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A DEMOGRAPHIC STUDY OF AN ISOLATED POPULATION OF THE GOPHER TORTOISE, *Gopherus polyphemus*; AND AN ASSESSMENT OF A RELOCATION PROCEDURE FOR TORTOISES

BY

TERRY J. DOONAN
B.S., University of Florida, 1977

THESIS

Submitted in partial fulfillment of the requirements
for the Master of Science degree in Biology
in the Graduate Studies Program of the College of Arts and Sciences
University of Central Florida
Orlando, Florida

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ABSTRACT

It is acknowledged that the gopher tortoise is declining in numbers throughout its geographic range primarily from degradation and loss of suitable habitat. This research project is part of a pilot program to study the effectiveness of relocation as a mitigation method for the conservation of gopher tortoises. There was an opportunity to gather information about the tortoise population prior to its relocation, and for that reason this thesis is presented in two sections.

The first section of this work involved the analysis of the tortoise population prior to its removal from the development site. Results of two methods for the estimation of population density from burrow counts seem to indicate that in some cases those procedures may over estimate tortoise density. Excavated burrows of hatchling and juvenile tortoises showed a significant correlation between carapace length and burrow length. A von Bertalanffy interval growth equation fit to carapace length and age data produced predicted ages from specific sized tortoises that were similar to previously published data.

The second section of this thesis describes the methods used to relocate a tortoise population and evaluates the success of that procedure. Use of enclosures around burrows when releasing the tortoises

did not lead to their becoming permanently established in those areas. The enclosures probably served to increase the survival rate of the tortoises by establishing a source of shelter. Twenty-five tortoises (12 relocated and 13 resident) were fitted with radio transmitters to document movements. The relocated tortoises generally moved greater overall distances than the residents. However, the differences were significant only in the number of moves per tortoise and not in distances per movement. The relocated tortoises did not always use burrows during their movements and often sought shelter in shallow pallets and forms.

ACKNOWLEDGEMENTS

First of all, I want to thank my major professor, Dr. I. Jack Stout, for his time, assistance and friendship throughout my work here at UCF. I am also grateful to the other members of my committee, Drs. F. F. Snelson and L. M. Ehrhart, for their valuable comments and their critical review of this thesis. I also want to thank Linda Songer, Richard Paglialonga and William Lites who assisted in the field work for this project and Barbara Erwin, Beverly Barnekow and Rita Greenwell of the Biology Department office for their day to day assistance. The Hardy-Lieb Development Corporation provided financial support for this work.

I am especially thankful for my wife Barbara. Without her support and understanding throughout this project, it could not have been completed.

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SECTION I

DEMOGRAPHY OF AN ISOLATED GOPHER TORTOISE POPULATION

INTRODUCTION

Longleaf pine-oak uplands are the principal habitat of the gopher tortoise, Gopherus polyphemus, throughout its range in the Southeastern United States. Of these upland sandhill communities, longleaf pine-turkey oak associations support the greatest density of tortoises (Auffenberg and Franz, 1982). The longleaf pine-turkey oak association occurs in Alabama, Georgia, Mississippi and South Carolina, but is most extensive in Florida. Auffenberg and Franz (1982) state that 57% of the area originally occupied by longleaf pine-oak communities in Florida had been lost as natural habitat. The conversion of these sandhill communities to pine plantations and citrus groves accounts for the majority of the losses. Within the past decade, a series of devastating winter freezes has resulted in the destruction and subsequent abandonment of many citrus groves across Central Florida.

This study reports the analysis of a tortoise population that recolonized an abandoned citrus grove in Central Florida that was formerly longleaf pine-turkey oak habitat. Impending commercial development of this site lead to the current study being done to test the feasibility of relocating gopher tortoises to mitigate the effects of development. The total removal of the population offered the opportunity to evaluate alternative methods for estimating tortoise density. In addition, demographic and distributional attributes of the population are examined in relation to site characteristics. The response of this tortoise population to habitat undergoing early secondary succession is compared to previous studies from more stable habitats.

STUDY AREA

The study area was a proposed development site, known as the Lake Mary Shopping Center (LMSC), located in Seminole County, Florida (28°45'N, 81°21'W) (Fig. 1). The site was relatively isolated from other suitable tortoise habitat. It was bordered to the north by Lake Mary Boulevard and to the west by Lake Emma Road (Fig. 2). Condominium and housing developments formed a barrier along the southern boundary. To the east, the middle third of the site was bordered by an area of bare sand with a steeply sloping sides that had been an old borrow pit. North of that was an area of bahia grass that was frequently mowed. A seasonal wetland area south of the old borrow pit was unsuitable as tortoise habitat. The elevation of the LMSC ranged 15-23m (50-75 feet) above sea level. Soils were primarily of the Blanton Series (Furman and White, 1966).

Of the LMSC's 19.43 ha, 1.25 ha remained as two islands of relatively undisturbed sandhill habitat located within the western third of the site (Fig. 3). In the islands, the primary tree layer was dominated by long-leaf pine (P. palustris), with turkey oaks (Q. laevis) and scrubby live oaks (Q. virginiana) as codominants in a secondary layer. Ground cover was primarily wire grass (Aristida stricta) though a variety of other grasses and herbaceous plants were present.

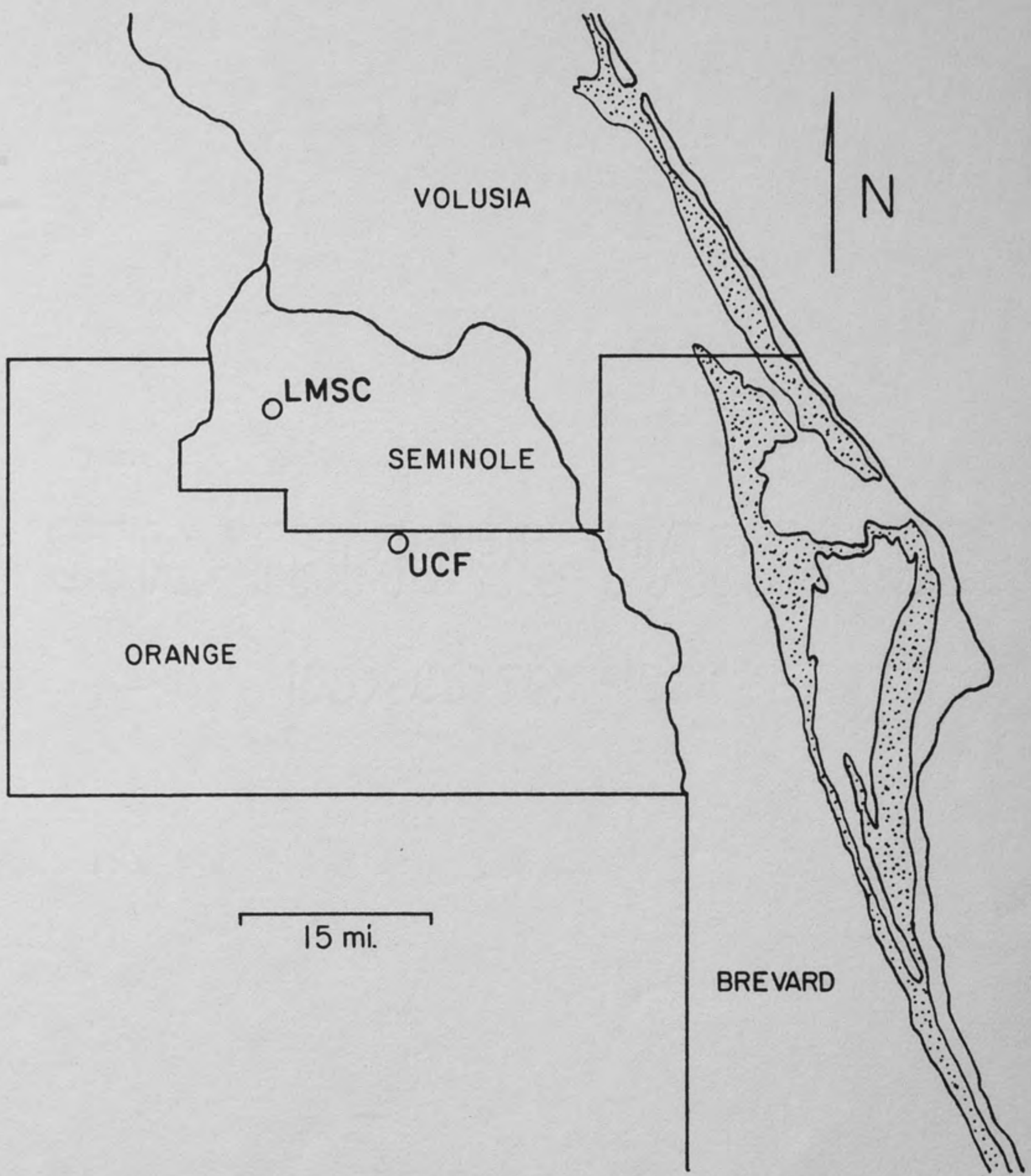

Fig. 1. East Central Florida showing the location of the Lake Mary Shopping Center (LMSC) in Seminole County and the University of Central Florida (UCF) in Orange County. Stippled areas indicate Mosquito Lagoon and the Indian River.

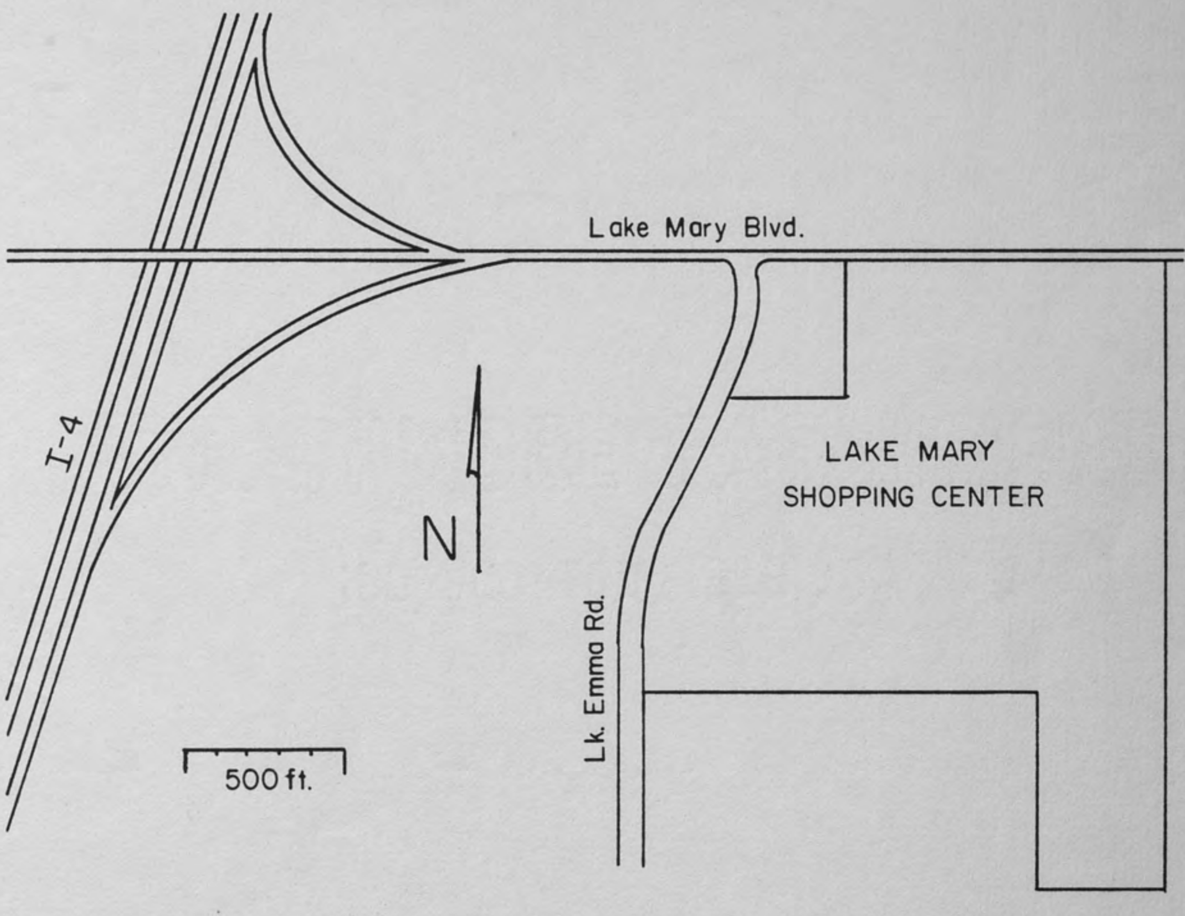

Fig. 2. Map of the Lake Mary Shopping Center (LMSC) in relation to the surrounding area.

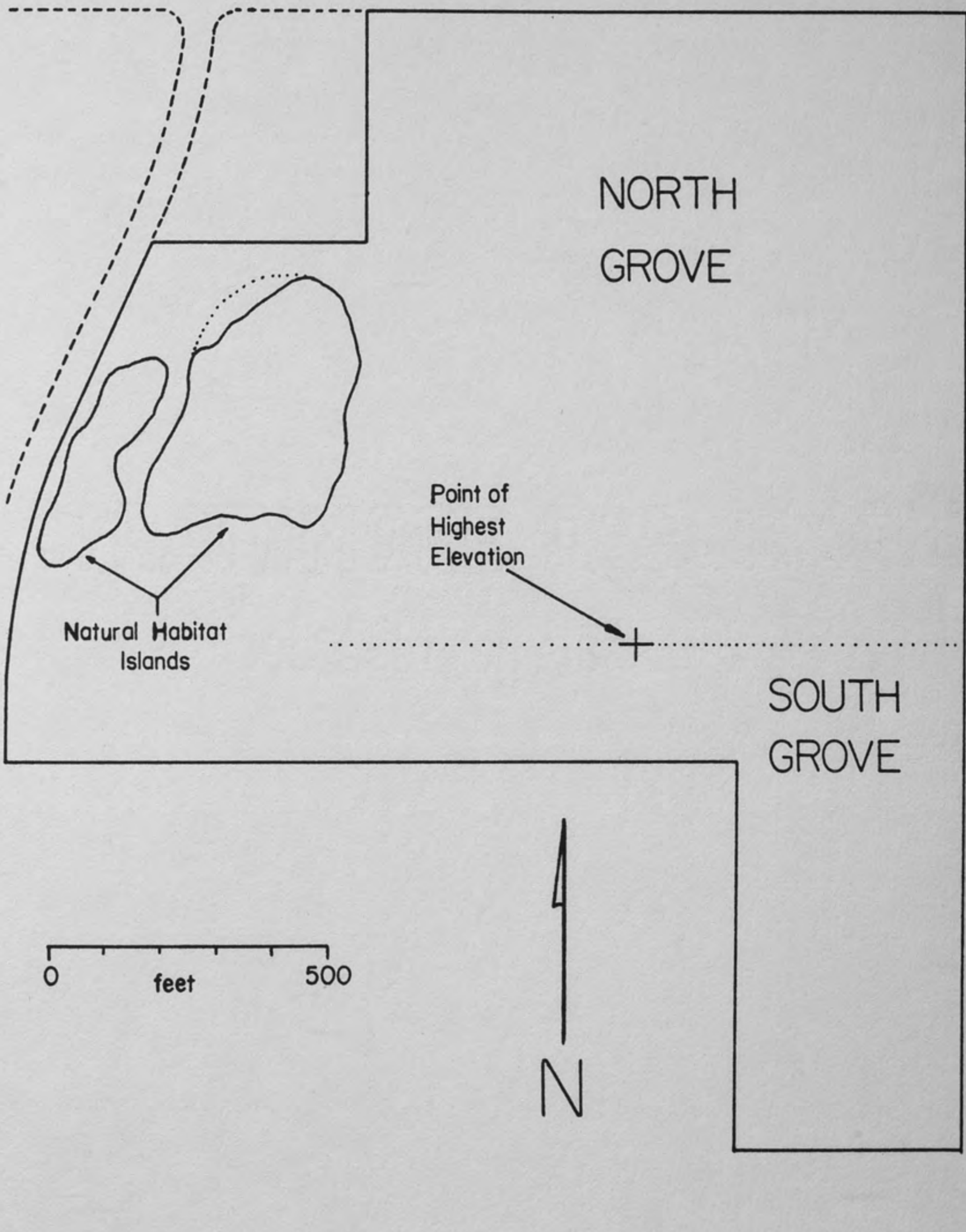

Fig. 3. The LMSC showing the location of the natural habitat islands and the division of the grove into north grove and south grove areas at the point of highest elevation.

as rotting stumps, the majority of which were less than 1m in height. The ground cover was dominated by golden aster (*Heterotheca scabrella*) a species of Panicum grass, and dog fennel (*Eupatorium capillifolium*) Passion flower (*Passiflora incarnata*), catbriar (*Smilax* sp.), and prickly-pear cactus (*Opuntia stricta*) were common. Young live oak (*Q. virginiana*), and cherry trees (*Prunus* sp.), all less than 5m tall, were scattered throughout the old grove area.

