BEHAVIOR AND ECOLOGY OF GOPHERUS FLAVOMARGINATUS IN AN EXPERIMENTAL ENCLOSURE

by

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May 17, 1979
Date

In loving memory of

Sadi and Aaron Nathan

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ABSTRACT

A captive population of bolson tortoises (Gopherus flavomarginatus) was observed in a 2-hectare enclosure and the animals' activities were analyzed in ecological and behavioral contexts. Observations covered most of the daylight hours of 46 days during the animals' summer active season (there was no above-ground activity at night).

The animals showed two daily peak periods of activity: one in this early morning, the other in the late afternoon. The duration and intensity of these activity periods was a function of seasonal changes in temperature, precipitation, and food availability.

Tortoises fed on a variety of plant species in the enclosure, but they preferred two common species of perennial grasses; Hilaria belangeri and H. mutica. The animals used trails to reach foraging areas and spent most of their time in areas near their burrows.

Use of a particular burrow by a given individual was common, although changes of home burrows were seen throughout the summer.

Observed mating activity involved a short sequence of precopulatory behavior similar to that shown by congenerics. The degree of mating success appeared to be related to the location of the encounter; i.e., all "complete" matings took place at burrows.

Bolson tortoises were observed to be solitary in their habits. When two animals met, they usually avoided each other. Occasionally, agonistic behaviors (ramming and/or chasing) ensued; these actions were often associated with burrow intrusion.

INTRODUCTION

The least known extant member of the genus Gopherus is G. flavomarginatus. It is known only from the Chihuahuan Desert in north-central Mexico where it inhabits Pleistocene lake basins (called "bolsons"). The bolson tortoise was first described by Legler in 1959. Detailed behavioral information on burrow use, foraging patterns, mating behavior, and other social interactions (in the wild or in captivity) is either unavailable or incomplete and is based on a small number of observations (Auffenberg 1969, Eglis 1962, Legler 1959, Legler and Webb 1961, Leon et al. 1979, Morafka in press, Pawley 1968 and 1975, and Weaver 1970).

Foraging strategies of wild populations in Mexico are presently being studied (Leon et al. 1979). Anecdotal information on the courtship of captive bolson tortoises is available (Eglis 1962, Legler and Webb 1961, and Morafka in press), but the reports are fragmentary and inconclusive. Successful courtship in the wild has yet to be described or documented.

I decided to study G. flavomarginatus since so little is known of its behavior and ecology and there are indications that it may become extinct in the near future. The bolson tortoise is unprotected by law[1] and wild population members have been reduced by the constant predation

1. The bolson tortoise was added to Appendix II ("endangered") of the United States List of Endangered Species on 14 February, 1979 (U.S. Fish and Wildlife Service 1979).

of resettled laborers and rail-line construction crews. If G. flavomarginatus were to become extinct, important behavioral comparisons with congenerics would obviously be impossible. Previous studies of the bolson tortoise in captivity have been in confined areas (e.g., back yards) which may have influenced the behavioral expressions of observed interactions. In the present study, the design of the captive environment was elaborate and selected for its similarity to the natural habitat in Mexico. This permitted intensive behavioral observations that would have been difficult, if not impossible, in the wild.

The study extended over a 10-week period during June, July, and August of 1977. One purpose was to record daily activity patterns, including basking habits, burrow use, foraging, and traveling patterns in relation to changing environmental parameters (temperature and rainfall) during the summer period of maximum activity. A second objective was to record social interactions with respect to burrow location. These included mating activity, and aggressive (e.g., ramming) and non-aggressive (tolerance and avoidance) encounters between individuals. For the sake of clarity and convenience in dealing with these different aspects of the work, the results are presented here in two major sections: Activity Levels and Social Interactions.

The Study Area

Field work was conducted at the Research Ranch near Elgin, in southeastern Arizona. The study site is located in the northeast corner of the ranch, on the western side of O'Donnell Canyon, elev. ca. 1433 m (31° 37' N, 110° 28' W). The enclosure can be reached by traveling east about 1.6 km along a dirt road which follows the boundary fence between the Research Ranch and the Babocomari Ranch. The 20,000 m^2, fenced, circular enclosure slopes gently downward from northwest to southeast. Two shallow washes cross the upper northern and western portions of the enclosure (Figure 1).

The Research Ranch receives most of its precipitation during the summer and winter months, a bi-seasonal pattern that is characteristic of southeastern Arizona (Sellers and Hill 1974). Approximately one half of the total yearly precipitation occurs during July and August as moist tropical air masses pass from the Gulf of Mexico through southeastern Arizona. As a result of these air movements, summer rains occur as localized thunderstorms with heavy precipitation for short periods (Humphrey 1958). Winter precipitation is usually due to storm fronts originating in the Pacific Northwest. These fronts usually produce less precipitation than the summer storms, although either snow or rain may occur. June was the driest month at the Research Ranch during the study period, precipitation during the first three weeks consisting mostly of light drizzles. The first heavy summer rain fell on June 22nd. Beginning in early July and continuing through late August, thunderstorms occurred almost daily. Most of these occurred in the mid-to-late afternoon and lasted from 20 minutes to a little over an hour (Table 1 summarizes precipitation during the study period).

The highest temperatures usually occur toward the end of June and early July before the onset of the summer rains (Sellers and Hill

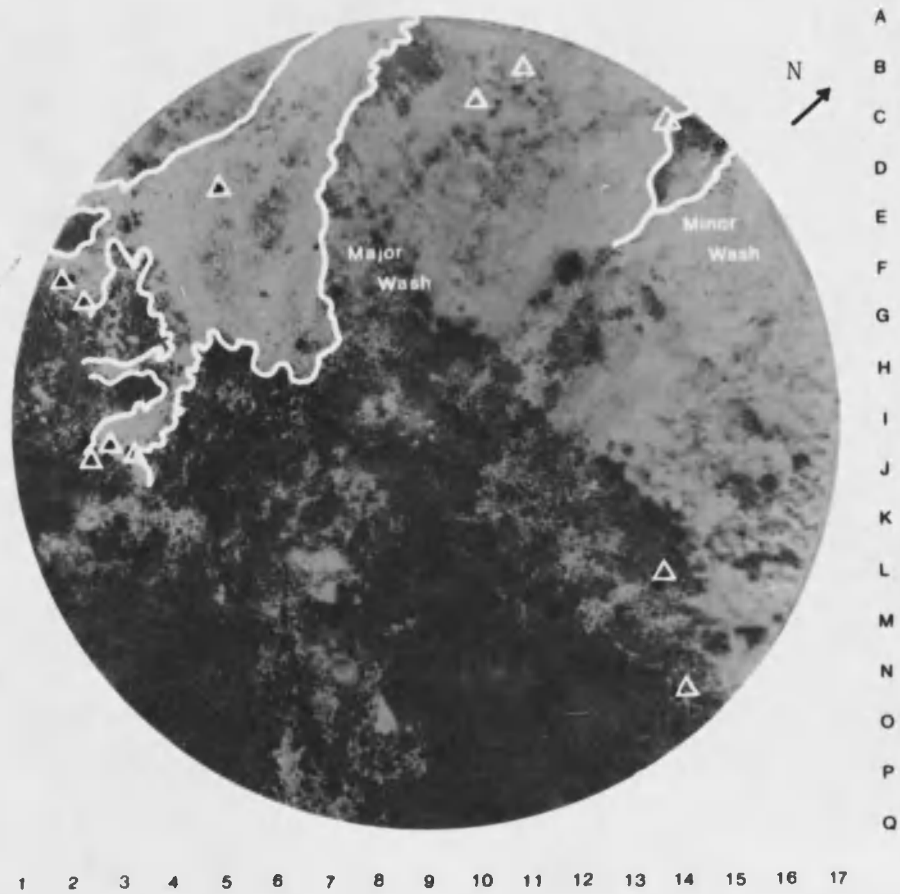

Figure 1. Tortoise enclosure showing the location of the two washes, and mesquite trees (<u>Prosopis juliflora</u>) utilized as shade areas.

(△) indicates mesquite trees.

Table 1. Precipitation at the study area during June, July, and August, 1977.

Dates	Total Precipitation (cm)	Mean Daily Precipitation (cm)
June 1 to 24	1.70	0.07
June 25 to July 31	6.43	0.17
August 1 to 25	5.54	0.22

1974). Mean daily temperatures during the study period were highest in June, and slightly lower in July and August (Table 2).

The study site falls within the desert grassland biome (Humphrey 1958). Dominant grass species include Hilaria mutica (Buckl.) Benth., H. belangeri (Steud.) Nash., and Bouteloua curtipendula (Michx.) Torr. Conspicuous small trees and shrubs include Prosopis juliflora (Swartz.) DC., several species of Haplopappus, and Baccharis pteronioides DC. (A list of all plant species found in the tortoise enclosure appears in Appendix A and code designations for most of these are in Appendix D).

The study area can be divided into two major vegetation types: the lower (south to southeastern) half falls within the Hilaria mutica/ Eriochloa lemmoni association, and the upper (north to northwestern) half falls within the Bouteloua chondrosioides/Hilaria belangeri/ Aristida divaricata association of Bonham (1972). The lower half of the area is nearly level and consists of a dense carpet of Hilaria mutica with little bare ground or other plant species. Soils in this portion are calcareous clay throughout, and are well drained with moderately slow permeabilities (Bonham 1972). The upper half of the area is a gentle slope dominanted by stands of Hilaria belangeri on a rocky substrate. Soils here are a well drained sandy loam with moderately slow to slow permeabilities (Bonham 1972).

Table 2. Mean daily minimum and maximum temperatures observed during June, July, and August, 1977.

Dates	Mean Daily Minimum Temperatures (^{o}C)	Mean Daily Maximum Temperatures (^{o}C)	Number of Observation Days
June 1 to 24	12.29	34.22	17
July 5 to 29	16.88	32.39	16
August 1 to 25	17.27	32.78	13

METHODS

Eleven tortoises,[2] imported from Durango, Mexico, with the cooperation of the Instituto de Ecologiá, Mexico,[3] were placed in the center of the 20,000 m^2, fenced, circular enclosure on August 16, 1976. Intensive daily observations on behavior were recorded on 17 days in May/June, 16 days in July, and 13 days in August, 1977. Most observations were made between 0600 and 1200 h, and between 1300 and 1900 h. During the summer, nocturnal observations were made four times between 2000 and 2200 h.

Each tortoise was permanently marked in 1976 by drilling one or more holes through the marginal scutes (system adapted from Cagle 1939). Individuals were identified by a binomial based on the position of the drill marks in the carapace. The first digit represented the position of the hole on the left side of the cervical scute; the second represented the hole on the right. A zero meant that no hole was drilled. For example, number 01 referred to a tortoise with one hole drilled into its carapace through the first marginal to the right of the cervical. These code numbers were painted in yellow on the front and rear of the carapace to facilitate easy identification from a distance.

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2. One tortoise, number 22, died shortly after introduction to the area.

3. Export permit no. 1897 (1976) from Dirección de la Fauna Silvestre, Mexico.

Tortoises were monitored from a platform 4.6 m high, located near the southern edge of the enclosure. A Bausch & Lomb 20X spotting scope mounted on a movable tripod and 7 X 35 binoculars were used to observe the tortoises. I attempted to scan the entire area every 5-10 minutes, recording identification numbers, locations, and apparent behaviors of all individuals which were in view.

I divided my observation time into three, arbitrary, 4-hour periods: morning (0600 to 1000 h), midday[4] (1000 to 1200 h and 1300 to 1500 h), and afternoon (1500 to 1900 h). I differentiated between "active" and "inactive" modes of behavior: all tortoises observed in any identifiable type of epigean activity (including basking) were considered "active"; all animals not so engaged (or in their burrows, out of view) were classified as "inactive"; this included times when animals used the shade of vegetation as an alternative to underground burrow retreat.[5] A Scheffé's multiple comparison test was used to determine if activity intensity differed significantly ($p \leq 0.05$) between the three daily activity periods and/or between June, July, and August.

Epigean activities were recorded in four categories: <u>basking</u>--postural orientation of tortoises to the sun's rays; <u>traveling</u>--moving about without foraging or encountering other individuals; <u>foraging</u>--eating various species of plants either while roaming or stationary;

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4. This period is divided into two, 2-hour intervals since no data were recorded between 1200 and 1300 h.

5. Audible digging activity that occurred while a tortoise was out of sight inside its burrow was a special case and considered separately.

and social encounters--all interactions involving two or more tortoises. The percentages of the total observation time in which individuals were recorded as engaged in these activities are presented as monthly activity budgets.

Tortoise movements were quantified by calculating straight-line distances between datum points for all trips which individuals were observed to make (data base explained below). A 1-way ANOVA was used to determine if there were significant differences ($p \leq 0.05$) in the mean trip lengths between months.

