

ORIENTATION OF THE GOPHER TORTOISE,
Gopherus polyphemus (DAUDIN)

By

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CHAPTER I

INTRODUCTION

Animal orientation may be defined as the ability of animals to find their way. Griffin (1952) classified it as follows: landmark orientation: reliance upon landmarks in or near familiar territory; compass orientation: maintenance of a certain direction by reference to celestial bodies; and navigation: ability to choose the correct homeward direction in unfamiliar territory. It is well known that celestial cues provide the information to an animal for maintenance of the direction in the second case, and there is good evidence that the third process occurs (Schmidt-Koenig, 1965). Thus it is obvious that there must exist some ability to compensate for the change in azimuth of these celestial bodies. This time-compensation is possible because animals have internal clocks (Hoffman, 1965).

Although much work has been done on orientation in animals (Cold Spring Harbor Symposia XXIV, 1960; *Ergeb. der Biol.* XXVI, 1963; *Animal Orientation and Navigation*, 1967), many problems, particularly in long-range orientation, remain unresolved. One of these is the question of the distribution and character of celestial orientation among species, genera, and

classes of vertebrates. Much evidence has been obtained with arthropods and birds, but little has been reported for the lower vertebrate classes.

There are considerable data that turtles are capable of landmark orientation (Ortleb and Sexton, 1964). There are also some reports that turtles are capable of compass orientation and perhaps of navigation by means of celestial cues (Gould, 1957, 1959; Fischer, 1964). However, Emlen (1965) could find no evidence to support either of these in Chrysemys picta, one of the species which Gould (1959) reported to be capable of navigation.

A terrestrial turtle that seems to be appropriate for orientation study is the gopher tortoise, Gopherus polyphemus, found in the southeastern United States. It makes burrows in which it dwells. These burrows provide relatively constant conditions of temperature and humidity, and are goals to which the tortoise regularly returns after foraging. Because these goals are small targets, the tortoises must have a precise means of finding them. This situation does not hold for other terrestrial or pond turtles, in which the homing drive may be only to regain contact with a somewhat diffused home range. Other advantages offered by the gopher tortoise as a subject

for orientation studies are that it is slow-moving, and thus easier to track accurately; and that it is diurnal, which permits the elimination of nocturnal celestial cues from consideration.

The aims of the present study have been as follows:

1. To establish the size of the home range in a population, in order to restrict the field of search for the cues which the tortoises may use for short-range orientation.
2. To determine some of the short-range cues used.
3. To determine the presence and accuracy of the internal clocks of the gopher tortoise.
4. To determine the existence and nature of any celestial orientation mechanism in this species.

CHAPTER II

HOME RANGE

There are several reasons for determining the home range of a population of gopher tortoises prior to studying the orientation mechanism itself. If it is found that the animal moves only short distances in its daily or seasonal wanderings then cues that are effective only over great distances can be discounted and attention focused upon the local cues. Second, if the home range can be clearly determined, then the set of stimuli potentially available to the tortoise for orientation can better be determined. Third, allowance can clearly be made for the fact that the tortoise may use more complex forms of orientation outside its home range but may rely upon simpler forms of orientation within its home range.

Home range is defined by Durt (1943) as "the area, usually around a home site, over which the animal normally travels in search of food." Homing cues are probably more plentiful inside the home range than outside it. In any case, successful return to the burrow must require fairly specific guidance information.

Method

A common method of determining the limits of a home range is to mark and release the animal, then to recapture it repeatedly. Because the gopher tortoise lives in a long, deep burrow, and when disturbed might remain in the burrow for at least four weeks, this method was not used. Instead, each of nineteen inhabited burrows at the Gainesville Municipal Airport (Alachua Co., T 9S, R 20E, S 24) was excavated, leaving the mouth and first four feet undisturbed. The tortoise was displaced a short distance from the mouth and allowed to wander for a period up to thirty minutes. Each tortoise was displaced six to ten times. Successful return to the home burrow was taken to mean that the tortoise was familiar with the intermediate area. The maximum displacement that still resulted in successful homing was regarded as an indicator of the size of the home range.

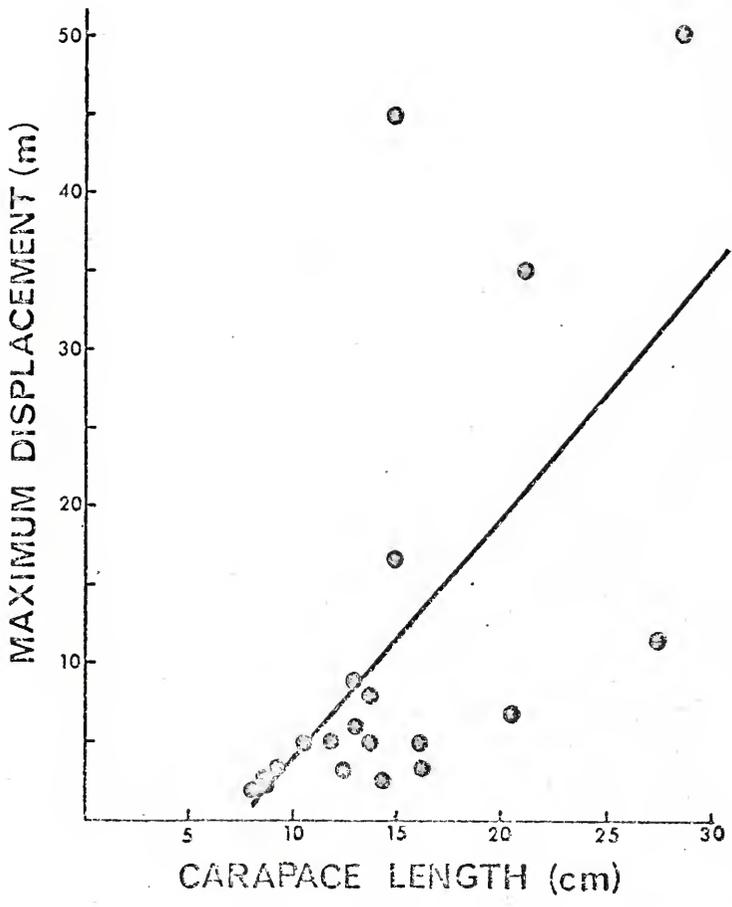
Results

In setting up the tests it was foreseen that three results might be obtained. First, the tortoise could return to its home burrow. Second, it could move to another burrow. Third, the tortoise might wander but not go to any burrow, even though its movements took it near burrows that appeared to be suitable. All three of these results were obtained, although under somewhat different circumstances.

The first possibility occurred when the displacement from the home burrow was 2.3 to 30 meters. The maximum displacement for an individual that resulted in a return to the home burrow varied directly with its age, determined by carapace length (Figure 1). This distance corresponded precisely with the maximum distance between the home burrow and the feeding areas. The feeding areas were apparent because of the closely-cropped vegetation. The tortoises had clearly delineated trails between their feeding areas and the home burrows.

The second possibility was obtained when a tortoise was displaced just beyond the feeding area. Tortoises with carapace lengths less than 12 cm proved to have no other burrows beyond the feeding area, but the larger tortoises

Figure 1. Relations of the size of tortoises and the maximum distances displaced from home burrows which resulted in direct return. Line is least-squares regression.



headed toward one of a number of other burrows. These burrows were from 6.7 to 100 meters from the home burrow. The distance from the home burrow to the most distant other burrow was directly related to the age, expressed as carapace length (Figure 2). There were few trails between the feeding areas and these other burrows. Such trails were much less distinct than the trails near the home burrow.

When the tortoise was displaced further from the home burrow than the most distant secondary burrow, the third possibility was realized. Small tortoises without other burrows gave this result when displaced beyond their feeding areas.

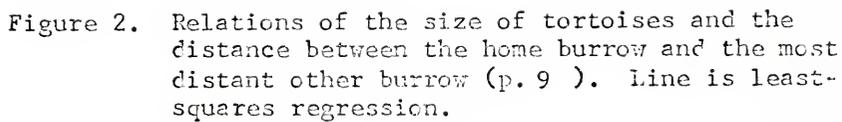
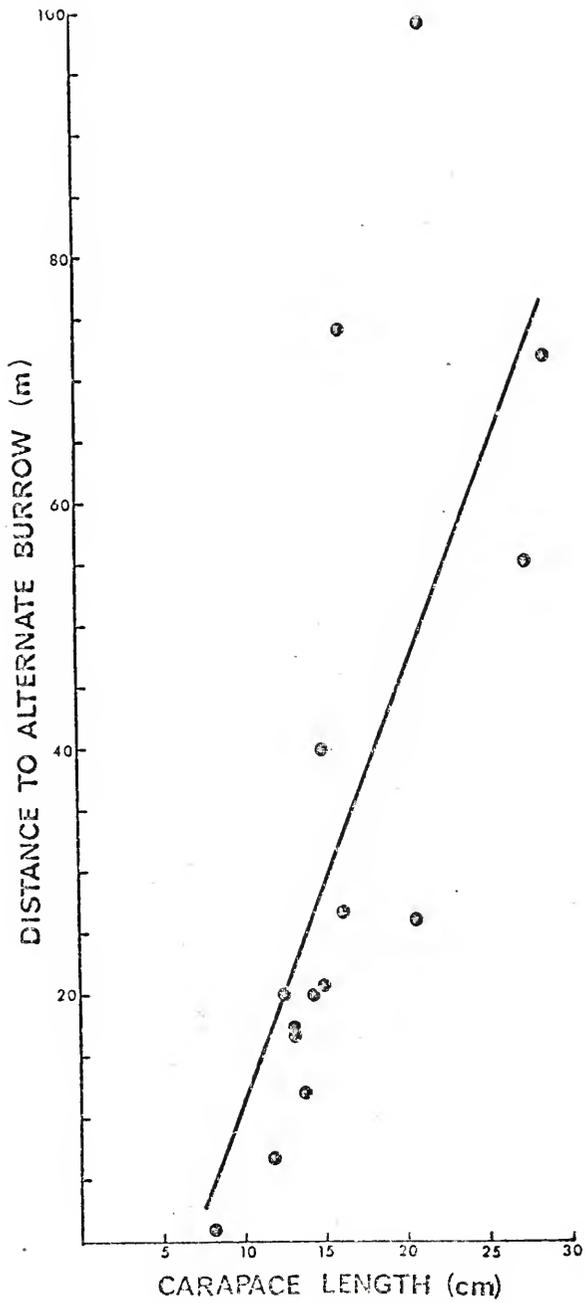


Figure 2. Relations of the size of tortoises and the distance between the home burrow and the most distant other burrow (p. 9). Line is least-squares regression.



Discussion

From the data, the dimensions of the home range of G. polyphemus may be estimated by several methods. The direct homing distance, which correlated well with the distance between the outer edge of the feeding areas and the home burrow, may be used as an indication of either the radius or the diameter of the home range, depending upon whether the home burrow was centrally or eccentrically located. This gave a home range area of 14.2 m^2 for the smallest tortoises and 6447 m^2 for the largest tortoises, providing that the burrow was centrally located. In the case of eccentrically located burrows, the home range areas varied from 4 m^2 to 1659 m^2 . If, on the other hand, the distance to the most distant other burrow is used as the criterion, then with a central burrow the home range is from 4 m^2 to $31,400 \text{ m}^2$.

Oliver (1954) stated that G. polyphemus seldom wanders further than 100 feet from the burrow, but this does not help to resolve the question of which criterion to use. The home range of G. agassizii varies from 10 to 100 acres in southwestern Utah. Differences in the size of the home ranges of these two species are undoubtedly attributable to

1) differences between the species, 2) differences in distribution of the food supply, and 3) to differences in the methods by which Woodbury and Hardy (1948) and I made the estimates involved. Their data does suggest that direct homing distance underestimates the size of the home range, and that calculations using the maximum distance to another burrow give a more valid area.

Further evidence of the value of distance to other burrows as a criterion of the size of the home range is suggested by the data of Blair (1951) on Peromyscus polionotus leucocephalus. The home range of this mouse normally contained 20 burrows. A mouse would rely upon five or six of these to escape predators. A parallel situation is obvious in the gopher tortoise. Blair (1951) also found that the animal was likely to be recaptured more often in certain parts of its home range than others, suggesting that not all parts of its home range are equally utilized. The areas used more often were generally near the present home site.

It could be argued that the tortoise spends most of its time above ground near the home burrow, and only occasionally wanders to the extremes of its home range. The trail systems are well maintained near the burrow, but few obvious

trails are found between the home burrow and the secondary burrows. If this interpretation is correct then several questions are raised. Which tortoise constructed the secondary burrows? Does a tortoise construct several burrows in succession and then abandon them in favor of other burrows which are built nearby? Or are these alternate burrows the work of tortoises that made them and then died or emigrated during courtship, or at some other time?

The following circumstantial observations support the idea that a tortoise will construct a number of burrows. In one burrow with a length of only 4 feet, a 20.3 cm tortoise was found. This burrow was extremely short for a tortoise of that size in that area. Also, there was little dung in the burrow and no arthropods were present. In another case a tortoise was taken from a long burrow (18 feet) in which there were few arthropods, and in which the grass in the mound piled at the mouth was still green, indicating that the burrow had been recently constructed.

On the other hand, there is also considerable evidence that tortoises will remain in their burrows for considerable lengths of time. Of 16 tortoises that were returned to their home burrows after these had been excavated, four were found in these same burrows eight months later. In each case the

tortoise had extended its burrow beyond its original length. Three other tortoises were recovered in freshly dug burrows--each of which had little or no dung at the bottom. Two tortoises were recovered from burrows which had been regarded as secondary burrows during the displacement tests. The burrowing history of the other seven tortoises was not known.

Why would a tortoise normally abandon a burrow?

Environmental conditions affect the habitability of the burrow. If the surrounding food supply decreased below a certain threshold the tortoise would have to emigrate. Also, if a tortoise wandered far afield during courtship and was not strongly motivated to return, or was unable to regain its home range, the burrow would be abandoned.

From the above I conclude that the home range of the gopher tortoise is relatively small. The larger tortoises are familiar with the positions of a number of secondary burrows, but it is not clear whether these burrows are the product of one tortoise or of several. Obviously, much work needs to be done on even some of the fundamental aspects of the life history of this species.

CHAPTER III

SHORT-RANGE ORIENTATION

The most readily observed feature of the home range of Gopherus polyphemus, besides the burrow, is the trail system converging on most of the burrows. The trails appear to be of primary importance in the short-range orientation of the gopher tortoise. The fundamental question as to how the original trail-blazing orientation was achieved still remains obscure. Once laid, the trails may provide visual, olfactory, and tactile cues.

In general, turtles have a good sense of vision (Walls, 1942), although they are probably not as sensitive as birds and mammals. They are able to discriminate form (Casteel, 1911) and color (Quaranta, 1952). Furthermore, most studies on turtle orientation have regarded visual cues as most important (Ortleb and Sexton, 1964).

Although olfaction has been shown to be important in the orientation of other lower vertebrates (fish: Wisby and Hasler, 1954, Groot, 1965; salamanders: Twitty, 1959), no experiment has yet shown that this sense is important in

turtle orientation. However, a number of reports suggest that olfaction may be important in the life of many species of turtles: Poliakov (1930) conditioned three European pond turtles, Emys orbicularis, and Boycott and Guillery (1962) conditioned red-eared turtles, Pseudemys scripta elegans, to discriminate between organic compounds. Allard (1949) attempted and failed to demonstrate that box turtles, Terrapene carolina, could discriminate between burlap-wrapped rocks and fish. Ortleb and Sexton (1964) were unable to show that the painted turtle, Chrysemys picta, could distinguish between "aromatic" water, i.e., water in which plants were grown, and plain tap water.

