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ORIENTATION IN JUVENILES OF A SEMIAQUATIC TURTLE, *KINOSTERNON FLAVESCENS*

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ABSTRACT: Hatchling orientation has been widely studied among marine turtle species, but much less so in nonmarine turtles. Yellow mud turtles (*Kinosternon flavescens*) exhibit an unusual semiaquatic life history with terrestrial estivation or hibernation in summer through winter and aquatic mating and feeding in spring and early summer. Hence, these turtles migrate between wetlands and uplands at least twice each year along the same migration path. To understand the orientation methods used by juvenile turtles, hatchling and second-year mud turtles emerging from hibernation were captured before reaching the water and released in one of two circular arenas placed out of sight of and on the opposite side of the wetland. Recapture locations of these turtles along the perimeter of the arenas suggested that hatchlings probably used visual (e.g., polarized light) or perhaps olfactory cues to orient toward water. However, second-year turtles maintained the same compass bearing used prior to initial capture, suggesting that they employed an internal compass mechanism that was not overridden by proximate cues from the wetland. The probable mechanism for setting that course was likely a sun and/or a magnetic compass.

Key words: Compass; Cues; Hatchlings; Migration; Mud turtle; Orientation

THE NAVIGATIONAL abilities of marine turtles have been well-documented in recent years (e.g., Lohmann et al., 1997). Upon emergence from the nest, hatchling sea turtles move to the ocean by orienting away from the darker, elevated landward horizon, and toward the lower, brighter seaward horizon, using vision as the primary orientation mechanism (Salmon et al., 1992). Once hatchlings reach the water they head out to sea by swimming directly into the oncoming waves (Lohmann and Lohmann, 1992, among others). Hatchlings acquire an internal compass course (probably magnetic) during the terrestrial migration (e.g., Stapput and Wiltschko, 2005) and/or the migration through the offshore waves (e.g., Goff et al., 1998). The acquisition of this magnetic compass is apparently the basis by which sea turtles navigate at sea and later return to their natal beach for nesting and mating (Lohmann et al., 1997; Freake et al., 2006).

Orientation (especially homing ability following displacement) in adult freshwater and terrestrial turtle species has also been well-studied. These turtles exhibit good homing and orientation skills, with ample evidence suggesting that a sun compass is a key mechanism. Indeed, sun-compass orientation ability has been demonstrated or suggested for at least 11 species (five families) of adult freshwater and terrestrial turtles (Carroll and Ehrenfield, 1978; DeRosa and Taylor, 1976, 1980, 1982; Ernst, 1970; Germano and Nieuwolt-Dacanay, 1999; Gibbons and Smith, 1968; Gould, 1957, 1959; Gourley, 1974; Graham et al., 1996; Lebbroni and Chelazzi, 2000; Metcalf and Metcalf, 1978; Murphy, 1970; Yeomans, 1995). Some evidence also exists for the role of geotaxis in this orientation (DeRosa and Taylor, 1980, 1982), but much less for the use of the Earth's magnetic field (Mathis and Moore, 1988). However, orientation in hatchling freshwater and terrestrial turtles is not as well studied as homing. Hatchlings of most freshwater turtle species emerge from their nest (or overwinter site; Costanzo et al., 1995) and migrate directly to wetlands (Burke et al., 2000; Ehrenfield, 1979), although a few apparently do not move directly to water (e.g., Burger, 1976; McNeil et al., 2000). In any case, very few experimental studies (Anderson, 1958; Burger, 1976; Noble and Breslau, 1939) have examined the orientation abilities and the theoretical mechanisms that displaced hatchling freshwater turtles employ.

