

# Current Biology

## Map-like use of Earth's magnetic field in sharks

### Highlights

- Sharks are known to undergo precise, long-distance migrations
- The navigational mechanism used to facilitate these movements is unresolved
- We show that sharks use the Earth's magnetic field for homeward orientation
- This ability is useful for navigation and possibly maintaining population structure

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### In brief

Keller et al. provide evidence that sharks use the map-like information from the geomagnetic field as a navigational aid. This ability is useful for navigating during the long-distance migrations that these species are known for and possibly maintaining population structure in marine environments, where few physical barriers limit movement.



## Report

## Map-like use of Earth's magnetic field in sharks

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## SUMMARY

Migration is common in marine animals,<sup>1–5</sup> and use of the map-like information of Earth's magnetic field appears to play an important role.<sup>2,6–9</sup> While sharks are iconic migrants<sup>10–12</sup> and well known for their sensitivity to electromagnetic fields,<sup>13–20</sup> whether this ability is used for navigation is unresolved.<sup>14,17,21,22</sup> We conducted magnetic displacement experiments on wild-caught bonnetheads (*Sphyrna tiburo*) and show that magnetic map cues can elicit homeward orientation. We further show that use of a magnetic map to derive positional information may help explain aspects of the genetic structure of bonnethead populations in the northwest Atlantic.<sup>23–26</sup> These results offer a compelling explanation for the puzzle of how migratory routes and population structure are maintained in marine environments, where few physical barriers limit movements of vagile species.

