

## **Orientation in Juveniles of a Semiaquatic Turtle, *Kinosternon Flavescens***

Authors: Iverson, John B., Prosser, Rebecca L., and Dalton, Evan N.

Source: *Herpetologica*, 65(3) : 237-245

Published By: The Herpetologists' League

URL: <https://doi.org/10.1655/07-090R1.1>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

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

JOHN B. IVERSON<sup>1</sup>, REBECCA L. PROSSER, AND EVAN N. DALTON

*Department of Biology, Earlham College, Richmond, IN 47374, USA*

**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 Wiltchko, 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; Lebbioni 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

<sup>1</sup> CORRESPONDENCE: e-mail, johni@earlham.edu

(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

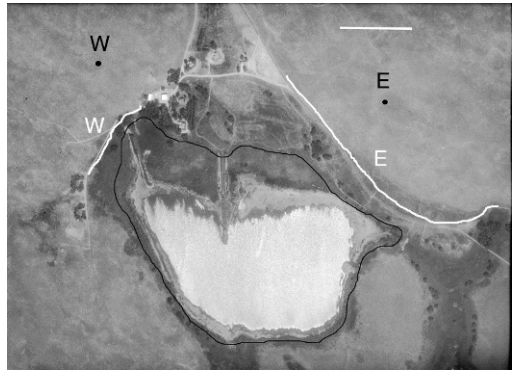


FIG. 1.—Aerial photo of Gimlet Lake study area in western Nebraska (north to top). Curved white lines indicate locations of East (E) and West (W) drift fences; solid black dots indicate east (E) and west (W) arenas. Black line encircling the wetland indicates the approximate shoreline during spring turtle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

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.

#### 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<sup>2</sup> area of rolling sand dunes now stabilized by mid-grass 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



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 =  $202.5^\circ$ ); those at the West Fence had moved at least 20 m (ca. ESE =  $112.5^\circ$ ).

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  $135^\circ$ , and from the east arena it was  $202.5^\circ$ . 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 =  $202.5^\circ$  for the west arena; ESE =  $112.5^\circ$  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

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  $0^\circ$  and  $360^\circ$  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  $121.3^\circ$  (Fig. 3), and was significantly clustered in the direction of the lake ( $135^\circ$ ;  $V = 0.49$ ;  $u = 3.93$ ;  $P < 0.0001$ ), as well as the direction to the site of original capture ( $120^\circ$ ;  $V = 0.51$ ;  $u = 4.04$ ;  $P < 0.0001$ ), but not toward the expected (original) migration vector ( $202.5^\circ$ ;  $V = 0.08$ ;  $u = 0.62$ ;  $P \gg 0.10$ ). Hatchlings in the east arena also moved nonrandomly, averaging  $170.1^\circ$ , and significantly oriented toward the lake ( $202.5^\circ$ ;  $V = 0.36$ ;  $u = 2.44$ ;  $P < 0.01$ ), but not toward the expected migration vector ( $112.5^\circ$ ;  $V = 0.23$ ;  $u = 1.16$ ;  $P > 0.10$ ), nor

