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Use of sun compass orientation during natal dispersal in Blanding's turtles: *in situ* field experiments with clock-shifting and disruption of magnetoreception

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Abstract

When hatchling freshwater turtles emerge from nests and first experience environmental stimuli, they primarily use visual cues to disperse toward nearby open horizons or far dark horizons. Within hours, hatchling Blanding's turtles (*Emydoidea blandingii*) develop compass mechanisms to maintain their headings when the initial dispersal targets become invisible. We captured hatchling Blanding's turtles during dispersal in natural habitat, attached a magnetic or non-magnet disk to each turtle, translocated them into an arena in a visually uniform field of corn, and measured their compass orientation (heading). Hatchlings from the magnet and no-magnet groups were evenly divided into two environmental chambers (6-h clock-shift or non-clock-shift) to create four experimental treatments. After 5 to 11 days hatchlings were re-released in the arena. If hatchlings used a time-compensated sun compass, then clock-shifting would cause a ~90° change in heading. If they used a geomagnetic compass, disruption of magnetoreception would cause wandering. If both compasses were used simultaneously or sequentially, we predicted a range of outcomes. All four treatment groups dispersed directionally during both trials, maintaining their prior headings in natural habitat except for the clock-shift treatment which changed heading ~90° as predicted. The ability of hatchlings to maintain prior headings despite the disruption of geomagnetism supports the absence, inactivity, or disregard of a geomagnetic compass. Only a time-compensated sun compass coupled with an internal clock was necessary and sufficient for hatchlings to maintain compass headings during natal dispersal when relocated from natural prairie habitat to a monoculture habitat with a relatively uniform visual horizon.

Significance statement

Individuals moving long distances (e.g., migrating birds or dispersing salamanders) often maintain their movement headings using compass orientation (i.e., a geomagnetic or time-compensated sun compass). When hatchling freshwater turtles emerge from underground terrestrial nests they initiate dispersal in search of wetlands primarily based on visual horizon cues. Because such cues often become obscured by uneven terrain or dense vegetation and because straight-line travel is more efficient and less risky, hatchlings soon develop a mechanism of compass orientation to maintain their dispersal headings. We disrupted their ability to use magnetoreception by attaching magnets to their shells, manipulated their sense of time-of-day with clock-shifting, and then monitored their dispersal in a visually uniform field of mature corn. Our results demonstrated that a sun compass was necessary and sufficient for hatchlings with dispersal experience to maintain their dispersal headings when natural environmental cues were not visible.

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Introduction

The concepts of landscape biology (Sumner et al. 2001; Wu 2006; Anderson et al. 2010) and core areas (Semlitsch and Jensen 2001; Crawford and Semlitsch 2007) combine to highlight the importance of short-distance and duration movements of individuals to population processes. Compared to strictly aquatic or terrestrial organisms, obligate use of more than one habitat to complete a life cycle can present a particularly challenging suite of problems for semi-aquatic organisms (Semlitsch and Bodie 2003; Anderson et al. 2010). For example, short-distance movements of semi-aquatic individuals can require a combination of spatial learning and compass orientation that guide movements between aquatic and terrestrial habitats in different seasons and during different life stages. Determining the variation in the phenology and spatial characteristics of movements of individuals in different age classes and in different situations can help reveal the ecological contexts of movements (Able 1980), and also reveal the role that early learning may have on spatial cognition (Congdon et al. 2015; Krochmal et al. 2015; Roth and Krochmal 2015).

Rapid learning is particularly important to naïve hatchling freshwater turtles (i.e., they have no previous exposure to environmental cues) when they emerge from terrestrial nests and confront a suite of problems related to orientation and dispersal toward wetlands or terrestrial overwintering sites (Butler and Graham 1995; Pappas et al. 2009). Because of their small body size, dispersing hatchlings often lose sight of visual environmental cues due to vegetation or uneven terrain but are able to maintain compass headings toward such targets (Noble and Breslau 1938; Anderson 1958; Pappas et al. 2009, 2013; Congdon et al. 2015). A hatchling's ability to maintain orientation and dispersal toward an obscured environmental target minimizes duration and distance of dispersal and the exposure to the risks of predators and abiotic extremes such as heat and dry conditions (Pappas et al. 2009; Congdon et al. 2011). However, even though dispersal distances of hatchling freshwater turtles from nests are relatively short (distances of 50 to 500 m and durations of hours to 3 days), individuals demonstrate partial compass navigation during their first hours of dispersal, and are able to maintain their headings with remarkable accuracy by the end of their first day of dispersal (Pappas et al. 2013; Congdon et al. 2015).