Yellow mud turtles (*Kinosternon flavescens*) in western Nebraska are diurnal, hibernate underground on upland sandhills, emerge and migrate to wetlands each spring, and return to the same uplands to estivate in mid-summer

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(Iverson, 1990, 1991; see also Christiansen et al., 1985, and Tuma, 2006). During autumn, estivation ends as turtles dig deeper to hibernate for the winter. Females nest in these same upland sandhills (Iverson, 1990); eggs hatch in the autumn, but hatchlings (mean carapace length = 22.1 mm; mean body mass = 2.92 g; $n = 206$) do not emerge from nests in the fall. Instead, they dig down below the nest to depths > 1 m to overwinter. In spring these hatchlings dig upward, emerge above ground for the first time, and then move directly to the wetlands (Costanzo et al., 1995; Iverson, 1990, 1991). One to two months later these neonates reverse their spring migration route, return to their natal upland habitat, and bury for estivation (and later hibernation). Hence, an individual turtle follows the same migration path at least twice each year, though in opposite directions (J. B. Iverson, unpublished data). We have documented the precision of this two-way migration over 27 years in some individuals and have never observed a mud turtle that switched migration routes from one side of the wetland to the other, despite nearly 24,000 captures over 27 years. Nonetheless, the orientation mechanisms and cues used are unknown.

Hatchling turtles could hypothetically orient using multiple cues during their initial diurnal descent from uplands to the wetland, including positive geotaxis, odors on the ground from older turtles, darker upland horizons, high light intensity and increased polarized light over the wetland, or even direct sight of water (Avens and Lohmann, 2003). Cues for the return trip are less obvious. We hypothesized that some kind of internal orientation compass was activated during that initial descent and that this compass was then simply reversed one to two months later when the yearling turtles returned to the same sandhill. An alternate hypothesis would suggest that hatchlings learn to read visual cues (terrestrial topography such as sandhills, shoreline markers such as vegetation; Emlen, 1969), and use them to move between their upland and wetland habitats.

To test whether post-hatchling turtles use an internal compass mechanism or simply the same cues that hatchlings use, we displaced hatchling and year-old turtles into distant arenas to determine whether they would continue on the same vector they were moving when initially captured, or whether they would reorient correctly toward the wetland. If they maintained the same vector on which they were initially headed, a compass mechanism must exist (though its basis would still be unclear). However, if they reoriented toward the lake, despite being out of direct line of sight and surrounded by a high horizon, a compass mechanism would not be evident and orientation would be based primarily on limited, proximate cues.

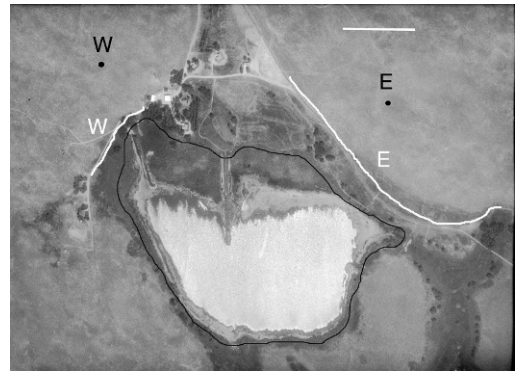


FIG. 1.—Aerial photo of Gimlet Lake study area in western Nebraska (north to top). Curved white lines indicate locations of East (E) and West (W) drift fences; solid black dots indicate east (E) and west (W) arenas. Black line encircling the wetland indicates the approximate shoreline during spring turtle migration. White scale in upper right measures 200 m.

MATERIALS AND METHODS

Our research was conducted at Gimlet Lake and its surrounding uplands on the Crescent Lake National Wildlife Refuge in Garden County, Nebraska (Fig. 1). The Refuge lies in the Nebraska Sandhills, a 50,000 km^2 area of rolling sand dunes now stabilized by midgrass prairie (Bleed and Flowerday, 1990). Because of the unique movements of yellow mud turtles between uplands and wetlands, since 1981 we have nearly annually erected 25 cm high drift fences parallel to the northeastern (East Fence) and northwestern (West Fence) shores of Gimlet Lake (Fig. 1). Turtles were captured, measured, and marked along these fences as part of long-term

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FIG. 2.—Placement of the west experimental arena (looking NNW) in a depression in the upland sandhills northwest of Gimlet Lake.

demographic studies of turtles (e.g., Converse et al., 2005; Iverson, 1991). Mud turtles to be displaced to arenas for our experiments were captured in the spring along the middle of these fences as they migrated directly to the wetland from their winter hibernation sites in the adjacent sandhills. When captured at the East Fence, turtles to be displaced had already traversed at least 60 m on their migration path to the lake (ca. SSW = 202.5°); those at the West Fence had moved at least 20 m (ca. ESE = 112.5°).

