Report

Current Biology

Evidence for Geomagnetic Imprinting and Magnetic Navigation in the Natal Homing of Sea Turtles

Highlights

- Sea turtle nesting density varies with slight changes in Earth's magnetic field
- Results imply that sea turtles locate nesting beaches using geomagnetic cues
- Turtles likely imprint on the unique magnetic signature of their natal beach
- Similar mechanisms may explain natal homing in diverse long-distance migrants

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In Brief

How sea turtles return to nest on their natal beaches after long migrations has remained enigmatic. Brothers and Lohmann report a relationship between sea turtle nesting density and small changes in Earth's magnetic field. Results imply that turtles use geomagnetic cues to find nesting areas and may imprint on the magnetic field of the natal beach.

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Report

Evidence for Geomagnetic Imprinting and Magnetic Navigation in the Natal Homing of Sea Turtles

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Summary

Natal homing is a pattern of behavior in which animals migrate away from their geographic area of origin and then return to reproduce in the same location where they began life [1–3]. Although diverse long-distance migrants accomplish natal homing [1–8], little is known about how they do so. The enigma is epitomized by loggerhead sea turtles (*Caretta caretta*), which leave their home beaches as hatchlings and migrate across entire ocean basins before returning to nest in the same coastal area where they originated [9, 10]. One hypothesis is that turtles imprint on the unique geomagnetic signature of their natal area and use this information to return [1]. Because Earth's field changes over time, geomagnetic imprinting should cause turtles to change their nesting locations as magnetic signatures drift slightly along coastlines. To investigate, we analyzed a 19-year database of loggerhead nesting sites in the largest sea turtle rookery in North America. Here we report a strong association between the spatial distribution of turtle nests and subtle changes in Earth's magnetic field. Nesting density increased significantly in coastal areas where magnetic signatures of adjacent beach locations converged over time, whereas nesting density decreased in places where magnetic signatures diverged. These findings confirm central predictions of the geomagnetic imprinting hypothesis and provide strong evidence that such imprinting plays an important role in natal homing in sea turtles. The results give credence to initial reports of geomagnetic imprinting in salmon [11, 12] and suggest that similar mechanisms might underlie long-distance natal homing in diverse animals.

Results and Discussion

Ever since John James Audubon tied silver threads to the legs of young songbirds and observed their return the following year [13], evidence has accumulated that many animals return to their natal areas after migrating to distant locations [1–8]. An extreme example exists in loggerhead sea turtles, which leave their natal beaches as hatchlings and traverse entire ocean basins before returning to nest, at regular intervals, on the same stretch of coastline where they hatched [9, 10, 14]. How sea turtles accomplish natal homing has remained an enduring mystery of animal behavior [1, 14–16].

Turtles derive long-distance navigational information from the Earth's magnetic field by detecting the intensity and inclination angle (the angle at which field lines intersect Earth's surface) [17–20]. These parameters vary predictably across the globe [21, 22]. As a result, each area of coastline is typically marked by a different isoline of inclination and a different isoline of intensity (Figure 1A) and thus has a unique magnetic signature [1]. In principle, if turtles were to imprint on the inclination angle and/or intensity of their natal beach, then returning might be relatively simple: a turtle might need only to locate the coast and then swim north or south until it encounters the correct magnetic signature (Figure 1A). No evidence presently exists, however, to support or refute this hypothesis.

An important consideration for the geomagnetic imprinting hypothesis is that Earth's magnetic field changes slowly over time. Because of this field change, known as secular variation [24], the magnetic signatures that mark natal sites often drift slightly along the coast while turtles are gone [1, 25]. Thus, if an adult female selects her nesting sites by seeking out the magnetic signature on which she imprinted as a hatchling, she will inevitably change her nesting location in accordance with secular variation [26, 27]. Such individual changes might result in detectable population-level shifts in nesting distributions, providing a unique opportunity to test the geomagnetic imprinting hypothesis.

Specifically, the hypothesis predicts that when isolines of inclination or isolines of intensity converge along the coast, the magnetic signatures marking natal locations between those isolines will also converge (Figure 1). Thus, returning turtles will nest on a shorter length of coastline, and the number of nests per kilometer should increase (Figures 1B and 1C). By contrast, when isolines diverge, magnetic signatures also diverge, so returning turtles will nest over a longer length of coastline and the concentration of nests should decrease (Figures 1B and 1C). Until now, this possibility has not been investigated.