METHODS

Though sections of the LMSC seemed to be unlikely tortoise habitat, work was begun without making assumptions as to the dispersion of the tortoises on the site. This was done to determine if an accurate estimate of the tortoise population could be derived by counting burrows in randomly selected portions of the site. The LMSC was divided into plots 150m x 7m (Auffenberg and Franz, 1982) with the long axes oriented north-south. Twenty of these plots were selected at random with the stipulation of no juxtaposition. These 20 plots represented approximately 10% of the 19.43 ha LMSC.

Two methods were used to estimate the number of burrows per ha (Burnham et al., 1980). First, the number of burrows within the 20 plots was determined, and the density of burrows on the site was extrapolated from that. This strip transect estimator is based on the assumption that 100% of all burrows within the 7m width of the transects were seen. The equation for this is:

$$D = \frac{n}{2Lw}$$

D is the estimated density, w is the distance from the mid-line of the transect to the boundary of the transect (the half-width of the transect), L is the total length of the transect (the sum of the lengths of all the individual transects), and n is the total number of burrows observed.

Secondly, the center line of each plot was treated as a line transect. A perpendicular distance was measured from the line to each burrow sighted, including those sighted beyond the 7m width of the plots. These data were subjected to Fourier Series analysis as outlined by Burnham et al. (1980). The equation for this is

$$D = \frac{nf(0)}{2L}$$

In this equation, $f(0)$ is the 'probability density function' at zero distance from the midline of the transect. It is estimated by:

$$f(0) = \frac{1}{w} + \sum_{k=1}^{m} a_k$$

In this equation, a_k is a constant. It is estimated by

$$a_k = \frac{2}{nw} \left[\sum_{i-1}^{n} \cos \left(\frac{k\pi x_i}{w}\right)\right]$$
$$k = 1,2,3,\ldots,m$$

where x_i is the perpendicular distance for each observation; $i=1,\ldots,n$. Burnham et al. (1980) suggested the use of a stopping rule for computing a_k, in which the value of m is chosen such that:

$$\frac{1}{w} \left(\frac{2}{n+1}\right)^{1/2} \geq |a_{m+1}|$$

This rule was followed for the density estimates reported here.

After completion of the transects, a thorough ground search of the entire site was conducted. Each tortoise burrow was marked with a numbered stake and orange plastic flagging tied on adjacent vegetation. The survey showed that the site could be effectively subdivided into: 1) the natural habitat islands, 2) the north grove, and 3) the south grove. An east-west line of division, at the point of highest elevation (Fig. 3), was used to divide the grove.

Every burrow was classified as either active, inactive, or old (Auffenberg and Franz, 1982). The height and width of each burrow was measured 15-20cm inside the entrance. The angle of declination and the compass orientation of the entrance were also recorded for each burrow.

Herbaceous biomass was measured at 20 randomly selected burrows evenly divided among the three subareas of the LMSC. Two $1m^2$ plots were selected at random from a 7m x 7m grid centered on the burrow entrance. A $0.25m^2$ frame was centered within each plot and all green, herbaceous vegetation rooted within it was clipped at ground level and oven-dried. Dried biomass was determined to the nearest 0.1g for each sample. Average biomass was calculated as kg/ha for each of the subareas.

The relative coverage of litter, grass, herbs, shrubs and trees in each of the subareas within the LMSC was analyzed with point-intercept line transects 100m in length. Transects were laid out from randomly selected points, and at 1m intervals all forms intercepting the line were recorded. Thus there were five possible intercepts at each point. These data were used to compute percent coverages for each vegetation form, in each subarea.

Removal of the tortoises was begun as soon as the ground survey of the burrows was completed. The majority of tortoises were collected with pit-fall traps (PFTs). These were five gallon plastic buckets set flush with the surface of the ground and covered with muslin that was lightly anchored with sand. A thin covering of sand was used to hide the traps. The PFTs were set as close as possible to active burrow entrances, either in the mounds or on paths obviously used by the tortoises.

Several tortoises were collected from burrows using a hand-pat technique (Osterman, 1984) that induced them to come up to the entrance where they could be captured by hand. Tortoises moving about on the ground were collected whenever they were encountered.

Active burrows less than 150mm wide were excavated with shovels to capture the tortoises. The length, depth at the end and degree of (horizontal) curvature were recorded for each burrow.

Captured tortoises were permanently marked by drilling small (2-3mm dia.) holes in the marginal scutes according to a predetermined pattern, thus individually numbering each tortoise (See Appendix I for a description of the marking system used.) Each tortoise was measured as detailed by McRae et al. (1981a) and weighed. Age was recorded for tortoises on which the annuli of the abdominal scutes could be clearly read.

Age and carapace length data were used to fit a von Bertalanffy interval growth equation. This equation was used to predict the maximum size of gopher tortoises, and to evaluate its use in predicting a tortoise's age from its size. The von Bertalanffy equation was derived from those presented by Frazier and Ehrhart (1985). The general von Bertalanffy equation they used was

$$L = a(1-be^{-kt})$$

where L is carapace length, a is asymptotic length, b is a parameter related to length at hatching, e is the base of the natural logarithms, k is the intrinsic growth rate, and t is age in years. They then presented an equality for b

$$b = 1 - \frac{h}{a}$$

where h is the mean carapace length at hatching. By combining these two equations, I derived a third equation that was used with the data from the gopher tortoises:

$$L = a - (a-h)e^{-kt}$$

The data were fit to this equation by means of the SAS (SAS Institute Inc., 1985) procedure NLIN (non-linear least squares regression).

RESULTS

Forty-six tortoises were removed from the LMSC (Table 1). The majority of the tortoises, 59%, were caught with pit-fall traps (PFTs). The average effort required for each tortoise caught in a PFT was 6.86 trap-days. One tortoise was caught the same day the trap was set, and several were caught on the next day. Other PFTs were set for periods of 2-4 weeks before tortoises were captured. Twenty-seven percent of the tortoises, all of which were juveniles, were collected by excavating burrows. The collection of the remaining 14% was evenly divided between the hand-pat technique, and the capture of tortoises encountered away from their burrows.

Of the 46 tortoises removed, 13 were living in the natural habitat islands, 15 were in the north grove, and 18 were in the south grove (Fig. 4). Except for one sub-adult, only juveniles were living in the natural habitat islands. Both adult females, and all of the hatchlings, were removed from the south grove area. The observed distribution pattern was tested with the nearest neighbor procedure (Poole, 1974) against the hypothesis of a random pattern. The results ($R = 0.474$; $var(R) = 0.00976$) indicated a significantly aggregated distribution ($z = -5.32$, $P < 0.01$) (Poole, 1974; Petrere, 1985).

Ninety-one gopher tortoises burrows were located on the LMSC (Fig. 5) yielding a density of 4.68 burrows per hectare (b/ha). Thirty-five burrows were located in the natural habitat islands, 30 in

Table 1. Population structure of gopher tortoises removed from the LMSC, Seminole County, Florida, September - October 1985.

Age group and sex	Natural habitat islands	South grove	North grove	Totals
Adult female	0	2	0	2
Adult male	0	2	5	7
Sub-adult	1	2	6	9
Juvenile	12	6	4	22
Hatchling	0	6	0	6
Totals	13	18	15	46

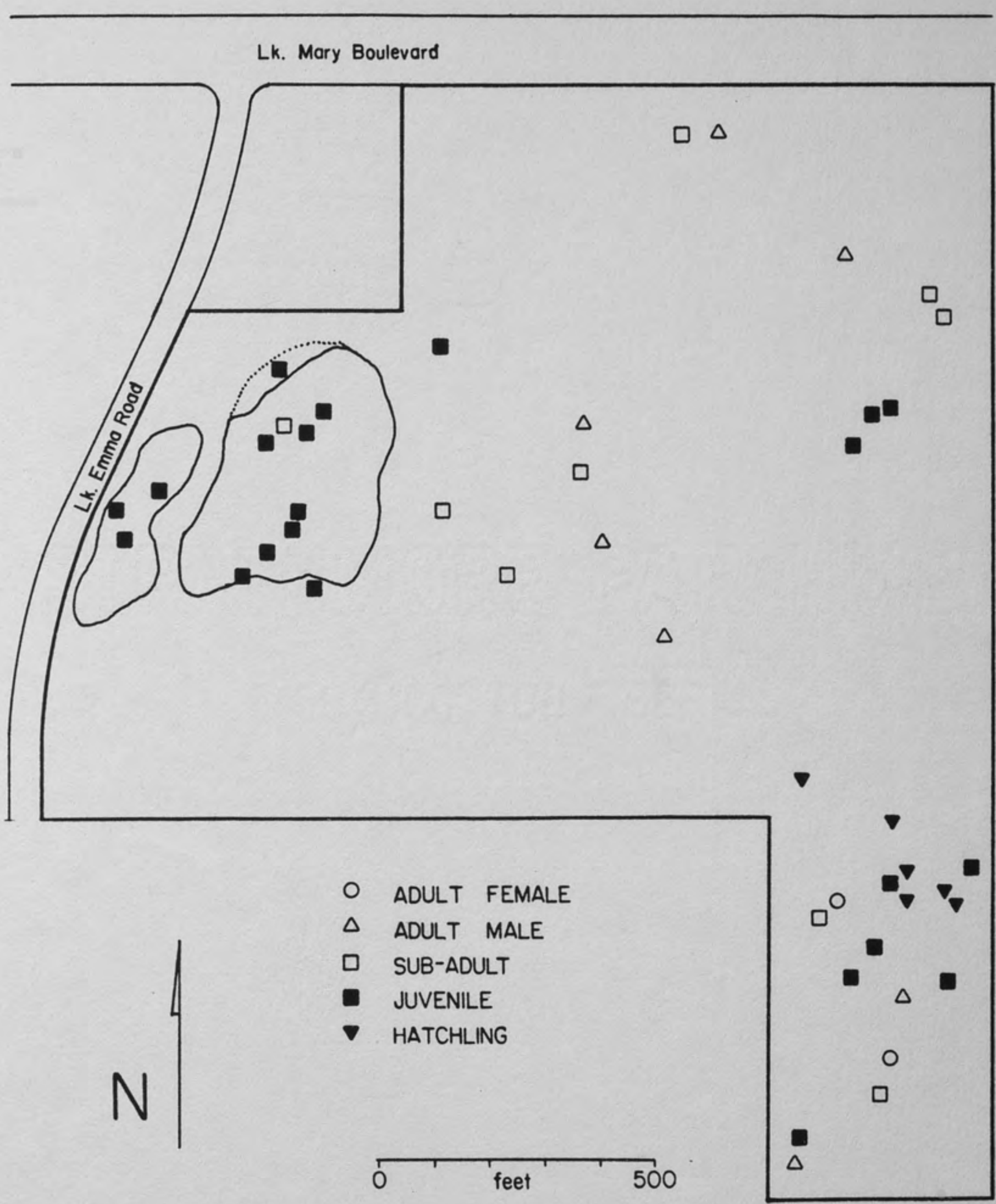

Fig. 4. Distribution of the gopher tortoises on the LMSC site by age group, and sex for adults.

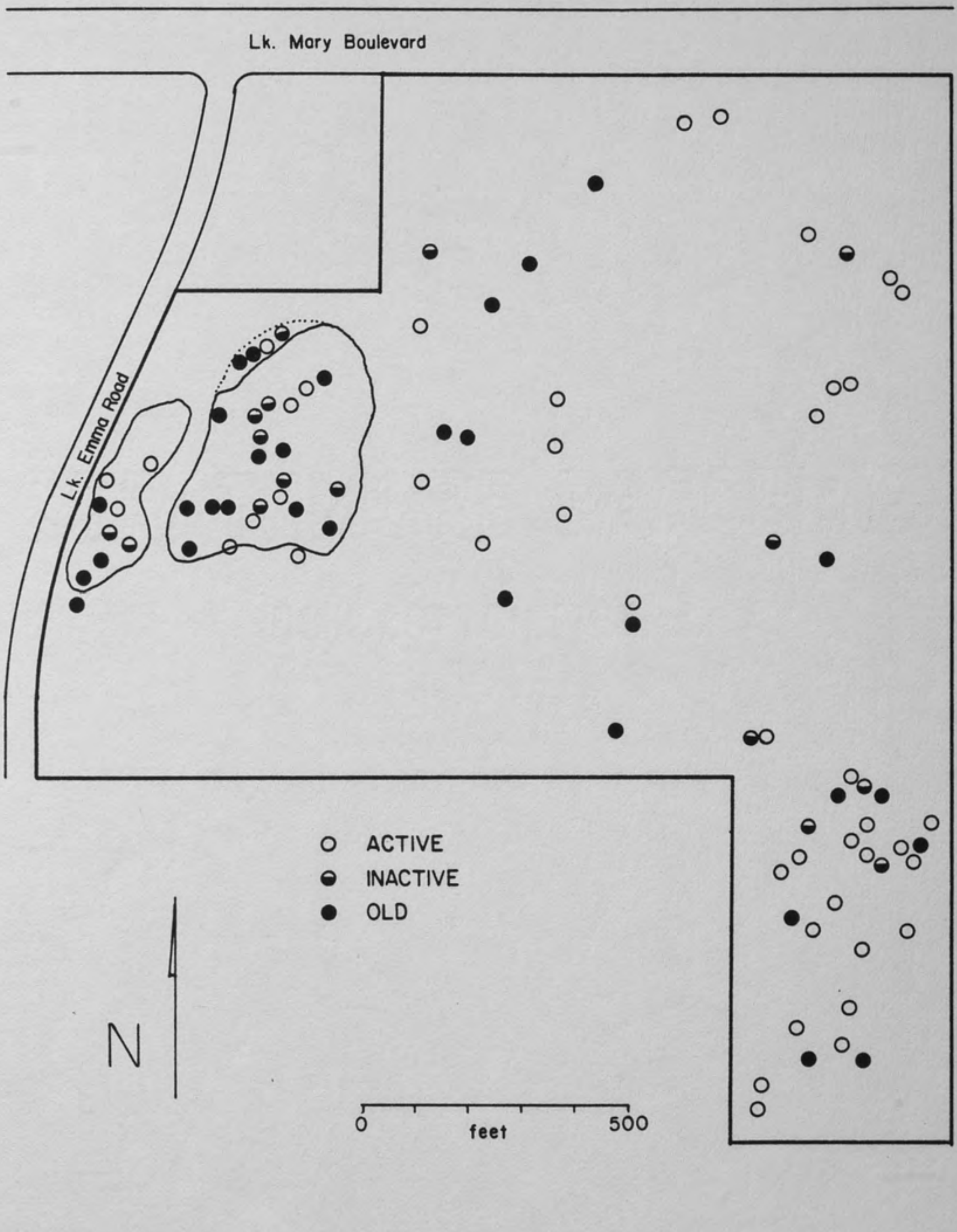

Fig. 5. Map of the LMSC showing the distribution and condition of all tortoise burrows.

the south grove, and 27 in the north grove. Of those burrows, 44 were active, 16 were inactive and 31 were old.

To analyze the transects with the methods described by Burnham et al. (1980), they were considered as a single transect with an overall length of 3000m (L). Along this transect, 24 burrows were located within 10m of the midline. Burnham et al. (1980) recommend truncating 1-3% of the outlying data points for the line transect estimation procedures by reducing the maximum half-width of the transect. Truncation of the LMSC data was accomplished by reducing the maximum half-width of the transect to 8m and thereby eliminating one data point (4%). Using that half-width the Fourier Series procedure generated an estimate of 7.76 b/ha.

The strip transect procedure is based on the assumption that 100% of all objects of interest are sighted. Thus, the 3.5m half-width of the plots was the maximum that could be used to calculate burrow density with this estimator. An estimate of 6.67 b/ha was generated by the strip transect procedure.

Correction factors that would generate the known tortoise density of 2.37 tortoises per hectare (t/ha) were calculated from the burrow density estimates of both procedures. The correction factor was .305 for the line transect procedure, and .355 for the strip transect procedure. Both values were well below the .614 correction factor used by Auffenberg and Franz (1982) to estimate tortoise density from burrow counts.

