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HOMING BEHAVIOR AND ORIENTATION IN THE GOPHER TORTOISE, *GOPHERUS POLYPHEMUS*

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CERTIFICATE OF APPROVAL

Master's Thesis

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the Examining Committee on January 30, 1996
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HOMING BEHAVIOR AND ORIENTATION IN THE GOPHER TORTOISE, *GOPHERUS POLYPHEMUS*

by

KEVIN MICHAEL CONNOR

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

May 1996

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

DEDICATION

To my wife, Diana, who has been my motivation for all that I have done since the day we met. And, to my parents and brothers and sisters, who have helped make me the person that I am today.

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Gopher tortoises are found in xeric habitats in the southeastern United States. In these xeric habitats, gopher tortoises excavate and reside in burrows which provide shelter and protection. Gopher tortoises are active throughout the year, often making several journeys a day away from their burrows. Although they may move substantial distances, they return to their burrows, suggesting that they posses a well-developed orientation and homing ability. This study investigated the ability of gopher tortoises to home from short distance (40 meters, just outside of or on the perimeter of their home ranges) and intermediate distances (200 meters, approximately 2 home range units) away from their burrows. This study also evaluated the roles of vision and olfaction in orientation by releasing tortoises with their vision blocked and/or nares plugged.

Gopher tortoises were found to be able to home from short distances away from their burrows. The mean angle they traveled was 4 degrees (0 degrees was the direction of the home burrow). The goal of the homing appeared to be the home range, not the specific home burrow. Only 1 of 15 tortoises returned to its home burrow, while 11 tortoises returned to their home range. The tortoises appeared to be well oriented as indicated by the low mean index of straightness of 1.62. Gopher tortoises also were found to be able to home from intermediate distance away from their burrows. The mean angle traveled was 358 degrees (0 degrees was the direction of the home burrow). Again, the goal of the homing appeared to be the home range, not the specific home burrow, as only 1 of 15 tortoises returned to its home burrow.

Vision and olfaction appear to be important senses for the orientation and movements of gopher tortoises. With the senses blocked, distances moved decreased significantly and no tortoises were able to home. The mean angle moved for tortoises with their vision blocked was 145 degrees, with their nares plugged was 301 degrees,

and with both vision blocked and nares plugged was 81 degrees (0 degrees was the direction of the home burrow). This study indicates that vision may be more important than olfaction for homing and orientation.

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INTRODUCTION

The gopher tortoise, *Gopherus polyphemus* (Daudin), is one of four extant North American species of tortoises. Gopher tortoises occur in the six coastal southeastern states, South Carolina to Louisiana. Within this range, gopher tortoise numbers are declining primarily because of habitat destruction (Auffenberg and Franz, 1982). Gopher tortoises inhabit xeric environments with well drained sandy soils and herbaceous ground cover. In Florida, one of the major tortoise habitats is longleaf pine (*Pinus palustris*) / turkey oak (*Quercus laevis*) uplands (Diemer, 1986). The physical structure of the habitat rather than the particular plant associations appears to be most important in determining which habitats gopher tortoises occupy (Campbell and Christman, 1982). The physical attributes of the habitat that are important to gopher tortoises include well drained loose sands in which to burrow (Hansen, 1963), adequate low growing herbs and grasses for food (Macdonald and Mushinsky, 1988), and sites with relatively low (20-40%) canopy cover (Mushinsky and McCoy, 1994).

Gopher tortoises excavate and reside in deep burrows in sandy habitats. Burrows of adult gopher tortoises in a northern Florida population averaged 4.7 meters in length, 2.0 meters in depth, and had a mean angle of declination of 29 degrees (Hansen, 1963). The burrow provides shelter for a tortoise from extreme climatic conditions, such as high temperature and drought, and also serves as a refuge from predators (Diemer, 1986). Because many other upland species are found in gopher tortoise burrows (Jackson and Milstrey, 1989), the gopher tortoise has been proposed as a keystone species (Eisenberg, 1983). Commensal organisms, such as the gopher frog, *Rana capito*, and the Florida mouse, *Podomys floridanus*, may have evolved a dependence on the gopher tortoise burrow for refuge and microhabitat requirements (Eisenberg, 1983).

The burrow serves as the focal point of the area of activity for a gopher tortoise (McRae *et al.*, 1981). This area of activity, also referred to as a home range, includes both social and feeding components of the tortoises' activities (Auffenberg and Iverson, 1979). Home range size for adult gopher tortoises varies seasonally as a function of social interactions among adults (McRae *et al.*, 1981). Males tend to have larger annual home ranges than females, usually because males move farther in the spring as they search for females (Auffenberg and Iverson, 1979). In a northern Florida population over a two year period, male adult gopher tortoises had an average home range of 0.88 ha, while females had an average home range of 0.31 ha; but because of high individual variation, no significant difference was detected between males and females (Diemer, 1992). In northern Florida, most individuals of both sexes moved less than 50 meters from their burrows to feed (Auffenberg and Iverson, 1979). Nearby, in southern Georgia, 95% of the adult tortoises had a feeding radius within 30 meters of their burrows and most individuals fed in circular or elliptical patterns around their burrows, with a mean radius of 13 meters (McRae *et al.*, 1981).

Movements by gopher tortoises away from their burrows are diurnal and vary with the time of year (Auffenberg and Iverson, 1979). Tortoise activity is greatest in the spring, declines slightly in the summer, increases again in the fall, and may continue at a reduced level through the winter. The spring peak in activity coincides with the reproductive season of the tortoises, when adults tend to make their longest movements. Daily activity is affected by temperature and moisture conditions within a season. In southern Georgia and northern Florida, tortoise activity was unimodal in the cooler months, occurring mostly during the hottest part of the day (0900-1900hr); and bimodal in the hotter months, occurring mostly before and after the hottest part of the day (1000-1200 hr and 1600-1800 hr) (Auffenberg and Iverson, 1979; McRae *et al.*, 1981). A study in south-central Florida, reported gopher tortoise activity to be unimodal throughout the year (0700-2000 hr) (Douglass and Layne, 1978).

Urbanization of upland habitat is one of the leading causes for the decline in the number of gopher tortoises (Auffenberg and Franz, 1982). As a result, gopher tortoises have been the subject of relocation projects, which involve the moving of tortoises from lands that are to be developed for human uses to recipient sites. Unfortunately, many of the relocated tortoises have not remained on the recipient sites. In central Florida, of 12 relocated tortoises, 58% were no longer on the relocation site after 12 months, as opposed to only 15% for resident tortoises (Bard, 1989). In the Mojave Desert, 31 desert tortoises, *Gopherus agassizii*, were relocated, and after 12-17 months, only 5 were found on the relocation site (Berry, 1986). At another site in the Mojave Desert, twelve desert tortoises were relocated 16.1 and 88.6 km from their home sites. Nine of these tortoises showed a tendency to orient homeward (Berry, 1986). Collectively, these observations suggest that the relocated tortoises may be trying to home and find their old burrows (Berry, 1986).

