

A compass without a map: tortuosity and orientation of eastern painted turtles (*Chrysemys picta picta*) released in unfamiliar territory

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Abstract: Orientation mechanisms allow animals to spend minimal time in hostile areas while reaching needed resources. Identification of the specific mechanism used by an animal can be difficult, but examining an animal's path in familiar and unfamiliar areas can provide clues to the type of mechanism in use. Semiaquatic turtles are known to use a homing mechanism in familiar territory to locate their home lake while on land, but little is known about their ability to locate habitat in unfamiliar territory. We tested the tortuosity and orientation of 60 eastern painted turtles (*Chrysemys picta picta* (Schneider, 1783)). We released turtles at 20 release points located at five distances and in two directions from two unfamiliar lakes. Turtle trails were quite straight (fractal dimension between 1.1 and 1.025) but were not oriented towards water from any distance (V -test; $u < 0.72$; $P > 0.1$). Turtles maintained their initially chosen direction but either could not detect water or were not motivated to reach it. Furthermore, paths were straighter at larger spatial scales than at smaller spatial scales, which could not have occurred if the turtles had been using a correlated random walk. Turtles must therefore be using a reference stimulus for navigation even in unfamiliar areas.

Résumé : Les mécanismes d'orientation permettent aux animaux de passer le moins de temps possible dans les espaces hostiles, alors qu'ils recherchent les ressources qui leur sont nécessaires. Il peut être difficile d'identifier les mécanismes spécifiques utilisés par un animal, mais l'examen du tracé de ses déplacements en terrains familier et inconnu peut fournir des indices sur le mécanisme en question. Il est bien connu que les tortues semi-aquatiques, se déplaçant au sol sur un territoire familier, utilisent un mécanisme d'orientation pour retrouver leur lac d'origine; mais, on sait peu de choses sur leur habileté à trouver un habitat dans un territoire non familier. Nous avons testé la tortuosité et l'orientation chez 60 tortues peintes de l'est (*Chrysemys picta picta* (Schneider, 1783)). Nous avons relâché les tortues à l'un de 20 points de libération. Ces points de libération se trouvaient à cinq distances et dans deux directions par rapport à deux lacs non familiers. Les tracés des déplacements des tortues sont remarquablement rectilignes (dimension fractal de 1,1 à 1,025), mais ils ne sont pas orientés vers l'eau, quelle que soit la distance (test de V ; $u < 0,72$; $P > 0,1$). Les tortues maintiennent l'orientation choisie initialement et elles n'arrivent pas à percevoir la présence d'eau ou alors elles ne sont pas enclines à s'y diriger. De plus, à des échelles spatiales plus grandes, les tracés des déplacements sont plus rectilignes qu'à de plus petites échelles spatiales, ce qui ne se produirait pas si les tortues se déplaçaient selon un trajet aléatoire corrélé. Les tortues doivent donc utiliser un stimulus d'orientation dans leurs déplacements, même en terrain non familier.

[Traduit par la Rédaction]

Introduction

To survive and reproduce, animals must locate necessary resources (i.e., food, shelter, others of the same species). Simply depending upon random movements for this purpose can be energetically inefficient. For this reason, most animals have evolved mechanisms and strategies to orient towards goals in their environment (Able 1991). When orientation is towards the site where an animal lives and has its shelter, den, or nest, it is referred to as homing (Papi

1992). If an animal is displaced far enough from where it lives that its home location is no longer detectable, or if its home is destroyed, the goal of orientation becomes habitat rather than home. Although the goal has changed, the principle remains the same. The animal must locate suitable habitat as quickly as possible or risk death. This is especially important in situations where there are well-defined patches of suitable habitat separated by inhospitable or unfavourable areas.

Animals use various orientation mechanisms to locate the nearest habitat patch. Mechanisms proposed for turtles include geotaxis (movement either up or down an incline; Emlen 1969; DeRosa and Taylor 1982), olfaction (Emlen 1969; Graham et al. 1996; Lebboroni and Chelazzi 2000), use of light characteristics (movement towards or away from light, orientation using gradients of light polarity or wavelength; Yeomans 1995; Lebboroni and Chelazzi 2000), use of local topographic landmarks (Emlen 1969), use of a sun compass (DeRosa and Taylor 1976, 1982), and use of a magnetic compass (Mathis and Moore 1988).

The first three of these suggested mechanisms (geotaxis,

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olfaction, and use of light characteristics) can be considered water-finding mechanisms. Geotaxis, for instance, is often successfully used to locate water because bodies of water are commonly found in low-lying areas. By orienting in the direction of a smell associated with water, an animal can also use olfaction to locate the nearest water body. The combination of incident and reflected light above bodies of water can change the polarity of light above water; an animal that can sense differences in polarity can use this ability to orient towards water. In a dense forest, simply moving towards lighter areas can also lead an animal to a body of water.