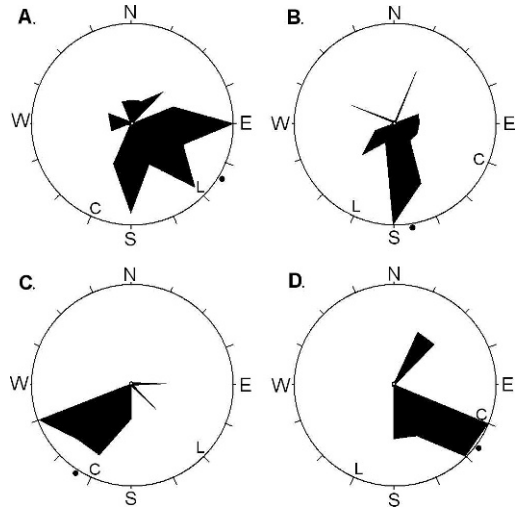


FIG. 3.—Recapture locations of hatchling (top) and second-year (bottom) yellow mud turtles in west (left) and east (right) experimental arenas. Mean bearing is indicated by solid black dot outside of circle. Directions to lake center (L) and for pre-capture migration bearing (C) are indicated. Maximum 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 ( $260^\circ$ ;  $V = 0.001$ ;  $u = 0.007$ ;  $P > 0.10$ ). 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,  $212.9^\circ$ ) and tended to move in the direction of the expected original migration vector ( $202.5^\circ$ ;  $V = 0.74$ ;  $u = 3.76$ ;  $P < 0.0001$ ), but not in the direction toward the water ( $135^\circ$ ;  $V = 0.16$ ;  $u = 0.80$ ;  $P > 0.10$ ), nor in the direction of the original capture site ( $120^\circ$ ;  $V = 0.04$ ;  $u = 0.19$ ;  $P > 0.10$ ). Second-year turtles in the east arena oriented nonrandomly (mean,  $127.9^\circ$ ), and tended to move in their expected original vector ( $112.5^\circ$ ;  $V = 0.77$ ;  $u = 2.86$ ;  $P < 0.005$ ), but not in the direction of the lake ( $202.5^\circ$ ;  $V = 0.21$ ;  $u = 0.79$ ;  $P > 0.10$ ), nor in the direction of their original capture ( $260^\circ$ ;  $V = -0.53$ ;  $u = -1.99$ ;  $P \gg 0.10$ ). These results demonstrate that second-year turtles maintained the same compass direction that they were moving before displacement (Fig. 3).



## 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

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 Wiltchko (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

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 Wiltchko, 2005), headstarting initiatives must account for this imprinting behavior (e.g., Fontaine and Shaver, 2005) or they may have significant negative fitness consequences.

**Acknowledgments.**—The managers and staff of the Crescent Lake National Wildlife Refuge provided permission for our work on the Refuge and allowed us to work in areas closed to the public. Scientific research permits were also provided by the Nebraska Game and Parks Commission. Support for the project was provided by Earlham College (the Matthews Fund and the Summer Science Initiative), the Howard Hughes Medical Institute, and the Joseph Moore Museum of Natural History. Comments provided by K. Adler, J. L. Christiansen, J. Tucker, and M. Salmon are greatly appreciated. We treated all turtles humanely and ethically.