We analyzed a 19-year (1993–2011) database of loggerhead nesting sites for each of the 12 counties on the east (Atlantic) coast of Florida [28], an area encompassing the largest sea turtle rookery in North America. To evaluate secular variation, we developed an objective metric (convergence index) that quantifies the degree of isoline movement along the coast within each county during 17 two-year time steps (see Experimental Procedures). A positive convergence index indicates that isolines within a particular coastal area moved closer together, with higher values indicating greater convergence. A negative convergence index indicates that isolines moved apart, with more negative values indicating greater divergence. For each county and time-step combination, we calculated two different convergence indices, one based on the movement of inclination isolines and the other based on the movement of intensity isolines. We then analyzed the relationship between each convergence index and changes in nesting density.

Analyses confirmed the predictions of the geomagnetic imprinting hypothesis. For inclination, regardless of year or location, isoline convergence was associated with increased nesting density, whereas isoline divergence was associated with decreased nesting density ($p = 5.34 \times 10^{-4}$) (Figure 2). Moreover, a linear mixed-effects model revealed a highly significant relationship between the magnitude of isoline movements and the magnitude of changes in nesting density ($p = 3.67 \times 10^{-4}$) (Figure 3; Table S1): the highest convergence indices were associated with the greatest increases in nesting

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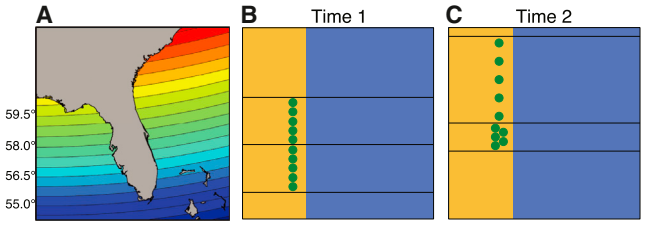

Figure 1. Map Showing Inclination Isolines near Florida and Diagrams Showing Predicted Effects of Isoline Movement on Nesting Density

(A) Because these isolines trend east/west whereas the coastline trends north/south, a unique inclination angle marks each area along Florida's east coast. Thus, turtles might locate natal beaches by returning to the appropriate isolines; locations to the north of the target area have steeper inclination angles, whereas locations to the south have shallower inclination angles. Black isolines bordering each color indicate increments of 0.5° and were derived from the IGRF model 11 [23] for the year 2012. The map for intensity isolines is not shown but is qualitatively similar, with different isolines of intensity existing at each area along Florida's east coast [16].

(B and C) Horizontal lines indicate three hypothetical isolines, and green dots represent nesting turtles, each of which has imprinted on the magnetic signature that marked her natal site as a hatchling. Over the past two decades, isolines near Florida have moved northward, but at variable rates. Sometimes, isolines to the south moved less than those to the north, resulting in divergence (C; upper two isolines). In these situations, the geomagnetic imprinting hypothesis predicts a decrease in nesting density, because turtles that imprinted on the fields between the isolines should return to nest over a larger area. In places where isolines converged (because those to the south moved more than those to the north), the hypothesis predicts that nesting density should increase (C; lower two isolines). Tan represents land; blue represents sea.

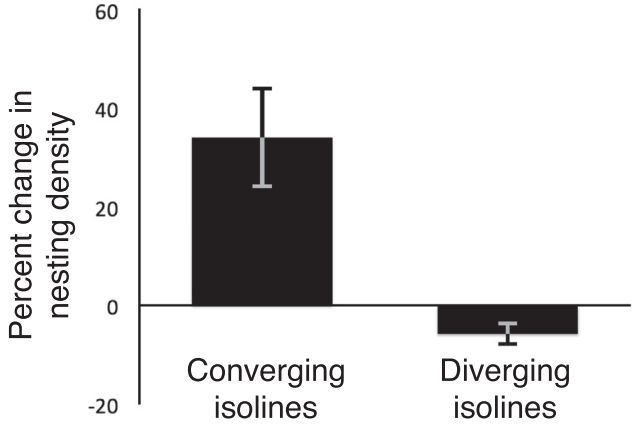

Figure 2. Changes in Nesting Density for Coastal Areas with Converging and Diverging Inclination Isolines

At times and places in which isolines converged (n = 29), nesting density increased by an average of 35%. At times and places in which isolines diverged (n = 172), nesting density decreased by an average of 6%. The mean changes of the two groups were significantly different ($p = 5.34 \times 10^{-4}$). Error bars represent standard error of the mean.

density, and the lowest convergence indices were associated with the greatest decreases in nesting density. This trend persisted within each of the 12 counties on Florida's east coast (Figure 4; Table S2).