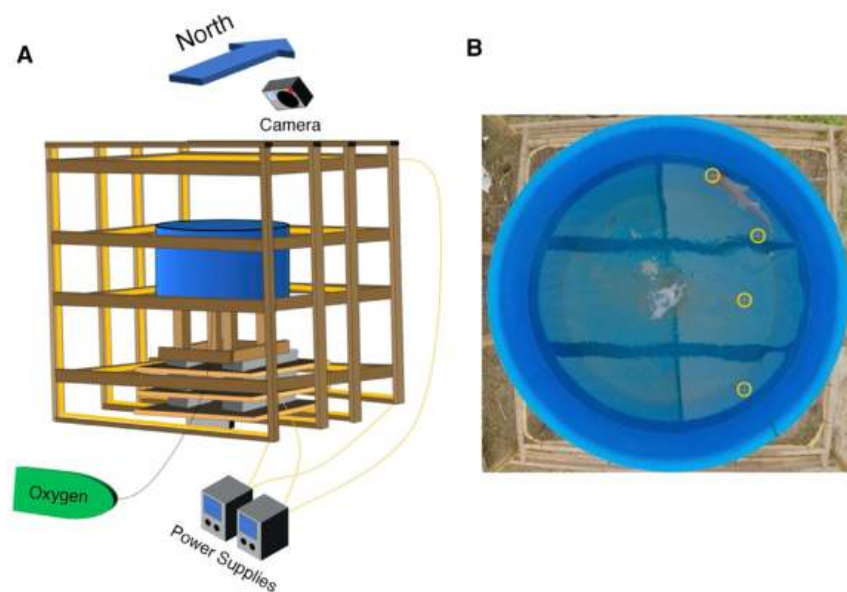
## RESULTS AND DISCUSSION

Navigating thousands of kilometers to a target location through a three-dimensional ocean is among the most impressive feats in nature and has important implications for the evolution, ecology, and conservation of many marine species.<sup>2</sup> Sharks, skates, and rays, from the subclass Elasmobranchii, are among the most ecologically important groups of marine fishes. Many species of elasmobranchs are highly mobile and their habitats can span thousands of kilometers,<sup>27,28</sup> with some migratory species exhibiting site fidelity, in which individuals return to specific locations.<sup>29,30</sup> Researchers have long known that elasmobranchs are sensitive to electromagnetic fields, and the possibility that sharks use their electrosensory organs in some capacity to glean information from Earth's magnetic field (hereby referred to as the geomagnetic field [GMF]) for navigational purposes has been widely discussed.<sup>21,31</sup> The GMF provides animals with both map and compass information.<sup>2,7,32</sup> The map allows animals to garner spatial information relative to their location,<sup>7</sup> while the compass allows animals to maintain a directed heading,<sup>32</sup> and together, these facilitate successful migrations toward targeted locations.<sup>9,33,34</sup> Elasmobranchs appear capable of discriminating between different components of the GMF<sup>14</sup> and have also been trained to respond to geomagnetic polarity and intensity.<sup>13,15,17,19</sup> Tracking studies of wild sharks have revealed striking associations between swimming trajectory and local magnetic maxima and minima extending from seamounts to feeding grounds,<sup>35</sup> however, whether sharks use geomagnetic cues for navigation remains unresolved. Our first aim was to experimentally determine whether sharks use magnetic cues to derive spatial information for orientation. Our second goal was to determine whether map-like use of the GMF could help explain spatial patterns of genetic variation in sharks. For both,

we studied the bonnethead (*Sphyrna tiburo*), a widely distributed, coastal shark that displays site fidelity to particular estuaries, bays, and sounds.<sup>30</sup>

We captured 20 juvenile bonnetheads from Turkey Point Shoal off the coast of Florida, USA, in the Gulf of Mexico (29.887°N, 84.511°W; Table S1). Sharks were transported to the Florida State University Coastal and Marine lab for experimentation (29.916°N, 84.511°W). We used “magnetic displacements” to expose animals to magnetic conditions representing locations hundreds of kilometers away from their capture location. The experimental approach is straightforward and allows specific predictions to be tested about how magnetic map information is used in orientation.<sup>9,33,34</sup> The manipulation of local magnetic fields was accomplished with Merritt coils, organized as two orthogonal series of horizontal and vertical lumber frames<sup>36</sup> (Figure 1). An experimental tank was positioned in the center of the coils and a GoPro camera recorded shark movements from above. Each shark was tested in three fields, presented in randomized order: (1) the field at the capture site as a control, (2) a field that exists ~600 km south of the capture site within the Gulf of Mexico (weaker magnetic intensity and decreased inclination versus control), and (3) a field that exists ~600 km north of the capture within the continental United States (stronger magnetic intensity and increased inclination versus control; Table 1). If sharks derive positional information from the GMF, then we predicted northward orientation in the southern magnetic field and southward orientation in the northern magnetic field (in each case to compensate for the perceived displacement), but no orientation preference in the magnetic field at the capture site. This design was chosen in part because of the geographic constraints of the study area, but also to explore whether sharks respond more robustly to changes in magnetic field conditions that are relevant from an ecological/evolutionary





**Figure 1. Merritt coil systems and shark tracking procedure**

(A) Our series of Merritt coils with the experimental tank in the center.

(B) A sample from our video analysis in which this shark has been tracked through 4 s. The O<sub>2</sub> aeration can be seen at the tank's center.

See Table S3.

perspective (i.e., the southern field) or whether they are equally adept at extrapolating magnetic information in an unnatural situation (i.e., the northern field).

The orientation of sharks tested in the capture site field (control) was indistinguishable from random (mean bearing = 186°; Rayleigh test:  $r = 0.055$ ,  $p = 0.942$ ,  $n = 20$ ), indicating that the testing procedure did not cause an obvious directional bias in the sharks (Figure 2). When sharks were exposed to the southern magnetic field, orientation was significantly northward (mean bearing = 347°; Rayleigh test:  $r = 0.406$ ,  $p = 0.035$ ,  $n = 20$ ; Figure 2). A paired Hotelling's test indicated a significant difference between the orientation of sharks in the control and the southern field ( $F = 5.835$ ,  $p = 0.011$ ). By contrast, when exposed to the northern field that exists in the continental United States, sharks were not oriented (mean bearing = 322°; Rayleigh test:  $r = 0.221$ ,  $p = 0.380$ ,  $n = 20$ ), and a paired Hotelling's test found no difference between the control and northern field ( $F = 1.055$ ,  $p = 0.369$ ). Details on the behavioral analysis can be found in the STAR Methods section.