Because only seven of the tortoises were adults, the measurements recorded were not used in a discriminant analysis to determine sexual dimorphism (McRae et al., 1981a). A frequency distribution of size classes based on carapace length measurements of the LMSC tortoises was compared (Fig. 6) to data from the Cape Sable population in south Florida (Kushlan and Mazzotti, 1984), and to data from north Florida populations studied by Alford (1980). Iverson (1980) stated that *Gopherus polyphemus* is sexually mature at carapace length (CL) of approximately 230mm. Thus, tortoises in size classes greater than 22.8cm were assumed to be adults for comparison of these three populations. Approximately 65% of the south Florida population was comprised of adults, while in the north Florida populations approximately 35% were adults. In the LMSC population, however, only 16% of the tortoises were adults. In addition, the maximum size of the LMSC tortoises was less than that reported for the tortoises in either of the other two studies. None of the LMSC tortoises had a carapace length greater than 30.0cm. Approximately 33% and 4% of the south Florida and the north Florida populations respectively, had carapace lengths greater than 30.0cm.

From the data fitted to the von Bertalanffy equation, estimates were obtained for a, the asymptotic carapace length, and for k, the intrinsic growth rate. These estimates are:

$$a = 338.726\text{mm}$$
(standard error = 47.409)

$$k = 0.0815198$$
(standard error = 0.018635)

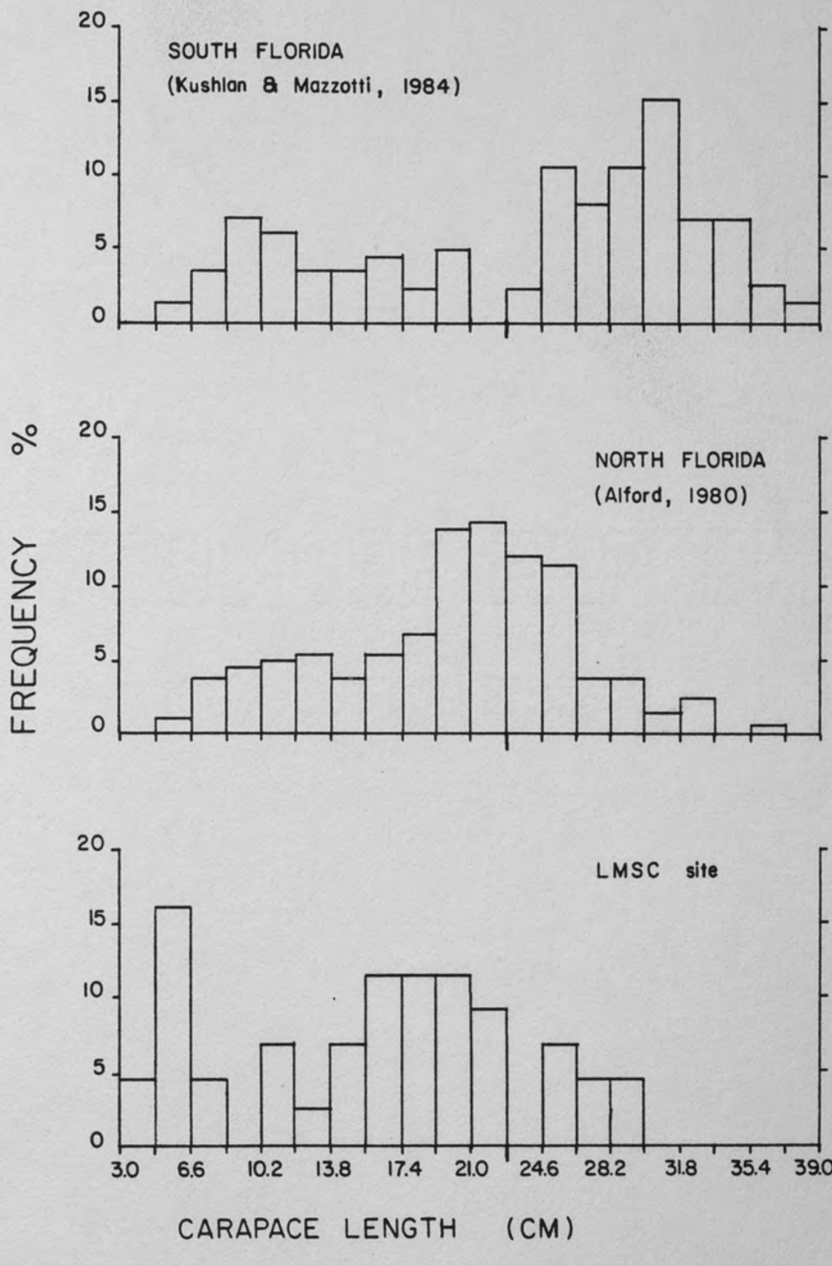

Fig. 6. Relative distribution of size classes for tortoises of the LMSC population, and a comparison to similar results from north Florida, and south Florida populations. Carapace length intervals of 1.8cm follow Alford (1980).

This asymptotic carapace length, plus one standard error, includes the record size tortoise listed by Conant (1975) of 368mm.

Inserting the estimates for a and k into the original equation along with a figure for h of 45mm CL (the size of the smallest hatchling collected on the LMSC site) gives a predictive equation:

$$CL = 338.726 - (293.726)e^{-.0815198t}$$

From this equation, size at age 13 years is predicted to be 236.94mm. This approximates data reported by Iverson (1980) for age at maturity (10-13 years) and size of maturity (226-236mm CL) from work on north Florida tortoise populations.

To predict age for tortoises of specific sizes, numbers were inserted into this equation as carapace length measurements (Fig. 7). The numbers used, and the predicted ages are presented as Appendix II. A carapace length of 338mm equated to a predicted age of 73.6 years. This is not an unreasonable estimate in light of known age records for other species of tortoises (Auffenberg and Iverson, 1979).

A breakdown of the ages recorded from the annuli on the abdominal scutes revealed that 58% of the LMSC population was eight years old or younger. In addition, 71% of the population was less than or equal to 10 years of age. None of the seven adults could be accurately aged. The largest tortoise (a female) was approximately 290mm CL, and the von Bertalanffy equation (above) predicted an age of 22 years for a tortoise of that size The age of that tortoise had been previously estimated at 20-25 years by examining the abdominal annuli.

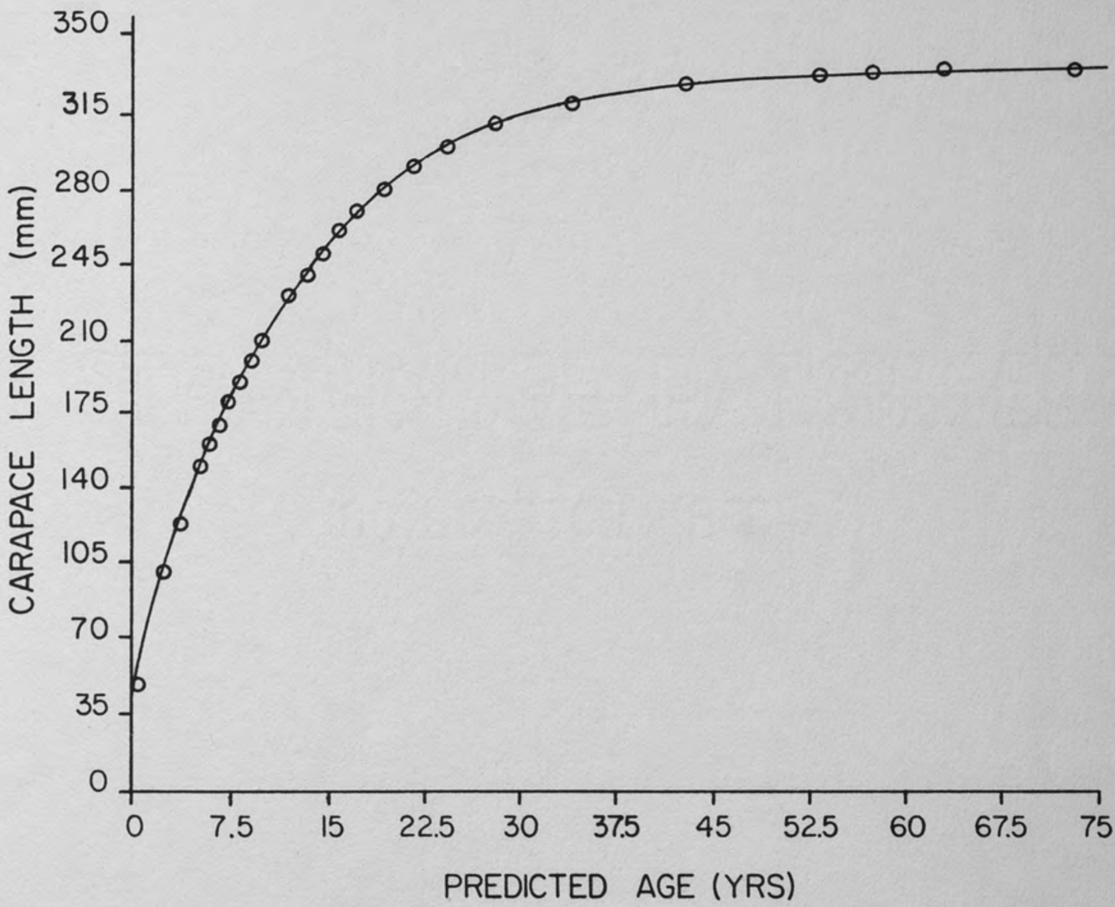

Fig. 7. Age predictions from numbers inserted as carapace length measurements into the von Bertalanffy equation. The fitted line represents a graph of the equation.

Measurements from the LMSC tortoise burrows were compared to similar data reported by Hansen (1963). The average angle of declination for the LMSC burrows of 28.1° was not significantly different from the average of 29° reported by Hansen ($t = 1.66$, d.f. = 50, $P > 0.05$). The average for the ratio of burrow height to burrow width found by Hansen was .51, and for the LMSC burrows it was not significantly different at .53 ($t = 1.03$, d.f. = 37, $P > 0.05$). Hansen found the average ratio of tortoise carapace width to the width of the burrow occupied by that tortoise to be .79. The ratio of .77 for the LMSC population was not significantly different ($t = 1.33$, d.f. = 35, $P > 0.05$).

The observed compass orientation of the active and inactive LMSC burrows was analyzed by chi-square test for differences from a random orientation. The percentages for each area and for the entire site were tested separately. A greater percentage (35%) of the burrows on the site faced west, though that difference was not significant ($X^2 = 3.92$, d.f. = 3, $P > 0.05$). Of the three areas, only the north grove exhibited a significant ($X^2 = 33.27$, d.f. = 3, $P < 0.05$) difference from the expected frequencies. That was caused primarily by a lack of south-oriented burrows.

Measurements recorded from all of the excavated juvenile burrows that contained tortoises are reported in Table 2. The burrow of the six year old tortoise had the appearance of having been started only a short time previously, but that could not be confirmed. For each of these excavated burrows, the ratio of burrow depth to burrow length

Table 2. Measurements recorded for all juvenile gopher tortoise burrows excavated as part of the removal process for the tortoises on the LMSC site. H=hatchlings of the current year. Burrow depth is the depth below the surface at the end of the burrow. Curvature represents any horizontal turn(s) in the burrow, recorded to the nearest 5°.

Tortoise number	Tortoise age(yrs)	Carapace length(mm)	Burrow length(mm)	Burrow depth(mm)	Depth/ length(%)	Curvature (degrees)
437	H	50	490	260	53	0
451	H	50	400	250	62	15 right
457	H	52	565	300	53	40 right
486	H	51	460	248	54	25 left
488	H	49	730	450	62	45 left & 15 right
489	1	65	1360	760	56	25 right & 20 left
490	1	67	1060	700	66	40 left
465	2	77	1740	960	55	80 right
462	3	115	2610	1360	52	90 left
476	3	110	2430	1090	45	30 right
483	3	127	3880	1940	50	45 left & 45 right
491	6	163	2900	1240	43	0

was calculated. They were compared by chi-square test to an expected ratio of 0.47 = sin 28° (opposite/hypotenuse = depth/length). None were significantly different from the expected (X^2 = 22.05, d.f. = 11, $P > 0.01$). Twenty-eight degrees was used as the expected since that was the average angle of descent for the burrows of the LMSC population. The regression of burrow length on carapace length (Fig. 8) yielded a significant correlation coefficient of 0.916 (d.f. = 10, $P < 0.001$).

Only two of the 12 excavated burrows had no (horizontal) curvature. In the burrows which did curve, there were no roots or other objects blocking them from continuing straight. The percentage of these juvenile burrows exhibiting curvature to some degree was apparently not unusual when compared to adult burrows on the LMSC site. Several adult burrows were partially excavated and all exhibited some degree of curvature. One adult burrow excavated 4.5m along its length, had turned almost 180° from its original heading. Burrows that exhibited horizontal curvature were evenly divided as to the direction (Table 2). In addition, 15 of the burrows that had been measured for height, width, etc. curved within 50cm of the entrance. Of those, eight curved to the left and seven curved to the right.

The vegetation on the LMSC site was sampled to determine whether it influenced the distribution of the tortoises (Table 3). Mean herbaceous biomass for each area was compared to the figure of 744.4 kg/ha reported by Auffenberg and Franz (1982) as average biomass for ruderal areas (the islands had been subjected to some disturbance and

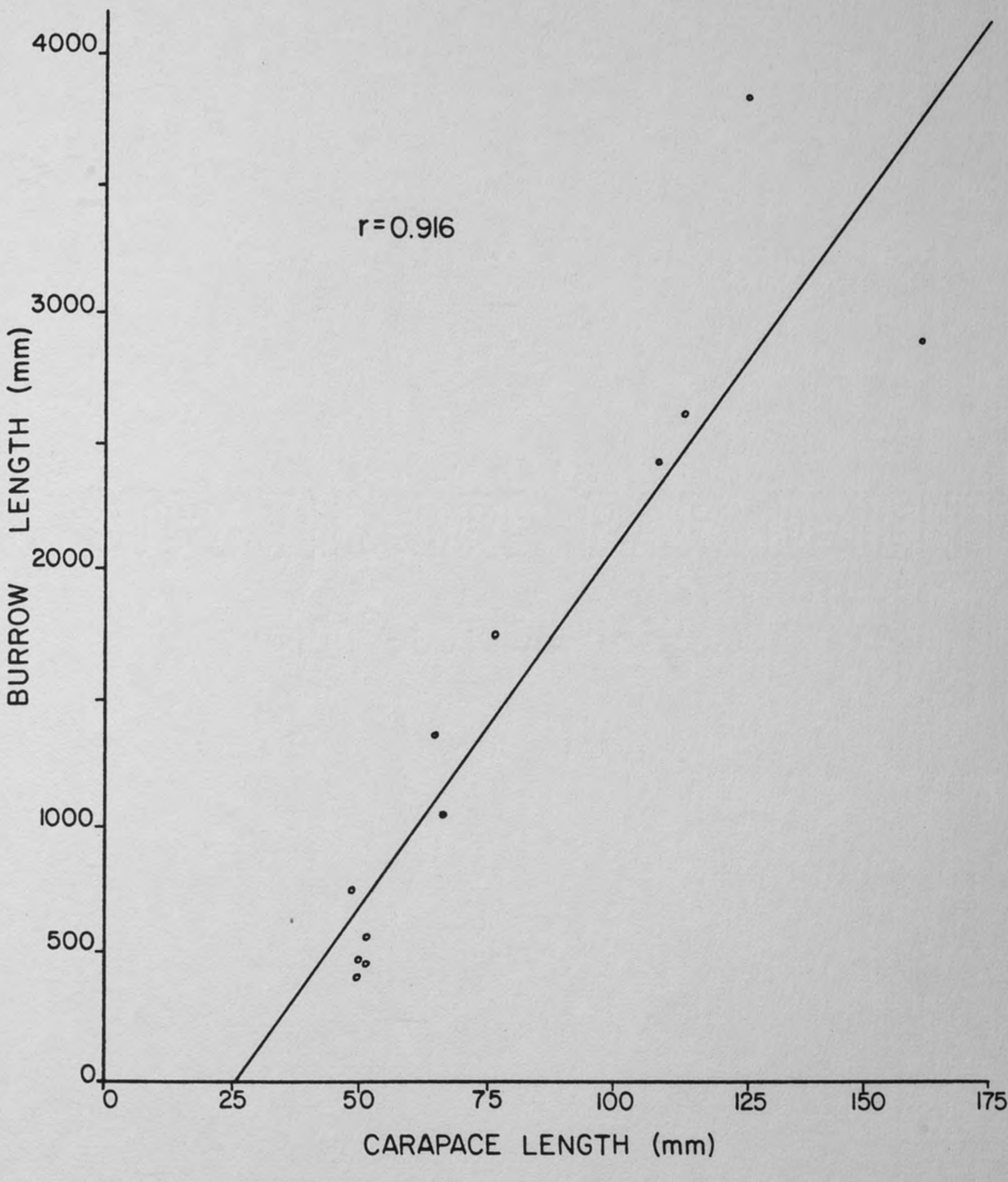

Fig. 8. Correlation between the carapace length of juvenile gopher tortoises and the length of the burrows they occupied. Burrow lengths were determined by excavating the burrows.