We built two circular arenas in natural depressions in upland sandhills that were out of direct sight of any wetland (Fig. 2), and far enough away to significantly reduce olfactory and auditory cues from the wetland. Each arena was 11 m in diameter and constructed with 30 cm wide aluminum coil stock buried ca. 5 cm in the ground and supported by pairs of wooden laths spaced about every 60 cm. Sixteen compass points were marked directly on the inside of the fence, and 200-ml paper cups were buried to ground level at each compass point. Moistened soil (ca. 3 cm) was placed in each cup and kept moist through the experiment in order to insure that no turtles desiccated.

These arenas were strategically placed such that the direction to the lake was distinctly different from the normal migration vector of turtles to be released there. The west arena was ca. 175 m from the west drift fence (ca. 190 m from the Gimlet Lake shoreline), and the east arena was ca.140 m from the east fence (ca. 210 m from the shoreline). We determined two predicted angles for each arena to account for our hypotheses. The direction to the center of the lake (presumably toward the highest intensity of reflected light or odor) from the west arena was 135°, and from the east arena it was 202.5°. If displaced turtles oriented toward these directions in their respective arenas, their primary orientation cue would likely have been light intensity, although olfactory cues could have been involved. If they maintained the same direction that they were headed when initially captured (SSW = 202.5° for the west arena; ESE = 112.5° in the east arena), then some mechanism of compass orientation must exist.

In May or June 2007, we individually marked 33 hatchlings (8–9 May) and 13 second-year yellow mud turtles (14 May–5 June) that were captured at the East Fence and released them into the west arena, and 25 hatchlings (9 May) and eight second-year turtles (14 May–6 June) captured at the West Fence and released into the east arena. Second-year turtles used in the experiment had all been captured and marked (at their respective fences) in May 2006 as hatchlings. Upon capture each turtle was individually marked with drops of fingernail polish on the plastral scutes. As soon as possible after capture (generally < 1 h), turtles were placed under moist native soil in a covered coffee can, carried to the appropriate arena, and released by burying them individually ca. 5 cm deep in the pre-moistened soil in a 0.5 m diameter area at the center (lowest point) of the arena. However, on a few extremely hot mornings, captured turtles were placed in covered coffee cans with 5 cm of moist soil and held inside a building until release in late afternoon of the day of capture. It was not practical to construct an individual arena for each hatchling release; however, given the small size of the turtles relative to the size of the arena, it is unlikely (though not impossible) that hatchlings followed the odors of other turtles. We checked the arenas twice a day, approaching them from random directions to minimize observer effects. Body mass, individual number, release and recapture date and time, and

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compass bearing on recapture were recorded for each turtle. Once a turtle was recaptured at an arena, either in a cup or along the fence, it was released on the lake side of the appropriate drift fence near where it was initially captured. One hatchling in the west arena, and two hatchlings and one second-year in the east arena were never recaptured prior to dismantling the fences on 14 June, and presumed to have died. Only 2.8 cm of rain fell during our experiment, all in light, brief afternoon or evening showers except during one larger rain event; 1.2 cm fell between 1500 and 2000 h on 29 May. Skies were mostly clear for most of every day, and hence cloud cover was not a significant climate variable.

Because of the nature of circular data, where 0° and 360° are equal (due north), the arithmetic mean of compass angles does not accurately represent the true mean direction. To determine the mean angle of orientation for each sample, and its difference from the predicted angles, we applied the circular statistics (*V*-test, with group correction factor for 16 compass sectors) outlined by Batschelet (1981:58).