These results suggest that sharks can differentiate geographic locations using map information from the GMF. Bonnetheads appeared to perceive the southern magnetic field as different from the field at the capture site and responded to the magnetic displacement with homeward orientation. It is tempting to

speculate that the northern field did not elicit different orientation from the field at the capture site because the sharks had no experience with such strong magnetic fields and that their magnetic map is "learned." Sharks in the Gulf of Mexico could learn that fields weaker than those at the capture site indicate more southward locations but would never experience stronger fields than the capture site and thus may not know how to respond to such conditions. However, the lack of response to the northern treatment is also

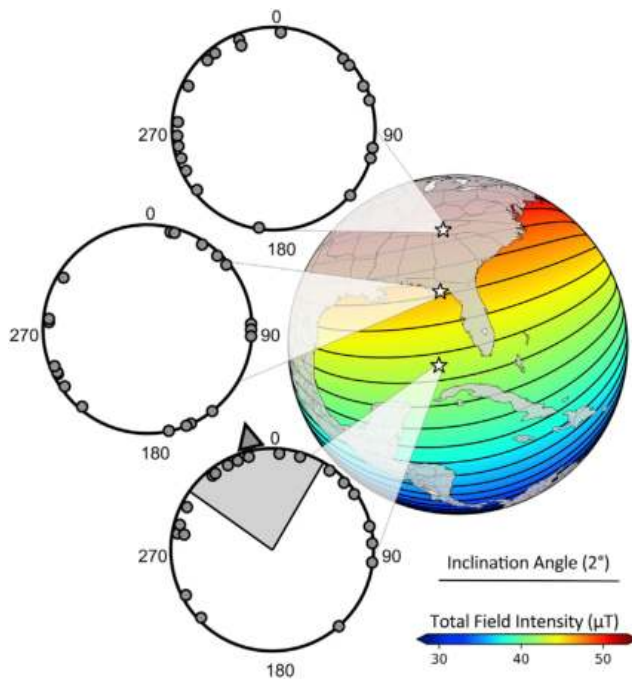
consistent with findings in animals with innate magnetic maps; hatchling loggerhead sea turtles (*Caretta caretta*) failed to orient in magnetic fields far outside of their normal migratory route, but were strongly oriented within the typical population range.<sup>37</sup> While our experiment suggests that magnetic fields that are more familiar (either from individual experience or evolutionary history) elicit more robust orientation responses, further study is required to conclude how bonnetheads derive and extrapolate magnetic map information. Regardless, the lack of response to a northern field does not disqualify the bonnethead from having a magnetic map, as information within a map may be tailored to the specific needs of an organism, and therefore maps may be unique to the spatial ecology of each species.<sup>7</sup> In this geographic setting, the map of bonnetheads may primarily be used to infer whether or how far south they are from their foraging site. It would be interesting to compare our findings with bonnetheads that are restricted in southward movements (e.g., populations along the Bay of Campeche in the southern Gulf of Mexico) and those not restricted in north-south movements (e.g., populations along the US Atlantic coast). Conducting longitudinal magnetic displacements would further inform what representation of space these sharks derive from the GMF.<sup>9,34,37</sup>

Our finding that bonnetheads derive spatial information from geomagnetic cues may have important implications for

**Table 1. Target location where sharks were magnetically displaced, and the associated synthetic magnetic fields created in our laboratory trials during the 2 study years**

	Coordinates		2018		2019		Test statistics		
	Latitude (°N)	Longitude (°W)	Intensity (nT)	Inclination	Intensity (nT)	Inclination	Mean heading	Rayleigh $r$	Rayleigh $p$
North	35.5°	84.5°	50,450	63.1°	50,670	62.6°	322°	0.221	0.380
Control	29.9°	84.5°	46,630	59.1°	46,880	58.6°	186°	0.055	0.942
South	24.5°	84.5°	43,550	53.8°	43,620	53.4°	347°	0.406	0.035

Due to the gradual drift of the geomagnetic field, we slightly modified intensity and inclination between study years to maintain continuity in relative differences between treatments. A statistically significant homeward orientation was observed for the southern treatment.  $n = 20$  for all treatments.