Table 3. Analysis of the vegetation coverage on the LMSC site. L=Litter, G=Grass, H=Herbs, S=Shrubs and T=Trees. In all cases, the figures presented are averages. For the point-intercept analysis, the percentage for each intercept was calculated separately, so it should not be expected that they add to 100%

	Point-intercepts, %					
Sampling area	L	G	H	S	T	Herbaceous biomass(kg/ha)
Natural habitat islands	11	54	32	23	14	988.3
South grove	21	58	33	0	0	1201.1
North grove	30	34	44	1	0	1071.0

were considered ruderal for this measure). Mean biomass in the islands was significantly greater than that average ($t = 2.33$, d.f. = 6. $P < 0.05$), and may be one reason for the relatively high density of tortoises in the islands (13 tortoises/1.25 ha). The biomass of neither grove area was significantly different (north grove: $t = 1.25$, $P > 0.05$; south grove: $t = 1.86$, d.f. = 6, $P > 0.05$), from the average reported by Auffenberg and Franz (1982). The rather patchy distribution of the vegetation in the grove areas produced a high standard deviation.

The results from the point-intercept analysis of the vegetation reflect the lesser density of trees and shrubs in the two grove areas. The density of trees in those areas was less that 10 per hectare. In the north grove dense patches of herbaceious vegetation produced a large amount of litter. In the south grove, and in the islands, there was a higher percentage of grass than any other form of vegetation. These two areas had correspondingly higher tortoise densities compared to the north grove (Fig. 5).

Predators of the gopher tortoise encountered on the LMSC site included humans, Colubrid snakes (2 *Masticophis flagellum*, and 1 *Pituophis melanoleucus*) and one canine (*C. familiaris*). Almost no signs of oppossums or armadillos were found. On 2-3 occasions the tracks of a single fox were seen. Raccoon tracks were seen occasionally. The relative isolation of this site was the only apparent factor to account for the low levels of predators.

DISCUSSION AND CONCLUSIONS

The distribution of gopher tortoises and inactive burrows on the LMSC suggested that the natural habitat islands had served as a refugium for the tortoises during the time the grove was in operation. Humphrey et al. (1985) reported that gopher tortoises will rapidly move into abandoned citrus groves from an adjacent area. The fact that nearly all of the tortoises in the islands were juveniles may be a result of their reduced propensity for movement relative to older tortoises (McRae et al., 1981b). In addition, of the juveniles in the islands, none were younger than six years of age. All of the tortoises younger than six years of age were collected in the south grove and the southern end of the north grove.

The size frequency distribution of the LMSC population also supports the hypothesis that a few adult tortoises from the natural habitat islands had recolonized the grove area within the past 8-10 years. For an animal such as the gopher tortoise with a low reproductive rate and long life span, a typical size frequency distribution would be expected to have relatively few individuals in each of the smaller size classes, and the majority of the population concentrated in the adult size classes. This is evidenced by both the south Florida and north Florida populations (Fig. 7). The LMSC population exhibits an opposite distribution (Fig. 7). An average of 3.3 individuals per year had been recruited into the LMSC population over the last ten years, a rapid rate of increase for a tortoise population. Gopher tortoises are 'K-strategists' (Pianka, 1974), with an inherently low reproductive rate (Iverson, 1980; Landers et al., 1980). The average reproductive success in most tortoise populations is approximately 5.8 hatchlings per mature female per ten years (Landers et al., 1980), or 0.58/year. Favorable soils, plentiful food, and little disturbance by humans have probably had a positive influence on reproductive success; however, a low level of predation was undoubtedly another contributing factor. In many areas, 90% of all clutches are destroyed by predators before the eggs hatch (Alford, 1980; Landers et al., 1980). The high rate of reproductive success exhibited by this population in the past 10 years seems to indicate that abandoned citrus groves could be effective preserves for tortoises, under similar circumstances.

The ability to accurately estimate gopher tortoise density is becoming increasingly important, both for small sites such as the one in this study and for large sections of the tortoises's geographic range. Because of the tendency for tortoise burrows to be aggregated, random samples through more densely occupied areas can produce estimates that are higher than the actual densities. This tendency for aggregation may affect sampling because of the necessity that sightings be independant events (Burnham et al., 1980), and is one reason the two procedures used in this study were compared over the same transects.

The fact that the density estimate from the strip transect procedure was higher than expected may indicate that in some cases previous tortoise density estimates based on this procedure should be reevaluated. The use of strip transects may only be appropriate for open habitats (e.g., sandhill or ruderal areas) because burrows are difficult to sight in thickly vegetated areas. Anything less than 100% certainty of locating all burrows would invalidate estimates from strip transects. Areas that contain a mixture of habitat types will also be difficult to sample with strip transects. Burnham et al. (1980) recommend selecting the half-width (w) prior to the start of sampling and using only that half-width for all transects. A strip transect with w = 10m might be reasonable for ruderal areas or sandhills while w = 3m may be too wide to be effectively searched in scrub or other areas.

The estimate of tortoise burrow density from the line transect procedure was also higher than expected. The thorough search required to satisfy the requirements of the strip transect procedure may have resulted in some burrows being sighted, and included, in the line transect estimate that would not usually be seen. Another consideration in assessing the line transect estimate is the sample size. Burnham et al. (1980) recommend a sample size of $n \geq 40$ for this Fourier Series estimation procedure though they state the estimator perfoms well with sample sizes as small as n = 30. This study was designed to sample 10% of the site, when w = 3.5m, with sampling to be stopped at that point. Ten percent is generally accepted as a reasonable percentage for a sample. The requirement, when using this line transect estimator, for a sample size of $n \geq 30$ may prove to be restrictive for some applications of this procedure.

The fact that both of the density estimation procedures used in this study produced estimates higher than the actual density of burrows on the LMSC site may simply be an artifact of random sampling. Of the two procedures, the line transect estimator seems to have the potential for greater accuracy in a wide variety of habitats. Confirmation of this will require additional work.

Even with a reliable estimate for burrow density, an accurate correction factor will be necessary to determine the tortoise density. It is the correction factor that is perhaps the most critical point, and the most difficult to determine. Humphrey et al. (1985) have stated that there is 'no known relation' between the number of burrows and the size of the tortoise population. However, to effectively survey sites for the tortoises themselves could require excessive amounts of time and there would be no guarantee that the results were reliable. In order to plan an effective conservation strategy for the gopher tortoise, including protection under the Federal Endangered Species Act, it will be necessary to accurately assess tortoise numbers across the entire geographic range of the animal (Pulliam, 1980). Based on the results of this work, the .614 correction factor of Auffenberg and Franz (1982) may produce tortoise density estimates that are greater than the actual densities. A more conservative correction factor should be considered for generating tortoise densities from burrow counts. I suggest the use of a 0.50 as a general correction factor. This is approximately the ratio of tortoises per hectare (2.37) to burrows per hectare (4.68) on the LMSC site.

The fitting of the data from the LMSC tortoises to the von Bertalanffy equation has produced a model for estimating the age of adult gopher tortoises from the length of their carapaces. This model fits well to data for age and size at maturity from north Florida tortoise populations studied by Iverson (1980). However, Landers et al. (1982) determined size and age at maturity for tortoises in south Georgia to be 230-265mm CL, and 16-21 years of age respectively, which is not in agreement with this model. Landers et al. (1982) state that maturity in the gopher tortoise is achieved at a 'physiological age' that varies across the geographic range of the animal. This variation may also be true for tortoises from different habitat types. Counts of abdominal annuli taken from tortoises on a site in central Florida that is predominantly sand-pine scrub and scrubby flatwoods have shown that tortoises with CL $\geq$ 230mm seem to be at least 15-20 years of age (Doonan, unpubl.). Predictions from the current model may only be applicable for tortoise populations from sandhill or ruderal habitats in central and north Florida. Before predicting the age of tortoises in other populations from this von Bertalanffy equation, it would be important to compare the age and size of younger tortoises in those populations against the figures in Appendix II. In many cases, it will undoubtedly be necessary to fit a different equation.

The close correlation of the measurements taken from the LMSC burrows to those of Hansen (1963) may partially be a result of similar soil types in both studies. Blanton (LMSC), Lakeland, Lakewood, and St. Lucie (Hansen, 1963) soils are all Regosols, typically found as deep deposits lacking definite horizons (Furman and White, 1966). Gopher tortoises could reasonably be expected to construct similar burrows in similar soils, even though on different sites, when not confronted with impediments to excavation. Horizontal curvature of tortoise burrows does not seem to be related to edaphic factors. The burrows from LMSC were evenly divided as to direction of horizontal curvature (i.e., right or left), while the majority of the burrows studied by Hansen (1963) curved to the right. This difference may be indicative that curvature of the burrow is an individual variable or that it varies between populations.

Hansen (1963) found no significant pattern to the orientation of tortoise burrows. The compass orientation of the burrows on the LMSC site also had a random distribution, except in the north grove area. Of all the burrows on the site with entrances that opened on sloping ground, the majority faced down-slope to some degree. In the north grove, where no burrows faced south, the ground sloped downward to the east, north, and west only.

Excavation of the juvenile tortoise burrows provided evidence that hatchlings will dig their own burrows soon after emerging from the nest. Douglass (1978) felt that hatchlings did not dig burrows until after their first winter. A strong correlation existed between the carapace length of the juvenile tortoises and the length of their burrows. In addition, the ratio of burrow depth to length showed no difference from that exhibited by the burrows of older tortoises. Hatchlings are, in effect, isolated from older individuals as they receive no parental care and have no opportunity to learn how to dig a burrow. This isolation, coupled with the similar ratio of dimensions from all burrows, indicates genetic control of digging behavior in the gopher tortoise (Marler and Hamilton, 1966). This is not unexpected; however, there had been no previous description of burrows excavated by hatchling tortoises to confirm this.

Analysis of the vegetation provided no definitive answers for explaining the dispersion of the tortoises on the LMSC site. The islands were the most densely populated (10.4t/ha) of the three areas. The south grove had a tortoise density of 3.9 t/ha while the north grove supported only 1.5 t/ha. The biggest difference between the vegetation of the islands and of the grove areas was in the percentages of the shrubs and trees. However that would not account for the absence of adult tortoises in the islands.

APPENDIX I

The marking system used for the tortoises in this study is similar to the shell-notching method described by Ernst et al. (1974). Their system made use of the digits 1, 2, 4 and 7 and the multiples of 1, 10, 100 and 1000 for each as does this current system (Fig. 9) The advantage of these digits and their multiples is that most numbers from 1 to 10,000 can be used with four marks or less without resorting to the plastron. The marks they used were v-shaped notches made with a file. One disadvantage of that type of marking is that there is a possibility of mistaking damage to the shell for a mark.

The numbering system for this study has been used in work on the Nature Preserve at the University of Central Florida (UCF) since 1970. The marks that have been used for virtually that entire period have been drilled holes 2-3mm in diameter. The advantage to drilling holes is lack of confusion with natural shell damage. The holes could still be easily recognized after 15 years (Doonan, unpubl.).

Another advantage of the UCF system is its simplicity. Other systems for marking the shells of turtles are often complicated and are usually difficult to remember (Cagle, 1939). The current system divides the carapace into four regions, with the numbering following a similar pattern in each region (Fig. 9). The carapace is divided longitudinally at the midline and transversely at the bridge. In each region numbering begins closest to the midline and proceeds laterally.

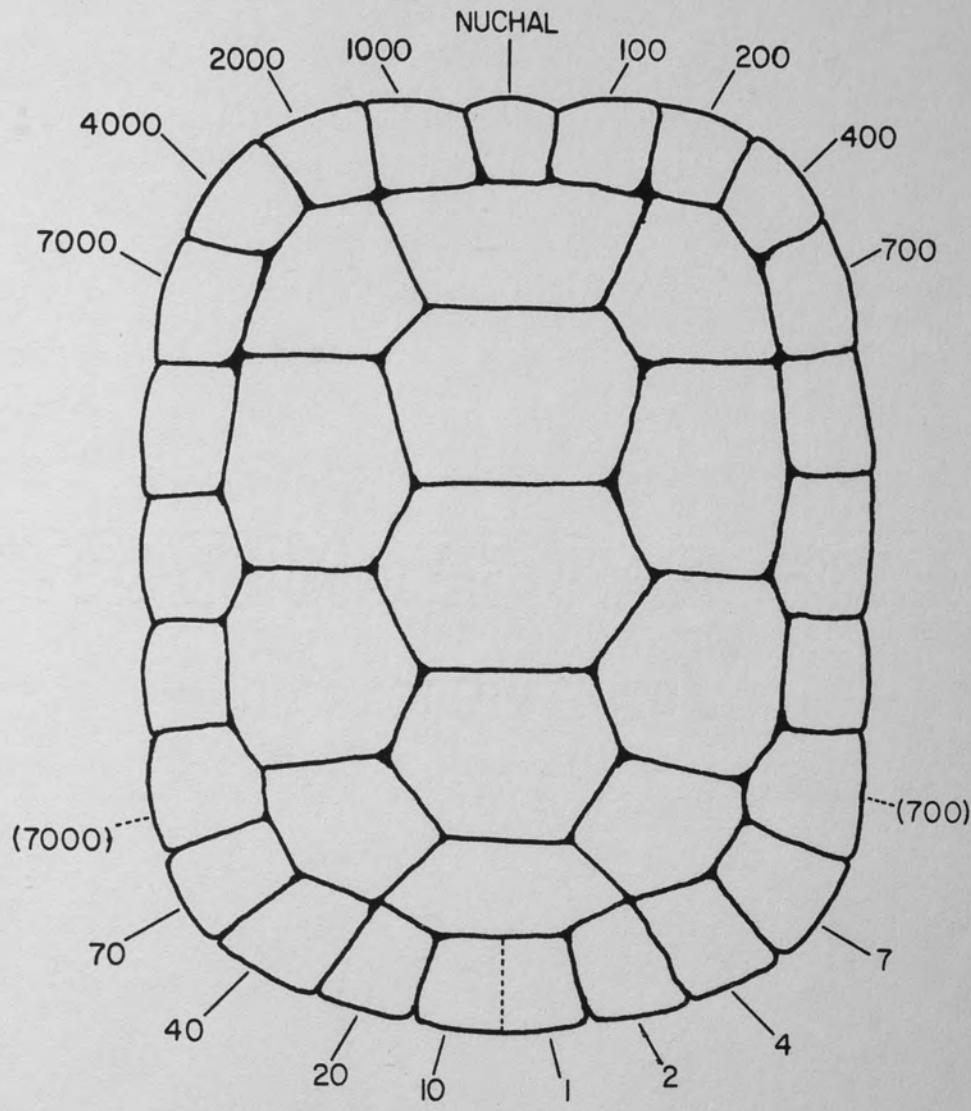

Fig. 9. Numbering pattern for marking tortoises and hard shelled turtles. A drilled hole, or a notch in the margin of a scute indicates inclusion of that number in the total (e.g., 4000 + 700 + 10 + 2 = #4712). Usually a maximum of only four marks are made on any one turtle. The numbers in parentheses are the optional location for those two numbers.

Anteriorly, the nuchal is not used and numbering begins to each side of it. Posteriorly, if there is a pygal scute (e.g., in the gopher tortoise) it is considered to be divided at the midline and both halves are used for numbering. If there is no pygal, the last two marginals are separated at the midline, and each begins the numbering sequence in their respective regions. It is the four regions, and the similar pattern of numbers in each region that makes this system easier to use.

One drawback to using drilled holes for the marks had been the necessity of bringing the animal back to the laboratory to mark it. The recent development of inexpensive, portable, cordless, rechargeable electric drills has made it possible to do this type of marking in the field. Drilling the holes is quick and relatively harmless to the turtles. Occasionally blood vessels are encountered with the drill, but leaving the spinning drill in the hole for 15-30 seconds seems to effectively cauterize the wound. The holes are drilled from the top down and an old soup spoon is used on the underside of the carapace as a shield to protect the turtles from injury when necessary. Tortoises with carapace length of less than 100mm have been drill-marked, though for the smallest tortoises notches are cut into the margin of the carapace with scissors.

The use of a drill for marking turtles means that the location of the bridge is more critical, and must be avoided. This is the reason there is an optional second location for the 7000 and 700 numbers. Because the basic system uses only four scutes to each side of the midline, a hole in the fifth scute from the midline at the posterior end of the carapace (or the fourth scute to one side or the other of the pygal) can be easily recognized as either 700 of 7000 depending on the side. This optional location would have to be used for gopher tortoises, and some Emydid turtles (e.g., Chrysemys floridanus).

APPENDIX II

Table 4. Age estimates predicted from the numbers listed as carapace length measurements that were inserted into the von Bertalanffy interval growth equation tht was fitted to the data from the LMSC gopher tortoise population.