The final three mechanisms (use of topographic landmarks, a sun compass, and a magnetic compass) can be used to locate water, but only if the animal has a knowledge of its surroundings (i.e., a mental map). With a mental map of topographic landmarks around a home lake, animals can navigate from one landmark to another, making their way home. A compass mechanism (sun or magnetic) can also be used in combination with a mental map to locate water. When an animal has a spatial sense of its surroundings it can initially orient its body in the direction of water using its mental map and then maintain that direction using a compass mechanism. A compass mechanism alone will allow an animal to maintain direction, but without a mental map, the initial choice of direction must be made randomly.

Each of these orientation mechanisms operates within a certain distance from the goal. Beyond this distance, navigation towards a goal becomes a search for resources. When an animal is moving towards a sensory stimulus, the limiting distance is the point at which the animal is no longer able to sense the stimulus (i.e., perception range). When the orientation mechanism involves stored information (i.e., memory) or experience, the distance is the point at which the animal is no longer in a familiar area. Beyond these distances, the direction of the goal is unknown and the animal must begin a search for the resources it needs to survive. Zollner and Lima (1999) simulated several search strategies in an attempt to test the relative effectiveness of each and found that nearly straight line searching was, in general, the most effective. Presumably, if turtles are placed where they can no longer detect water, they will begin searching and may use such a straight line search strategy.

Determining the spatial limitations of orientation can provide clues to the mechanisms or combinations of mechanisms used. These spatial limitations can also have implications for conservation. If the habitat of a primarily aquatic turtle is destroyed because of drought, for instance, the spatial limitation of the turtle's homing or water-finding ability can affect its survival (Gibbons et al. 1983). If the direction of water is unknown and turtles must begin searching for water, they are less likely to reach safety and could die from desiccation or starvation.

Semiaquatic turtles are ideal organisms for studying orientation and search strategies, as they have distinct habitat patches (bodies of water) and must traverse hostile areas to reach these patches. The absence of food (Ernst and Barbour 1989) and shelter (Sexton 1959) and the increased risk of predation (Gilhen 1984) on land make the terrestrial environment hostile for semiaquatic turtles. To make these necessary but dangerous overland trips as short as possible,

several turtle species have developed homing mechanisms to help them locate and navigate back to their home lake (Williams 1952; Gould 1957; Emlen 1969; Carroll and Ehrenfeld 1978; Lebboroni and Chelazzi 2000).

Some turtles can also locate a body of unfamiliar water from some distance away. For example, when their home pond had dried up, 50% of red-eared slider turtles (*Trachemys scripta elegans* (Wied-Neuwied, 1839)) and 70% of Florida cooter turtles (*Pseudemys floridana floridana* (LeConte, 1830)) relocated to a pond 400 m away (Gibbons et al. 1983). In another example, when moved to an unfamiliar site, yellow-bellied slider turtles (*Trachemys scripta scripta* (Schoepff, 1792)) oriented towards an unfamiliar body of water 300 m away (Yeomans 1995). In both studies, turtles had to move through inhospitable areas (land) to reach a suitable habitat patch (water) unfamiliar to them.

There have been no studies testing the effect of distance on the water-finding abilities of turtles in unfamiliar territory. However, Yeomans's (1995) study suggested that the spatial limitation of water finding for the yellow-bellied slider turtle in unfamiliar territory is beyond 300 m, and the study by Gibbons et al. (1983) suggested that for red-eared slider turtles and Florida cooter turtles, the distance is beyond 400 m. We studied the water-finding ability of the eastern painted turtle (*Chrysemys picta picta* (Schneider, 1783)). Painted turtles can home from somewhere between 100 m and 1.6 km (Emlen 1969), but there have been no studies of the ability of these turtles to locate habitat when released in an unfamiliar area.

We had two objectives in this study. The first was to determine whether eastern painted turtles use an orientation mechanism when placed in an unfamiliar area. If they use such an orientation mechanism to maintain direction, then the tortuosity (opposite of straightness) of their movement paths should either decrease or remain constant with an increase in spatial scale. Our second objective was to determine whether turtles navigate towards the nearest body of water in an unfamiliar area. If they are using an orientation mechanism involving movement towards a sensory stimulus, they should be able to navigate towards water from distances at which they perceive that stimulus, but not from greater distances. Their movement paths should, therefore, be straighter and more directed toward water the closer they are to the water. However, if they are using a compass mechanism they may not be able to navigate towards the nearest body of water at any distance because they have no mental map of the area.

Materials and methods

Our general procedure was to release turtles at various distances from the nearest water in unfamiliar territory. We analyzed the structure of the movement paths to gather information about the orientation mechanisms used.

Experimental procedure

Between June and September of 2002 we removed eastern painted turtles from their home lake and released them on land at five distances from an unfamiliar lake. To ensure that any pattern found in the trail characteristics was not unique to one particular lake or one direction to water, we

used two release lakes and two release directions at each of those lakes.

