ORIENTATION IN BOX TURTLES, TERRAPENE c. CAROLINA (LINNAEUS)

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Homing ability of the box turtle, *Terrapene carolina,* was reported by Breder (1927) and by Nichols (1939), who recorded several returns to the home territory after transportation to distances as great as 4200 feet. Stickel (1950) estimated the average diameter of the range of this species to be about 350 feet, basing this estimate on 440 recoveries of 55 turtles. Home ranges of individual turtles overlap, and most recorded territories were quite similar in succeeding years. Longer journeys may be made to lay eggs or for other reasons, and some turtles had two home ranges. The longest spontaneous movement recorded was 2540 feet. But these important observations give no indication of the means of orientation employed by these turtles in finding their way home.

During the summer and fall of 1956, while stationed at the Army Chemical Center, Edgewood, Maryland, the author had the opportunity to experiment with over 100 of these turtles in an area only thirty-five miles from the location of Stickel's studies. The results demonstrate that many turtles of this species start to walk in the homeward direction within a few minutes after being released in unfamiliar territory, and furthermore, that the sun is one of the cues on which this orientation is based. These preliminary findings are of considerable interest, since they demonstrate that box turtles are capable of at least the same order of precision in celestial navigation as the birds studied by Matthews (1955) and Kramer (1953).

I am greatly indebted to the members of Boy Scout Troop 369, who brought many turtles and helped with certain field experiments which would have been impossible without them. Special thanks go to James Laney, who was particularly helpful in actively searching for turtles when they were most needed. My appreciation is also extended to Kile R. Barbehenn, Kenneth S. Rawson, and Lucille F. and William H. Stickel for their advice, to John R. Audett for drawing the figures, and to Jason I. Adleman for statistical advice. To Donald R. Griffin I am particularly indebted for his encouragement and numerous important suggestions concerning the planning of the experiments and the analysis of the resulting data.

Methods

Turtles were picked up in the fields and woodlands about Edgewood. The source of each turtle was carefully noted on a topographic map and it was given a permanent number denoted by combinations of notches filed into the edges of the posterior carapace (Cagle, 1939). In order to facilitate visual recognition in the field, its number was also painted on the shell or written with a wax pencil and covered with balsam.

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When observing a turtle for a short period it was of the utmost importance that it continue its heading as long as possible rather than stopping to make a form—a well-shaped cavity made by digging with the front feet and pushing and moving about from side to side in high grass or soft soil (Stickel, 1950). Level fields having closely cut grass were found to be most suitable for release areas. In hot weather the turtles would often head for a shady spot, and release points were therefore located insofar as possible near the center of large open areas such as a parade ground or golf course. The three areas used for most of these observations are described below.

Release Point G. Part of a golf course, this area is 350 yards long running east and west and about 125 yards wide, with a northern border formed by a vine-covered fence and high trees several hundred feet in the background. Along the southern edge stands an almost unbroken line of buildings. To the east is a well-traveled road bordered by large shade trees spaced about 80 feet apart. The western portion narrows to a blunt point of a few buildings and some low shrubs.

Release Point P. A parade field, 250 by 400 yards, was found to be the most suitable release point available. Its length runs north and south; the southern end was not visible to the turtles, due to the slight elevations of the ground. A line of buildings and shrubs are to the north. Along the west side is a broken line of mixed coniferous and deciduous trees, and to the east is a road beyond which lies another group of buildings.

Release Point B is located 0.35 mile south of G, and P is 1.55 miles south-southwest of B. For the various turtles used, the distances from the release points to the home ranges varied between 0.28 and 5.80 miles; and since all release points are located within an active military post and surrounded by roads, fences, ditches, and numerous buildings irregularly situated, there was little chance that they were within territory previously visited by these turtles.

Methods of observation

Forty-three box turtles were released and observed at least once, and 22 proved to be suitable for these experiments. Selection was based on whether the turtle headed in approximately the homeward direction, and whether it moved any appreciable distance during the first period of observation, which lasted for from ten minutes to two hours. Carr (1952) mentions the various differences in the personality of turtles, and I found, for example, that some would never even open the hinges of their plastrons during a 60-minute period of observation; others would not pull themselves in unless touched, and were quite active when let alone; still others were completely at ease even when approached or picked up.

Groups of two to twelve turtles were placed at numbered stakes on the same part of one of the three fields in each release. The head of the turtle was faced opposite to the homeward direction so that a heading in the direction faced would not be confused with an accurate heading. As each turtle walked away from its stake, the compass bearing of its course was read by a compass accurate to two degrees; then the distance traveled was paced off and a piece of cloth dropped just behind the turtle. After recording one I then went to another turtle and checked its progress so that the first was not disturbed in my absence. Unless witnessed, it is difficult to imagine how little effect the observer has upon the heading of the turtle under

these conditions. It is true that some will often stop suddenly and pull into their shells when closely approached, but this seemed to have no effect whatever upon the direction in which they continued to travel. Movements over distances from 65 to 600 feet were measured, the distance depending on the time available and the activity of the individual turtle.