Eglis (1962) described head-bobbing movements in tortoises when they were presented with a novel food item. He had no other reasonable hypothesis for this behavior and attributed it to an olfactory response. Auffenberg (1965, 1966) described similar head-bobbing in three species of tortoises (Geochelone carbonaria, Geochelone denticulata, and Gopherus polyphemus) during courtship. He attributed this to a visual recognition cue evolved from the original responses to olfactory stimuli. He further demonstrated the importance of olfaction in tortoise courtship by rubbing

cloacal secretions on the rear of a skeletonized shell and eliciting attempts at mounting by a male. Based on experimental evidence, Weaver (1967) concluded that in Gopherus berlandieri head-bobbing was primarily an olfactory response. Electrophysiological recordings from the nasal epithelium of G. polyphemus (Tucker, 1963) demonstrated that stimulation by amyl acetate, benzyl amine, butyric acid, and geranoil elicited neural responses. These observations clearly show the potential importance of olfaction in the life of turtles.

Any short-range orientation by the gopher tortoise probably involves the use of visual or olfactory cues. Because the trails surrounding the burrows can provide such cues, I regarded the trails as the primary source of short-range orientation information to the tortoise.

Methods and Materials

Experiments with Artificial Trails

In an attempt to determine whether running on familiar trails would account for the successful short range orientation of the gopher tortoise, I made test trails outside the home range of the experimental subjects. Before a tortoise establishes a distinct trail system around the burrow, it must be able to return to the burrow, and if the trails are the important devices by which the return is made, the tortoise must be able to follow cues which are not obvious to a human observer. To test this possibility, trails which were discernable to me only as strips of bent-down grass were formed by dragging a sandbag in a series of straight lines, each 60 feet long, through a grassy field. Each of ten tortoises was tested on one of these trails.

The trail systems surrounding most burrows were much more distinct than the artificial trails formed by dragging the sandbag. To simulate a well-established trail a series of straight paths 60 feet long were cut with a grass clipper in the grassy field. Each of ten tortoises was tested on a single trail. The natural trail systems of

the tortoise consist of intersecting paths, rather than of a series of straight trails. To approximate this condition in the experiment artificial trails were cut at right angles to the original cut trails.

Another series of cut trails were made to investigate behavior on complex trail systems in another way. These were Y-shaped, with each arm 2 feet long. The floors of two of the arms were covered with Benchkote, a paper that is absorbent on one side and has a plastic coating on the other side. This permitted the manipulation of possible odor trails by moving the Benchkote. Ten of these trails were provided for tests with each of twelve tortoises. The starting positions and the arm down which the tortoise was to be forced to run were predetermined and all tortoises followed the same sequence of starting positions and turns.

Procedure

Each tortoise was placed at one end of a straight trail and the distance it travelled before it completely left the trail was recorded. For the indistinct trails, where there was potential directional information from the warp of the grass, each tortoise was started at both ends of the trail.

Each tortoise was placed at the end of the trails cut at right angles to the straight trail, and was permitted to move down this trail and turn onto the straight trail. The tortoise was tested once on each of ten of these intersecting trails to determine whether it would follow the original straight trail. After testing the tortoise was forced to run the length of the straight trails five more times. Two days elapsed between the forced runs down the straight trail and the testing on the side trails. After fifteen forced runs and two tests had been recorded the nares of five animals were blocked with Carbowax 3000 and Carbowax 1500 (in the ratio of 3:1). The other five animals were used as a control. Both groups were then retested.

In the tests on the Y-trails the tortoises were started at the uncovered branch and were forced to turn right or left on the Benchkote according to a predetermined sequence. After five of these forced runs a tortoise was permitted to choose between the two directions. A turn in the direction of the forced run was recorded as a positive response. This same procedure was repeated for a total of twenty forced runs and four test runs. Tortoises were not tested immediately after the forced runs; an interval of a day elapsed between the two types of runs.

When a series of tests was completed the Benchkote was reversed and the tortoises were retested. Then the original orientation of the Benchkote flooring was restored and each tortoise was forced five more times. The next day the tortoises were divided into two groups. The nares of one group were blocked with Carbowax. The other group was used as a control. Both groups were then retested.

Laboratory Experiments

Materials

To investigate the possibility that olfactory stimuli provide orientation information, the tortoises were tested in a T maze, the inside of which had been coated with white fiberglass resin. The runway was 24 inches long and choice arms extended 12 inches to either side. All passageways were 11 inches wide, thus permitting the tortoises to turn around, and all had walls 3 inches high. An aluminum door separating the starting box (8" x 11") from the rest of the maze was kept closed until the start of each trial, at which time it was removed. The maze was roofed with 1/4 inch mesh hardware cloth, covered with opaque plastic tape to minimize visual cues that might confuse the turtles.

Each choice arm led into a wooden box with the same dimensions as the starting box. One of these boxes served as a home for each tortoise at least a week before starting the tests; the other was a dummy box in which a tortoise had never been kept. To the insides of both boxes several coats of white fiberglass resin were applied to prevent penetration of odorants into the wooden floor. In the home box food and water were provided at all times, except during the tests.

Procedure

The home box and each neutral box were attached to the ends of the choice arms. Each tortoise tested was placed in the starting box with the aluminum door in place. The position of the home box was randomly alternated from side to side between tests. The tortoise was subjected to the heat generated by a 150 W infra-red bulb hung over the starting box. The length of time the tortoise was retained in the starting box varied from 2 to 15 minutes, depending on the ambient temperature. When the animal attempted to escape, the door was removed and the trial begun.

Continuous observations were made during each trial. Records were made of the choice taken, of the time spent at the choice point, of any head-bobbing behavior, of putting

the snout down on the floor, and of any unusual behavior patterns. A choice was not recorded until the tortoise had moved down one of the maze arms far enough so that it was no longer visible from the starting box. No time limit was placed on a trial, because the tortoises often showed considerable hesitation at the choice point, not related to correctness of choice.

After each trial the tortoise was placed in its home box until the next run. In a few cases I varied the procedure, placed a tortoise in a neutral box after it had made a negative choice, but this had no obvious effect on subsequent tests. Between trials the T maze was washed with Alconox solution and thoroughly rinsed with distilled water to minimize extraneous odors. Before each trial the home was wiped out with paper towels to eliminate humidity and visual marks of dung or food. The neutral box was also wiped out with paper towels to control for odorants on the toweling itself.

To maximize the amount of any odorant deposited by the tortoise, the floors of the choice arms were covered with Benchkote. It was assumed that the tortoise deposited a scent trail as it walked over the Benchkote. This "scented" Benchkote was subsequently placed in the positive choice arm, i.e., on the same side as the home box.

Results

Artificial Trail Experiments

The tortoises placed on the indistinct trails (p. 19) invariably followed them for short distances before wandering off. Although the distances travelled on the trails were so small that they could be attributed to chance, no statistical test of their significance was found to be appropriate. The distances travelled down the grain of bent grass (mean = 5.7 ft. \pm S.E. = 1.5 ft.) were not significantly different from those travelled against the grain (mean = 3.2 ft \pm S.E. = 1.1 ft), although the tortoises appeared to follow the trails somewhat longer in the direction of the bend of the grass. The tortoises stayed on the distinct trails for significantly greater distances (mean=22.5 ft \pm S.E. 7.0 ft) than they did on the indistinct trails (t-test, $P < .05$).

The tortoises placed on the side trails, after being forced down the straight trails, turned in the same direction onto the straight trails as they had been forced, with frequencies significantly different from random ($z=3.70$, $P < .0001$). It is clear that this significance applies to the behavior of half of the group of tortoises, the other half chose randomly (Table 1). When the external nares were blocked, random choices were made (Table 2).

Table 1. Preference of tortoises to turn onto a straight trail in the same direction in which they had been forced previously on the straight trail (positive choice). The data represent the number of positive choices out of ten.

Subject	Number of positive choices after ten forced runs	z score
SFV 2	10	2.85
AC 3	10	2.85
JJ 1	10	2.85
SF 1	9	2.21
A 15	9	2.21
AC 1	6	0.32
X 1	5	0.00
A 19	4	-0.32
SFV 1	4	-0.32
F 1	3	-0.95
		11.70
		$\frac{z}{\sqrt{n}}$ 3.70
		P < 0.001

Table 2. Comparison of preferences of tortoises to turn onto a straight trail in the same direction that they had been forced previously with nares blocked with wax and unblocked.

<u>Nares Blocked</u>		
Subject	Number of positive choices after fifteen forced runs	z score
SF 1	10	2.85
AC 3	8	1.58
F 1	8	1.58
A 19	2	-1.58
A 15	2	-1.58
	z	<u>2.85</u>
	$\frac{z}{\sqrt{n}}$	1.03
	P > 0.70	
<u>Nares Unblocked</u>		
X 1	10	2.85
JJ 1	10	2.85
SFV 1	10	2.85
SFV 2	8	1.58
AC 1	4	-0.32
	z	<u>9.81</u>
	$\frac{z}{\sqrt{n}}$	3.10
	P < 0.001	

On the Y-trails the results were similar to those obtained on the side trails (Table 3). There was a gradual improvement in the turning of the tortoise toward the training direction with a greater number of forced trials. Again, half of the subjects showed this improvement while the choices of the other half was not different from random. Blocking the nose with wax destroyed the direction preference ($z=0.99$, $P > .10$). Reversing the Benchkote which covered the floors of the choice arms, however, did not cause the tortoises to reverse their preferred choices. Instead, they turned non-randomly ($z=1.79$, $P < .05$) in the same direction as previously.

Laboratory Experiments

Analysis of results in the T maze tests showed no significant preference for the home box (Table 4). Behavioral differences were observed between trials resulting in the choice of the home box and those which did not. These differences related mainly to the amount of head-bobbing (mean for positive trials = 7.0, for negative trials = 3.2) and lowering the snout on the substrate (mean for positive trials = 5.6, for negative trials = 2.2). There was also some difference in the amount of time spent at the choice point (mean for positive trials = 20.9 min., for negative trials = 3.3 min.).

Table 3. Preferences of tortoises to turn in the same direction in which they had previously been forced to turn on Y-shaped trails (positive choice). The ranked data represent the number of positive choices out of ten trails on ten separate Y-trails per tortoise.

<u>Number of forced runs before testing</u>							
5		10		15		20	
No.	z	No.	z	No.	z	No.	z
7	0.95	9	2.21	8	1.58	9	2.21
7	0.95	8	1.58	8	1.58	8	1.58
7	0.95	7	0.95	8	1.58	8	1.58
6	0.32	6	0.32	7	0.95	8	1.58
6	0.32	6	0.32	7	0.95	8	1.58
6	0.32	6	0.32	6	0.32	7	0.95
6	0.32	6	0.32	6	0.32	6	0.32
6	0.32	6	0.32	6	0.32	6	0.32
5	0.00	6	0.32	6	0.32	6	0.32
5	0.00	5	0.00	6	0.32	6	0.32
4	-0.32	5	0.00	5	0.00	4	-0.32
4	-0.32	5	0.00	4	-0.32	4	-0.32
<hr/>		<hr/>		<hr/>		<hr/>	
z	3.81		6.66		7.92		10.12
$\frac{z}{\sqrt{n}}$	1.10		2.24		2.29		2.92
P	<0.14		<0.01		<0.01		<0.002

Table 4. Results of tests in the T-maze. Positive refers to the trials in which the tortoise chose the arm leading to the home box (p.23). Negative refers to the trials in which the tortoise chose the other arm. Except for the choices, the numbers represent the average number of responses per trial. Probabilities refer to the expectation that the numbers of responses for positive and negative choices are equal.

Subject	Choice		Head Bobbing		Head Lowering		Time (Minutes)		pb			
	+	-	+	-	+	-	+	-				
Ar 1	18	12	.50	8.7	5.0	.05	6.5	3.7	.04	22.9	6.0	.05
W 1	5	5	.90	1.4	0.2	.06	4.2	0.6	.01	3.7	0.8	.17
A 4	4	5	.90	18.5	9.4	.14	15.8	5.4	.16	75.8	8.4	.06
Wes 1	2	8	.05	5.5	1.0	.13	0.5	0.8	.18	1.7	0.6	.40
Wes 2	3	7	.90	1.1	0.4	.01	1.1	0.3	.002	0.5	0.6	.17

a z test

b Mann-Whitney U Test (Siegel, 1956)

Discussion

The results of the tests on the "indistinct" trails suggest that these were not very effective orientation stimuli. Perhaps the weak trails lacked some factor that a tortoise recognizes as being indicative of a trail. Repeated testing of a tortoise on the same trail resulted in a slight improvement in trail-following, perhaps because the trails became increasingly more distinct. Although there was a slight improvement in trail-following when the tortoise was going with the direction of the bend of the grass, rather than against it, there was no significant difference (t test, $P > .05$) because of the short distances travelled. This suggests that weak tactile or visual stimulation is of little use to the tortoise for orientation.

The cut trails, on the other hand, were readily followed over significantly greater distances (t test, $P < .05$) distances than on the indistinct trails. This suggests that strong tactile or visual stimuli can direct the tortoises along the path of least resistance. This may explain the formation of the distinct trails near the burrows.

The short side trails cut into the straight cut trails were made to see whether tortoises which had wandered

down the straight trails would turn onto one of these trails after being placed on the side trails. They did indeed turn consistently onto the trails suggesting that the features of the trails themselves stimulated the tortoise directly. It is unlikely that they utilized a kinesthetic pattern for this. An interesting side result was obtained. In a significant number of cases ($z = 3.70$, $P < .0001$) tortoises turned down the straight trail in the same direction in which they had headed when tested on the straight trail alone. With very little experience the tortoises had learned to travel in a particular direction. Cues that may have controlled this behavior could have been either a scent trail with directional properties deposited by the tortoises during the straight-trail tests, or landmarks such as clumps of grass or the tree-line. Still another possibility was that the straight trails chanced to run in a direction matching an innate direction preference (e.g., sun compass). The latter possibility seems unlikely because of the pronounced variability of direction preference among individual tortoises (p. 80).

To test the possibility that the tortoises use odor trails, the nares of five specimens were blocked with wax. This resulted in the loss of directional preference estab-

lished in earlier series. Control animals with the nares unplugged retained and improved their preference for the direction they had travelled down the straight trail. Much individual variation existed within each of these two groups. The rigorous analysis with the z test indicated that only half of the tortoises showed this preference; they did it so strongly that one could get the impression that, on the average, the entire group was demonstrating a directional preference. Still another test was necessary.

The experiment was repeated on Y-trails. Each tortoise was started from a different position on each of a series of these trails to minimize any possible use of a solar compass in the directional choice. The tortoises turned in the correct direction significantly greater ($z = 2.92$, $P < .002$) than random expectation. Again, only half of the animals showed a strong directional preference; with their nares blocked with wax their preference was lost. Thus, the tortoises showed comparable results on the two types of trails. However, when the Benchkote that covered the floor of the choice arms of the Y-trails was changed to the negative runway, the tortoises did not reverse their preferred directions, but retained a preference for the original choice. This

suggests that blocking the nares with wax, rather than merely preventing olfactory input, upset the tortoises' behavior. These data suggest that for short-range orientation visual cues are more important to the tortoise than olfaction. The tortoises seem to learn the landmarks at each choice point after only a few experiences. The observation that only half of the subjects showed a direction preference in the experiments is attributed to individual variation in learning ability and motivation.

The lack of evidence for the use of olfaction in short-range orientation, as revealed in the preceding tests, does not exclude the possibility that it is used by Gopherus. The T maze tests were designed to eliminate all stimuli except olfactory ones. The lack of preference for the home box in the T maze parallels the findings of Boycott and Guillery (1962), but the differences in head-bobbing and snout-lowering between successful and unsuccessful trials suggests that olfaction may be involved. The time spent at the choice point was also longer in two cases for the successful trials, although the rates of bobbing and lowering were actually less than for the unsuccessful trials, suggesting that these responses may not be accurate indicators of olfactory input or that tortoises

unsuccessful in picking up the odors kept trying but showed the response only when they could perceive the odors. These data suggest that, although the tortoise may be capable of perceiving olfactory stimuli which they themselves have produced, either the experimental conditions were not appropriate to elicit this behavior or the tortoises do not rely upon olfactory cues for directional information.