We captured adult eastern painted turtles from two home lakes, Grays Lake and Anthony Lake, in Hants County, Nova Scotia, Canada, using hoop traps baited with sardines (Legler 1960). We used only adult turtles, defined as those with carapace length >13 cm, as in Gilhen (1984). We marked turtles by filing notches into the marginals of the carapace (Cagle 1944) to ensure that they were not used more than once.

Within 8 h of capture, turtles were transported to one of 20 release points in an opaque plastic container with sufficient water to prevent desiccation. Release points were situated at five distances (100 m, 500 m, 1500 m, 1000 m, or 2000 m) in two directions from two unfamiliar lakes. We chose the release point for each turtle randomly. We released only one turtle at a time in a given direction from a release lake to minimize the possibility that a turtle would be able to follow another turtle's trail.

We chose release lakes and directions such that release points were closer to the study lake than to any other lake. Since the furthest release distance was 2 km, study lakes had to be at least 4 km from any other lake. We chose the eastern and western directions from Shields Lake and the northeastern and southern directions from Anthony Lake based on these criteria. Since Anthony Lake was also a capture lake, we released any turtles captured in that lake at Shields Lake.

We released turtles far enough from their home lake to make homing unlikely. We released turtles from Anthony Lake at least 3.6 km away and those from Grays Lake at least 7.5 km away. These distances were considered sufficient because painted turtles released even 1.6 km from a home lake were not able to home (Emlen 1969).

Habitat varied among release points. Most release points were in dense mixedwood forests, but some were in clear-cut areas. Release points closer to water tended to be in areas with fewer softwood trees and more tall grass. Although there were roads within 100 m of some release points, all roads within 1.4 km of any of the release points were loose-surface, one-lane logging roads. All release points were located on government-owned land with little human disturbance.

To track movement paths, we fitted each turtle with a thread packet consisting of three internally wound cocoon thread bobbins (Imperial Threads Inc., Northbrook, Illinois; approximately 1500 m). We shrink-wrapped bobbins in plastic (Boonstra and Craine 1986) and attached them to the turtle's carapace with duct tape. We attached one end of the thread to a wooden stake at the release point and as the turtle moved forward, the thread snagged on vegetation and left a trail indicating the turtle's path. Due to the negligible resistance in the spool, the turtle was not hindered from forward movement and there was not enough tension in the thread to artificially straighten the trail.

We chose the initial direction in which to place each turtle randomly and recorded this direction for later analysis. We also recorded the direction in which we left the release area. This allowed us to later test for observer effect. Approximately 24 h following release, we recaptured turtles,

using the thread trail to locate them, and returned them to their home lake.

Data collection

We recorded each turtle's path by walking along the thread trail with a global positioning system (GPS) backpack unit (Leica GS50, Leica Geosystems). In open areas under clear skies, the accuracy of the readings was estimated by the GPS unit to be ± 0.5 m, but this error increased in dense forest and overcast conditions. To minimize the error, a threshold was set at 2 m. If this was exceeded, no readings were recorded by the GPS unit. In cases where the threshold was exceeded, we would wait at that location until a more accurate reading could be collected by the GPS before continuing along the trail. On average, we gathered coordinates every 2 to 3 s (approximately every 1 to 1.5 m) and tried to maintain a constant walking speed while following the turtle's trail.

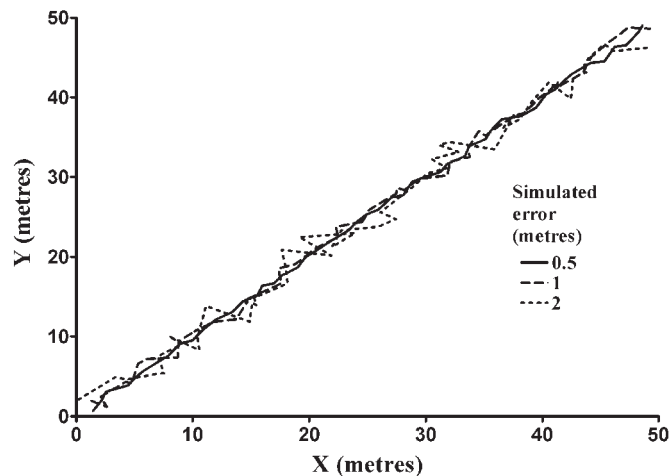
Tortuosity analysis

To determine the tortuosity of each trail, we used fractal analysis. A shape that is fractal has the same pattern regardless of the scale at which it is examined (Mandelbrot 1982). If the image were magnified, the same pattern would remain. Fractal dimension is a measure of the tortuosity of a line over a range of scales. It is also the continuous analogue of geometric dimensions. Thus, the fractal dimension of an animal's path in two dimensions is limited to values between 1 (a completely straight path) and 2 (a path that is so tortuous as to cover a two-dimensional plane) (Dicke and Burrough 1988; Sugihara and May 1990). For each movement path, we used the program "Fractal" (Nams 1996) to calculate a mean fractal dimension, as well as fractal dimensions at specific spatial scales, for 18 equally (log) spaced spatial scales between 1 and 100 m.

