ORIENTATION OF FRESHWATER HATCHLING BLANDING'S (EMYDOIDEA BLANDINGII) AND SNAPPING TURTLES (CHELYDRA SERPENTINA) **DISPERSING FROM EXPERIMENTAL NESTS IN AGRICULTURAL FIELDS**

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Abstract.—Tilled crop fields and natural nesting areas of many freshwater turtles have common characteristics that attract nesting females, but as some crops mature, their canopies block access to natural environmental cues used by hatchlings during orientation and dispersal from nests. We examined orientation of 417 naïve and 232 experienced hatchling Blanding's Turtles (Emydoidea blandingii) and Snapping Turtles (Chelydra serpentina) during dispersal from experimental nests in three 60-m square arenas located in soybean and corn fields or by tracking re-located experienced hatchlings in a corn field at Weaver Dunes, Minnesota, USA. For both species, orientation patterns of naïve hatchlings in crop fields were primarily random (indicating no environmental cues were available) and secondarily bimodal in both directions of crop row alignment (a dispersal pattern consistent with following paths of least resistance). In contrast to naïve individuals, dispersal patterns of natural-experienced hatchling Blanding's Turtles were non-random, not in the direction of crop row alignment, and in the directions they had been moving prior to being released in crop fields. Hatchling Blanding's and Snapping Turtles with 45-150 minutes dispersal experience at different times of day in a prairie arena were able to disperse directionally when rereleased in a corn plot, a result that supports rapid development of a compass for maintaining headings when targets are not visible. Morning- and afternoon-experienced hatchling Blanding's Turtles dispersed in different directions in a corn plot and in a different direction or pattern (random versus directional) from their previous dispersal in the prairie arena. The results of our study indicate that mature crop canopies that block access to natural environmental cues used for dispersal from nests pose more substantial orientation problems for naïve hatchlings than for experienced hatchlings that are able to use a compass to maintain dispersal headings when environmental cues are not available.

Key Words.—Chelydra serpentina; compass, crop fields; dispersal from nests; Emydoidea blandingii; hatchling freshwater turtles; orientation

INTRODUCTION

Selection of a nest site is one of the last components of reproductive investment of female freshwater turtles that determines the biophysical conditions necessary for successful embryo development. In addition, location of the nest determines the suite of environmental cues available to hatchlings as they emerge from nests and initiate orientation and dispersal (Noble and Breslau 1938; Anderson 1958; Iverson et al. 2009; Pappas et al. 2009). Because natural nesting areas of freshwater turtles and tilled agriculture fields have many characteristics in common (e.g., sparse vegetation cover and loose, well-drained soil), nesting females are attracted to crop fields that represent a large and occur between mid-September and late October growing category of human disturbed areas. For (Thiesse, K., Corn, soybean harvest progressing

example, 169 million acres were planted in soybeans and corn in the United States in 2007, an increase of about 23 million acres over recent years (2007 Prospective Plantings report, National Agricultural Statistics Service, U.S. Department of Agriculture).

From the time female turtles select nest sites in crop fields and hatchlings emerge from nests, subsequent growth of dense and tall monocultures (e.g., soybean, corn, and other grains) dramatically alters the characteristics of pre-harvest fields. The majority of fall hatchling emergence from nests by freshwater turtles in the northern hemisphere occurs from mid-August through late-September (Carroll and Ultsch 2007; Baker 2008). Soybean and corn harvests

rapidly; Corn and Soybean Digest, CSD Blogs and Opinions, October 2010.). Therefore, some hatchlings emerge from nests where canopies of soybean and corn fields block visual access to the typical environmental cues used for orientation and dispersal. In addition, hatchlings in crop fields are presented with relatively uniform, near-horizon cues in all directions, a situation equivalent to having no dispersal target. Hatchlings with previous dispersal experience in natural habitats may also face similar problems if their dispersal route requires crossing mature crop fields.

Although previous studies of marine turtles indicate that visual cues are the most important sensory mechanism used by dispersing hatchlings (Mrosovsky and Carr 1967; Ehrenfeld 1979; Lohmann and Lohmann 2003), а combination of visual, olfactory, and magnetic cues are also used by hatchling sea turtles to move from nests to water (Fuentes-Farias et al. 2011). In addition to vision (Noble and Breslau 1938, Pappas et al. 2009; Congdon et al. 2011), other mechanisms used during orientation and dispersal of freshwater turtles include geotaxis, odors and humidity gradients associated with wetlands, sounds created by running water or calling frogs (Noble and Breslau 1938; Burger 1976; Butler and Graham 1995; Tuttle and Carroll 2005), and light reflected off of water (i.e., polarized light; Iverson et al. 2009). Social facilitation (i.e., naive hatchings following other naïve hatchlings during dispersal from nests) has also been suggested to occur in freshwater turtles (Butler and Graham 1995; Tuttle and Carroll 2005), but the value of that mechanism has been questioned (Pappas et al. 2009). Two types of compasses (sun and magnetic) have been suggested as mechanisms allowing experienced hatchlings to maintain headings when dispersal targets are obscured (Pappas et al. 2009; Iverson et al. 2009).

