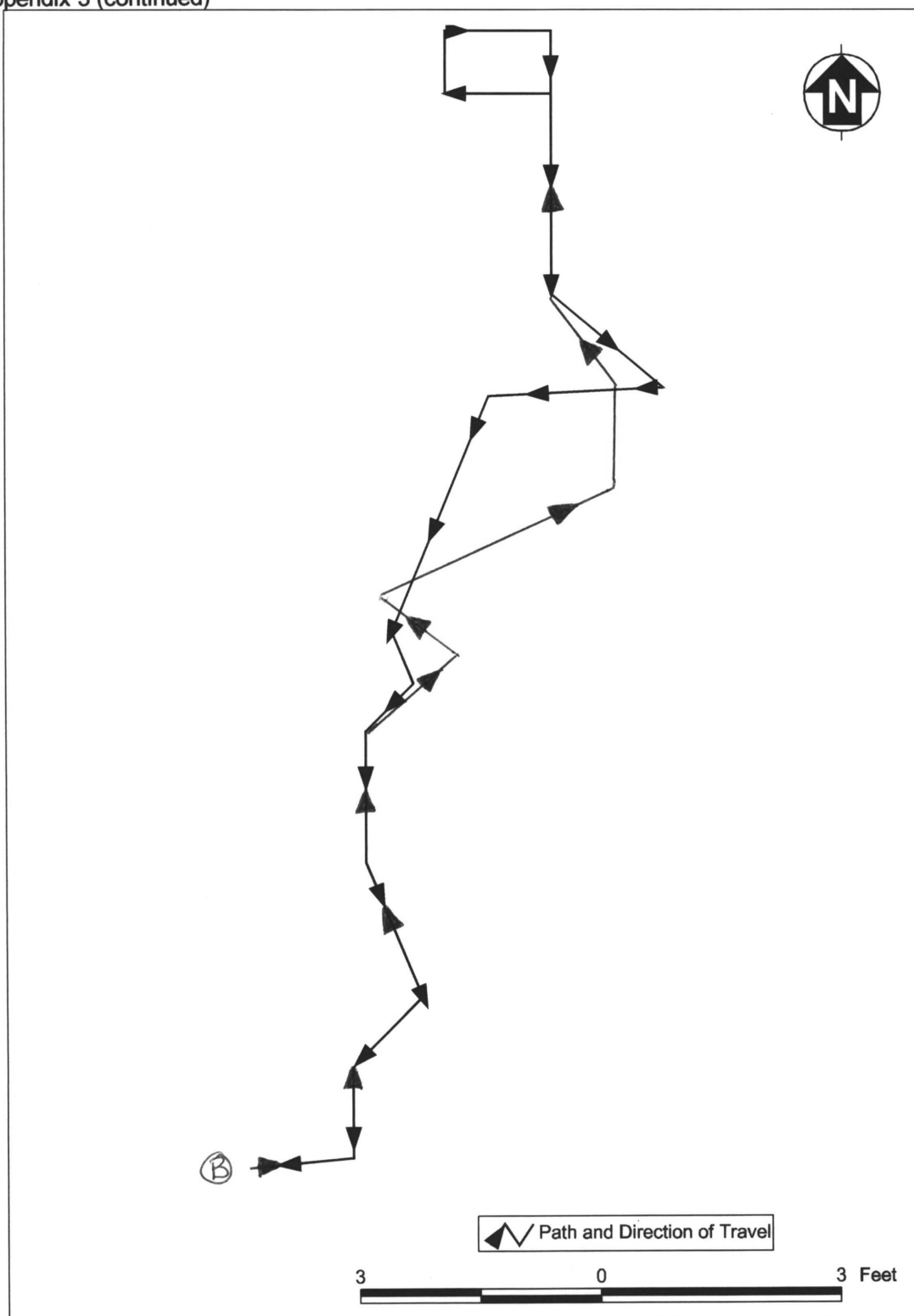
Start and end time of each foraging path are provided; for incomplete observations (see above), start time is the time the tortoise was discovered.