The overall fractal dimension allowed us to test for water detection distance. We would expect that if turtles had detected and were travelling towards water, they would travel in a straighter path than if they were searching for water. Thus, fractal dimension would be lower closer to water. The original fractal dimensions (D) were non-normal (Anderson-Darling normality test, $P < 0.001$), but a transformation of $\log(D - 1)$ resulted in normality ($P = 0.568$). We then used a one-way analysis of variance to compare fractal dimensions among the five release distances.

Estimating fractal dimension at specific spatial scales allowed us to investigate orientation mechanisms. If a turtle is travelling with a correlated random walk, fractal dimension would be low at small spatial scales and would increase with scale (Turchin 1996). Thus, a constant or decreasing fractal dimension should indicate orientation. We calculated a mean slope of fractal dimension versus $\log(\text{spatial scale})$ for a range of scales from 10 to 100 m as follows. For each trail, we calculated the fractal dimension for specific scales between 10 and 100 m. We then performed a linear regression on the calculated fractal dimensions to determine a slope for each trail, thus treating each trail as a single sampling unit. Finally, we calculated the mean slope from the slopes of the individual trails. We found the slope data to be non-normal ($P < 0.001$) and therefore used a nonparamet-

Fig. 1. Simulation of straight paths with three different levels of GPS error.



ric Wilcoxon signed-ranks test to determine whether the slope was increasing, constant, or decreasing with scale.

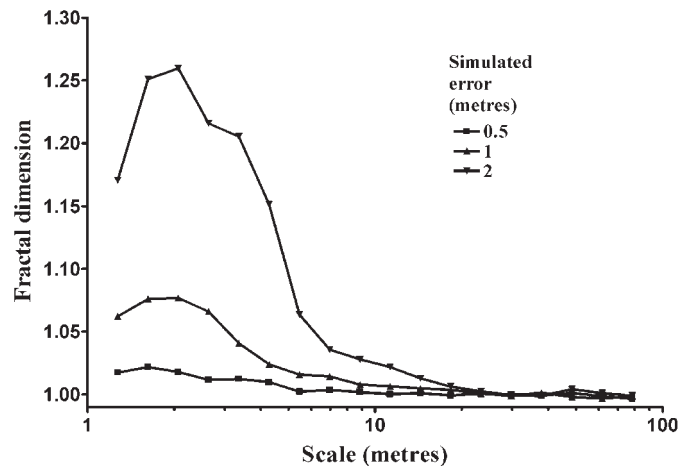
We minimized the effects of GPS error on our fractal dimension analyses as follows. To separate the tortuosity of the trail from that produced by the GPS error, the size scales that were most influenced by the error had to be determined. We did this by creating a simulated straight trail 420 m long and then simulating GPS error in an open area under clear skies by adding a random distance between -0.5 and 0.5 m to each x and y coordinate. We then repeated this procedure with random errors of ± 1 and ± 2 m to simulate the effect of GPS error under less ideal conditions. We then calculated fractal dimension at each scale. A straight trail should have a fractal dimension of 1 at all scales; those scales with a fractal dimension greater than 1 are those that are affected by the simulated GPS error. The simulated straight-line trails with errors of 0.5, 1, and 2 m (Fig. 1) had fractal dimensions that were larger on a small scale and decreased at larger scales, approaching a fractal dimension of 1 (Fig. 2). All three plots level off at a scale of approximately 10 m, revealing that the main effects of the GPS error on tortuosity calculations occurred at scales below 10 m. Thus, only scales between 10 and 100 m were used in calculating fractal dimension for the turtle trails.

Some trails were too short. To calculate fractal dimension, trails must have sufficient straight-line distances to allow for at least three segments of a scale size to cross the trail. Any trails that did not have sufficient straight-line distances to allow calculations of fractal dimension at scales above 10 m were removed from this analysis.

Directional analysis

To determine whether turtles oriented in a waterward direction (direction with the shortest path to the test lake) at any of the five release distances, we used a circular statistic called the V -test (Batschelet 1981). The V -test tests the directedness of a sample of angular values. The null hypothesis is that the sample is uniformly distributed in the range of possible values, as compared with a specific expected direction (e.g., towards water). We calculated a mean vector for each turtle using the initial (release point) and final (recap-

Fig. 2. Fractal dimensions of simulated straight-line paths with three different GPS errors at scales of between 1 and 100 m (on a log scale). The effects of GPS error are minimal at scales greater than 10 m.



ture point) trail coordinates and then converted the vector into an angular value. We assumed that turtles that did not move more than 10 m had not made a decision on their direction of movement, and we therefore removed trails less than 10 m long from the analysis.

We used V -tests to determine whether turtles oriented towards water and to test whether there was an observer effect. To test whether turtles oriented towards water, we performed separate V -tests for each of the release distances. To test for effects of release direction, we performed separate V -tests for each of the four release directions. To test whether the turtles moved away from us, we performed a V -test on all of the trails with the expected direction being the opposite direction from which we left. To test whether the turtles moved in the direction in which we initially placed them, we performed another V -test on all trails with the expected direction being the placement direction.