A χ^2 test was used to determine if the observed behavior of tortoises approaching occupied burrows differed significantly ($p \leq 0.05$) from that of individuals approaching empty burrows.

A record was made of the plant species observed being eaten during the summer. After watching the tortoises for several weeks, it became apparent that they were foraging more often in some areas than in others. To determine if certain plant species, especially *Hilaria belangeri* and *H. mutica*, were taken more often than other species on a basis of relative abundance, observed and expected diets were compared. A χ^2 test was used to determine if these differences were significant ($p \leq 0.05$). Observed diets were defined in terms of the number of times each species was seen being eaten, regardless of quantity. Expected diets were calculated by weighting the relative availability of different plant species in foraging areas by the number of visits to those areas. Thus an "expected" diet is a representation of plant species in direct proportion to their availability as tortoise food.

Environmental temperature extremes were obtained from a maximum-minimum thermometer enclosed in a standard U.S. Weather Bureau shelter adjacent to the southwest border of the enclosure (Figure 2). Burrow and shaded-surface ambient temperatures were recorded with a Yellow Springs two-point thermograph; the burrow probe rested on the tunnel floor about 1 m back from the entrance; the surface ambient temperature probe was mounted 6 cm above the ground in a small protective shelter. Precipitation was measured by a rain gauge attached to the perimeter fence.

The area was divided into a grid of ten-meter squares using wooden stakes, each marked with a letter and number code (e.g., A-1) to serve as reference points for location data (Figure 2). When a tortoise was observed, its location was recorded by the code designation of the nearest stake.

Two artificial burrows were built in the early fall of 1976. These were large enough to accommodate several tortoises in case the already-existing, natural burrows were not deep enough to protect them from freezing temperatures during the winter. Two drinking basins were built near burrow sites I and III to provide supplementary water during drought periods (Figure 2).

Species composition and plant biomass were estimated by weight (Appendix B). On October 9 and 10, 1976, data were obtained on plant composition and species biomass[6] on 26 belt transects 0.32 m by 3.2 m

6. The standing crop biomass equalled 3500 kilograms/hectare. This figure represents an estimate of the forage standing crop in the enclosure when the sample was taken in October, 1976.

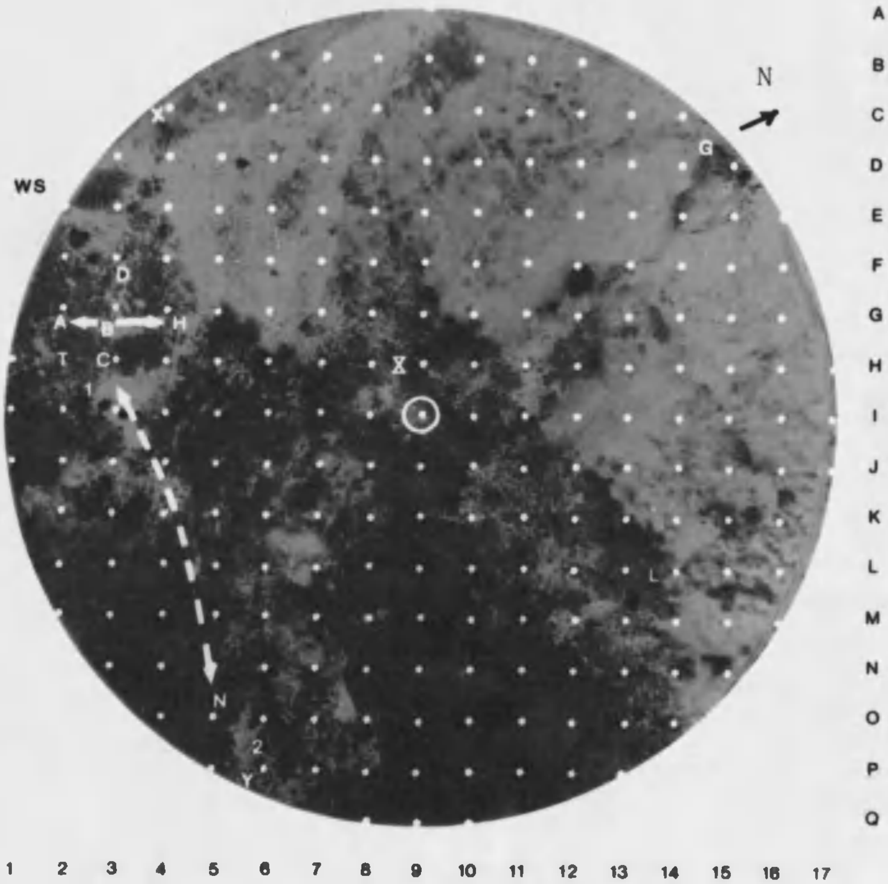

Figure 2. Tortoise enclosure showing the grid pattern, burrow locations, trails, artificial basins, and weather station.

T, observation tower; 1 and 2, artificial drinking basins; X and Y, pallets; A, B, C, D, and G are burrows dug by tortoises and present during the study; L and $\overline{X}$, new burrows dug by tortoises during the latter part of the summer; H and N, artificial burrows; ⊙ , center of study plot; ↔ , trails; (···), grid pattern (position of reference post at 10 m intervals). Burrow site I, includes burrows A, B, C, D, and H; site II, includes burrow G; and site III, includes burrow N and pallet Y.

(method suggested by Dr. E.M. Schmutz, School of Renewable Natural Resources, University of Arizona). These transects were evenly spaced on each side of the plot center (Figure 3). All plants within each transect were clipped at ground level, separated as to species, dried in an oven at 70°C for 72 h, and weighed to the nearest 0.1 g.

Point-plot estimation was also used to determine species composition (Figure 4). This method consisted of recording all vegetation touched or "hit" by a series of needles (spaced 10 cm apart and held in a 1-m-long frame) that were lowered to the ground along a transect (method adapted from Levy 1933). Species composition was derived by expressing the number of "hits" for each species as a percentage of the total number of "hits" per transect (Appendix C). Point-plot transects were subjectively located after careful examination of the surroundings, while the number of unit transects measured was dictated by the statistical requirements of the method.

Prior to placing the tortoises in the enclosure, I subdivided it into four tentative vegetational types. Subsequently, after analyzing the biomass and point-plot data, five vegetational facies were delineated.

Phenological changes of the principal plant species were recorded weekly. Several plants of each species were examined, and leaf development, stem elongation, leaf death, and floral development were scored numerically throughout the summer (Appendix E).

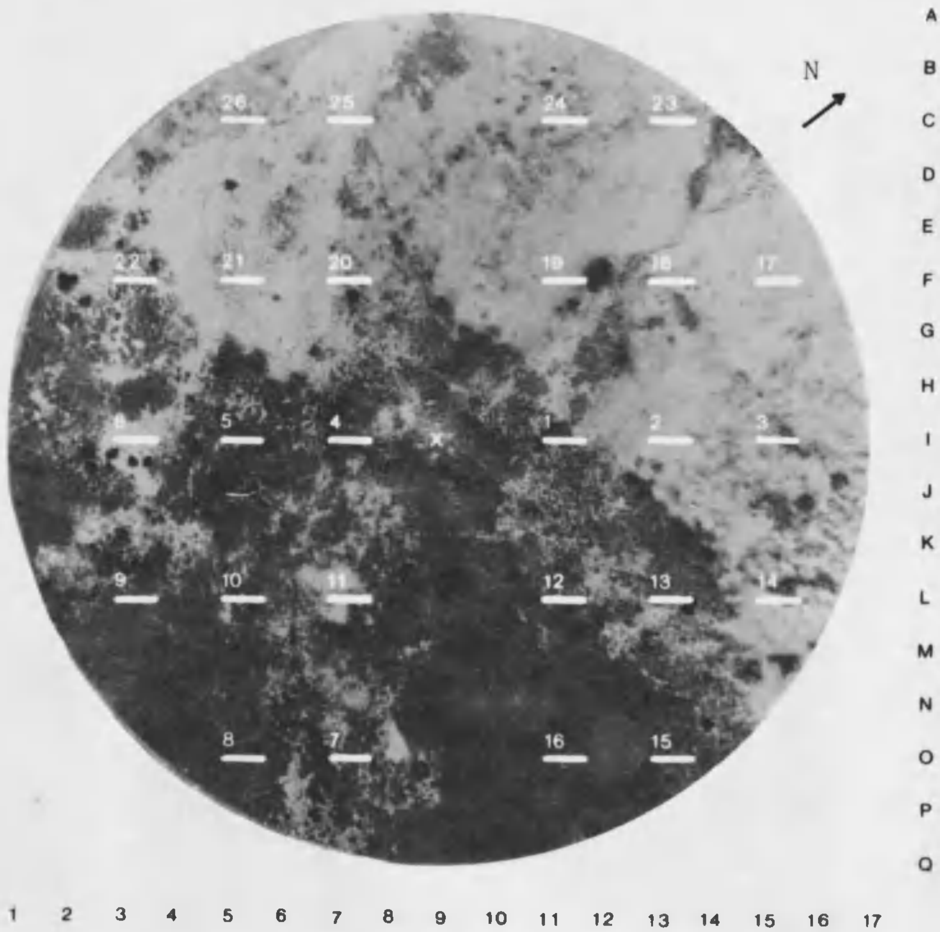

Figure 3. Tortoise enclosure showing the layout of the 26 belt transects (.32 m by 3.2 m) used for plant biomass measurements.

X, plot center; transect numbers correspond with those in Appendix B.

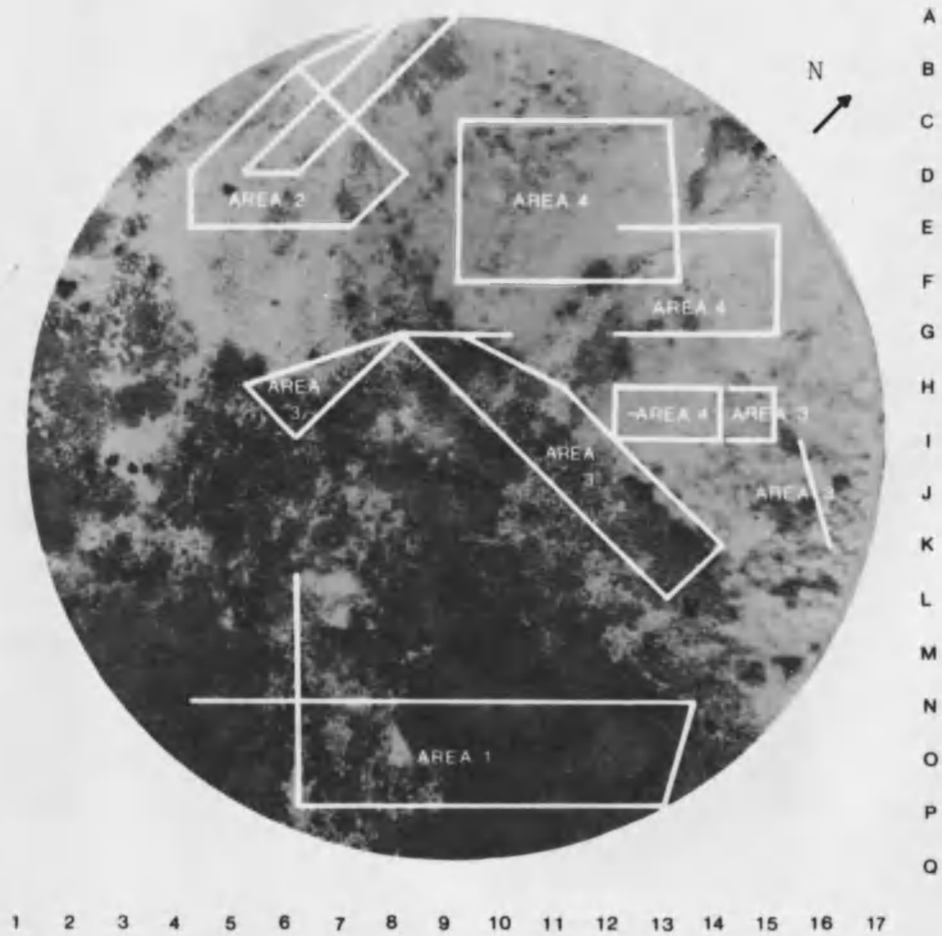

Figure 4. Distribution of the point-plot transect lines.

Area 1--*Hilaria mutica* zone; Area 2--Heterogeneous zone with *H. belangeri*, *H. mutica*, and *Bouteloua curtipendula*; Area 3--*B. curtipendula* zone; Area 4--*H. belangeri* zone. White lines are the transect lines used for point-plot analyses. All areas correspond with those in Appendix C.