Carapace length (mm)	Predicted age (years)
50	0.21
100	2.54
125	4.12
150	5.43
160	6.09
170	6.80
180	7.55
190	8.35
200	9.20
210	10.12
220	11.11
230	12.19
240	13.37
250	14.68
260	16.15
270	17.82
280	19.75
290	22.04
300	24.85
310	28.52
320	33.77
330	43.13
335	53.57
336	57.41
337	63.01
338	73.64

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SECTION II

ASSESSMENT OF A RELOCATION PROCEDURE FOR GOPHER TORTOISES

INTRODUCTION

Gopher tortoises, _Gopherus polyphemus_, have a preference for well-drained areas with deep sandy soils throughout their range in the Southeastern United States (Carr, 1952; Ernst and Barbour, 1972). Unfortunately, these areas are also prime sites for development. The increasing rate of development, particularly in Florida, has meant an increasing rate of tortoise habitat loss, and that has been the primary cause of decreasing tortoise numbers (Diemer, 1986). The gopher tortoise is considered a keystone species of these sandhill areas because the burrows it excavates are homes for a variety of commensals (Eisenberg, 1983). Extinction of the gopher tortoise will undoubtedly lead to the extinction of some other species dependent upon the shelter provided by the tortoise burrows.

One approach to reduce the conflict between development and the preservation of gopher tortoises would be to preserve tortoise habitat within development projects. In some cases, in situ preservation of tortoises will not be feasible. A possible solution to that problem may be to remove the gopher tortoises from those areas and relocate them to areas with suitable habitat that will not be developed and are capable of supporting additional tortoises (e.g., nature preserves).

An interim protocal for gopher tortoise relocation was written by the Florida Game and Freshwater Fish Commission in 1985. A pilot program was initiated in cooperation with the Department of Community

Affairs to evaluate relocation strategies. The present study is one of six relocation projects authorized as a part of that program (Don Wood, pers. comm.). The tortoises relocated in this study were removed from a tract of land scheduled for development as the Lake Mary Shopping Center (LMSC) in Lake Mary, Seminole County, Florida (see Sec. 1, this report).

The objective of this work was to study the feasibility of using relocated tortoises to establish new colonies or supplement existing colonies within predetermined release sites without disrupting resident tortoises. A literature review was conducted to compile relevant information from previous mitigation and relocation studies. These data were integrated with details of gopher tortoise biology to plan and evaluate the success of this project. I hypothesized that establishment of the tortoises within the release areas could be maximized if each tortoise was initially released into a small enclosure that contained a burrow as well as food. Three release areas were used. A subsample of the relocated and resident tortoises in each area were equipped with radio transmitters to document the results of the relocation.

METHODS AND MATERIALS

Study Area - - The tortoises from the LMSC site were moved to the University of Central Florida (UCF) during September-October 1985. UCF is approximately 24km (15 miles) from the LMSC site (Fig 1) in Orange County, Florida (28° 36' N, 81° 12' W), 21km (13 miles) east of downtown Orlando. UCF consists of 1227 ha of which 50-60% remains undeveloped. A parcel of land to the north of UCF as well as a large tract of land to the west of the campus also remain undeveloped at this time. The areas to the west and the south of UCF are currently undergoing development.

Three release sites, Areas A, B and C, were used on the UCF campus (Fig. 2). In describing these areas, and throughout this paper, the designation of vegetation associations follows Laessle (1942). The soil designations are from Leighty et al. (1960).

Of the three release areas, Area A initially seemed to be the best tortoise habitat. It was comprised mostly of sandhill and sand-pine scrub vegetation associations. The shrub layer was generally open with grass and other herbaceous vegetation present throughout the area. However, this area also suffered relatively greater disturbance from humans, primarily because it was bound to the west by a heavily traveled two-lane highway. There was also a ruderal section in Area A that formed the northern boundary. This was a firebreak that was partly bare sand and partly covered with weedy herbaceous vegetation.

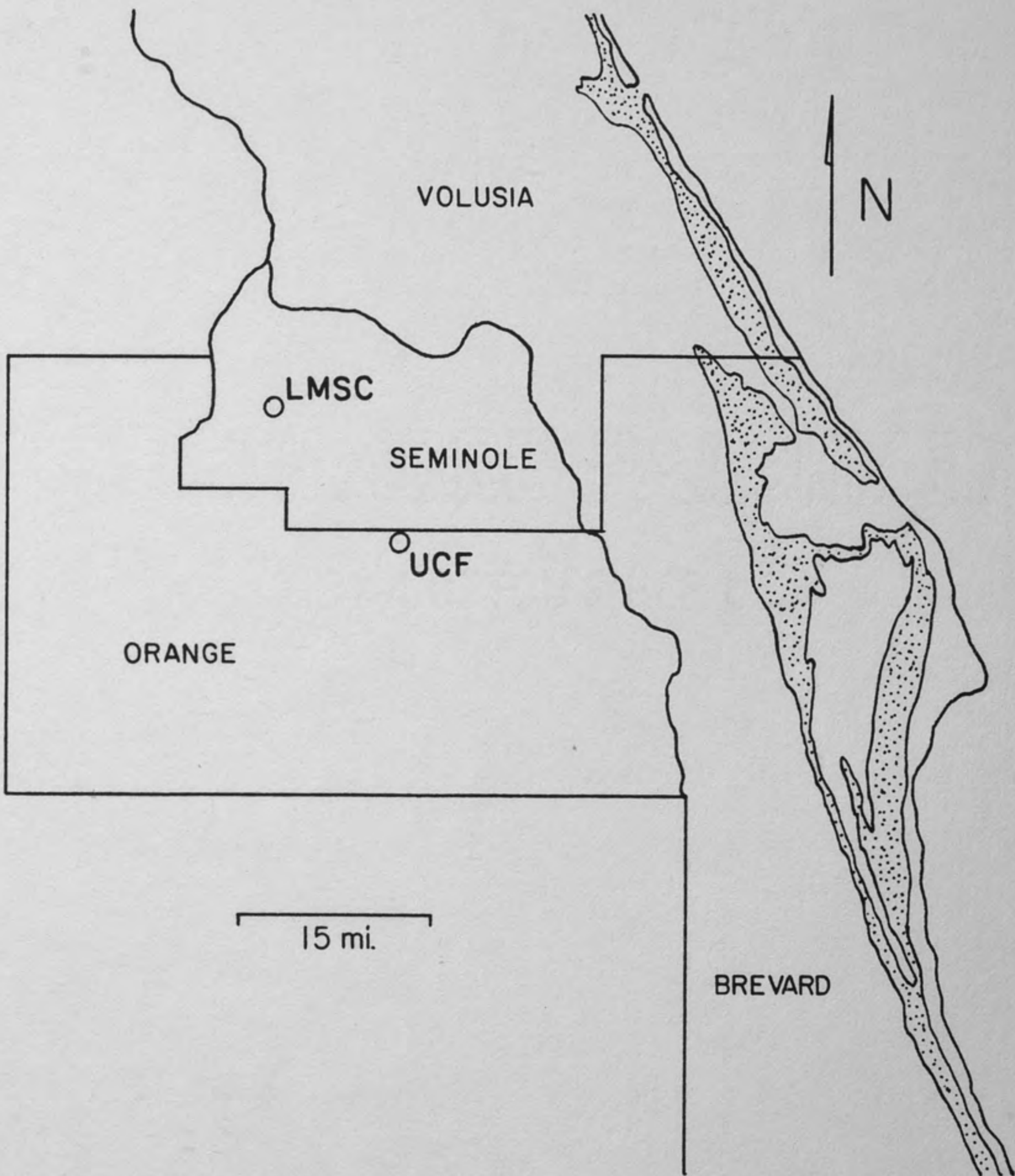

Fig 1. East Central Florida showing the location of the Lake Mary Shopping Center (LMSC) in Seminole County and the University of Central Florida (UCF) in Orange County. Stippled areas indicate Mosquito Lagoon and the Indian River.

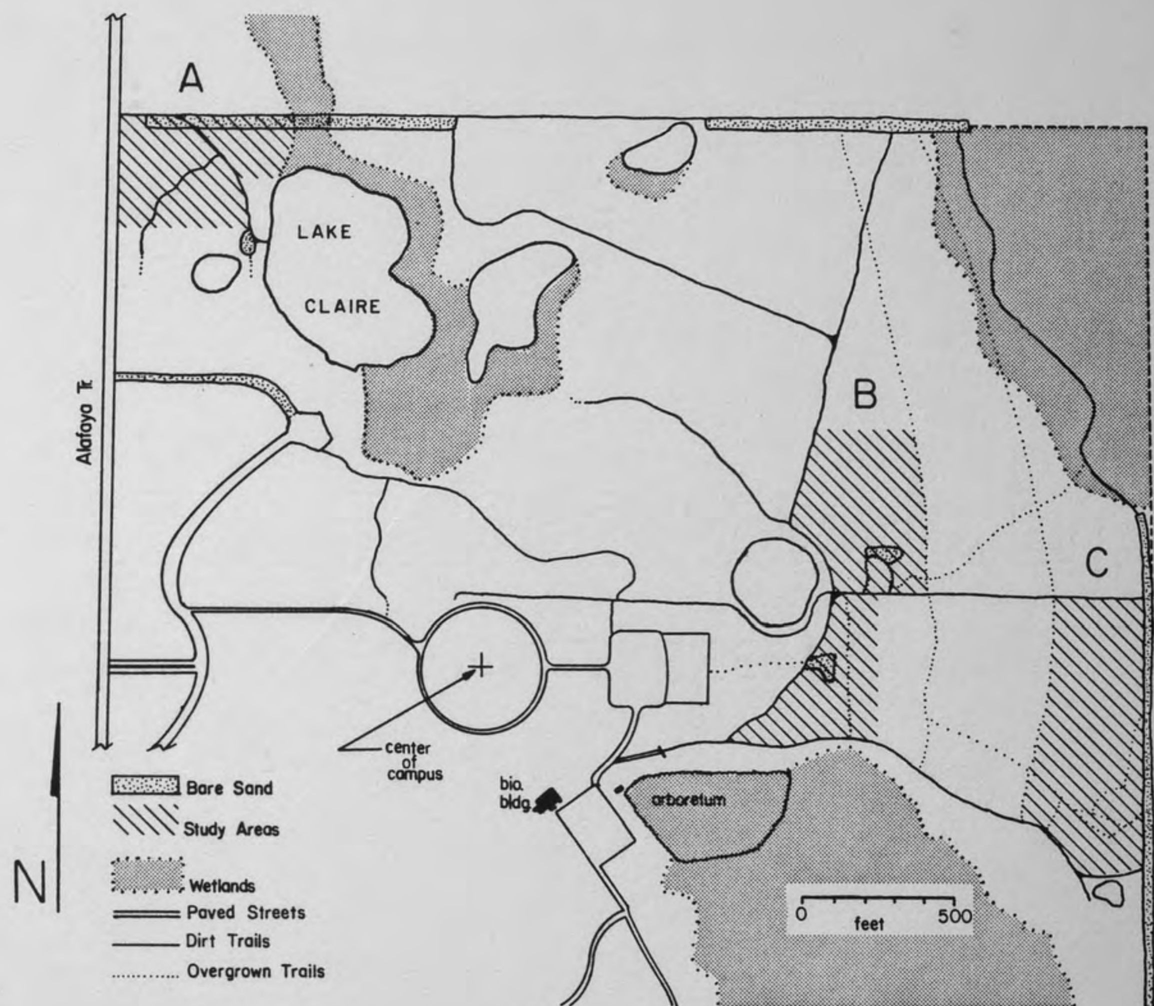

Fig. 2. Location of the 3 release sites (A, B and C) used for this study within the undeveloped area of the UCF campus. Developed areas are south and west of the center of campus, except for one parking lot to the east of that point.

It had originally been cleared ca. 1972, and was 10-15m wide with a 0.5-1.0m tall ridge of sand along its southern edge. The elevation in this area ranged from 20-23m (65-75 feet) above sea level (ASL). The soils were primarily Blanton sands, with some St. Lucie and Leon fine sand.

Area B encompassed scrubby flatwoods and sand-pine scrub. The shrub layer was generally thick, but patchy enough for there to be good forage for tortoises in some places. The section of Area B north of the trail running east-west (Fig. 2) was primarily sand-pine scrub. South of that trail, Area B was mostly scrubby flatwoods. The ecotone between the two habitat types was at, or just north of the trail. Elevations in this area were 20-21.5m (65 -70 feet) ASL. The soils were St, Lucie, Pomello, and a small area of Leon fine sand.

The eastern third of Area C was mostly true flatwoods and the remaining two-thirds was primarily scrubby flatwoods. The shrub layer was generally thick, especially in the true flatwoods sections. The relative density of grasses and herbaceous vegetation was greatest in the ecotones. Elevations ranged from 17-18.5m (55-60 feet) ASL. Soils were mostly Pomello fine sand.

Methods. - - Tortoises with carapace lengths (CL) of 150mm or greater were initially held in an outdoor temporary enclosure adjacent to the release sites. The enclosure was 3.75m X 3.75m and consisted of 50cm wide sheet metal sunk 10cm in the ground and supported by wooden stakes. The ground cover within the enclosure was primarily bahia grass. A shelter consisting of corrugated roofing panels set on 20cm (8 inch) concrete blocks was placed within the enclosure. Supplemental food (e.g., lettuce, corn, bananas, etc.) was provided regularly. The tortoises less that 150mm CL were maintained indoors in terrariums and also provided with supplemental food. Food preferences exhibited by the tortoises were recorded.

While the LMSC tortoises were in the temporary enclosure, a survey was conducted of tortoises resident within the release areas. Pit-fall traps (PFTs) were set at all active burrows (see Sec. 1 for a description of the procedure). Captured tortoises were measured as detailed by McRae et al. (1981a) and weighed. Age was recorded for tortoises on which the annuli of the abdominal scutes could be clearly read. After processing, each tortoise was returned to the place where it was captured.

Twelve of the tortoises relocated from the LMSC site were fitted with HMPCB-1110-LD radio transmitters (Wildlife Materials, Inc. Carbondale, Illinois), as were 13 tortoises from the resident population. Ten of the resident tortoises were collected during the trapping survey of the release areas and fitted with the transmitters at that time. The remaining three tortoises were collected from areas of the UCF campus near the release areas in order to compare their movement patterns with the other tortoises. The protocol for this study, dictated by the Florida Game and Freshwater Fish Commission, called for the radio transmitters to be evenly divided between adult males, adult females and sub-adults.

Transmitters were mounted on the marginal scutes of the carapace to left of the nuchal. They were attached with two, 3mm diameter machine screws inserted from the underside in holes drilled through the marginal scutes and the base plate of the transmitter. The area around the base plate and the ends of the screws was filled and smoothed with florist's clay. That area, as well as the screw heads, was then covered with Orthodontic Resin (L. D. Caulk-Dentsply, Milford, Delaware). This protected the tortoise from abrasion on the underside of the carapace and reduced the probability of the transmitter catching on obstructions. The antenna of each transmitter extended posteriorly around the left side of the carapace and was attached with Orthodontic Resin. Each transmitter operated on a separate frequency between 150.8 and 151.8 MHz.

The relocated tortoises were released between December 1985 and February 1986. Tortoises with carapace length greater than 150mm were released separately into enclosures 7.5m in circumference, containing a burrow and natural food plants. A burrow was either an old abandoned burrow cleared of debris and reopened or it was a hole newly excavated by hand at an angle of declination of approximately 30°. All of the burrows were either cleared or excavated to a depth at least twice the length of the tortoise that was to be released there. Each tortoise was released at the top of the slide, facing the entrance of the burrow. The slide is defined as the area leading up from the entrance to the top of the mound and is the path taken by the tortoise when entering and leaving the burrow. Those tortoises with carapace length of 150mm or less were released as two groups into larger enclosures, in the same manner. Four hatchlings, two yearlings, and 1 two-year-old were released into an enclosure in Area B that was 15m in circumference and contained 11 burrows of appropriate sizes. Two four-year-olds, 1 five-year-old, and 1 six-year-old tortoise were released into an enclosure in Area A of 22.5m circumference that contained seven burrows of appropriate sizes.

All of the tortoises equipped with radio transmitters were located at least twice per week. They were located with a three-element, folding Yagi antenna connected to a TRX-1000S receiver (both manufactured by Wildlife Materials, Inc. Carbondale, Illinois). Whenever relocated or resident tortoises without radio transmitters were encountered, their position and the time of day were recorded. All movements by the tortoises of 100m or less were recorded as straight line distances with a 100m tape measure. The compass angle of each of those movements was also recorded. The length and direction of movements greater than 100m were recorded from an aerial photograph of the area (1 inch = 200 ft.). The movements of each radio-tagged tortoise, and of other tortoises located at least three times, were plotted on grid paper. The total distance moved, exclusive of feeding forays, was determined for each radio-tagged tortoise. In addition, an estimate of range size was calculated for each radio-tagged tortoise with the minimum polygon method (McRae et al., 1981b) using a Graphics Tablet connected to an Apple II computer. In instances when the only recorded movements for a tortoise were linear, the longest of those movements was used as the radius of a circle for calculating the range size.