The tortoises in the present study may not have deposited the usual scent cues, although dung was occasionally deposited. When this was left for a subsequent trial by that tortoise, most of the tortoises showed no reaction to its presence. One appeared to avoid the side with the dung on it, but this avoidance was not seen the next day. Possibly dehydration or decomposition of an aversive odorant altered the stimulus properties of the dung. Rehydration with distilled water did not restore the original aversion.

The tortoises also urinated on the Benchkote during some of the trials. One tortoise, with its nose blocked with wax, followed the urine-soaked trails ten times in ten runs. The result was not conclusive because the urine made dark spots on the floor. It seems likely that the tortoise followed the visual cues.

Although the number of tortoises tested in each of these experiments was not large, the conclusion is inescapable that visual cues provide the primary directional information to the tortoise. These may be rapidly learned under novel conditions. Although only slight evidence that olfaction was used as a directional stimulus, the possibility remains. Perhaps with appropriate training techniques the tortoises can subsequently be shown to utilize olfactory stimuli as supplementary short-range cues.

CHAPTER IV

BIOLOGICAL CLOCK

Although Gould (1957,1959) suggested that turtles utilize the sun for orientation, he did not examine their internal chronometer. If a mechanism of celestial orientation is to be functional for a long time over a long distance, the organism must compensate for the characteristically and continually changing angle between the sun's azimuth and the goal direction. The procedure of resetting the internal clock by changing the beginning and end of the light-dark cycle has become a useful technique to demonstrate the interaction between the internal chronometer and solar orientation. Most phase-shifting work has been done with invertebrates, birds, and mammals, but Birukow et al. (1963) obtained similar deviations from the trained direction in three species of lizards, Lacerta viridis, L. sicula, and L. muralis, when these were phase-shifted.

Because so many organisms, including mammals, birds, lizards, and insects, have been shown to have an internal clock (Hoffman, 1965) Pittendrigh (1960) maintains that

circadian rhythms are ubiquitous in living systems. The presence of a circadian rhythm is demonstrated by placing an animal under constant environmental conditions and observing whether an activity pattern whose frequency approximates that of the solar day is maintained. Results obtained from a wide variety of organisms have been very consistent. The circadian rule states that a diurnal animal in constant light will show a shorter circadian frequency than it will in complete darkness, the reverse being true for nocturnal animals (Aschoff, 1960). With few exceptions, much evidence supports this generalization (Hoffman, 1965). The presence of an internal clock does not imply that it is functional in orientation. In fact, the inaccuracy of these internal clocks has often been cited as evidence that the current theories of celestial orientation are not sufficient to explain the ability of some organisms to return home from relatively short distances (Adler, 1963a, 1963b; Meyer, 1964; Walraff, 1960, 1967).

The purposes of this phase of the study were:

1. To learn whether the gopher tortoise possesses an internal clock.
2. If so, to determine its accuracy.

3. To provide a basis for phase-shifting in order to investigate the possibility of celestial orientation.

Methods and Materials

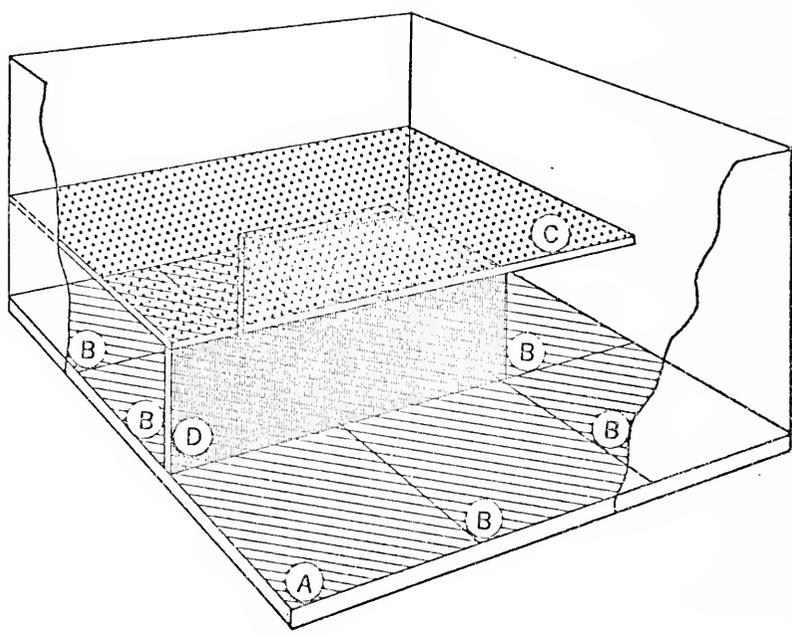
The method to determine the existence of a circadian rhythm was to record the locomotor activity of tortoises under various conditions. The daily patterns were determined in automatically monitored activity boxes in which light and temperature were kept under control.

Activity Box

Two wooden boxes (37 x 31 x 16 inches) with nine wooden floor panels (each 10 x 12 inches) were used. Only one of the panels, serving as a feeding platform, was rigidly mounted on wooden blocks. The other panels were supported on small springs and connected to adjustable micro-switches. When the tortoise depressed a panel the micro-switch was closed; this information was fed into an Esterline-Angus Event Recorder. A wooden partition (Figure 3) prevented the tortoise from depressing more than two panels simultaneously. The partition also directed the tortoise to cross the panels in a regular sequence.

A wooden cover was placed above six of the panels (Figure 3) to determine the effect of the presence of a refuge from the imposed light condition on the activity

Figure 3. Activity box used for determining locomotor activity patterns of tortoises. A, panel upon which food and water was supplied; B, panels which activated micro-switches; C, removable cover; D, wooden partition.



pattern. Harker (1960, p. 354) suggested that a clearer rhythm is found when such a dark shelter is provided.

Procedures

Each freshly-caught tortoise was kept for seven days in an activity box under twelve hours of light alternating with twelve hours of dark, in order to acclimate it to the experimental situation. Records were kept of the total activity and of the pattern of activity during this period.

Each tortoise was then subjected to one or more of the following conditions: constant light, constant dark, or a regimen in which the light-dark pattern was phase-shifted either six or twelve hours. The illumination in all cases came from a 100 W light bulb approximately 2 feet above the floor of the activity box. The incident light 4 inches above the surface was approximately 350 lux. The temperature was kept constant for each individual tortoise and did not vary more than from 26 C to 29 C in all experiments. Each tortoise remained under the constant conditions for at least seven days, or until the activity pattern had changed in response to a phase-shifted light-dark cycle. ◦

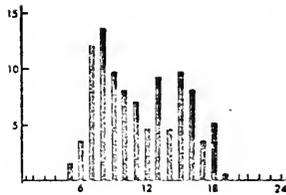
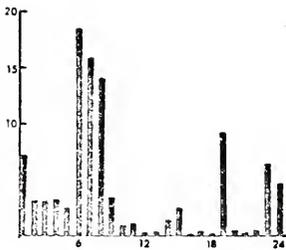
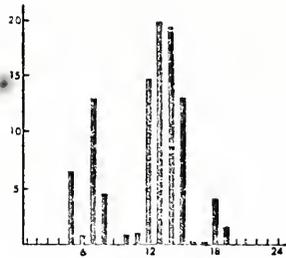
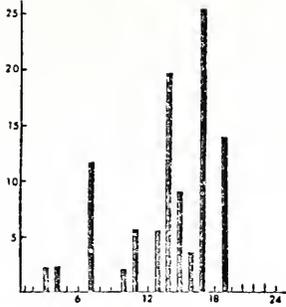
Results

Under the alternating twelve hours of light and twelve hours of dark, single individuals showed fairly regular activity patterns, but there was considerable variation between individuals, with from two to four peaks of activity (Figure 4). Usually the tortoise became inactive near solar noon.

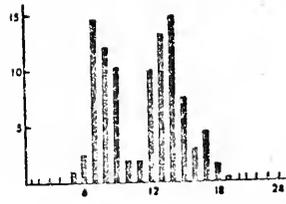
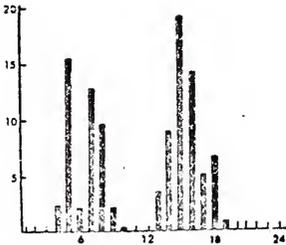
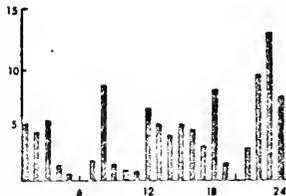
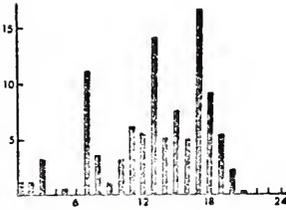
The tortoises subjected to a six-hour phase-shift adjusted their activity patterns within one or two days (Figure 5). A twelve-hour phase-shift required approximately four days of adjustment, although there were conspicuous changes on the first day (Figure 6).

In constant light each individual showed a progressive shift of onset of activity in the direction expected for a diurnal animal: each successive activity period began earlier (Figure 7). The length of the period is subject to various interpretations depending on the method of analysis (p. 59), but the differences are not great (Table 5). Offset of activity was also determined, and similar results were obtained. An individual exposed to constant light and fluctuating temperatures did not show a regular shift of onset of activity. Instead the onset appeared to be related to the temperature fluctuations (Figure 3).

Figure 4. Mean per cent of daily activity each hour under approximately 12 hours of dark alternating with 12 hours of light. Light on at approximately 0700 and off at approximately 1900.



ACTIVITY (%)



HOURS

Figure 5. The effect on the activity pattern of shifting the phase of the artificial light-dark conditions 6 hours. Vertical bars represent periods during which the tortoises were active; shaded areas, the periods of imposed darkness. To more clearly illustrate the rhythmicity, the succeeding day is shown above the numbered day. A shows a retarded shift; B shows an advanced shift.

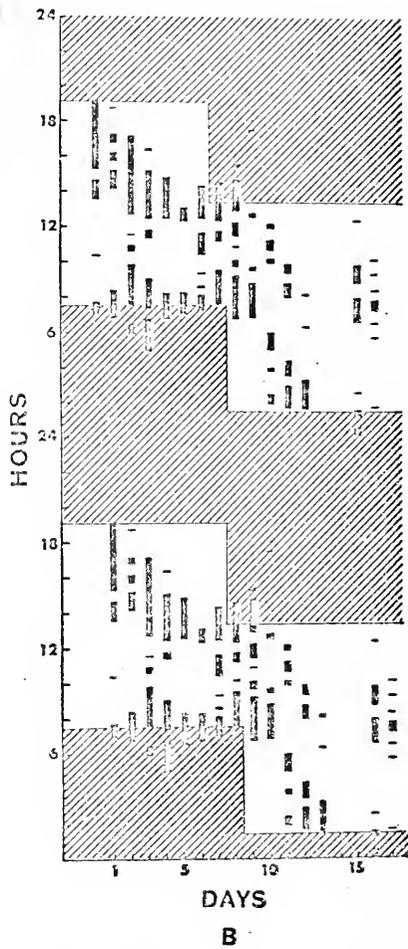
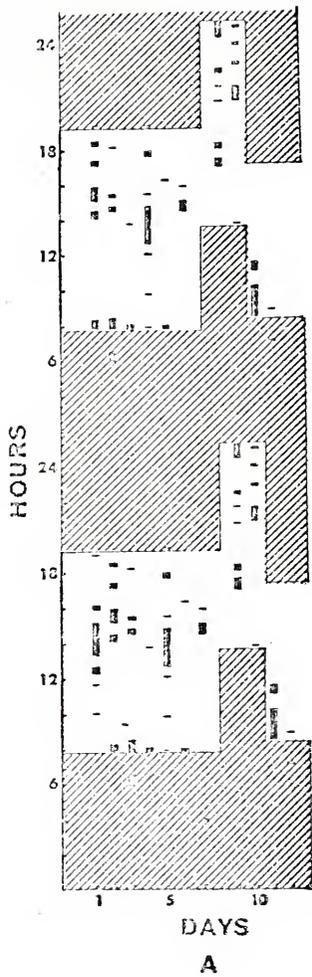


Figure 6. The effect on the activity pattern of a tortoise shifting the phase of the artificial light-dark conditions 12 hours. Data presented as explained for Figure 5.

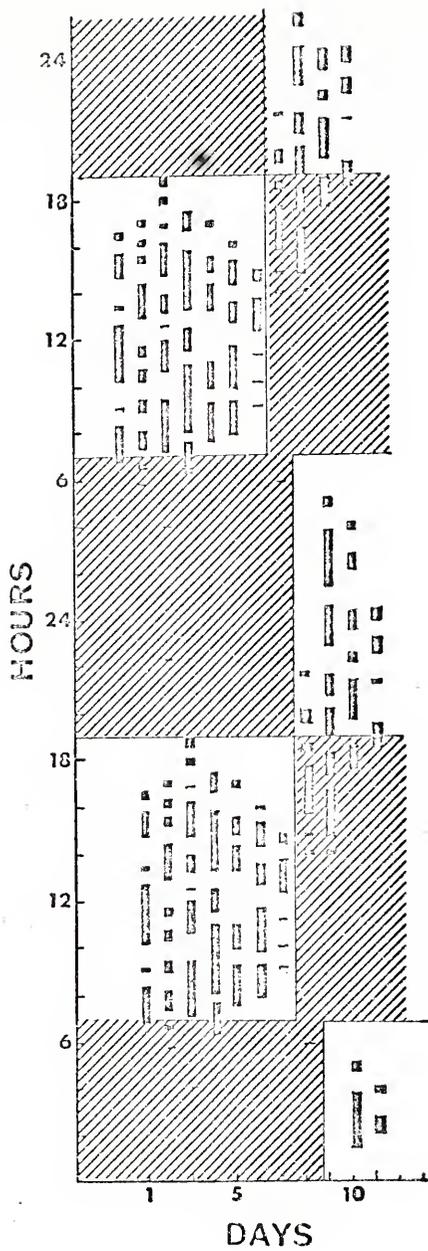


Figure 7. Activity patterns of tortoises under alternating light-dark conditions and under constant light. Data presented as explained in Figure 5.