**Figure 2. Orientation of bonnetheads to magnetic displacements**  
Orientation of bonnetheads in the 3 magnetic treatments (white stars). Adjacent rose diagrams detail individual headings of each shark (gray circles,  $n = 20$ ) in the corresponding magnetic fields. Significant, homeward orientation was elicited by the southern magnetic field. The shaded area represents the 95% confidence interval (CI) and the outer triangle represents mean bearing ( $347^\circ$ ). No orientation preference was elicited in the control field (capture site) or the northern field that exists outside the range of the bonnethead. The intensity of the total magnetic field is represented by the color bar, and the inclination is represented by  $2^\circ$  contours. See Table S3.

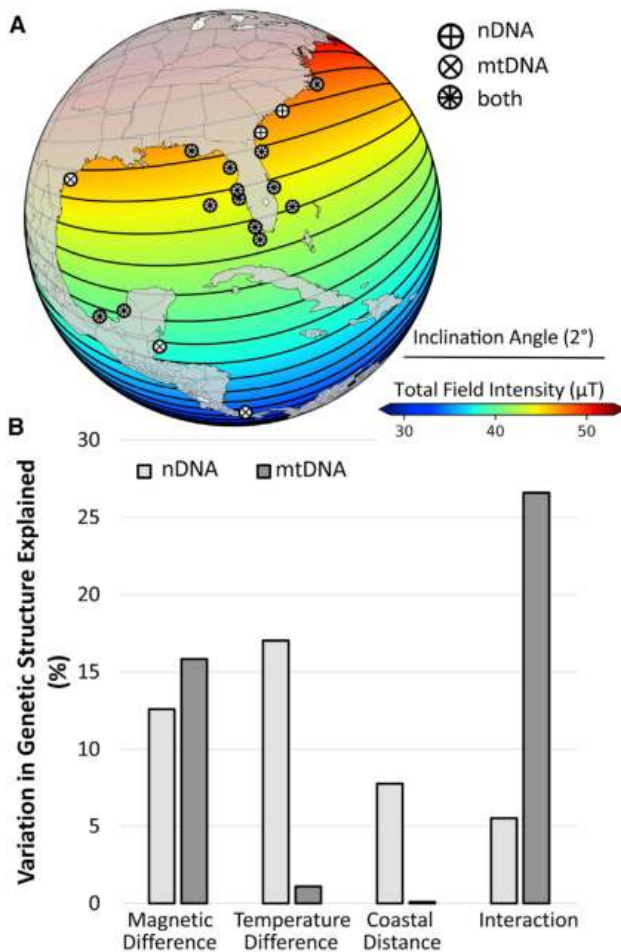
understanding their current migrations and biogeographic patterns.<sup>2,38,39</sup> One such example is that genetic differences between populations of sharks may be predicted by spatial variation in the GMF.<sup>40</sup> Population structure can be a function of geographic distance, and in an isolation by distance model, populations will be more diverged if separated by greater distances. Likewise, environmental conditions can affect components of genetic variation, with organisms in disparate habitats experiencing reductions in gene flow.<sup>41</sup> In addition, if sharks use magnetic maps to home on particular locations, then magnetic differences between sites may be a better predictor of divergence than geographic distance. We explored this hypothesis by comparing genetic distances between bonnetheads sampled at discrete geographic locations in the northwest Atlantic (estimated as  $F_{ST}$  in one published nDNA dataset and  $\Phi_{ST}$  in three mtDNA datasets) to the percentage of difference in magnetic field values, coastal distance, and difference in mean sea surface temperature between sites (a proxy for environmental distance). Multiple regression and variance partitioning analyses indicated that the combination of these three variables accounted for 42.86% of the variance genetic distance inferred from nuclear DNA (nDNA) and 42.94% of the variance genetic distance inferred from mtDNA. For nDNA, variation partitioning analyses uniquely ascribed 12.58% of the variation to magnetic differences,

17.03% to temperature differences, and 7.74% to the coastal distances between sites. For mtDNA, 15.83% of the variation ascribed to magnetic differences, 1.10% to temperature differences, and  $-0.60\%$  to coastal distances (Figure 3; Table S2).