Although gopher tortoises may move substantial distances away from their burrows, they return to them, often many times a day, suggesting that they possess a well-developed orientation and homing ability. Orientation is a selective process in which environmental stimuli elicit a response sequence that results in a nonrandom pattern of locomotion (Adler, 1970), while homing is orientating and moving in the homeward direction. The orientation and homing abilities of other turtle species are well documented. Celestial cues, especially the sun; visual landmarks; olfactory cues; magnetic fields; and geotactile cues are all possible cues for orientation and homing. For example, green sea turtles, *Chelonia mydas*, and box turtles, *Terrapene carolina*, use celestial cues for orientation (Nichols, 1939; Gould, 1957, 1959; Carr, 1964; Lemkau, 1970). Box turtles also recognize magnetic fields, and magnetic disturbances on their outward journeys influence their orientation (Mathis and Moore, 1988). Painted turtles, *Chrysemys picta*, can orient homeward and visual landmarks are important in their homing ability (Gould, 1959; Emlen, 1969). Painted turtles, box turtles and spiny softshell turtles,

Trionyx spinifer, possibly use geotactile and sun compass orientation (DeRosa and Taylor, 1982). The use of olfaction is important in the homing of Herman's tortoise, *Testudo hermanni* (Chelazzi and Delfino, 1986).

Little is known about the orientation and homing abilities of the gopher tortoise. Research on members of the genus *Gopherus* suggests that they rarely move more than 3.2 km from their hatching site during their lives (Auffenberg and Iverson, 1979). When they move, they may use celestial cues for orientation (Gibbons and Smith, 1968), or possibly several different mechanisms may be used in orientation (Gourley, 1969). Gopher tortoises have demonstrated the ability for sun compass orientation, but it appears to be used secondarily to visual landmarks (Gourley, 1974). Landmarks may be important cues for both long and short range orientation. When a gopher tortoise is seeking its home burrow, it may search for familiar landmarks surrounding the burrow, or if it is trying to find an area for establishing a new burrow, similar landmarks might indicate suitable areas. Gopher tortoises travel along well worn paths and other burrows are possible landmarks used in movement (Douglass, 1990). In a long range orientation study, gopher tortoises released between five and seven kilometers from their home area used a sun compass and landmarks for orientation (Gourley, 1974). Tortoises consistently walked in a straight line upon release, but the direction of orientation was not necessarily homeward. The ability to move in a straight line demonstrates type II orientation, which is the selection of a compass heading and traveling in a straight line for several hundred meters (Able, 1980). In the long range orientation studies, only slight evidence was found for the use of olfaction by gopher tortoises, but the possibility of olfactory cues as a directional stimulus still exists (Gourley, 1969). Olfactory cues appear to be used in directional movement within the tortoise's home range (Gourley, 1969).

Homing ability in gopher tortoises has been suggested, but never demonstrated. Most previous studies of the homing and orientation of gopher tortoises were performed in arenas or test fields where the animals were allowed to move only 100 meters or less.

Such studies, therefore, could only demonstrate an ability to orient and a tendency to home. These studies did not show successful homing, i.e. movement back to the home range or burrow. Also, some of these previous studies were not able to determine which of the many possible cues available were actually used by the gopher tortoises for orientation.

My study investigated the homing ability and use of olfaction and vision in orientation by gopher tortoises. Because extremely long movements, movements greater than 3.2 km, are rare and sun compass orientation and use of landmarks for long range navigation have been demonstrated, I focused on the intermediate and short range movements. The concept of intermediate range homing is useful for considering orientation mechanisms because intermediate range homing takes place outside of the animals home range, so that the animals do not have direct contact with the home range, but are close enough to be influenced by local cues (Carroll and Ehrenfeld, 1978).
I evaluated homing ability by releasing tortoises outside their home ranges, and the role of olfaction and vision in orientation by releasing tortoises with their vision blocked and/or nares plugged.

MATERIALS AND METHODS

Study Site

All research was conducted at the 200 ha University of South Florida Ecological Research Area located in Hillsborough County, west-central Florida (28.05° N; 82.20° W). The study site is xeric uplands, consisting of well drained yellowish sands (Lakeland series) with a limestone base (Mushinsky, 1985). Vegetation is typical of sandhill habitat, consisting of grasses (*Aristida stricta* and *Andropogon* spp.); a variety of herbs (*Pityopsis graminifolia*, *Aster* spp., and *Baptista lecontei*); shrubs, predominantly saw palmetto (*Serenoa repens*); and trees, predominately longleaf pine (*Pinus palustris*), slash pine (*P. elliottii*), turkey oak (*Quercus laevis*), and sand live oak (*Q. geminata*) (Myers, 1990). The Ecological Research Area is divided into study plots (1-2 ha each) which are maintained on different frequencies of prescribed burns. The period between controlled burns on the study plots varies from every year, two years, five years, and seven years, to unburned plots which have not been burned in more than thirty years.

Homing Study

Tortoises were captured by burying bucket traps at the burrow openings, to capture tortoises as they emerged from their burrows. The burrow at which a tortoise was captured wass considered its home burrow. The study began in April 1994 and continued through September 1994. Only adult tortoises with carapace lengths greater than 220 mm were used. After being captured, individuals were taken to the laboratory, where they were measured and fitted with a thread trailing device (Wilson, 1994), and then they were

released the following morning. This procedure minimized the amount of time the tortoises were out of their natural habitat.

Tortoises were released and followed using thread trailing techniques. Thread trailing allows for the observation of the path taken by the turtle (Breder, 1927). The thread trailing consists of a precision wound cocoon bobbin of nylon thread (Culver Textiles, New Jersey). Each bobbin is wrapped in plastic wrap and dipped in a rubber-like coating (Plasi-Dip) for support and protection (Wilson, 1994). The thread bobbins were attached to the rear of the carapace with duct tape. When an individual was released, the thread was secured to a marking flag and as the tortoise moved, it left a thread trail behind. A trial continued for as long as the thread bobbin and string remained intact.

Short Range Homing

Short range homing was evaluated by releasing gopher tortoises 40 meters from their burrows. Using Diemer's (1992) home range value of 0.88 ha and assuming a burrow is in the center of the home range, a displacement of 40 meters would place the individual near the perimeter of its home range. Considerable individual variation was reported by Diemer (1992), but no significant difference was found between males and females; therefore, males and females were treated alike in my study. A tortoise could not see its burrow from 40 meters away and would need to use cues to find it. Fifteen tortoises were released in randomly selected directions from their burrows, either north, south, east, or west. The tortoises also were released facing in randomly selected directions, either north, south, east, or west.

Individual gopher tortoises were released in the late morning (900-1100hr), so that each tortoise had sufficient time to reach its burrow before the hottest part of the day. Individuals were left alone to prevent any disturbance or distraction from observers. A tortoise was checked after a few hours. For each individual, three pieces of data were

collected. First, and most important, success or failure in reaching its home range and burrow was determined. Second, the length of the path taken was measured from the length of the string trail. Third, the compass direction of the burrow which the tortoise entered, relative to the release point, was determined.

Intermediate Range Homing

Intermediate range homing was tested by repeating the procedure used for short range homing, but releasing fifteen tortoises a distance of 200 meters, or about two home ranges, from their burrows. Because of the shape of the Ecological Research Area, tortoises could not always be released 200 meters north or south of their burrows, so northeast, northwest, southeast, and southwest releases occasionally were substituted. Success of the homing event, and distance and direction traveled were recorded, as described above.

Orientation Study

Vision and olfaction are the two mechanisms of orientation that have been demonstrated in gopher tortoises (Gourley, 1969 and 1974). In the absence of one of the senses, the most likely cue used for orientation is the other sense. By releasing tortoises with their vision blocked and/or nares plugged, the importance of vision and olfaction in orientation and homing was assessed.