Map 2: Burrow 13, 7/15/99 Tortoise Unknown 1320-? hrs



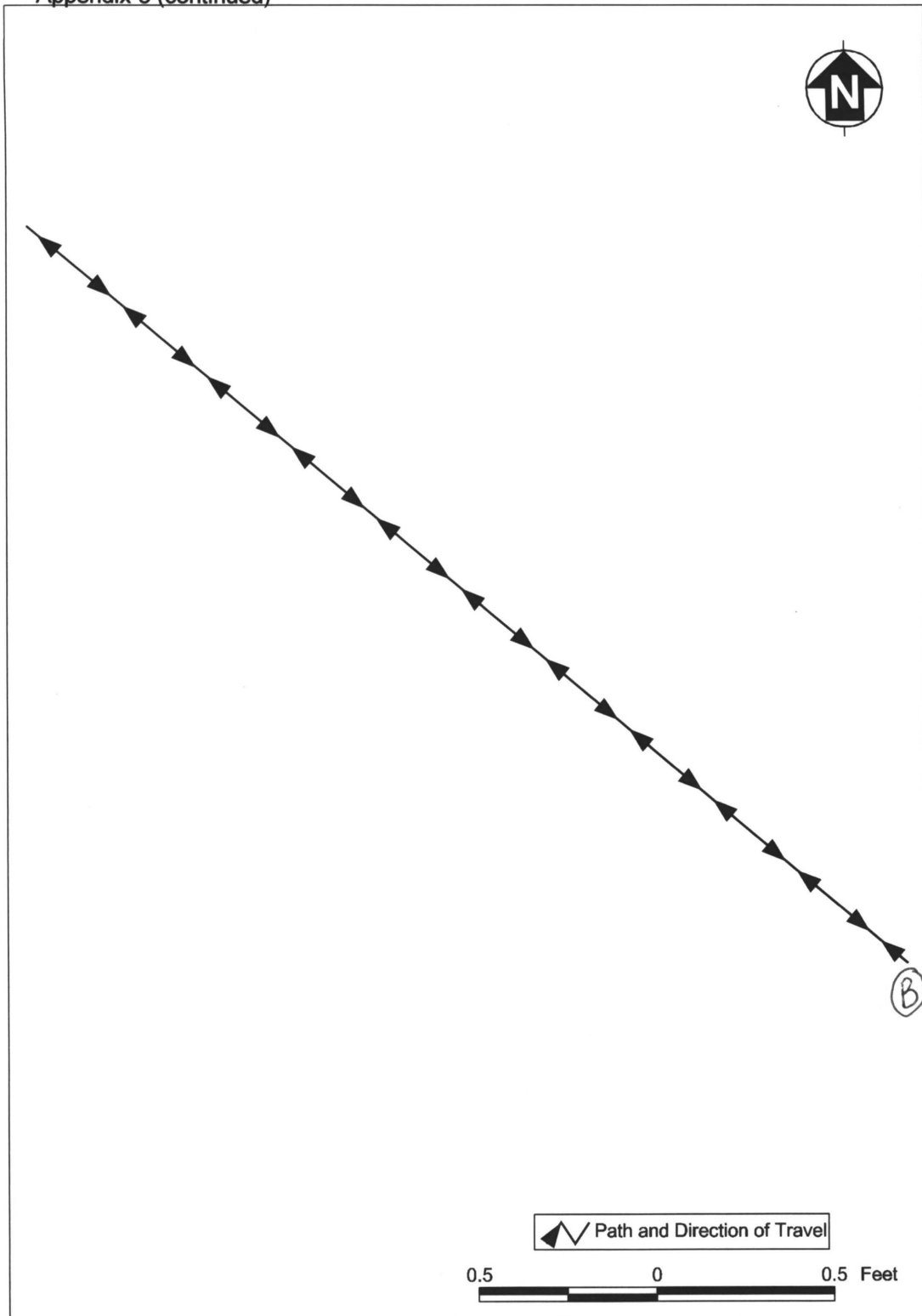
Map 4: Burrow 13, 7/22/99 Tortoise 502 1309-1316 hrs