These findings provide an important test of the hypothesis that genetic structure in populations may be shaped by magnetic-based navigation. Brothers and Lohmann<sup>40</sup> developed this hypothesis from genetic patterns in mtDNA of female loggerhead sea turtles nesting across the peninsula of Florida. Our study extends this initial work by analyzing nDNA and mtDNA from both sexes of a shark species across a wider geographic area (Figure 3A). We find that magnetic differences account for more variation in mtDNA than temperature differences or coastal distance, but in nDNA, a similar amount of variation is explained by each of these variables. This result is consistent with an earlier study assessing the genomic diversity of bonnetheads in the eastern Gulf of Mexico and US Atlantic.<sup>42</sup> Genetic markers putatively under selection were associated with latitude, while neutral markers were more correlated to distance.<sup>42</sup> The authors speculated that patterns observed at loci under selection were due to site fidelity of breeding females and localized adaptation, while patterns observed in the neutral markers reflected gene flow resultant of nomadic males. It is likely that our observations are due to the magnetic similarities between locations that were originally colonized by females, with philopatry to these locations driving the observed patterns in maternally inherited mtDNA. As with sea turtles, this effect results from Florida's peninsula, where geographically distant sites can be more magnetically similar than those that are closer.<sup>40</sup> Over evolutionary timescales, the nomadic tendencies of males, which contributes to patterns of genetic variance in bi-parentally inherited nDNA, likely accounts for coastal distance and temperature difference contributing similarly to magnetic differences in the microsatellite dataset. It is important to note that all three variables are correlated and distinguishing the relative importance of each factor is difficult. We encourage future studies in which geographic sites are not simply sampled opportunistically but specifically chosen so that these three variables show different trends across locations, and their relative contributions to observed genetic population structure can be more clearly assessed.<sup>2</sup>

Even so, our experiment provides evidence that sharks have a magnetic map that is used for orientation and that this ability may contribute to population-level processes. These findings complement recent research that has shown elasmobranchs likely have a polarity-based magnetic compass.<sup>15</sup> The combination of magnetic map and compass senses would likely be highly adaptive and allow the evolution of complex movement patterns that are a hallmark of elasmobranch life histories. Our results are significant because for 50 years researchers have highlighted the importance of determining whether sharks and rays use the GMF to aid in orientation and navigation.<sup>15–17,21</sup> Multiple species of elasmobranchs have been shown capable of detecting various components of the magnetic field,<sup>13,15,17,19,22</sup> and this research provides ecologic context for how these abilities may be used.

The use of magnetic maps appears to be a fundamental tactic of how marine animals migrate,<sup>2</sup> and we have added evidence that this is also the case for an ecologically important taxonomic group. To date, most studies on magnetic-based



**Figure 3. Relationships between genetic structure of bonnetheads in the northwest Atlantic Ocean relative to the geomagnetic field**

(A) Sites where genetic samples were obtained for bonnetheads. Circles with crosses, nDNA; circles with x's, mtDNA. Map conventions as in Figure 2.

(B) Results of variation partitioning procedures for multiple linear regression in predicting  $F_{ST}$  values for nDNA (light gray bars) and  $\Phi_{ST}$  values for mtDNA (dark gray bars) based on the maximum percentage of magnetic difference, the mean annual sea surface temperature difference, and the coastal distance between sites.