Fifteen gopher tortoises were captured and released in the manner discussed above and released 200 meters from their burrows. This study was conducted in September and October 1994 and February and March 1995. Success of the homing event, and distance and direction traveled were recorded as described above in the homing study. The fifteen individuals were divided into three groups. The first group of 5 tortoises had their vision

blocked by means of small circular band aids (Curad Sensitive Skin - 2.3 cm in diameter with a 1 cm diameter pad in the middle to protect the eye of the tortoise), one covering each eye. The second group of 5 tortoises had their nares blocked with a small piece of Parafilm held in place with duct tape. The third group of 5 tortoises had both their eyes covered and their nares blocked. After being released, each individual was observed from a distance, to minimize additional disturbance. The observations were completed when the tortoise entered a burrow or ceased to move for 20 minutes. Upon completion of the observations, each individual was recaptured and all eye patches and nare plugs were removed. The tortoises were observed several weeks later, and no ill effects as a result of the manipulations were observed.

Statistical Analysis

Both linear and directional data were collected in this study. The linear data consisted of the distances traveled by the tortoises. Straight line distances and actual distances were measured. These distances were used to calculate the index of straightness, which is the ratio of the actual distance traveled to the straight line distance (Emlen, 1969). The index of straightness provides an indicator of how well an organism is oriented. Well oriented individuals have an index of straightness approaching one. The distances traveled by the tortoises in the Intermediate Range Homing Study and the Orientation Study were compared using single factor analysis of variance (ANOVA) to determine if differences existed between the tortoises with no senses impaired, with their vision blocked, with their olfaction blocked, and with both their vision and olfaction blocked (Zar, 1984). If the ANOVA revealed a significant difference, Tukey tests were used to determine which treatments differed (Zar, 1984).

The second type of data collected were compass directions. Compass directions are an example of a circular scale measurement, a specific type of interval scale

measurements in which a circle is divided into 360 equal intervals with an arbitrary zero point. To interpret such data, statistical analyses for circular distributions are required (Zar, 1984). Descriptive statistics were calculated to determine the mean angle moved by the tortoises in each study, circular standard deviation, and concentration (r). The measure of concentration (r) indicates how clustered or distributed the data are around the mean: a high r (approaching 1) indicates that most of the data are concentrated near the mean, and a low r (approaching 0) indicates that the data are randomly distributed. Chi-square statistics were used to test the goodness of fit of observed circular frequency distributions to theoretical random distributions (Zar, 1984). Rayleigh tests were performed to determine if the mean angle moved by the tortoises was significant. A significant Rayleigh test indicates that the mean angle results from a nonrandom distribution (i.e., the tortoises are moving in a particular direction), and is not a mean angle mathematically calculated from a random distribution (i.e., the tortoises are moving randomly, not in a particular direction) (Zar, 1984). Rayleigh tests also were used to determine if the directions traveled by the tortoises were influenced by the direction in which they were facing when released. The V test is a modification of the Rayleigh test when a specific mean angle is expected a priori (Zar, 1984). When the Rayleigh test indicated that the mean angle was significant, V tests were performed to determine if the mean angle moved was homeward.

RESULTS

Short Range Homing Study

Five male and ten female gopher tortoises, averaging 279 mm in carapace length, were used in the short range homing study (Table 1). With 0 degrees as the homeward direction, the average direction moved (i.e., the direction to the burrow which the tortoise entered) by the tortoises after being released was 4 degrees, with a circular standard deviation of 85.3 degrees and an r value of 0.33 (Figure 1). The mean direction moved by the tortoises was not significant (Rayleigh test, $z=1.64$, $P>0.05$), indicating that the directions moved by the tortoises cannot be distinguished from random. The heading the tortoise was facing when it was released did not influence the direction in which it moved (Rayleigh test, $z=1.23$, $P>0.05$).

Gopher tortoises released on the edges of their home ranges traveled an average of 38.2 m and entered burrows an average of 22.8 m from the release point (Table 2). Actual travel distances ranged from 2.8 m to 122.4 m, while the straight line distances from the release points to the burrows which the tortoises entered ranged from 2.8 m to 68.0 m. The tortoises did not necessarily move toward the closest burrow and they often passed several burrows which they did not enter. The mean index of straightness for the tortoises movements was 1.62. The tortoises may not have always been moving in the direction of the burrow in which they were captured, but the low index of straightness indicates that the tortoises were oriented and moved in straight paths.

Of the fifteen tortoises, only one returned to its home burrow. This individual traveled 91.2 m to return the 40.0 m straight line distance to its home burrow. The index of straightness was 2.28, the third highest of the fifteen tortoises. While only one tortoise

Tortoise #	Sex	Carapace Length (mm)	Homeward Direction	Heading at Release	Direction Moved (Degrees)	Direction Moved with Zero as the Homeward Direction (Degrees)
1	M	268	N	W	300	300
2	F	272	E	S	225	135
3	F	309	W	E	260	350
4	F	325	W	N	270	0
5	F	262	W	S	240	330
6	F	289	W	N	285	15
7	F	272	E	W	250	160
8	M	274	E	S	60	330
9	F	310	W	E	320	50
10	F	272	S	N	340	160
11	M	252	E	N	5	275
12	F	298	E	W	90	0
13	M	250	N	E	10	10
14	M	233	N	W	180	180
15	F	296	S	S	230	50
MEAN		279				4
STANDARD DEVIATION		25.4				85.3

Table 1. Tortoise information and release directions, headings, and directions moved for the short range homing study.

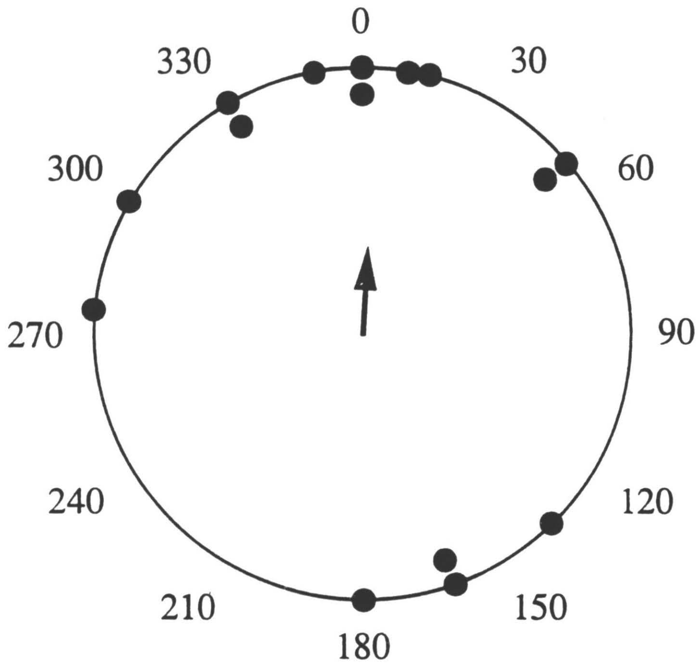

Figure 1.

Directions moved by tortoises when released 40 meters from burrow.
0 = Homeward Direction, N = 15, Mean = 4 degrees, Circular Standard Deviation (s') = 85.3 degrees, and r = 0.33. The arrow indicates the mean direction and the length of the arrow represents the measure of concentration (r).