For intensity, there were no areas along the coast where isolines converged; thus, all convergence indices were negative. In all other regards, however, the results of the analysis were qualitatively identical to those of the inclination analysis. A linear mixed-effects model revealed a strong positive relationship between convergence index and changes in nesting density ($p = 8.2 \times 10^{-4}$) (Figure 3; Table S1): as convergence index increased, so did the percent change in nesting density. This trend persisted within all 12 counties on Florida's east coast (Figure 4; Table S2).

These results provide strong evidence that nesting sea turtles use Earth's magnetic field to locate their natal beaches. Although the exact geomagnetic component (or components) exploited by turtles cannot be determined from the analyses, the findings are consistent with the hypothesis that nest site selection depends at least partly on magnetic signatures consisting of inclination angle, field intensity, or a combination of the two.

In a previous study, the migratory route of salmon approaching their natal river was shown to vary with subtle changes in the Earth's field [11]. Whereas the endpoint of the salmon spawning migration was presumably the same regardless of route, our findings demonstrate for the first time a relationship between changes in Earth's magnetic field and the locations where long-distance migrants return to reproduce.

Sea turtles are long lived, and females undertake reproductive migrations periodically throughout their adult lives [29]. Thus, the population of turtles that migrate to a given beach to nest each year consists of two subsets: a group of first-time nesters, and another, typically larger group of older "re-migrants" that have nested in the area during previous years. Genetic analyses indicate that both groups display natal homing [3, 5, 9, 14]. An unresolved question, however, is whether both reach the natal region by using the same navigational strategy and sensory cues [26].

At least two possibilities are compatible with the data. One is that hatchling turtles imprint on the magnetic signature of the natal beach and retain this information into adulthood [1]. Alternatively, nesting females might somehow reach the natal beach the first time without relying on magnetic information (e.g., by following an experienced nester or by using nonmagnetic cues) and then learn the magnetic signature of the beach and use it to return during subsequent nesting migrations. Although neither possibility can be excluded, we presently favor the first because "socially facilitated" migration has never been observed in sea turtles [3, 30], and because no nonmagnetic cue has been identified that can provide the necessary positional information for long-distance navigation [16]. Regardless of how the first return to the natal region is accomplished, turtles might periodically update their knowledge of the magnetic field at the nesting area each time they visit so as to minimize navigational errors that might otherwise accrue due to secular variation [25, 26].

Given the strong relationship between subtle changes in Earth's magnetic field and sea turtle nesting density, one possibility is that turtles are highly sensitive to small differences in magnetic fields. Alternatively, however, the same relationship can be explained if, in a typical nesting area, numerous error-prone individuals seek out a magnetic signature but miss the target by varying distances. Such imperfect navigation might, through a process resembling a "wisdom of the crowd" phenomenon [31, 32], give rise to a nesting distribution centered on the magnetic signature and, in effect, coupled to it. Thus, when Earth's field changes slightly and magnetic signatures move, the population-level nesting distribution might change even if individual turtles have relatively low magnetic sensitivity and make considerable navigational errors.

Our findings do not imply that turtles reflexively nest at a particular magnetic signature regardless of other environmental

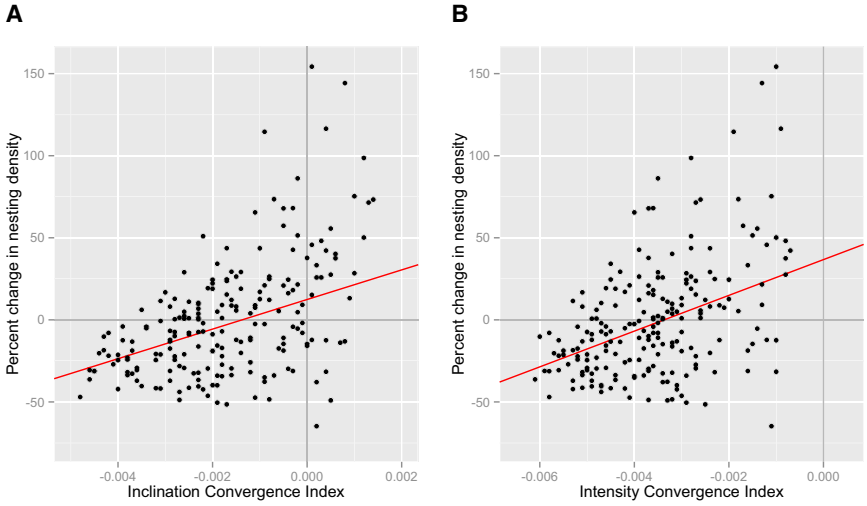

Figure 3. Relationship between Isoline Movement and Change in Nesting Density

Each data point represents values for one county in one time step.