See Tables S2, S4, and S5.

navigation in marine animals have relied on species with either a terrestrial or freshwater component of their life cycles (e.g., sea turtles, salmonids, anguillid eels). Our findings suggest that the same sensory basis for navigation extends to fully marine taxa as well. This work points to a solution for a major puzzle in biogeography: how are migratory routes and population structure maintained in marine environments, where few physical barriers limit movements of vagile species? The ability for marine animals to discriminate different oceanic regions using geomagnetic cues is a possible answer.<sup>2,4</sup> Moreover, the importance of magnetic maps in the spatial ecology of animals likely extends well beyond migratory marine taxa. The use of magnetic maps appears to be a widely shared trait in species that occupy a variety of habitats, possess divergent life history strategies, and move over a wide range of spatial scales.<sup>39,43,44</sup>

Our work adds to the growing body of literature that the map-like use of the GMF is an evolutionary underpinning for how animals across a variety of taxa successfully derive spatial information from diverse habitats.

## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact
  - Materials availability
  - Data and code availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
  - Experimental design and magnetic field treatments
  - Behavioral trials and analysis
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Genetic structure of bonnetheads

## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2021.03.103>.

A video abstract is available at <https://doi.org/10.1016/j.cub.2021.03.103#mmc3>.

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## AUTHOR CONTRIBUTIONS

B.A.K., N.F.P., R.D.G., and T.P.M. conceived the experiment and designed the project. All of the authors assisted with the formal analysis and contributed written sections. B.A.K. secured the funding and conducted the field work. N.F.P., B.A.K., D.S.P., and R.D.G. conducted the population structure analyses. The authors are listed in the order of their contributions to the study.

## DECLARATION OF INTERESTS

The authors declare no competing interests. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect the views of NOAA or the US Department of Commerce.

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## STAR★METHODS

### KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
<b>Deposited data</b>		
Raw and analyzed data	This paper	N/A
Temperature data	Optimum Interpolation Sea Surface Temperature (OISST) v2.0, NOAA	<a href="https://www.ncdc.noaa.gov/oisst/optimum-interpolation-sea-surface-temperature-oisst-v20">https://www.ncdc.noaa.gov/oisst/optimum-interpolation-sea-surface-temperature-oisst-v20</a>
Geomagnetic Data	National Centers for Environmental Information, NOAA	<a href="https://www.ngdc.noaa.gov/geomag/">https://www.ngdc.noaa.gov/geomag/</a>
Genetics data on bonnethead population structure	<a href="#">23–26</a>	<a href="https://doi.org/10.1371/journal.pone.0220737">https://doi.org/10.1371/journal.pone.0220737</a> , <a href="https://doi.org/10.1093/jhered/esv030">https://doi.org/10.1093/jhered/esv030</a> , <a href="https://doi.org/10.1111/jfb.13025">https://doi.org/10.1111/jfb.13025</a> , <a href="https://doi.org/10.1002/aqc.3434">https://doi.org/10.1002/aqc.3434</a>
<b>Experimental models: organisms/strains</b>		
Bonnetheads, <i>Sphyrna tiburo</i>	Turkey Point Shoal, FL	N/A
<b>Software and algorithms</b>		
ImageJ	<a href="#">45</a>	<a href="https://imagej.nih.gov">https://imagej.nih.gov</a>
MtrackJ	<a href="#">46</a>	<a href="https://imagescience.org/meijering/software/mtrackj/">https://imagescience.org/meijering/software/mtrackj/</a>
Excel	Microsoft Office	<a href="https://www.microsoft.com/en-us/microsoft-365/excel">https://www.microsoft.com/en-us/microsoft-365/excel</a>
Oriana 4.0	Kovach Computing Services	<a href="https://www.kovcomp.co.uk/oriana/">https://www.kovcomp.co.uk/oriana/</a>
Google Earth	Google	<a href="https://www.google.com/earth/">https://www.google.com/earth/</a>

### RESOURCE AVAILABILITY

#### Lead contact

Further information and requests should be directed to and will be fulfilled by the Lead Contact, Bryan Keller ([bryan.keller@noaa.gov](mailto:bryan.keller@noaa.gov))

#### Materials availability

This study did not generate reagents.

#### Data and code availability

The published report and supplementary information include all datasets generated or analyzed during this study.