Results

We captured and released 60 turtles (39 female and 21 male) under a variety of weather conditions (I.R. Caldwell and A. Georgallas, unpublished data) between 17 June and 27 September 2002. The average overall distance moved by turtles between release and recapture was 218 m. Of the 60 turtles released, 10 did not move further than 10 m and their trails were therefore excluded from further analysis. Of these 10, 5 were released at Anthony Lake (3 from the south and 2 from the northeast) and 5 at Shields Lake (3 from the west and 2 from east), indicating that release habitat was likely not the reason for their lack of movement. Trail lengths of the remaining 50 turtles varied from 14 to 1326 m. Forty of these trails were long enough for fractal analysis. The behaviour of turtles at the time of recapture also varied. Some turtles were buried in moss, whereas others were walking when we recaptured them. All of those turtles that moved less than 10 m, however, were stationary at the time of recapture.

There were no significant differences in overall fractal dimensions of the trails among the five release distances

Fig. 3. Fractal dimensions of turtle trails at each of five release distances from an unfamiliar lake (error bars are 95% confidence intervals).

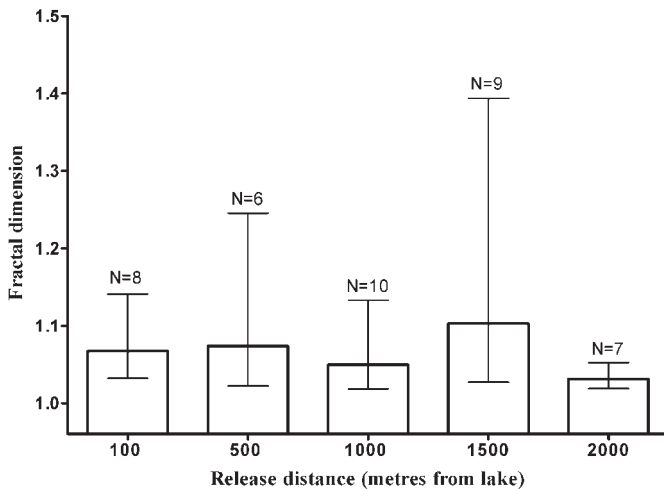
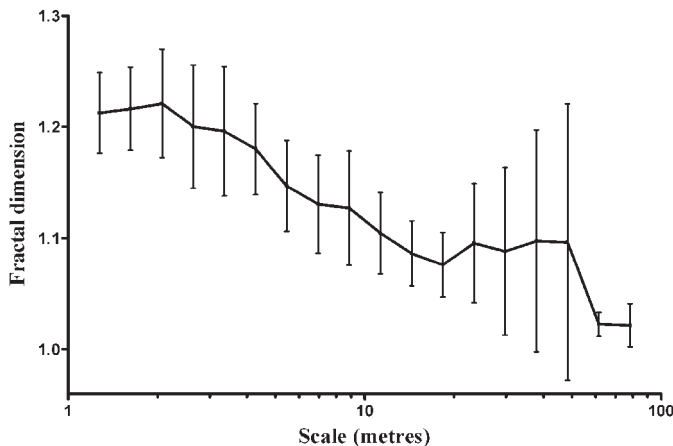


Fig. 4. Fractal dimensions for scales between 1 and 100 m (on a log scale). Values from trails of all turtles released near an unfamiliar lake were combined (error bars are 95% confidence intervals).



(Fig. 3; ANOVA, $P = 0.210$). Although confidence intervals were larger at the 500 and 1500 m distances, variances did not differ significantly (Bartlett's test for equal variance, $P = 0.181$) and trail lengths at these distances were not significantly different from those at other distances (ANOVA, $P = 0.601$). We therefore combined data from all distances to determine how fractal dimension varied with scale (Fig. 4).

For each trail, we calculated the fractal dimension at specific spatial scales (chosen by the program "Fractal" after setting the minimum scale at 10 m, the maximum scale at 100 m, and the number of divisions at 20). We then calculated the mean fractal dimension and the confidence interval at each scale from the fractal dimensions of all trails at that scale. As the scale increases, there are fewer trails of sufficient length for a fractal dimension to be calculated, and this is what leads to the larger confidence intervals seen at higher scales. Oddly, at the two largest scales, however, confidence intervals become quite small and it is not clear why this occurred. As in the GPS error simulations, fractal dimension was higher at scales below 10 m. At scales above

10 m the mean fractal dimension of the turtle trails was between 1.1 and 1.025.

Fractal dimension changed significantly with spatial scale. The mean slope of fractal dimension versus log(spatial scale) for the range of scales from 10 to 100 m was -0.00104 . This was significantly less than zero (Wilcoxon's signed-ranks test, $P = 0.03$). Thus, the turtle trails were straighter at larger scales than at smaller scales.