ACTIVITY LEVELS

Daily and Seasonal Patterns

During this study, tortoise activity was observed only between 0600 and 1900 h. They usually first emerged from their burrows between 0645 and 0715 h, while burrow temperatures were still higher than outside ambient temperatures (Figure 5). Emergence at this time favored heat gain from the external environment as ambient temperatures began to rise quickly. Most of the burrows faced (opened) south to southeast so that the rays of the morning sun fell directly on the burrow mounds and even into some burrows.

The first early emergence was followed by basking on the burrow mound (the raised, loose pile of dirt in front of the burrow entrance) for periods of 30 to 120 minutes. During this basking period tortoises usually extended their limbs, apparently to obtain maximum exposure to the sun's rays. When basking thus, they closed their eyes and rested their heads and necks on their gular projections. After basking, they usually either left the burrow area for a short period, or pivoted and retreated inside. By 1030 h, when ambient temperatures had reached about 34^{o}C, surface activity decreased, the tortoises usually remaining inside their burrows or in the shade of emergent vegetation during the late morning and early afternoon. Surface activity resumed around 1500 h as the heat of midday subsided. Basking for 3-5 minutes often preceeded the afternoon bout of activity. Late afternoon retreat to a

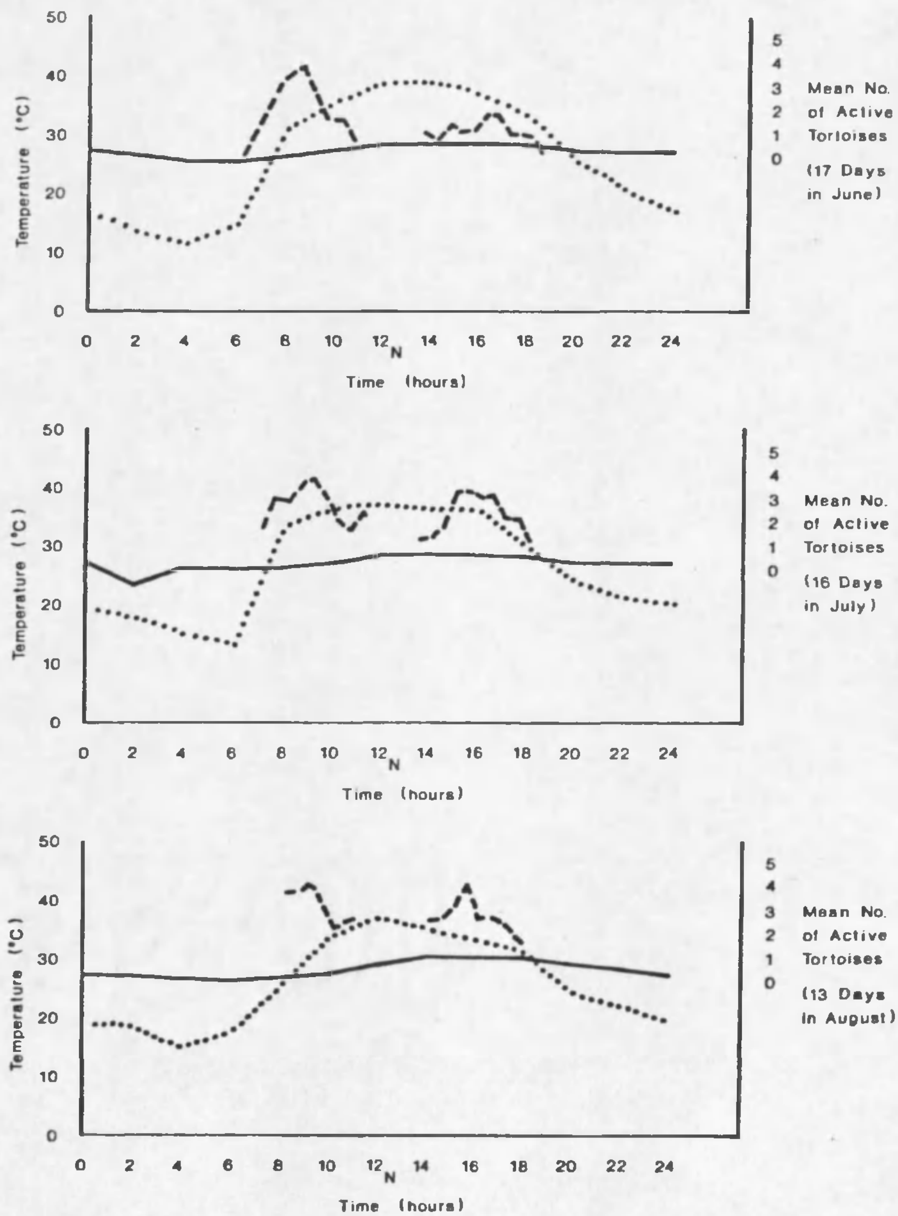

Figure 5. Tortoise activity during June, July, and August, 1977, in relation to burrow and ambient temperatures.

(——), burrow temperatures; (···), surface ambient temperatures; (---), mean numbers of active tortoises. Temperatures were recorded every two hours, while the mean numbers of active tortoises were recorded over half hour intervals.

burrow or to the shelter of protective vegetation was most often observed between 1815 and 1845 h, while ambient temperatures were falling, but were still higher than burrow temperatures (Figure 5). Because of the slope of the ground, shade fell quickly over the area in late afternoon. Tortoises usually paused for several minutes on the mounds of their burrows and extended their limbs in the basking posture before retreating for the day. Burrow retreat at this time reduced body heat loss to the environment. Tortoises were inactive at night.

Observed tortoise activity on the surface was usually bimodal, with the morning peak higher than the afternoon peak (Figures 5 and 6). Although tortoises were not inactive at midday, the level of surface activity was generally lower then than at other times of the day. This bimodal pattern was less apparent in June than during July and August because of relatively less afternoon activity (see Figure 6). Throughout the study, significant differences in the numbers of active tortoises existed between the morning and midday periods, but not between morning and afternoon, or between midday and afternoon (Table 3).

A bimodal pattern of activity has also been reported for _G. berlandieri_, but that species is more active during the afternoon (Auffenberg and Weaver 1969, Rose and Judd 1975). Variations of observed activity patterns between the two species may be attributed to differences in habitat, use and construction of burrows, and basking habits (the latter suggesting different physiological abilities to withstand solar radiation). _G. berlandieri_ inhabits dense, shrubby

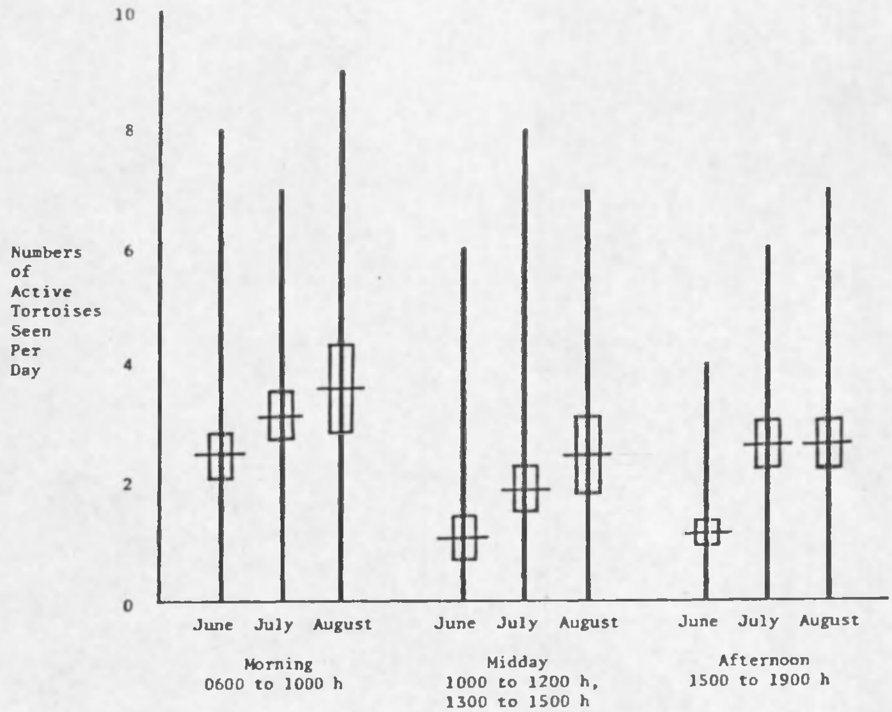

Figure 6. Mean numbers of active tortoises in relation to month and different periods of the day.

The mean (horizontal line), 95% confidence interval (box), and the range (vertical line) are shown.

Table 3. Mean number of active tortoises during morning, midday, and afternoon portions of the day.

Time of Day	Midday	Afternoon	Morning
Mean* No. Active	1.79	2.04	2.66

* Any pair of means not underscored by the same line are significantly different at the 0.05 level as judged by Scheffé's Test (Standard Error of Difference = 0.33).

areas in southern Texas. They do not usually burrow, but dig out shallow depressions in the ground called pallets that only partially cover their bodies (Auffenberg 1969). They do not usually bask (Ernst and Barbour 1972), but "warm up" in their pallets prior to emergence (Voigt and Johnson 1976). In contrast with this environment, *G. flavomarginatus* in the Research Ranch enclosure live in a desert grassland habitat with few, scattered shrubs. They dig burrows, bask several times during the day, and are active for periods lasting several hours. Grant (1960) reports that *G. berlandieri* restricts its activity to short periods in the morning and afternoon.

The ability of *G. flavomarginatus* to withstand increasing morning temperatures, which might cause overheating in the smaller *G. berlandieri*, suggests a resemblance to the pattern reported for *G. agassizi*. *G. agassizi* remained active and maintained deep body temperatures within its viable limits while the shell acted as a buffer against solar radiation, and heated up well above lethal limits (McGinnis and Voigt 1971).

The level of observed activity increased throughout the summer (Figure 6). Activity levels differed significantly between June and July/August, but not between July and August (Table 4).

Despite the existence of the artificial drinking basins, the low level of tortoise activity may have been due to physiological restraints imposed on them by the lack of available water in their diet. Water loss through evaporation during surface activity was probably not compensated by dietary intake from the dry plant material available.

Table 4. Mean number of active tortoises during June, July, and August, 1977.

Month	June	July	August
Mean* No. Active	1.49	2.38	2.61

* Any pair of means not underscored by the same line are significantly different at the 0.05 level as judged by Scheffé's Test (Standard Error of Difference = 0.33).

Accumulation of toxic levels of potassium in the urinary bladder may occur if there is extensive foraging "at a time when insufficient water is available to excrete it" (Minnich 1977). The increase in tortoise activity between June and July appeared to be in response to greater food availability (i.e., greater plant productivity) and more abundant environmental moisture. Stem elongation and leaf production in most perennial grass species began with the moderate-to-heavy showers in July, but only after rain began falling regularly over the area every several days.

In addition to affecting the growth of plants, rainfall altered activity periods in a direct way. Light rain did not usually affect tortoise movements, but heavy showers forced temporary retreat to burrows. When heavy thunderstorms occurred in the late afternoon, tortoises stayed inside their burrows for the remainder of the day. Douglass and Layne (1978) observed similar behavior in *G. polyphemus* in southern Florida.

Activity Budgets

Throughout the summer, tortoises spent more than 60% of the daylight hours inside their burrows. As the summer progressed, they spent a greater proportion of time above ground basking, traveling, foraging, and interacting with other tortoises. Figure 7 represents graphically the proportions of time the subject animals engaged in these activities. The amount of time spent traveling increased steadily and almost doubled from June to August. During the summer, tortoises spent between 16% and 20% of the time basking. The proportion of time

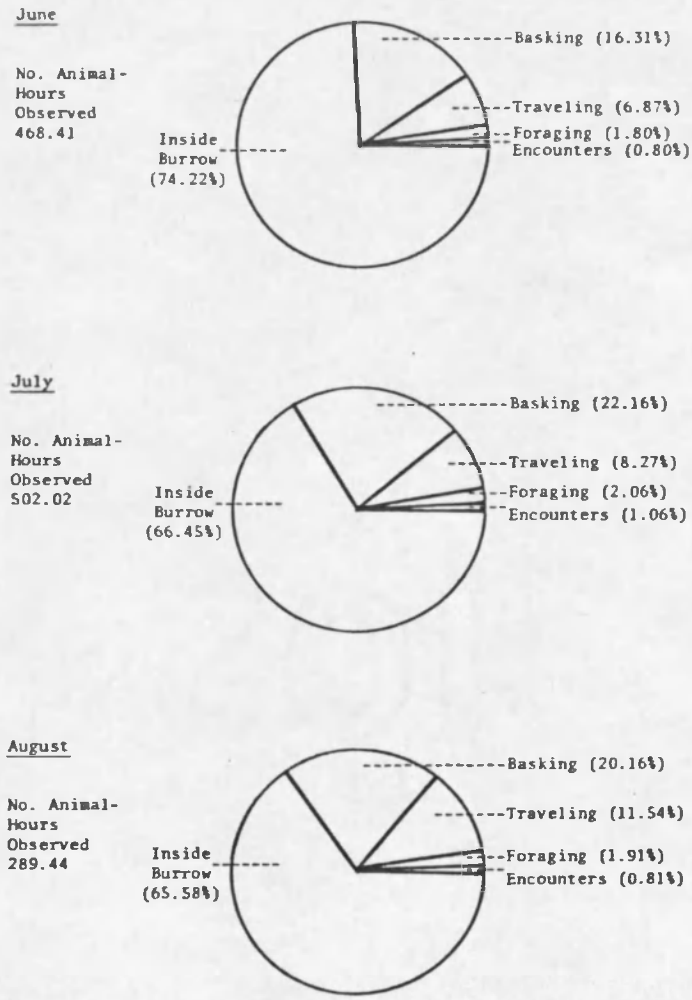

Figure 7. Combined activity budgets of five tortoises (numbers 01, 07, 10, 11, and 80) during June, July, and August, 1977.

spent basking increased from June to July, and then decreased again in August. The same pattern was observed for foraging; however, this activity only represented about 2% of the tortoises' time budget. The rate of encounter was low throughout the summer, with a maximum in July.