### EXPERIMENTAL MODEL AND SUBJECT DETAILS

The use of animals conducted in accordance with institutional guidelines and approved under Florida State University Institutional Animal Care and Use Committee protocol #1737. Data pertaining the individual sharks used can be found throughout the manuscript and in the supplementary information. Sharks were collected from Turkey Point Shoal (29.887°N, 84.511°W; [Table S1](#)), within 5 km of the Florida State University Coastal and Marine Lab, from Apr 2018 to Jul 2019. We captured sharks with an experimental gillnet consisting of three panels, each 30.5 m long by 3.05 m tall, with stretched mesh measuring 7.62 cm, 8.89 cm and 10.16 cm, respectively. The gillnet was anchored on both ends and marked with surface buoys. We closely monitored the gillnet, checking the entire net every 15 minutes or upon hearing a splash. Captured Bonnetheads were immediately removed from the gillnet and measured on-board our research vessel. Sharks that were less than 58 cm in fork length (tip of cephalofoil to fork in caudal fin) were placed in a



transport tank and brought back to the FSU Coastal and Marine Lab. All other animals were released. Sharks were kept in a 9,500 L holding tank supplied by a closely monitored flow through system connected to St. George Sound. We monitored dissolved oxygen, salinity, ammonia, nitrate and nitrite to ensure levels mirrored those in the adjacent bay.

All sharks were fed frozen squid at 3% body weight per day, as is common for captive elasmobranchs.<sup>15</sup> Sharks were never fed the morning of trials and were rested for at least one day between trials.

## METHOD DETAILS

### Experimental design and magnetic field treatments

We followed established methodologies,<sup>9</sup> which exposed animals to “magnetic displacements” whereby the magnetic field around animals was precisely manipulated using a series of Merritt coils.<sup>36</sup> We built two orthogonal four-coil systems with 14 AWG solid copper wire, which were independently manipulated to control the horizontal and vertical magnetic field. The two coil systems were aligned to 0° Magnetic North. The vertical coil system (side length,  $d = 293$  cm) controlled the horizontal component of the magnetic field and the horizontal coil system (side length,  $d = 268$  cm) controlled the vertical component of the magnetic field. Each coil system was connected to an adjustable DC power supply (Korad, KD3005D), which allow us to independently modify each field.

Due to the dimensions of our coil-systems the most uniform area of the magnetic field was  $\sim 117$  cm wide by  $\sim 107$  cm tall and our 790 L experimental tank was placed within these confines in the cube. The tank was centered within the cube, with the base being 83 cm from the frames of the horizontal coil system. We measured the resulting magnetic fields in the tank with a tri-axial magnetometer (Alpha Lab, MR3) to ensure that field uniformity was at or better than 3% across the arena.

To test our sharks, we created three magnetic fields: 1) a southern treatment representing a location  $\sim 600$  km south of the capture locations, 2) a control treatment representing locations at the shark’s capture location and 3) a northern treatment representing locations  $\sim 600$  km north of the shark’s capture location. To account for secular variation (gradual drift) in the magnetic field, we modified the magnetic field intensity and inclination for our treatments between study years to maintain the same relative differences in intensity and inclination from the year prior. The intensity and inclination for each treatment for both years can be found in [Table 1](#).

### Behavioral trials and analysis

Sharks were kept in captivity for two weeks to acclimate to captive conditions before any trials were conducted. For behavioral trials, the test tank was filled with seawater from the holding tank. An air stone was installed in the middle of the tank’s bottom surface and  $O_2$  aerated the tank. We verified the tank was centered within the cube and then placed a Go Pro camera above the coil system to record trials. Sharks underwent two acclimation days where they were individually placed in the experimental tank for 15 minutes with the control field activated (the total field intensity and inclination angle at the sharks capture location). No data were collected from these trials. This acclimation process was to familiarize the sharks with the experimental procedure, which is common in behavioral trials.<sup>47</sup> After each shark went through two acclimation trials, we began the three treatment trials.