(A) For inclination, a significant, positive relationship exists between convergence index and change in nesting density ($p = 3.67 \times 10^{-4}$; $n = 204$) (Table S1). As the degree of isoline convergence increased, so did the change in nesting density; the greatest increases in nesting were associated with the highest rates of convergence, and the greatest decreases in nesting were associated with the highest rates of divergence.

(B) For intensity, a significant positive relationship also exists between convergence index and change in nesting density ($p = 8.2 \times 10^{-4}$; $n = 204$) (Table S1). The slope and intercept for each red line were estimated with mixed-effects models that included convergence index as a fixed effect and a random slope and intercept for time step.

conditions, or that nesting distributions will track the steady movement of isolines along a coast no matter what. Successful nesting requires deposition of eggs in a location suitable for incubation. Factors such as beach erosion, sand quality, visual cues, and predation are known to influence where turtles nest on a local scale [1, 26]. Because these and other environmental conditions also affect the likelihood that a nest will yield viable hatchlings [26, 33], natural selection is likely to act against turtles that choose nesting locations by relying on magnetic cues to the exclusion of all else. Moreover, sensory cues other than geomagnetism are likely to help guide natal homing, especially once turtles have arrived in the vicinity of the nesting area [25, 26].

Given that geomagnetic cues appear to play an important role in natal homing, an intriguing speculation is that, over evolutionary time, turtles might have had difficulty locating their natal beaches during brief periods of rapid field change, as are thought to have occurred during some magnetic polarity reversals [34]. During these intervals, turtles might have had a tendency to stray into new nesting areas, which subsequent generations could then locate reliably as the field stabilized and geomagnetic imprinting once more became an effective strategy for natal homing [1].

Because sea turtles nest in different environmental settings worldwide, it is possible that different nesting populations exploit geomagnetic cues in different ways during natal homing [1, 16, 35]. Our analysis suggests that turtles use geomagnetic cues to locate natal areas along continental coastlines, the most common setting for large sea turtle rookeries worldwide [16]. In other settings, such as on small islands, turtles must nest in specific, restricted areas because no alternative exists. In such situations, a clear relationship between field changes and nesting sites is unlikely because, over time, magnetic signatures that once marked the natal site drift offshore where nesting is impossible [1, 26]. In these cases, turtles might use magnetic cues to navigate to the vicinity of the island and then use odorants or other supplemental local cues to locate the nesting beach [16, 35, 36].

Regardless of these considerations, our results provide the strongest evidence to date that sea turtles find their nesting areas at least in part by navigating to unique magnetic signatures along the coast. In addition, our results are consistent with the hypothesis that turtles accomplish natal homing largely on the basis of magnetic navigation and geomagnetic imprinting. These findings, in combination with recent studies on Pacific salmon [11, 12], suggest that similar mechanisms might underlie natal homing in diverse long-distance migrants such as fishes [2, 4], birds [37, 38], and mammals [6].

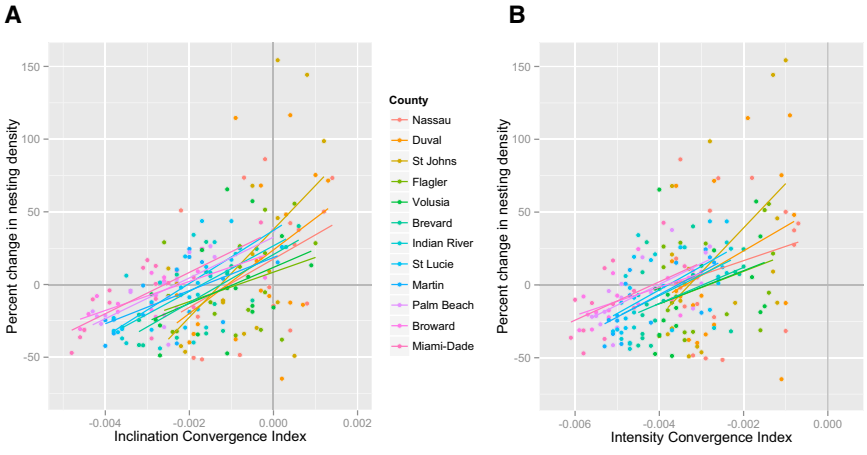

Figure 4. Relationship between Isoline Movement and Change in Nesting Density for Individual Counties