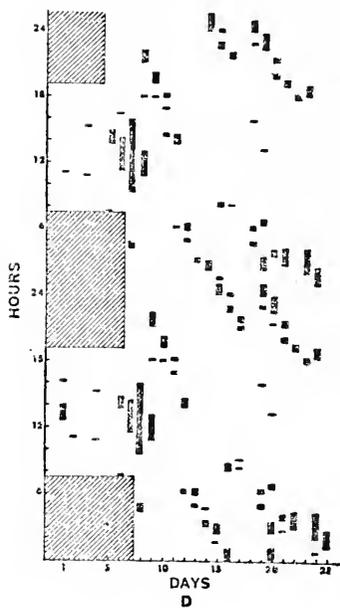
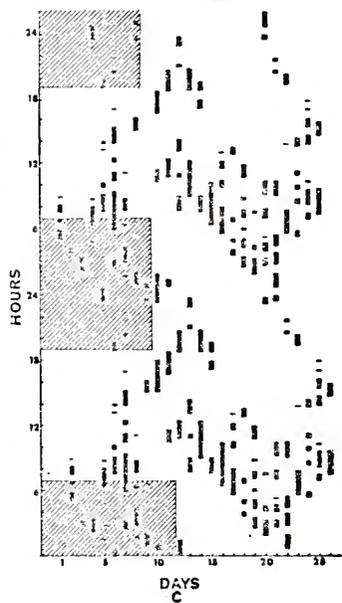
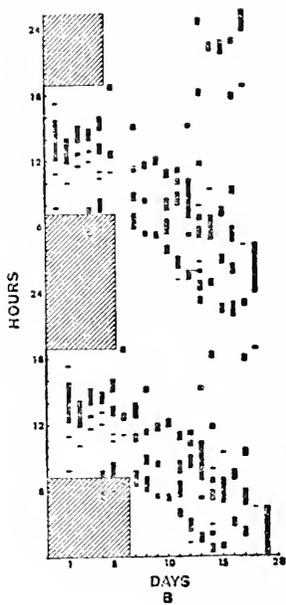
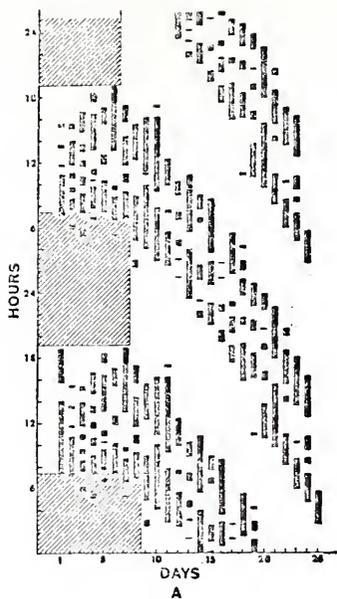


Figure 7. (Continued)

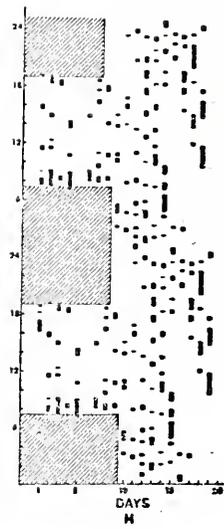
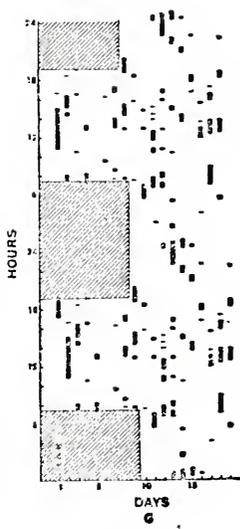
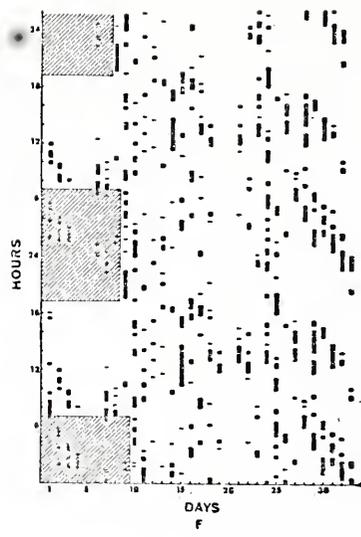
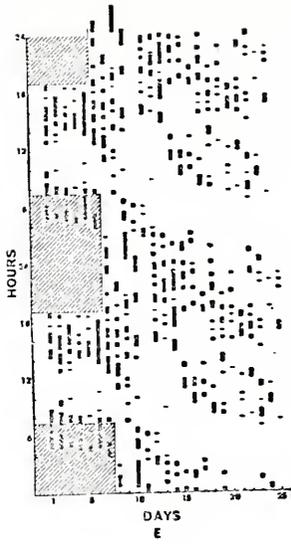
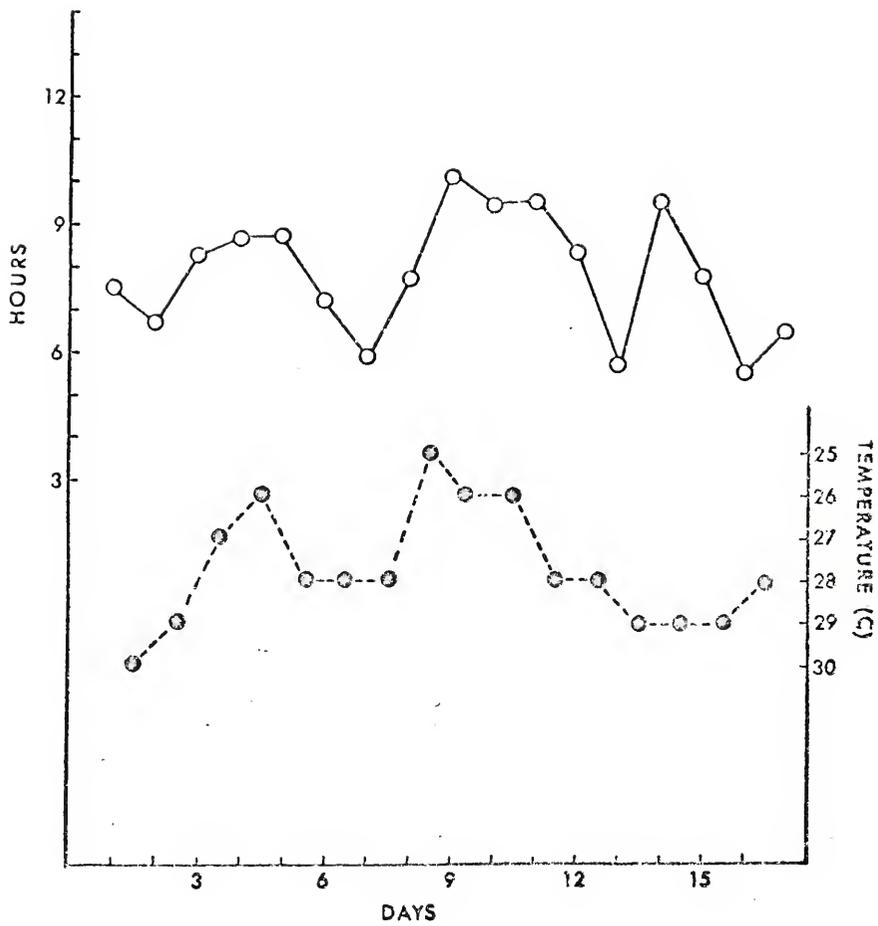


Table 5. Comparison of length of circadian period under constant light based on time of onset of activity by the two methods of mean-period length by the classical method and by linear regression (see p. 59).

Condition	Tortoise	Classical			Linear Regression		
		n	mean (hrs)	S.E. (min.)	n	mean (hrs)	S _b (min)
Cover off activity box	A 1	10	21:27.9	47.3	11	21:21.5	12.7
	A 2	10	22:14.0	57.8	11	22:29.9	15.3
	BUC1	18	23:27.7	1:17.9	19	23:00.3	12.5
	BUC2	8	24:32.4	1:38.3	9	23:43.2	33.2

Cover on activity box	P 1	16	22:28.3	19.3	17	22:21.5	3.9
	P 2	11	22:55.2	26.8	12	22:51.8	5.7
	C 1	13	23:35.5	42.2	14	23:25.0	12.0
	BC1	18	23:03.9	67.5	19	22:55.9	9.3

Figure 8. The effect of temperature on the onset of activity under constant light. Solid line, representing onset of activity, to show parallel pattern; dashed line represents temperature.



Discussion

Comparison of the onset of the tortoises' activity with the onset of light under twelve hours of light alternating with twelve hours of dark indicates that the rhythmic behavior is entrained by light onset, although some individuals remain active well into the dark period, and some "anticipate" the onset by an hour. This might have adaptive significance for the poikilothermous tortoise, whose activity is dependent upon relatively high ambient temperatures. The inactivity at midday may reflect an adaptive avoidance of the extremes of heat that prevail at that time during the summer. This midday inactivity was evident in tortoises observed in the laboratory throughout the year.

More pertinent to the demonstration of an internal clock in the gopher tortoise is the evidence that tortoises maintain circadian activity patterns under constant light and temperature conditions. The period of the activity cycle is less than twenty-four hours as would be expected for a diurnal animal. The mean period length was calculated according to the classical method

$$t = \frac{(t_2-t_1) + (t_3-t_2) + \dots + (t_n-t_{n-1})}{n-1}$$

where t is the mean period and t_1 , t_2 , t_3 , and t_n refer to the time of initiation of activity. However, I concur with the argument of Lowe et al. (1967) that regression analysis results in a more precise estimate of the natural period.

The classical method results in a range of 21:37.9 hours to 24:32.4 hours with a mean of 22:58.1. By the regression method the range was 21:21.5 to 23:43.2 with a mean of 22:47.1. However, analysis of covariance (Snedecor and Cochran, 1967) indicates that the regressions obtained from tortoises examined with the cover absent cannot be pooled. The tortoises with the cover present can be pooled (F test, $P < .05$). The period length calculated by either analysis supports Aschoff's (1960) circadian rule for diurnal animals, and also agrees with values obtained with other animals--23 to 26 hours (Bünning, 1964). Similar values were obtained when the offset rather than the initiation of activity was used as the criterion for the limit of the activity period.

The variances of the pooled data under the two conditions, cover present and absent, are significantly different (F test, $P < .05$), the variance obtained with the cover off being greater, thus supporting Harker's (1960, p. 354) suggestion that providing a refuge from constant light results in a more distinct rhythm. These data suggest that

the gopher tortoise may behaviorally affect the rhythm. However, the tortoise's activity rhythm is more variable than has been reported for other animals, e.g., Glaucomys volans, DeCoursey (1960), which had a minimum standard deviation of only two minutes (by the classical method). The standard error of the mean calculated by the classical method was 26.8 minutes; the minimum standard deviation of the slope by the regression method was 3.9 minutes.

Aschoff's (1960) rule further predicts that under constant dark conditions the period of a diurnal animal is lengthened, as compared with that developed under constant light. Actually, in the single animal which showed rhythmicity under these conditions the period was 22:34.4 hours, which is not a statistically significant deviation from the results obtained under constant light. However, only two tortoises were subjected to this condition; a larger sample might show the expected results. In constant dark the onset and offset of the animals' activity was not clear cut and rhythmic pattern was lost. One tortoise rapidly became inactive, the other was active in bursts throughout the testing period. Therefore, little valid comparison can be made between the results obtained and those predicted by Aschoff's circadian

rule. However, if upon subsequent examination of a larger sample this discrepancy remains, it may be attributed to the fossorial habit of this species. At present there is no evidence that the internal clock of the gopher tortoise is different from that found in any other species of diurnal animals.

It seems evident that under natural patterns of light and dark the tortoises adjust their locomotor patterns to the natural conditions. The factors which keep an animal in phase with the diurnally fluctuating conditions are called entraining agents; most important are light and temperature (Bruce, 1960). Under alternating light and dark conditions it is clear that light-dark cycles are important entraining agents in this species as well. Adjustments to phase-shifts further support this idea. It only took one or two experiences of a six-hour phase-shifted light pattern before the tortoises were in phase with the shift. A twelve-hour shift required several days to reach the same result of a new steady-state. That these were not merely immediate responses to the onset of light is indicated by the "anticipatory" activity prior to the onset of light.

The experiments demonstrated that temperature fluctuations have an effect on the periodicity of the tortoise.

During a single test made over several days in constant light, the temperature fluctuated between 25 C and 30 C; the onset of the tortoise's activity fluctuated correspondingly, beginning earlier when the temperature was high and later in a lower temperature. A similar result was reported by Hoffman (1968) who found that lizards were entrained by temperature fluctuations as small as 0.9 C.

If Hoffman's (1965) suggestion that a rigid or very slowly shifting clock is necessary for bicoordinate navigation is valid, as seems self-evident, then the internal chronometer of the gopher tortoise would appear to be poorly suited for such position-finding. On the other hand, a rapidly shifting clock such as that found in these tortoises would appear adequate for compass orientation. Hoffman (1954), for example, found that starlings started to shift in response to a six-hour phase-shift after one day but had not completed the shift until the thirteenth day. This is a much slower shift than that demonstrated by the gopher tortoises.

Among students of animal navigation there is some opinion that the accuracy of the internal chronometer has not been shown to be sufficient for effective bicoordinate navigation (Adler, 1963a, 1963b; Meyer, 1964; Walraff, 1960,

1967). The accuracy of the clock is usually indicated by the standard deviation from the mean frequency. As mentioned above, the internal clock of the gopher tortoise is less accurate than that of some other organisms which would also argue against the possibility that bicoordinate navigation is used in travel orientation.

CHAPTER V

LONG-RANGE ORIENTATION

Recent investigations have revealed that many species of animals are capable of orienting even when they are not in direct sensory contact with familiar fixed landmarks. Most of the work to date has been concerned with migratory birds, although fish and reptiles also have been considered (Matthews, 1955; Hasler, 1964; Carr, 1967).

Some species of turtles, especially marine forms, are migratory and capable of long-range orientation, but the nature of this orientation is unknown. Little experimental evidence has been obtained to support any of the various hypotheses formulated to explain the mechanism of long-range, open-sea orientation. One of the major obstacles to such experimentation is the difficulty of accurately tracking individuals over open ocean for long periods of time. In turtles several investigators have tried to solve the homing-orientation problem by examining hatchling sea turtles, fresh-water or terrestrial species. There have been numerous observations of turtles returning to their

home ponds or to particular portions of the pond (Cagle, 1944), to their burrows (Woodbury and Hardy, 1948), or to the same corner of a room (Mertens, 1958). Although this homing phenomenon may or may not be directly related to the problem of sea turtle navigation, its investigation should provide clues to the mechanism of turtle orientation.

The major hypotheses to explain turtle orientation involve reference to fixed landmarks along the travel path, especially horizon effects (Ortleb and Sexton, 1964); olfaction; and celestial orientation. Other types of guidance such as magnetic orientation and inertial control have been suggested for birds, but the evidence of their existence remains controversial and no attempt to show their utilization in lower vertebrates has been made.

Landmarks are usually regarded as short-range stimuli, but they may interfere with other orientation stimuli (Schmidt-Koenig, 1965).

Olfactory orientation may, theoretically, be a long-range cue under certain conditions--for example, where a prevailing current of wind or water from the goal maintains a gradient. This may account for the island-finding orientation of green turtles, Chelonia mydas (Carr, 1967). Another situation in which olfaction may be utilized for long-range

orientation is where scent trails are deposited by the animal, which can then home by retracing its trail. However, a terrestrial or semi-aquatic animal is still able to orient in spite of living in an area where the currents are not constant and displaced beyond its scent trails.

Celestial orientation has been suggested several times as possible means of turtle orientation. Fischer (1964) found that hatchling green turtles, C. mydas, possess a time-compensated sun compass and perhaps are capable of true solar navigation, which is defined by Schmidt-Koenig (1965) as a phenomenon in which the compass direction is goal-related. Carr (1962, 1963, 1964) suggests that adult green turtles utilize some form of celestial orientation and implies that more than a compass sense is involved. Ehrenfeld and Koch (1967) found that green turtles are extremely myopic in air, which argues against the utilization of stars for navigation.

Gould (1957, 1959) obtained evidence that the terrestrial box turtle, Terrapene c. carolina, and the aquatic painted turtle, Chrysemys picta, are capable of true celestial navigation. Ehlen's (1965) re-examination of C. picta provided no evidence that this species was capable of celestial orientation.

Gopher tortoises, Gopherus polyphemus, would seem to be good subjects to test for celestial guidance capacity. First, they are terrestrial, which permits the accurate tracking of their paths. Second, they live in permanent or semi-permanent burrows, so that the goal to which they may be assumed to return is very limited in area. Third, they are diurnally active, which obviates the necessity of determining their possible use of stellar or lunar orientation. The limited range of their travels suggests that a capacity for bicoordinate position finding would be altogether superfluous, and physiologically unachievable. It does not, however, preclude the possible use of a sun-compass sense.