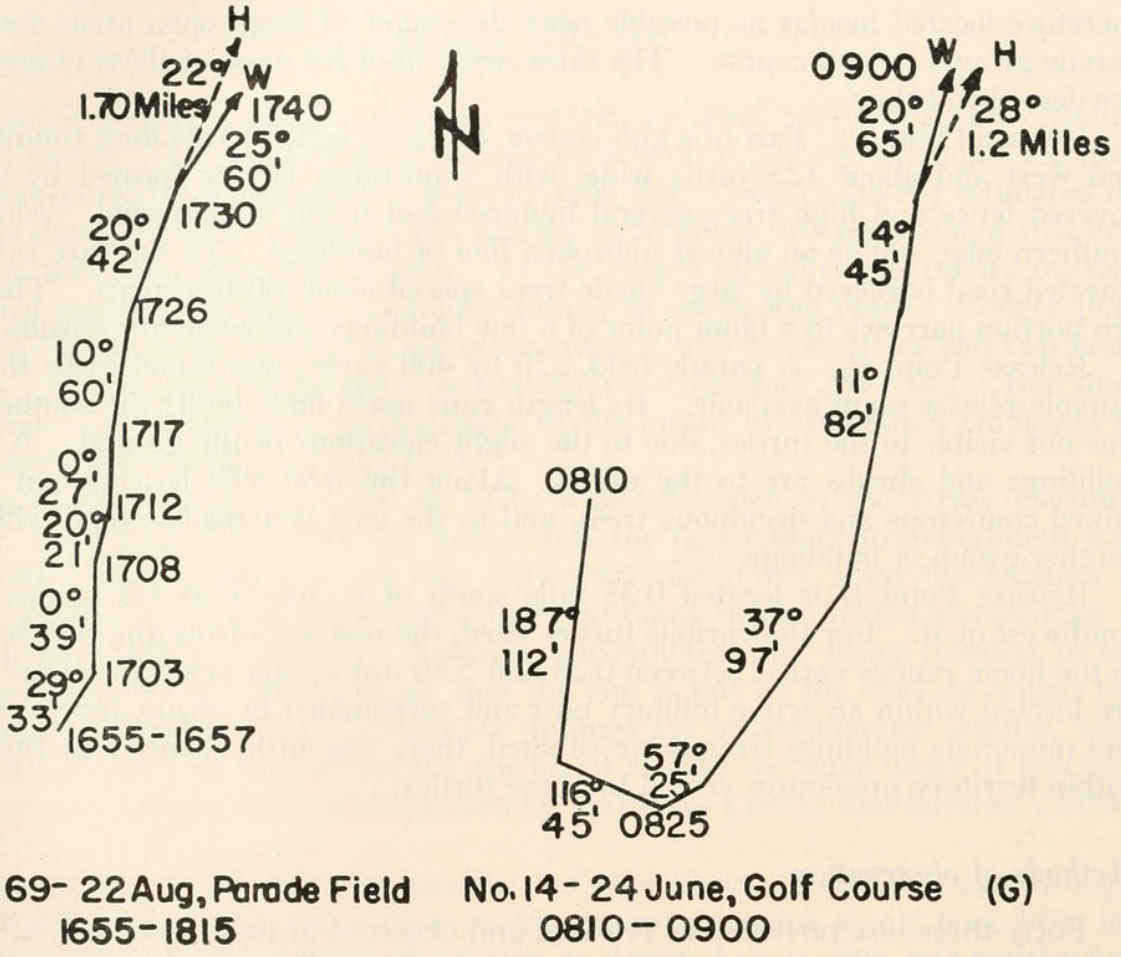


FIGURE 1. Two typical headings. H is home direction; W is direction in which the turtle went. Each straight portion of a turtle's course indicates the direction and distance traveled between compass readings. Time of day (EST) is also noted beside most of the bearings.

Because it was sometimes impossible to spend an hour watching the turtles, they were often left alone and their course recorded by attaching a spool of thread to the top of the carapace, a modification of the procedures described by Breder and Stickel. The end of the thread was fastened to a stake and unwound as the turtle walked off. Even in the short grass the slack thread would catch on small uncut weeds and the like, and would leave an accurately plotted course. A total of forty-five observations out of approximately 200 were made in this way. There were never any apparent differences noted in the headings between those recorded with and those without the use of thread. Both Breder and Stickel agree that turtles carrying the spools of thread move and behave quite normally. Stickel compared recorded movements of both and could find no discernible difference.

The turtles were transported in cloth bags or in closed boxes so that they could see nothing of their surroundings, and they were taken to the release areas by auto-

