Correspondences

Compatibility of magnetic imprinting and secular variation

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Diverse ocean migrants, including some sea turtles, elephant seals, and salmon, begin life in particular reproductive areas along coastlines, disperse across vast expanses of sea, and then return as adults to their natal areas to reproduce [1–3]. Little is known about how such marine animals guide themselves to the correct coastal region from hundreds or thousands of kilometers away and after absences ranging in duration from a few months to a decade or more. One hypothesis is that animals imprint on the magnetic field of their home area and use this information to return [1]. The Earth's field varies predictably across the globe, so different geographic areas are marked by distinctive magnetic fields that might, in principle, provide unique magnetic signatures for natal areas [4]. A potentially serious complication for this hypothesis is that the Earth's field changes gradually over time [1,4], causing the magnetic signatures that define natal areas to slowly drift. This secular variation could make natal homing via magnetic imprinting impossible if the magnetic signatures moved too far from the natal area [1,5,6]. To investigate whether magnetic imprinting is compatible with secular variation, we sought a species with a life history that poses challenges for the hypothesis, reasoning that if magnetic imprinting is consistent with natal homing under unfavorable circumstances, then it would also be plausible in most other cases. We chose the Kemp's ridley sea turtle (*Lepidochelys kempii*), an endangered species that ranges widely over the Gulf of Mexico, northern Caribbean, and the eastern U.S. coast, but returns to nest along a single, limited region of coastline in northern Mexico [7]. This species requires approximately 10–15 years to reach sexual maturity [7] and is thus absent from its natal area for much longer than animals such as salmon and elephant seals [2,3]. Given this long absence, the Kemp's ridley appears to be particularly susceptible to effects of secular variation if it relies on magnetic imprinting. The modeling results we report here show that the magnetic imprinting hypothesis can account for how the Kemp's ridley turtle returns to its natal region even after absences of a decade or more.

In principle, an animal might exploit geomagnetic cues in several different ways to identify its natal area, with the optimal strategy differing depending on whether the target area is along a continental coastline or on an island [1,4]. For species such as the Kemp's ridley that nest along continental coastlines, each coastal area typically has a different magnetic field associated with it [1,4] (Figure 1). Sea turtles detect two elements of the magnetic field: the inclination angle (angle at which the field lines intersect the Earth's surface) and the total field intensity [1]. Our model, based on a hypothetical strategy of magnetic navigation proposed previously for turtles that nest on continents [1], assumes that Kemp's ridley turtles imprint on one of these geomagnetic elements and return at sexual maturity to the coastal location marked by the same magnetic value. One analysis assumed turtles mature at 10 years, whereas a second assumed 15 years; these values bracket most estimates [7]. The model further assumed that turtles could not compensate for field change. Two geomagnetic models [8,9] were used in combination with GIS software to quantify the movement of the magnetic field between the years 1600 and 2010 at Rancho Nuevo, the beach with the highest nesting density (Figure 1).

Results indicate that, since 1900 (when the most detailed geomagnetic model begins), Kemp's ridley turtles imprinting on the inclination angle of Rancho Nuevo would return to the coast an average of about 23 km away from their natal site if absent for 10 years or an average of about 32 km if absent for 15 years (Figures 1A and 2). Imprinting on field intensity would lead to returns that average 89 km from the natal site for a 10-year absence and 132 km for a 15-year absence (Figures 1B and 2). Geomagnetic models for the period

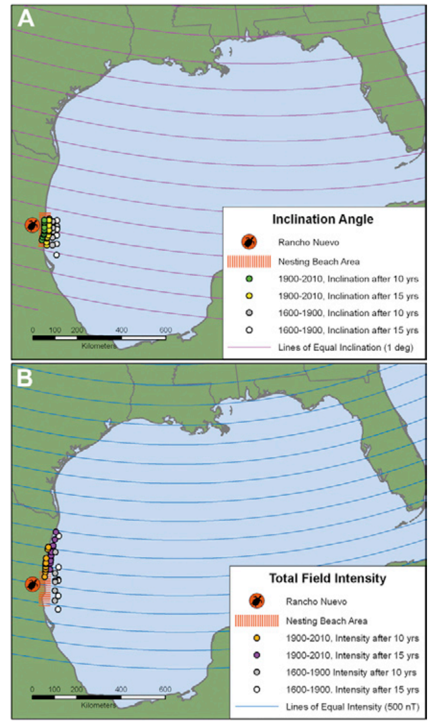

Figure 1: Map of the Gulf of Mexico indicating the nesting area of the Kemp's ridley turtle and the locations to which turtles would hypothetically return under two simple magnetic imprinting strategies.

The red hatched lines indicate the region of coastline (approximately 160 km) in which 98% of nests of the species are deposited [7,10]. The turtle symbol indicates the location of Rancho Nuevo, Mexico (23.20°N, 97.77°W), the site of peak nesting density [7,10]. Isolines in (A) indicate 1° increments of magnetic inclination; in (B) they indicate 500 nT increments of total intensity. Because the coastline is aligned approximately north–south while the isolines trend east–west, each area of coastline is marked by a different magnetic inclination and magnetic intensity [1,4]. In effect, the coast serves as one coordinate, so that the navigational problem can be reduced to arriving at a coastal area with the correct latitude. (A) Predicted locations of returns if turtles imprint on the magnetic inclination angle at Rancho Nuevo and then return 10 or 15 years later to the coastal location with the same inclination angle. Each colored dot indicates the return location for a turtle leaving the coast in a specific year (1900, 1905, and so on). Because some return locations are nearly identical, not all dots are visible; see Supplemental Data for complete results. (B) Predicted locations of returns if turtles imprint on the magnetic intensity at Rancho Nuevo. Conventions are as before; see Supplemental Data for complete results.