Each data point represents values for one county in one time step; each county is represented by a different color. In the color key, counties are arranged from north (top) to south (bottom). For both the inclination analysis (A) and the intensity analysis (B), all counties show a positive relationship between convergence index and change in nesting density ($n = 17$ for each county) (Table S2). The greatest increases in nesting were associated with the highest rates of convergence, and the greatest decreases in nesting were associated with the highest rates of divergence. For inclination, this relationship was significant in eight individual counties ($p < 0.05$), and the trend was present in all. For intensity, the relationship was significant in seven individual counties ($p < 0.05$), and the trend was present in all.

Experimental Procedures

Using data from Florida's Statewide Nesting Beach Survey [28], which reports the number of kilometers surveyed within each county and the corresponding number of sea turtle nests counted, we calculated the loggerhead turtle nesting density in Florida's 12 east coast counties for each of 19 years (1993–2011). We then calculated each county's percent change in nesting density for 17 two-year time steps (e.g., from 1993 to 1995, 1994 to 1996, and so on). Because the total number of loggerhead nests on Florida's east coast varied from year to year [39], we estimated the change in nesting density attributable to population fluctuations by calculating the average change in nesting for all counties and time steps. We then calculated the difference between this average and each data point and used the resulting value in our analyses.

Two-year time steps were used because adult female loggerheads typically return to nest on their natal beach every two to three years [29]; thus, this time step reflects isoline movement that turtles realistically encounter during successive reproductive migrations. Ideally, an analysis of nesting data designed to test geomagnetic imprinting would be limited to first-time migrants and would also use a longer time step that coincides with the interval between hatching and first migration, but this was impractical because no existing dataset spans a sufficient time period or distinguishes between first-time and experienced migrants.

To assign coastal position, we used Google Earth to calculate distance along a line parallel to the east coast of Florida (Figure S1). We then used data from the International Geomagnetic Reference Field model 11 (IGRF-11) [23] to calculate the distance isolines traveled along the coast over the same two-year time steps for which we evaluated changes in nesting density. We described isoline movement as a function of coastal position (Figure S2A). The derivative of this function, with respect to position, quantifies isoline convergence or divergence (Figure S2B). This metric, referred to as the convergence index, was calculated at the midpoint of each county for each time step. A convergence index was calculated for both inclination and intensity isolines.

Over the past two decades, isolines near Florida have moved northward, but at variable rates. At some times and places, isolines to the south moved less than those to the north, resulting in the divergence of isolines. In such cases, the derivative (convergence index) is negative (Figure S2). At other times and places, isolines to the south traveled farther than those to the north, resulting in the convergence of isolines. In these places, the derivative (convergence index) is positive (Figure S2). In addition, the degree of isoline convergence or divergence is proportional to the magnitude of the derivative; a more positive derivative indicates high rates of convergence, while a more negative derivative indicates high rates of divergence.

To characterize the relationship between convergence index and change in nesting density, we evaluated several linear models, including ordinary least-squares regression, mixed-effects regressions with random effects for time step, and mixed-effects regressions with random effects for county. The random effects included in the models take into account the year-to-year variations in nesting density along the Florida coast, as well as the county-to-county variations. While all models revealed equivalent results, the best-fit models for both the inclination analysis and the intensity analysis include convergence index as a fixed effect and a random intercept and slope for time step (Table S1). We evaluated the difference between nesting changes for areas with converging or diverging inclination isolines using a mixed-effects model with convergence or divergence as a fixed effect and time step as a random effect. This last analysis was not performed for intensity isolines because there were no coastal areas with converging intensity isolines.

Supplemental Information

Supplemental Information includes two figures and two tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.12.035.

Author Contributions

The study was conceived by J.R.B. and K.J.L. The data were analyzed by J.R.B. The manuscript was written by J.R.B. and K.J.L.

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