Tortoise #	Distance Travelled (m)	Straight Line Distance (m)	Index of Straightness
1	43.0	27.6	1.56
2	16.2	8.9	1.82
3	43.8	28.4	1.54
4	122.4	68.0	1.80
5	22.8	18.7	1.22
6	11.3	10.2	1.11
7	2.8	2.8	1.00
8	70.7	37.8	1.87
9	9.6	4.1	2.34
10	27.1	20.1	1.35
11	8.6	6.9	1.25
12	91.2	40.0	2.28
13	41.3	34.4	1.20
14	36.5	24.1	1.51
15	25.2	10.2	2.47
MEAN	38.2	22.8	1.62
STANDARD DEVIATION	33.5	17.5	0.46

Table 2. Distances moved by tortoises in the short range homing study and the index of straightness.

returned to its home burrow, another individual returned to a burrow it was known to have inhabited previously and a second was found in its home burrow two months after the study.

Thus far, I have assumed that the home burrow is in the center of the home range and that a distance of 40 m would place the resident tortoise on the edge of its home range. With these assumptions, movements by the tortoises toward the home range, as opposed to the specific burrow, can be determined. When displaced 40 m and placed on the edge of its home range, a tortoise's movement in a 180 degree range toward the home burrow (90 degrees to either side of the homeward direction) would be homeward, toward the home range. Of the 15 tortoises in the study, 11 moved in the direction of their home ranges. By relaxing the previous assumptions that the burrows are in the center of the home range and that the 40 m displacement resulted in the tortoises being on the edge of their home ranges, various homing scenarios can be evaluated. A more difficult homing senario is if the burrows were on the edge of the home ranges and the tortoises were displaced 40 m from their home ranges. Assuming the home range is equally long as it is wide, a home range of 0.88 ha (as found in males by Diemer, 1992) would be 94 m wide and 94 m long. When displaced 40 m from its home range, a tortoise's movement in a 100 degree range toward the home burrow (50 degrees to either side of the homeward direction) would be toward its home range (Figure 2A). Of the 15 tortoises in the study, 9 of the tortoises moved in the direction of their home ranges (Figure 3A). The movements of the tortoises were not randomly distributed: more tortoises than expected by chance moved toward their home ranges (Chi Square, $X^2 = 8.52$, $P<0.05$). Assuming a home range of 0.31 ha (as found in females by Diemer, 1992) and that it is equally long and wide, the home range would be 56 m long and 56 m wide. When displaced 40 m from its home range, a tortoise's movement in a 60 degree range toward the home burrow (30 degrees to either side of the homeward direction) would be toward its home range (Figure 2B). Of the 15 tortoises in the study, 7 of the tortoises moved in the direction of their

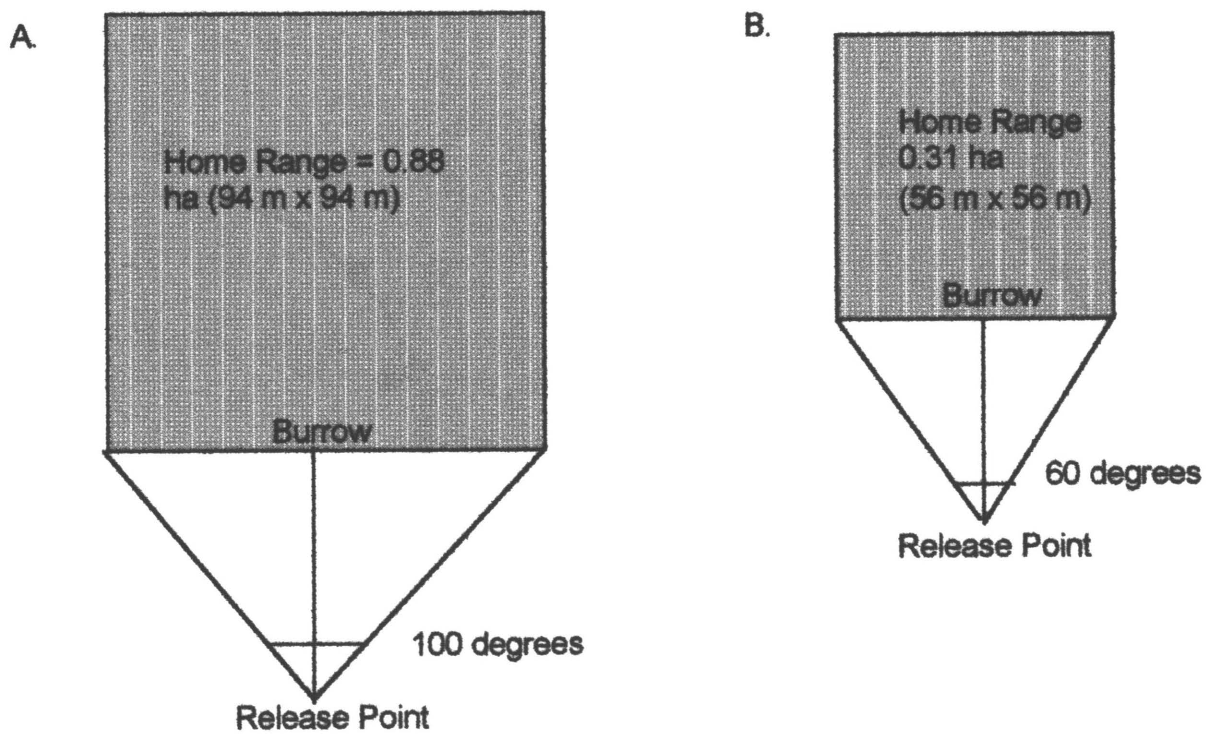

Figure 2. Range of directions for movement towards the home range for different home range sizes.