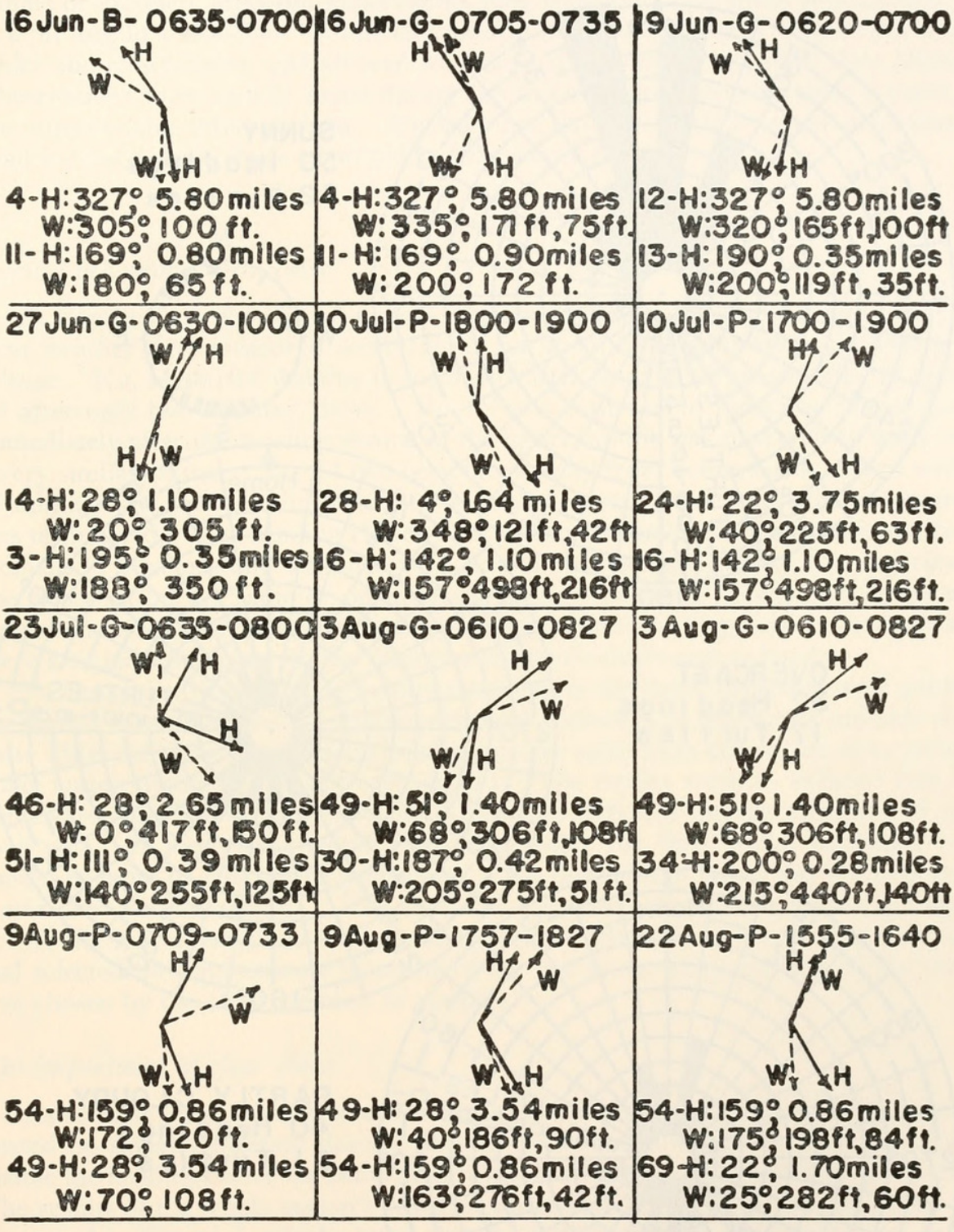
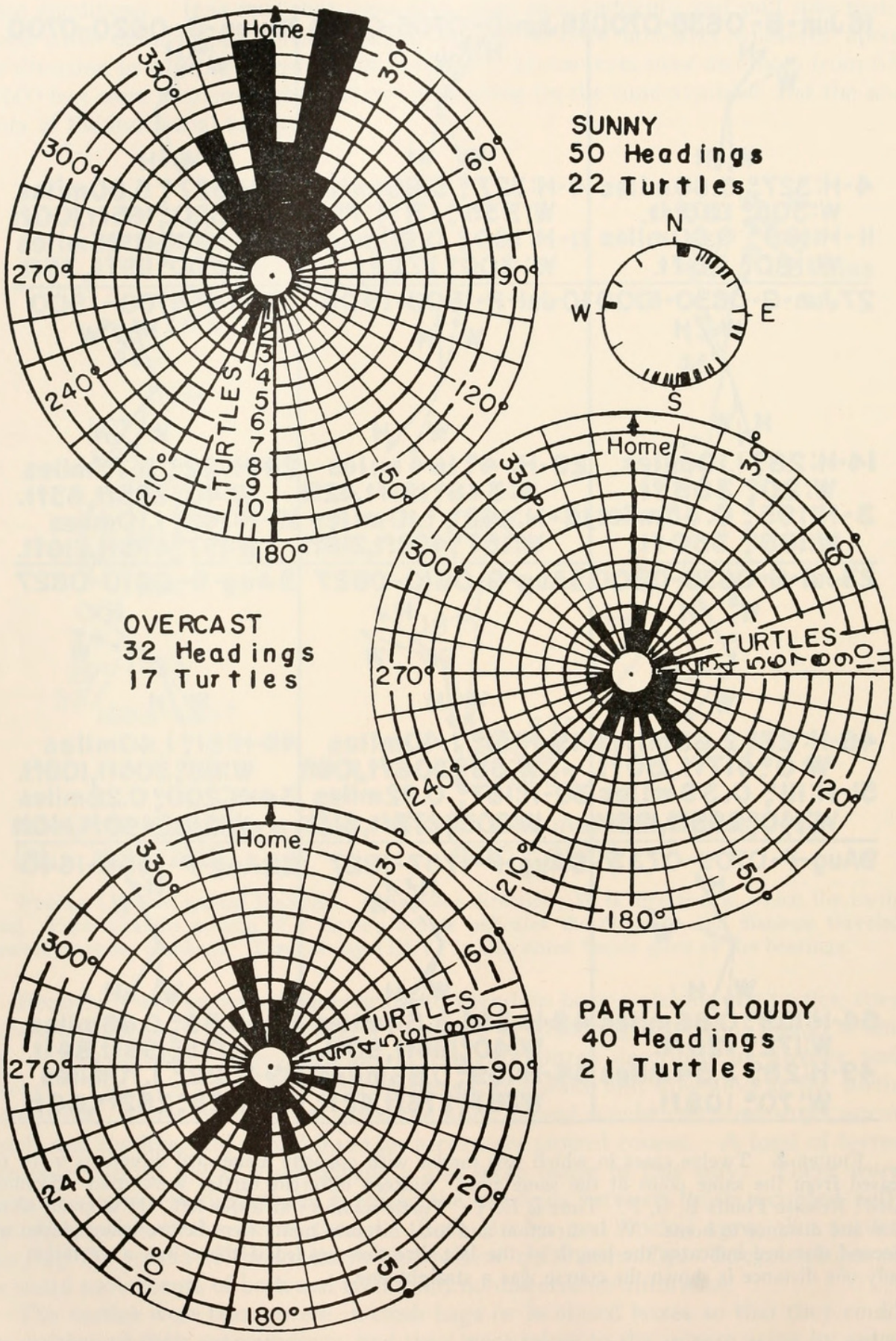


FIGURE 2. Twelve cases in which two turtles with opposite homeward directions were released from the same point at the same time. Sixteen different turtles were used. Symbols used: Release Points B, G, P. Time is EST. Turtle numbers at lower left. H is home direction and distance to home. W is direction and total distance turtle went before being picked up. Second distance indicates the length of the last direction headed if there was a variation. If only one distance is shown the course was a straight line.