Although there was an unequal ratio[7] of males to females which might influence the results, there were differences in activity levels between sexes. Figure 8 represents graphically the activity budgets of four females (numbers 07, 10, 11, and 80) and the one definitive male (number 01) during the study period. The percentage of time spent basking by the male and the females was nearly equal during June, but during July and August the male basked almost twice as much as did the females. During June, the male spent twice as much time traveling as did the females. As the summer progressed, this pattern reversed so that the females traveled twice as much as did the male during August. During June, the females spent more time foraging than did the male; however, the opposite was true during July and August. Most importantly, the encounter rate of the male was several times greater than that of the females during the entire summer.[8] (Appendix F shows activity budgets of individual females). Since the rate of encounter between individuals was generally low, it is assumed that most of the

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7. Definitive sexing by external characters was impossible; as best as I could determine from behavioral data, the population consisted of one male and nine females.

8. These data include encounters with animals other than those in this sample

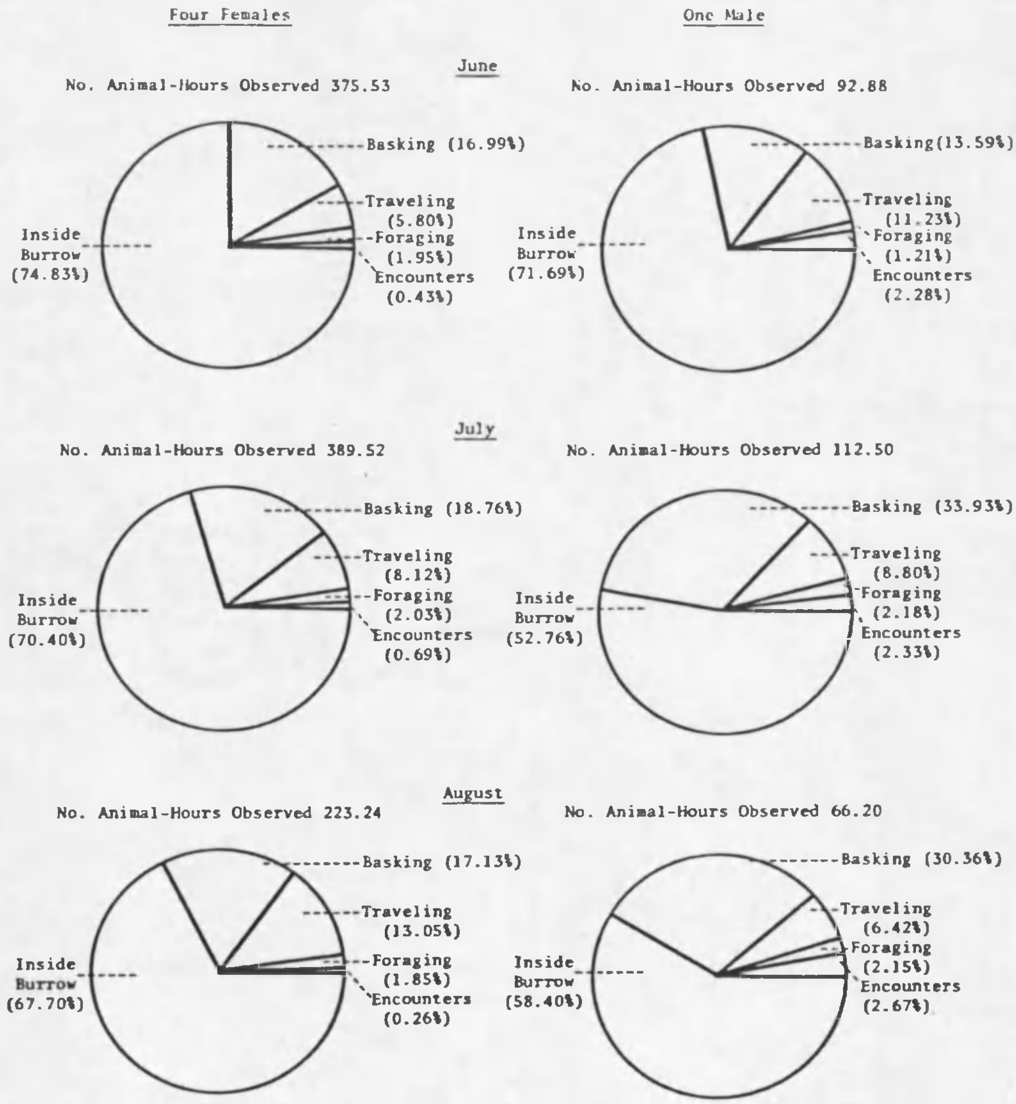

Figure 8. Combined activity budgets of 4 females (numbers 07, 10, 11, and 80) compared with the 1 male (number 01).

traveling observed consisted of exploration for food and burrow sites instead of being socially motivated.

Patterns of Burrow Use

Individuals used their burrows for basking, overnight retreat, and as "home base" after a period of activity. The tortoises dug their burrows in three kinds of sites: in areas that bordered grass tufts and bare ground (sites I and III); in washes (site II); and at the bases of emergent vegetation such as Prosopis juliflora trees or bushes (Figure 2). Most of these burrows were between 1 and 1.5 m in length.[9]

Burrows are important in both temperature and moisture regulation. During the summer, temperatures in the instrumented burrow fluctuated less than did ambient temperatures (Table 5 and Figure 5, page 17). The observed pattern of early morning emergence when both ambient and burrow humidities were high, followed by retreat in mid-to-late morning when the general evaporation rate increased rapidly (Auffenberg 1969), suggests that the burrow aids in water conservation. Auffenberg (1969) also points out that breathing of tortoises inside the burrow adds moisture to the air, lowering evaporation rates. Hourly and monthly differences in activity levels noted in this study may reflect both humidity and temperature differences between the air and the burrow. Rainfall occurred infrequently in June, and burrow humidities were probably much higher than in the outside air. Rain fell regularly

9. Tortoises were apparently unable to dig extensive burrows because of the dense soil. One exception was a burrow dug near the northern edge of the enclosure, at the base of a wash; this burrow was more than 2 m in length.

Table 5. Mean monthly burrow and shaded, surface ambient temperatures.

Dates	Burrow Temperatures (°C)		Ambient Temperatures (°C)	
	Low	High	Low	High
June 1 to 30	25.49	29.58	10.93	42.25
July 5 to 31	26.09	29.74	16.72	44.27
August 1 to 31	25.33	32.62	16.26	41.35

during July and August and air humidities often reached 100% in the early morning; burrow and air humidities were probably similar at this time.

Tortoises did not always retreat to burrows to escape high temperatures. Individuals often remained in the shade of mesquite trees (*Prosopis juliflora*) and/or tall grass clumps (e.g., *Sporobolus wrightii*, *Hilaria mutica*, and *Bouteloua curtipendula*) collectively called shade spots (Appendix G). Judd and Rose (1977) observed that in areas where shrubs provided shade, *G. berlandieri* did not gain any thermal advantage from pallets. This alternative use of vegetation by captive *G. flavomarginatus* probably allowed them to increase their range of activity.

The captive animals improved their burrows throughout the summer and early fall of 1977. Burrows that I visited in October, 1977, were larger than when seen previously in mid-August. Digging was usually observed in the morning between 0800 and 1100 h, when tortoises retreated into their burrows (Appendix G). Sporadic digging was sometimes observed in the afternoon.

Digging took two forms: "scraping" and "clearing". The term "scraping" is used here to designate the hard, clawing action of the front limbs at the hard, clay substrate to deepen the burrow. "Clearing" is a sweeping action similar to that achieved through use of a broom. This is done mostly with alternate strokes of the front limbs, with similar use of the rear limbs on occasion. In this way, loose material accumulated in and near the entrance of the burrow is removed. Because of the looseness of this debris, "clearing" did not appear to be as physically demanding as "scraping".

A tortoise might dig inside its burrow for several hours during the day. This was usually done in spurts, alternating with rest periods in the burrow or spells of basking on the mound. In contrast with time spent scraping, clearing periods were usually brief, lasting less than a minute. After periods of scraping, individuals were seen backing out of a burrow, basking, clearing some loose material, and then resuming digging inside. Although most of this activity took place at an individual's home burrow, this was not always the case.

Foraging and Drinking Patterns

Tortoise foraging patterns consisted of short, sporadic sampling lasting less than a minute, and long forays (called "feeding bouts") which consisted of wandering along trails for extended periods, lasting from several minutes to over an hour. These bouts were not always continuous and were often interrupted by basking, traveling, or other activities.

Insofar as could be determined by this study, the diet of *G. flavomarginatus* consisted of a variety of perennial grasses, forbs, and (occasionally) shrubs (Table 6). Approximately 31% (15 species) of the total number of plant species available in the enclosure were taken. Of these, *Hilaria belangeri* and *H. mutica* were observed to be taken more often than other species by most tortoises. Fecal pellet analysis showed that 80% of the diet of *G. flavomarginatus* living in the Mapimi Biosphere Reserve in Durango, Mexico, is composed of five species:

Table 6. Individual tortoise diets observed during June, July, and August, 1977.

Plant Species Consumed	Tortoise Numbers 01	02	07	08	09	10	11	20	80	90	Totals
	Number of Feeding Observations per Plant Species										
Hilaria belangeri	10	15	17	9		12	15	2	14	1	95
H. mutica	29	1	11	1	3	24	4		10		83
Bouteloua curtipendula	5	2				1	1		5		14
B. gracilis			1				1				2
B. hirsuta		1	7			1	1		1		11
Panicum obtusum	1				1	1					3
Sida procumbens			1				1				2
Solanum eleagnifolium			2								2
Andropogon barbinodis	1					1					2
Euphorbia albomarginata							1				1
Perezia nana						1			2		3
Prosopis juliflora			1								1
Sporobolus wrightii	1										1
Viguiera annua			1			1	1				3
Desmanthus cooleyi									1		1
Number of Plant Species Taken per Tortoise	6	4	8	2	2	8	8	1	6	1	
Total Number of Feeding Observations per Tortoise	47	19	41	10	4	42	25	2	33	1	224

Bouteloua gracilis, H. mutica, Sida leprosa, Tridens pulchellus, and Sphaeralcea angustifolia (Leon et al. 1979).

Tortoises fed primarily on the succulent parts of plants: stems, leaves, and flowers.[10] Several times they were seen to avoid a particular plant after inspecting (smelling) it. On two occasions, I saw animals avoid Haplopappus spinulosus; I never saw it eaten. Perezia nana was avoided once in early June, but was eaten by two tortoises later in the season.

Diet variety decreased as the season progressed and plant productivity increased (Table 7). During July and August, species other than Hilaria belangeri and H. mutica gradually disappeared from the diet. This pattern of increasing specialization coincident with greater plant productivity is in accordance with optimal foraging theory (Pyke, Pulliam, and Charnov, 1977).

Fecal pellet analysis of G. flavomarginatus at the Mapimi Biosphere Reserve in Durango, Mexico, suggests that a seasonal shift in diet occurs. Scats collected during the summer contained B. gracilis and H. mutica, while those collected at other times of the year contained mostly H. mutica. Other perennials were eaten during the dry season but H. mutica was taken more often, supposedly because it was more abundant (Leon et al. 1979).

Observed diets of individual tortoises were compared with "expected" diets (see methods). A χ^2 test showed that individuals

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10. In one instance, part of a fecal pellet was ingested during a feeding bout.

Table 7. Plant species other than Hilaria belangeri and H. mutica taken by individual tortoises.

