

HOME RANGE AND MOVEMENT PATTERNS OF THE BOLSON TORTOISE, *GOPHERUS FLAVOMARGINATUS*

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ABSTRACT

A colony of *G. flavomarginatus* was studied during two consecutive summers at the Mapimi Biosphere Reserve, Durango, México. Movements and behavior of individuals living in a 77 ha area were recorded by means of radiotelemetry. Objectives of this study were to determine home range and movement patterns, and to evaluate these using probabilistic (Jennrich and Turner, 1969; Calhoun and Casby, 1958; Koepl *et al*, 1975, and a variant of this model named 68% bivariant ellipse) and non-probabilistic models (Harvey and Barbour, 1965 and minimum convex polygon). According to direct observation of movements in the field, home ranges are not overestimated only by the minimum modified polygon and the 68% bivariant ellipse, respectively: 3.1 and 4.1 ha for adult males; 2.5 and 3.1 ha for adult females, and 0.4 and 1.2 ha for immature individuals. Correlation values (r) of carapace length vs. home range area and several motility measures vary from 0.54 to 0.85. Sixty four percent of tortoises in the colony use one or two burrows, and 36% use four to eight burrows. An analysis by the Poisson distribution showed aggregation for both burrow dispersion ($t = 3.66$ $p < 0.05$) and activity center ($t = 5.20$ $p < 0.05$) patterns. These data suggest definite ecological and behavioral relationships within the context of a social hierarchy system.

RESUMEN

Durante dos veranos sucesivos se estudió una colonia de *G. flavomarginatus* en la Reserva de la Biosfera de Mapimí, Dgo. Por

medio de radiotelemetría se registraron los movimientos y comportamiento de 31 individuos (juveniles, subadultos y adultos) establecidos en una superficie de 77 ha. Los objetivos de este estudio fueron determinar el ámbito hogareño de esta especie y su patrón de uso, y evaluar el área de actividad por medio de modelos probabilísticos y no probabilísticos. Los modelos probabilísticos empleados fueron el índice de Jenrich y Turner (1969), la función de probabilidad de densidad (Calhoun y Casby, 1958), el modelo bivalente de Koepl *et al* (1975) y una variación de este modelo denominada elipse bivalente del 68%. Los no probabilísticos fueron el polígono mínimo convexo y el modelo de área mínima modificada (Harvey y Barbour, 1965). Con base en observaciones continuas de los desplazamientos de los individuos sólo los modelos del polígono mínimo modificado y la elipse bivalente del 68% arrojan valores que no sobreestiman la superficie del ámbito hogareño, respectivamente: 3.1 y 4.1 ha para los machos adultos, 2.5 y 3.1 para las hembras adultas y 0.4 y 1.2 ha para los individuos sexualmente inmaduros. El análisis de la dispersión de las madrigueras y de los centros de actividad de las tortugas muestran un alto índice de agregación ($t = 3.66$ y 5.20 , respectivamente, $p < 0.05$). Los valores de correlación (r) entre longitud de caparazón, área de actividad y diversas medidas de desplazamiento varían entre 0.54 y 0.85. El 64% de las tortugas de la colonia usan de 1 a 2 madrigueras y el 36% ocupan de 4 a 8 madrigueras. Esta variación en el grado de correlación, junto con el patrón de uso de madrigueras y la variación en el solapamiento de los ámbitos hogareños de adultos y juveniles implican relaciones ecológicas y conductuales marcadas y una organización social de jerarquías, las cuales pueden verse determinadas de manera importante por requerimientos metabólicos y la concentración local del forraje. Todos estos factores junto con el alto grado de movilidad mostrado por individuos inmaduros posiblemente contribuyen al remplazo de individuos dentro de una misma colonia y a la formación y expansión de nuevos núcleos.

INTRODUCTION

The Bolson Tortoise, *G. flavomarginatus*, is the least known species of the North American genus *Gopherus* of land tortoises. Knowledge of Bolson Tortoise home ranges is comprised within a broader study of the autoecology of this endangered species. The main goal is to gather abundant and quantifiable information about life history that will eventually lead to the implementation of a coherent plan for protection and management.

The data here reported complement aspects about the species status and ecology published elsewhere (Morafka et al, 1981; Morafka, 1982) and specifically contribute to clarify matters related to the amount of home range required to accomplish portions of the life cycle as well as the relationship of area to body size, sex and social system.

MATERIALS AND METHODS

The study took place in the Mapimí Biosphere Reserve (40 km NE of Ceballos, Durango, Mexico, located between the parallels 26°29' and 26°52' and the meridians 103°58' and 103°32') between 1979 and 1981, with intensive observations concentrated during the time of maximum tortoise activity (summer). Observations were made during July and August, 1979; March, April, May, July, August and November, 1980, and July, 1981.

The study area is located 600 m north of the base of a low, 2.5 km long hill. The slope varies between 1° and 3°. The areas of minor slope, which comprise the majority of the study area and contain the greatest tortoise density, are located in playas with vegetation dominated by *Hilaria mutica*, *Larrea divaricata* and *Prosopis juliflora*. Between these vegetated areas are areas lacking perennial vegetation.

A quadrat of 77 ha (1 100 m X 700 m) was established and marked with banded stakes at 100 m intervals. Ninety percent of a colony of *G. flavomarginatus* was included in the quadrat.

Each tortoise captured was marked with a number painted on both sides of the shell for long-distance identification and by filing the marginal scales. Tortoises were measured in length by a straight line from the top of the nuchal plate to the tip of the pygal plate. The sex of animals was estimated by evaluating morphological characteristics, observing behavior and was later confirmed by cloacal palpation and otoscopic examination. All these methods were of use in sex determination only on adults and subadults; we were not able to determine sex in juveniles using these methods.