Regardless of which cues or compasses are used by hatchling freshwater turtles, both the durations and distances of terrestrial dispersal should decrease when hatchlings move directly

toward wetlands or terrestrial overwintering sites. Shortened dispersal times and distances should reduce risks associated with: (1) not finding wetlands or suitable overwintering sites; (2) exposure to predators; (3) desiccation; (4) overheating; (5) farm machinery; (6) road traffic; and (7) trap hazards (Gibbs and Shriver 2002; Steen and Gibbs 2004; Saumure et al. 2007; Castellano et al. 2008; Tingley et al. 2009).

Blanding's Turtles (Emydoidea blandingii) are designated as Threatened or Endangered in many states and provinces within its range in the United States and Canada; whereas, Snapping Turtles (*Chelydra serpentina*) are designated as a Species of Concern in some states and species of special concern in Canada. Hatchling Blanding's Turtles orient toward far dark horizons (Pappas et al. 2009) and hatchling Snapping Turtles orient toward near open horizons (Noble and Breslau 1938; Congdon et al. 2011). Because Blanding's and Snapping turtles orient toward different horizons and both species frequently nest in or near agricultural fields, those fields may present different types of problems for hatchlings dispersing from nests.

The primary goal of this study was to determine whether the essentially closed canopies of mature crop fields pose problems for naïve (i.e., no previous exposure to environmental cues) and experienced (i.e., previous exposure to environmental cues; Table 1) hatchling Blanding's and Snapping Turtles dispersing from nests. We tested whether: (1) the target/compass relationship of naturalexperienced hatchling Blanding's Turtles could be reset; (2) limited dispersal experience in a prairie arena would be sufficient to result in development of compass in hatchling Blanding's and Snapping Turtles; and (3) the time experience was gained (morning and afternoon) in a prairie arena influenced subsequent dispersal of hatchling Blanding's Turtles in a corn plot. To those ends, we documented the orientation and dispersal patterns of naïve hatchlings of both species, four categories of experienced hatchling Blanding's Turtles, and one category of experienced Snapping Turtles (Table 1) in large arenas (60-m square) in one soybean and two corn fields. Using different species and categories of hatchlings and placing them in a variety of situations makes inferences drawn from comparisons among dispersal patterns more robust (Able 1991).

MATERIALS AND METHODS

Study sites .- The Weaver Dunes area in southeast Minnesota is approximately 600 ha of glacio-alluvial sand terraces bordered on the west by 1,500 ha of wetlands and deciduous riparian habitats in the McCarthy Wildlife Management Area and on the east by the Weaver Bottoms, a 1,600-ha open-water wetland (see Pappas et al. 2000 for more detailed descriptions). Lower dune areas closest to wetlands were often used for agriculture while higher elevation dunes are frequently used for nesting because vegetation cover is minimal due to low water holding capacity and low organic content.

square arenas were constructed on flat terrain by burying 15-cm aluminum flashing 5 cm deep in the soil in one soybean and two corn fields in 2007 and 2008. Arenas were square to minimize crop damage by allowing two sides of the fencing to be placed in the space between rows. We also constructed one 100-m diameter circular arena in a flat area of prairie habitat with a wetland 120 m to the west (the same 2008 arena shown in Fig. 2a; Pappas et al. 2009). The arena perimeter fences were labeled with the numbers 0, 4, 8, and 12, located at the cardinal directions (N, E, S, and W), the numbers 2, 6, 10, and 14 at the primary inter-cardinal bearings (45°, 135°, 225° , 315° , respectively), and the numbers 1, 3, 5, 7, 9, 11, and 13 spaced evenly between the other directions. Blanding's and Snapping Turtle females nest in the area of the prairie and all of the crop fields chosen for hatchling releases.