The purpose of this phase of the study is to determine whether gopher tortoises are capable of solar orientation, or if so, to determine the nature of such an orientation whether a compass sense or true navigation is involved.

Methods and Materials

Open Field Tests

Source and Care of the Experimental Animals

Twenty-three tortoises were used in these tests. Twelve were from the Gainesville Municipal Airport (Alachua County, T 9S R 20E, S 24), located approximately seven miles from the open field in which they were tested. The remaining tortoises were from several Florida localities. To avoid the presence of landmarks with which the tortoise was familiar, no tortoise whose home burrow was less than five miles from the test site was used.

The tortoises were either housed for six weeks in terraria and wooden pens in the laboratory or in an outdoor pen 11.5 miles south-southeast of the test field. Light for the laboratory animals was provided either through a north-facing window or by fluorescent lighting which was automatically turned on and off at approximately sunrise and sunset. The tortoises were permitted to feed during each testing period and also provided with fresh lettuce, grapes, melons, and water. There was no significant change in the weight of the tortoises during these tests, nor was

there any detectable difference in behavior between those held indoors and those kept under more natural conditions.

Description of Test Field

All twenty-three tortoises were released and studied in an open field of closely cropped grass, on the University of Florida Experimental Station grounds (Alachua Co., T 10S, R 20E, S 1). The field measured 245 yards in a north-south direction and 65 yards in the east-west direction. The northern edge of the field was bounded by a dirt road. A twelve-foot-wide strip of grass on the other side of the road separated it from a large plowed field. The road could not be seen by tortoises located in the center of the field because of a slight rise at this end of the field. The eastern edge of the field was bordered by a row of two- to four-foot fruit tree saplings, which marked the edge of an adjoining orchard. To the south the field widened slightly. There was a clump of trees to the southeast in which a trailer park was located. From the trailer park a line of longleaf pine trees ran almost all the way across the southern end of the field. Toward the southwestern corner there was a gap in this row of trees. Approximately 50 yards beyond this first row of trees was a second which

almost filled this gap on the horizon. A dense border of shrubs separated the pines from the edge of the cut grass in the field. The western edge of the field consisted of an irregular row of live-oak and longleaf pines; this was the edge of a mixed oak-pine woods which extended to the west. There was a relatively dense growth of shrubs along this border, but under the trees were few plants near the ground.

Procedure

All of the tortoises were transported to the test field by automobile in closed styrofoam ice chests. They were carried to the three release points in the field in these chests. The twenty-three tortoises were released singly from the release points, which were in the middle of the field, about 50 feet apart. The first three tortoises were allowed to move unimpeded for periods of 10 to 90 minutes, depending on the activity of the tortoise. To avoid excessive heating and yet permit the tortoise to make a usefully long run, 30 minutes appeared to be the optimum period for each trial. Accordingly, the remaining twenty tortoises were observed for one-half hour. I moved slowly at least 15 feet behind the tortoise, and my presence did not appear to disturb the experimental animal. The initial

direction upon release was chosen at random by me, so that each of the cardinal compass points were faced at least once during each individual's test.

The paths of travel were tracked in three ways. First, the tortoises were followed and their trails plotted. This was possible because of their slow gait and because they depressed the grass as they moved over it. The distance travelled was then calculated by means of a properly calibrated map reader. Second, the position of the tortoise was marked every 5 minutes by pushing a nail into the ground. After the test the directions could be determined by sighting on the nails with a compass, with an accuracy of approximately $\pm 2^\circ$. The distances from the starting point were paced. The two methods resulted in angular differences within 8° , and the linear distances within 5 feet.

The third method used was that of the thread trailer of Breder (1927) and Stickel (1950). Although this method worked well and the results agreed with those obtained with the other two methods, it required two persons to untangle the thread and measure it in a short time.

The mean direction for each test was determined by the polar angle from the starting point to the position of the tortoise at the end of the test period.

Arena Tests

Elimination of all fixed landmarks should result in disruption of any direction tendency not based upon a sun compass sense. Such tests were carried out in an orientation arena.

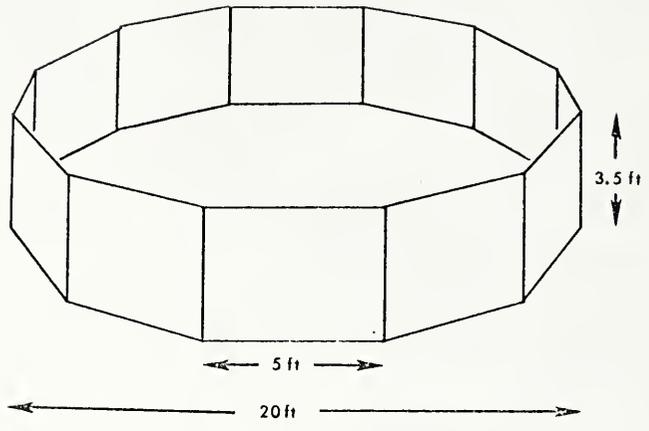
Arena

The arena had a diameter of 20 feet and consisted of twelve panels, each measuring 42 inches high and 60 inches long. The height was sufficient to exclude from view of the tortoises any trees or other features of the outside landscape. The panels were of black polyethylene sheeting mounted on a wooden framework (Figure 9). To minimize glare the polyethylene was sprayed with a dull black paint. The panels were connected by strips of Velcro, a nylon zipper material, which permitted rapid assembly and dismantling of the arena after each day's tests. A regular dodecagon was formed by the panels constituting the arena. The panels were individually numbered and interchangeable so that they could be randomly placed in the arena wall to eliminate cues from individual panels.

Heating and cooling effects during the tests caused wrinkles to form in the polyethylene, but this was approxi-

Figure 9. Arena used for testing tortoise orientation in the absence of landmarks. A, dimensions; B, arena set up in field.

A



B



indicate the approximate location where turn takes effect. For the higher Reynolds number case, the local Nusselt numbers near the inlet region of the present study deviate only slightly from the Hornbeck's results.

For all the cases studied for the heat exchanger, a large Nusselt number is found near the inlet, the turning point, and in the reattachment region and low Nusselt number occurs in the recirculation region.

It is clear that once the flow is deflected into the annulus, a redevelopment of flow occurs. In the annulus region, a fully developed condition is reached earlier for fluid of low Peclet number, see figures 18 through 20. In order to check on the computations of the present work, Lundberg and coauthors' results [24] are used. As shown in Table 4, Lundberg's results for fully developed velocity and temperature profiles in an annulus appear to be in good agreement with the present investigation that is computed at $Pr=0.7$ and $Re=100$. If a linear interpolation based on Lundberg's results at $r^+=0.5$ and 1.0 can serve as a guide, then the error is only 1.3%.

VI.6 Mean Nusselt Number

Figure 21 presents mean Nusselt number as a function of Reynolds number with Prandtl number as a parameter. This figure shows that mean Nusselt number increases with both the Reynolds and Prandtl numbers. A correlation of

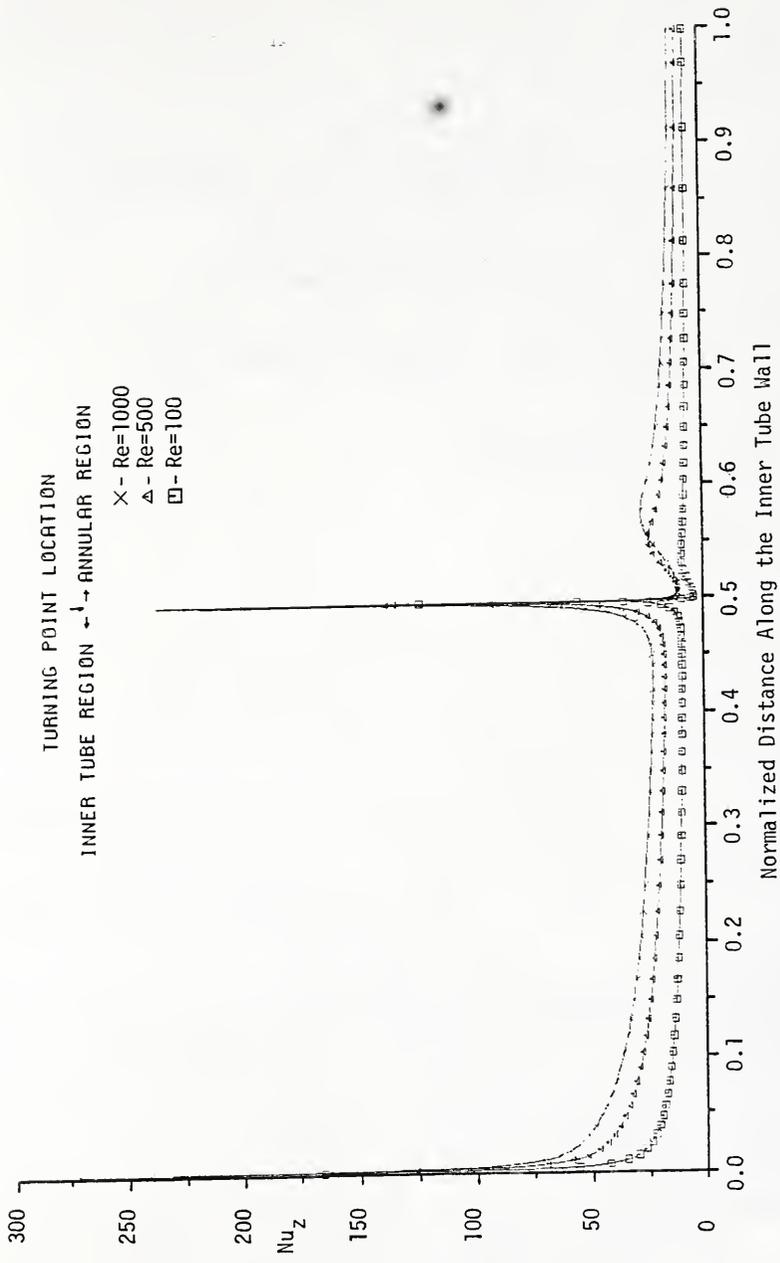


Figure 19 Local Nusselt Number for $Pr=20$ and $Re=100, 500, \text{ and } 1000$

The tortoises from the previous arena tests which had shown a significant preferred direction were subjected to a phase-shift six hours advanced. Light onset was approximately 0045 LST and light offset was approximately 1410 LST. The light source was a 150 W sun lamp. Three other tortoises that had shown a preferred direction in the arena were also brought into the laboratory but were kept in phase with local solar time by an open window and fluorescent lamps which went on at approximately natural sunrise.

One of the animals subjected to the phase shift was kept in the previously described activity box (p.40) to verify that the locomotor activity pattern shifted. The tortoises were all kept under these artificial conditions for at least seven days before beginning of tests in the arena, to make certain that not only the locomotor activity internal but also the orientational clock had been shifted. Others (e.g., Hoffman, 1960) have found that it takes longer for the orientational clock to be shifted than it takes the activity clock.

These tortoises were then tested in the arena as described above each tortoise was tested eight times during the morning (0900 to 1030 LST). Upon completion of each day's

testing they were returned to the laboratory. Each was then tested eight times in the arena at midday (1130 to 1300 LST). All tortoises required at least two days to complete testing for each time of day.

Statistics

The directions which an individual chose each time were compared to determine whether a non-random distribution resulted. Such a distribution indicated that a particular direction was preferred. Mean angles and their angular deviations were determined by methods described by Batschelet (1965), as follows:

$$x = \frac{\sum \text{Cos}}{n} \quad \text{where } n \text{ is the number of observations}$$

$$y = \frac{\sum \text{Sin}}{n}$$

$$r = \sqrt{x^2 + y^2} \quad \text{where } r \text{ is a measure of the concentration around the mean direction.}$$

$$z = nr^2 \quad \text{where } z \text{ is a statistic for non-random direction preference. The critical values for } z \text{ have been calculated by Greenwood and Durand (1955) and are given by Batschelet (1965)}$$

$$\frac{X}{r} = \cos \text{ of mean angle}; \quad \frac{Y}{r} = \sin \text{ of mean angle.}$$

Although repeated tests of the same individual are not totally independent, the movement of the arena to different parts of the field and the use of several release points in the open field minimizes the possibility of learning, and the z statistic is used with the assumption that the runs are independent, even though this condition is not rigidly met.

When the preferred directions between individuals are compared, only the mean direction is used, rather than the individual tests. Thus, the statistics are not biased by an artificially inflated sample size.

For comparison of preferred directions and homeward directions the F test of Watson and Williams (1956) as summarized by Batschelet (1965) was used. The null hypothesis is that there was no difference between the preferred direction and the home direction.

The arena tests were analyzed similarly but because the actual degree headings were not made, a correction for grouping data was made. The Gilroy (1965) correction factor for grouping data into twelve sectors is 1.0115 (Batschelet, 1965). This gives a corrected r , r_c , which better indicates the concentration around the mean direction than does an uncorrected r .

Results of Field and Arena Tests

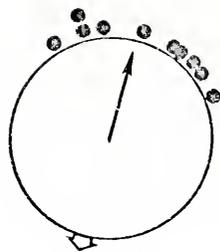
Open Field Tests

The tortoises released in the field showed no tendency to head in the same direction (Figure 10). Tortoises from the same geographic population (Figure 11) also showed no uniformity. They were neither motivated nor able to head in a direction which would take them back to their home burrows.

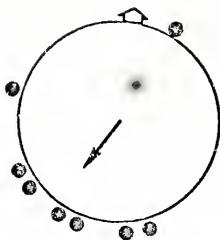
However, as is indicated by the high r values, and the z statistics at the 0.05 level of significance, thirteen of the twenty-three (56.5%) tortoises repeatedly chose the same individual non-random directions from the release point. This individual preferred direction is not homeward directed, but the data nevertheless indicate that the individuals were oriented.

Further evidence that the tortoises were oriented is that the paths taken by each individual were relatively straight. If the straight line distance between the release point and the end point of each run (best path) is plotted against the actual path taken by tortoises (Figure 12), a linear relation becomes evident, which would not be expected in the absence of orientation. The mean ratio of best path to actual path is 1.6:1.

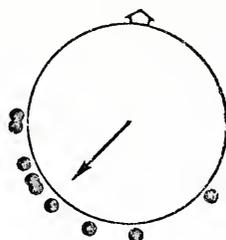
Figure 10. Preferred directions of travel shown by individual tortoises taken from different geographic populations. Tests were performed in an open field. Arrows inside circles indicate mean preferred directions; length of arrow indicates strength of the concentration around the mean direction, r . When the length of the arrow equals the radius perfect correlation of preferred directions among trials is indicated.



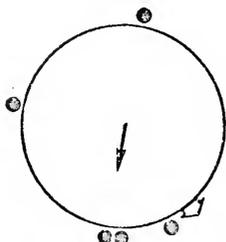
H 1



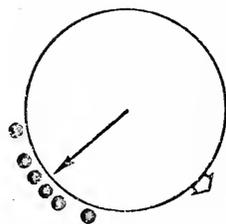
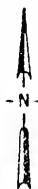
P 1



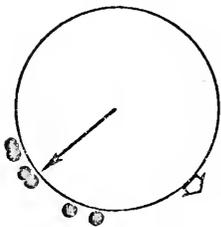
P 2



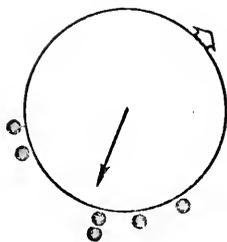
L 1



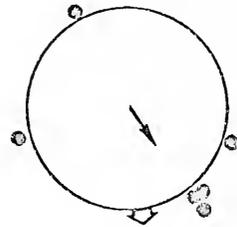
O 1



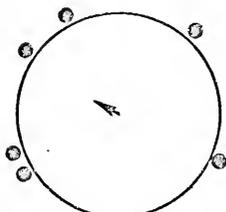
RS 1



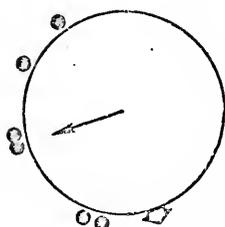
ACP



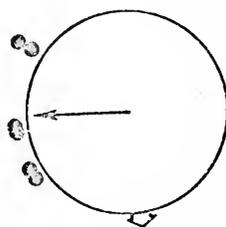
M 1



Haw 1

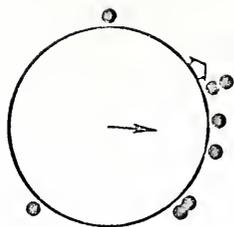


HCl

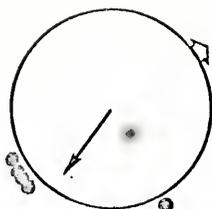


N 1

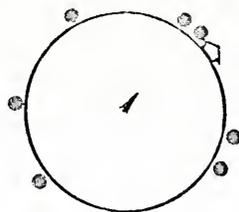
Figure 11. Preferred directions of travel shown by individual tortoises taken from the same geographic population. Data presented as explained in Figure 10.