Radio telemetry was used to study movements and behavior of tortoises. Following anesthesia (0.33 cc Ketaset/kg total body weight, axillary subcutaneous injection) thermal transmitters (Minimitter Co., Model L) were introduced orally into the digestive tract of some individuals. Directional, long-distance transmitters (AVM Co., Model SM 1) as well as photosensitive non-crystal controlled transmitters were cemented to the marginal plates with epoxy cement and covered with the same material. Once installed, recordings of tortoise movements were made in two ways: a) continuous recordings of thermal transmitter-equipped animals for 13 hours daily (0700-2 000) and b) time sampling of the tortoise population by locating the photo transmitters and long-distance transmitter-equipped animals an average of 10 times daily and recording the routes followed by the tortoises until the tortoise discovered the observer or ceased activity. Precautions were taken in order to reduce the observer's influence on tortoise behavior.

The photo transmitters were used principally for continuous observation. A sudden increase in the click rate (pulse rate) of the radio signal permitted knowledge of the exact instant of emergence of the tortoise even though the observation post was out of sight of the tortoise. Also, wooden sticks 10 cm long were placed in the majority of burrow entrances. These sticks could be observed from a distance without interfering with tortoise activity by approaching too closely and, upon being knocked down by an entering or leaving tortoise, allowed inferences about the activity and whereabouts of the occupant tortoise. In this manner, estimates of activity times could be obtained for those intervals when no direct observations or tracking occurred. Once located, tortoises were followed slowly at a distance which appeared to not interfere with their behavior. The number of continuous observations on tortoises was 150 and the number of activity points was 2 500.

Movements and positions were recorded directly by measuring in paces the distances covered by individuals and situating by triangulation their locations relative to the quadrat stakes. Orientations were measured with a Brunton compass. These movements were transferred to a map of scale 1:500 on which the moved distances were also measured using a planimeter. The difference between the than 5%. The map-measured distances were then used to normalize all

field-measured distances and those measured from the map were less calculations. We believe that this method gives results which reliably reflect the actual distances covered by tortoises in the field.

To calculate areas of tortoise activity both probabilistic and non-probabilistic methods were employed. The probabilistic methods included: the density probability function (Calhoun and Casby, 1958), the index of Jennrich and Turner (1969), the bivariate model of Koepl et al. (1975), and a variation of this last model which we call 68% bivariate ellipse. The non-probabilistic methods used were the minimum convex polygon and the modified minimum polygon (Harvey and Barbour, 1975). In order to apply these methods, the maps of tortoise displacement were converted to a pattern of random points transformed to a coordinate system in which the center of activity (Hayne, 1949) was calculated as well as the median radius of activity for each individual tortoise. The patterns of random points were used to construct the polygons for the non-probabilistic methods.

In order to arrive at the shape of the distribution of the random points (circular or elliptical) required for the application of each of the probabilistic methods, the data were subjected to a circularity test by means of a principal axes method and calculation of the confidence ellipse (Sokal and Rohlf, 1969). The correspondence to a normal bivariate distribution was tested by calculating the frequency of random points in various intervals of the confidence ellipse ($p = 0.01, 0.05, 0.10, 0.25, 0.50$ and 0.75) by means of the direct search method of Hooke and Jeeves (Himmelblau, 1972) and measuring the goodness of fit for the null hypothesis (= normal bivariate distribution) and alternative hypothesis (= distribution different from the normal bivariate).

By means of one-way ANOVA the differences in area of activity of males, females and juveniles, calculated by the aforementioned methods, were tested. Two-way ANOVA was used to analyze the differences in ambient temperatures and precipitation between two periods with different climatic conditions in the summer of 1980. The Student's test was used to analyze differences between sexes and ages in the following comparisons: median and maximum distance moved in two periods of differing climate (within and between periods), radius of activity, and percentage of overlap of areas of activity.

RESULTS

The results presented here correspond to the time of maximum activity: July through mid-September. Comparable data were not obtained for the spring and autumn months but it was possible to determine through radiotelemetry that in these non-summer activity periods the level of activity diminishes an average of 80% and the areas of activity comprise between 5 and 10% of those occupied during the summer. *Gopherus flavomarginatus* hibernates from the end of November until the end of February.

The colony, defined by means of population sampling, is composed of a nuclear area of greater burrow density and individual density (3 tortoise/ha) and a peripheral area with individual density decreasing to a minimum of 1 tortoise/8-10 ha. All individuals living in the area were marked, and unmarked tortoises have not been captured or observed for three years. The absence of unmarked individuals is an additional criterion we use for delimiting the tortoise colony.

Movements

The daily movement of adult tortoises follow typical elliptical or triangular patterns (Fig. 1). These patterns are principally associated with foraging movements and with exploratory surveys. In the case of adult males, trips are related to courtship and searching for females following a linear movement pattern between visited burrows.

The tortoises can also follow paths in the most dense vegetation, generally in patches of *H. mutica*, and do so in very localized areas for periods of up to 25 consecutive days. This type of movement is more marked in females than males.

During the spring and fall, the movements of juveniles (80-180 CL) are practically null. Juvenile movements are essentially concentrated in the time of maximum adult activity, whereas adults do have activity in other seasons.