Home
30°
60°
90°
120°
150°
180°
210°
240°
270°
300°
330°
TURTLES
1
2
3
4
5
6
7
8
9
10
SUNNY
50 Headings
22 Turtles
N
W
E
S
OVERCAST
32 Headings
17 Turtles
PARTLY CLOUDY
40 Headings
21 Turtles

mobile or bicycle. Between experiments they were kept in a small storage shed or in a pit dug in a woodlot. While in captivity they were well fed with fruits, vegetables and cockroaches, and allowed to wallow in muddy water when they pleased. Observations were usually made during the morning and late afternoon because of the objectionable effect of heat. On very hot days the turtles would immediately head for the nearest shade or would burrow into a form.

Observations

Typical behavior after release

In Figure 1 are shown two typical cases in which the headings of two turtles in clear weather were measured several times for about three-quarters of an hour after release. No. 14 started walking immediately after being set free, and No. 69 moved off after only two minutes' delay. No. 69 was returned to the same release point immediately after the heading shown in the figure, and it was observed to walk over a very similar course. No. 14 had been faced away from home, but it turned within 15 minutes and then continued in an essentially correct course until the observation was terminated. The heading chosen by a particular turtle was thus consistent from moment to moment, and was also very similar in most cases when the experiment was repeated on the same or on different days. On seven occasions a turtle was moved about 300 feet after it had indicated a definite heading, and in no case was there a significant change in the direction the turtle continued to head.

To determine whether local factors unrelated to the home direction were guiding the turtles, a total of twelve experiments were performd in which two animals from quite different home ranges were released at the same time and at the same release point (often within ten feet of each other). The turtles were so selected that the homeward direction would be 90 to 180 degrees different for the members of each such pair. If some local factor were responsible for their initial headings, both should be more or less similarly affected; if the direction of home was the important factor, they should separate. The results of these experiments are shown in Figure 2. While not all headings were perfectly correct, there is no doubt that each animal selected the approximate direction of its own home independently of the direction chosen by the other member of the pair.