In May 1986, measurements were taken of all burrows that were determined to be either active or inactive according to the criteria of Auffenberg and Franz (1982). The height and width of those burrows were measured 25-50cm inside the entrance. The angle of declination of each burrow and the compass orientation of the entrance were also recorded. Any prominent fixed object such as a tree or large bush, a fallen log or a palmetto stem within 1m of the burrow entrance was noted.

Data collection for this study was terminated on 20 June 1986 for a preliminary evaluation of the success of this relocation procedure. This coincided with the approximate end of the nesting period (Iverson, 1980; Landers et al., 1980), Tortoise movement patterns have been reported to become more widespread and less stable after the nesting season (McRae et al., 1981b).

Throughout this paper, tortoises will be referred to by number. Those tortoises with numbers $\geq$ 400 are from LMSC, while those with numbers $\leq$ 200 are from UCF. Temporary shelters, other than burrows, used by tortoises in this study will be referred to as either pallets or forms. A pallet is a shallow excavation which may be only deep enough to cover the anterior half of the tortoise or it may be large enough for the entire tortoise to be covered (Auffenberg and Weaver, 1969). A form is a shelter just large enough to conceal the tortoise located beneath dead palmetto fronds, pine needles or other vegetation, usually in the shade, in which little or no digging is done (Ernst, 1986).

RESULTS

Tortoise Densities. -- During the trapping survey of the resident tortoises, many old and abandoned burrows were seen in each of the three release areas, and it appeared as though all three areas had previously supported higher levels of tortoises. A total of 40 tortoises were collected from the active burrows in the three release areas (Table 1), although that probably did not account for all of the tortoises that used those areas.

Six juvenile tortoises were collected from the ruderal section of Area A, more than from both of the other two areas (Table 1). In Area A the density of the residents was 2.6 tortoises per hectare (t/ha) prior to the release of the LMSC tortoises. After their release, the maximum possible density would have been 4.8 t/ha.

The majority of the tortoises collected from Area B were in the scrubby flatwoods or in the ecotone. Over 50% of the resident tortoises collected during the trapping survey were from this area, with the majority being adults (Table 1). The only sub-adult tortoise (#149) collected during the trapping survey was also from Area B. The density of resident tortoises was 2.8 t/ha, and after the release of the LMSC tortoises the density was 4.5 t/ha.

Only two resident tortoises were collected from Area C (Table 1), though at least 15-25 old burrows were located there. Some of those burrows were still partly open, while others were completely blocked

Table 1. Size of the release areas used in this study and the distribution of resident (UCF) amd relocated (LMSC) gopher tortoises among those areas. A = Adults, S = Sub-adults, J = Juveniles and H = Hatchlings.

Release area	Size of the area (ha)	LMSC	UCF	Totals
Area A	5.03	2 A	6 A	8 A
		2 S	1 S	3 S
		7 J	6 J	13 J
Area B	8.93	3 A	21 A	24 A
		2 S	2 S	4 S
		6 J	2 J	8 J
		4 H	0 H	4 H
Area C	7.14	3 A	2 A	5 A
		4 S	0 S	4 S
		6 J	0 J	6 J
Totals		39	40	79

by leaf-litter and sand. The tortoises, and most of the old burrows were in the scrubbier sections of Area C. The density of resident tortoises collected from this area was 0.14 t/ha, and after the release of the LMSC tortoises the density was 2.1 t/ha. During the second week of January several of the old burrows in Area C were observed filled with water within 20cm of ground level because of heavy rains the previous week.

Between 1969-1972, 75 tortoises from the UCF property were marked. During this study, three of those tortoises, all females, were recaptured. One (Tortoise #40) measured 219mm CL in July 1970, and 247mm CL in March 1986. The second (Tortoise #99) measured 148mm CL in June 1971, and 228mm CL in November 1985. The third measured 200mm CL in December 1971, and 221mm CL in April 1986.

Release of LMSC Tortoise. - - Of the 46 tortoises from the LMSC, only 39 were eventually relocated to the release sites at UCF. Three escaped the enclosure and three were stolen. One juvenile (6 years old) died just prior to release. It had been in the outdoor enclosure, but was indoors and appeared healthy up until the time it died.

I attempted to divide the 39 LMSC tortoises evenly among the three release areas (Table 1). However, the hatchlings, and the three youngest juveniles were released together in Area B. The other four young juveniles were released together in Area A. Of the two adult females, both from the south grove area of LMSC (see Sec. 1), one was released in Area B and one in Area C. For the remainder of the tortoises, whenever possible I released those collected close together at LMSC in the same release area.

Eighty percent of the enclosures used for the release of the LMSC tortoises were left in place from 5-15 days. The minimum period was three days and the maximum was 24 days, not including the enclosure used for the hatchlings and juveniles in Area B. That enclosure was left in place for 77 days because several of those tortoises had done little digging at the burrows and were therefore somewhat exposed to predators. Data on the enclosure of the radio-tagged tortoises (Table 2) indicates little correlation between the period they were enclosed and the length of time they remained at their release burrows before abandoning them ($r = 0.367$, d.f. = 10, $P > 0.05$).

There were three principal behavior patterns exhibited by the relocated tortoises while confined within the enclosures. Some went into the burrows and there was no subsequent sign of activity until the day they abandoned the burrows. The radio-tagged tortoises that exhibited this behavior were Nos. 464, 475, 471, 435 and 480 (Table 2). On the other extreme were tortoises that were active during the time the enclosure was in place, digging in the burrow and moving around the enclosure. The radio-tagged tortoises that exhibited this behavior were Nos. 467, 458 and 474. The remaining tortoises exhibited behavior intermediate between these two extremes. Generally they moved about the enclosure but did little or no digging.

Once the enclosures were removed, most of the tortoises abandoned their release burrows within a week. The only tortoise that used its release burrow (an old burrow that was reopened) throughout this study was a juvenile (#472) in Area A. Tortoise #458 (Table 2) actively used its release burrow (also old and reopened) longer than any other tortoise except #472. Little was seen of the other relocated tortoises after the enclosures were removed, though newly excavated burrows were located in all three release areas, and other burrows that had been inactive or old showed new activity. However, few sightings of the tortoises themselves prevented a determination of the level of establishment by the LMSC tortoises, especially the juveniles. Of the hatchling and juvenile tortoises from the enclosure in Area B, only one (a hatchling) continued to use the release burrows for any length of time. The hatchling's burrow continued to remain active for two months after removal of the enclosure, and then became inactive with no evidence of disturbance. One month after the enclosure was removed, both of the yearling tortoises were found dead on the surface of the ground within a week of each other. They were within 3m of the area were they had been released. There were no signs of injury, though ants (species unknown) were found feeding on both carcasses. Both yearlings exhibited little activity while the enclosure was in place. The four juveniles from the large enclosure in Area A left the burrows they were using as soon as the enclosure was removed. One, #469, was located five weeks later using a newly excavated burrow 35m northwest of where the enclosure has been.

Tortoise Movements. - - The pattern of movements exhibited by the radio-tagged tortoises from the UCF population showed considerable individual variation (Table 3). A comparison at each of the four time intervals of the average distance moved by the adult females with the average for the adult males indicated no significant differences. The difference between males and females for average distance from the release point was also not significant ($t = 0.47$, d.f. = 10, $P > 0.05$). As of 20 June, the maximum distance moved by a male was 642m, and the maximum distance moved by a female, excluding tortoise #162, was 576m. Tortoise #162 was the only UCF tortoise that was lost (lost = could not be located within 2km of the release area). For the calculation of average movements, a figure of 2000m was used for this tortoise. The distance moved by the only sub-adult at each of the four time intervals, and its distance from the release point as of 20 June were within the range for those measures exhibited by the adults.

It may be significant that two of the radio-tagged UCF tortoises (#40 and #99) exhibiting the least movement (Table 3) had originally been captured and marked 15 years previously. During this study, tortoise #40 was recaptured ca. 400m from where it was released in 1970 and tortoise #99 was recaptured ca. 300m from where it was released in 1971.

Two UCF tortoises (#151 and #147), both adult males, were located in the same burrow on 9 December 1985. They were then located in separate burrows 12 times from 10 December-4 January 1986. On

Table 3. Cumulative movements, excluding feeding forays, for each radio-tagged gopher tortoise from the resident (UCF) population. Distance from the release point is the approximate distance, as of 20 June 1986, from the tortoise's position to its point of release as determined from an aerial photo of the area. >2km indicates the tortoise could not be located within 2 kilometers of the release area.

Age group	Tortoise number	Month re-released	Distance moved (m)				Distance (m) from release pt.
			At end of one month	At end of two months	By 1 June	By 20 June	
Adult female	40	March	43	43	43	43	40
	99	November	0	14	98	121	0
	142	January	25	25	25	25	20
	144	November	130	130	218	576	130
	158	December	65	65	235	333	160
	162	February	205	250	>2km	>2km	>2km
	166	April	11	11	11	11	11
Adult male	145	December	172	172	642	642	480
	147	December	28	28	290	290	15
	151	November	149	280	452	490	0
	155	November	257	257	437	554	135
	168	May	132	---	132	132	120
Sub-adult	149	December	0	200	344	455	25

4 January they were again located together in a burrow. Between that time and 19 January they were located in separate burrows on five occasions, before again being located together in one burrow on 21 January. From 21 January-21 February they were located 11 times together in that burrow. They were not located together after 21 February. They had originally been captured at burrows that were within 50m of each other, and were always located within 200m of each other throughout this study.

After abandoning their release burrows, 50% of the radio-tagged LMSC tortoises initially moved eastward, between 46°-135° (Table 2). The initial movements of the remaining radio-tagged tortoises were evenly divided among the other three cardinal directions. The movement patterns of the radio-tagged LMSC tortoises varied between individuals (Table 4), but because of small sample sizes for adult females, within population statistical comparisons could not be done. As of 20 June, the average distance moved by the adult females was 867m. For adult males the average was 863m, including a figure of 2000m for #471 and #474, both of which were considered lost. The average distance moved by the four sub-adults was 968m as of 20 June. The average distance from the release point for the adult females was 685m. That average for the males was 784m. The sub-adults's average distance from the release point of 217m was markedly less than that of the adults. These could not be compared statistically because of the small numbers of females and sub-adults.

Table 4. Cumulative movements, excluding feeding forays, for each radio-tagged gopher tortoise from the relocated (LMSC) population. Distance from the release point is the approximate distance, as of 20 June, from the tortoise's position to its point of release as determined from an aerial photo of the area. ?-Indicates the tortoise could not be located at that time. *-Tortoises that moved out of the release area, were returned and re-released. >2km-indicates the tortoise could not be located within 2 kilometers of the release area.

			Distances moved (m)				
Age Group	Tortoise number	Month enclosure removed	At end of one month	At end of two months	By 1 June	By 20 June	Distance (m) from release pt.
Adult female	476	January	130	130	142	947	830
	458	January	0	0	442	787	540
Adult male	468	February	0	41	1056	1310	180
	464	November	0	27	609	638	175
	425	February	61	94	184	252	210
	475	February	0	77	157	157	140
	471	February	0	250	>2km	>2km	>2km
	474	February	118	118	160	>2km	>2km
Sub-adult	432	February	?	1890	*2315	*2530	---
	435	February	0	0	87	187	115
	466	February	215	222	*540	*811	---
	480	February	0	0	95	345	320

In Fig. 3, the population averages for the cumulative movements of the radio-tagged tortoises from the LMSC are shown along with those of the radio-tagged tortoises from UCF at each of the four time intervals used in Tables 3 and 4. Note that only after one month was the average movement by the UCF tortoises greater than that for the LMSC tortoises. The differences were compared statisticaly, and found to be significant at the end of one month ($t = 2.62$, d.f. = 22, $P < 0.05$) and not significant at the end of two months ($t = 0.75$, d.f. = 23, $P > 0.05$) or as of 1 June ($t = 0.86$, d.f. = 23, $P > 0.05$). As of 20 June, the difference was again significant ($t = 2.46$, d.f. = 23, $P < 0.05$). The difference in mean distance from the release point as of 20 June for the radio-tagged tortoises from each population was also compared statistically, and not found to be significant ($t = 1.69$, d.f. = 21, $P > 0.05$).

The movements of the radio-tagged tortoises from both populations were analyzed by month on the basis of average number of movements per tortoise, and the average distance per movement (Fig. 4). The tortoises from both populations exhibited relatively fewer movements in February-March than in any of the other months, though the variation in the distance per movement was less pronounced. The means from both populations for each parameter, over the months January-June, were compared by analysis of variance. There was significant variation between the means for movements per tortoise ($F = 2.32$; $d.f._1 = 11$, $d.f._2 = 113$; $P < 0.05$). To determine if the difference between populations was significant for any month, pairwise comparisons were

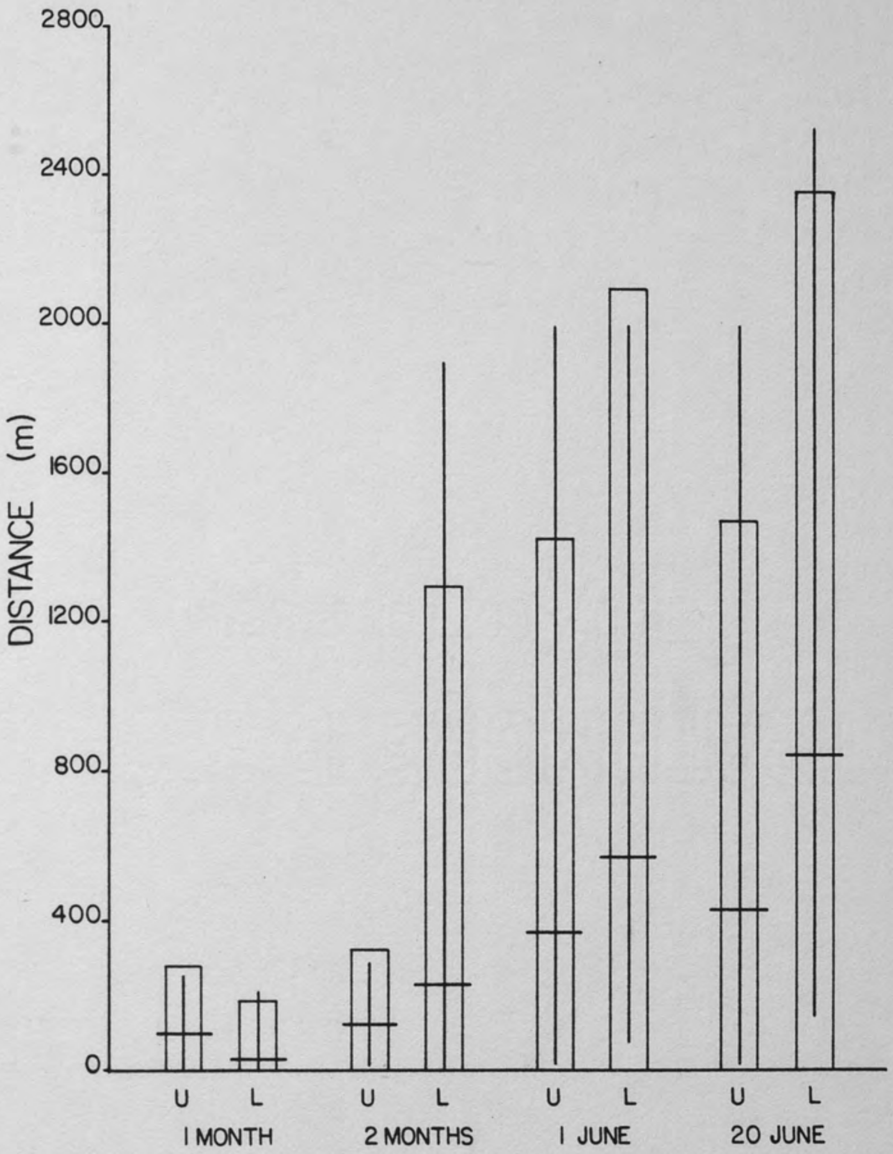

Fig. 3. Average cumulative movement of the radio-tagged tortoises at four time intervals following their return (U = UCF) or the removal of their enclosure (L = LMSC). Horizontal lines represent the means and the vertical lines the ranges. The open boxes represent two standard deviations of the mean, truncated at zero.