Field research on compass use is difficult to conduct because almost all field settings expose animals to a variety of environmental cues that can be the proximate causes of orientation. However, naïve hatchling Blanding's turtles (*Emydoidea blandingii*) in natural habitat dispersed directionally toward far dark horizons in natural habitat (Pappas et al. 2009), but primarily dispersed randomly in homogeneous monocultures of agricultural fields of mature soybeans or corn (Pappas et al. 2013; Congdon et al. 2015). The contrast in dispersal patterns of naïve hatchlings in natural habitat versus agricultural fields indicated that such fields provide no visual cues useful for initial orientation and dispersal and therefore provide a setting where the influences of environmental cues and compass orientation are not confounded (i.e., a location where the proximate causes of compass orientation could be examined outside the laboratory; Congdon et al. 2015).

Authors of field studies of adult and hatchling freshwater turtles in natural habitat have suggested that a time-compensated sun compass enabled adult and hatchling freshwater turtles to maintain their headings when environmental cues were not visible (DeRosa and Taylor 1978, 1982; Caldwell and Nams 2006; Pappas et al. 2009), but were not able to rule out use of a geomagnetic compass. Indeed, little is known about magnetoreception in freshwater turtles. Recent documentation that yearling snapping turtles (*Chelydra serpentina*) use a geomagnetic compass to orient in a laboratory setting (Landler et al. 2015) suggests that freshwater turtles may have the ability to use one or both compass types during dispersal as do other vertebrates (e.g., salamanders, sea turtles, and birds; Wiltschko and Wiltschko 1976, 2001; Wiltschko 1983; Wiltschko et al. 1987; Phillips and Moore 1992; Lohmann and Lohmann 1996; Avens and Lohmann 2003). When experienced hatchling Blanding's turtles (i.e., individuals captured during dispersal from nests in natural habitat) were released in a variety of novel locations and habitats, they maintained their prior headings thus demonstrating use of a compass mechanism (Pappas et al. 2009, 2013). In another study, Blanding's turtle hatchlings with magnets (strong enough to disrupt magnetoreception) attached to their anterior carapace retained their ability to maintain prior headings established in natural habitats when released in a field of mature corn. Because there are only two compass mechanisms known, the results provided evidence supporting the use of a sun compass (Congdon et al. 2015). However, at present, it is not known whether existence of a magnetic compass is widespread in freshwater turtles or whether freshwater turtle hatchlings use a sun or geomagnetic compass (simultaneously or conditionally) to maintain prior dispersal headings when orientation targets are not visible.

Our primary objective was to conduct a comparative and manipulative field experiment that would determine whether hatchling Blanding's turtles with previous dispersal experience maintain their orientations using a geomagnetic compass, a time-compensated sun compass, or both. The two key experimental manipulations were to attach disk magnets to the hatchlings to disrupt reception of geomagnetism and to expose them to a shifted photoperiod (i.e., clock-shift) to detect use of a time-compensated sun compass adjusted by their internal biological clock.

Control treatments were the attachment of aluminum disks and exposure to natural photoperiod. Manipulated and control individuals were subsequently released simultaneously in an experimental arena in a mature corn field. We tested the following predictions: (1) If a geomagnetic compass is used, then a magnet will cause the animal to wander unless it uses a sun compass simultaneously; (2) if a geomagnetic compass is not used, magnets will have no effect; (3) if a sun compass is used, clock-shifting will rotate their compass orientation and heading commensurately (unless obfuscated by simultaneous use of a geomagnetic compass). Four experimental treatments were generated by crossing two photoperiods (non-clock-shift and 6-h clock-shift) with the presence or absence of disruption of magnetoreception (non-magnet and magnet). Further, four patterns of experimental outcomes are possible depending on hatchling use of one or both compasses (Table 1).

Methods

Experimental arena

A circular arena (approximately 90-m diameter) was constructed each fall in 2012 and 2013 in a relatively level field of mature corn (approximately 2.5 m tall) located adjacent to prairie habitat used for nesting by female Blanding's turtles. The arena perimeter was constructed of solid aluminum flashing, 15 to 25 cm in height and buried 5 cm deep. As much of the arena fence as possible was placed in the spaces between rows to minimize damage to the corn. A compass was used to sight the location of 16 pitfall traps adjacent to the inside wall of the fence at intervals of 22.5° with flags marking smaller intervals between the traps.

Capture and preparation of hatchlings

During late August and early September of each year, we captured hatchlings while they were dispersing in a westerly direction from natural nests in an elevated sand dunes habitat bounded on the west side by a large wetland complex and riparian forest. The locations of the nests were not precisely known, so the durations and distances of their dispersal experience, and the resulting variation in compass development were unknown. However, knowledge of the location of the nesting habitat relative to the capture locations, coupled with the results of previous experiments on dispersal speed and compass orientation with hatchlings captured at this location (Pappas et al. 2009, 2013), allowed us to estimate that the majority were 1 to 2 days post-emergence and with well-developed compass orientation.