Figure 1
Typical movement pattern of *G. flavomarginatus* (162 mm CL)
Circles represent random points on actual motility paths.
Dark semicircles represent burrows

The distances covered by tortoises were analyzed in two ways: 1) considering the global movements occurring during the summers of the study periods and 2) comparing movements in

a dry period and a wet period within the summer of 1980 (significantly different, $p < 0.01$).

The results of the first analysis are shown in Table 1. The adult males exhibited a statistically greater mean daily movement (265.2 m) than both adult females and juveniles ($p < 0.05$). The daily distances moved by females and juveniles was similar (164.9 m versus 155.7 m) and insignificant statistically. The maximum displacements of juveniles were less than those of adults of both sexes, associated fundamentally with burrow changes and the search for new excavation sites. In the adults, these maximum displacements are associated with reproductive activities.

Comparing the distances covered in dry and wet periods, it is observed that during the dry period the adult males and the juveniles move greater distances than the adult females (Table 2). The difference between the distances moved by the adults of both sexes and that covered by juveniles is not statistically significant ($p > 0.05$), but that between the distances moved of adult males and females is ($p < 0.01$). In the course of the wet season, females as well as males increase the daily average distance covered in comparison with the dry season ($p < 0.05$), and adults of both sexes move greater distances than juveniles ($p < 0.05$) in comparison with the dry season.

Table 1.
Mean and maximum distance traveled by day (m) during the summer

	Mean distance				Maximum distance			
	N	\bar{X}	S.D.	Range	N	\bar{X}	S.D.	Range
♂♂	37	265.2	187.1	30-910	5	505.4	271.5	204-910
♀♀	87	164.9	169.6	14-988	6	559.5	243.8	250-988
JUV	60	155.7	107.9	10-460	11	256.1	105.5	95-460

Any pair of values joined by the same line are not significantly different at the 0.05 level

Table 2.
Mean distance/day (m) traveled in two periods with different climatic conditions during the summer

	Dry period				Wet period			
	N	\bar{X}	S.D.	Range	N	\bar{X}	S.D.	Range
♂♂	16	171.0 ¹	152.2	5-470	22	318.9 ^{2,3}	20.2	33-910
♀♀	42	86.9	84.9	4-441	36	229.7 ^{2,3}	194.4	15-759
JUV	25	114.8	82.4	100-289	19	195.8 ³	119.7	10-460

¹Significantly larger than female mean within the same period ($p < 0.01$)

²Significantly larger than juvenile mean within the same period ($p < 0.05$)

³Significantly larger between periods ($p < 0.05$)

The analysis of the degree of correlation between shell length (CL) by sex or age class and various measures of displacement appears in Table 3. In the case of females, high negative correlations were obtained between CL and average distance moved per day ($r = -0.8767$) as well as average distance between burrows

Table 3.
Correlations for different motility measures with carapace length (CL)

	Activity radius vs. CL	Mean distance traveled by day vs. CL	Mean distance between burrows vs. CL
♂♂	0.6489	0.3211	0.6285
♀♀	-0.4473	-0.8767*	-0.7758*
JUV	0.6335	0.7591*	0.1155

*Significant at the 0.05 level

($r = -0.7758$). A high positive correlation between CL and the average daily distance moved by juveniles was obtained ($r = 0.7591$).

Table 4 presents the radii of activity calculated for adults and juveniles. The same tendencies are demonstrated as the other measures considered, that is, greatest in adult males and females and least in juveniles. Activity radius did not show correlation with CL in any case, unlike the other measures of displacement.

Table 4.
Activity radii (m)

	N	\bar{X}	S.D.	Range
♂ ♂	211	94.1 ¹	61.3	(45 -193)
♀ ♀	289	92.5 ²	28.7	(52 -129)
JUV	209	47.4	20.9	(17 - 73)

¹ Significantly larger than juvenile mean ($t = 2.6$, $p < 0.05$)

² Significantly larger than juvenile mean ($t = 3.5$, $p < 0.05$)

Movements outside the colony

Extensive displacements of some individuals were registered which included areas distant from the region in which they commonly concentrated the majority of their activity. This type of movement was exhibited by 14% of the adults and 18% of the juveniles captured within the limits of the colony and occupying one or two burrows constantly for two years. These individuals were not encountered or recaptured in the colony area after 11 months. The displacements of these individuals are characterized as being erratic at first and within an area of 0.2 to 0.7 ha and, later, consisted of large, almost straight, advances generally following the same direction. The following displacements were registered: (distance, CL and sex or age class, period in which the movement occurred) 1 500 m-136 mm juvenile/13 days; 4 000

m-149 mm juvenile/15 days; 4 500 m-248 mm (sex?)/29 days; 6 000 m-256 mm female/10 months.

Area of activity

A total of 20 tortoises (5 males, 6 females and 9 juveniles) out of 35 animals observed produced an adequate number of observations to calculate areas of activity.

The pattern of dispersion of the burrows and of the centers of activity was evaluated by the method of Poisson distribution. Both patterns are clumped ($t = 3.66$ for burrows, $t = 5.20$ for centers of activity, $p < 0.05$). The distribution of centers of activity is "tightly tied" to the distribution of the burrows and these in their turn are closely related to areas with high density of *Hilaria mutica*.

Table 5 shows areas of activity calculated by the different methods. The areas of smallest size resulted from using the minimum modified polygon method (Fig. 2) and the 68% bivariate ellipse (Fig. 3). In each case the results are different but all the methods produce the same relation between areas: male areas $>$ female areas $>$ juvenile areas. The differences between sexes or age classes are not statistically significant in any cases. Only in the average areas calculated by the minimum convex polygon method are the adults of both sexes significantly greater than those of the juveniles.