Results

Displaced hatchlings were recaptured after a mean of 3.5 days (range, 0.5–11.5 d; median, 2.5 d; $n = 32$) at the west arena and 3.8 days (range, 1–11 d; median, 1 d; $n = 23$) at the east arena. Second-year turtles were recaptured after a mean of 2.4 days (range 0.5–7 d; median, 1 d; $n = 10$) at the west arena and 4.0 days (range 1–10.5 d; median, 2 d; $n = 7$) at the east arena.

The orientation direction of hatchlings in the west arena was nonrandom, averaged 121.3° (Fig. 3), and was significantly clustered in the direction of the lake (135°; $V = 0.49$; $u = 3.93$; $P < 0.0001$), as well as the direction to the site of original capture (120°; $V = 0.51$; $u = 4.04$; $P < 0.0001$), but not toward the expected (original) migration vector (202.5°; $V = 0.08$; $u = 0.62$; $P \gg 0.10$). Hatchlings in the east arena also moved nonrandomly, averaging 170.1°, and significantly oriented toward the lake (202.5°; $V = 0.36$; $u = 2.44$; $P < 0.01$), but not toward the expected migration vector (112.5°; $V = 0.23$; $u = 1.16$; $P > 0.10$), nor

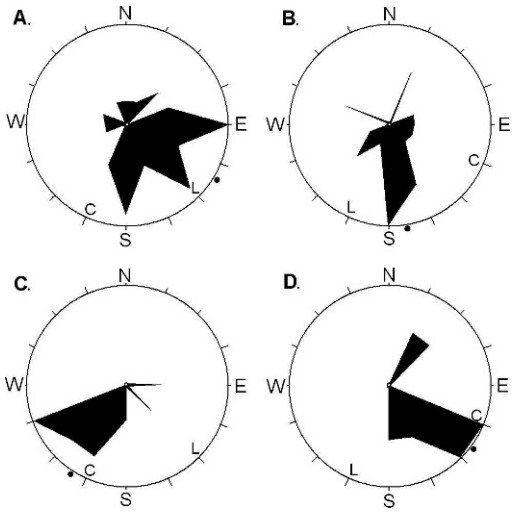


Fig. 3.—Recapture locations of hatchling (top) and second-year (bottom) yellow mud turtles in west (left) and east (right) experimental arenas. Mean bearing is indicated by solid black dot outside of circle. Directions to lake center (L) and for pre-capture migration bearing (C) are indicated. Maximum capture frequency for a compass bearing on each plot (i.e., scale of radius of circle) is 6 (A, B), 4 (C), and 2 (D).

toward the site of original capture (260°; $V = 0.001$; $u = 0.007$; $P > 0.10$). Thus, following displacement, hatchling mud turtles reoriented toward the water, which, because of the location of the west arena, happened to be in the same direction as the original capture site for that arena.

In contrast, second-year turtles in the west arena also oriented nonrandomly (mean, 212.9°) and tended to move in the direction of the expected original migration vector (202.5°; $V = 0.74$; $u = 3.76$; $P < 0.0001$), but not in the direction toward the water (135°; $V = 0.16$; $u = 0.80$ $P > 0.10$), nor in the direction of the original capture site (120°; $V = 0.04$; $u = 0.19$; $P > 0.10$). Second-year turtles in the east arena oriented nonrandomly (mean, 127.9°), and tended to move in their expected original vector (112.5°; $V = 0.77$; $u = 2.86$; $P < 0.005$), but not in the direction of the lake (202.5°; $V = 0.21$; $u = 0.79$; $P > 0.10$), nor in the direction of their original capture (260°; $V = -0.53$; $u = -1.99$; $P \gg 0.10$). These results demonstrate that second-year turtles maintained the same compass direction that they were moving before displacement (Fig. 3).