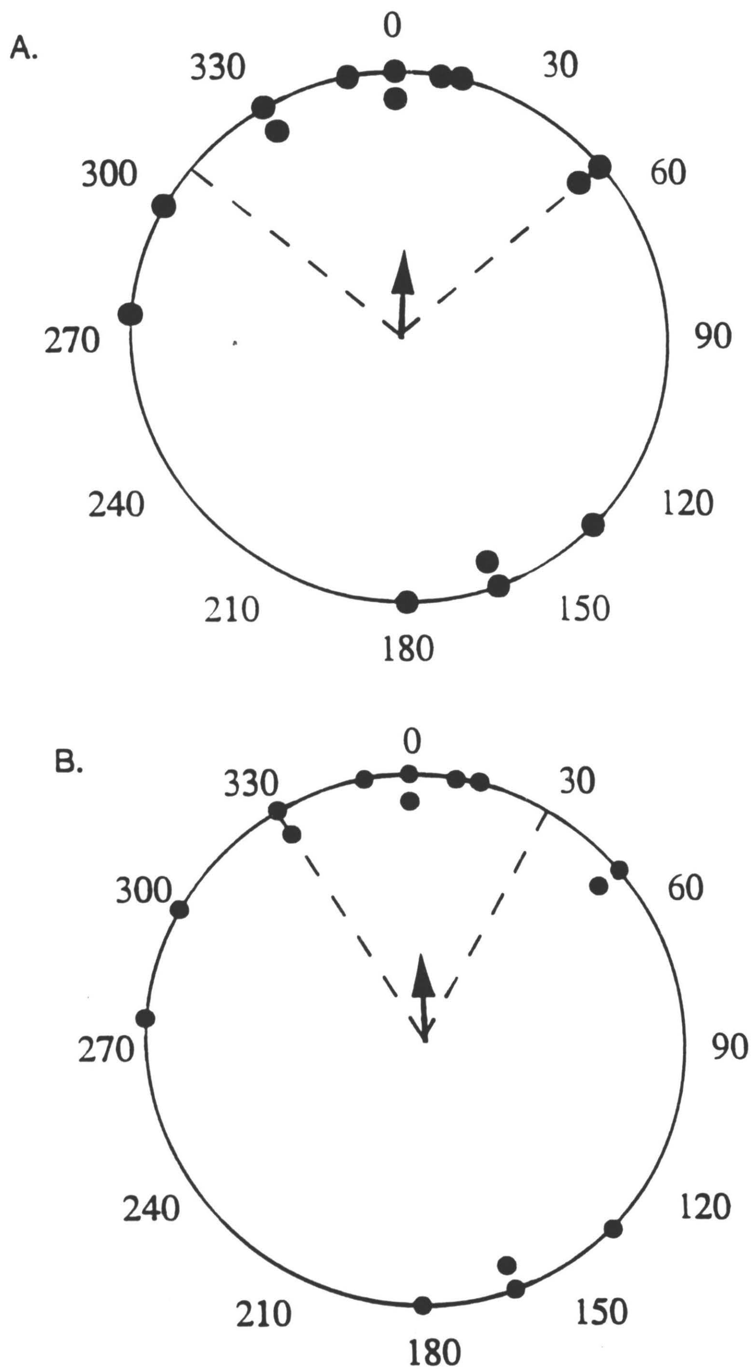

Figure 3.

Directions moved by tortoises when released 40 meters from burrow.
0 = Homeward Direction, N = 15, Mean = 4 degrees, Circular Standard Deviation (s') = 85.3 degrees, and r = 0.33. The arrow indicates the mean direction and the length of the arrow represents the measure of concentration (r).
A. Dashed Lines = Home Range (100 degrees, 310-50 degrees)
B. Dashed Lines = Home Range (60 degrees, 330-30 degrees)

home range (Figure 3B). The movements of the tortoises again were not randomly distributed: more tortoises than expected by chance moved toward their home ranges (Chi Square, $X^2 = 9.72$, $P<0.05$). About half of the tortoises moved in a range of directions that covers only 1/6th all possible directions. The tortoises appear to be homing, but to the home range, rather than the home burrow, and appear to be oriented, walking in straight paths.

Intermediate Range Homing Study

Three male and twelve female tortoises averaging 274 mm in carapace length were used in the intermediate range homing study (Table 3). With 0 degrees as the homeward direction, the average direction moved by the tortoises after being released was 358 degrees with a circular standard deviation of 40.6 degrees and an r value of 0.78 (Figure 4). The mean direction moved by the tortoises was significant (Rayleigh Test, $z=9.07$, $P<0.05$), meaning the tortoises showed a tendency to move in that direction. Also, the mean direction in which the tortoises moved was in the direction of the home burrow (V Test: Modification of Rayleigh Test for an in advance specific mean angle, $u=4.26$, $P<0.05$). When displaced 200 m, the range of directions toward the home range a tortoise could move is small. As a result of this small range, the tests could not distinguish between movement toward the home burrow and movement toward the home range.

The tortoises traveled an average of 235.5 m and entered burrows that were an average of 99.2 m from the release point (Table 4). Actual travel distances ranged from 95.2 m to 399.3 m, with the straight line distances from the release points to the burrows in which the tortoises entered ranged from 15.6 m to 228.3 m. The tortoises did not necessarily move toward the closest burrow and they often passed several burrows which they did not enter. The average index of straightness for the tortoises movements was 3.74. This index of straightness is greater than in the short range homing study,

Tortoise #	Sex	Carapace Length (mm)	Homeward Direction	Heading at Release	Direction Moved (Degrees)	Direction Moved with Zero as the Homeward Direction (Degrees)
1	F	269	SW	E	245	20
2	M	250	W	W	265	355
3	F	272	E	S	300 (85)	120 (355)
4	F	282	W	N	240	330
5	F	302	SE	E	90	315
6	M	224	SW	S	240	30
7	F	283	W	W	270	0
8	F	272	E	N	130 (95)	40 (5)
9	F	289	W	N	250	340
10	F	283	N	S	10	10
11	F	272	NE	W	340	65
12	F	275	E	N	90	0
13	F	298	E	E	45	315
14	F	267	W	N	150 (245)	240 (335)
15	M	268	NW	W	330	15
MEAN		274				358 (1)
STANDARD DEVIATION		18.9				40.6 (13.8)

Table 3. Tortoise information and release directions, headings, and directions moved for the intermediate range homing study. The numbers in parentheses in the Direction Moved column are the re-evaluated initial move for the tortoises who would not enter the unburned plots.

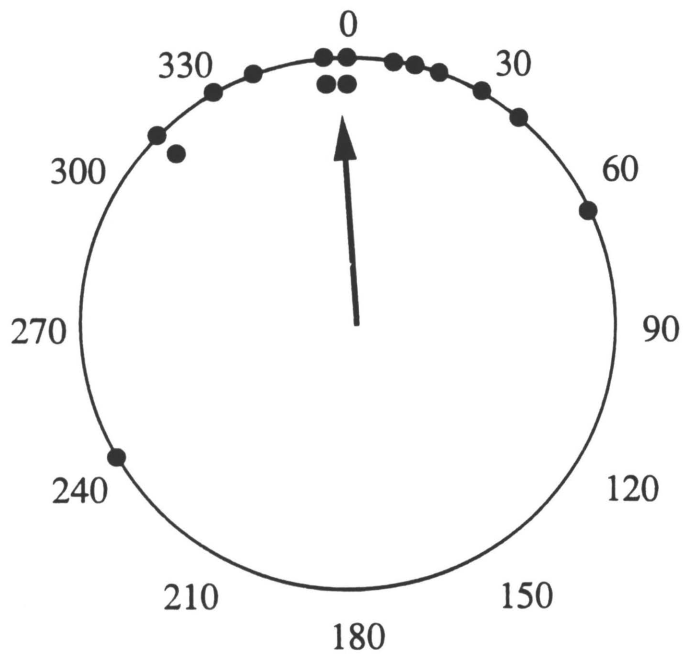

Figure 4.

Directions moved by tortoises when released 200 meters from burrow.
0 = Homeward Direction, N = 15, Mean = 358 degrees, Circular Standard Deviation (s') = 40.6 degrees, and r = 0.78. The arrow indicates the mean direction and the length of the arrow represents the measure of concentration (r).

Tortoise #	Distance Travelled (m)	Straight Line Distance (m)	Index of Straightness
1	95.2	15.6	6.10
2	352.4	228.3	1.54
3	317.2	64.6	4.91
4	333.3	45.2	7.37
5	134.0	32.4	4.14
6	399.3	173.3	2.30
7	254.0	200.0	1.27
8	218.5	24.3	8.99
9	329.0	113.3	2.90
10	197.1	69.4	2.84
11	136.4	52.4	2.60
12	220.8	191.9	1.15
13	179.3	138.1	1.30
14	174.6	25.0	6.98
15	191.2	114.8	1.67
MEAN	235.5	99.2	3.74
STANDARD DEVIATION	91.2	72.0	2.55

Table 4. Distances moved by tortoises in the intermediate range homing study and the index of straightness.

suggesting that the tortoises were not as well oriented when released from the greater distance.