Males showed the greatest variability in the size of the area of activity. Considering all the methods, the largest male area is an average of 37 times greater than the smallest area. In contrast, the largest female area is only 7 times greater than the smallest female area and 28 times larger than the smallest juvenile area.

Upon applying the test of circularity to the distribution of the random points, it was found that only 37% of the tortoises exhibited a circular distribution in their movements. The remaining 63% present a component of the distribution, such that the method of density probability function, which assumes circularity in the distribution, is not completely applicable. For comparative purposes, Table 5 includes the values obtained by this method.

Table 5.
Mean home range (ha) as calculated through different models

	Minimum Convex Polygon		Minimum Modified Polygon (Harvey & Barbour, 1965)		Jennrich & Turner Index	
	\bar{X}	S.D.	\bar{X}	S.D.	\bar{X}	S.D.
♂♂	5.35 ¹	6.42	3.07	4.17	6.59	7.34
♀♀	4.72 ²	2.87	2.48 ³	1.95	5.91 ⁴	2.54
JUV	1.10	1.19	0.42	0.73	2.02	1.43
	Koepl et al Bivariant Model (1975)		68.27% Ellipse (This study)		Probability density function (Calhoun & Casby, 1959)	
	\bar{X}	S.D.	\bar{X}	S.D.	\bar{X}	S.D.
♂♂	11.20	13.71	4.13	5.14	19.90	30.50
♀♀	8.26	3.17	3.12	1.96	11.04	5.19
JUV	3.73	1.86	1.24	0.72	3.39	3.13

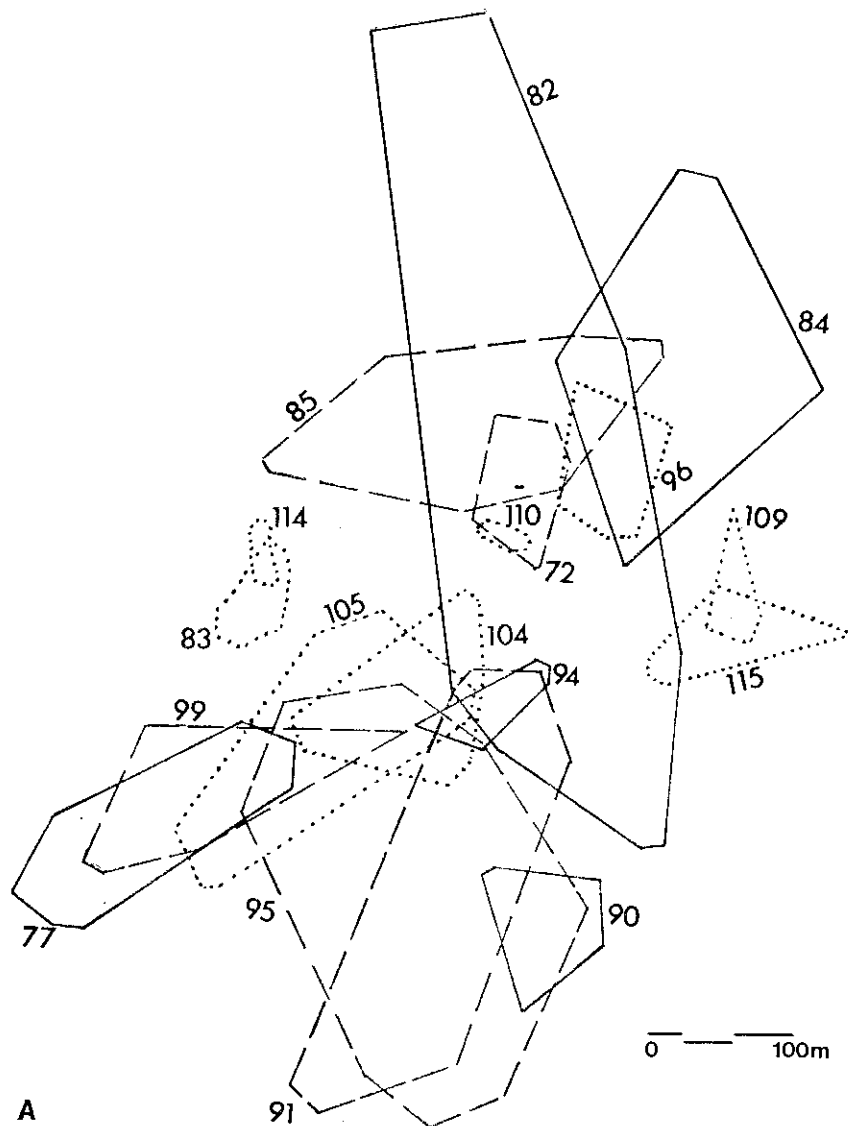
¹Significantly larger than juveniles ($F = 10.46$, $p < 0.01$)

²Significantly larger than juveniles ($F = 6.21$, $p < 0.05$)

³Significantly larger than juveniles ($F = 7.37$, $p < 0.05$)