The turtle trails showed no significant directionality. Neither the initial direction chosen for each turtle (V -test; $u = -0.479$, $u_{0.05} = 1.646$, $n = 50$, $P > 0.10$) nor the direction chosen for our departure (V -test; $u = 1.262$, $u_{0.05} = 1.646$, $n = 50$, $P > 0.10$) had a significant effect on the directions of the turtles' paths. For each of the distances, turtle trail vectors did not significantly cluster around the expected (waterward) direction (Fig. 5). In all five cases, mean vector length was small, indicating that there was very little clustering of turtles' orientation directions.

Discussion

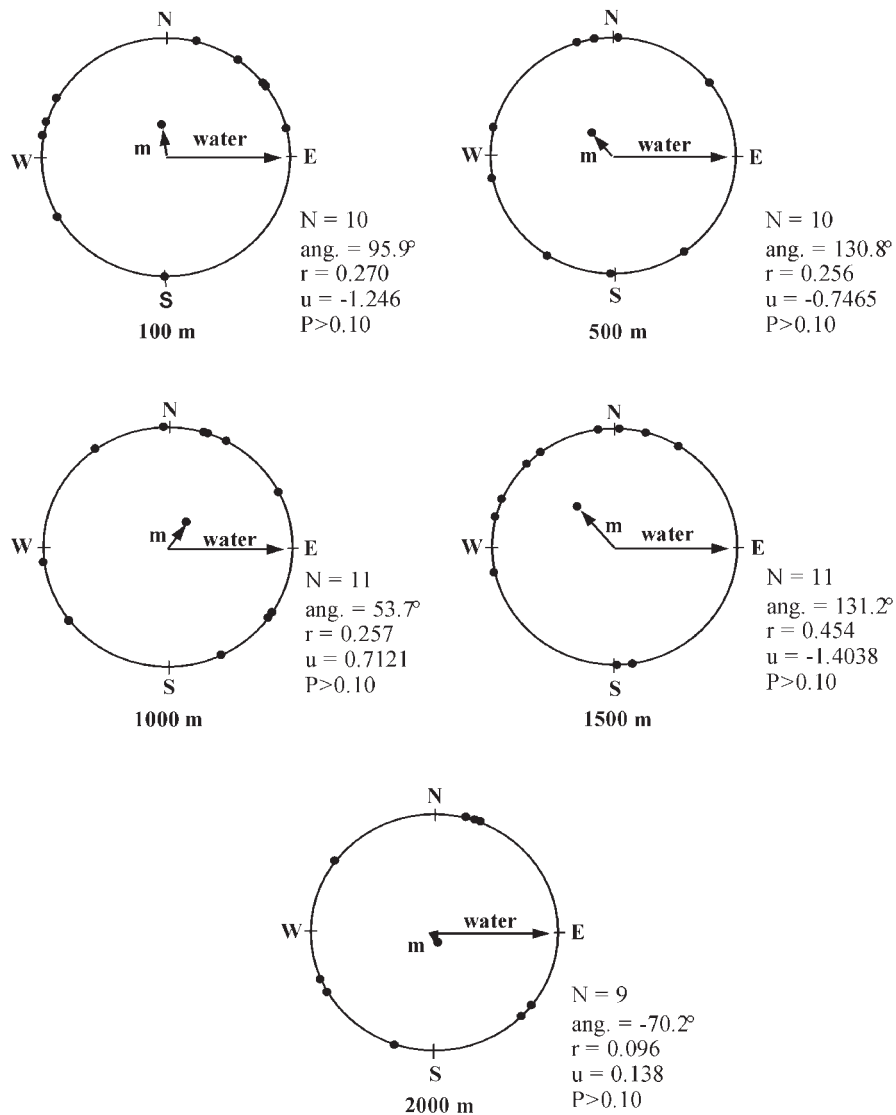
Tortuosity and orientation of turtle trails

Turtles travelled in relatively straight paths for hundreds of metres, well beyond the distance they could see in the dense forests in which they were released. These results are not expected of animals walking randomly. Turtles might maintain their direction by taking each successive step in the same approximate direction as their last step. This is known as a correlated random walk and can result in low tortuosities at small scales. At larger scales, however, without a constant frame of reference to maintain direction, the path will become more tortuous. If the turtles were maintaining their direction using a correlated random walk, the fractal dimension of their paths should have increased at larger scales (Turchin 1996).

This did not happen. Not only did tortuosity not increase at larger scales, but it significantly decreased (Fig. 4), even after eliminating scales below 10 m, which might be influenced by GPS error. Although fractal analysis made it necessary to remove trails with insufficient straight-line distances, their removal only resulted in decreased tortuosities at small scales, making our results more conservative. Clearly, the turtles were using some mechanism to choose their steps in a nonrandom manner and travel in such a straight line. Unfortunately, this trend could not be confirmed at scales below 10 m, as the tortuosities at smaller scales were probably influenced by GPS error and are not representative of the turtles' movement. Future studies using more accurate locational equipment may allow the examination of tortuosity at smaller scales to determine whether the trend continues.