Tortoise Number	June	July	August
01	Bouteloua curtipendula Sporobolus wrightii Panicum obtusum Andropogon barbinodis	B. curtipendula	
07	B. curtipendula B. gracilis B. hirsuta Solanum eleagnifolium* Prosopis juliflora Sida procumbens*	B. hirsuta+ Viguiera annua**	B. hirsuta S. eleagnifolium*
10	B. curtipendula A. barbinodis P. obtusum Perezia nana++	B. hirsuta+ V. annua**	
11	B. curtipendula B. gracilis S. procumbens* Euphorbia albomarginata*	B. hirsuta+ V. annua**	
80	B. curtipendula P. nana++	B. curtipendula	B. hirsuta Desmanthus cooleyi*

*, plant in flower
+, new growth
**, elongation of green stems
++, some dry plants, but others with new buds and leaves

selected *H. belangeri* and *H. mutica* more often and other less abundant species less often than predicted (Appendix H). Although one tortoise (number 11) did not appear to be selective, this individual was observed less often (25 feeding observations) than the others in the sample.

Foraging patterns may have been influenced by the presence of 10-70 m trails leading from burrows (Figure 2). These trails were either created by continuous use, or occurred naturally as bare ground surrounded by perennial grasses. Near burrows, little foraging occurred along these paths. The trails apparently functioned as guides to and from foraging areas. A continuous trail around the periphery of the enclosure was mechanically created when the boundary fence was installed. Tortoises were often observed traveling along the fence as if looking for a way out of their confinement.

In the wild, *G. flavomarginatus* has been observed to wander along well-defined grazing trails that lead 10-20 m from a burrow (Morafka in press). *G. polyphemus* uses a number of paths which radiate from the burrow entrance and most of its activity centers around these paths and the areas immediately adjacent to burrows, the tortoises foraging along these paths and enlarging them as their feeding needs increase (Auffenberg 1969).

Differences in the relative abundance of plant species and the presence of shade spots, combined with individual foraging preferences and the availability of trails probably determined the foraging areas used by my captive bolson tortoises. The sheer density of vegetation may also have affected foraging patterns. For example, one of the least visited areas was the _Hilaria mutica_ zone--a dense carpet of _H. mutica_ with few trails, little shade, and little bare ground (Figure 9). Tortoise travel may have been impeded by this tall tobosa grass. Most plant species eaten, including _H. mutica_, were taken from the _Bouteloua curtipendula_ and _H. belangeri_ areas (Table 8). These areas provided more diversity, and more shade spots at comparable distances from most tortoise burrows.

The tortoises drank readily from artificial, shallow water basins near their burrows. Upon approaching a basin, they lowered their heads to the ground and sniffed around the edge. Moving closer, they immersed their heads and necks in the water for several seconds at a time to drink. Individuals paused approximately five seconds between drinks, raising their heads above the level of the water. After several short drinks of 5-10 seconds duration, they frequently moved into the basin until their bodies were partly submerged. Drinking resumed as before, except that it lasted for longer periods of 15-20 seconds. After 2-3 minutes, tortoises usually left the pool. Urination occurred both in the basin and while leaving it. Defecation was seen only after exiting. A loud squirt was audible from at least 15 m away as the tortoises, on more than one occasion, voided their bladders. Return to the basin for shorter drinking bouts usually occurred after several minutes. The number of drinking observations decreased as rainfall and the moisture content of plants increased from June to August until, by August, use of these basins ceased entirely. In contrast with my

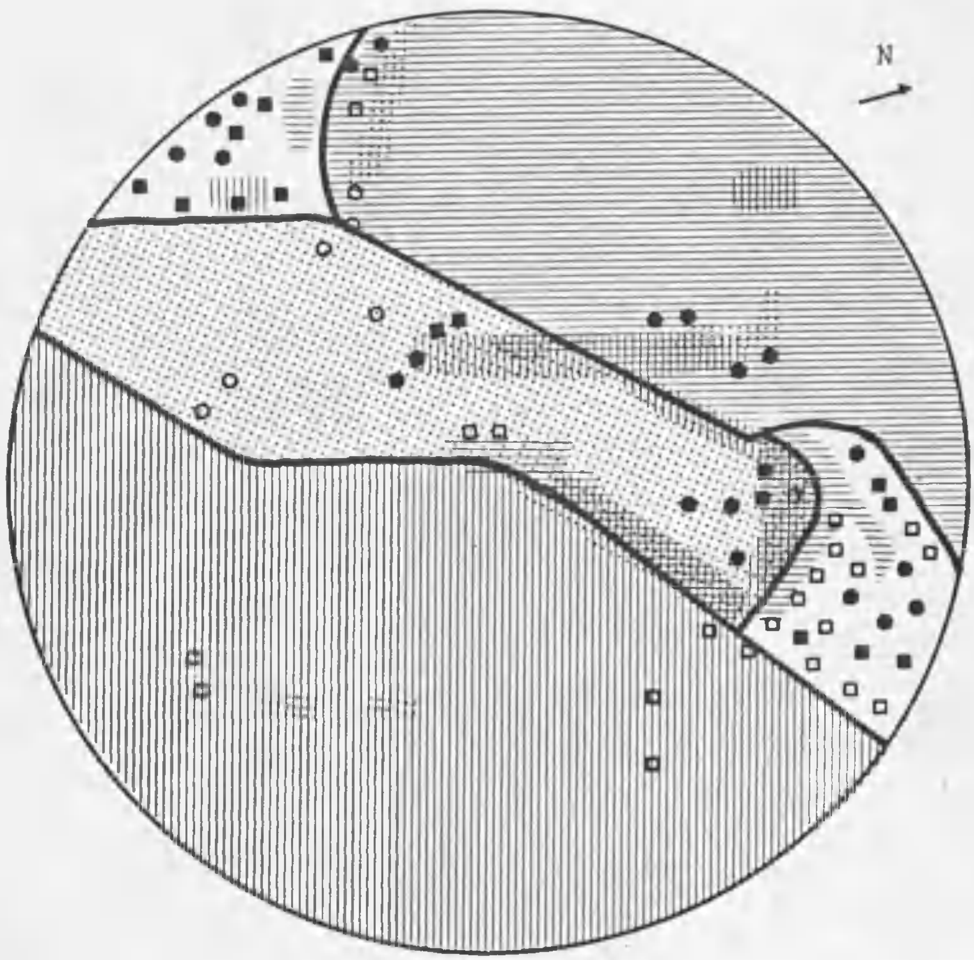


Figure 9. Tortoise enclosure showing the five different vegetational areas.

Area 1--Hilaria mutica zone; Area 2--Heterogeneous zone with H. belangeri, H. mutica, and Bouteloua curtipendula; Area 3--B. curtipendula zone; Area 4--H. belangeri zone; and Area 5--Mixed zone with B. chondrosioides, B. gracilis, and B. hirsuta. (■), Bouteloua chondrosioides; (∷), B. curtipendula; (O), B. eriopoda; ( ), B. gracilis; (●), B. hirsuta; (≡), Hilaria belangeri; (|||), H. mutica.

Table 8. Mean percent of foraging observations in different vegetational facies.

Totals	Vegetation Areas				
	1	2	3	4	5
$\bar{X}$	7.74	25.30	30.08	36.31	0.57
S	8.22	21.62	28.08	37.51	1.51

The mean ($\bar{X}$) and standard deviation (S) are shown. The vegetation areas are coded as follows: (1)--*Hilaria mutica* zone; (2)--Heterogeneous zone with *H. belangeri*, *H. mutica*, and *Bouteloua curtipendula*; (3)--*B. curtipendula* zone; (4)--*H. belangeri* zone; and (5)--Mixed zone with *B. chondrosioides*, *B. curtipendula*, *B. gracilis*, and *B. hirsuta*. The ranking is from greatest to least number of observations. N = 224 feeding observations.

observations, other captive G. *flavomarginatus* were not observed to drink even when placed in a shallow water basin (Legler and Webb 1961).

Traveling Patterns

The tortoises traveled more in June than they did in July and August (Table 9); however, a one-way ANOVA showed that the differences from month to month were not significant (Table 10). There was no correlation between the sizes of tortoises and mean distances traveled ($r = 0.1$, $p > 0.25$).

Tortoises may have traveled greater distances during June because the food supply was low and the plants were dry, requiring time to search for adequate succulent vegetation. In July and August, the average trip distance was shorter, and presumably related to greater food availability.

Table 9. Trip lengths (all tortoises) during June, July, and August, 1977.

Month	Mean (m)	Standard Deviation	No. of Trips
June	102.35	85.51	72
July	79.79	77.00	98
August	89.58	69.88	88

Table 10. 1-way ANOVA of trip lengths observed during June, July, and August, 1977.

Source	DF	MS
Total	257	
groups	2	10555.50*
error	255	4514.55072

* F test non-significant for group means at 0.05 level.

SOCIAL INTERACTIONS

Behavioral Responses during Burrow Approach

Tortoises approaching a burrow may behave in one or more of several ways: "head-bob" (vertical movements of the head and neck region); "flatten" (lower the body to the ground, with the entire plastron touching the substrate, while simultaneously raising the head and neck region). Occasionally they do not behave in any of these ways. The approach behavior at occupied burrows was significantly different from that shown at unoccupied ones (Appendix I). Tortoises usually head-bobbed upon approaching an occupied burrow and flattened upon approaching an empty one (Table 11).

The fact that head-bobbing took place more often at occupied burrows than at empty ones suggested that this behavior may function as a visual signal. Bobbing was usually initiated when a tortoise was several meters away from the burrow and became more pronounced as it moved closer towards the burrow mound. Bobbing continued once the tortoise was on the mound, and also occurred after flattening; sometimes it continued while retreating. Head-bobbing was also observed during courtship and is discussed later in that context.

The fact that tortoises flattened more often at empty burrows than at occupied ones suggested that this action was not a visual signal to other animals. I believe it afforded a tortoise with a better view of a dark burrow before entering. Flattening was

Table 11. Head-Bobbing and flattening responses upon approach to occupied and empty burrows.

	Head-Bobbing* versus No Head-Bobbing		Flattening+ versus No Flattening		Total No. Observations
Burrow Status	Percent	N	Percent	N	N
Empty	20.18	22	43.12	47	109
Occupied	45.90	28	16.39	10	61

* alone or in combination with flattening
\+ alone or in combination with head-bobbing

observed only once away from a burrow. In this instance, a female dropped suddenly to the ground and ceased feeding as a second female approached to within two meters. The approacher stopped, looked at, and then moved away from the flattened tortoise, which resumed feeding.

When one tortoise approached another at a burrow entrance, the behavior of the approaching individual varied. Male #01 head-bobbed every time he approached a female. When females approached #01, the responses varied. Although females sometimes responded (26.3%) to approaching females, this was not the usual pattern. Table 12 summarizes male and female responses during burrow approach.

Observed behaviors upon burrow approach were apparently unrelated to the period of vacancy (Table 13). Although responses of individuals varied, the same behaviors were observed at burrows vacated for either short or long periods of time.

Bobbing and flattening of tortoises at empty burrows may have been influenced by the scent emanating from scats inside the burrows. Patterson (1971) reports that fecal pellets influenced the behavior of captive G. agassizi, causing the dispersal of conspecifics until the pellets dried up.

There was no exclusive use of burrows, although burrows were seldom occupied by more than one tortoise at any one time during the study. In 55 of 450 burrow or shade spot observations (12.2%), I observed two or three tortoises together at a shade spot or burrow. Tolerance of another individual at this time varied; table 14 summarizes the degree of tolerance when several tortoises were at a burrow or

Table 12. Individual responses of approaching tortoises at burrows.

	Approachers				
Approachees	01♂	07♀	10♀	11♀	80♀
01♂	X	OO FO OO FO FB FO	OO OO	FO BO	BF BO
07♀	BO BO BO BO BO	X	BO	OO OO BO FO	BO
10♀	BO BO		X		
11♀	BO	OO OO		X	
80♀	BO BO BO BO BO BO BO BO BO	OO OO OO	OO OO OO OO	OO OO OO BO	X

01 is presumed to be the only male in the colony (see page 25). Action types: OO, no response; BO, bobbing only; FO, flattening only; BF, both bobbing and flattening. Blank boxes indicated that no approaches were observed.

Table 13. Responses of tortoises to empty burrows following short, intermediate, and long periods of vacancy.