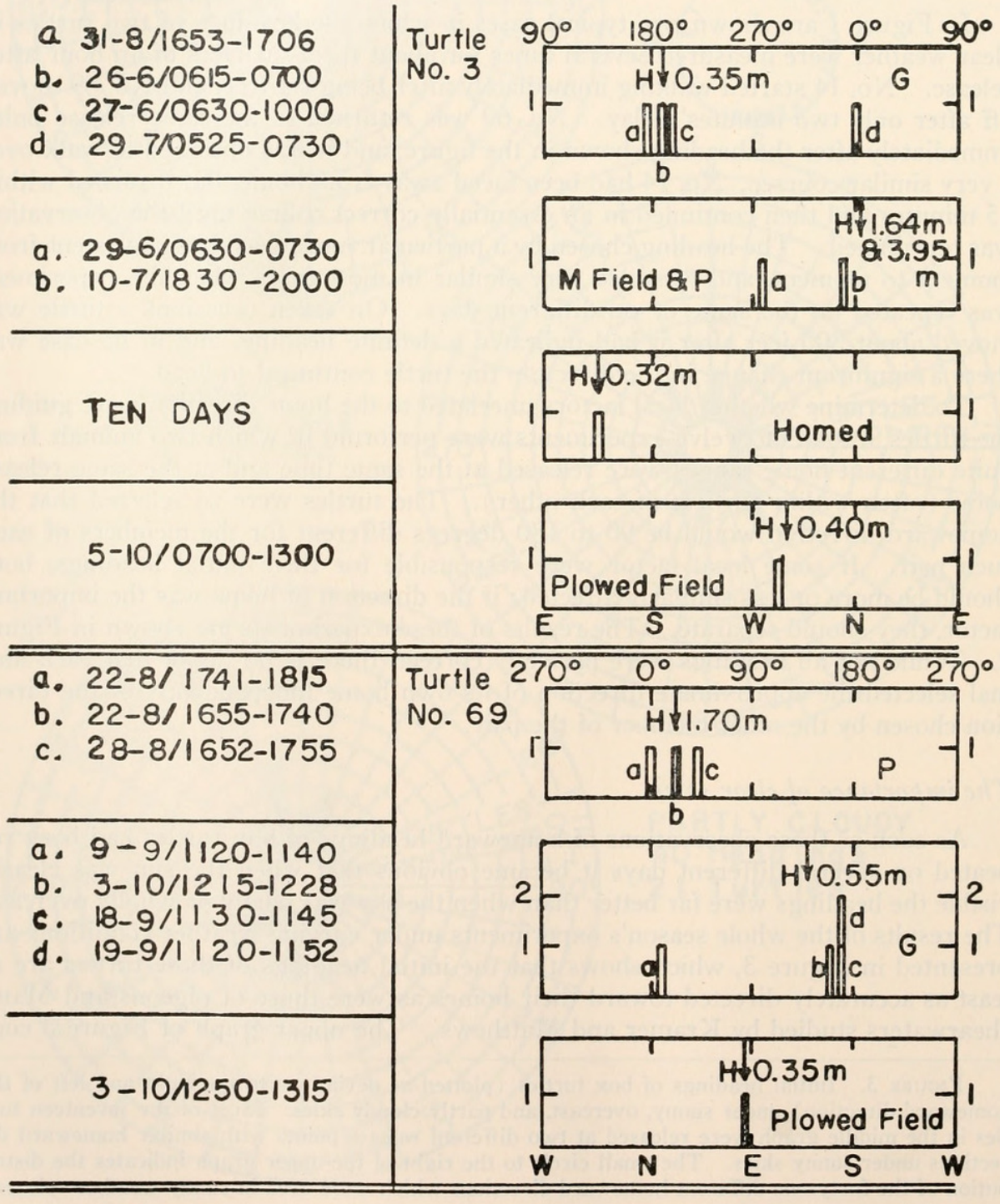
The importance of clear skies

As soon as these observations of homeward headings of box turtles had been repeated on several different days it became obvious that when the sun was clearly visible the headings were far better than when the sky was partly or wholly overcast. The results of the whole season's experiments under varying weather conditions are presented in Figure 3, which shows that the initial headings of these turtles are at least as accurately directed toward their homes as were those of pigeons and Manx shearwaters studied by Kramer and Matthews. The upper graph of Figure 3 con-

Figure 3. Initial headings of box turtles (plotted as deviations to the right and left of the homeward direction) under sunny, overcast, and partly cloudy skies. Most of the seventeen turtles in the middle graph were released at two different release points with similar homeward directions under sunny skies. The small circle to the right of the upper graph indicates the distribution of the forty-one different homeward directions which were used in sunny-weather releases.

tains the observations of twenty-two turtles which in most cases were tested at two or more release points as described above. The actual homeward directions were widely distributed around the compass. As has already been made clear in Figure 2, these headings represent in most cases a definite choice of the homeward direction.

It is of great interest that these accurate homeward headings largely disappeared under partly or completely overcast skies, for this at once indicates that the turtles were choosing the home direction by some form of celestial navigation similar to that studied in birds by Matthews, Kramer, and others. These releases were made at distances varying from 0.28 to 5.6 miles away from the place where the turtles