An unexpected and interesting result of this study was that although turtles walked in straight paths, they did not orient towards water or in any specific direction. The inconsistency in orientation direction between turtles further indicated a lack of homing. Overall path tortuosity also did not differ among distances. This suggests either that the turtles wanted to find water and could not or that they could perceive the water but it was not their goal. If the former is correct, it may mean that turtles cannot find water in unfamiliar territory or, if they can, they can do so only at distant

Fig. 5. Orientation of turtles released at five distances from an unfamiliar lake in relation to waterward direction. Each dot on the perimeter of the circles represents an individual turtle's heading; *m* represents the mean vector. *N* is the number of turtles released, *ang.* is the angular difference between the expected and mean vectors, *r* is the length of the mean vector, and *u* is the test statistic. Although the waterward direction was not eastward for all of the turtles, all angles from waterward were transformed to an angle from eastward to make the figure easier to interpret.



ces less than 100 m. If the latter is correct, it calls into question whether the need for water was the driving motivation for the turtles' movement in this study.

We assumed that turtles would want to orient towards water for several reasons. First, they spend the majority of their lives in an aquatic environment. Their only known food sources are aquatic animals and plants, and their risk of predation is greater on land than in the water (Gilhen 1984). Second, our study lakes were suitable turtle habitat: they were trapped and found to contain their own populations of eastern painted turtles. Finally, other studies of orientation of freshwater turtles released on land (Emlen 1969; DeRosa and Taylor 1976, 1982; Yeomans 1995; Graham et al. 1996; Lebboroni and Chelazzi 2000) have been based on the assumption that turtles are guided by their need for water. Thus, it is unlikely that in this study the turtles had

no desire for water and it is more likely that they wanted to reach a suitable aquatic habitat but could not.

The eastern painted turtles' inability to find water provides clues to the mechanism they use when homing. Midland painted turtles (*Chrysemys picta marginata* Agassiz, 1857), a closely related subspecies, can locate their home lake from a distance of 100 m but not from a distance of 1 mile (Emlen 1969). In our study, however, we found that even those turtles released 100 m from water did not orient towards water. If the eastern painted turtle uses the same mechanism as the midland painted turtle to find its home lake, then the mechanism for water finding at distances of 100 m must function only when turtles are in familiar territory. The mechanism used by these turtles might, therefore, include the use of local landmarks, a sun compass, or a magnetic compass, as all of these mechanisms are ef-

fective for navigation to a specific goal only in familiar areas.

Other species can find water in unfamiliar habitat. Yellow-bellied slider turtles released in unfamiliar territory successfully oriented towards water from 300 m away (Yeomans 1995). During a period of drought, more red-eared slider turtles and Florida cooter turtles than would be expected by chance relocated to the nearest pond 400 m away (Gibbons et al. 1983). All three of these turtles belong to the same family (Emydidae) as the eastern painted turtle and spend the majority of their lives in freshwater (Ernst and Barbour 1989).

Why has the ability to locate water in unfamiliar territory evolved in some species and not others? Water-finding abilities may have evolved in some turtle species because the conditions in which they live (e.g., drought, temporary water bodies) make it necessary to move between habitats regularly. The yellow-bellied slider turtle makes overland trips between aquatic habitats (Yeomans 1995), and both the red-eared slider turtle and the Florida cooter turtle are well adapted to temporary bodies of water (Gibbons et al. 1983). Our study animal does not live in such conditions and thus would not have evolved this ability.

Turtles have been shown to move in straight paths in familiar habitats, but these movements could be the result of memory-based mechanisms. The trails of midland painted turtles (Emlen 1969) and eastern long-necked turtles (*Chelodina longicollis* (Shaw, 1794); Graham et al. 1996) had very low straightness indices (i.e., the ratio of gross trail length to net distance travelled). In both of these studies, though, the turtles were in familiar surroundings, orienting in the direction of home water, indicating that a memory-based mechanism could have led to such straight paths.

Some turtles follow natural guidelines such as ditches and waterways. As in our study, Lemkau (1970) found that box turtles (*Terrapene carolina carolina* (L., 1758)) did not consistently orient in any particular compass direction but maintained relatively straight paths. However, their straight paths could be explained by their tendency to follow natural guidelines. Although a small number of our turtles followed a ditch for a short distance, other turtles crossed ditches and waterways without following them for any distance. It is, therefore, unlikely that the use of natural guidelines led to the straightness of the turtle paths in our study.

Use of fractal dimension

Criticism has arisen for measuring the fractal dimension of movement paths when it varies with spatial scale (Turchin 1996). For example, the fractal dimension of correlated random walks increases with spatial scale (i.e., paths get more tortuous at larger scales). The overall fractal dimension for a correlated random walk is thus dependent upon the range of scales used for its calculation. We minimized this problem by using the same range of scales for all movement paths. Furthermore, the non-fractal nature of correlated random walks was useful in testing for the presence of an orientation mechanism. Thus, we used fractal dimension as a measure of tortuosity rather than other measures (e.g., the index of straightness (Claussen et al. 1997) or sinuosity (Bovet and Benhamou 1988)) because fractal dimension allows testing for a correlated random

walk. The other measures do not give estimates of tortuosity as a function of spatial scale. Furthermore, sinuosity assumes that the trail is a correlated random walk to begin with.