Of the fifteen tortoises, only one returned to its home burrow. The tortoise traveled 254.0 m to return the 200.0 m straight line distance to its home burrow. The index of straightness was 1.27 the second lowest of the fifteen tortoises. While only one tortoise returned to its home burrow, one returned to a burrow it was known to have inhabited previously, and three others returned to the same plot in which their home burrows were located. The ten remaining tortoises entered burrows that they were not known to have previously inhabited or were not in the same plot as their home burrows. Of those ten remaining tortoises, I observed that the three tortoises which had an unburned plot between their release points and home burrows would not cross or enter into the unburned plots. The unburned plots, which had not been burned in over 30 years, were darker at ground level, with nearly 100% canopy coverage, as opposed to the 30-40% cover in the plots which are frequently burned. The ground cover also differed, with the ground in the unburned plots being covered with leaf debris instead of herbaceous vegetation, as in the frequently burned plots. If the tortoises had to cross an unburned plot to return to their home burrows, they would walk to the unburned plot, walk along its edge, but not enter into it. The tortoises would eventually turn and move away from the unburned plot. The results were re-evaluated to include the direction in which these three tortoises first moved (i.e., the direction the tortoises were headed as they approached the unburned plots), rather than the direction they eventually traveled. The results indicate an even stronger tendency to move in the homeward direction (Figure 5). The mean direction moved was 1 degree with a circular standard deviation of 13.8 and an r value of 0.89 (Rayleigh Test, $z=11.79$, $P<0.05$; and V Test, $u=4.85$, $P<0.05$). When displaced 200 m from their home burrows, the tortoises tended to travel back to their home ranges.

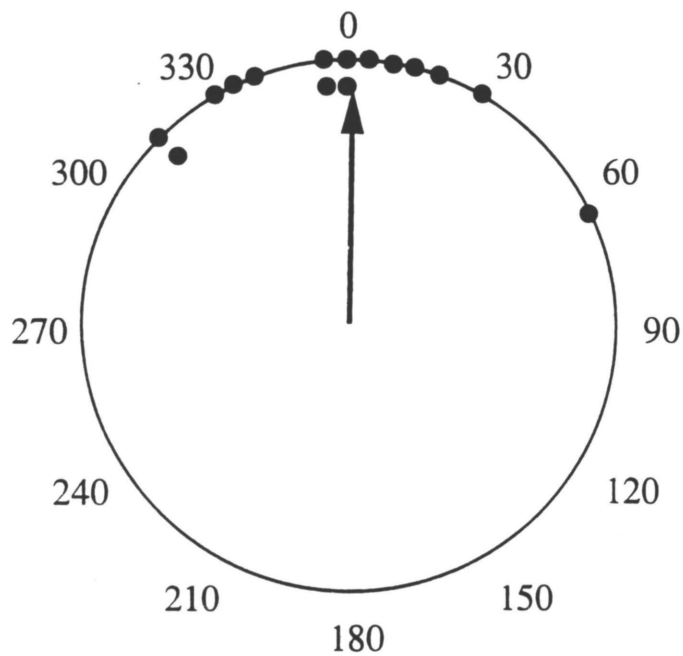

Figure 5.

Re-evaluated first directions moved by tortoises when released 200 meters from burrow. 0 = Homeward Direction, N = 15, Mean = 1 degree, Circular Standard Deviation (s') = 13.8 degrees, and r = 0.89. The arrow indicates the mean direction and the length of the arrow represents the measure of concentration (r).

Orientation Study - vision blocked

Five tortoises, 2 males and 3 females, averaging 279 mm in carapace length, were released 200 m from their burrows with their eyes covered (Table 5). With 0 degrees as the homeward direction, the average direction moved by the tortoises was 145 degrees with a circular standard deviation of 23.4 degrees and an r value of 0.92 (Figure 6). The mean direction the tortoises moved was significant (Rayleigh Test, $z=4.22$. $P<0.05$), meaning the tortoises showed a tendency to move in that direction. The direction the tortoises moved however, was not toward their home burrows (V Test, $u=-2.38$, $P>0.05$). The heading in which the tortoises were released did not influence the direction in which they moved (Rayleigh Test, $z=0.83$, $P>0.05$).

The tortoises traveled an average of 24.9 m and entered burrows that were an average of 10.1 m from the release point (Table 6). Actual travel distances ranged from 10.2 m to 46.9 m, while the straight line distances from the release points to the burrows in which the tortoises entered ranged from 3.7 m to 20.9 m. The average index of straightness was 2.68. Non-impaired tortoises traveled an average of 235.5 m while the vision impaired tortoises traveled significantly less, an average of 24.9 m (ANOVA, $F=69.06$, $P<0.05$; Tukey Test, $q=11.14$, $P<0.05$). None of the tortoises returned to their home burrows or even to the plot in which their home burrows were located. The absence of vision deterred the tortoises from venturing far to find their home burrows or home ranges.

Orientation Study - olfaction blocked

Five tortoises, 1 male and 4 females, averaging 275 mm in carapace length, were released 200 m from their burrows with their nares blocked (Table 5). With 0 degrees as the homeward direction, the average direction moved by the tortoises was 301 degrees

Tortoise #	Sex	Carapace Length (mm)	Homeward Direction	Heading at Release	Direction Moved (Degrees)	Direction Moved with Zero as the Homeward Direction (Degrees)
Vision Blocked Tortoises						
1	F	284	SE	N	250	115
2	F	293	E	W	210	120
3	M	261	W	E	80	170
4	F	282	W	N	80	170
5	M	275	W	S	60	150
MEAN		279				145
STANDARD DEVIATION		11.9				23.4
Olfaction Blocked Tortoises						
1	F	283	W	N	155	245
2	F	260	W	W	250	340
3	F	255	S	E	60	240
4	F	303	NE	E	350	305
5	M	275	E	S	120	30
MEAN		275				301
STANDARD DEVIATION		19.2				60.8
Vision and Olfaction Blocked Tortoises						
1	F	292	W	N	280	10
2	F	280	E	S	150	60
3	F	258	W	E	40	130
4	F	298	SE	S	345	120
5	M	274	NW	S	230	265
MEAN		280				81
STANDARD DEVIATION		15.7				84.2

Table 5. Tortoise information and release directions, headings, and directions moved for the orientation study.

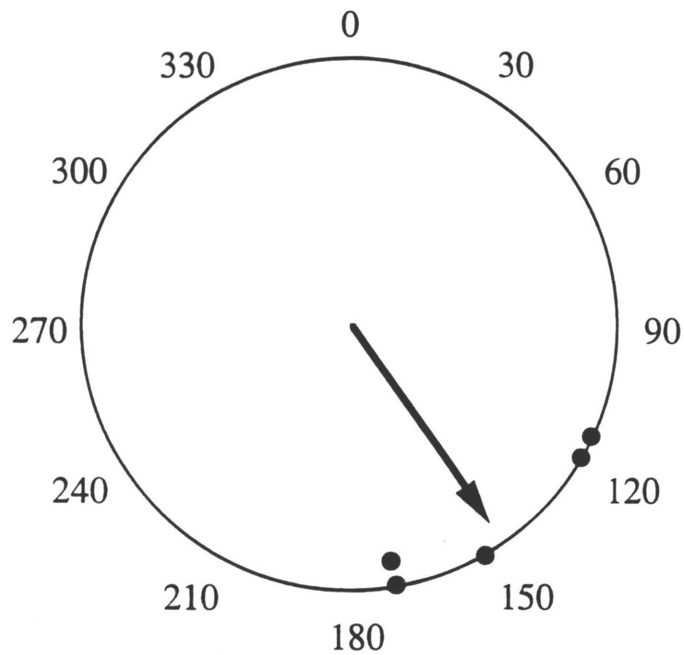

Figure 6.

Directions moved by tortoises with vision blocked when released 200 meters from burrow. 0 = Homeward Direction, N = 5, Mean = 145 degrees, Circular Standard Deviation (s') = 23.4 degrees, and r = 0.92. The arrow indicates the mean direction and the length of the arrow represents the measure of concentration (r).