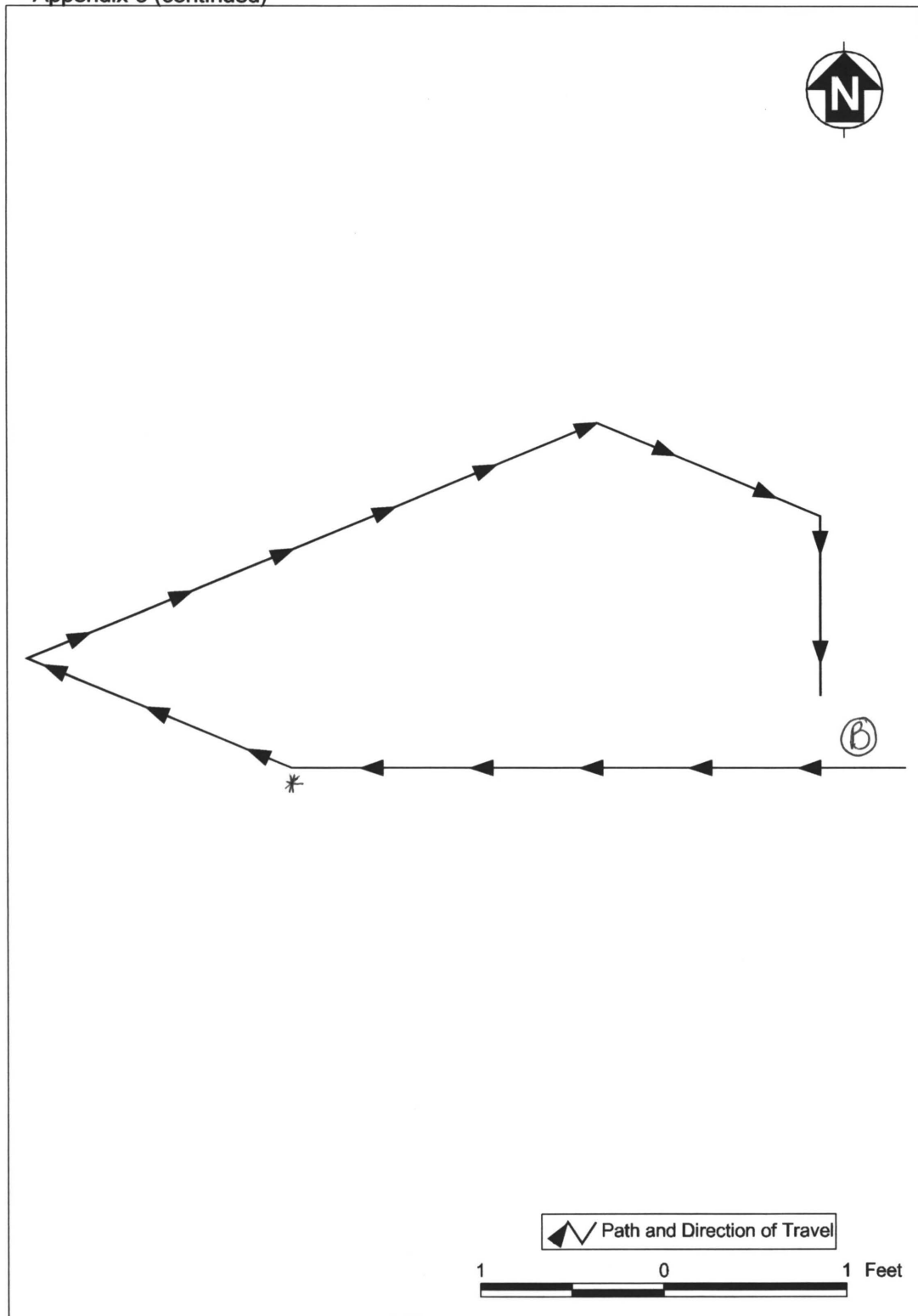
Map 5: Burrow 13, 3/7/00 Tortoise 502 1250-1320 hrs

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