Possible mechanisms used

The straightness of the paths we observed suggests that the turtles were using an orientation mechanism. To maintain a specific direction over great distances, there must be a continuously consulted, constant frame of reference. At limited distances, directionality can be maintained by focusing on and moving towards a distant landmark, but this becomes increasingly difficult when the line of sight is reduced. In our study, the turtles were often released in areas with dense undergrowth. This would have considerably reduced their line of sight, making it unlikely that visual landmarks were used to maintain direction.

None of the water-finding mechanisms proposed for freshwater turtles could be used to maintain direction over the large distances turtles travelled in our study. Geotaxis (orientation up or down a slope) would allow turtles to maintain direction only until they encountered a change in slope. Also, geotaxis would result in all turtles released at the same point following similar paths; this did not occur in our study. Olfaction would cause turtles to orient towards water at short distances; this did not occur either. The use of light characteristics above water requires a clear line of sight, which was not available in our study. Thus, these mechanisms cannot be responsible for the straightness of turtle paths in our study.

The only mechanisms that can explain the straightness are sun and magnetic compasses; these provide a constant frame of reference for movement over hundreds of metres. As long as the direction of the sun is visible and an animal can correct for the sun's movement across the sky throughout the day, the sun can be used as a constant reference. The earth's magnetic field can always be used as a constant reference. However, both of these mechanisms are effective in locating water only if the direction of the water is known. This may explain why painted turtles found their home lake when they were released on land in familiar territory (Emlen 1969) but did not orient towards water in our study. We cannot speculate about which type of compass mechanism was used, although the use of a sun compass by painted turtles has been shown by DeRosa and Taylor (1976, 1982).

A compass mechanism is the only proposed mechanism that could explain why painted turtles in our study, in unfamiliar habitat, moved in such straight paths yet could not find water, whereas those in other studies could find their home lake. A compass mechanism would allow turtles to maintain a direction but would not help them choose that direction. The turtles have a compass, but in unfamiliar territory they lack a map.

Search strategies

What use is a compass without a map? Zollner and Lima (1999) showed that nearly straight line movement was a highly effective search strategy for animals attempting to locate habitat patches. Although they modelled small forest-dwelling mammals moving across hostile agricultural fields in search of forest fragments, this situation is similar to that

of turtles moving on land in search of aquatic habitat. To locate another nearby body of water, a turtle has to move across hostile land where there are no available food resources and there is an increased risk of predation.

We found that turtles did not perceive the direction of water even when water was nearby. They were not orienting towards a known goal but were searching for a habitat patch using an orientation mechanism. Zollner and Lima (1999) showed that with high mortality risks, low energy reserves, and a uniform landscape, a straight line search was the best strategy. A nearly straight line search, however, was superior to a straight line search in general. The nearly straight line paths of our turtles would thus be an effective strategy for finding nearby water if the distribution of water bodies was unknown. In other words, without a map, a compass would still help turtles in their search for water.

Our study points out another aspect of search strategy. Zollner and Lima's simulations used a correlated random walk, whereas we found that our turtles used a directed walk. It is unclear whether a nearly straight directed walk would be more or less efficient than a nearly straight correlated random walk. A directed walk should cover a greater distance at larger scales but less area at smaller scales. More work is needed to compare search efficiency of directed versus non-directed movement.

Other studies have found quite straight movement paths. Bowne and White (2004) found that painted turtles had straight paths at both small and large spatial scales and that straightness did not decrease at the large scale. However, most of the turtles they tested at the large scale found water. Thus it is not known whether the straight-line movement was due to a compass or simply detection of and travel towards water.

Male prairie rattlesnakes (*Crotalus viridis* (Rafinesque, 1818)) move in relatively straight paths when searching for mates (Duvall and Schuett 1997), and female cabbage white butterflies (*Pieris rapae* (L.)) do so when searching for cabbage plants on which to lay their eggs (Jones et al. 1980). Unfortunately, neither of these studies determined whether animals were using a correlated random walk or a directed walk.

Cactus bugs (*Chelinidea vittiger* Uhler, 1863) also travel in relatively straight paths and do not use correlated random walks (Schooley and Wiens 2003). However, these cactus bugs also tended to orient towards upwind habitat patches and may simply have been orienting towards their goal using olfaction and not employing a search strategy.

Although it is important to establish whether animals are moving in relatively straight search paths, it is equally important to determine whether these paths are due to directed or non-directed movement. To our knowledge, our study is the first to show that turtles use a directed walk in their search for resources in unfamiliar territory. Determining which other animals use such a strategy should be a focus of future studies.

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