Hatchlings were transported to the laboratory (< 2 km away) and held in natural photoperiod lighting. We painted a unique number on each turtle and haphazardly assigned individuals to the magnet group or the non-magnet group. Magnets were neodymium disks (6.3 mm diameter and 1.5 mm thick, 330,900 micro Tesla (μT), part number D41-N52, K&J Magnetics, Inc.). Magnets or non-magnetic aluminum disks were adhered to the anterior carapace of hatchlings in the evening of the same day as capture. At 21 mm from the magnet (i.e., greater than the distance from the magnet to the head of a walking hatchling), flux densities were ~1000 μT, 20 times the mean geomagnetic field at the earth's surface (50 μT; Lanzerotti and Krimigis 1985). In laboratory tests, a compass needle always became fixed toward a disk magnet placed 25 mm away in any direction (Congdon et al. 2015).

Hatchlings were released in the center of the corn arena (first trial) the first or second morning after capture depending on weather; we conducted trials under only sunny or partly

Table 1 Four distinct patterns of predicted changes in dispersal heading between first and second arena trials depending on activity or inactivity (or absence) of sun and geomagnetic compasses. Each 2 × 2 pattern consists of four treatments as defined by photoperiod (non-clock-shift or 6-h clock-shift) and disruption of magnetoreception (non-magnet or magnet). Predictions assuming both compasses are active (upper-left quadrant) vary depending whether individuals use the compasses simultaneously or sequentially

Geomagnetic compass	Magnetoreception	Sun compass			
		Active		Inactive	
		Photoperiod			
		Non-clock-shift	Clock-shift	Non-clock-shift	Clock-shift
Active	Non-magnet	0°	− 90° to 0°	0°	0°
	Magnet	0° or random[a]	− 90° or random	random	random
Inactive	Non-magnet	0°	− 90°	0°	0°
	Magnet	0°	− 90°	0°	0°

[a] Random because a turtle with an active geomagnetic compass but bearing a disruptive magnet is expected to wander (non-linear path) because the perceived magnetic field is not stationary relative to the landscape

sunny conditions because, in our previous experiments involving both naïve and experienced hatchlings, trials occurring under cloudy skies resulted in little movement by hatchlings. We recaptured hatchlings at the arena fence, recorded their identities and compass headings, returned them to the laboratory, and haphazardly assigned them to one of two photoperiod chambers where they were held 5 to 11 days (depending on weather conditions) before being re-released in the corn arena (second trial). Both photoperiod chambers were illuminated with two 75-W fluorescent grow-lights suspended 2 m directly overhead. Chamber temperatures were ~20 °C and moist sand substrates with free water were provided. One chamber simulated the natural photoperiod (non-clock-shift); the other chamber's photoperiod was identical but 6 h earlier (clock-shift). By dividing the magnet and non-magnet groups into the two photoperiod groups, four experimental treatments were created.

Trial protocol

On each trial day, only one group of hatchlings was released at the center of the arena between 8:00 and 10:00 h when ambient air temperature was ~21 °C. Each group was composed of all first-trial hatchlings in the laboratory (hatchlings captured 1 or 2 days earlier) and all second-trial hatchlings that had been in the photoperiod chambers for at least 5 days). Each group including second-trial hatchlings consisted of approximately equal shares from all four treatments. During transport, non-magnet hatchlings were haphazardly placed in four compartments in a circular plastic container (38-cm diameter) and each compartment had a covered opening at ground level facing one of four opposite directions; magnet hatchlings were transported in small individual plastic containers to prevent magnet-to-magnet contact. To begin the trial, we placed the large container at the center of the arena, removed the covers, and up-ended the smaller containers nearby at 1-m intervals to prevent magnet-to-magnet contact. We patrolled the arena perimeter at intervals of ≤ 20 min to recapture the majority of turtles along the fence and approximately 10% in pitfall traps. Continuous patrol and use of pitfall traps reduced the potential for substantial movement of hatchlings along the fence. We recorded identity, time, and dispersal heading for each hatchling recaptured. At the arena fence, researchers were blind to the photoperiod treatment that was recorded earlier for each hatchling, whereas magnets and aluminum disks were painted different colors to assure correct identification of treatment upon capture.

Statistical analysis

Although we monitored the fence until the late afternoon of each trial, we excluded from the analysis six hatchlings (5%) that were not captured at the arena fence within 4 h of release in both the first and second trials. A small number of hatchlings were excluded because they had lost their magnet or aluminum disk. For the estimation of treatment effects, the response variable was the difference in compass heading between the pre-clock-shift trial and the post-clock-shift trial for each individual. All dispersal heading data were analyzed as circular data (Oriana Version 4). Within each treatment, we tested for non-random distributions using a Rayleigh test and tested for no change in dispersal heading using Moore's paired test. We tested for the significance of treatment effects using Watson's test. Because hatchlings within each daily group may have not behaved independently (e.g., by scent trailing other individuals) we also conducted a second-order analysis of daily group means. We used One-sample Hotelling tests to detect non-random distributions within each treatment and a Two-sample Hotelling test to estimate the significance of treatment effects. Second-order mean vectors were calculated as the addition of daily (group) mean vectors.