Our decision to use large arenas without bucket traps was based on giving hatchlings an area to make exploratory movements related to locating orientation targets before beginning dispersal toward the fence. We also considered the relative sampling errors that result from our *Arenas.*—Three approximately $60 \text{ m} \times 60 \text{ m}$ protocol versus those associated with installing

Hatchling Category	Definition			
Naive	Individuals with no previous exposure to environmental cues.			
Natural-experienced	Blanding's Turtles captured while dispersing west from natural nests in prairie habitat.			
Modified natural-experienced	Initially natural-experienced hatchling Blanding's Turtles dispersing west that were then held for 7–9 d in an outdoor aquarium with a view restricted to a far dark horizon to the east.			
Morning and afternoon arena-experienced hatchling Blanding's Turtles	Initially naïve hatchling Blanding's Turtles that were given limited morning or afternoon experience (at least 50 m movements over 45–150 mins) dispersing in an arena located in a natural prairie habitat. All hatchlings were re-released in a corn field in the following morning.			
Morning arena-experienced hatchling Snapping Turtles	Initially naïve hatchling Snapping Turtles that were given limited morning experience (at least 50 m movements over 45–150 mins) dispersing in an arena located in prairie habitat. Only those individuals captured on the southwest quadrant of the arena fence were used.			

TABLE 1. Categories and definitions of hatchling Blanding's (Emydoidea blandingii) and Snapping Turtles (Chelydra serpentina) dispersing from nests at Weaver Dunes, Minnesota, USA.

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bucket traps to be similar in magnitude in a large E-W crop row alignment. Due to a dry summer, arena. Walking arena fences with no bucket the corn stalks were partially dry and shorter traps creates a potential sampling error by allowing some hatchlings a maximum of 20 mins to move the 13 m (crop arenas) or 21 m (prairie arena) between numbered fence locations. Bucket trap errors would have included: (1) those related to the number of buckets and the distance between them; (2) whether a hatchling moves toward or away from the closest bucket; and (3) whether or not some hatchlings avoid buckets.

In 2007, one arena was constructed in a dense area of a 525 m \times 100 m soybean field with plants approximately 1–1.2 m in height and row alignment N to S with a wetland located approximately 40 m to the west of the field (Fig. 1a). A second arena in 2007 was located in the south end of a 650 m \times 560 m corn field with an



FIGURE 1. (a) Aerial photograph (white square = arena, dashed arrow = crop row alignment) and rose diagrams of initial dispersal in a morning release of (b) naïve, and (c) modified natural-experienced hatchling Blanding's Turtles (Emydoidea blandingii) and (d) naïve hatchling Snapping Turtles (Chelvdra serpentina) in a mature soy bean field (2007) at Weaver Dunes, Minnesota, USA.

(1.8–2.3 m tall [i.e. the min-max of stalk heights in the dry year]) than occur in wetter years. A large wetland was located about 60 m south of the arena (Fig. 2a). In 2008, an arena was constructed in a wildlife corn plot (110 m \times 70 m) with dense 3-m tall green corn stalks with row alignment from NNW to SSE. Wetlands were located approximately 60 m from the eastern and southwestern edges of the corn plot. For hatchlings at ground level, essentially all



FIGURE 2. (a) Aerial photograph (white square = arena, dashed arrow = crop row alignment) and rose diagrams of initial dispersal of hatchling Blanding's Turtles (Emydoidea blandingii), (b) naïve and (c) modified natural-experienced, and (d) naïve hatchling Snapping Turtles (Chelydra serpentina) released in a mature corn field (2007) at Weaver Dunes, Minnesota, USA.

access to environmental cues beyond the crop fields was blocked and penetration of direct sunlight to ground level was minimal. In 2008, we constructed a circular arena in an area of prairie to convert naïve hatchlings to arenaexperienced hatchlings (Table 1).

Naïve hatchlings.—Eggs were obtained directly from gravid female Blanding's and Snapping Turtles using oxytocin (Ewert and Legler, 1978) or from natural nests. Eggs were incubated in perforated plastic containers (10 cm \times 15 cm) buried approximately 15 cm deep in an area of nesting dunes protected with hardware cloth. We excavated the protected nests at night under a black tarp in late August and transported unhatched eggs and hatchlings in light-proof containers to a dark room where they were held until hatchlings were prepared for release in arenas.

Because crop monocultures present hatchlings with a uniform set of near horizon cues that are similar in all directions, we expected that the initial dispersal of naïve hatchling Blanding's and Snapping Turtles would be random or, because dispersing hatchlings Blanding's Turtles follow animal trails (Butler and Graham 1995; Pappas et al. 2009), hatchlings of both species would follow the spaces between crop rows as paths of least resistance.

Categories of experienced hatchlings (Table 1).—Natural-experienced hatchling Blanding's Turtles captured during dispersal from natural nests were able to use a compass to maintain their headings when translocated and released in new locations in prairie habitat with different sets of environmental cues (Pappas et al. 2009). We translocated and released a sample of natural-experienced hatchling Blanding's Turtles just outside and within the eastern edge of a mature corn field to determine if those released on the outside edge would enter the corn field, and whether both groups would be able to maintain their previous dispersal headings without access to natural cues used for in a prairie arena was obtained by naïve

orientation.