Tortoise #	Distance Travelled (m)	Straight Line Distance (m)	Index of Straightness
Vision Blocked Tortoises			
1	46.9	20.9	2.24
2	26.1	12.4	2.10
3	10.2	3.7	2.76
4	16.4	7.4	2.22
5	24.8	6.1	4.07
MEAN	24.9	10.1	2.68
STANDARD DEVIATION	13.9	6.8	0.82
Olfaction Blocked Tortoises			
6	103.2	36.1	2.86
7	125.2	60.2	2.08
8	50.6	31.5	1.61
9	79.3	28.4	2.79
10	94.7	42.5	2.23
MEAN	90.6	39.7	2.31
STANDARD DEVIATION	27.8	12.6	0.52
Vision and Olfaction Blocked Tortoises			
11	9.9	5.0	1.98
12	15.1	9.2	1.64
13	18.2	6.1	2.98
14	8.7	5.6	1.55
15	13.6	6.3	2.16
MEAN	13.1	6.4	2.06
STANDARD DEVIATION	3.9	1.6	0.57

Table 6. Distances moved by tortoises in the orientation study and the index of straightness.

with a circular standard deviation of 60.8 degrees and an r value of 0.57 (Figure 7). The mean direction the tortoises moved was not significant (Rayleigh Test, $z=1.61$, $P>0.05$), indicating that the directions moved by the tortoises cannot be distinguished from random. The heading in which the tortoises were released did not influence the direction in which they moved (Rayleigh Test, $z=1.33$, $P>0.05$).

The tortoises traveled an average of 90.6 m and entered burrows that were an average of 39.7 m from the release point (Table 6). Actual travel distances ranged from 50.6 m to 125.2 m, while the straight line distances from the release points to the burrows in which the tortoises entered ranged from 28.4 m to 60.2 m. The average index of straightness was 2.31. Non-impaired tortoises traveled an average of 235.5 m while the olfaction impaired tortoises traveled significantly less, an average of 90.6 m (ANOVA, $F=69.06$, $P<0.05$; Tukey Test, $q=7.67$, $P<0.05$). None of the tortoises returned to their home burrows or even to the plot in which their home burrows were located. Orientation capabilities appeared to be better for the non-olfactory tortoises than for the non-vision tortoises. The olfaction impaired tortoises traveled an average of 90.4 m, 65.7 m more than the vision blocked tortoises (ANOVA, $F=26.60$, $P<0.05$; Tukey Test, $q=8.11$, $P<0.05$). The absence of olfaction appears to have deterred the tortoises from finding their home burrows or home range, but not to the same degree as the vision blocked tortoises.

Of the five tortoises released, one had an unburned plot between its release point and home burrow. The tortoise behaved as the non-impaired tortoises did in the intermediate range homing study and would not venture through the unburned plot that was between the release point and its home burrow. It walked to the unburned plot and turned away, not entering into it.

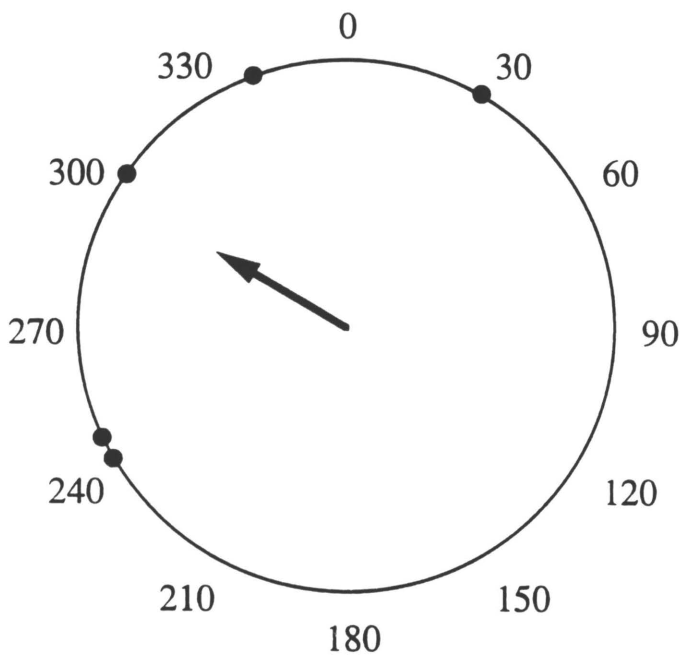

Figure 7.

Directions moved by tortoises with nares blocked when released 200 meters from burrow. 0 = Homeward Direction, N = 5, Mean = 301 degrees, Circular Standard Deviation (s') = 60.8 degrees, and r = 0.57. The arrow indicates the mean direction and the length of the arror represents the measure of concentration (r).

Orientation Study - vision and olfaction blocked

Five tortoises, 1 male and 4 females, averaging 280 mm in carapace length, were released 200 m from their burrows with both their eyes covered and their nares blocked (Table 5). With 0 degrees as the homeward direction, the average direction moved by the tortoises was 81 degrees with a circular standard deviation of 84.2 degrees and an r value of 0.34 (Figure 8). The mean direction the tortoises moved was not significant (Rayleigh Test, $z=0.57$, $P>0.05$), indicating that the directions moved by the tortoises can not be distinguished from random. The heading in which the tortoises were released did not influence the direction in which they moved (Rayleigh Test, $z=0.67$, $P>0.05$).

The tortoises traveled an average of 13.1 m and entered burrows an average of 6.4 m from the release point (Table 6). Actual travel distances ranged from 8.7 m to 18.2 m, while the straight line distances from the release points to the burrows in which the tortoises entered ranged from 5.0 m to 9.2 m. The average index of straightness was 2.06. Non-impaired tortoises traveled an average of 235.5 m while the tortoises with both their vision and olfaction impaired traveled significantly less, an average of 13.1 m (ANOVA, $F=69.06$, $P<0.05$; Tukey Test, $q=11.77$, $P<0.05$). None of the tortoises returned to their home burrows or even to the plot in which their home burrows were located. The tortoises appeared to be completely lost and disoriented. These tortoises moved enough to find some shelter or protection in the high grass or palmetto bushes and then stopped moving and covered up. No apparent attempt was made to find a burrow. The tortoise moved significantly less than the olfaction impaired tortoises (ANOVA, $F=26.60$, $P<0.05$; Tukey Test, $q=9.57$, $P<0.05$); however, no difference was found between the tortoises with both vision and olfaction impaired and the tortoises with only their vision blocked (ANOVA, $F=26.60$, $P<0.05$; Tukey Test, $q=1.46$, $P>0.05$).

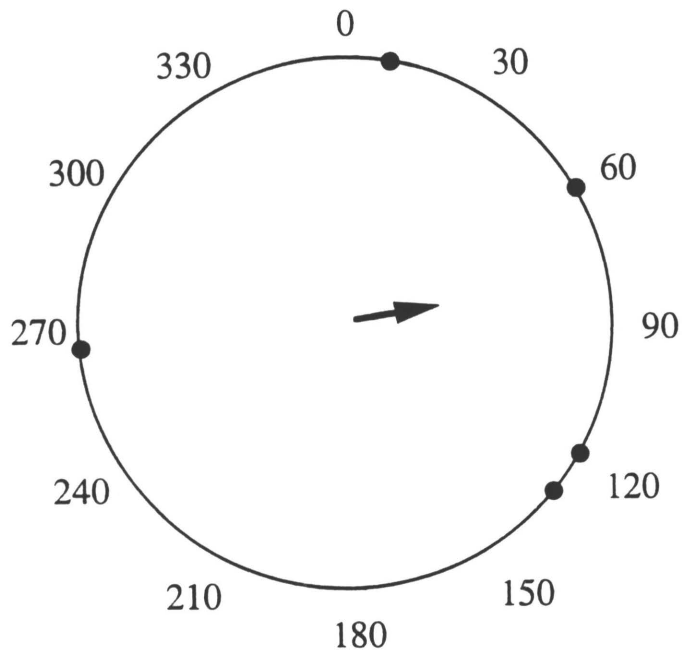

Figure 8.