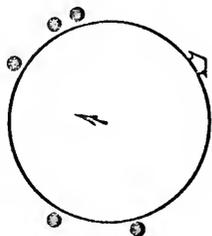
A 2



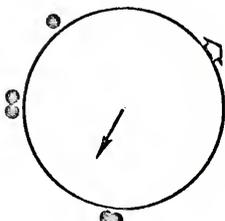
A 4



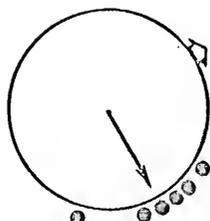
A 5



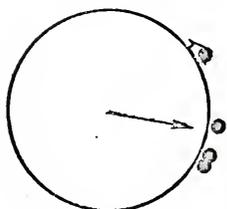
A 6



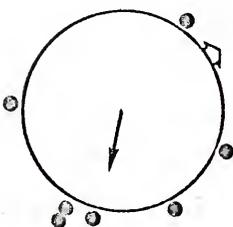
A 7



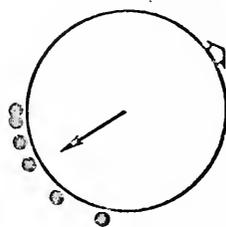
A 8



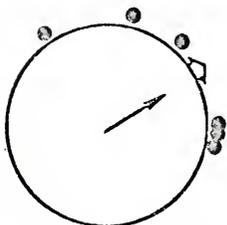
A 11



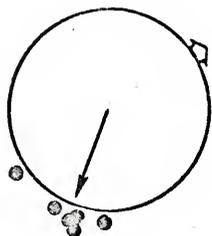
A 12



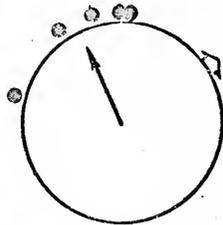
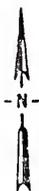
A 13



A 14

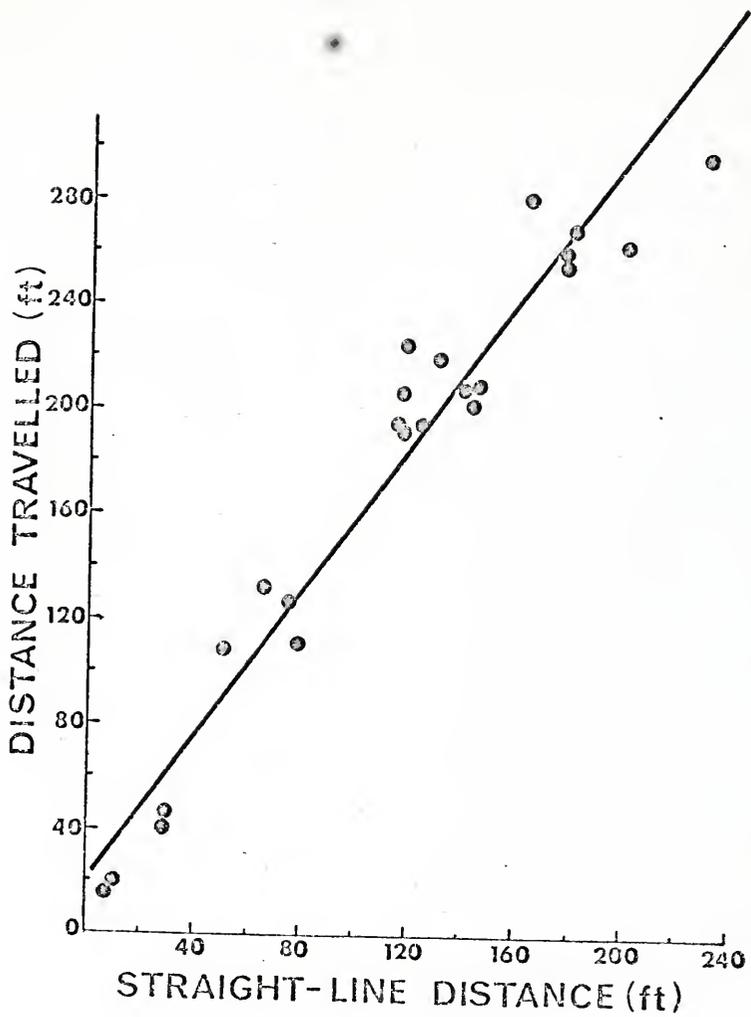


A 15



A 16

Figure 12. lengths of paths travelled by tortoises and the straight-line distances from starting point to end point of each run. Trails were performed in an open field. Points represent the mean values obtained for an individual. Line is least-square regression.



Arena Tests

In the arena nineteen of thirty-seven (51.4%) showed a particular direction preference throughout the day (Table 6). There was no tendency for the group to head in the same direction, even among tortoises from the same population. The preferred directions had no relation to the homeward direction, although there was some similarity between those taken by the same individuals in the open field tests (Table 7). There was considerable variation in the tortoises' demonstration of a direction preference at different times of day, although the mean directions which were shown were very consistent (Table 8).

After the internal clocks of the tortoises which showed a direction preference in the arena were advanced 6 hours, a significant change in preferred direction was noted. Preferred directions of the tortoises before and after phase-shifting the internal clocks were compared, but only if the individual oriented at the same solar time under both conditions (Figures 13,14). The mean directional shift from the original preferred direction for six tortoises, in the morning, was 121° counterclockwise. Four of the tortoises which had not shown a preferred direction at noon did so after being phase-shifted. The controls showed no significant change in

Table 6. Mean preferred directions; concentration around mean direction, r_c , and z statistic for significance of tortoises tested in the arena throughout the day.

Tortoise	r_c	z	Angle
67A15	0.4795	4.1379**	279°
67A22	0.0769	0.1066	94°
67A19	0.2924	1.2679	294°
67AC1	0.0169	0.0046	30°
67AC2	0.1565	0.4406	161°
67AC3	0.4065	2.9738*	54°
67AC4	0.3746	2.1045	10°
67MH1	0.3351	2.0763	150°
67SF2	0.3098	1.7274	262°
67SVF1	0.2312	0.9521	85°
67F1	0.5730	5.9090**	300°
67X1	0.5594	5.6329**	356°
67GC1	0.1318	0.5286	335°
68A1	0.7485	11.2040**	182°
68A2	0.2615	1.3660	140°
68A4	0.6843	9.3640**	167°
68A5	0.3780	2.8560	307°
68A6	0.2133	0.9140	238°

Table 6 (Continued)

Tortoise	r_c	z	Angle
68A7	0.5958	7.0980**	107°
68A8	0.2050	0.8400	132°
68A9	0.0942	0.1760	230°
68A10	0.6973	9.7240**	107°
68JJ1	0.6685	8.9360**	93°
68M1	0.5050	5.1000**	131°
68M2	0.7367	10.8540**	169°
68S1	0.4733	4.4805**	173°
68SF1	0.1989	0.7900	79°
68L1	0.3070	1.3853	341°
68HC1	0.6558	8.6010**	304°
68MI	0.4966	4.4394*	358°
68CJ1	0.6170	7.6127**	329°
68HAW1	0.5836	6.8117**	42°
68RS1	0.5918	7.0055**	298°
68ACP	0.4020	3.2318*	260°
68RCG	0.3568	2.5467	249°
68O1	0.5646	6.3750**	232°
68N1	0.2575	1.3263	287°

* indicates significance at the 0.05 level.

**indicates significance at the 0.01 level for non-random, preferred direction.

Table 7. Comparison of preferred directions in open field and arena tests.

Tortoise	Open Field Heading (deg)	Arena Heading (deg)	Remarks
68 L1	----	----	No orientation under either set of conditions.
68 O1	231**	232**	Same direction preference under both sets of conditions.
68 RS	230**	298**	Orientation, but shift in preference
68 ACP	202*	260*	"
68 HAW 1	302**	42**	"
68 M I	----	358	Orientation in arena only.
63 HCl	----	304**	"
68 N1	268**	----	Orientation in field only.

* indicated 0.05 level of significance;

**indicates 0.01 level.

Table 8. Mean preferred directions; concentration around mean direction, r_C ; and z statistic for significance of tortoises tested in the arena at three different times of day.

Tortoise	Morning			Noon			Afternoon		
	r_C	z	Anglea	r_C	z	Anglea	r_C	z	Anglea
67A15	0.9025	4.8859**	265	0.1514	0.1036	170	0.6991	2.9322**	509
67A22	0.4460	1.1956	249	0.1686	0.1705	190	0.4036	0.9774	129
67A19	0.6936	2.8366**	305	0.3770	0.8526	203	0.5057	1.0231	150
67A21	0.4905	1.4433	170	0.5774	2.0005	319	0.4885	0.9546	75
67A22	0.1686	0.1705	30	0.1951	0.2285	70	0.6411	2.4664	191
67A23	0.3170	0.6030	53	0.3619	0.7857	84	0.6124	2.2502	38
67A24	0.0873	0.0457	15	0.5905	2.0919	532	0.6513	1.2723	15
67NH1	0.2267	0.2056	135	0.4768	1.3642	135	0.5058	1.0231	130
67SF2	0.6513	2.5455	225	0.3372	0.6821	0	0.4905	1.4433	260
67SF1	0.2539	0.3867	355	0.3257	0.6364	105	0.4129	1.0231	105
67F1	0.5070	1.5469	275	0.6300	2.3872	304	0.6513	2.5455	315
67A1	0.4847	1.4093	335	0.4606	1.2727	30	0.8495	4.5297**	350
67G21	0.2920	0.5115	0	0.1951	0.2284	542	0.2267	0.2056	255
68A1	0.8173	5.3457**	180	0.8495	4.3297**	170	0.6124	2.2502	202
68A2	0.4983	1.9858	131	0.3770	0.6526	63	0.4847	1.4098	215
68A4	0.5849	2.7958	156	0.8154	3.9980*	168	0.7198	3.0571*	178
68A5	0.3165	0.8016	333	0.4221	1.0688	533	0.3898	4.7500**	315
68A6	0.2190	0.3837	30	0.6124	2.2502	218	0.4036	0.9774	249
68A7	0.5213	2.1740	106	0.5453	1.7843	122	0.7797	3.6477*	96
68A8	0.5644	2.5465	180	0.0973	0.6457	165	0.6124	2.2502	52
68A9	0.5202	2.1649	125	0.6936	2.8866*	325	0.5453	1.7843	212
68A10	0.7328	4.2955**	105	0.4036	0.9774	129	0.9809	5.7731**	100

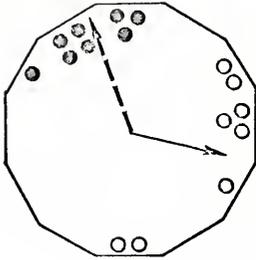
Table 8. (Continued)

Tortoise	Morning			Moon			Afternoon		
	r _c	z	Angle ^a	r _c	z	Angle ^a	r _c	z	Angle ^a
68JJ1	0.6115	2.9916*	132	0.7306	3.2733*	95	0.9564	5.2616**	70
68N1	0.7691	4.7319**	125	0.2539	0.5867	115	0.4625	1.2824	156
68M2	0.7543	4.5513**	149	0.7761	3.6142	153	0.9472	5.3326**	205
68S1	0.5355	2.2928	122	0.4460	1.1936	169	0.9066	4.9314**	214
68SF1	0.3636	1.0574	95	0.5453	1.7643	28	0.3255	0.6354	195
68L1	0.5720	2.6170	99	0.7791	3.6477**	326	0.8616	4.4546**	296
68HC1	0.3366	5.5995**	304	0.6572	2.5912	323	0.4905	1.4433	280
68NI	0.6673	3.5625*	345	0.5453	1.7843	2	0.2529	0.2558	120
68CJ1	0.7001	3.9210*	236	0.6936	2.8865*	5	0.8462	4.2963**	344
68UAN 1	0.7676	4.7134**	49	0.4036	0.9774	51	0.5206	1.6261	44
68RS	0.0868	0.0603	122	0.2920	0.5115	0	0.9335	5.2281**	316
68ACP	0.4385	1.9091	225	0.4606	1.2727	330	0.6513	2.5455	255
68RCG	0.6594	3.4781*	222	0.4036	0.9774	351	0.4905	1.4433	250
68O1	0.6909	3.8183*	210	0.1745	0.1823	285	0.9475	5.3864**	245
68N1	0.5821	2.7108	327	0.5259	1.6595	143	0.7138	3.0571*	272

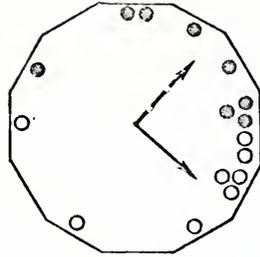
* indicates significance at the 0.05 level.

** indicates significance at the 0.01 level for non-random preferred direction.
a Angles in degrees.

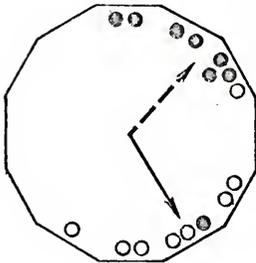
Figure 13. Comparison of original preferred directions of tortoises in the arena during the morning testing period and the preferred directions after the tortoises had been subjected to a phase-shift 6 hours advanced. Open circles, original directions; solid circles, directions after phase-shifting. Solid arrows indicate original mean preferred directions; dashed arrows indicate shifted mean preferred directions; arrow lengths indicate r_c values.



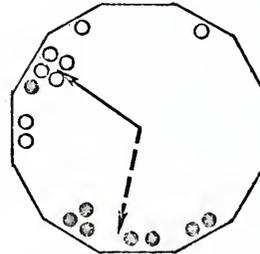
A 10



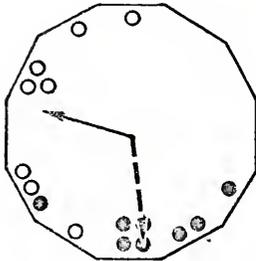
JJ 1



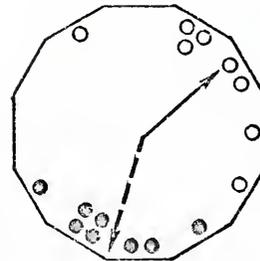
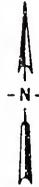
M 2



HC 1

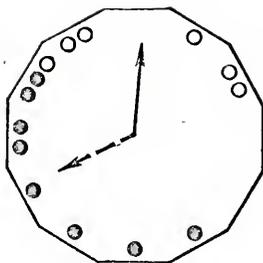


CJ 1

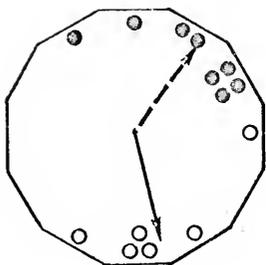


How 1

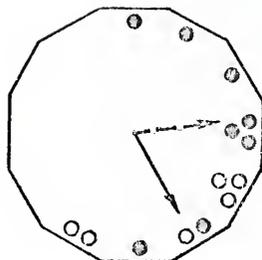
Figure 14. Comparison of original preferred directions of tortoises in the arena during the noon testing period and the preferred directions after the tortoises had been subjected to an advanced phase-shift of 6 hours. Data presented as explained for Figure 13.