Time of Vacancy	Tortoise Number	Time Burrow is Empty	Flatten	Head-Bob	Burrow Letter
	01	13 minutes	no	yes	B*
		26 "	no	no	C*
SHORT	07	12 "	no	no	A*
	10	7 "	yes	yes	C*
	80	17 "	no	no	H*
	01	70 minutes	yes	no	B
		46 "	no	no	C*
INTERMEDIATE		46 "	no	yes	C*
		38 "	yes	no	C*
	07	67 "	no	no	A*
	10	73 "	yes	yes	A
	80	89 "	no	yes	H*
		46 "	no	no	H*
		52 "	no	yes	H*
LONG	01	101 minutes	no	yes	B*
	10	175 "	no	yes	C*
VERY LONG	01	12+ hours	no	no	C*
		15+ "	no	no	C*
	11	12+ "	no	no	D*

* indicated a home burrow. Time of vacancy indicated that a burrow was not visited by another tortoise during the interim period. Time periods were as follows: short, several minutes; intermediate, between 30 and 90 minutes; long, between 1.5 and 3 hours; and very long, many hours, possibly overnight.

Table 14. Summary of behavioral observations when 2 or more tortoises shared a burrow or shade spot.

Frequency of Recorded Observations	Behavioral Responses
30	Tortoises were tolerant of each other.
20	The resident attempted to prevent entry of an intruder by bracing its legs against the sides of the burrow.
3	The resident braced its legs against the sides of the burrow, and slowly moved out towards the burrow entrance, evicting the intruder.
1	The intruder backed out of the burrow after an unsuccessful attempt to enter.
1	The resident was displaced from its burrow by an intruder. The former resident rammed the new occupant for several hours, but was unable to dislodge it.

N = 55 Observations

shade spot. Tortoises already inside their burrows (residents) were usually tolerant of other individuals sharing their quarters (intruders). Pallets of G. berlandieri were observed to be used on a first-come, first-served basis and late arrivals tried to push themselves into occupied pallets (Rose and Judd 1975).

Mating Activity

Eighteen mating attempts were recorded during the summer and early fall, 1977. In full knowledge of the fact that I could not tell whether full intromission and effective sperm transmission had occurred, I nevertheless differentiated between (apparently) "complete" matings with repeated thrusting motions by the mounted male and "incomplete" matings in which thrusting did not usually occur. Four of the eighteen matings were considered "complete"; all took place at burrow mounds. Six "incomplete" matings took place at burrow mounds, and eight occurred away from them.

Courtship behavior consisted of three phases, (two precopulatory and one copulatory), during which the male was apparently either successful or unsuccessful in his attempts to copulate. When the female was unreceptive to the male's advances, additional phases were added as the behavioral repertoire became increasingly complex and repetitive.

"Complete" Mating Sequence

The male approached a female at her burrow and bobbed at her, regardless of her orientation. She presented her posterior end either by turning around or pivoting if she was outside her burrow, or by backing out if inside. The male mounted the female. To facilitate intromission, the male thrust his body up and down by alternately extending and retracting the front and rear limbs, while almost vertical in stance (Figure 10). When the male simultaneously pushed down with his front limbs and extended his rear limbs, he also extended his head and neck region. Alternately, the head and neck became relaxed (no longer extended) when he shifted his balance and retracted his legs. During thrusting, his front legs remained resting on the female's carapace. After coition had apparently been accomplished, the male dismounted and the female retreated into her burrow. The male did not always leave immediately and often tried to engage her in additional courtship. Figure 11 diagrams the above pattern.

"Incomplete" Mating Sequence

Incomplete courtships were behaviorally similar to complete ones except there was no obvious coition. Mating attempts away from burrow mounds were more complex than those at burrows. The male was often seen trailing a female. While trying to overcome her, he usually circled around her with his mouth open, as if to bite her. This led either to a circular pursuit by the male with the female retreating backwards in an inner circle terminating with the male's departure, or the female walked away from the male and he resumed trailing her. No contact was made during these sequences. Incomplete courtship sequences are indicated in Figures 12 and 13.

Away from burrows, ancillary behaviors occurred when the male trailed a female. These actions by the male may have 1) identified him

Figure 10. Photograph of the thrusting stage during a "complete" mating sequence.

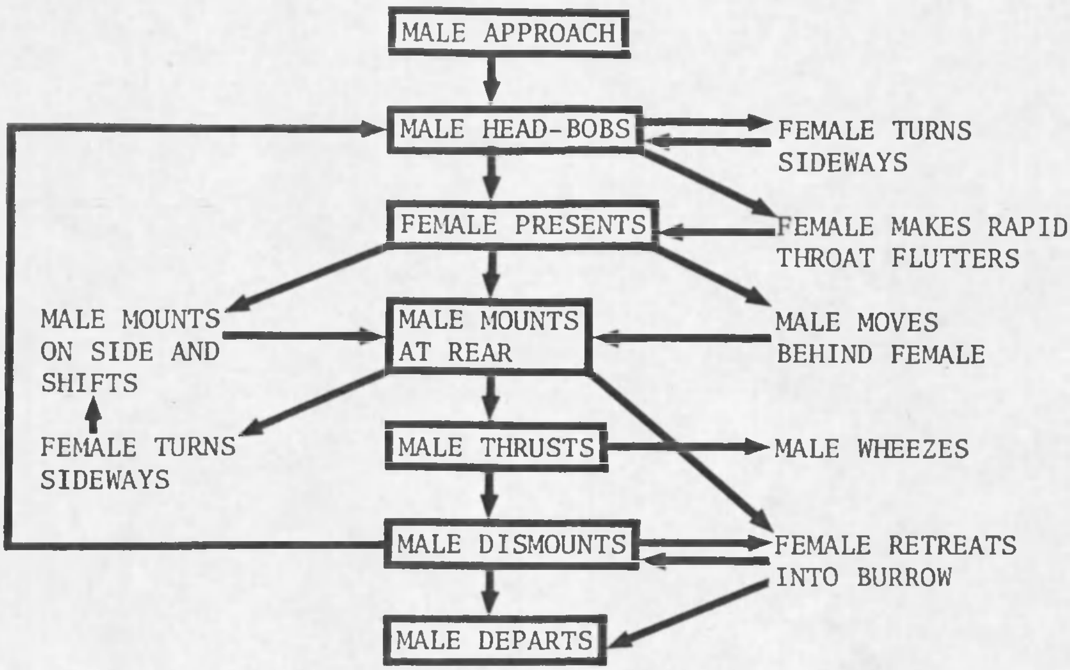


Figure 11. Complete mating sequence at burrow mounds.

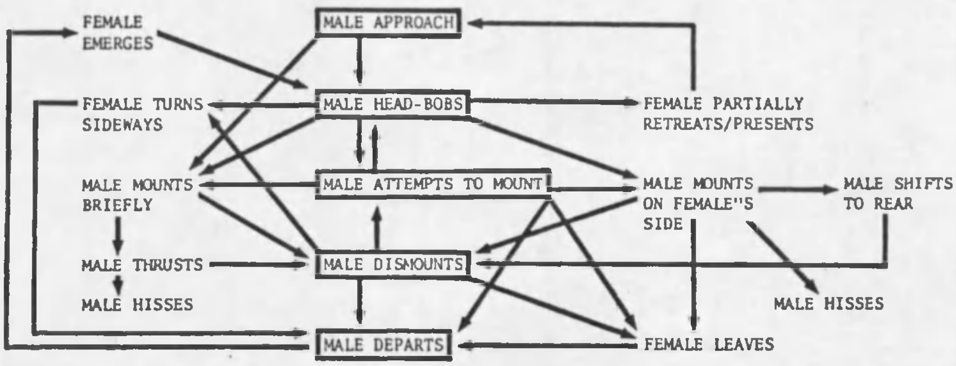


Figure 12. Incomplete mating sequence at burrow mounds.

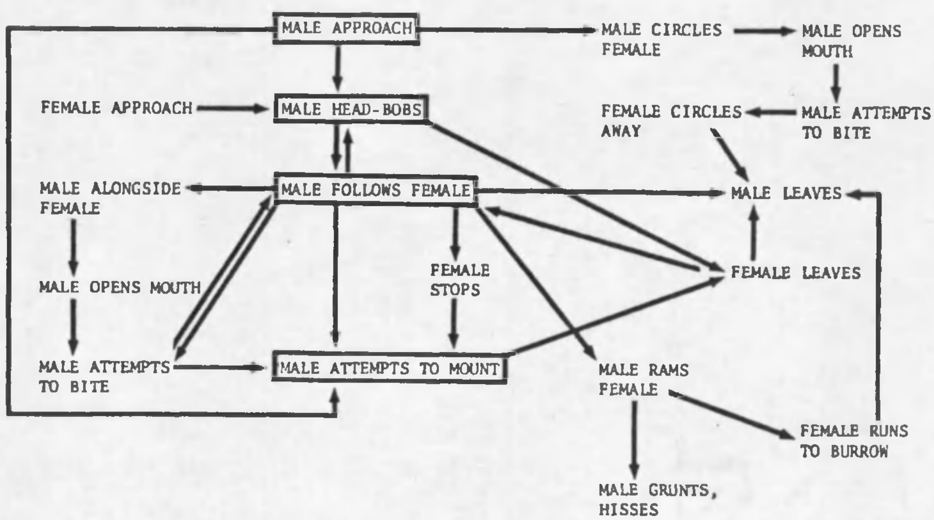


Figure 13. Incomplete mating sequence away from burrow mounds.

as a member of the same species, 2) helped overcome and immobilize the female, and/or 3) further excited her, or 4) served in some other way as visual signals important in sex and species recognition (Auffenberg 1964). At a burrow, females blocked mounting attempts by turning sideways or retreating. A male mounted a female on the side of her carapace or alternately tried to mount while bobbing at her. The male's response in this situation was not as complex or variable as it was away from the burrow. This may have been because the female's responses were physically limited, due to restraints imposed by the burrow walls.

Visual, Olfactory, and Auditory Cues during Courtship

Head-bobbing in captive G. flavomarginatus probably served as a visual signal during courtship, and may have had some olfactory function; enabling the male to pick up scent from the female's cloaca. The male (01) usually head-bobbed at the female upon approaching her burrow. Only once was a female observed to present her posterior end to the male without seeing him. While sight may not be necessary for sex and species recognition (e.g., Geochelone travancorica relies only on olfactory signals, Auffenberg 1964), most observed matings of G. flavomarginatus occurred only after the partners had initially faced each other.

The role of scent in courtship is not fully understood. Female and male G. polyphemus were observed rubbing their forearms near their chin glands during courtship (Auffenberg 1966, Weaver 1970). This apparently had some visual and/or olfactory effect on courting tortoises (Rose, Drotman, and Weaver 1969). The only time I saw a male or female

G. flavomarginatus rub its forearms against the sides of its head was during solitary basking and this may have been associated with some "waking-up" function.

During all courtings, the male produced various sounds which were never produced by any female. These sounds were of three distinct types: grunting, wheezing, and hissing. Grunting is a plosive sound of low frequency; it was heard during ramming of a female and, on one occasion, during ejaculation while mounted on the side of a female. Wheezing consists of a series of high-pitched, breathy sounds with some tonal quality; it was audible during mounting. Hissing is an atonal, "white" sound produced by expulsion of air under pressure; it also was heard during mounting, and it is a normal concomitant of rapid withdrawal into the shell. Vocalization occurs in several species of tortoises, but its function is unknown (Gans and Maderson 1973).

Non-Courtship Encounters

In addition to courtship, tortoises occasionally encountered other individuals at various locations in the area. In these instances, there was either avoidance, tolerance, or antagonism, regardless of location. Tortoises avoided one another 77.6% of the time (38 of 49 non-courtship encounters). They tolerated the other's presence 6.1% of the time (3 times), and exhibited agonistic behavior in the form of ramming and/or chasing 16.3% of the time (8 times).

When encounters were observed at burrows, avoidance usually occurred as the approached tortoise retreated inside its burrow and the other individual left the area. Away from burrows, both tortoises usually swung wide of each other and increased their pace for several meters before slowing down.

Tortoises tolerated the presence of other individuals at shade spots. The approached animals were probably sleeping and initially unaware of any intrusion or, did not respond by leaving or chasing the other tortoise because temperatures were high.

Agonistic behaviors were usually observed at burrows and involved attempts by one tortoise to dislodge another already inside the burrow. The aggressor rammed the burrow occupant, retracting its head into its shell while backing off, and then moving forward and quickly making contact with the shell of the other tortoise. In one instance, ramming of a female by a male (01) was heard (the tortoises were shielded from my view by vegetation) following an unsuccessful mating attempt. The female was motionless in the shade of a tall mesquite tree (Prosopis juliflora) when the male came over and apparently rammed her. It was possible that the sounds heard were not those of ramming but those of an awkward attempt by the male to mount her near the base of the tree. The female departed quickly and returned to her burrow. The male remained in the shade for several minutes and then left. Surprisingly, he passed in front of her burrow but did not show any interest in her.

Changes in the behavior of the approached and/or approaching tortoise(s) were observed when individuals were within a certain distance of each other, called a threshold distance (TD). Observed differences in the TD when behavioral responses were noted may have been due to the location of the encounter (at or away from a burrow), the orientation of the two tortoises, the specific individuals, and the approacher's intent.