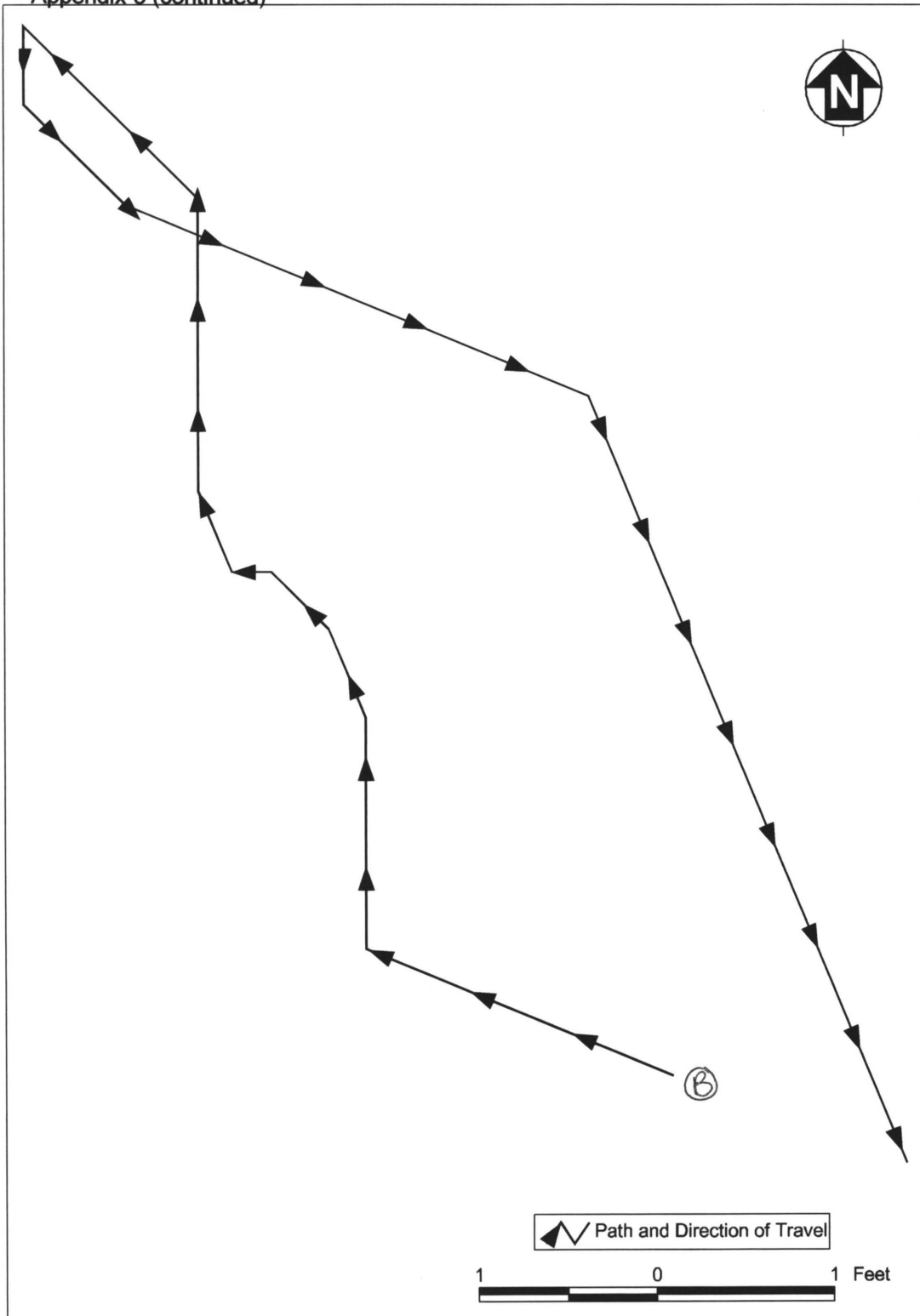
Map 8: Burrow 32, 6/3/99 Tortoise 499 1435-1501 hrs

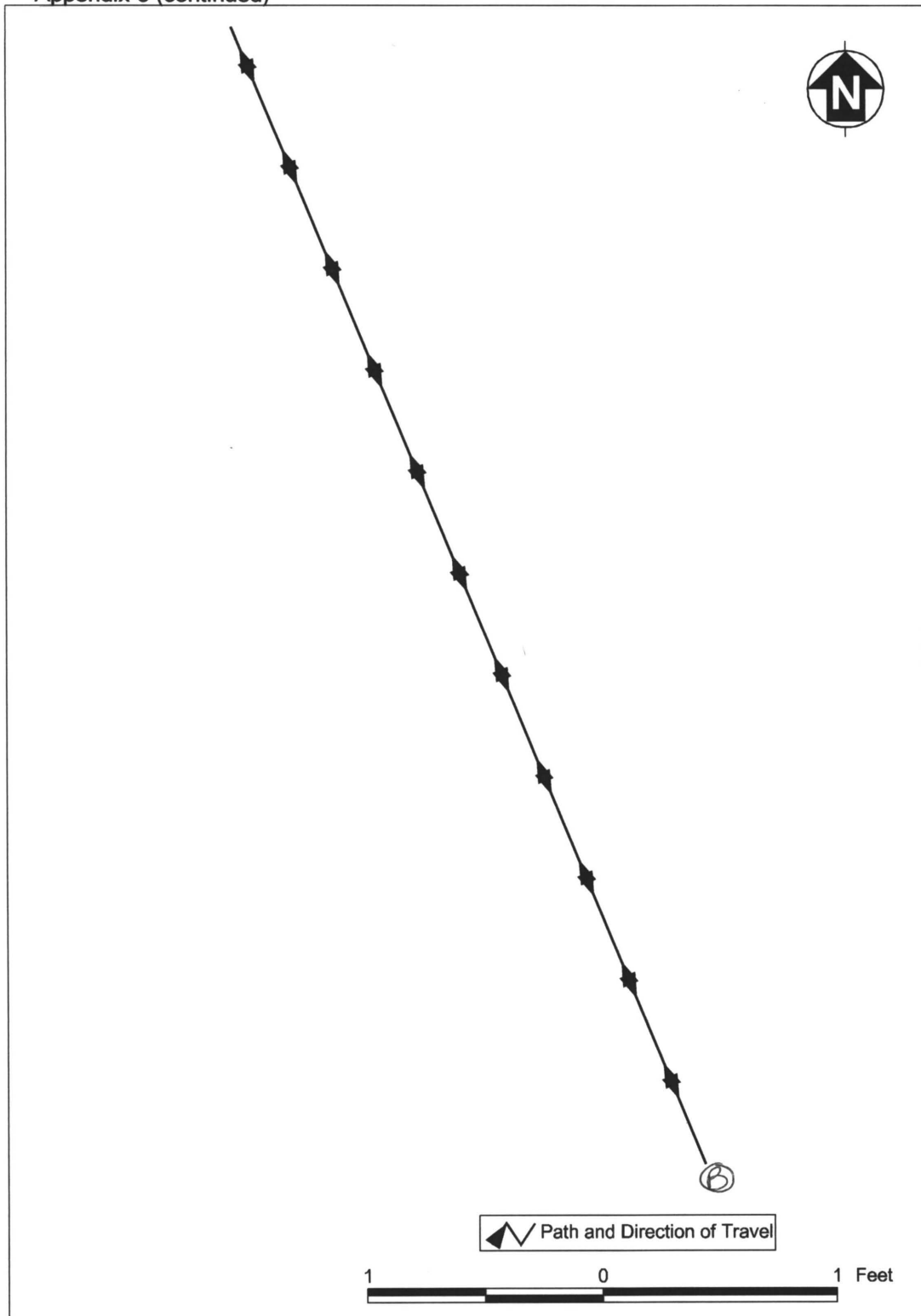


Map 9: Burrow 37c, 11/23/99 