Results

The experienced hatchlings captured during their westerly dispersal from natural nests demonstrated a long-lasting compass sense and ability to maintain their prior headings after being relocated to the corn field arena. Hatchlings in all four treatment groups exhibited significant directionality in both trials. The influence of the clock-shift treatment was apparent in as few as 5 days, and non-clock-shift hatchlings were able to maintain their prior headings after spending up to 11 days in the photoperiod chambers. The only change in performance was a reduction in dispersal velocity correlated with duration of photoperiod treatment: hatchlings kept 5 or 6 days were not significantly slower during their second trial (mean 100 min, first trial; mean 111 min, second trial; paired $t_{47} = 1.98$, $P > 0.05$), whereas animals kept 10 or 11 days were significantly slower (mean 97 min, first trial; mean 230 min, second trial; paired $t_{33} = 14.90$, $P < 0.001$). Hatchlings that bore magnets did not differ in dispersal speed from non-magnet hatchlings in both the 5-to-6-day group (mean 111 min, magnet; mean 114 min, non-magnet; $t_{28,20} = 1.19$, $P = 0.74$) and the 10-to-11-day group (mean 228 min, magnet; mean 233 min, non-magnet; $t_{21,11} = 0.33$, $P = 0.94$). However, regardless of dispersal speed of hatchlings, duration of photoperiod treatment had no effect on fidelity of headings in both clock-shifted and non-clock-shifted groups (Fig. 1).

During their first trial, experienced hatchlings were non-randomly directional and the mean dispersal headings of hatchlings in the both the magnet and non-magnet groups were not significantly different (mean magnet 292°, mean non-magnet 285°; Watson's $U^2_{48,54} = 0.042$, $P > 0.50$) and consistent with the westerly headings in previous experiments (Congdon et al. 2015). During the second trial, the presence of magnets did not influence change in heading in either
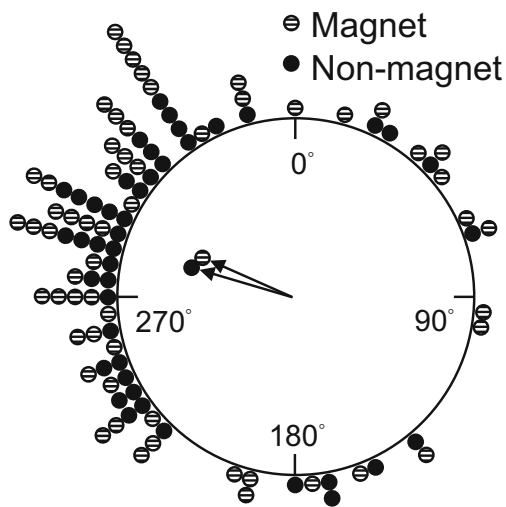
Fig. 1 Headings of hatchlings in magnet and non-magnet treatments during first trial, prior to photoperiod treatment. Each circle is an individual hatchling. Arrows indicate mean heading and length of vector (r). Groups were each significantly directional (magnet $r = 0.51$, Rayleigh's $Z = 15.0$, $P < 0.001$, $n = 58$, mean $= 292°$, SE $= 9.7°$; non-magnet $r = 0.59$, Rayleigh's $Z = 15.1$, $P < 0.001$, $n = 44$, mean $= 285°$, SE $= 9.3°$) but not different in mean orientation (Watson's $U^2 = 0.042$, $P > 0.50$)

photoperiod treatment (clock-shift, Watson's $U^2_{21,27} = 0.06$, $P > 0.50$; non-clock-shift, Watson's $U^2_{23,31} = 0.03$, $P > 0.50$; Table 2). Therefore, we pooled the data from hatchlings with magnets and non-magnets for subsequent analysis. In both the clock-shift and non-clock-shift treatments, the distributions of differences in headings were non-random (Rayleigh tests, both $P < 0.001$). Hatchlings in the non-clock-shift treatment did not change heading (mean difference 2.1°, SE 7.2°, Moore's $R'_{54} = 0.81$, $P > 0.10$), whereas hatchlings in the

clock-shift treatment exhibited a significant difference in heading (mean − 109.3°, SE 8.3°, Moore's $R'_{48} = 1.75$, $P < 0.001$). The effect of clock-shifting was significant (Watson's $U^2_{48,54} = 1.38$, $P < 0.001$; Table 2, Fig. 2a). The pattern of results matches the lower-left quadrant of Table 1, indicating the use of a sun compass but not a geomagnetic compass.

A second-order analysis of daily group means produced the same pattern of results as the analysis of individuals. Distributions of differences in hatchling compass heading were non-random for both photoperiod treatments (Table 2, Fig. 2b). The effect of a 6-h clock-shift was a mean change in heading of − 95.5° that was significantly different from the 2.6° difference in heading of individuals exposed to a natural photoperiod (Two-sample Hotelling $F = 18.5$, $P < 0.001$; Fig. 2b). In combination, the results are concordant with the first-order analysis: the 6-h advance in photoperiod caused the animals to alter their heading as predicted by sole use of a sun compass.