We also tested whether a previously established relationship between a target and compass could be reset by exposing a subsample of natural-experienced hatchlings to new cues (e.g., eastern-only visual exposure) to convert them into modified natural-experienced hatchlings (Table 1). Because new target habitats become available during dispersal from nests, we expected that modified naturalexperienced hatchlings would reset their target/compass relationship and disperse to the east when released in arenas in soybean and corn fields.

In 2008, we converted naïve hatchling Blanding's and Snapping Turtles to arenaexperienced hatchlings (Table 1) by giving them 45–150 mins of dispersal experience in a prairie arena before they were released in a corn plot to see if limited experience is sufficient for hatchlings to develop a compass. Naïve hatchling Blanding's Turtles were released in the prairie arena in the morning and afternoon and hatchling Snapping Turtles in the morning only (Table 1). Because female Snapping Turtles nest relatively close to wetlands, use of a compass by hatchlings may not often be necessary during dispersal from those nests; however, development of a compass has not been documented in hatchling Snapping Turtles. Based on the non-random SW dispersal heading of hatchling Snapping Turtles in an arena in the same general area of prairie in 2006 (Fig. 4b; Congdon et al. 2011), we selected only those individuals captured on the southwest quadrant of the prairie arena fence in 2008 to be released in the corn plot (Table 1).

We tested whether morning and/or afternoon arena-experienced hatchlings of both species would disperse non-randomly when re-released on the following morning in a mature corn plot that blocked access to typical environmental cues, a result that would indicate rapid development of a compass. We also examined whether the time of day that previous experience

hatchling Blanding's Turtles influenced the patterns and directions of subsequent dispersal in a corn arena.

Preparing hatchlings for release.—Naïve and experienced hatchings were marked in a dark room illuminated by a 5-watt red photographer's bulb located directly overhead. Naïve, and each category of experienced hatchlings (Table 1), were each given different paint codes or colors on the vertebral and marginal scutes. On the morning of the release, clutches of naïve hatchlings or samples of experienced hatchlings were distributed as uniformly as possible among four, equally-sized compartments within circular release buckets (38-cm diameter). Each compartment had a 3-cm diameter escape hole covered with tape to prevent hatchlings from exiting until they were at the release area. The release buckets were wrapped in two layers of black vinyl prior to transport to the arenas or release sites.

Release protocols.—A release (notations R1 or R2) is a group of hatchlings of a particular type (i.e., naïve or categories of experienced) simultaneously released at an arena. The species, category, and numbers of hatchlings released and recaptured at each arena and morning and afternoon releases are presented in Table 2. The majority of releases were conducted in morning or late afternoon on sunny days (although some days became partly cloudy after releases) in early September when hatchlings were dispersing from natural nests.

Between 0830–0900 h (morning releases) or 1600–1630 h (afternoon releases), one person: (1) placed a release bucket in the center of an arena; (2) removed the black plastic covering; (3) aligned the exit holes to the four compass directions to evenly distribute the initial direction of hatchling emergence; (4) removed tape from the exit holes; and (5) immediately left the arena. A naïve hatchling's first exposure to natural environmental cues occurred when they exited the release bucket. After one hour, we checked

TABLE 2. Descriptions of arena locations, identification of figures related to the arenas, and hatchling release data including hatchling species, category (Exp. = experienced), and sample sizes (n; * = hatchlings used during re-release in a corn plot) at Weaver Dunes, Minnesota, USA.

Year	Species	Hatchling category	Figure	Field	Release (R)/ time of day	n released/ recaptured
2007	E. blandingii	Naïve	1b	Soybean	R1/AM	50/48
		Exp. (modified-natural)	1c		R1/AM	50/47
	C. serpentina	Naïve	1d		R1/AM	106/100
	E. blandingii	Naïve	2b	Corn	R1/AM	60/57
		Exp. (modified-natural)	2c		R1/AM	51/45
	C. serpentina	Naïve	2d		R1/AM	95/86
2008	E. blandingii	Naïve	3b	Corn	R1/PM	47/19
		Naïve	3c		R2/AM	51/37
	C. serpentina	Naïve	3d		R1/PM	45/37
		Naïve	3e		R2/AM	40/33
	E. blandingii	Exp. (arena morning)	3f		R2/AM	40/40*
		Exp. (arena afternoon)	3g		R2/AM	28/25*
	C. serpentina	Exp. (arena morning)	3h		R2/AM	60/40*
2010	E. blandingii	Exp. (natural)	4b	Corn	R1/AM	13/13
		Exp. (natural)	4c		R2/AM	22/22

the release bucket to ensure that all hatchlings *Statistical analyses.*—Prior to analyses, all had exited (the few turtles that failed to exit capture locations on the arena fences were release buckets were not used in the study). converted to degrees by multiplying the