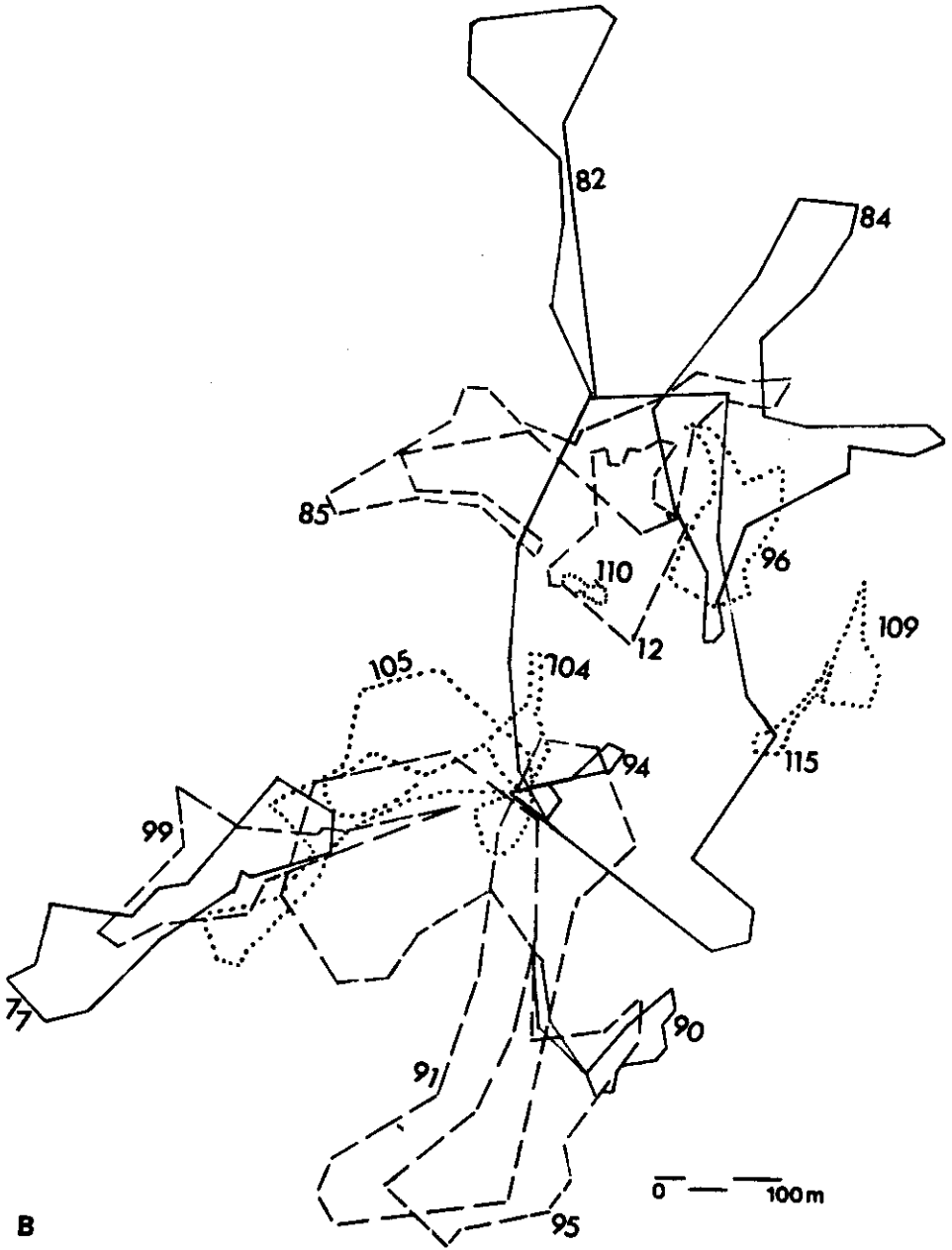
⁴Significantly larger than juveniles ($F = 6.53$, $p < 0.05$)

In the tortoises which exhibited circular distributions (37%), the activity area was calculated by the ellipsoidal methods and by that of density probability. There are no significant differences between these values so they are included in the calculation of the averages of the elliptical areas.



Figures 2 A/B

Home range of *G. flavomarginatus* calculated by two polygonal models:
 A) Minimum Convex Polygon, and B) Minimum Modified Polygon.
 Males in solid line, females in broken line and juveniles in dotted line.
 Each number represents one individual.



B

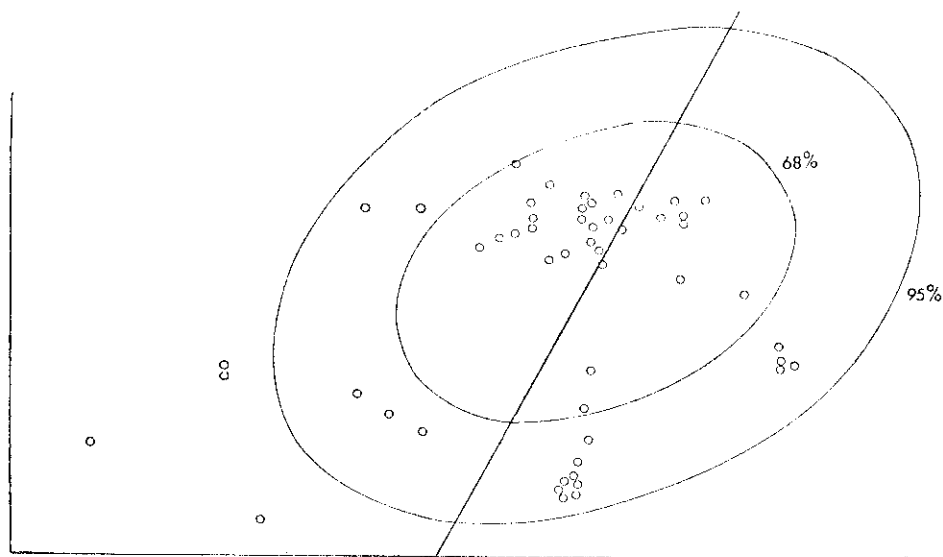


Figure 3
Home range of *G. flavomarginatus* calculated by 95 and 68% bivariate ellipses. Circles represent "recapture" random points delineated by real movement patterns. Axis represents principal component.