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Discussion

Orientation Cues

Emerging yellow mud turtles have a number of potential cues available to them: an elevated, darkened horizon (Anderson, 1958; Noble and Breslau, 1939; Salmon et al., 1992; Tuxbury and Salmon, 2005); a topography sloping downward as much as 45° toward the wetland (Burger, 1976; Salmon et al., 1992); direct visual site of water; increased light (especially reflected) over the wetlands (Anderson, 1958; Lohmann et al., 1997); increased humidity in low wetlands (Ehrenfield, 1979; Noble and Breslau, 1938); possible odors (from other turtles [Tuttle and Carroll, 2005] or from the wetlands [Graham et al., 1996; Hays et al., 2003; Salmon et al., 1992]); calling anurans (as for some amphibians: e.g., Pupin et al., 2007), and the Earth's geomagnetic field (Avens and Lohmann, 2003; Mathis and Moore, 1988). Under undisturbed conditions, hatchlings may integrate the information from these cues to direct their initial migration (Salmon et al., 1992), since there would only rarely be incongruity among them. However, our experimental arenas offered elevated horizons and increased slopes in all directions, offered no direct sight of water, were located beyond the upland habitat used for hibernation by other mud turtles, and were far enough away from the wetland that olfactory cues were probably minimal. Furthermore, experiments were conducted at a time when the only calling anuran in the wetland was the chorus frog (*Pseudacris* sp.), which rarely called during the day. Because yellow mud turtle emergence is diurnal (J. B. Iverson, R. L. Prosser and E. N. Dalton, personal observations), the only apparent cues remaining are variation in the intensity of reflected light, the position of the sun, and the Earth's magnetic field.

Following displacement, hatchling yellow mud turtles changed the direction of their migration to orient correctly toward the lake. They probably used the increased reflected light intensity over the lake to do this, although wetland-associated odors might have been involved. This result is consistent with other studies of hatchling dispersal from nest to water in marine and freshwater turtles (Ehrenfield, 1979; Lohmann et al., 1997; Salmon et al., 1992). Light cues are probably nearly always the most reliable cues for orientation toward water in hatchling turtles (but see Tuxbury and Salmon, 2005).

Our experiments also suggest that even in the absence of other cues, indirect light intensity alone may be sufficient to allow hatchling orientation (and hence migration) to the wetland. Unfortunately, we could not create arenas that isolated each one of the other possible cues, so we cannot conclude that other factors (e.g., geotaxis or odor) might also be sufficient by themselves to guide hatchlings to water. Examination of other potential cues that could override visual cues was also beyond the scope of this study. However, slope may be of particular interest in such studies (DeRosa and Taylor, 1982; Salmon et al., 1992), given the height of the adjacent sandhills from which the hatchlings emerge.

Compass Activation

Our data suggest that hatchling yellow mud turtles were orienting based primarily on cues emanating from the wetland during their initial migration to water. They may have an internal compass, but apparently lack the experience to use it. However, by their second year, a compass mechanism had been acquired (presumably through experience), and it either replaced or over-rode the cues used as hatchlings. Unfortunately, the mechanism behind that compass setting is still unknown (e.g., magnetic field, sun angle, etc.). More research will be necessary to determine when during their one to two months of aquatic activity hatchling yellow mud turtles set the compass for future orientation, when they lose (or reduce) the initial cue-based orientation ability, and what the mechanism is behind that compass.

We did not allow hatchlings access to water before displacement because the natural pattern of behavioral migration might have been disturbed. It is possible that a compass mechanism is ingrained only after a successful migration (i.e., after finding water). Testing hatchlings in arenas after access to water and at different times during their first summer of activity would be informative; however, first-year juveniles are nearly impossible to capture

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in the wetland. Displacement experiments of yellow mud turtles in other age classes would also be helpful in determining the ontogeny of orientation ability in these long-lived turtles. Nevertheless, our results differ significantly from those of Stapput and Wiltschko (2005), who found that hatchling olive ridley sea turtles acquired and used a compass setting after as few as 5 m migration toward the ocean.