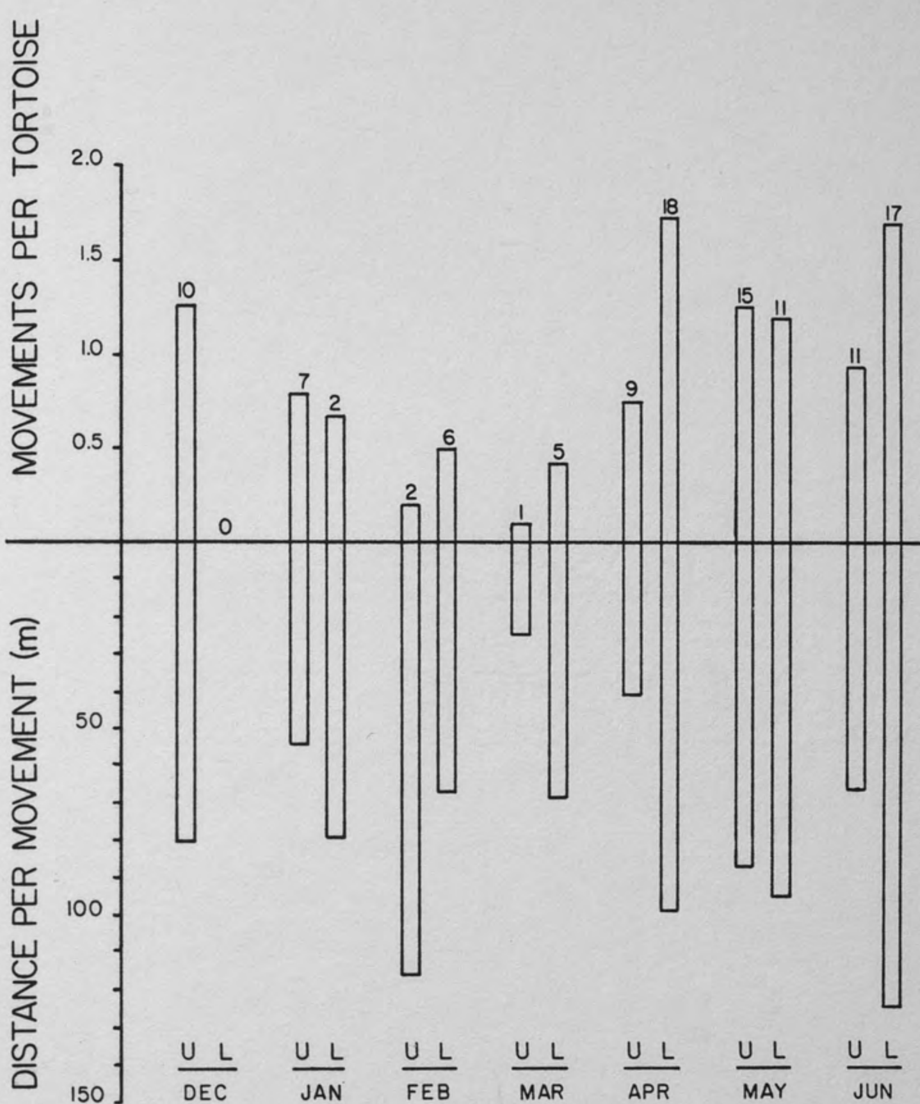

Fig. 4. Monthly comparison of the average number of movements per tortoise, and the average distance per movement for the radio-tagged tortoises from the resident, UCF population (U) and the relocated, LMSC population (L). The numbers above each bar indicate the sample size (i.e., number of movements) for both averages.

conducted using the Tukey-Kramer procedure (Ott, 1984). Significant differences were found in April ($W = 0.98$, $P < 0.05$), and in June ($W = 0.78$, $P < 0.05$). The variation in the means for distance per movement was not significant ($F = 0.89$; $d.f._1 = 11$, $d.f._2 = 92$; $P > 0.05$).

The size of the activity ranges used by the radio-tagged tortoises from both populations are reported in Table 5. The average range for each population was calculated and the difference was not significant ($t = 1.65$, $d.f. = 19$, $P > 0.05$). The difference in average range of the radio-tagged males from each population was also tested and not found to be significant ($t = 0.63$, $d.f. = 9$, $P > 0.05$. Because of small sample sizes, the ranges of the adult females and the sub-adults were not compared statistically between populations. However, the ranges of both LMSC females were greater than those for any of the UCF females, while the range sizes for the sub-adults from both populations were similar (Table 5).

I considered the relocations of four LMSC tortoises (Nos. 474, 471, 466, 432) to have been dispersal failures (Leopold, 1933) because they were either lost (i.e., could not be located) or moved off the UCF property and had to be returned and re-released. Below I detail the movements of those four tortoises as well as several of the other LMSC tortoises in order to more completely describe the variety of movement patterns they exhibited.

Tortoise #471: released in Area A; abandoned its release burrow; first movement was 250m north to another burrow; stayed at that burrow

Table 5. Area of the ranges used by radio-tagged gopher tortoises from the resident (UCF) and the relocated (LMSC) population, as of 20 June. LOST indicates tortoises which could not be located within 2 km of the release areas.

UCF			LMSC		
Age group	Tortoise number	Area of range(ha)	Age group	Tortoise Number	Area of range(ha)
Adult female	40	0.02	Adult female	467	10.09
	99	0.02[a]		458	3.83
	142	0.01	Adult male	468	11.58
	144	119		464	2.91
	158	1.00		425	0.55
	162	LOST		475	0.25
	166	0.04[a]		471	LOST
Adult male	145	2.94		474	0.68[b]
	147	0.64	Sub-adult	432[c]	----
	151	0.29		435	0.42
	155	0.54		466[c]	----
	168	415[a]		480	0.59
Sub-adult	149	0.41			

[a]Areas calculated as the area of a circle (see methods).

[b]This area was calculated as of 3 June, after which the tortoise was LOST.

[c]No areas were calculated because those tortoises had to be re-released.

three weeks, exhibited little activity; left that burrow and could not be located.

Tortoise #474: released in Area A; active within 100m of its release burrow for four months; used two other burrows during that time; located once 125m north of that area, then could not be located.

Tortoise #432: released in Area A; temporarily lost (Table 4); moved more than 2000m south along the highway through several intersections; found in an area of relatively undisturbed long leaf pine-turkey oak vegetation at the south end of the UCF campus; left that area and crossed the highway; returned to Area C and re-released.

Tortoise #466: released in Area C; moved 465m east over seven weeks off the UCF property; located several times using forms but no burrows; reached a bayhead area bordering a stream, and was returned to Area C and re-released.

Tortoise #467: left release burrow almost immediately; moved 130m to an old burrow, stayed there four months; began a series of long movements in June (800m over approximately three weeks); used no burrows, only forms.

Tortoise #468: left release burrow, moved 26m to old burrow; used that one month; moved 1030m in one month - first went northwest, then south, then southeast; stopped at old burrow; stayed one month then moved 15m to burrow often used by #99; stayed there four days; moved to old burrow, 180m from release burrow.

Tortoise #425: left release burrow; never used another burrow, only forms; moved through scrubby flatwoods, into true flatwoods; used first form for one month, second for 1.5 months; used five other forms 1-3 weeks each.

Tortoise #464: used release burrow six weeks, left when heavy rains raised water table and flooded burrow; moved 28m and dug a pallet; stayed there five weeks, little activity; moved to old burrow, stayed three weeks; moved 275m southeast, then 275m east within one week; ended at old burrow.

Tortoise #458: used release burrow 93 days; over two weeks it moved to a form, to an old burrow, to a burrow used by #158 (stayed at that burrow one week, #158 never went back), and back to its release burrow; stayed at release burrow three weeks; moved 600m northwest over 10 days; ended at old burrow in thick flatwoods near bayhead.

Tortoise #480: left release burrow; moved 100m to old burrow; stayed there two months; moved 150m to a form, in flatwoods, next to (< 15cm from) #425; #425 had moved 225-250m to get there; both at that form one week; #480 moved 100m east to old burrow, scrubby flatwoods; #425 moved 15m northeast to a form.

Burrow and Tortoise Measurements. - - Measurements taken from active and inactive burrows in the three release areas at UCF were compared to similar measurements taken at LMSC (Sec. 1). The average ratio of burrow height to width from UCF was 0.49. This is not significantly different ($t = 0.75$, d.f. = 94, $P > 0.05$) from the average of 0.53 for that ratio from LMSC. The average angle of declination (23.7°) for the UCF burrows was significantly different ($t = 1.97$, d.f. = 105, $P < 0.05$) from the average for the LMSC burrows (28.1°). The orientation of the UCF burrows was not significantly different from a random pattern of orientation ($X^2 = 8.92$, d.f. = 3, $P > 0.05$), which was also true for the LMSC burrows (Sec. 1). I also compared the placement of the burrows on the two sites relative to fixed objects. At the LMSC, 85% of the burrows were not located near a fixed object. At UCF, 65% of the burrows were located under, next to, or within 1m of a fixed object. For burrows occupied by tortoises at UCF, the ratio of carapace width to burrow width was 0.72. That was compared to the ratio of 0.77 from LMSC and found to be significantly different ($t = 2.38$, d.f. = 59, $P < 0.05$).

The average for the ratio of tortoise thickness to tortoise width was 0.57 for the UCF population, exactly the same as the average for the LMSC tortoises. The average carapace length of the UCF adult male tortoises was 241.5mm which was not significantly different ($t = 0.38$, d.f. = 18, $P > 0.05$) from the average carapace length of 252.8mm for the adult male LMSC tortoise. The same comparison was done for the adult female tortoises, and the average of 229.3mm CL for the UCF population was not significantly different ($t = 0.54$, d.f. = 12, $P > 0.05$) from the LMSC average of 286.0mm CL. A size frequency distribution of the resident, UCF tortoises was compiled for comparison with a size frequency distribution for the LMSC population (Fig. 5).

Over 50% of the UCF population were adults (CL $\geq$ 22.8cm, see Sec 1 for explanation), while over 50% of the LMSC population were juveniles (Sec. 1). A size frequency distribution of the combined population that resulted after the release of the LMSC tortoises is shown in the lower graph of Fig. 5.

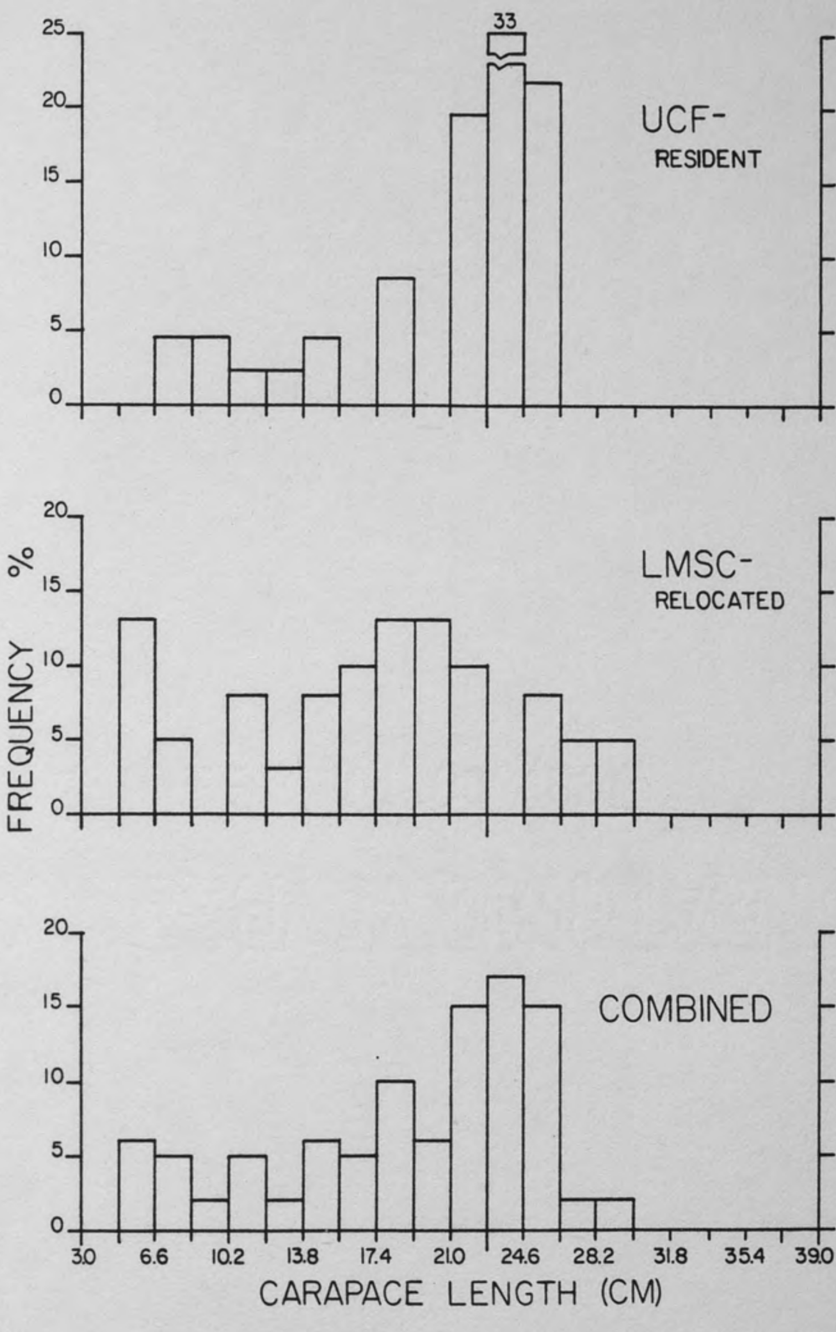

Fig. 5. Relative distribution of size classes for the resident tortoises from the release areas at UCF (top), and the relocated tortoises from LMSC (middle). At the bottom is the relative frequency for the combined populations after the release of the LMSC tortoises. Carapace length intervals of 1.8cm follow Alford (1980).

DISCUSSION AND CONCLUSIONS

Based on the vegetation associations of the three release areas used in this study, the carrying capacity for tortoises in those areas should have been sufficient for the residents and the relocated tortoises. Auffenberg and Franz (1982) reported densities as high as 10.23 t/ha within colonies from longleaf pine-turkey oak (LLP-TO) habitats and 26.61 t/ha within colonies from ruderal areas. Auffenberg and Iverson (1979) reported an average density of 5.45 t/ha for LLP-TO habitat, and they reported four densities from sand pine scrub sites that ranged from 3.11-6.94 t/ha. There is no previously published report for tortoise density in scrubby flatwoods habitat.

In assessing carrying capacity for gopher tortoises, the vegetation association of an area does not appear to be as important as the percent ground cover of grasses and other herbaceous plants that serve as food for the tortoises (Auffenberg and Iverson, 1979; Garner and Landers, 1981). Data presented by Auffenberg and Iverson (1979) for nine sites in Georgia and Florida show a significant correlation ($r = 0.760$, d.f. $= 7$, $P < 0.05$) between tortoise density and percent basal cover by grasses. Though the percent basal area of herbaceous vegetation in the three release areas was not quantified, it was considered to be of sufficient density to support the LMSC tortoises being released in those areas. While the density of food plants was sufficient to support the relocated tortoises it may have affected their movements; however, that could not be determined. A continued lack of prescribed burning in the UCF natural preserve areas will undoubtedly lead to a decrease in the density of herbaceous plants in the future. Fires are considered important for tortoise habitat management because they increase the density of food plants (Diemer, 1986). A long-term decrease in the density of the grasses and herbs will probably cause the emigration of tortoises from portions of the release areas (Aufenberg and Iverson, 1979).

Use of the enclosures when releasing the LMSC tortoises did not cause them to become established at those burrows. I initially believed that in suitable habitat, forcing the tortoises to utilize the release burrows for a short period of time would increase the rate of establishment at those burrows. The lack of correlation between enclosure period and establishment period indicates that is not the case. It is possible that if wire-mesh hardware cloth (Orr, 1966) had been used for release enclosures instead of the sheet metal the rate of establishment could have been increased. A tortoise's behavior while within the enclosure was not indicative of its behavior once the enclosure was removed. Even those tortoises which actively excavated the release burrow usually remained at the release burrow for only a short period of time after the enclosure was removed.

R. Lohoefener (pers. comm.) stated that the instances of successful establishment he had when relocating groups of gopher tortoises in larger ($\leq$ 15m dia.) enclosures occurred when he used hand started burrows within the enclosure, even though none of the tortoises became established at those burrows. The hand started burrows used in this study seemed to be acceptable temporarily and, although it is possible the movements of some tortoises may have been influenced by a drive to seek-out natural burrows, the hand started burrows should be provided as a source of shelter for relocated tortoses when natural burrows are not available.

When 50% of the radio-tagged LMSC tortoises oriented their initial movements eastward upon removal of the enclosures it was probably not due to homing, as the LMSC is northwest of UCF. It may be that this tortoise population exhibited nonsense orientation. Matthews (1966) described nonsense orientation as a situation in which the majority of a population, when released, initially displays orientation in a direction other that that of home. It is also possible tht this apparent eastward orientation by the LMSC tortoises was simply the result of random chance. Gourley (1969) in open field tests with gopher tortoises found that while 56% of the animals exhibited non-random orientation, not associated with the direction of home, there was no population specific consistency to this orientation.