The test of fit to a normal bivariate distribution showed that 81% of the tortoises had this type of distribution.

Table 6 shows the correlations between CL and area of activity calculated by the different methods. The correlation of the different values of activity area with CL is moderate ($r = 0.5$) and there is no correlation with the areas calculated by the method of Koeppl and that of the 68% bivariate ellipse.

In the case of distance, there is a greater correlation between the maximum distance moved per day and CL ($r = 0.67$, $p < 0.01$) than in the average distance moved per day ($r = 0.44$, $p < 0.05$). Table 7 shows the correlations between the different methods of activity area estimation with the mean and maximum distance co-

Table 6.
Correlation coefficients (r) for linear regression of home range
calculated through different models vs. CL
(adults and juveniles combined)

Model	r	p
Minimum Convex Poligon	0.5639	< 0.05
Minimum Modified Poligon (Harvey & Barbour, 1965)	0.5360	< 0.05
Ellipse (Jennrich & Turner 1969)	0.5332	< 0.05
Ellipse (Koepl et al, 1975)	0.4298	> 0.05
68% Bivariant Ellipse (this study)	0.4307	> 0.05

Table 7.
Correlation coefficients for linear regressions of home range (calculated
through different models) vs. maximum and mean distance
traveled by day (adults and juveniles combined)

Model	Max. Dist./day	Mean Distance
Minumum Convex Poligon	0.8554, p < 0.01	0.7748, p < 0.01
Minimum Modified Poligon (Harvey and Barbour, 1965)	0.8554, p < 0.01	0.7279, p < 0.01
Ellipse (Jennrich & Turner, 1969)	0.8104, p < 0.01	0.8192, p < 0.01
Ellipse (Koepl et al, 1975)	0.7680, p < 0.01	0.8404, p < 0.01
68% Bivariant Ellipse (this study)	0.7813, p < 0.01	0.8334, p < 0.01

vered daily. In all cases the correlation is high ($r = 0.7279 - 0.8554$, $p < 0.01$).

The percentage intrasexual overlap of the adult areas and the overlap between juvenile areas calculated by the minimum

convex polygon and minimum modified polygon was calculated (Table 8). In agreement with our observations, the limits of the polygonal areas represent in the most objective manner the limits of real movements of individuals in comparison with the limits of the areas calculated by probabilistic methods. During spring and autumn overlap was not present existing spatial isolation between members of the colony.

If we consider the areas of the minimum modified polygon, the males overlap more between (31.7%) than the females (23.8%) and more than the juveniles (8.9%). However, the differences are not statistically significant.

The results obtained through minimum convex polygon show differences with those obtained by the minimum modified

Table 8.
Percent overlap of home range calculated by two models

Overlapping	Minimum Modified Polygon			
	N	\bar{X}	S.D.	Range %
♂♂	4	31.7	37.4	3.2-85.2
♀♀	6	25.8	18.2	2.3-53.7
JUV	4	8.9	7.9	1.6-20.2
	Minimum Convex Polygon			
	N	\bar{X}	S.D.	Range %
♂♂	4	26.3	33.9	2.0-76.2
♀♀	6	38.9	25.6	7.6-78.5
JUV	6	44.9 ¹	22.6	24.0-74.8

¹Significantly larger than juveniles calculated by the other model
 (t = 3.01, p < 0.05)

polygon, resulting in a reversal in the overlap; the females exhibit greater overlap than the males and the juveniles overlap more (44.9%) than the males (26.3%) or than the females (38.9%) although, again the values do not differ significantly.

Regardless of method, the only statistically significant differences occur in juvenile overlap value.

In agreement with the pattern of continuously observed actual movement, the percentages of overlap estimated by means of minimum modified polygon are representative of real overlap. The high overlap percentages of females and juveniles obtained by means of the minimum convex polygon involve areas in which never or rarely are movements or interactions of tortoises seen (Fig. 2). In the majority of cases these areas contain a high vegetation density which does not offer possibilities of locomotion nor other type of utilization.

Use of Burrows

Adult males occupy a greater number of burrows, on the average, than either adult females or juveniles (Table 9) which is related to the visits to other burrows by courting males in search of females. Young tortoises excavate their own burrows and exhibit very

Table 9.
Number of utilized burrows and mean distance between burrows

	Burrows			Distance between burrows		
	N	\bar{X}	Range	N	\bar{X}	S.D.
♂♂	6	3.5	(1-8)	15	146.0	60.9
♀♀	7	2.7	(1-4)	11	183.3*	92.
JUV	17	1.8	(1-3)	13	107.7	74.6

*Significantly larger than juvenile mean ($t = 2.2$, $p < 0.05$)

restricted movements. A tortoise of 54 mm CL (estimated age: 6 months) was found occupying an apparently self-excavated burrow. Tortoises up to 175 mm CL occupy only one burrow. Social interactions between juveniles, with the exception of one double burrow occupancy early in summer, were not observed.

The average distance between burrows (Table 9) is similar for those occupied by adults and juveniles; however, the mean distance between female burrows is significantly larger than that for juveniles (183.3 m vs 107.7 m).

Gopherus flavomarginatus exhibits adult and juvenile multiple burrow use. During the summer there is a maximum interchange of burrows; during the spring no burrow changes were registered and during the fall only two burrow changes, by a dominant male, were recorded.