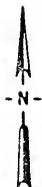
C J 1



A 4



M 2



direction preference in the morning; and showed no improvement of orientation at noon.

Discussion

It was hoped that by carrying the tortoises to the test field in covered ice chests, and starting them in randomly chosen directions, directional cues could be limited. Testing in a field distant from the home burrow, and moving the release point between trials should have prevented any recognition of familiar landmarks by the tortoises and reduced the possibility of their learning new landmarks in the test situation.

Even with these precautions thirteen of twenty-three tortoises tested (56.5%) demonstrated a significant ($P < .05$) non-random directional preference. It might be argued that repeated testing may cause an individual to respond in later trials as it did in earlier trials, or to improve its ability to orient. Such a situation has been reported in birds. Schmidt-Koenig (1963) and Graue (1965) found that homing pigeons would alter their orientation with experience. The tortoises, however, were not returned to their home areas between trials as were the pigeons, so that intertrial reinforcement was avoided. Furthermore, there was no obvious improvement in homeward orientation upon repeated testing. Learning, of course, may have occurred, but the stimulus

that provided the tortoise with directional information still must be determined.

The relative straightness of the paths taken by individuals during these tests provides additional evidence of orientation by the tortoises displaced from their home ranges. In the absence of orientation it would be expected that longer paths would result in greater deviations from a straight line. It is apparent (Figure 12) that, instead, a linear relationship between actual path and straight-line path was obtained ($r = .97$), which would not be expected in the absence of orientation. The mean ratio between actual path and straight-line path is 1.6:1 with a 95 per cent confidence interval of 1.5 to 1.7. Although this is significantly greater than the 1:1 ratio expected in perfect orientation, it is not expected that a terrestrial animal encountering tufts of grass and other small obstacles could achieve such a degree of orientation. The ratio corresponds well with the ratio of 1.46:1 obtained with Chrysemys picta released 100 meters from their home pond (Emlen, personal communication). This same species when displaced one mile from the home pond achieved a ratio of 2.33:1. Using these values for comparison, it is apparent that the gopher tortoises

were orienting, even though they were at least 5 miles from home and well beyond any familiar landmarks.

These two measures, direction preference and straightness of path, indicate that the tortoises were oriented in individual directions. This was true even for tortoises from the same geographic population. There is no preference for the homeward direction. These results bolster the assumption that the tortoises are not capable of true navigation under these conditions. "Nonsense" orientation was defined by Matthews (1961) to be a population-specific variable. There is no such population-specific consistency in the tortoises. However, this possibility cannot be dismissed because landmarks are known to disrupt the orientation of birds (Schmidt-Koenig, 1965), and potentially disrupting landmarks were present during these tests.

The straightness of the paths suggests that the tortoises are capable of perceiving these stimuli anywhere in the field and are continuously orienting by them. What stimuli are responsible for this orientation? The possibilities fall into two major categories: internal, such as kinesthetic sense and inertial guidance; and external. Kinesthetic orientation could account for the straightness

of the path but not for the consistent directional preference on succeeding trials, particularly when the starting directions were randomized. Inertial guidance has been suggested as a possible means of orientation (Barlow, 1964, 1965, 1966). This remains an interesting possibility, but it has not yet been clearly shown to be present in animals.

The external cues suggested as possibilities by these open field data are gravity, earth's magnetic field, large landmarks, and position of the sun. Geotactic guidance has been reported in hatchling Caretta trying to escape from the nest (Moble and Breslau, 1938), but observations on pond turtles whose supposed goal, the pond, is often downhill have not supported the existence of geotaxis in adults (Dolen, 1965). In any case, relative flatness of the test field in the present study and the dispersed preferred directions suggest that this cue is not involved in tortoises.

At present there is no evidence that any reptile is capable of detecting the earth's magnetic field. Recently there has been a renewed interest in this phenomenon and its effect on bird orientation (Merkel and Wiltschko, 1965), but there is little evidence to support its existence.

A large landmark that the field data suggest might have been used by the orienting tortoises is the tree-line obstructing the horizon. The effect of the horizon on the orientation of turtles has been well documented. Caretta (Noble and Breslau, 1938), Dermochelys (Carr and Ogren, 1959), and Chelonia (Carr and Ogren, 1960; Ehrenfeld and Carr, 1967) hatchlings move away from a blocked horizon or toward a clear horizon; or away from dark shapes (Caretta, Daniel and Smith, 1947; Trionyx, Graptemys, Anderson, 1958). The tortoises in the present study showed no uniform reaction to the horizon in the test field, indicating that a simple phototaxis is not involved. Instead, the individuals may have responded to particular features of the horizon, or perhaps even to particular trees. This could account for the scattered direction preferences among individuals, as well as for the straight paths.

The results also suggest the need to postulate that some sort of solar orientation is utilized. There is some evidence that reptiles are capable of using the position of the sun for orientation (see p.66). . Solar orientation may take the form of a compass sense alone, with each individual simply using it to take a particular direction of travel

adaptively useful in establishing the position of the supposed goal, the home burrow, so long as no untoward displacement from familiar territory has occurred. In the present case compass orientation could also explain the data obtained.

Thus the two possible guidance systems suggested by the present experiments are: landmark orientation and solar orientation. To distinguish between them it is necessary to examine one in the absence of the other. This was done in the arena which excluded landmarks and provided the tortoises with the position of the sun as an orientational reference.

Arena Tests

Even with landmarks screened from the tortoises by the wall of the arena, nineteen of thirty-seven (51.4%) animals showed a non-random directional preference throughout the day. Sixteen of these preferences were significant at the 0.01 level and the other three were significant at the 0.05 level. There was no difference between the percentage of animals orienting in the open field and in the arena, which suggests that solar orientation was involved.

Most of the tortoises that demonstrated a direction preference throughout the day did not orient well during

at least one of the three testing periods (0900-1030 LST, 1130-1300, LST, and 1500-1630 LST). Some tortoises that did not orient throughout the day did show a directional preference during one of these periods, but the chosen directions were so scattered during the other periods that the z statistic indicated no preferred direction throughout the day. Other tortoises that did show a preferred direction through the entire day, showed no orientation during any of the periods separately. In this case the scatter overall was very little and a preferred direction was indicated. These two situations might have been clarified if the number of runs per tortoise had been increased. However, the disorientation at one or more times of day seems to have been a real phenomenon.

One explanation for this could be that the increasing temperature during the day interfered with motivation to orient. If this were the case it would be expected that the temperature and the disorientation are directly related. The mean temperature was least for the morning period, greater at noon, and greatest in the afternoon, but 35.1 per cent of the tortoises oriented in the morning, 13.9 per cent oriented at noon, and 37.8 per cent oriented in the afternoon. Although temperature undoubtedly has an effect on the activity of

these poikilotherms, there is no direct relation between temperature and the ability of the tortoises to show a direction preference.

It is apparent that the ability of the tortoises to orient parallels their activity pattern under controlled conditions as described previously (p. 44): an activity peak in the morning, a decrease of activity at noon, and another peak in the afternoon. This suggests that the tortoises oriented themselves only during the periods in which they are normally active, and that they are disoriented during their normally inactive periods. After phase-shifting the internal clock, seven tortoises showed a direction preference at noon, while only four had shown a preference prior to shifting. This lends credence to the suggestion that lack of orientation at noon reflects the midday inactive period. Further evidence supporting this idea would require the examination of the natural activity periods of a number of tortoises which would subsequently show a preferred direction in the absence of landmarks, but this was not obtained in this study. It should be noted that in the open field tests there was no apparent period of disorientation for an individual, although this was not rigorously examined.

If the above hypothesis is true, then it can be further concluded that the tortoises relied upon a diurnally fluctuating stimulus for their orientation. This adds further support that the position of the sun was used for orientation and reduces the probability that the stable cues--gravity, the earth's magnetic field, or inertial guidance--were involved.

It is apparent (Figures 10,11) that the individuals' preferred directions in the arena are not homeward directions. Furthermore, there is no tendency for individuals from the same geographic population to prefer the same direction. These results are similar to those obtained in the open field. Although the field results may have been affected by the presence of landmarks which might have had a disrupting influence on the orientation of the tortoises, this cannot be true in the arena tests. The direction preferences in the arena strongly imply that the tortoises utilize a sun-compass, and that this could not be true bicoordinate navigation because the preferred directions were not home-directed. Still, it is possible that some factor other than the position of the sun is responsible.

Assuming that the sun's azimuth shifts at an average uniform rate of 15° per hour, a six-hour phase-shift then is

equivalent to a 90° change of azimuth. If the animal is subjected to such a shift by altering the light-dark cycle and the animal orients by maintaining a time-compensated compass direction based on the sun's position, then the animal's preferred direction should shift 90° in a direction appropriate to the direction of the phase-shift (clockwise if the clock is retarded; counterclockwise if the clock is advanced). Ten tortoises were subjected to a six-hour shift before local solar time after demonstrating a direction preference in the arena throughout the day. Comparison of the preferred directions under these two sets of conditions shows a mean shift of 121° for the six tortoises which showed a preferred direction during the morning testing period. This is not a statistically significant difference ($P > .05$), Watson and Williams Test (1956), from the expected 90° shift and is in the expected counterclockwise direction. One tortoise (Haw 1) either shifted in the appropriate direction but greatly overshot the magnitude of the shift or shifted in the opposite direction. Because no shift in the opposite direction has yet been reported in phase-shifted animals, I assume that this individual was merely overcompensating in the counterclockwise direction and have treated these results accordingly. These data indicate that the tortoises are able to utilize a time-compensated sun-compass.

Only three individuals were oriented at noon and displayed a directional preference at local noon after a six-hour phase-shift. The observed shift in preferred direction was also counterclockwise, with a mean of 107° , even less of a difference from the expected 90° shift than was the morning shift, but because of the small sample I was not able to analyze this statistically. Thus there is no difference in the behavior of the shifted tortoises at the two times of day.

The compass orientation of the tortoises is not very precise under the experimental conditions, although it may be more precise under natural conditions. The mean values of the shifted directions were not significantly different from those expected, but there was considerable variation among individuals and there was a tendency for an overshoot. This inaccuracy may be due to several factors. First, although the average rate of change of the sun's azimuth is 15° per hour, the rate is faster around noon and slower in the morning and evening (Braemer, 1960). Thus, to expect a directional change of 90° resulting from a six-hour phase-shift may not be valid. Another factor is the accuracy of the tortoises' internal clocks. The mean circadian period under constant

light is 22:33 hours (p. 59). If this period were used as a basis for time measurement, this means that the internal clock is running faster than solar time and would result in an average hourly change of 15.8° . A six-hour phase-shift would then cause an expected deviation of 94.8° rather than 90° from the original preferred direction. Individuals also showed considerable variability of period length. A tortoise which showed shorter periods would be expected to show a greater difference between expected and shifted directions. The relatively small number of trials per tortoise may also have introduced a sampling error. Any or all of these uncontrolled factors may account for the discrepancy between the expected and the actual shifts in preferred direction.

Another question concerns which aspect of the sun's position is being used by the tortoises for compass orientation. Hoffman (1960) has pointed out that besides a time sense an animal utilizing the sun for time-compensated solar orientation may use either the altitude or the azimuth. The tortoises which were phase-shifted and tested at noon made alterations in preferred directions in the correct

direction, and of approximately the expected magnitude, even though the sun was not correct for their subjective time (1800 LST). Also, there was no obvious conflict between their original preferred directions and the shifted directions as Braemer (1960) reported for fish. Braemer regarded such a conflict as evidence for the utilization of the sun's altitude. The results obtained with the tortoises parallel those obtained by Hoffman (1960) with starlings and I conclude that the gopher tortoises used only the sun's azimuth for sun-compass orientation.

The ability to orient correctly at noon presents still another problem because some of the tests were run on the summer solstice, when the sun's position was only 7° from the zenith at the experimental site (Alachua, Florida). It would be expected that unless the tortoises could distinguish a radial position difference of only 7° from the zenith they could not determine the azimuth. No data concerning this aspect of visual acuity have been reported for tortoises. Psychophysical approaches to this phenomenon have been conducted on other species. Leibowitz et al. (1955) report that humans can localize the radial position of a light with an error of 4.64° . Pigeons (McDonald, 1968)

can discriminate a difference of position of 3.4° . Neither of these involved the position of a celestial body, but tortoises may be able to determine a 7° difference from the zenith and thus determine the azimuth. Another possibility is that the walls of the arena cast shadows when the sun is not at the zenith position. Shadows may provide the azimuthal information to the tortoises at noon. Further studies are needed to resolve this question.

Having established the utilization of a sun-compass by the gopher tortoise, the question of adaptive significance of such a mechanism arises. Until the life history of this species is better known the answer must remain conjectural. As has been mentioned earlier in this study, gopher tortoises seldom wander far from their burrows. At close range a time-compensated sun-compass would seem to be of only secondary importance, with the primary cues being landmarks and trails. It might be of some use in making a choice between the forks of a branching trail, but topical cues would be far more accurate.

It is only when the tortoise has lost sensory contact with familiar landmarks that the utility of a sun-compass would be apparent. There are several situations when this

might occur and when the animal might try to regain this contact: when the food supply near the burrow fails, or when travel out of known territory in search of a mate might become necessary. In such cases the ability to determine directions by a solar compass would greatly increase the wanderer's chances of renewing sensory contact with familiar landmarks leading to its burrow. The individuality of direction preference of tortoises from the same geographic population suggests that their directional preferences have been learned. If this is true then perhaps these individuals have acquired a particular direction tendency because they previously had found food, a mate, or an alternative burrow in that direction.

However, it is not necessary to assume that the tortoise is attempting to re-establish contact with familiar landmarks in every case in which a direction preference is shown. There are situations which would cause the burrow to lose its attractiveness to the tortoise. A fire that destroyed the food supply near the burrow might send the tortoise off in search of a better place or a new burrow. In locating a new habitable site the tortoise would traverse the greatest distance with the least expenditure of energy

if it travelled in a straight line. Such movements do not preclude the use of landmarks. It has often been remarked that all travel orientation by animals is almost certainly composite, involving a number of different sensory cues and sources of information.

Comparison of data obtained in the field and in the arena for the same individuals is summarized in Table 7. It appears that where landmarks are present these override sun-compass direction as a guidance mechanism. The disruptive effect of landmarks has been described previously for birds (Schmidt-Koenig, 1965). Only one tortoise was unable to orient under either the conditions of the open field or those of the arena. One tortoise oriented in the field but not in the arena. The preferred direction of this individual was directly toward the tree-line and may reflect an attempt at behavioral thermoregulation. The remaining tortoises oriented similarly under both sets of conditions although a statistically significant shift is apparent in three individuals. It seems likely that any tortoise displaced from familiar territory may use both a sun-compass and fixed features of the landscape in its orientation. If the tortoise were attempting to find its home burrow,

then it would probably be searching for the familiar landmarks surrounding the burrow. Landmarks similar to familiar ones might confuse the experimental tortoise. If, on the other hand, a tortoise were trying to find an area suitable for establishing a new burrow then certain landmark types might indicate the suitability of the area..