There was a slightly greater TD away from burrows; however, a t-test indicated this difference was not significant (Table 15). The mean TD for all tortoises was 1.16 m. There did not appear to be any patterns of responses between individual pairs.

Away from burrows, tortoises appeared to be startled as other individuals approached to within several meters; they may have mistaken them for potential predators. In contrast, tortoises were able to get closer at burrows before any behavioral change was noticed, presumably because both animals saw and identified each other at a distance, and the intent of the approacher was more apparent (e.g., the pattern of head-bobbing upon approaching a burrow when it was occupied). The burrow also provided a quick retreat to safety. In one instance, a tortoise which approached another from behind was able to get very close before any noticeable behavioral change in either animal was observed. The approaching individual was within 0.2 m when both tortoises departed suddenly, swinging wide of each other.

Table 15. Threshold distances (meters) at and away from burrows.

Condition	Mean*	S	N
At Burrows	1.09	0.80	19
Away From Burrows	1.31	0.70	9

* Means are not significantly different at 0.05 level (t = -.379).

SUMMARY OF FINDINGS

Observed shifts in activity appeared to be responses to changing environmental parameters during the summer. Daily temperature fluctuations affected the activity intensity the tortoises maintained in two peaks of activity: morning and afternoon, with more tortoises seen outside their burrows during the morning. Perennial grasses responded quickly to the July and August rains and tortoise foraging increased as plants became more succulent.

Tortoises preferred foraging on two species of perennial grasses, _Hilaria belangeri_ and _H. mutica_. Other forbs, grasses, and shrubs supplemented their diets. However, as the season progressed and all plants became more productive, tortoise diets became restricted and included fewer species.

Tortoises drank readily from artificial basins constructed near their burrows. Drinking decreased from June to July as the plants became more succulent, finally ceasing in August.

Burrows were used by all the tortoises in the enclosure. Tortoises usually returned to the same burrow daily. Several times during the summer, tortoises shifted their home burrow. Burrow improvement (digging) was observed throughout the summer. Burrow digging was of two types: clearing and scraping. Scraping was by a clawing action of the front limbs inside the burrow walls. Clearing was similar to sweeping with a broom and involved removing loose debris from the burrow area.

Tortoises spent the majority of time in or near to their home burrows. Trails produced by vegetation cropping were used as guides to reach other areas. Shady spots located throughout the enclosure were used as an alternative to burrow retreat when surface ambient temperatures were presumably prohibitive.

Tortoises typically head-bobbed and/or flattened upon approaching a burrow site. Head-bobbing was observed to occur more often at occupied burrows while flattening was seen more often at empty burrows.

Courtship activity occurred throughout the summer. Similar to that of other congeneric species, mating involved a short sequence of pre-copulatory activity. A male pursued females at and away from burrows for purposes of copulation, but the only complete matings (with thrusting) observed were at burrows.

The tortoises studied appeared to prefer a solitary existence except when courting and mating. When confronted with another individual, the usual response was mutual avoidance. Occasionally, two tortoises engaged in aggressive behavior such as shell-ramming and/or chasing, but this was restricted to burrow intrusion.

APPENDIX A

LIST OF PLANT SPECIES IDENTIFIED IN THE TORTOISE ENCLOSURE, SUMMER OF 1977

Starred species contributed 0.1% or more to standing crop biomass measurements--see Appendix B.

Grasses

Andropogon barbinodis
Aristida adscensionis
A. bigelovii
A. tagetinus
A. ternipes

Bouteloua chondrosioides
*B. curtipendula
*B. eriopoda
*B. gracilis
*B. hirsuta

B. radicosa
Chloris virgata
Eragrostis lehmanniana
Eriochloa lemmoni
*Hilaria belangeri

*H. mutica
Muhlenbergia repens
*Panicum obtusum
*Sporobolus wrightii

Trees and Shrubs

Agave palmeri
Baccharis pteronioides
Ephedra trifurca
Haplopappus gracilis
H. spinulosus

H. tenuisectus
Prosopis juliflora

Forbs

Aster tagetinus
Astragalus bigelovii
Cassia leptadenia
Croton corymbulosus
Dalea nana

*Desmanthus cooleyi
Dichelostemma pulchellum
*Euphorbia albomarginata
E. hyssopifolia
Evolvulus arizonicus

Gomphrena nitida
Jatropha macrorhiza
Melampodium longicorne
Perezia nana
Portulaca retusa

P. suffrutescans
Salsola kali
Salvia subincisa
Sida procumbens
Solanum eleagnifolium

Sphaeralcea angustifolia
*Viguiera annua

Sedges

Cyperus rusbyi

APPENDIX B

STANDING CROP BIOMASS OF DIFFERENT PLANT SPECIES IN THE TORTOISE ENCLOSURE, SUMMER OF 1977

Transect						Species							Totals
	Bocu	Boer	Bogr	Bohi	Deco	Eual	Hibe	Himu	Paob	Spwr	Vian	Misc*	
26	48			16	tr		75				tr	39	181
25	1				2		133						136
24				13			172				2	18	205
23				4	tr	tr	258					1	263
22	416											3	419
21	149											1	150
20	40	86	2		tr		47					7	182
19					5		332						337
18	54						190						244
17	2						353						355
6								21			7	3	31
5						28		401				3	432
4	24							355			2		381
1	462											1	463
2	11				6		181						198
3				25			93					91	209
9								403					403
10	2							416	30	233		15	696
11	5				4			213					222
12	1					17		244			11	10	283
13	56							414					470
14			710									3	713
8								445					445
7								421			1		422
16								644				2	646
15								969					969
Totals	1271	86	712	58	17	45	1834	4946	30	233	23	197	9455
Percent Contributed to Total	13.4	0.9	7.5	0.6	0.2	0.5	19.4	52.3	0.3	2.5	0.2	2.2	

Legend

* No single species in the " Misc " category contributed more than 0.1% of the total biomass measurements.

Bocu- *Bouteloua curtipendula*
Boer- *B. eriopoda*
Bogr- *B. gracilis*
Bohi- *B. hirsuta*
Deco- *Desmanthus cooleyi*
Eual- *Euphorbia albomarginata*
Hibe- *Hilaria belangeri*
Himu- *H. mutica*
Paob- *Panicum obtusum*
Spwr- *Sporobolus wrightii*
Vian- *Viguiera annua*

APPENDIX C

POINT-PLOT DATA FOR FOUR DIFFERENT VEGETATIONAL AREAS IN THE ENCLOSURE, SUMMER OF 1977

	Areas			
Species*	1	2	3	4
Bare Ground	10.3	26.9	6.1	5.2
Rock/Litter	6.0	28.0	13.6	24.2
Anba		0.7	2.3	
Arbe				0.1
Arta			0.3	0.7
Arte		0.1	1.0	0.1
Boch		3.0	5.1	3.6
Bocu	0.1	9.5	22.6	3.5
Boer		0.2		
Bogr	0.4	0.2	3.3	
Bohi		1.5	5.1	3.6
Cale			0.1	
Crco		0.3		
Deco	0.5	1.4	0.4	3.2
Eual	0.1		0.4	0.1
Euhy	0.1			
Hibe		8.9	11.1	53.5
Himu	82.0	16.0	23.7	2.1
Mure			0.6	
Paob	0.1	0.8	0.2	0.5
Pena		0.2	0.2	
Prju		1.6		
Span			0.5	
Spwr	0.4		1.0	
Vian		0.4	2.0	0.2

* The code designations of all plant species used are listed in Appendix D. Five different vegetational types are described in the text and delineated in Figure 9; only 4 of these appear in the above data; the decision to identify the 5th type as distinctive was made after this data had been collected. Area 1--*Hilaria mutica* zone; Area 2--Heterogeneous zone with *H. belangeri*, *H. mutica*, and *Bouteloua curtipendula*; Area 3--*B. curtipendula* zone; and Area 4--*H. belangeri* zone.

APPENDIX D

CODE DESIGNATIONS OF PLANT SPECIES RECORDED AT THE RESEARCH RANCH STUDY PLOT

Scientific Name	Species Code	Scientific Name	Species Code
Andropogon barbinodis	Anba	*Gomphrena nitida*	Goni
Aristida adscensionis	Arad	*Haplopappus gracilis*	Hagr
A. bigelovii	Arbi	*H. spinulosus*	Hasp
A. tagetinus	Arta	*H. tenuisectus*	Hate
A. ternipes	Arte	*Hilaria belangeri*	Hibe
Baccharis pteronioides	Bapt	*H. mutica*	Himu
Bouteloua chondrosioides	Boch	*Jatropha macrorhiza*	Jama
B. curtipendula	Bocu	*Melampodium longicorne*	Melo
B. eriopoda	Boer	*Muhlenbergia repens*	Mure
B. gracilis	Bogr	*Panicum obtusum*	Paob
B. hirsuta	Bohi	*Perezia nana*	Pena
B. radicosa	Bora	*Portulaca suffrutescens*	Posu
Cassia leptadenia	Cale	*Prosopis juliflora*	Prju
Chloris virgata	Chvi	*Salsola kali*	Saka
Croton corymbulosus	Crco	*Salvia subincisa*	Sasu
Cyperus rusbyi	Cyru	*Sida procumbens*	Sipr
Dalea nana	Dana	*Solanum eleagnifolium*	Soel
Desmanthus cooleyi	Deco	*Sphaeralcea angustifolia*	Span
Dichelostemma pulchellum	Dipu	*Sporobolus wrightii*	Spwr
Ephedra trifurca	Eptr	*Viguiera annua*	Vian
Eragrostis lehmanniana	Erle		
Eriochloa lemmoni	Erle		
Euphorbia albomarginata	Eual		
E. hyssopifolia	Euhy		
Evolvulus arizonicus	Evar		