We began walking the arena perimeter fences within 30 mins of hatchling release and walked the fence continually during peak activity and at 20-min intervals during periods of reduced activity. Fences were monitored into the evening until an hour had elapsed without any hatchling activity. We recorded the identification code of each hatchling captured, the time, and location number on the arena perimeter fence (estimated to the nearest 0.1 of a fence number). Releases were terminated at the end of the first day to reduce differences in times of dispersal (i.e., data from hatchlings released in the afternoon and spent the night within the arena and then dispersed during the following morning were not used in analyses). All hatchlings captured at the fence were released at the edge of wetlands: (1) near the location of their natural nest site; (2) where their mother was captured; or (3) in the direction that experienced hatchlings were dispersing before capture.

Tracking natural-experienced hatchlings in corn fields (2010).—A sub-sample of naturalexperienced hatchling Blanding's Turtles (n = 35) captured as they moved from E to W were relocated and released in the morning within or adjacent to a 285 m \times 650 m corn field with N-S alignment of crop rows (Fig. 4a). Hatchlings were dusted with one of four differently colored fluorescent powders (Butler and Graham 1995). To prevent overlap of trails of same colored powder, a maximum of four hatchlings were released at different sites (> 10 m apart) located 5 m inside the eastern edge (n = 13) and 7 m outside of the eastern edge (n = 22) over a 7-d period. We followed the fluorescent trails using ultraviolet lights on the following night and trails were flagged at approx.10-m intervals. The next day, the directions from release sites to the ends of all trails were determined with a compass and straight-line distances were measured with a 50m tape.

Statistical analyses.—Prior to analyses, all converted to degrees by multiplying the locations by 22.5°. Tests for non-random dispersal (Rayleigh-test) of groups of hatchlings were calculated with Oriana2TM program (version 2.02a, Kovach Computing Services, 85 Nant-y-Felin Pentraeth, Isle of Anglesey LL75 8UY Wales, U.K.) for circular statistics (sample sizes are in Table 2). Mean vectors of dispersal are presented when bimodal dispersal patterns were significantly different from random, but not when dispersal was random and bimodal. Because a release in an arena represents a sample size of one, significant differences in dispersal of hatchlings in different releases and arenas was established by non-overlap of a mean vector of one group or arena with the 95% confidence interval around the mean dispersal vector of a second group of hatchlings.

Rose diagrams of dispersal are presented with aerial photographs showing the location arenas (Google EarthTM version 7.0.3.8542, Mountain View, California, USA) and straight-line distances from the center of arenas to features in the surrounding area (measured with the ruler tool in Google EarthTM, *op. cit.*). In the following sections of this paper "significantly different from random" and "directional dispersal" are used interchangeably. The directions of the fluorescent trails of experienced hatchlings were examined for concordance with original direction of movement before being relocated using Oriana2TM (*op. cit.*), and visually compared to alignment of crop rows.

Because our paper is only about hatchlings, we refer to the individuals used in this study as Blanding's Turtles or Snapping Turtles rather than hatchling Blanding's or Snapping Turtles. When we cite other papers, we identify whether the reference is to hatchlings, juveniles, or adults.

RESULTS

Soybean field (2007).—Orientation of naïve

Blanding's Turtles in the soybean field was not along the alignment of crop rows and parallel to significantly different from random (Rayleightest: Z = 1.67, P = 0.190), but dispersal was strongly bimodal along both directions of crop row alignment (N-S) and parallel to the wetland to the west (Fig. 1b). Orientation of modified natural-experienced Blanding's Turtles was directional (Rayleigh-test: Z = 7.33, P < 0.001) to the ENE (mean vector = 61°), across crop rows, away from the nearby wetland to the west, and different from the dispersal pattern of naïve hatchlings (Fig. 1c). The 95% confidence interval of the mean vector of dispersal of modified natural-experienced hatchlings overlapped with the eastern exposure during the holding period and did not overlap with the direction (W) that they were dispersing from natural nests when initially captured.

Orientation of naïve Snapping Turtles in the soybean field was directional to the SW (mean vector = 223.2°; Rayleigh-test: Z = 14.3, P <0.001). Even though the orientation was directional, the pattern of dispersal was primarily bimodal to the N and S along crop row alignment and parallel to the wetland (Fig 1d).