#### LITERATURE CITED

- ANDERSON, P. K. 1958. The photic responses and water-approach behavior of hatchling turtles. *Copeia* 1958:211–215.
- AVENS, L., AND K. J. LOHMANN. 2003. Use of multiple orientation cues by juvenile loggerhead sea turtles, *Caretta caretta*. *Journal of Experimental Biology* 206:4317–4325.
- BATSCHLET, E. 1981. *Circular Statistics in Biology*. Academic Press, London, UK.
- BINGHAM, V. P., AND K. CHENG. 2005. Mechanisms of animal global navigation: Comparative perspectives and enduring challenges. *Ethology, Ecology, and Evolution* 17:295–318.
- BLEED, A., AND C. FLOWERDAY (Eds.). 1990. *An atlas of the Sandhills. Conservation and Survey Division, Institute of Agriculture and Natural Resources, Resource Atlas* 5a:1–265.
- BOWEN, B. W., AND S. A. KARL. 1996. Population structure, phylogeography, and molecular evolution. Pp. 29–50. In P. L. Lutz and J. A. Musick (Eds.), *The Biology of Sea Turtles*. CRC Press, Boca Raton, Florida, USA.
- BOWEN, B. W., A. L. BASS, S.-M. CHOW, M. BOSTROM, K. A. BJORNDAAL, A. B. BOLLEN, T. OKUYAMA, B. M. BOLKER, S. EPPERLY, E. LACASELLA, D. SHAVER, M. DODD, S. R. HOPKINS-MURPHY, J. A. MUSICK, M. SWINGLE, K. RANKIN-BARANSKY, W. TEAS, W. N. WITZELL, AND P. H. DUTTON. 2004. Natal homing in juvenile loggerhead turtles (*Caretta caretta*). *Molecular Ecology* 13:3797–3808.
- BURGER, J. 1976. Behavior of hatchling Diamondback Terrapins (*Malaclemys terrapin*) in the field. *Copeia* 1976:742–748.
- BURKE, V. J., AND J. W. GIBBONS. 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in a Carolina bay. *Conservation Biology* 9:1365–1369.
- BURKE, V. J., J. W. GIBBONS, AND J. L. GREENE. 1994. Prolonged nesting forays by Common Mud Turtles (*Kinosternon subrubrum*). *American Midland Naturalist* 131:190–195.
- BURKE, V. J., J. E. LOVICH, AND J. W. GIBBONS. 2000. Conservation of freshwater turtles. Pp. 156–179. In M. W. Klemens (Ed.), *Turtle Conservation*. Smithsonian Institution Press, Washington, D.C., USA.
- CARROLL, T., AND D. EHRENFIELD. 1978. Intermediate-range homing in the wood turtle, *Clemmys insculpta*. *Copeia* 1978:117–126.
- CHRISTIENSEN, J. L., AND B. J. GALLAWAY. 1984. Raccoon removal, nesting success, and hatchling emergence in Iowa turtles with special reference to *Kinosternon flavescens* (Kinosternidae). *Southwestern Naturalist* 29:343–348.
- CHRISTIENSEN, J. L., J. A. COOPER, J. W. BICKHAM, B. J. GALLAWAY, AND M. A. SPRINGER. 1985. Aspects of the natural history of the yellow mud turtle, *Kinosternon flavescens* (Kinosternidae) in Iowa: A proposed endangered species. *Southwestern Naturalist* 30:413–425.
- CONVERSE, S. J., J. B. IVERSON, AND J. A. SAVIDGE. 2005. Demographics of an ornate box turtle (*Terrapene ornata ornata*) population experiencing minimal human-induced disturbances. *Ecological Applications* 15:2171–2179.
- COSTANZO, J. P., J. B. IVERSON, M. F. WRIGHT, AND R. E. LEE. 1995. Cold hardiness and overwintering strategies of hatchlings in an assemblage of northern turtles. *Ecology* 76:1772–1785.
- DEGENHARDT, W. G., AND J. L. CHRISTIANSEN. 1974. Distribution and habitats of turtles in New Mexico. *Southwestern Naturalist* 19:21–46.
- DEROSA, C. T., AND D. H. TAYLOR. 1976. Sun-compass orientation in the painted turtle, *Chrysemys picta* (Reptilia, Testudines, Testudinidae). *Journal of Herpetology* 12:25–28.
- DEROSA, C. T., AND D. H. TAYLOR. 1980. Homeward orientation mechanisms in three species of turtles (*Trionyx spinifer*, *Chrysemys picta*, and *Terrapene carolina*). *Behavioral Ecology and Sociobiology* 7:15–23.
- DEROSA, C. T., AND D. H. TAYLOR. 1982. A comparison of compass orientation mechanisms in three turtles (*Trionyx spinifer*, *Chrysemys picta*, and *Terrapene carolina*). *Copeia* 1982:394–399.
- EHRENFIELD, D. W. 1979. Behavior associated with nesting. Pp. 417–434. In M. Harless and H. Morlock (Eds.), *Turtles: Perspectives and Research*. John Wiley and Sons, New York, New York, USA.
- EMLER, S. T. 1969. Homing ability and orientation in the painted turtle, *Chrysemys picta*. *Behaviour* 33:58–76.
- ERNST, C. H. 1970. Homing ability in painted turtle, *Chrysemys picta* (Schneider). *Herpetologica* 26:399–403.
- FONTAINE, C., AND D. SHAVER. 2005. Head-starting the Kemp's ridley sea turtle, *Lepidochelys kempi*, at the NMFS Galveston Laboratory, 1878–1992: A review. *Chelonian Conservation and Biology* 4:838–845.
- FORDHAM, D. A., A. GEORGES, AND B. W. BROOKS. 2008. Indigenous harvest, exotic pig predation and local persistence of a long-lived vertebrate: Managing a tropical freshwater turtle for sustainability and conservation. *Journal of Applied Ecology* 45:52–62.