Data availability statement The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Discussion

Prior research demonstrated Blanding's turtle hatchlings emerging from natural nests develop partial compass orientation within the first 2 hours of dispersal and within the first day fully develop the ability to accurately maintain their initial headings in natural habitat and crop fields when environmental cues were obscured (Pappas et al. 2013; Congdon et al.

Table 2 All treatment groups maintained significant directionality during first and second trials (Rayleigh tests). Differences in mean heading between first and second arena trials were not affected by the disruption of magnetoreception by magnets but were significantly affected by clock-shifting (Watson tests). The differences in dispersal

heading caused by clock-shifting (first order, 109.3°, Fig. 2; second order, 95.5°, Fig. 3) was approximately equal to the change in the sun azimuth for a 6-h period beginning at the time of day and latitude of our trials (see Fig. 3 for explanation)
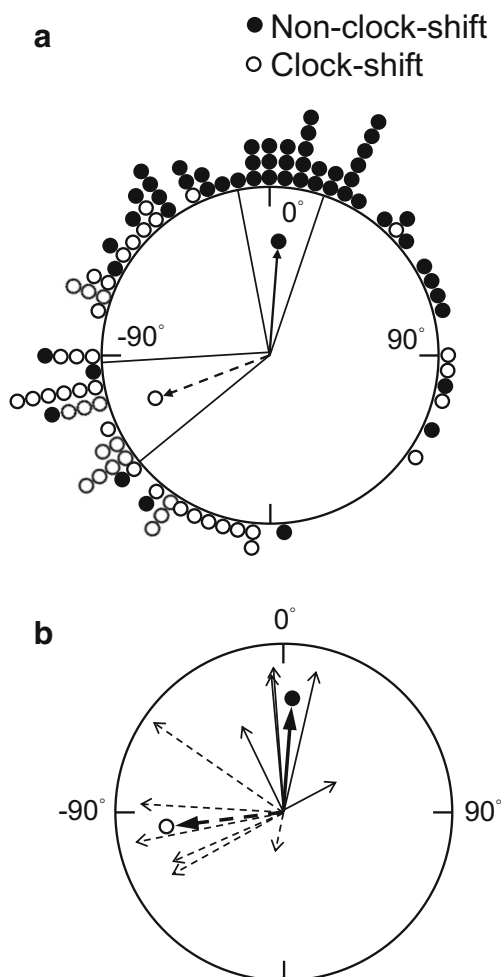
Experimental treatment		Difference in heading (degrees)				Directionality test		Treatment effect test	
Internal clock	Magnetoreception								
First-order analysis		n	Mean	SE	r	Rayleigh's Z	P	Watson's U^2	P
Clock-shift	Non-magnet	21	− 94.2	12.8	0.65	7.8	< 0.001		
Clock-shift	Magnet	27	− 119.8	10.4	0.61	11.5	< 0.001	0.06	> 0.50
Non-clock-shift	Non-magnet	23	− 3.4	10.9	0.66	10.1	< 0.001		
Non-clock-shift	Magnet	31	6.3	9.5	0.66	13.5	0.013	0.03	0.50
Clock-shift	Pooled	48	− 109.3	8.3	0.62	18.3	< 0.001		
Non-clock-shift	Pooled	54	2.1	7.2	0.66	23.5	< 0.001	1.38	< 0.001
Second-order analysis						Hotelling one-sample F	P	Hotelling two-sample F	P
Clock-shift	Pooled	6	− 95.5	20.3	0.81	10.4	0.026		
Non-clock-shift	Pooled	5	2.6	19.0	0.87	10.4	0.045	18.53	< 0.001

Fig. 2 a Difference in heading between first and second trials of individual hatchlings in non-clock-shift (filled circles) and clock-shift (open circles) treatments (magnet and non-magnet treatment data pooled). Lines are vector 95% confidence intervals. Photoperiod treatment groups were each significantly directional and differed significantly (rows five and six, Table 2). Vectors were not different than as predicted assuming the operation of a time-compensated sun compass and the absence of an active geomagnetic compass (lower-left quadrant, Table 1). **b** Second-order analysis of difference in heading between first and second trials in non-clock-shift (solid vectors) and clock-shift treatments (dashed vectors). Light vectors are daily means; bold vectors are grand means. Both treatment groups were significantly directional and different (see second-order statistics, Table 2)

2015). Straight-line travel toward a dark horizon can reduce risks associated with overland travel by reducing the distance and duration of movements to suitable aquatic or overwintering sites. Optimal foraging models of dispersal in fragmented landscapes indicate that the most efficient and least risky way to utilize habitat patches is through straight-line movements (Pyke 1984; Van Dyck and Baguette 2005). The use of a sun compass or a geomagnetic compass have both been suggested as mechanisms that allow adult freshwater turtles to maintain their orientation when displaced laterally to novel locations (Caldwell and Nams 2006; Iverson et al. 2009; Pappas et al. 2009). However, data from field studies

are difficult to interpret in relation to compass orientation because it is difficult to eliminate the influence of environmental cues (but see Congdon et al. 2015).