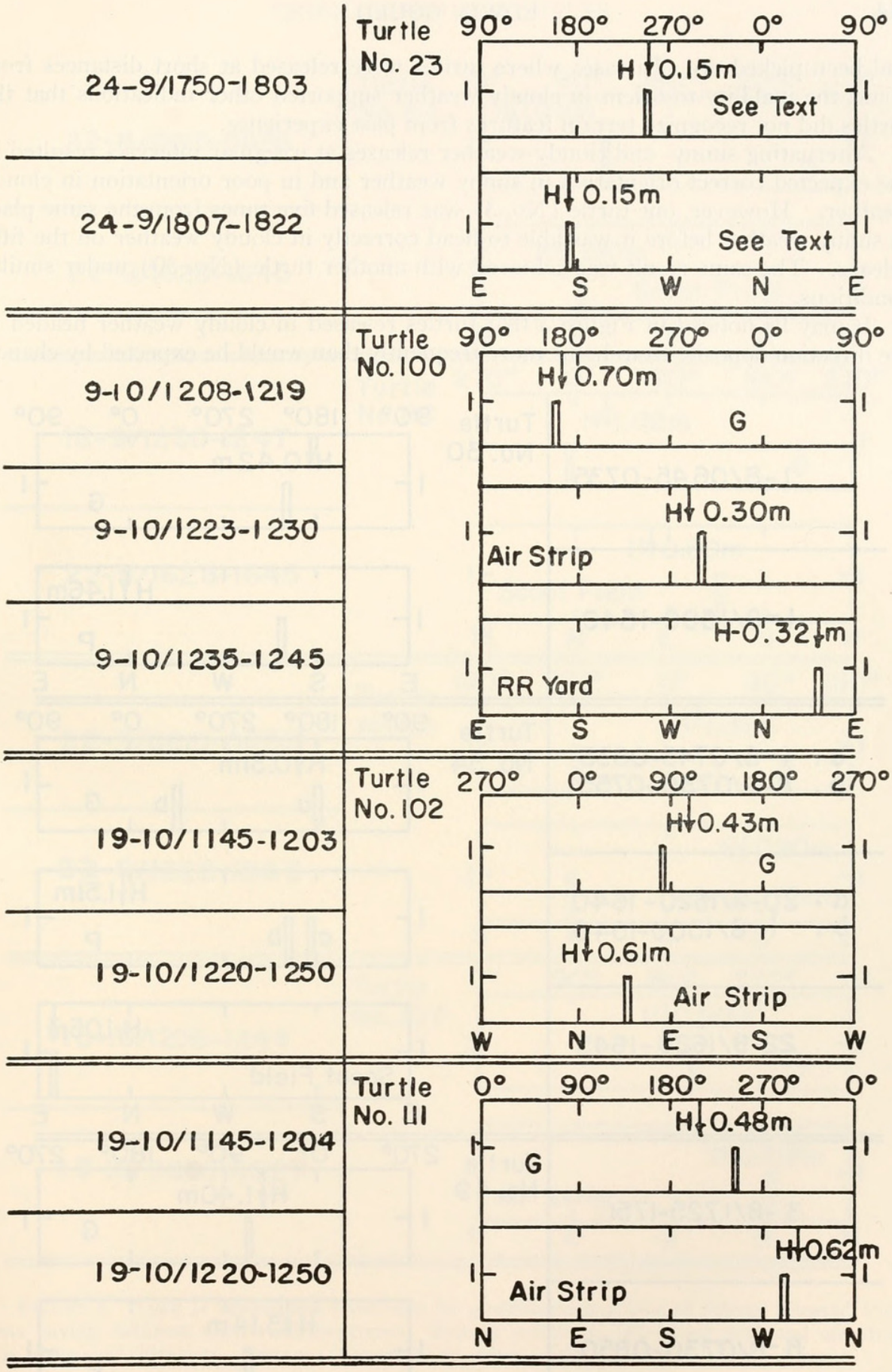
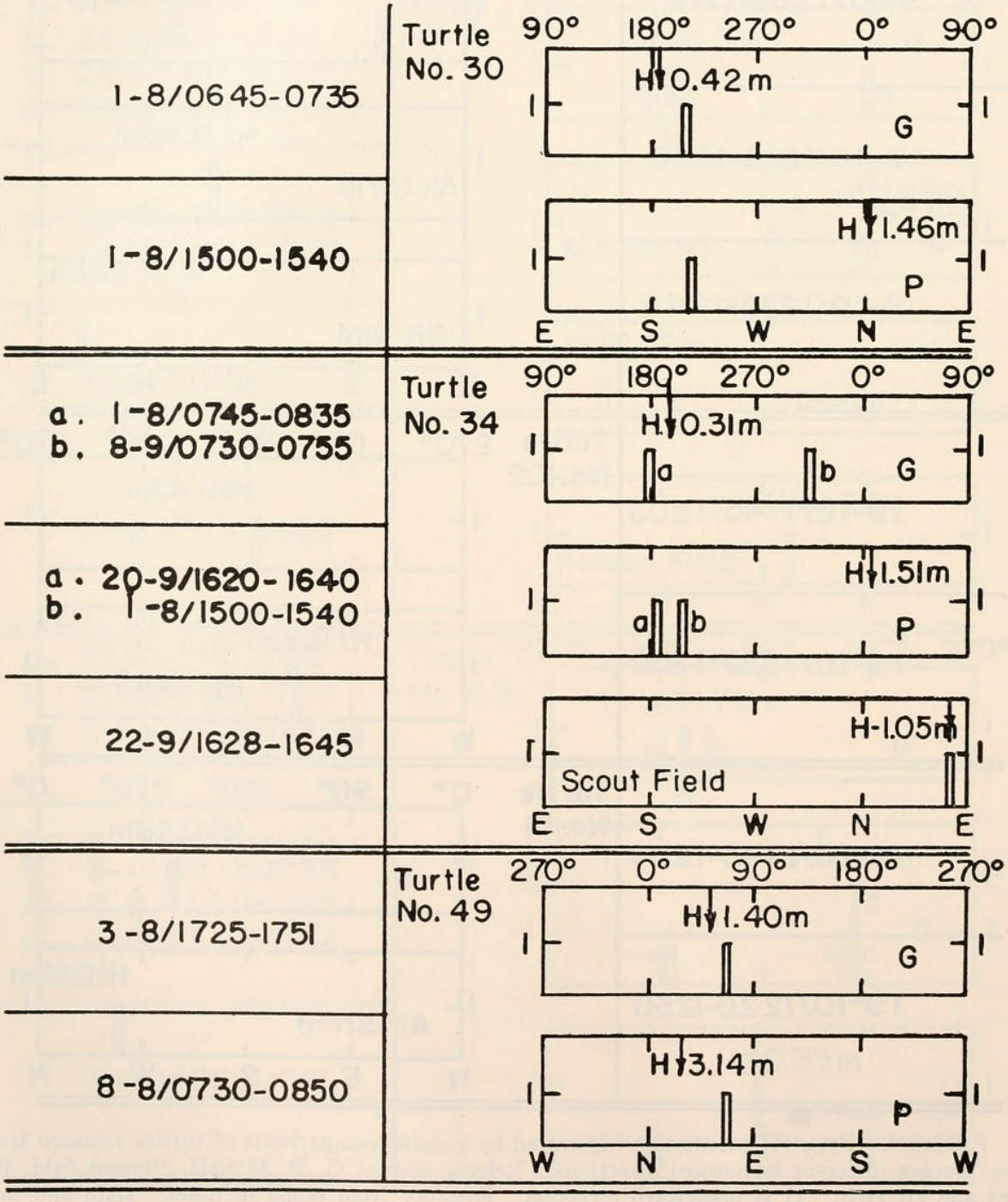


FIGURE 4. Type III orientation illustrated by graphic comparisons of turtles released from areas having different homeward directions. Release points: G, P, M field, Plowed field, RR yard and air strip. H is homeward direction. Distance from home in miles. Date and time in left column.

had been picked up. In cases where turtles were released at short distances from home, the inability to orient in cloudy weather supported other indications that the turtles did not recognize terrain features from past experience.

Alternating sunny- and cloudy-weather releases at irregular intervals resulted in the expected correct orientation in sunny weather and in poor orientation in cloudy weather. However, one turtle (No. 3) was released five times from the same place in sunny weather before it was able to head correctly in cloudy weather on the fifth release. The same result was achieved with another turtle (No. 30) under similar conditions.

It may be noticed in Figure 3 that turtles released in cloudy weather headed in the direction opposite from home more frequently than would be expected by chance.