- FRAZER, N. B. 1992. Sea turtle conservation and halfway technology. *Conservation Biology* 6:179–184.
- FREAKE, M. J., R. MUHEIM, AND J. B. PHILLIPS. 2006. Magnetic maps in animals: a theory comes of age? *Quarterly Review of Biology* 81:327–347.
- FREEDBERG, S., M. A. EWERT, B. J. RIDENHOUR, M. NEIMAN, AND C. E. NELSON. 2005. Nesting fidelity and molecular evidence for natal homing in the freshwater turtle, *Graptemys kohnii*. *Proceedings of the Royal Society B* 272:1345–1350.
- GERMANO, D. J., AND P. M. NIEUWOLT-DACANAY. 1999. *Terrapene ornata luteola* (Desert Box Turtle): Homing behavior. *Herpetological Review* 30:96.
- GIBBONS, J. W., AND M. H. SMITH. 1968. Evidence of orientation by turtles. *Herpetologica* 24:331–333.
- GOFF, M. D., M. SALMON, AND K. J. LOHMANN. 1998. Hatchling sea turtles use surface waves to establish magnetic compass direction. *Animal Behaviour* 55:69–77.
- GOULD, E. 1957. Orientation in box turtles, *Terrapene carolina* (Linnaeus). *Biological Bulletin* 112:336–348.
- GOULD, E. 1959. Studies on the orientation of turtles. *Copeia* 1959:175–176.
- GOURLEY, E. V. 1974. Orientation of the gopher tortoise, *Gopherus polyphemus*. *Animal Behaviour* 22:158–169.
- GRAHAM, T., A. GEORGES, AND N. MCELHINNEY. 1996. Terrestrial orientation by the eastern long-necked turtle, *Chelodina longicollis*, from Australia. *Journal of Herpetology* 30:467–477.
- HAUSWALDT, J. S., AND T. C. GLENN. 2005. Population genetics of the diamondback terrapin (*Malaclemys terrapin*). *Molecular Ecology* 14:723–732.
- HAYS, G. C., S. AKESSON, A. C. BRODERICK, F. GLEN, B. J. GODLEY, F. PAPI, AND P. LUSCHI. 2003. Island-finding ability of marine turtles. *Proceedings of the Royal Society of London* 270B(Supplement): S5–S7.
- HEPPELL, S. S., L. B. CROWDER, AND D. T. CROUSE. 1996. Models to evaluate headstarting as a management tool for long-lived turtles. *Ecological Applications* 6:556–565.
- IVERSON, J. B. 1989. The Arizona mud turtle *Kinosternon flavescens arizonense* (Kinosternidae) in Arizona and Sonora. *Southwestern Naturalist* 34:356–368.
- IVERSON, J. B. 1990. Nesting and parental care in the turtle, *Kinosternon flavescens*. *Canadian Journal of Zoology* 68:230–233.
- IVERSON, J. B. 1991. Life history and demography of the yellow mud turtle, *Kinosternon flavescens*. *Herpetologica* 47:371–393.
- IVERSON, J. B. 1998. Molecules, morphology, and mud turtle phylogenetics. *Chelonian Conservation and Biology* 3:113–117.
- LEBBORONI, M., AND G. CHELAZZI. 2000. Waterward orientation and homing after experimental displacement in the European Pond Turtle, *Emys orbicularis*. *Ethology, Ecology, and Evolution* 12:83–88.
- LOHMANN, K. J., AND C. M. F. LOHMANN. 1992. Acquisition of magnetic directional preference in loggerhead sea turtle hatchlings. *Journal of Experimental Biology* 190:1–8.
- LOHMANN, K. J., B. E. WITHERINGTON, C. M. F. LOHMANN, AND M. SALMON. 1997. Orientation, navigation, and natal beach homing in sea turtles. Pp. 107–136. *In* P. Lutz and J. Musick (Eds.), *The Biology of Sea Turtles*. CRC Press, Boca Raton, Florida, USA.
- LUSCHI, P., S. BENHAMOU, C. GIRARD, S. CICCIONE, D. ROOS, J. SUDRE, AND S. BENVENUTI. 2007. Marine turtles use geomagnetic cues during open-sea homing. *Current Biology* 17:126–133.
- MACNEIL, J. A., T. B. HERMAN, AND K. L. STANDING. 2000. Movement of hatchling Blanding's Turtles (*Emydoidea blandingii*) in Nova Scotia in response to proximity to open water: a manipulative experiment. *Chelonian Conservation and Biology* 3:611–617.
- MATHIS, A., AND F. R. MOORE. 1988. Geomagnetism and the homeward orientation of the box turtle, *Terrapene carolina*. *Ethology* 78:265–274.
- METCALF, A. L., AND E. METCALF. 1978. An experiment with homing in Ornate Box Turtles (*Terrapene ornata ornata* Agassiz). *Journal of Herpetology* 12:411–412.
- MITRUS, S. 2005. Headstarting in European pond turtles (*Emys orbicularis*): Does it work? *Amphibia-Reptilia* 26:333–341.
- MURPHY, G. 1970. Orientation of Adult and Hatchling Red-eared Turtles, *Pseudemys scripta elegans*. Ph.D. Dissertation, Mississippi State University, State College, Mississippi, USA.
- NARO-MACIEL, E., J. H. BECKER, E. H. S. M. LIMA, M. A. MARCOVALDI, AND R. DESALLE. 2007. Testing dispersal hypotheses in foraging green sea turtles (*Chelonia mydas*) of Brazil. *Journal of Heredity* 98:29–39.
- NICHOLSON, B. J., AND J. B. SWINEHART. 2005. Evidence of Holocene climate change in a Nebraska Sandhills wetland. *Great Plains Research* 15:45–67.
- NOBLE, G. K., AND A. M. BRESLAU. 1939. The senses involved in the migration of young fresh-water turtles after hatching. *Journal of Comparative Psychology* 25:175–193.
- PUPIN, F., R. SACCHI, A. GENTILLI, P. GALEOTTI, AND M. FASOLA. 2007. Discrimination of toad calls by smooth newts: Support for the heterospecific attraction hypothesis. *Animal Behaviour* 74:1683–1690.
- RODDA, G. H. 1984. The orientation and navigation of juvenile alligators: Evidence of magnetic sensitivity. *Journal of Comparative Physiology* 154A:649–658.
- SALMON, M., J. WYNEKEN, E. FRITZ, AND M. LUCAS. 1992. Seafinding by hatchling sea turtles: Role of brightness, silhouette and beachslope as orientation cues. *Behaviour* 122:56–77.
- SERB, J., C. PHILLIPS, AND J. B. IVERSON. 2001. Molecular phylogeny and biogeography of *Kinosternon flavescens* based on complete mitochondrial control region sequences. *Molecular Phylogenetics and Evolution* 18:149–162.
- SHAVER, D. J. 2005. Analysis of the Kemp's Ridley imprinting and headstart project at Padre Island National Seashore, Texas, 1978–88, with subsequent nesting and stranding records on the Texas coast. *Chelonian Conservation and Biology* 4:846–859.
- SHEDLOCK, A. M., C. W. BOTKA, S. ZHAO, J. SHETTY, T. ZHANG, J. S. LIU, P. J. DESCHAVANNE, AND S. V. EDWARDS. 2007. Phylogenomics of nonavian reptiles and the structure of the ancestral amniote genome. *Proceedings of the National Academy of Science* 104:2767–2772.
- SINKS, P. Q., G. B. PAULY, J. J. CRAYON, AND H. B. SHAFFER. 2003. Survival of the western pond turtle