Tortoise Unknown 1440-1452hrs



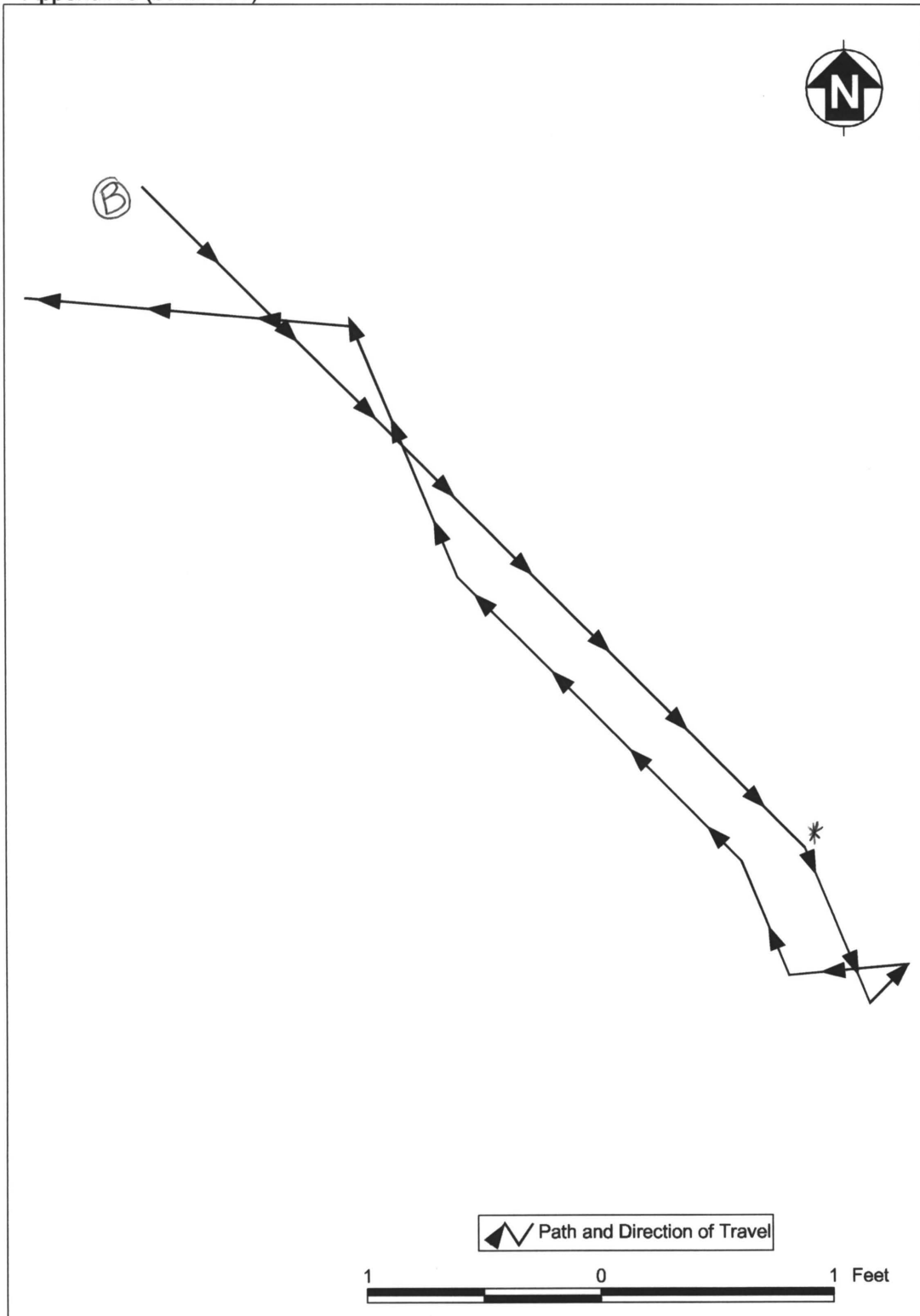
Map 12: Burrow 54, 3/30/99 Tortoise Unknown 1431-1445 hrs





Map 14: Burrow 58, 7/22/99 Tortoise Unknown 1430-1435 hrs

Map 15: Burrow 58, 8/3/99 Tortoise 700 1320-1347 hrs



Map 17: Burrow 59, 11/26/99 Tortoise 515 1300-1319 hrs