Corn field (2007).—Initial orientation of naïve Blanding's Turtles released in the corn field in morning was non-random (Rayleigh-test: Z =3.87, P = 0.020) with a mean SW vector of 246° (Fig. 2b). Orientation of modified naturalexperienced Blanding's Turtles was non-random (Rayleigh-test: Z = 15.63, P < 0.001) to the ENE (mean vector = 51° ; Fig 2c), parallel to or away from the wetland to the south, and in essentially the opposite direction taken by naïve hatchlings. The 95% confidence interval of the mean dispersal vector of modified natural-experienced hatchlings overlapped with the direction of exposure during the holding period, but not with the direction (W) that they were dispersing from natural nests at initial capture in prairie habitat.

Orientation of naïve Snapping Turtles released in the corn field in the morning was not different from random (Rayleigh-test: Z = 0.51, P =0.600), but primarily bimodal to the E and W the wetland (Fig. 2d).

Corn plot (naïve hatchlings, 2008).— Dispersal of naïve Blanding's Turtles released in the corn plot in late afternoon (Fig. 3b) or in the morning (Fig. 3c) were both not different from random (Rayleigh-tests: Z = 2.61, P = 0.070 and Z = 1.93, P = 0.150, respectively). However,



FIGURE 3. (a) Aerial photograph (white square = arena, dashed arrow = crop row alignment) and rose diagrams of orientation and initial dispersal of naïve hatchling Blanding's (E. b.) and Snapping Turtles (C. s.) released in a mature corn field (2008) at Weaver Dunes, Minnesota, USA; releases include naïve hatchling Blanding's Turtles in (b) late afternoon and in (c) morning; and naïve hatchling Snapping Turtles released in (d) late afternoon, and (e) morning, and two groups of arena-experienced hatchling Blanding's Turtles with (f) morning and (g) afternoon experience and one group of arena-experienced hatchling Snapping Turtles were released in the corn plot in the morning (h). Only when dispersal of naïve hatchlings was non-random (f, g, & h) are arrows through rose diagrams presented for mean vectors of the direction of dispersal during the previous release in a prairie arena.



FIGURE 4. (a) Aerial photograph (dashed arrow = crop row alignment), of general release areas (2008) and rose diagrams summarizing the dispersal releases of naturalexperienced hatchling Blanding's Turtles (b) within the corn field (square) and (c) just outside of the corn field (circle) at Weaver Dunes, Minnesota, USA.

more hatchlings dispersed away from wetlands (WNW) in the afternoon (Fig. 3c) than in the morning (SE; Fig. 3b).

Orientation of naïve Snapping Turtles in an afternoon release in the corn plot (Fig. 3d) was not different from random (Rayleigh-test: Z =0.82, P = 0.440), whereas in the release on the following morning (Fig. 3e), dispersal was directional to the SSE (mean vector = 151.7° , Rayleigh-test; Z = 0.32.82, P = 0.001), primarily bimodal, and in both directions of crop row in the prairie arena (arrow in Fig. 3h). alignment.

Prairie arena (converting naïve hatchlings to (2010).—Natural-experienced arena-experienced hatchlings, 2008).— Orientation of naïve Blanding's Turtles released in the prairie arena in the morning was not edge of a corn field. Hatchlings were tracked an significantly different from random (Rayleigh- average of 100.5 m (range: 45-148 m) and 51.3 test: Z = 0.69, P = 0.510); whereas, orientation m (range: 45–121 m), respectively. Orientation

of those released in the afternoon was directional with a mean vector to the S (195.0°, Rayleightest: Z = 6.24, P = 0.001; see arrow in Fig. 3g). All arena-experienced Blanding's Turtles were re-released in a corn plot to examine the influence of time of experience (morning or afternoon). We also selected a sample of Snapping Turtles restricted to only those that had dispersed to the southwest quadrant of the prairie arena fence with a mean dispersal vector of 211° (Rayleigh-test: Z = 27.0, P < 0.001; see arrow in Fig. 3h) and re-released them in the corn plot on the following morning to determine if they would be able to maintain their previous heading (i.e., evidence for development of a compass).

Corn Plot (re-release of arena-experienced hatchlings, 2008).—In contrast to the random dispersal in the prairie arena, morning arenaexperienced hatchlings released in a corn field dispersed directionally to the SW (mean vector $= 254^{\circ}$; Rayleigh-test: Z = 14.69, P < 0.001) and across crop rows (Fig. 3f). Afternoon arenaexperienced Blanding's Turtles dispersed directionally to the NW (mean vector = 298° ; Rayleigh-test: Z = 15.37, P < 0.001) in one direction of crop row alignment; a mean westerly dispersal direction (118° W) of the previous dispersal direction (S) in prairie habitat (arrow in Fig. 3g).