APPENDIX E

PHENOLOGIC SUMMARY

Species	Floral Development (Week No. 1 2 3 4 5 6 7 8 9 10)	Stem Elongation (Week No. 1 2 3 4 5 6 7 8 9 10)	Leaf Death (Week No. 1 2 3 4 5 6 7 8 9 10)	Leaf Development (Week No. 1 2 3 4 5 6 7 8 9 10)
Anba	1 1 5 - 0 0 0 0 0 0	1 1 0 - 1 1 1 1 3 3	0 0 0 - 0 0 0 0 0 0	1 2 0 - 1 3 3 3 3 3
Arad	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -
Arbi	4 4 5 - - 1 - - 5 5	3 3 3 - - 2 - - 3 3	2 2 - - - 0 - - 2 2	3 3 3 - - 3 - - 3 3
Arta	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -
Arte	- - - - 0 - - - 3 4	- - - - 1 - - - 3 4	- - - - 0 - - - 0 0	- - - - 1 - - - 3 3
Bapt	4 3 3 3 3 3 4 1 5 5	2 3 3 3 3 3 3 3 3 3	0 0 0 1 0 1 2 1 1 1	3 - 1 3 - 3 3 3 3 3
Boch	0 - - - - - - - 1 4	1 - - - - - - - 2 3	0 - - - - - - - 0 0	0 - - - 0 - - - 3 3
Bocu	0 0 0 - 0 0 0 1 1 3	1 2 0 - 1 1 2 2 3 3	0 0 0 - 0 0 0 0 0 0	0 0 1 - 1 2 3 3 3 3
Boer	- 0 0 - 0 0 0 0 - -	- 2 1 - 1 0 1 1 - -	- 0 0 - 0 0 0 0 - -	- 1 0 - 1 2 3 3 - -
Bogr	0 0 0 - 0 0 0 0 1 -	1 1 0 - 1 1 2 2 2 -	0 0 0 - 0 0 0 0 0 -	0 1 0 - 1 2 3 3 3 -
Bohi	0 0 0 0 0 0 0 1 1 4	1 1 0 1 1 1 2 2 1 2	0 0 0 0 0 - 0 0 0 0	0 1 0 0 1 2 3 3 3 3
Bora	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -
Cale	- - - - 2 - - - 0 2	- - - - - - - - 2 2	- - - - - - - - - 0	- - - - - - - - - 3
Chvi	- - - - - - - - - -	- - - - - - - - - 3	- - - - - - - - - -	- - - - - - - - - -
Crco	- - - - - - 0 2 2 1	- - - - - - 2 2 2 2	- - - - - - 0 0 0 0	- - - - 3 - 3 3 3 3
Cyru	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -
Dana	4 4 4 4 - - - - - 3	2 2 3 3 - - - - - 2	0 0 0 1 - - - - - 0	3 3 3 3 - - - - - 3
Deco	- - - - 0 - 3 3 3 3	- - - - - - 2 2 3 3	- - - - - 0 0 0 0 0	- - - - - - 3 3 3 3
Dipu	4 - - - - - - - - -	3 - - - - - - - - -	2 - - - - - - - - -	3 - - - - - - - - -
Eptr	- - 0 0 0 0 0 0 0 0	- - 3 3 3 3 3 3 3 3	- - 0 1 0 0 0 0 0 0	- - 2 3 3 3 3 3 3 3
Erle	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -
Erle	- 0 - - - - - - - 4	- 1 - - - - - - - 2	- 1 - - - - - - - 0	- 1 - - - - - - - 3
Eual	4 4 4 4 5 5 3 4 5 4	2 2 1 2 3 2 2 2 3 3	1 1 1 1 1 0 0 1 1 0	3 3 3 3 3 3 3 3 3 3
Euhy	- - - - 0 - - - - -	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -
Evar	- - - - 2 4 3 4 4 4	- - - - 2 3 2 3 3 3	- - - - 0 0 0 0 0 0	- - - - 3 3 3 3 3 3
Goni	0 - - - - - - - - -	1 - - - - - - - - -	0 - - - - - - - - -	1 - - - - - - - - -
Hagr	3 - 1 - - - - - - -	2 - 2 - - - - - - -	0 - 0 - - - - - - -	3 - 3 - - - - - - -
Hasp	4 4 4 - 3 5 5 - 5 2	2 3 2 - 2 3 2 - 3 2	0 0 1 - 0 1 1 - 2 0	3 3 3 - 3 3 3 - 3 3
Hate	0 - - - 0 0 - 0 - 1	1 - - - 2 2 - 3 - 2	0 - - - 0 0 - 0 - 0	3 - - - - 3 - 3 - 3
Hibe	0 0 0 0 0 0 0 1 4 4	1 1 1 1 1 1 2 2 3 3	0 0 0 0 0 0 0 0 0 0	1 1 1 1 1 3 3 3 3 3
Himu	0 0 0 0 1 1 3 3 4 4	1 1 1 1 2 2 2 2 3 3	0 0 0 0 0 0 0 0 0 0	1 1 1 1 2 3 3 3 3 3
Jama	- - - - 2 3 3 4 4 4	- - - - 2 2 2 3 3 3	- - - - 0 0 0 0 0 1	- - - - - 3 3 3 3 3
Melo	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -
Mure	0 1 0 0 5 - 5 0 5 0	0 1 1 1 3 - 1 1 1 2	0 0 0 0 0 - 0 1 0 0	1 1 1 0 2 - 3 3 3 3
Paob	0 0 0 0 0 0 - 0 - -	1 1 1 1 1 1 - 1 - -	0 0 0 0 0 0 - 0 - -	0 1 1 1 1 2 - 3 - -
Pena	2 3 3 5 2 - 4 1 5 1	2 2 3 3 3 - 3 3 3 3	0 1 1 1 1 - 1 0 1 1	3 3 3 3 3 - 3 3 3 3
Posu	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -
Prju	1 1 1 0 0 0 1 2 1 1	3 3 3 3 3 3 3 3 3 3	0 0 0 0 0 0 0 0 0 0	3 3 3 3 3 3 3 3 3 3
Saka	5 4 5 5 5 5 5 5 5 5	3 3 3 3 3 3 3 3 3 3	1 0 1 2 3 1 2 1 2 3	3 3 3 3 3 3 3 3 3 3
Sasu	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -
Sipr	3 4 - - - 0 1 1 1 2	2 2 - - - 1 2 2 2 2	1 1 - - - 0 0 0 0 0	3 3 - - - 3 3 3 3 3
Soel	3 3 3 4 3 3 4 3 3 4	2 2 3 3 3 2 3 2 3 3	0 0 1 1 1 1 0 0 0 0	3 3 3 3 3 3 3 3 3 3
Span	4 3 5 5 5 5 1 2 3 4	3 3 3 3 3 3 3 3 3 3	1 1 1 2 2 1 1 0 0 0	3 3 3 3 3 3 3 3 3 3
Spwr	0 0 0 0 0 0 0 0 3 4	2 1 1 0 1 1 1 2 3 3	0 0 0 0 0 0 0 0 0 0	1 - 1 1 1 3 2 3 3 3
Vian	- - - 0 0 0 - 0 0 0	- - - 2 2 3 - 2 3 3	- - - 0 0 0 - 0 0 0	- - - 3 3 3 - 3 3 3

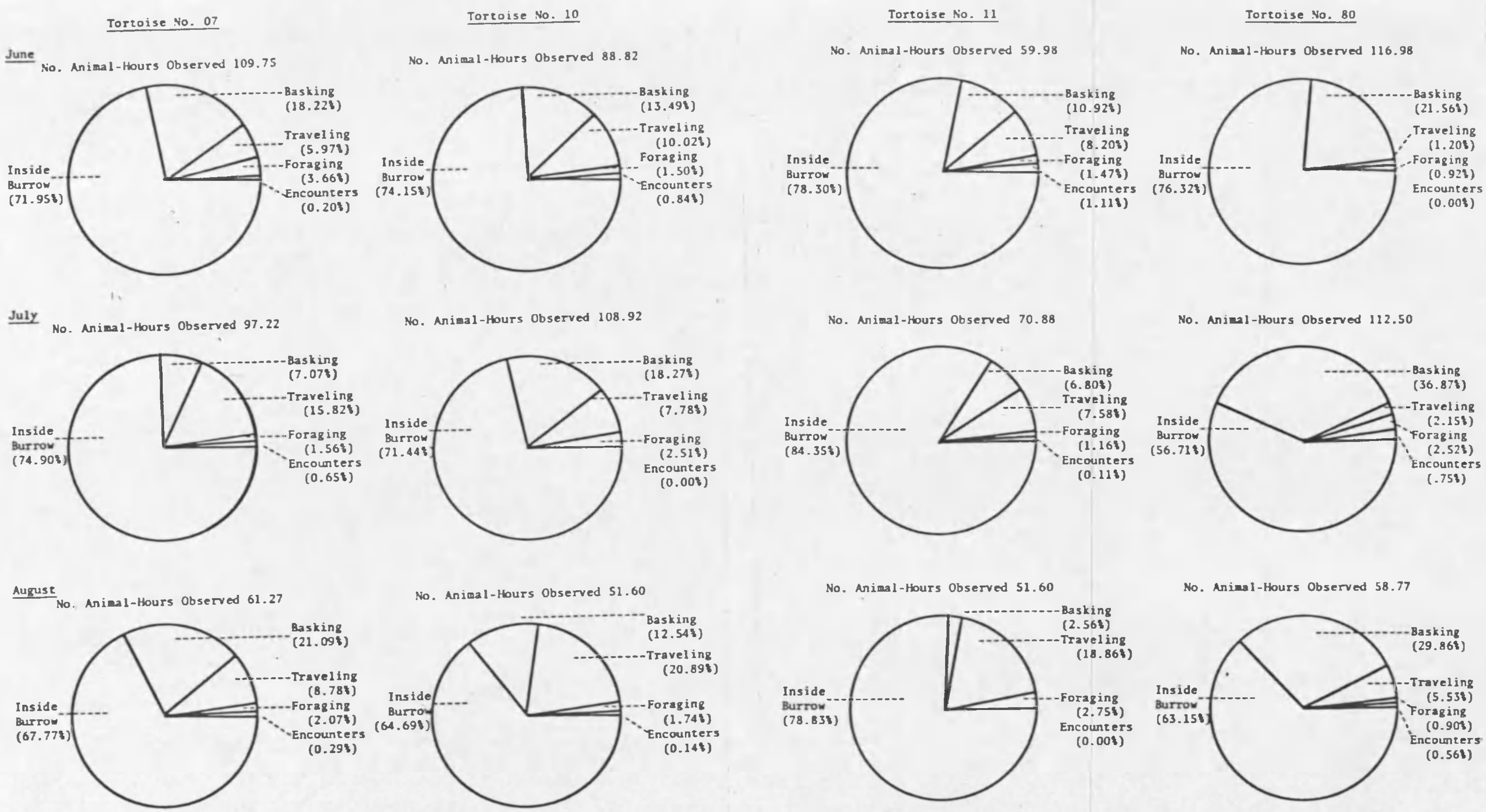
Weeks 1-4 were in June; weeks 5-8 were in July; and weeks 9 & 10 were in August, 1977.

Numerical scoring of each category:

Code	Identification	Code	Identification	Code	Identification	Code	Identification
0	none	0	none	0	none	0	none
1	immature buds	1	sparse	1	light	1	initiating
2	opening buds	2	moderate	2	moderate	2	immature
3	partial bloom	3	full	3	heavy	3	mature
4	full bloom	-	no observation	4	complete	-	no observation
5	buds dead			-	no observation		
-	no observation						

APPENDIX F

ACTIVITY BUDGETS OF INDIVIDUAL FEMALES, NUMBERS 07, 10, 11, AND 80, DURING JUNE, JULY, AND AUGUST, 1977


Tortoise No. 07
Tortoise No. 10
Tortoise No. 11
Tortoise No. 80
June
No. Animal-Hours Observed 109.75
Basking (18.22%)
Traveling (5.97%)
Foraging (3.66%)
Encounters (0.20%)
Inside Burrow (71.95%)
No. Animal-Hours Observed 88.82
Basking (13.49%)
Traveling (10.02%)
Foraging (1.50%)
Encounters (0.84%)
Inside Burrow (74.15%)
No. Animal-Hours Observed 59.98
Basking (10.92%)
Traveling (8.20%)
Foraging (1.47%)
Encounters (1.11%)
Inside Burrow (78.30%)
No. Animal-Hours Observed 116.98
Basking (21.56%)
Traveling (1.20%)
Foraging (0.92%)
Encounters (0.00%)
Inside Burrow (76.32%)
July
No. Animal-Hours Observed 97.22
Basking (7.07%)
Traveling (15.82%)
Foraging (1.56%)
Encounters (0.65%)
Inside Burrow (74.90%)
No. Animal-Hours Observed 108.92
Basking (18.27%)
Traveling (7.78%)
Foraging (2.51%)
Encounters (0.00%)
Inside Burrow (71.44%)
No. Animal-Hours Observed 70.88
Basking (6.80%)
Traveling (7.58%)
Foraging (1.16%)
Encounters (0.11%)
Inside Burrow (84.35%)
No. Animal-Hours Observed 112.50
Basking (36.87%)
Traveling (2.15%)
Foraging (2.52%)
Encounters (.75%)
Inside Burrow (56.71%)
August
No. Animal-Hours Observed 61.27
Basking (21.09%)
Traveling (8.78%)
Foraging (2.07%)
Encounters (0.29%)
Inside Burrow (67.77%)
No. Animal-Hours Observed 51.60
Basking (12.54%)
Traveling (20.89%)
Foraging (1.74%)
Encounters (0.14%)
Inside Burrow (64.69%)
No. Animal-Hours Observed 51.60
Basking (2.56%)
Traveling (18.86%)
Foraging (2.75%)
Encounters (0.00%)
Inside Burrow (78.83%)
No. Animal-Hours Observed 58.77
Basking (29.86%)
Traveling (5.53%)
Foraging (0.90%)
Encounters (0.56%)
Inside Burrow (63.15%)

APPENDIX G

SUMMARY OF OBSERVED TORTOISE ACTIVITY AT BURROWS

Tortoise Number	Number of Retreats to a Burrow to Shade		Total No. Retreats, Burrow & Shade	Number of Times Tortoise Returns to Same/Different Burrow		No. Times Tortoise Observed Digging at Retreat Site	Home* Burrow
	Burrow	Shade		Same	Different		
01	83	2	85	23	6	9	B & C
02	6	9	15	0	0	-	G
07	57	22	79	15	9	22	A
08	9	9	18	1	0	5	B & G
09	19	-	19	1	0	-	N
10	67	8	75	8	11	22	A & C
11	35	2	37	1	8	4	?
20	3	10	13	1	0	-	N
80	95	-	95	19	0	2	H
90	-	14	14	-	-	-	G & L13
Totals	374	76	450	69	34	64	

* Figure 2, page 12 shows locations of burrows.

APPENDIX H

DIET SELECTIVITY OF TORTOISES

Tortoise Number	No. of Feeding Observations			Chi Square	P Value*
	Hibe	Himu	Others		
01	10	29	8	21.648	< 0.001
07	17	11	15	8.118	< 0.25
10	12	24	6	16.536	< 0.001
11	15	4	6	4.990	< 0.10
80	14	10	9	34.488	< 0.001

* P value indicates degree of significance between observed and expected diets. Hibe, Hilaria belangeri; Himu, H. mutica; and others, all other plant species eaten by tortoises.

APPENDIX I

APPROACH BEHAVIORS AT OCCUPIED AND EMPTY BURROWS

Condition	Head-Bob	Flatten	Both	Neither	Totals
Empty Burrows	10	35	12	52	109
Occupied Burrows	25	7	3	26	61
Totals	35	42	15	78	170

$\chi^2 = 27.82$ DF = 3 $p < 0.001$

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