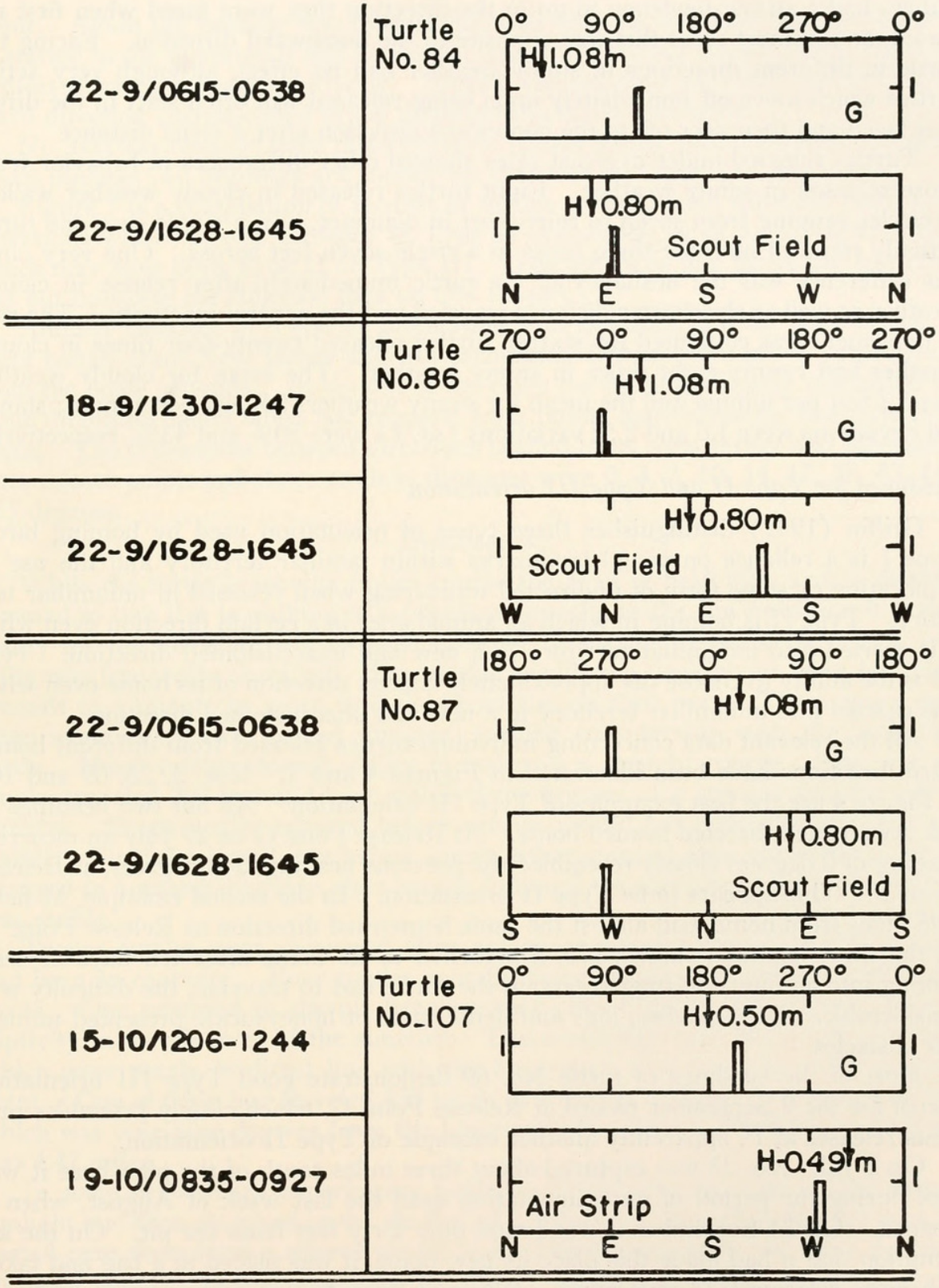


FIGURE 5. Type II orientation illustrated by graphic comparisons of turtles released from areas having different homeward directions. Release points: G, P, Scout field and air strip. H is homeward direction. Distance from home in miles. Date and time in left column.

Others had a strong tendency to go in the direction they were faced when first released, and in most cases this was opposite to the homeward direction. Facing the turtle in different directions in sunny weather had no effect, although very active turtles which move off immediately upon being released will often start in the direction faced and then veer off to the homeward direction after a short distance.

Turtles released under overcast skies showed other differences in behavior from those released in sunny weather. Eight turtles released in cloudy weather walked in circles ranging from seven to thirty feet in diameter. In a single case one turtle actually retraced its track three times in a circle seven feet across. One very obvious difference was the hesitancy of the turtle immediately after release in cloudy weather as well as the shorter distance traveled and the general inactivity. The rate of movement was computed for sixteen turtles released twenty-four times in cloudy weather and twenty-eight times in sunny weather. The mean for cloudy weather was 3.2 feet per minute and the mean for sunny weather, 5.8 feet per minute; standard deviations were 1.6 and 2.5; variations ($sd/\bar{x}$) were 50% and 43%, respectively.

Evidence for Type II and Type III orientation

Griffin (1952) distinguishes three types of orientation used by homing birds. Type I is a reliance on visual landmarks within familiar territory and the use of exploration or some form of undirected wandering when released in unfamiliar territory. Type II is homing in which an animal goes in a certain direction even when it is carried into unfamiliar territory in a new and unaccustomed direction. Type III is the ability to choose the approximately correct direction of its home even when it is carried into unfamiliar territory in a new and unaccustomed direction.

All the relevant data concerning individual turtles released from different homeward directions have been illustrated in Figures 4 and 5. Nos. 3, 23, 69 and 100 in Figure 4 are the best examples of Type III orientation. All but two headings of No. 3 were well-directed toward home. At Release Point G on 29 July an incorrect heading of 0 degrees closely resembled the previous heading, 348 degrees, at Release Point P. This appears to be Type II orientation. In the second example, M field, 3.95 miles from home, had almost the same homeward direction as Release Point P. In the third example shown, No. 3 returned to its home after ten days or less. Taking into account the rugged terrain the turtle had to traverse, the difficulty was considerable. Deep ditches, logs and dense mats of honeysuckle presented numerous obstacles.