Tortoises possess primary burrows in which they spend the majority of their time and these burrows are defended against intrusion by other tortoises. This burrow defense is common to both adults and juveniles. The maximum number of relocations (defined as entire nights passed in one burrow) is similar between males, females and juveniles (Table 10): 10, 12 and 9 respectively. Males exhibit a greater average number of relocations than do females or juveniles but

Table 10.
Burrow usage and relocations

	N	Relocations X±S.D. (Range)	% Burrow usage Primary (Range)	X±S.D. Secondary (Range)
♂♂	6	75.0±14.4 (61.5-93.1)	5.4±2.7 (3-10)	23.3 ±13.8 (6.9-38.5)
♀♀	7	72.8±10.9 (60.0-86.7)	4.2±3.9 (1-12)	25.5 ± 9.5 (13.3-40.0)
JUV	13	79.1±12.9 (65.0-97.0)	2.9±2.5 (1-9)	20.3 ±12.7 (3.0-35.0)

the differences are not statistically significant. Adults, as well as juveniles, show similar behavior in how much average time they spend in their primary burrows (73-79%) and their secondary burrows (20-26%).

Tables 11 and 12 exhibit the use of burrows according to the percent of burrows used by one or more tortoises and the percent of tortoises that make individual and multiple use of the burrows. Seventy-two percent of the burrows of the colony are used exclusively by one individual (Table 11) as follows: primary burrows (63% of cases), secondaries (37%). The remaining 28% of the available bur-

Table 11.
Percentage of burrow usage according to number of dwellers

Tortoises	Burrows	
	N	%
1	43	71.7
2	13	21.6
3	3	5.0
4	1	1.7

Table 12.
Percentage of tortoises showing single and multiple burrow usage

Burrows	Tortoises	
	N	%
1	11	33.3
2	10	30.3
3	9	27.3
4	2	6.1
8	1	3.0

rows are used in decreasing order by 2, 3 and 4 tortoises not necessarily in a simultaneous manner. The maximum number of tortoises that occupy one burrow at the same time is two and generally only one of the tortoises among the several that may use it uses it as a primary burrow (59% of the cases).

This species tends to use and maintain a low number of primary burrows, usually two. Sixty-four percent of the tortoises of the area use from one to two burrows and the remaining 36% occupy from 4-8 burrows (Table 12). In the last case the principal use consists of short visits.

DISCUSSION

In contrast to what happens in other species of *Gopherus*, decreasing the quantity or diversity of food does not seem to have an influence in expanding the area of activity. The tendency in *G. flavomarginatus* is to lower movements during the season of less diversity and abundance of forage and increase movements during the season of major productivity. In *G. polyphemus* (McRae et al., 1981) and in *G. agassizii* (Burge, 1977) it has been observed that the distance for grazing increases with the decrease of available food. The differences between these species and *G. flavomarginatus* may be explicable based on interspecific metabolic differences. Results of blood tests taken during the dry season (unpublished data) show that *G. flavomarginatus* is capable of taking advantage of the availability of any food. The blood shows a high content of uric acid, implicating a diet of low water intake and concentrated proteins, mainly coming from *Hilaria mutica*. Also correlated is the high content of this grass in feces (90% dry weight) in this same period. These results suggest a strong relationship between metabolic requirements, local concentration of food, and the magnitude of the displacements inside the area of activity. *Hilaria mutica* is usually available within a radius of 20-30 m of the majority of the burrows. If our interpretation is correct, the correlations between mean traveled distance per day and the size of the area with respect to the size of the individuals (Tables 3 and 6) come to be secondary relationships.

The distances considered for movements of the tortoises showed differences according to age class, and CL. The following considerations indicate for this species that the best parameters for the degree of motility are the mean distance and the maximum distance traveled per day in opposition to the radius of activity that for other reptiles has come to be a parameter with biological significance (Tinkle, 1967). The differences between sexes in the mean distance traveled per day, reflects the displacement of the males in searching for females throughout the season of maximal activity. The males maintain a large, constant displacement but the maximum distance they are able to travel per day is not significantly different than that of the females. Moreover, the long travels done by the females were not associated with any apparent specific behavior such as enlarging the foraging area or interacting with other tortoises. These movements may be better associated with changes of burrows that would potentially be related with a search for nesting sites.

The major movements by the males during any summer period, dry or wet, show that the displacements related with courtship are initiated well before the females have a pronounced activity. In fact, in spring of 1980, when the activity of the females was practically null, courtship and displacement by some males was still observed.

The high negative correlations, in the case of the females, between CL and the mean traveled distance per day imply a more sedentary life and restriction of movements by the older females. This phenomenon may have implications in the stability and permanence of the reproductive nucleus of females of one colony. In the case of the males, the lack of correlation between CL and distance can be explained by the individual variability of movements of certain dominant males, that even though they are not the largest members of the colony, maintain areas of activity six times higher than other males of similar size.

The juveniles show a high motility in comparison to the adult males. This is reflected in the overall mean traveled distance per day and, in particular, during the dry period of the summer. The high correlation of CL and mean traveled distance per day, indicate that there is a gradual expansion of the area of activity of the juveniles. This high motility can be related with the dispersion of the juveniles at

a certain age and possibly contributes to the enlarging of the colony, to the replacement of individuals, and to the formation of new colonies.

The movements of the greatest distances (outside the colony) do not correlate obviously with any factor, such as the low forage density and diversity season, the courtship season or the exclusion by dominant individuals (one young adult that was never observed in interactions with other males of the colony exhibited extensive movements). The lack of space does not seem to be a factor stimulating immigration either because all the tortoises that moved outside the colony had two burrows that they alternatively used before leaving and the overlapping with areas of other individuals was very low: 10% on average. Individuals that show this type of displacement are not just transient in the area. They can stay in the colony for continuous periods up to at least approximately two years (the duration of this study) before the initiation of these movements.