When morning arena-experienced Snapping Turtles captured only in the southwest quadrant $(180^{\circ}-270^{\circ})$ of the prairie arena fence were rereleased in a corn plot in the morning, dispersal was non-random to the SSW (Rayleigh-test: Z =5.72, P < 0.003, mean vector = 200°; Fig. 3h), essentially the same direction they had dispersed

Trails of experienced Blanding's Turtles Blanding's Turtles were released approximately 5 m inside (n = 13) and 7 m outside (n = 22) of the eastern of both groups of hatchlings was non-random trails or other less vegetated pathways in natural (Rayleigh-test: Z > 8.600, P < 0.001), across corn row alignment (mean vectors = 291.7° and 298.9°, respectively; Fig. 4b & c), and in the same general direction they had been moving (W) in prairie habitat.

DISCUSSION

Orientation and dispersal of naïve *hatchlings.*—In the 2007 corn field, an area of relatively stunted stalks in the west end may have provided some naïve Blanding's Turtles access to far dark horizon cues (e.g., tall riparian trees) to the W and S (Fig. 2a & b) that resulted in directional dispersal. For the seven other releases of naïve hatchlings of both species, patterns of dispersal in soybean and corn fields were random (n = 3), random and bimodal (n =3), and directional and bimodal (n = 1). Random dispersal and following crop rows resulted in the majority of naïve hatchlings dispersing either parallel to, or away from wetlands. Those results indicate that the majority of naïve hatchlings did not have access to cues typically used for orientation (far dark horizons for Blanding's Turtles and near open and most illuminated horizons for Snapping Turtles), and that crop row alignment influenced dispersal. In contrast, dispersal was directional in the majority of releases of naïve hatchlings of both species in prairie habitat (Pappas et al. 2009; Congdon et al. 2011).

When hatchlings move in one direction of crop row alignment they could be following a path of responding least resistance or to an environmental cue (e.g., a difference in illumination). Because of the low probability that identical cues could occur in both directions of crop row alignment (i.e., being equally illuminated in both directions at the same time of day), hatchling dispersal in both directions of crop row alignment provides strong support for following a path of least resistance in the absence of a cue. During dispersal from natural nests, some naïve Blanding's turtles followed animal indicates that they were able to rapidly develop

environments (Butler and Graham 1995; Pappas et al. 2009).

Orientation and dispersal of modified natural-experienced Blanding's Turtles.—In both 2007 releases of modified naturalexperienced Blanding's Turtles in soybean and corn fields, mean vectors of dispersal were: (1) different from their W direction of dispersal when initially captured; (2) non-random to the ENE and similar to the direction of exposure during the holding period; (3) across crop rows; and (4) different from the random and bimodal dispersal patterns of naïve hatchlings. Collectively, the results indicate that the relationship between their compass and the initial environmental target to the west was reset by the eastern exposure during the holding period. A lack of a plastic response would have been surprising since new dispersal targets may frequently become available to hatchlings.

Orientation of arena-experienced Blanding's and Snapping Turtles (rapid development of a *compass*).—We created arena-experienced Blanding's (one morning and one afternoon release) and Snapping Turtles (one morning release) to determine whether initial dispersal (50 m movements in 45–150 mins) in a prairie arena was sufficient to initiate development of a compass. Because female Snapping Turtles nest relatively close to wetlands, use of a compass by hatchlings may not often be necessary during dispersal from those nests; however, evidence for use of a compass during hatchling dispersal has not been previously documented.

In contrast to the random dispersal of naïve hatchlings in other releases in the corn plot (Fig. 3b, c, and d), the dispersal of arena-experienced hatchlings of both species was directional in all releases (Fig. 3f, g, & h). For both species, the ability of arena-experienced hatchlings to maintain a dispersal heading in a corn field (without access to natural environmental cues)

a compass/target relationship during their limited individuals were able to maintain movement dispersal experience in prairie habitat.

Influence of previous prairie arena experience on Blanding's Turtle dispersal in a *corn plot.*—Time of day that previous dispersal experience of naïve Blanding's Turtles was obtained (morning or afternoon at the prairie arena) influenced their subsequent dispersal in the morning in a corn plot. Dispersal of naïve hatchlings released in the prairie arena was random in the morning and directional to the S in the afternoon (arrow in Fig. 3g). When released in the morning in a corn plot, dispersal of the morning arena-experienced hatchlings was directional to the WSW (Fig. 3f) whereas the dispersal of afternoon arena-experienced hatchlings was to the NW (Fig. 3g). Dispersal in the corn plot by both categories of arenaexperienced Blanding's Turtles was: (1) different from their previous dispersal in the prairie arena; (2) different from each other (Fig. 3f & g); and (3) different from the random dispersal of naïve turtles in other releases in the corn plot. Collectively, the results indicate that the time of day influenced the dispersal of Blanding's Turtles in the prairie arena and that experience subsequently influenced their dispersal as arenaexperienced hatchlings as they dispersed in the corn plot.