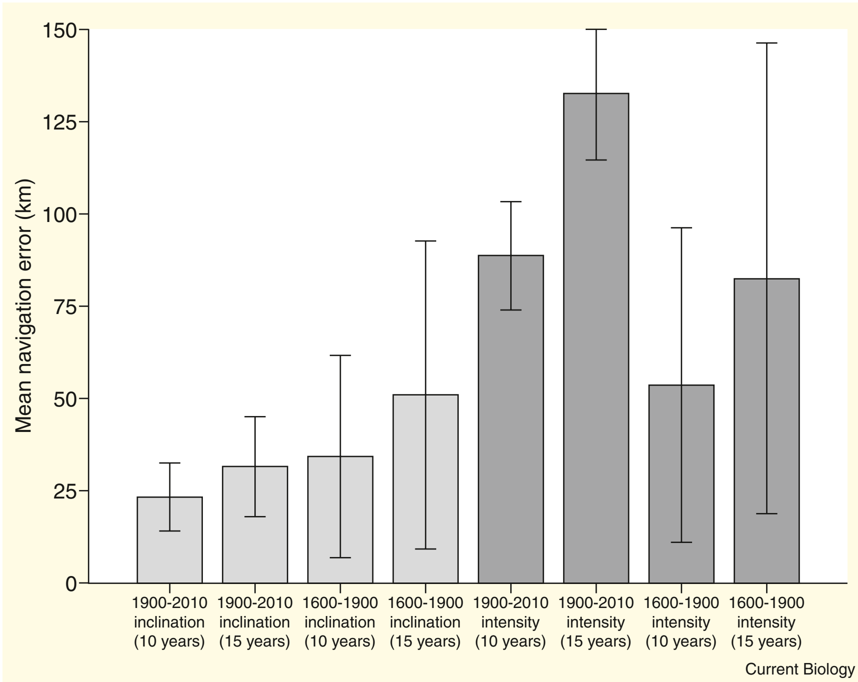

Figure 2. Bar graph showing hypothetical navigational errors for turtles that imprinted on inclination angle or intensity at specific points in time and returned to the coastal location marked by the same magnetic value 10 or 15 years later.

For simplicity all turtles were assumed to enter the ocean as hatchlings at Rancho Nuevo (indicated by 0 km on the vertical axis), the beach with the highest concentration of nesting. Light-colored bars on the left half of the graph indicate outcomes if turtles imprint on inclination angle; the different means indicate results for different periods (1900–2010 or 1600–1900) and different assumptions about time to maturation (10 years or 15 years) as indicated below each bar. Dark bars on the right half of the graph indicate outcomes if turtles imprint on total intensity. Error bars indicate the 95% confidence interval for the mean. For the period 1900–2010, simulations were run for each 5-year period (for turtles entering the sea in 1900, 1905, 1910, and so on); thus, the reported means are based on n = 21 for 10-year results and n = 20 for 15-year results. For the period 1600–1900, the geomagnetic model provides estimates of field change only for 50-year increments; thus, n = 6. The rates of secular variation (field change) at Rancho Nuevo appear to be typical of those that occur in other geographic areas used by other species that display natal homing (see Supplemental Data for comparisons and for complete results of analysis summarized above).

1600–1900 are not as detailed as those for the past century, but analyses indicate that similar outcomes during the two time spans would be expected (Figures 1 and 2).

The results demonstrate that the precision of natal homing predicted by the magnetic imprinting hypothesis is consistent with the precision known to occur in the Kemp's ridley turtle. The modeled returns of turtles imprinting on the inclination angle at Rancho Nuevo indicate that, for the past 400 years, first time nesters could consistently home to the narrow stretch of beach where 98% of nests are presently deposited by this species (Figure 1A). Though modeled returns of Kemp's ridley show that imprinting on field intensity does not always lead turtles directly back to the species' main nesting area, turtles would arrive near their natal region (Figure 1B). In principle, simple strategies of magnetic imprinting can return turtles to their natal region, at which point they might use other, local cues to pinpoint particular nesting areas. Short-range cues available in the vicinity of nesting beaches might include pheromones secreted by females aggregating offshore in preparation for mass nesting events [7], visual cues associated with the nesting areas, or distinctive chemical cues from the nesting beach leaching into the sea. Thus, magnetic imprinting might serve to return turtles to a general coastal location, around which they search for their final target.

The precision of magnetic navigation might improve after the initial return migration because female Kemp's ridley turtles nest every 1–2 years once they have matured [7]. Thus, experienced nesters return at much shorter intervals which provide less time for the field to change; moreover, turtles might update their knowledge of the magnetic field at the nesting beach each time they visit and use this information to target the natal area more accurately [1].

Our study demonstrates that the magnetic imprinting hypothesis can plausibly account for how the Kemp's ridley turtle, and perhaps other species, return to natal regions along continental coastlines even after absences of a decade or more. Additional studies will be needed to determine whether magnetic imprinting does in fact occur in sea turtles, as well as in other diverse migrants.

Supplemental data

Supplemental data are available at http://www.current-biology.com/cgi/content/full/18/14/R596/DC1

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