Among the non-probabilistic methods for the calculation of the area of activity the convex polygon has been the most commonly employed for reptilian studies. The minimum modified polygon has had a limited use and it has been applied principally to the areas of activity of aquatic tortoises.

Of the probabilistic methods, the adjustment proposed by Jennrich and Turner (1969) has been moderately employed in studies of the area of activity in reptiles while other methods, such as the one of Koepl *et al.* (1975) have not been employed in this group. We consider that the areas calculated with the method of the minimum modified polygon (MMP) and the 68% bivariate ellipse are the most representative of the areas traveled and really utilized by tortoises. In comparison with other methods, the overestimation of the above two cited methods is 5 times on average. The method of the MMP precisely delineates the limits of the area of activity associated with the burrows. The polygon obtained in this manner permits realistic estimations of behavioral (and social) phenomena such as the overlapping of areas and the social system of the species.

Waldschmidt (1979) demonstrated that the employment of probabilistic methods (of Fitch, 1960; Jennrich and Turner, 1979; Koepl *et al.*, 1975) result in an overestimation of the area of

activity of *Uta stansburiana* in comparison with the areas obtained by the convex MMP.

Statistically, considering an ellipse (or a circle) of 95% confidence (corresponding to 2 S.D. in a normal distribution) instead 68% (corresponding to 1 S.D.) introduces an error in the calculation of the area really utilized. This method includes localized points in the periphery of the home area that represent zones of accidental or rare usage and that do not form a consistent part of the home range.

Other authors have exposed ideas about the inconvenience of considering the extreme points of movements inside the area of activity. McRae et al. (1981) suggested that in order to have a model that does not obscure interesting aspects of the movements of *G. polyphemus*, one should consider a feeding radius that, according to the method of density probability function, delimits a circular area corresponding to approximately 60% of the total area defined in terms of the MMP. Moreover, these authors considered that, according to the type of movements by the tortoises, the circular feeding area so estimated results in a overestimation of the feeding area actually used.

Our observations of aggressive behavior, courtship, use of burrows, and overlap show that there is a social structure in *G. flavomarginatus* that corresponds more to a hierarchial system than to territoriality. Behaviors that suggest a weak territoriality occur in relation to burrow defense by adults of both sexes and some juveniles during the high activity season, and also in relation to spatial-temporal isolation occurring during low activity periods.

The evidence suggestive of a hierarchial system is more abundant: *G. flavomarginatus* does not exhibit strong defense of a specific area, or of receptive females inside an area, or formation of harems. Also, there is no evidence for the defense, on the females' part, of optimal nesting areas. A hierarchial system of dominance is established where a small percentage of adult males are responsible for the majority of reproduction. The dominant males stay constantly in the area of the colony, while the subordinates can either stay in the colony or else immigrate from the area corresponding to the reproductive nucleus of the colony. Our observations of courtship between adult

individuals of the colony in 3 successive summers show the existence of a social system of this type in Mapimí.

The centers of activity of the dominant males are found close to those of the females most frequently courted, but not those of the subordinate males. The dominant males thus don't continually and aggressively exclude the subordinates from an area with receptive females and interaction is restricted.

The number of burrows used or visited is not correlated with the size of the males, but is related to the hierarchical situation inside the colony. In this study, the two dominant males used the highest number of burrows (4-8). Generally, all the largest males move freely inside the colony. The males of smaller size did not exhibit comparable movements. Our data suggest that size is of secondary importance in determining hierarchical relationships and female selection because the dominant and most mobile males are not the biggest in size although they are in the large size categories.

The degree of overlap between areas of activity is a potential indicator of the social structure of a population. This phenomenon has been observed in lizards (Tinkle, 1967; Krekorian, 1976). The observed overlap in adults of both sexes of *G. flavomarginatus* indicates that there is no mutual exclusion between individuals and that there exists a tendency towards a social organization in the shared areas.

There is no defense of an area for food resources. This becomes evident when we consider the reduced percentage of the area of activity that is intensively used for foraging (10% on average even in dry periods with scarce and low diversity of forage) and the absence of intra and intersexual overlapping of these portions of the area of activity.

Other considerations about the social organization of *G. flavomarginatus* are concerned with the size of the area. When the sexes are of the same size, as in this species (Morafka et al., 1981), one expects that the areas of activity should be similar in size unless other factors are operating (Turner et al., 1969). The mean areas of activity do not differ significantly between sexes, although the mean for the males is bigger than the females.

In the other species of *Gopherus*, the males occupy larger areas than the females (Rose and Judd, 1975; Burge, 1977; McRae et al., 1981).

The high variability in the size of the areas of males may be related to hierarchical variation in which dominant males move more as they court a greater number of females. The greater mean area of the males may also be caused by the movements of the dominant males during the reproductive season. The large activity areas for the females, comparable to those of some males, may be advantageous for two reasons: the location of optimal nesting places and the increase in probability of contact with reproductive males. This latter hypothesis may explain observed behavior of females that were not included in the areas of the dominant males. They moved gradually to the periphery of the area of the males and stayed in these zones for several days.

The social system of *G. flavomarginatus* is similar to that of *G. polyphemus* described by McRae et al. (1981). The most noticeable difference is the absence in Bolson Tortoise of the dense gathering that *G. polyphemus* shows during the reproductive period in which the reproductive individuals of a colony concentrate in an area of one hectare.

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