The interpretation of our statistical results assumes independence of hatchling behavior. Because the hatchlings experienced arena trials in groups, a reasonable question arises on whether scent trailing occurs. We have two lines of evidence that such behavior does not occur. First, the second-order analysis (treating each daily group as a single datum to avoid any potential non-independence of hatchlings in the same arena trial) results produced the same conclusions as the first-order analysis (see Results and Table 2). If scent trailing occurred, then trial-to-trial variation would be much greater than we observed. Secondly, in our previous papers on orientation of naïve hatchlings (those with no dispersal experience and without any exposure to light prior to the arena trial), we found that hatchling Blanding's turtles and snapping turtles dispersed directionally when visual environmental cues were available. However, when naïve hatchlings were released in crop fields that provide no visual dispersal cues (mature soybean and corn fields), they dispersed randomly (a result that does not support scent trailing). If scent trailing occurs, it should begin at the nest, rather than being suggested by dispersal trails that converge some distance from nests (as suggested by Butler and Graham (1995) for Blanding's turtles and Tuttle and Carroll (2005) for wood turtles), and hatchlings that we tracked with fluorescent powder left trails that converged and then diverged (Pappas et al. 2009). A basic issue with the costs and benefits of scent trailing by naïve hatchlings is that one individual following another would have to be based on a high probability that the leader was dispersing in the correct direction (Pappas et al. 2009).

Redundant use of sun and geomagnetic compasses has been reported in vertebrate taxa including sea turtles (Wiltschko and Wiltschko 1996; Johnsen and Lohmann 2008). The existence of a geomagnetic compass in freshwater turtles was only recently documented in snapping turtles (*C. serpentina*; Landler et al. 2015), suggesting that it may exist in Blanding's turtle and other freshwater turtles. Hatchlings with and without magnets exhibited remarkable ability to maintain their prior headings when released in a mature corn field, as did those in the non-clock-shift treatment. In contrast, clock-shifting caused changes of −96° (first-order analysis) and −109° (second order), supporting the prediction of −90° for a 6-h advance in photoperiod (Table 2; Fig. 2). Our results and those of Congdon et al. (2015) support the hypothesis that the sun compass is necessary and sufficient for compass orientation of hatchling Blanding's turtles during natal dispersal and that the geomagnetic compass is either absent, inactive, or if active is disregarded by hatchlings.

The accuracy in maintaining prior headings in the arena trials by the experienced hatchlings used in our experiments indicates

that they had fully developed sun compass mechanisms. However, it is possible that magnetoreception and a magnetic reference were temporarily involved in the development of the sun compass. However, independent development of a sun compass during early dispersal without involvement of magnetoreception is the more parsimonious explanation for the short time it takes to fully develop a sun compass. It will take future research specifically designed to discern whether magnetoreception augments the early development of a sun compass by hatchlings during the first hours of dispersal.

In a laboratory experiment by Mora et al. (2004), magnetoreception by pigeons of a magnetic field anomaly was blocked by the attachment of neodymium magnets to their beaks, but only temporarily. After about 8 days, the pigeons recovered their magnetoreceptive ability despite the magnets intact. Their results cause caution in the interpretation of experiments like ours that employ magnets to disrupt magnetoreception. But, although some of our hatchlings bore magnets for as many as 11 days, recovery of magnetoreception (*sensu* Mora et al. 2004) would have resulted in magnet hatchlings in the clock-shift treatment to exhibit a smaller difference in heading than the non-magnet hatchlings; however, the differences in headings were similar for both groups (Table 2). Further, recovery may occur when a magnet position is fixed relative to the magnetoreceptive tissue (e.g., the beak in pigeons), but not when magnets are not fixed relative to the magnetoreceptive tissue (i.e., the magnet on the anterior carapace is not fixed in relation to the head of the turtle).
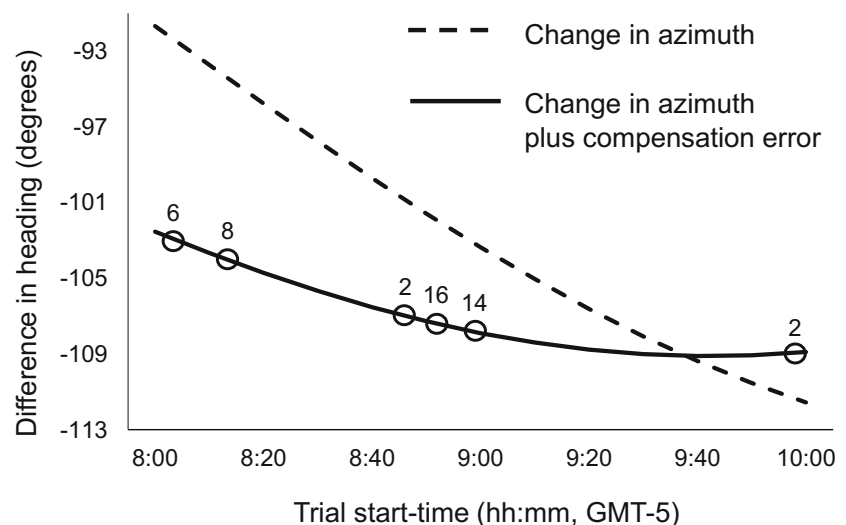
The prediction of a 90° change in heading caused by a 6-h clock-shift is intuitive but incorrect because, at the latitude and dates of our trials, the sun's azimuth moves 92° to 112° in 6 h, depending on time of day; the azimuth moves more quickly at mid-day than in the morning or the evening. Further, if time-compensation has evolved to attain straight-line travel, then clock-shifted hatchlings would err, veering left in the morning (over-compensation) and veering right later in the day (under-compensation). For the six trials we conducted involving clock-shifted hatchlings, the expected mean change in dispersal heading was − 106° (Fig. 3). We suggest that in future experiments involving clock-shifted animals, more-accurate predictions of change in heading will account for the time of day of the trial and for rate of change in azimuth anticipated by the animal.