Given historic changes in the Earth's magnetic field (Freake et al., 2006), the significant changes that have occurred to these wetlands in Nebraska over the last 12,000 years (Nicholson and Swinehart, 2005), and the short migration distances involved (compared to marine turtles), an innate magnetic compass may not be important to yellow mud turtle hatchlings. Experiments to test for the use of magnetic fields by nonmarine turtles are clearly needed. However, given the typical clarity of the skies at this site, the generally open horizons (with few trees), and the strictly diurnal movements of these turtles, a compass based on the sun (e.g., DeRosa and Taylor, 1982) may be the most likely explanation for their orientation ability after their initial migration to the wetland.

Adaptive Significance

Yellow mud turtles on the Great Plains are unusual among turtles in being highly adapted to ephemeral wetland habitats (Degenhardt and Christiansen, 1974). The precision of the migration paths of yellow mud turtles to and from the wetland, and the movement of all age classes of these turtles from permanent as well as temporary wetlands in mid-summer for estivation (Christiansen et al., 1985; Tuma, 2006; this study), suggest that seasonal migratory behavior is of significant adaptive advantage over remaining in the wetland. Clearly, the ability to migrate successfully between upland sites (where nesting and hibernation were successful) and ephemeral wetland sites (for feeding and mating) must be under intense selective pressure.

Phylogenetic Aspects

Kinosternon flavescens belongs to a clade of kinosternid turtles (including *K. baurii*, and *K. subrubrum*; Iverson, 1998; Serb et al., 2001) that are all semi-aquatic and migrate between wetlands and terrestrial estivation/hibernation sites (Burke et al., 1994; Burke and Gibbons, 1995; Christiansen and Gallaway, 1984; Christiansen et al., 1985; Iverson, 1989; Tuma, 2006; Wilson et al., 1999; Wygoda, 1979; this paper). Comparative phylogenetic studies of orientation behavior in at least this clade of kinosternids would be illuminating, particularly since they are apparently derived from much more highly aquatic ancestors (outgroups include *Sternotherus*, and *Staurotypus*; Iverson, 1998).

Furthermore, given that most available evidence suggests the existence of magnetic map navigational abilities in birds (e.g., Freake et al., 2006), alligators (Rodda, 1984), sea turtles (Bingham and Cheng, 2005; Freake et al., 2006; Luschi et al., 2007), and possibly box turtles (Mathis and Moore, 1988), this ability is possibly ancestral for at least the clade including all archosaurs and chelonians (Shedlock et al., 2007). Further study in nonmarine turtles and lepidosaurs could resolve whether these abilities are plesiomorphic for all Sauropsid reptiles or simply the result of convergence evolution in clades exhibiting long-distance migrations.

Conservation Aspects

Increasing evidence suggests that both marine (Naro-Maciel et al., 2007; among many others) and freshwater turtles (e.g., Freedberg et al., 2005; Valenzuela, 2001) are capable of natal homing, that is, returning to their natal nest sites later in life for feeding (e.g., Bowen et al., 2004) or breeding and nesting (Bowen and Karl, 1996). Considerable controversy surrounds the value of headstarting as a conservation strategy for turtles (e.g., Frazier, 1992). For example, sensitivity analyses based on demographic data suggest that protecting nests and hatchlings is not sufficient to reverse declines in populations (e.g., Heppell et al., 1996; but see Fordham et al., 2008); however, recapture data exist that suggest some effectiveness of the technique in supplementing populations and imprinting turtles to new nesting beaches (Shaver, 2005). Despite the controversy, the technique is still employed for freshwater turtles (Hauswaldt

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and Glenn, 2005; Mitrus, 2005; Spinks et al., 2003; among others). If the acquisition of compass orientation abilities during the first few weeks of life applies to other turtles besides yellow mud turtles (this study) and sea turtles (e.g., Stapput and Wiltschko, 2005), headstarting initiatives must account for this imprinting behavior (e.g., Fontaine and Shaver, 2005) or they may have significant negative fitness consequences.

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