The random dispersal of naïve hatchlings of both species in the majority of releases in crop fields indicates that they had no access to cues for orientation and argues that experienced hatchlings also had no access to cues for dispersal, but used a compass to maintain their headings. Use of a sun compass to maintain a heading during movements has also been reported in adult freshwater Painted Turtles (*Chrysemys picta*) and Box Turtles (*Terrapene* carolina; Derosa and Taylor 1978, 1982; Caldwell and Nams 2006), and in juvenile Green Sea Turtles (Chelonia mydas; Mott and Salmon 2011). In addition, Yeomans' (1995) study of adult Yellow-bellied Pond Sliders (Trachemys *scripta*) supports use of a sun compass because clumps on the periphery of pothole wetlands in

headings during clear conditions, but when overcast their headings became random (i.e., a magnetic compass should not be influenced by cloud cover). None of the above studies, however, can rule out use of a magnetic compass. Furthermore, adult Box Turtles apparently use a magnetic compass for orientation (Mathis and Moore 1988).

Biological and conservation issues.—The dispersal patterns of naïve hatchlings of both species in crop fields provided no evidence that olfactory cues or humidity gradients are primary mechanisms for orientation (i.e., very few naïve and experienced hatchlings moved toward nearby wetlands). Vision appeared to be the primary sensory mechanism used by hatchling Blanding's and Snapping Turtles during orientation and dispersal in a variety of natural and atypical locations in prairie habitat (Pappas et al. 2009; Congdon et al. 2011). Vision is a robust sensory mode because the relationship between environmental cues and hatchlings remains constant over a wide range of conditions. In contrast, a hatchling's olfactory or auditory assessment of humidity gradients, odors, and sounds from wetlands (e.g., frogs calling, running water, etc.) are all potentially influenced by factors such as temperature, humidity, rainfall, wind speed, and wind direction, even in proximity to their source.

Although data are accumulating that suggest some hatchling Blanding's Turtles overwinter on land (Butler and Graham 1995; Pappas et al. 2000; Dinkelacker et al. 2004), the direction of dispersal from natural nests of hatchling Blanding's Turtles at Weaver Dunes was toward the riparian habitat and associated wetlands. Movement toward riparian areas suggests that suitable overwintering sites are probably rare or not available in upland prairie habitats. Overwintering hatchling Blanding's Turtles marked in previous fall orientation studies (Pappas et al. 2009) were captured in sedge

early spring (M. Pappas, unpubl. data). should time of day have such a strong influence Movement toward riparian areas can also result on hatchling orientation and dispersal? in hatchlings having to cross crop fields on the way to riparian areas.

influence the probability of successful hatchling dispersal may be resisted by land owners due to increased costs, types of machinery, or tradition (Saumure et al. 2007). One potential mitigation tool would be to compensate landowners for not planting portions of some tilled fields close to wetlands. Unplanted areas would not be covered by crop canopies during development of turtle embryos and at nest emergence would provide hatchlings access to natural environmental cues used during dispersal from nests. However, few and relatively small nesting set-asides may result in high turtle nest densities that result in high depredation rates, and may require predator control measures.

Our study documents that novel changes in landscape mosaics caused by rapid development of dense canopies of agriculture crops pose more severe problems for naïve than for experienced Blanding's and Snapping Turtles dispersing from nests to wetlands. Crop fields near wetlands may also create similar problems for some age classes of semi-aquatic snakes (Roe et al. 2004) and amphibians, such as frogs, toads, and salamanders, as they migrate between wetlands or move among locations within terrestrial core areas (Mazerolle and Vos 2006; Semlitsch 2000, 2008; Semlitsch and Bodie 2003).

Answers to the following questions are needed to determine the severity of the problems that crop fields cause for dispersing hatchlings: what are the relative numbers of turtle nests located in natural areas versus crop fields?; during dispersal from nests, do naïve hatchlings that orient toward open horizons (e.g., Snapping and Painted Turtles) avoid entering the dark horizons presented by crop fields?; does additional dispersal time and distance caused by crop fields increase hatchling mortality?; and finally, because the relationships between nest sites and wetlands (or overwintering sites) are fixed, why

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