A geomagnetic compass would seem to be more constant and reliable than the use of solar cues (the sun itself or the pattern of polarized light in the sky; Phillips and Moore 1992), because geomagnetism (1) is available at all times, (2) is relatively constant over short distances (Wyeth 2010), and (3) does not require coordination with an internal circadian clock. Although use of geomagnetism would allow hatchling dispersal at night to avoid excessive heat and desiccation, it would result in exposure to nocturnal predators. Hatchling Blanding's turtles in our study use only solar cues to maintain dispersal headings.

Previous studies on naïve hatchling freshwater turtles have shown that even a brief dispersal experience in a field arena (dispersal distance of 50 m and duration of 45 to 75 min) resulted in partial development of compass orientation and moderate ability to replicate headings in crop-field arenas (Pappas et al. 2013; Congdon et al. 2015). Our observations show hatchling Blanding's turtles with more extensive dispersal experience possess well-developed compass orientation (a mechanism that endured an 11-day holding period), and they use only a solar compass to maintain prior headings with remarkable accuracy when translocated into an arena located in a visually uniform corn field.

Fig. 3 Predicted change in dispersal heading accounting for actual azimuth change and mis-compensation by clock-shifted hatchlings depending on trial start time. The 6-h change in sun azimuth depends on trial start time (dashed line); additional change is caused by hatchlings over-compensating for a slowly changing morning azimuth (veering left) in expectation of a faster mid-day azimuth (solid line). The mean change for the six trials of clock-shifted hatchlings (circles) weighted by number of hatchlings (numerals) was calculated as − 106°

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The study was conducted under permits (13808 and 15422) from Richard Baker, Jaime Edwards, Gary Nelson, and Don Ramsden of the Minnesota Department of Natural Resources, and permit 2007-17R from Richard Biske of The Nature Conservancy.

The methods of care and use for this study were approved by the Institutional Animal Care and Use Committee at Minnesota State University.

References

Able KP (1980) Mechanisms of orientation, navigation and homing. In: Gauthreaux SA Jr (ed) Animal migration, orientation, and navigation. Academic Press, New York, pp 283–373

Anderson PK (1958) The photic responses and water-approach behavior of hatchling turtles. Copeia 1958:211–215

Anderson CD, Epperson BK, Fortin MJ, Holderegger R, James P, Rosenberg M, Scribner KT, Spear S (2010) Considering spatial and temporal scale in landscape-genetic studies of gene flow. Mol Ecol 19:3565–3575

Avens L, Lohmann KJ (2003) Use of multiple orientation cues by juvenile loggerhead sea turtles (*Caretta caretta*). J Exp Biol 206:4317–4325

Butler BO, Graham TE (1995) Early post-emergent behavior and habitat selection in hatchling Blanding's turtles, *Emydoidea blandingii*, in Massachusetts. Chelonian Conserv Bi 1:187–196

Caldwell IR, Nams VO (2006) A compass without a map: tortuosity and orientation of eastern painted turtles (*Chrysemys picta picta*) released in unfamiliar territory. Can J Zool 84:1129–1137

Congdon JD, Pappas MJ, Brecke BJ, Capps JD (2011) Conservation implications of initial orientation of naïve hatchling snapping turtles (*Chelydra serpentina*) and painted turtles (*Chrysemys picta belli*) dispersing from experimental nests. Chelonian Conserv Bi 10:42–53