To evaluate the movements of the LMSC tortoises, they should be compared to previously published averages for tortoise movements as well as to the movements exhibited by the UCF tortoises. McRae et al. (1981b) reported that the mean feeding radius of the adult tortoises they studied was 13m, with 95% of all feeding within 30m of the burrow. They also stated that for sub-adults, 95% of all feeding was done within a radius of 25m. They stated that the average home range of adult males was 0.45 ha and for females it was 0.21 ha. Auffenberg and Iverson (1979) reported an average recapture radius of 46.8m for adult males and 28.3m for females, and that the recapture radius is inversely related to percent herbaceous ground cover.

The majority of the radio-tagged LMSC tortoises exhibited movements much greater than these averages Only tortoises #475 and #435 may have used feeding radii similar to the published figures, though that was not verified by sightings. The remainder of the radio-tagged LMSC tortoises moved in more linear patterns. The majority used a burrow (or form, or pallet) for a short period of time and then moved on to a different location. Comparison of the activity ranges for the LMSC tortoises in Table 5 with the published figures does not seem accurate in itself. The minimum polygon method generated relatively small ranges for the LMSC tortoises which moved in relatively straight lines. It may be that the most accurate analysis of the movements exhibited by the LMSC tortoises can be achieved by evaluating both the area of the range and the distance from the release point as of 20 June. This seems to indicate that tortoises #475, an adult male, and #435, a sub-adult, were probably the most stably established of the radio-tagged LMSC tortoises.

There was no indiction why the tortoises from both populations exhibited a greater number of movements in December and January than in February and March. Auffenberg and Iverson (1979) reported the average monthly movements of tortoises from Alachua County, Florida over bi-monthly periods. In their work, the average movements for tortoises of 201-300mm CL (the size range that includes all but one of the radio-tagged tortoises in this study) were lowest in January-February, and highest in May-June. It may be that the greater number of movements exhibited by both populations in the current study for December-January was a response to the handling they had undergone to mark them and attach the radio transmitters.

Comparison of the cumulative movements exhibited by the UCF and the LMSC tortoises showed a statistically significant difference after one month, and as of 20 June (Fig. 3). However, only after one month was the average for the UCF tortoises greater than that for the LMSC tortoises. That may have been due to the UCF tortoises being in familiar territory while the LMSC tortoises needed a period of acclimation before actively exploring the area. As of 20 June most of the LMSC tortoises had moved greater over-all distances than had the UCF tortoises, and that is consistent with the significant differences in number of movements for April and June between the two populations (Fig. 4). The differences in distance per movement were not significant, which seems to indicate that the tortoises of both populations were moving similar amounts each time they moved, but the LMSC tortoises were moving move often. The average ranges of the two populations were not significantly different partly because there was considerable variation within both populations.

Analysis of movement patterns of all the radio-tagged tortoises in Area A seems to indicate that area may not be a suitable habitat for gopher tortoises. Of the five radio-tagged tortoises released there, three were lost (2 LMSC, 1 UCF), one (LMSC) had to be returned to another area and re-released, and only one (UCF) remained in Area A. The level of human disturbance in Area A may have been a factor in causing increased movement as the LMSC tortoises were from a relatively isolated site (see Sec. 1). Griffo (1961) felt that the artificial movement of animals could cause a form of stress and bring about 'a search for familiar territory'. Griffo's hypothesis could explain the situation in Area A as well as the relatively longer movements exhibited by a majority of the radio-tagged LMSC tortoises in this study. The presence of the highway adjacent to Area A was probably a contributing factor to the loss of all three tortoises because the relatively clear shoulders of the road would expedite movement in a linear pattern. McRae et al. (1981b) stated that open areas along the edge of roads produced more linear movements by tortoises when feeding.

The radio-tagged tortoises were located every 3-4 days, and when they could not be located the search was extended at least 2000m in all directions. Thus if a tortoise was lost it was probably because either the transmitter failed, or the tortoise had moved out of range of the receiver in that 3-4 day period. While it cannot be proven that all of the lost tortoises moved our of range along the highway, the loction of #432 over 2000m south of where it was released in Area A, indictes such movements were possible.

There is a possibility the UCF tortoise that was lost, #162, was really a transient. Kiester et al. (1982) defined a transient as an individual that does not remain in any area, but seems to continually move, generally in a linear manner. Tortoise #162 was captured near the edge of the highway, and remained near the highway until it was lost. Dispersal of gopher tortoises along highways in this manner could be important for maintaining gene flow between populations (Kiester et al., 1982). In addition, otherwise isolated populations could be effectively connected by these right-of-ways to form a network of populations (Noss and Harris, 1986).

The use of forms and pallets by tortoises from both populations in this study seems to indicate that their movements may not always be restrained by the presence of burrows. Tortoise #145 moved almost 400m through flatwoods over a week and was located twice using forms. Tortoise #162 was locted once using a pallet almost identical to the one excavated by tortoise #464 after it left its release burrow. The degree to which the LMSC tortoises utilized forms and pallets was probably greater than should be expected from an established resident population with access to burrows. However, the use of these shelters by gopher tortoises may be relatively more common among established populations than had been previously expected. Douglass and Layne (1978) observed overheated tortoises moving under leaf-litter to reduce heat stress. The lower layers of leaf-litter are generally moist and could provide the same type of protection against water loss that the burrow provides. In sand pine scrub and sandhill habitat the sand is often damp 10-20cm below the surface and a shallow pallet could serve to reduce water loss in the same manner.

Movement patterns of the radio-tagged LMSC tortoises seemed to have been influenced by old, partly overgrown firebreaks and trails that are common throughout the undeveloped areas of the UCF property. These old trails provided relatively vegetation free paths, and the tortoises seemed to show a preference for them. When locating the radio-tagged tortoises I was repeatedly walking along these paths. Although the tortoises may be simply taking the course of least resistance, it is also possible that they interpret those paths as cues for orientation. Gourley (1969) reported that trails made by the tortoises during their normal movements appeared to be the primary method used for orientation during short range movements. It has also been shown that gopher tortoises will use vehicle trails in their movements (Douglass and Layne, 1978; McRae et al., 1981b). On the UCF property the resident tortoises are a relatively common sight along the vehicle trails, however because none of the tortoises in this study were equipped with trailing devices (McRae et al., 1981b) to mark exact movements, the extent to which the resident tortoises utilize the paths and the vehicle trails during long-range movements could not be accurately determined. Three of the radio-tagged UCF tortoises (Nos. 145, 158, 155) exhibited moves of 100m or more. Of those three, #145 apparently did not make use of paths while moving within a flatwoods area. Tortoise #158 made use of sections of the vehicle trails but probably did not use any of the other paths. After being returned to the burrow where it was captured, tortoise #155 (an adult male) apparently followed a path along an old firebreak approximately 135m to an active burrow previously observed being used by an adult female. When #155 was next located three days later, it had apparently followed the path back again, as it was in another burrow within 15-20m of the burrow where it had been released.

The average angle of declination of the burrows and the average ratio of a tortoise's carapace width to the width of its burrow measured at UCF, were significantly different from similar measurements recorded at LMSC (see Sec. 1). The difference in the angle of declination may be due to different soils at UCF relative to LMSC. None of the UCF burrows were excavated, but several old burrows in scrubby flatwoods habitat which had partially collapsed could be traced for 2-3m along the ground, as though they remained within one meter of the surface for at least that distance. This may have been due to the presence of a hard, organic pan layer of soil that was impenetrable to the tortoise. Leon and Pomello soils are both Ground-Water Podzols underlain by this type of hard-pan layer that generally begins 0.5-1.5m below the surface (Leighty et al., 1980). This would also account for the flooded burrows seen in Area C, as these soils have relatively poor drainage.

The difference in the ratio of carapace width to burrow width between UCF and LMSC may have been a result of burrow placement. Many of the UCF burrows were located near trees or palmetto stems, while the majority of the LMSC were not located near any object. The wider cross section of the UCF burrows relative to the LMSC burrows could be due to the tortoises moving laterally to avoid roots. The tortoises from the two populations were identical in the ratio of thickness to width of their shells, thus the proportions of the tortoises's shells could not be affecting the width of the burrows.

Although no quantitative analysis of predator species was done, observations and signs of known tortoise predators (Douglass and Winegarner, 1977; Ernst and Barbour, 1972; Auffenberg and Iverson, 1979) were noted. Armadillos seemed to be the most common tortoise predator in all three areas. Digging by armadillos was frequently seen on the mounds of active and inactive tortoise burrows. Two juvenile hogs (Sus scrofa) were seen in Area B, and tracks and rooting from hogs were seen regularly in Area C. Raccoon tracks were frequently seen, especially in Area B. Oppossum tracks were seen occasionally in Areas B and C. The only species of snake encountered during this study was Coluber constrictor. Although these snakes were frequently observed in all three areas, all were less than 1m snout-vent-length and therefore unlikely to prey upon tortoises.

The size frequency distribution for the UCF population seems to indicate that this population has a low rate of recruitment. Only ca. 20% of the population was smaller than 17.4cm CL. Most of the predator species seen on the UCF property are nest predators, and that may be one cause of the low rate of recruitment. The frequency distribution for the combined population that resulted after the release of the LMSC tortoises appears more robust. Thus if the LMSC tortoises become established, they may serve to effectively restock the UCF property by producing a more typical balance between juveniles and adults in the population.

In assessing the success of the relocation procedure used in this study, the rate of establishment by the LMSC tortoises must be evaluated. In all three release areas, a greater number of active burrows were seen after the relocation than prior to it. However, only the establishment of the radio-tagged tortoises can be clearly determined. Of those, eight (67%) were established on the UCF property as of 20 June without having to be re-released. Over the summer as tortoise movements become longer and less predictable (McRae et al., 1981b) it seems possible that other currently established LMSC tortoises may move off the UCF property, thus bringing the establishment rate down to, or below 50%. Landers (1981) stated that just under half of all relocated tortoises should be expected to become established at the release areas. Only four of the eight radio-tagged tortoises on the UCF property were within the release areas (one in Area B and three in Area C) as of 20 June. Using Leopold's (1933) list of possible outcomes for the translocation of game species, I believe that the preliminary evaluation of this relocation project should be as either a dispersal or straggling failure, or a colony survival. A true evaluation of this project will be possible in 2-3 years when current reproductive success can be assessed to determine if there has been an increase since the relocation of the LMSC tortoises.

Because the current rate of development occurring in Central Florida is expected to continue through the forseeable future, it should be expected that a large number of tortoises will need to be relocated. Thus, potential release sites throughout the state of Florida should be identified now. Release sites should be protected areas with suitable habitat such as state and national parks and wildlife management areas. Those sites should then be surveyed to determine their actual quality and the potential number of tortoises which could be stocked there. The costs and time that would be needed to prepare those sites for the release of tortoises would have to be determined, and when possible they should be passed on proportionally to those groups (developers, etc.) creating the problem. Permanent enclosures should be established within, or adjacent to those release areas. This will permit holding the tortoises for site acclimation, and ensure proper captive maintenance of the tortoises. A grant proposal to the Non-Game Fund of the Florida Game and Freshwater Fish Commission could be a source of financing for this type of work.

Relocation programs are expensive, time consuming, and labor-intensive (Noble, 1958; Conover and Chasko, 1985; McArthur, 1981; O'Bryan and McCullough, 1985; Diemer, 1984). In some cases relocation programs are ineffective solutions to problems caused by human interactions (Fritts et al., 1984; McArthur, 1981), and they may produce more problems than they are designed to solve (Kushlan, 1980;

Petrides, 1968). Regardless, the reloction of gopher tortoises will often be seen as the best solution to enviromental problems, which have no easy solutions. Case by case decisions will be required to adequately address all pertinent factors. In every case though, relocation should only be considered as the last alternative. The goal for tortoise preservation should be to integrate reasonable sized areas of suitable tortoise habitat into development projects whenever possible. Those patches of natural habitat should be planned in ways that would enable them to serve as additions to statewide natural habitat corridors. Inducements for developers such as tax rate reductions or similar financial benefits may promote the maintenance of on-site natural areas within developments.

APPENDIX I

Food Preferences. - - Maintaining the LMSC tortoises in the temporary outdoor enclosure provided the opportunity to observe their preferences in food items they were, and were not, familiar with. Large patches of bahia grass had been present at the LMSC, and the bahia grass within the enclosure was completely eaten by the tortoises. Passion flower (Passiflora incarnata) was a common plant on the LMSC, and often appeared cropped in areas where the tortoises were concentrated. Passion flower fruit that were brought back from LMSC on several occasions were always eaten by the tortoises in the enclosure.

Bruised and damaged vegetables and fruit were obtained and used as supplemental food for the tortoises in the outdoor enclosure. Food items the tortoises seemed to prefer the most included lettuce and other green leafy vegetables except cabbage, watermelon with the rind, bananas (and sometimes the peel), yellow crook-neck squash, grapes, oranges including the rind, and corn on the cob (and sometimes the husk from the corn). The corn on the cob was usually the first food eaten if present. Other foods that were eaten less readily included green beans, okra, apples, cabbage, and butternut squash. Onions and potatoes were the only foods that the tortoises consistently did not eat.

The fact that the tortoises showed definite preferences for some food items while in the temporary enclosure was not completely unexpected. Garner and Landers (1981) stated that tortoises in the wild will preferentially take higher quality (in terms of nutrients and palatability) food items including soft fruits and berries when they are available. It could not be determined if the color or shape of some food items affected the choices made by the tortoises. The bananas, crook-neck squash, and corn on the cob were yellow, similar in shape and seemed to be preferred by the tortoises. The apparent preference of the tortoises for passion flower (Passiflora incarnata) fruit may be significant. There appeared to be some correlation between tortoise density and the density of passion flower plants at the LMSC, though was not tested. The viability of passion flower seeds retrieved from tortoise scats remains to be tested.

APPENDIX II

<u>Behavioral Interactions</u>. - - There were no serious interactions between tortoises while they were in the temporary enclosure. Some confrontations occurred, generally when one tortoise was more aggressive and initiated the action. While bobbing its head up and down, the aggressor would approach a second tortoise and begin to butt that tortoise with its gulars. This behavior was generally of short duration and usually ended when the second tortoise moved. Males, females and sub-adults were all observed initiating this type of behavior, but it was usually initiated by tortoises newly introduced into the enclosure. Size was not always a factor in determining which tortoise would initiate the action. Sometimes a smaller tortoise would confront a larger one in this manner. On one occasion I observed a larger tortoise apparently become tired of a smaller aggressor after being butted several times. The larger one raised itself up with its hind legs, pushed forward and got its gulars under the side of the smaller one. With another quick push forward it flipped the smaller one onto its back. The larger tortoise then quickly repeated the action, and flipped the smaller tortoise right-side up again.

Other interactions observed between tortoises in the enclosure involved mounting behavior by the males. They did not always attempt to mount females, and even juveniles were sometimes mounted. On several occasions tortoises were observed attempting to mount the front or side. Neither of the adult females ever appeared receptive when males attemped to mount them. The smallest male (extruded penis observed) that exhibited mounting behavior was 195mm CL.

At night all of the tortoises in the outdoor enclosure generally congregated under the shelter. This was especially true during the periods of colder weather, though it could not be determined if the tortoises did this for conservtion of heat. During periods when the air temperture was 5-10°C at night, I attempted to insulate the tortoises by piling straw on the shelter and around the edges of it. Fresh cut green grass was a better insulating material because it would generate a small amount of heat, but there was never enough available. This insulation method maintained temperatures under the shelter 2-5° C above the ambient temperature at night, and worked well as long as the temperature during the day reached 20-25° C. In January after three days continued cold weather with overcast skies when the daytime temperature did not rise above 10-15° C, the tortoises were moved indoors.

The fact that no serious confrontations occurred within the temporary enclosure was probably due in part to the time of year they were confined. The enclosure was relatively small in size ($14m^2$) and a larger enclosure would undoubtedly have been needed if the same tortoises were held in that manner during the breeding season when the mating and competitive interactions between tortoises tend to become more aggressive (Carr, 1952; McRae et al., 1981b).

The incidences of mounting behavior observed in the enclosure may not be aberrant in themselves. Douglass was cited in Landers et al. (1980) as reporting courtship behavior by male gopher tortoises through the fall. The attempted mounting of other males and juveniles could have been due to the unusually close proximity of a large number of other tortoises. There have been no reports of similar captive behavior by gopher tortoises.

The successful maintenance of these tortoises outdoors during part of the winter may indicate that this type of maintenance for gopher tortoises is possible where winter weather is not severe. Complete outdoor winter maintenance could be successful in Central Florida if a wind resistant shelter that contains some type of heat source is provided.

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