Directions moved by tortoises with both vision and nares blocked when released 200 meters from burrow. 0 = Homeward Direction, N = 5, Mean = 81 degrees, Circular Standard Deviation (s') = 84.2 degrees, and r = 0.34. The arrow indicates the mean direction and the length of the arrow represents the measure of concentration (r).

DISCUSSION

The gopher tortoises in this study have demonstrated their ability to home when displaced short and intermediate distances from their home ranges. The home range of the gopher tortoise appears to be the principle target of short range and intermediate range homing. Tortoises displaced from their home ranges were not necessarily moving in the direction of their home burrows (the burrow in which a tortoise was captured); instead, they were moving in the direction of their home ranges.

Gopher tortoise burrows appear to play some role in homing, in that they are where the tortoises go once inside of the home ranges. In both the short range and intermediate range homing experiments, several tortoises did return to their home burrows or to burrows they were known to have used previously. The primary homing objective appears to be to return to the home range and within the home range any burrow, or possibly a select few burrows, can be suitable to enter.

Equally important as demonstrating that the tortoises moved in the homeward direction, is how they moved in that direction. The movements the displaced tortoises made while homing had a low index of straightness (less than 2). Their movements were straight, not wandering, suggesting that they were well oriented, able to detect and utilize the necessary cues to home. The specific cues used by the displaced tortoises to home, however, are not revealed in this study.

An interesting observation resulting from the intermediate range homing experiment is that all three tortoises which had an unburned plot between their release points and home burrows would not enter or cross the unburned plots. The three tortoises moved in the homeward direction to the unburned plots, indicating that the unburned plots

did not interfere with their homing and orientation capabilities. Instead, the tortoises perceived and treated the unburned plots as a barrier to movement.

In both the short range homing study and the vision impaired orientation study, the tortoises which did not head toward their home ranges headed in virtually the opposite direction. Several tortoises are clustered in this opposite direction, suggesting that it is not a random event. Instead, the tortoises appear to be avoiding and moving away from their home ranges. The tortoises may not have returned to their home burrows because of the disturbance of the bucket trapping at the mouths of their burrows. Physical disturbances at the burrows often cause the tortoises to relocate to a new burrow (Wilson *et al.*, 1994). While all efforts were made to minimize the disturbance caused by the trapping, it was still a disturbance. The tortoises could have been moving away from their home ranges to avoid further disturbance.

Based on the limited experimentation in the orientation study, visual and olfactory cues appear to be utilized by the tortoises for homing and orientation. The absence of vision and olfaction appears to have prevented the tortoises from utilizing their orientation capabilities and, therefore, they were unable to find their previous burrows or home ranges. With visual and/or olfactory senses absent, the tortoises did not move as far as the non-impaired tortoises. The movements were longer relative to the straight line distance traveled, and often circular in path. The tortoises often appeared to be searching for the first burrow that they could find, especially the tortoises with both senses impaired.

The results of the orientation study suggest that vision is more important than olfaction in the movement, homing, and orientation of gopher tortoises. Tortoises with olfactory senses impaired, but with vision, moved farther than the tortoises with their vision impaired, but with olfactory abilities, and tortoises without either of the senses. While the tortoises with olfactory senses impaired, but with vision, traveled farther and straighter, they still were not oriented homeward. The only tortoise in the orientation study which had an unburned plot between its release point and its home burrow was an

olfaction impaired tortoise. Interestingly, the tortoise behaved similarly to the non-impaired tortoises who faced the same situation. The tortoise moved in the homeward direction until it reached the unburned plot, at which time it turned and moved away from the unburned plot. The tortoise appeared capable of determining which direction was homeward, but came across the apparent barrier of the unburned plot. Possibly, some sort of visual cue indicated to the tortoise not to enter the unburned plot, so it turned away.

Previous studies have also determined that vision and olfaction are involved in the homing and orientation capabilities of gopher tortoises. Gopher tortoises may use celestial cues (Gibbons and Smith, 1968), a sun compass (Gourley, 1974), visual landmarks (Gourley, 1974), or olfactory cues (Gourley, 1969) for homing, orientation, and movement. My study did not thoroughly investigate all of the possible cues used for homing and orientation, and these results can not distinguish among the possible visual cues used: sun compass, visual landmarks, or other visual cues. My study leaves open the opportunity for additional research on other cues, such as geotactile or magnetic cues, known to function in orientation by other turtle species. Gopher tortoises are known to travel along well worn paths (Douglass, 1990). The tortoises I observed often traveled along the fire lanes between the various burn plots and along paths which were well established in the ground vegetation. Further studies with larger sample sizes, replicates at different sites, and laboratory/arena tests are needed to determine the specific cues used and their relative importance.

My research shows that gopher tortoises possess a well-developed homing and orientation ability, thereby able to locate their home ranges from short range and intermediate range distances. Similar homing abilities have been documented in other turtle species. Box turtles (*Terrapene carolina*) showed a homing instinct or a tendency to return to a territory from which they were removed (Nichols, 1939). Ornate box turtles (*Terrapene ornata ornata*) have been shown to home distances greater than 3 kilometers (Metcalf, 1978). Wood turtles (*Clemmys insculpta*) would regularly home from distances

of 2 kilometers (Carroll and Ehrenfeld, 1978). Painted turtles (*Chrysemys picta marginata*) have been shown to home when displaced 100 meters from their home ponds (Emlen, 1969). This ability of painted turtles to home was also reported by Ernst (1970), Williams (1952), and Cagle (1944). A leopard tortoise (*Geochelone pardalis*) was observed to return to its home range 7.3 kilometers away (Bertram, 1979). Homing is not unique to gopher tortoises and is commonly found in other chelonians.

In addition to studies specifically addressing the homing of displaced turtles, the ability to return to a specific location has been studied in several other turtle species. During nesting, Blanding's turtles (*Emydoidea blandingi*) have shown site fidelity over several years, having nested at the same nest sites, often moving distances greater than 1 kilometer to reach nesting sites and then returning to their original aquatic habitat (Congdon *et al*., 1983). Painted turtles (*Chrysems picta*) have been observed nesting within 5 meters of previous years nesting sites (Lindeman, 1992). Ouachita map turtles (*Graptemys ouachitensis*) and false map turtles (*Graptemys psuedogeographica*) also exhibit nesting site fidelity, nesting on the same beach over several seasons (Vogt and Bull, 1982). These turtles' abilities to return to the same location to nest year after year, demonstrates that they also possess well-developed homing and orientation abilities.

While this study demonstrates that gopher tortoises have the capabilities of orientation and homing from both short and intermediate distances, many important questions still need to be answered for a complete understanding of the homing and orientation capabilities of gopher tortoises. Determining the specific cues that the tortoises are using and understanding why the unburned plots act as a barrier to movement are important for learning about how tortoises interact with there environment.

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