Orientation in gopher tortoises thus seems to involve two mechanisms: a time-compensated sun-compass, perhaps used to establish contact with landmarks; and the landmarks themselves, which provide precise information regarding the position of the home burrow or a suitable site for establishing a new burrow.

CHAPTER VI

SUMMARY

Twenty-two tortoises were displaced short distances from their burrows. If the distance was not great they were able to return to this burrow. When the distance of displacement was somewhat greater the larger tortoises headed directly to one of a number of other burrows. Displaced still farther the tortoises wandered. The maximum size of the home range, determined on the basis of the distance from the home burrow to the most distant other burrow, is 31,400 m² for a 20 cm tortoise in a pine-grassland ecotone in north-central Florida.

Between the home burrow and the feeding areas are distinct trails which appear to be the primary short-range orientation cues. Experiments with twenty-two tortoises on artificial trails indicate that visual and tactile stimuli are utilized by the tortoises on these trails. No evidence was obtained for the use of olfactory cues although blocking the nose with wax and testing the tortoises in a T maze was done. However, this remains a possibility.

Gopherus polyphemus has an internal clock similar to that described for other animals. Under constant light the mean circadian period is 22:47.1 to 22:53.1 hours depending on whether the linear regression or the classical method of calculating mean period length is used. The former seems to best analyze the data. There is, however, considerable variation among tortoises; although an individual's period length is relatively constant, particularly when provided with a refuge from the imposed light conditions. Under constant darkness a tortoise either became totally inactive or showed a period length of about 22:34.4 hours, but these data were obtained from two individuals.

The inaccuracy of the internal clock, compared with values obtained for other animals, suggests that it is not suitable for use in celestial navigation-- position finding-- but might be sufficient for compass orientation. This is further supported by the relative ease with which the activity pattern can be phase-shifted, requiring only one to two days for a six-hour phase-shift; and seven days for a twelve-hour shift.

To test the possibility that tortoises are capable of orienting outside their home range, twenty-three tortoises were released in an open field at least 5 miles

from their home burrows. Over half (56.5%) showed a statistically significant individual direction preference. Their preferred directions had no relation to the homeward direction and were widely divergent even among individuals from the same geographic population.

Thirty-seven tortoises were tested in an arena which excluded all outside landmarks. Nineteen of these tortoises (51.4%) showed a significant direction preference in these tests. Comparison of eight individuals tested in the open field and in the arena showed that in only one case was the direction preference the same under both conditions, suggesting that landmarks may have a disruptive effect on the tortoise's orientation.

To show that this direction preference in the arena was due to sun-compass orientation, ten tortoises were subjected to a phase-shift of six hours earlier than natural onset of light. This resulted in a change in the expected counterclockwise direction and the mean shift in preferred direction was not significantly different from the expected shift of 90° . Because the only parameter that was changed was the phase of the internal clock and the only diurnally

fluctuating cue in the arena was the position of the sun, it is concluded that the gopher tortoise is capable of sun-compass orientation.

Therefore, at least one species of turtle has been shown to be capable of sun-compass orientation. However, many questions remain to be answered. What is the activity pattern under natural conditions? Will a tortoise maintain its preferred direction over long periods of time? What is the value to a tortoise of being able to utilize a sun-compass? Much of the ecology and behavior of these tortoises must be examined before a definite answer can be given.

LITERATURE CITED

- Adler, H. 1963a. Psychophysical limits of celestial navigation hypotheses. *Ergeb. der Biol.* 26: 235-252.
- _____ 1963b. Sensory factors in migration. *Animal Behav.* 11: 566-577.
- Allard, H. 1949. The eastern box turtle and its behavior. *J. Tenn. Acad. Sci.* 25: 146-152.
- Anderson, P. 1958. The photic responses and water-approach behavior of hatchling turtles. *Copeia*. 1958: 211-215.
- Animal Orientation and navigation. 1967. R. Storm (ed). Univ. Oregon Press, Corvallis: 1-134.
- Aschoff, J. 1960. Exogenous and endogenous components in circadian rhythms. *Cold Spr. Harb. Symp. quant. Biol.* 25: 11-26.
- Auffenberg, W. 1965. Sex and species discrimination in two sympatric South American tortoises. *Copeia*. 1965: 335-342.
- _____ 1966. On the courtship of Gopherus poly-
phenus. *Herpetologica*. 22: 113-117.
- Barlow, J. 1964. Inertial navigation as a basis for animal navigation. *J. Theor. Biol.* 6: 76-117.
- _____ 1965. Inertial navigation and animal navigation. *New England J. Med.* 273: 1090-1092.
- _____ 1966. Inertial navigation in relation to animal navigation. *J. Inst. Navigation*. 19: 302-316.
- Batschelet, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. *A.I.B.S. Monograph*. Washington, D.C.
- Birukow, G., K. Fischer, and H. Bottcher. 1963. Die Sonnenkompassorientierung der Eidechsen. *Ergeb. der Biol.* 26: 216-234.

LITERATURE CITED (Continued)

- Blair, F. 1951. Population structure, social behavior, and environmental relations in a natural population of the beach mouse (Peromyscus polionotus leucocephalus). Contrib. Lab. Vert. Biol. 48.
- Boycott, B. and R. Guillery. 1962. Olfactory and visual learning in the red-eared terrapin, Pseudemys scripta elegans (Wied.). J. Exp. Biol. 39: 567-577.
- Braemer, W. 1960. A critical review of the sun-azimuth hypothesis. Cold Spr. Harb. Symp. quant. Biol. 29: 413-427.
- Breder, R. 1927. Turtle trailing: a new technique for studying the life habits of certain testudinata. Zoologica. 9: 231-243.
- Bruce, V. 1960. Environmental entrainment of circadian rhythms. Cold Spr. Harbor Symp. quant. Biol. 25: 29-48.
- Bünning, E. 1964. The physiological clock. Springer Verlag. Berlin.
- Burt, W. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24: 346-357.
- Cagle, F. 1944. Home range, homing behavior, and migration in turtles. Misc. Publ. Mus. Zool. Univ. Mich. 61: 1-34.
- Carr, A. 1963. Panspecific reproductive convergence in Lepidochelys kempi. Ergeb. der Biol. 26: 298-303.
- _____ 1964. Transoceanic migration of the green turtle. Bioscience. 14: 49-52.
- _____ 1967. Adaptive aspects of the scheduled travel of Chelonia. Animal orientation and navigation. R. Storm (ed.). Oregon State Univ. Press. Corvallis. 35-55.

LITERATURE CITED (Continued)

- Carr, A. and L. Ogren. 1959. The ecology and migrations of sea turtles. 3. Dermodochelys in Costa Rica. Amer. Mus. Novitates. 1958: 1-29.
- _____ 1960. The ecology and migrations of sea turtles, 4. The green turtle in the Caribbean Sea. Bull. of Amer. Mus. Nat. Hist. 121: 1-48.
- Casteel, D. 1911. The discriminative ability of the painted turtle. J. Anim. Behav. 1: 1-28.
- Cold Spring Harbor Symposium on quantitative Biology. 1960. C.P. Pittendrigh (ed.). 25: 1-524.
- Daniel, R. and K. Smith. 1947. The migration of newly-hatched loggerhead turtles toward the sea. Science. 106: 398-399.
- DeCoursey, P. 1960. Phase control of activity in a rodent. Cold Spr. Harb. Symp. quant. Biol. 25: 49-55.
- Eglis, A. 1962. Tortoise behavior: a taxonomic adjunct. Herpetologica. 18: 1-8.
- Ehrenfeld, D. and A. Carr. 1967. The role of vision in the sea-finding orientation of the green turtle (Chelonia mydas). Anim. Behaviour. 15: 25-36.
- _____ and A. Koch. 1967. Visual accomodation in the green turtle. Science. 155: 827-828.
- Emlen, S. 1965. Homing and orientation in the painted turtle, Chrysemys picta marginata. Amer. Zoologist. 5: 703. Abstract.
- Ergebnisse der Biologie, 1963. H. Antrum (ed.) Springer-Verlag. 26: 1-313.
- Fischer, K. 1961. Untersuchungen zur Sonnenkompassorientierung und Laufaktivität von Smaragdeidechsen (Lacerta viridis Laur.). Z. Tierpsychol. 13: 450-470.

LITERATURE CITED (Continued)

- Fischer, K. 1964. Spontanes Richtungsfinden nach dem Sonnenstand bei Chelonia mydas L. (Suppenschildkröte). *Naturwissenschaften*. 51: 203.
- Gilroy, J. 1965. Corrections for grouping in the case of circular distributions. (Cited in Batachelet, 1965).
- Gould, E. 1957. Orientation in box turtles, Terrapene c. carolina (Linnaeus). *Biol. Bull.* 112: 336-343.
- _____ 1959. Studies on the orientation of turtles. *Copeia* 1959: 174-176.
- Graue, L. 1965. Experience effect on initial orientation in pigeon homing. *Anim. Behaviour*. 13: 149-153.
- Greenwood, J. and D. Durand. 1955. The distribution of length and components of the sum of n random unit vectors. *Ann. Math. Stat.* 26: 233-246.
- Griffin, D. 1952. Bird navigation. *Biol. Rev.* 27: 360-393.
- Groot, C. 1965. On the orientation of young sockeye salmon (Oncorhynchus nerka) during their seaward migration out of lakes. *Behaviour Suppl.* 15: 1-198. E.J. Brill. Leiden.
- Harker, J. 1960. In discussion. *Cold Spr. Harb. Symp. quant. Biol.* 25: 354.
- Hasler, A. 1966. Underwater guideposts: Homing of salmon. The Univ. of Wisconsin Press. Madison.
- Hoffman, K. 1954. Versuche zu der im Richtungsfinden der Vogel enthalten Zeitschätzung. *Z. Tierpsychol.* 11: 453-475.
- _____ 1960. Experimental manipulation of the orientational clock in birds. *Cold Spr. Harb. Symp. quant. Biol.* 25: 379-387.

LITERATURE CITED (Continued)

- Hoffman, K. 1965. Overt circadian frequencies and circadian rule. *Circadian Clocks*. J. Aschoff (ed.). North-Holland Publishing Co., Amsterdam.
- _____ 1963. Synchronisation der circadianen Aktivitätsperiodik von Eidechsen durch Temperaturecyclen verschiedener Amplitude. *Z. Vergl. Physiol.* 58: 225-228.
- Leibowitz, H., N. Myers, and D. Grant. 1955. Radial localization of a single stimulus as a function of luminance and duration of exposure. *J. Opt. Soc. Amer.* 45: 76-78.
- Lowe, C., D. Hinds, P. Lardner, and K. Justico. 1967. Natural free-running period in vertebrate populations. *Science*. 156: 531-534.
- McDonald, D. 1963. Bird orientation: A method of study, *Science*. 161: 486-487.
- Matthews, G. 1955. *Bird navigation*. Cambridge Univ. Press. N.Y.
- _____ 1961. 'Nonsense' orientation in Mallard, Anas platyrhynchos, and its relation to experiments on bird navigation. *Ibis*. 103: 211-230.
- _____ 1963. 'Nonsense' orientation as a population variant. *Ibis*. 105: 185-197.
- Merkel, F. and W. Wiltshko. 1965. Magnetismus und Richtungsfinden zugunruhiger Rotkehlchen (Erithacus rubecula). *Vogelwarte*. 23: 71-77.
- Mertens, R. 1953. Wie orientieren sich die Schildkröten? *Natur und Volk*. 88: 116-121.
- Meyer, M. 1964. Discriminative basis for astronavigation in birds. *J. Comp. Physiol. Psychol.* 58: 403-406.

LITERATURE CITED (Continued)

- Nichols, J. 1939. Range and homing of individual box turtles. *Copeia*. 1939: 125-127.
- Noble, G. and A. Breslau. 1938. The senses involved in the migration of young fresh water turtles after hatching. *J. Comp. Psychol.* 25: 175-193.
- Oliver, J. 1954. The natural history of North American amphibians and reptiles. Von Nostrand. Princeton, N.J.
- Ortleb, E. and O. Sexton. 1964. Orientation of the painted turtle, *Chrysemys picta*. *Amer. Midland Naturalist*. 71: 320-334.
- Pittendrigh, C. 1960. Circadian rhythms and the circadian organization of living systems. *Cold Spr. Harb. Symp. quant. Biol.* 25: 159-184.
- Poliakov, K. 1930. The physiology of the olfactory and auditory analysers in the turtle *Emys orbicularis*. (Russian, German summary). *Russ. Fiziol. Zh.* 13: 162-178.
- Quaranta, J. 1952. An experimental study of the color vision of the giant tortoise. *Zoologica*. 37: 295-311.
- Schmidt-Koenig, K. 1958. Experimentelle Einflussnahme auf die 24-Stunden-Periodik bei Brieftauben und deren Auswirkungen unterbesonder Berücksichtigung des Heimfindevermögens. *Z. Tierpsychol.* 15: 301-331.
- _____ 1963. Neuere aspekte uber die Orientierungsleistungen von Brieftauben. *Ergeb. der Biol.* 26: 286-297.
- _____ 1965. Current problems in bird orientation. In *advances in the study of behavior*. (E. Hinde, D. Lehman, E. Shaw ed.) N.Y. 217-278.
- Siegel, S. 1956. *Non parametric statistics for the behavioral sciences*. McGraw-Hill. N.Y.

LITERATURE CITED (Continued)

- Snedecor, G. and W. Cochran. 1967. Statistical methods. 5th ed. The Iowa State Univ. Press. Ames.
- Stickel, L. 1950. Populations and home range relationships of the box turtle, Terrapene c. carolina (Linnaeus). Ecol. Monogr. 20: 351-378.
- Tucker, D. 1963. Physical variables in the olfactory stimulation process. J. Gen. Physiol. 46: 453-489.
- Twitty, V. 1959. Migration and speciation in newts. Science. 130: 1735-1743. 1
- Walraff, H. 1960. Does celestial navigation exist in animals? Cold Spr. Harb. Symp. quant. Biol. 25: 451-461.
- _____ 1967. The present status of our knowledge about pigeon homing. Proc. XIV Int. Orn. Cong. Oxford. 331-358.
- Walls, G. 1942. The vertebrate eye and its adaptive radiation. Cranbrook Inst. Science, Bloomfield Hills, Mich.
- Watson, G. and E. Williams. 1956. On the construction of significance tests on the circle and the sphere. Biometrika. 43: 344-352.
- Weaver, W., Jr., 1967. Courtship and combat behavior in Gopherus berlandieri. Doctoral dissertation. University of Florida, Gainesville.
- Wisby, W. and A. Hasler. 1954. The effect of olfactory occlusion in migrating silver salmon (O. kisutch). J. Fish. Res. Bd. Can. 11: 472-478.
- Woodbury, A. and R. Hardy. 1943. Studies of the desert tortoise, Gopherus agassizii. Ecol. Monogr. 18: 145-200.

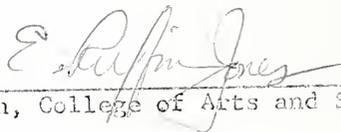
BIOGRAPHICAL SKETCH

Eugene Vincent Gourley was born November 15, 1940, at Detroit, Michigan. In June, 1958, he graduated from Southfield High School, Southfield, Michigan. He attended the University of Michigan, from September, 1958, to June, 1960. He attended Wayne State University during the Summer of 1960. In September, 1960, he enrolled in Eastern Michigan University, and received the degree of Bachelor of Arts in June, 1962. He enrolled in the graduate school of Eastern Michigan University in September, 1962, working as a teaching assistant until June, 1964, when he received the degree of Master of Science. From September, 1964, until the present time he continued his work toward the degree of Doctor of Philosophy, while serving as a research and teaching assistant, and also was awarded a graduate school fellowship from 1966 until 1967. He is presently an interim instructor in Zoology for the University of Florida.

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This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

March, 1969



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