Congdon JD, Pappas MJ, Krenz JD, Brecke BJ, Schlenner MA (2015) Compass orientation during dispersal of freshwater hatchling snapping turtles (*Chelydra serpentina*) and Blanding's turtles (*Emydoidea blandingii*). Ethology 120:1–10

Crawford JA, Semlitsch RD (2007) Estimation of core terrestrial habitat for stream-breeding salamanders and delineation of riparian buffers for protection of biodiversity. Conserv Biol 21:152–158

DeRosa CT, Taylor DH (1978) Sun-compass orientation in the painted turtle, *Chrysemys picta* (*Reptilia*, *Testudines*, *Testudinidae*). J Herpetol 12:25–28

DeRosa CT, Taylor DH (1982) A comparison of compass orientation mechanisms in three turtles (*Trionyx spinifer*, *Chrysemys picta*, *and Terrapene carolina*). Copeia 1982:394–399

Iverson JB, Prosser RL, Dalton EN (2009) Orientation in juveniles of a semiaquatic turtle *Kinosternon flavescens*. Herpetology 65:237–245

Johnsen S, Lohmann KJ (2008) Magnetoreception in animals. Phys Today 61:29–35

Krochmal AR, Roth TC Jr, Rush S, Wachter K (2015) Turtles outsmart rapid environmental change: the role of cognition in navigation. Commun Integr Biol 8:e1052922

Landler L, Painter MS, Youmans PW, Hopkins WA, Phillips JB (2015) Spontaneous magnetic alignment by yearling snapping turtles: rapid association of radio frequency dependent pattern of magnetic input with novel surroundings. PLoS One 10:e0124728

Lanzerotti LJ, Krimigis SM (1985) Comparative magnetospheres. Phys Today 38:25–34

Lohmann KJ, Lohmann CM (1996) Detection of magnetic field intensity by sea turtles. Nature 380:5–61

Mora CV, Davison M, Wild JM, Walker MM (2004) Magnetoreception and its trigeminal mediation in the homing pigeon. Nature 432:508–511

Noble GK, Breslau AM (1938) The senses involved in the migration of young fresh-water turtles after hatching. J Comp Psychol 25:175–193

Pappas MJ, Congdon JD, Brecke BJ, Capps JD (2009) Orientation and dispersal of hatchling Blanding's turtles (*Emydoidea blandingii*) from experimental nests. Can J Zool 87:755–766

Pappas MJ, Congdon JD, Brecke BJ, Freedberg S (2013) Orientation of freshwater hatchling Blanding's (*Emydoidea blandingii*) and snapping turtles (*Chelydra serpentina*) dispersing from experimental nests in agricultural fields. Herpetol Conserv Biol 8:385–399

Phillips JB, Moore FR (1992) Calibration of the sun compass by sunset polarized light patterns in a migratory bird. Behav Ecol Sociobiol 31:189–193

Pyke GH (1984) Optimal foraging theory: a critical review. Annu Rev Ecol Syst 15:523–575

Roth TC, Krochmal AR (2015) The role of age-specific learning and experience for turtles navigating a changing landscape. Curr Biol 25:333–337

Semlitsch RD, Bodie JR (2003) Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conserv Biol 17:1219–1228

Semlitsch RD, Jensen JB (2001) Core habitat, not buffer zone. Natl Wetl Newsl 23:5–11

Sumner J, Rousset F, Estoup A, Moritz C (2001) 'Neighbourhood' size, dispersal and density estimates in the prickly forest skink (*Gnypetoscincus queenslandiae*) using individual genetic and demographic methods. Mol Ecol 10:1917–1927

Tuttle SE, Carroll DM (2005) Movements and behavior of hatchling wood turtles (*Glyptemys insculpta*). Northeast Nat 12:331–348

Van Dyck H, Baguette M (2005) Dispersal behaviour in fragmented landscapes: routine or special movements? Basic Appl Ecol 6:535–545

Wiltschko W (1983) Compasses used by birds. Comp Biochem Phys A 76:709–717

Wiltschko W, Wiltschko R (1976) Interrelation of magnetic compass and star orientation in night-migrating birds. J Comp Physiol 109:91–99

Wiltschko W, Wiltschko R (1996) Magnetic orientation in birds. J Exp Biol 199:29–38

Wiltschko R, Wiltschko W (2001) Clock-shift experiments with homing pigeons: a compromise between solar and magnetic information? Behav Ecol Sociobiol 49:393–400

Wiltschko W, Wiltschko R, Keeton WT, Brown AI (1987) Pigeon homing: the orientation of young birds that had been prevented from seeing the sun. Ethology 76:27–32

Wu J (2006) Landscape ecology, cross-disciplinarity, and sustainability science. Landsc Ecol 21:1–4

Wyeth RC (2010) Should animals navigating over short distances switch to a magnetic compass sense? Front Behav Neurosci 4:42