Most of the headings of turtle No. 69 demonstrate good Type III orientation except for the 9 September record at Release Point G, which closely resembles previous releases at P, apparently another example of Type II orientation.

On 2 July, No. 23 was captured about three miles south of the pit where it was kept during the period of experimentation until the last week of August, when it escaped. On 24 September it was found only forty feet from the pit. On the assumption that it had made this place its new home, it was placed in a bag and taken to a large clearing 0.15 mile away. While walking to this release point I rotated and spun the turtle in various directions so as to remove any possibility of its remembering the movements. It was in my pocket for the remainder of the short journey. Upon release, No. 23 headed accurately toward the spot where it had just been recaptured. Following a similar procedure, it was again released from a point having a homeward direction 72 degrees different from the previous release

point. Again the heading was toward the spot where it had just been recaptured. It started in the direction it had proceeded from the previous release point, but after a short distance it headed correctly. Neither the previous direction nor the homeward direction corresponded to the direction the turtle was faced.

No. 100 was released from three different release points within a period of thirty-seven minutes; all headings are supportive evidence for Type III orientation.

Figure 5 is a compilation of records of turtles released from different homeward directions which showed evidence of Type II orientation or of an ambiguous type which may have been Type II or Type III. The others in this figure are less obvious but complete the collected data on this subject.

Another instance of Type II orientation was demonstrated by ten releases of eight turtles from New Jersey and Massachusetts, 180 and 400 miles, respectively, from the home grounds. In six out of ten cases the headings closely resembled the same directions taken when last released from points approximately one mile from home. The differences between directions headed from New Jersey and Massachusetts release points and those at close distances were 0, 3, 3, 10, 14, 17, 38, 43, 148, 155 degrees.

Discussion

While the turtle is moving on its course the head is held high and is directed forward so that if it is walking in a direction opposite to the sun's position it is necessary for the turtle to turn its head in order to see the sun directly. This very thing was frequently observed. The turtles would stop, look about them for thirty seconds to a minute or more, and then continue on their way. These stops were often made every two to four minutes, varying considerably with the individual turtle. Many turtles showed ability to maintain a straight course. One, for example, traveled 200 feet and kept within three degrees of a straight line for twelve minutes. Seven turtles released before sunrise moved but little until the sun was visible. Turtles released just before sunset either stopped after the sun had set or changed to a wrong direction after having followed the correct course while the sun was visible.

Twelve turtles were recovered after escape or release from a pit where they had been in captivity. Four turtles actually homed from distances of 405 to 563 yards. One returned to the pit from another release point after having been in captivity in the pit most of the summer. The remainder were picked up at points which were nearly in direct line with the homeward direction from their starting point. One of these had traveled 458 yards in less than six days in a presumed line which was only nine degrees from the homeward direction. The distance to home was 4.47 miles.

In some preliminary experiments turtle headings were recorded under natural sunlight and then observed in the shadow of a person or tree when the sun was reflected onto them from a mirror placed about 180 degrees from the sun's position. In all of twenty observations using ten turtles they changed their courses significantly when the sun's image fell upon them. In nearly all cases the turtles headed toward the mirror. Furthermore, in all cases the headings which were initially taken in the sun were resumed after the mirror was removed and the turtle was returned to natural conditions of direct sunlight. The exact meaning of these observations remains obscure, but they do support the hypothesis that it is the sun which enables these turtles to exhibit Type II and Type III orientation.

Summary

1. An investigation was made to test the hypothesis that box turtles [*Terrapene c. carolina* (Linnaeus)] employ a means of sun orientation similar to that found in birds. Box turtles from different localities were taken in closed containers to unfamiliar territory and released in large open fields 0.28 to 5.80 miles from their homes. (According to Stickel the home range is about 300 feet in diameter.) They were then observed over periods varying from ten minutes to two hours, and with the aid of a compass their headings during that period were plotted, and the distances traveled were paced off. After the observation they were again placed in closed containers and returned to a pit where they were kept until the next release.

2. Of forty-three turtles released and observed in this manner, twenty-two headed toward home; seventeen of the latter were released under sunny and overcast skies and in most cases this was done from at least two different release areas. Homeward headings were observed in sunny weather, but under overcast skies orientation broke down (Fig. 3). Twelve examples, two turtles each, of situations in which sixteen turtles with opposite homeward directions headed toward their respective homes at the same time from the same place, demonstrated that the heading was not dependent on some local environmental factor at the release point (Fig. 2).

3. Of sixteen turtles released from several completely different homeward directions, four showed definite ability to orient correctly (Fig. 4).

4. There were ten releases under sunny skies more than 150 miles from home. Nine turtles were used in these experiments. In seven of these headings the turtles went in a direction which seemed to correspond to the direction last chosen when close to home, regardless of the actual homeward direction. At short distances of a mile or less from home several turtles also headed in consistent directions regardless of the homeward direction.

5. Ten turtles in twenty experiments were first observed for directional heading in natural sunlight, and then observed in the shade while the sun's image was reflected upon them with a mirror. The direction of heading was altered in all cases and usually resulted in the turtles' heading for the mirror.

6. While walking, turtles stopped frequently and turned their heads as though looking at the sun.

7. These findings seem to support the hypothesis that turtle orientation resembles the type of orientation found in birds; however, more data are necessary to clarify numerous factors which may bring to light conflicting differences and close resemblances. Work is continuing and new developments will be reported as they are observed.

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