- (*Emys marmorata*) in an urban California environment. *Biological Conservation* 113:257–267.
- STAPPUT, K., AND W. WILTSCHKO. 2005. The sea-finding behavior of hatchling olive ridley sea turtles, *Lepidochelys olivacea*, at the beach of San Miguel (Costa Rica). *Naturwissenschaften* 92:250–253.
- TUMA, M. W. 2006. Range, habitat use, and seasonal activity of the yellow mud turtle (*Kinosternon flavescens*) in northwestern Illinois: Implications for site-specific conservation and management. *Chelonian Conservation and Biology* 5:108–120.
- TUTTLE, S. E., AND D. M. CARROLL. 2005. Movements and behavior of hatchling wood turtles (*Glyptemys insculpta*). *Northeastern Naturalist* 12:331–348.
- TUXBURY, S. M., AND M. SALMON. 2005. Competitive interactions between artificial lighting and natural cues during seafinding by hatchling marine turtles. *Biological Conservation* 121:311–316.
- VALENZUELA, N. 2001. Genetic differentiation among nesting beaches in the highly migratory giant river turtle (*Podocnemis expansa*) from Colombia. *Herpetologica* 57:48–57.
- WILSON, D. S., H. R. MUSHINSKY, AND E. D. MCCOY. 1999. Nesting behavior of the Striped Mud Turtle, *Kinosternon baurii* (Testudines: Kinosternidae). *Copeia* 1999:958–968.
- WYGODA, M. L. 1979. Terrestrial activity of Striped Mud Turtles, *Kinosternon baurii* (Reptilia, Testudines, Kinosternidae) in west-central Florida. *Journal of Herpetology* 13:469–480.
- YEOMANS, S. R. 1995. Water-finding in adult turtles: Random search or oriented behavior? *Animal Behavior* 49:977–987.

Accepted: 25 July 2009

Associate Editor: Alicia Mathis