The three treatments were a control (as described above), a southern treatment (the total field intensity and inclination angle  $\sim 600$  km south of the capture location), and a northern treatment (the total field intensity and inclination angle  $\sim 600$  km north of capture location). Each of the 20 sharks was tested in each of the three treatments, the order of which were randomized. Trials were 15-minutes long and began with a 5-minute acclimation to the control field. For the control treatment, the magnetic field then remained unchanged. For the northern and southern treatments, the magnetic field was switched after 5-minutes. After the field was switched (or at the 5-minute mark for the control treatment), we allowed the sharks 2.5 minutes to acclimate to the new field. Data collection then occurred up until 15 minutes had transpired from the trial’s start. Magnetic conditions within the testing arena were confirmed each trial day with a three-dimensional magnetometer (MR3, Alpha Lab). All trials occurred during daylight hours during July-August of 2018 and 2019.

A reoccurring critique of a previous study examining magnetoreception in sharks<sup>22</sup> was that possible electric artifacts could be responsible for the observed behavioral responses.<sup>6</sup> Recent research showed a transient in the applied field within 2 ms of a field switch and demonstrated this was unlikely to affect the shark’s behavior.<sup>17</sup> In order to remove this possible source of uncertainty we integrated measures to reduce any systematic errors resulting from potential electrical artifacts. Our Merritt coil system was offset 0.75 m between the coils and our tank, which helped decouple electrical and mechanical artifacts resulting from coil operations. Furthermore, we incorporated a latency period of 2.5 minutes after changing the field before data collection occurred. Lastly, at least 0.103 A was always supplied to the coils to remove the possibility of magnetic field transients being created by energizing the power supply and to recreate the magnetic field at the capture site. When DC power supplies are energized there is an inrush current into the power supply’s transformer that results in a transient, or spike in the output current. The value of this transient is difficult to reproduce since it depends on what part of the 60 Hz, 120 VAC, sinewave that is passing through the primary side of the transformer when the power switch closes.

## QUANTIFICATION AND STATISTICAL ANALYSIS

We analyzed our trials using the GoPro footage obtained from the camera above the coil system. Videos were imported into ImageJ<sup>45</sup> and sharks were tracked with MtrackJ.<sup>46</sup> To track sharks, we placed a point on the shark’s cephalofoil every second during the data collection process. These tracking data were then uploaded to Excel and standardized to circular data, with the center of the tank

representing coordinates (0,0) and with x and y values ranging from  $-1$  to  $1$ . These points were then translated to headings. The average heading per shark per trial was then calculated (Table S3). We then used a Rayleigh test per treatment to determine if there was a statistically significant mean direction for the unweighted headings. Finally, we conducted a pairwise comparison between the control treatment and each of the displacement fields using a paired Hotelling's test to determine if orientation differed in response to the change in magnetic conditions. All statistical tests were carried out in Oriana 4.0. Statistical details can be found in the Results and discussion section of the main text. Significance was set at alpha ( $\alpha$ ) equal to 0.05. In each test, "n" represents the number of sharks used per trial. We used the same 20 sharks for each trial and thus  $n = 20$ .

### Genetic structure of bonnetheads

If Bonnetheads use geomagnetic cues as a proxy for geographic position, it is possible that genetic differences between populations of sharks might be predicted by spatial variation in the GMF.<sup>40</sup> Over evolutionary timescales some individual sharks will disperse from natal areas, but dispersal is non-random; movement is more likely to locations that are geographically closer or have habitat characteristics similar to the natal site. Additionally, if sharks use a magnetic map to assess where they are, then when navigational errors are made or when storms or other disturbances cause sharks to depart from an area, sharks may be more likely to travel to (or remain at) sites that are more magnetically similar to their home than sites that are more magnetically different. We tested this hypothesis using location and genetic data from four published datasets from studies examining Bonnethead population structure in the north-western Atlantic that differed in geographic sampling locations and the portion of the genome sampled.<sup>23–26</sup> Regions of the genome included the control region of the mitochondrial genome (mtDNA)<sup>23–25</sup> and nuclear-encoded microsatellite loci (nDNA).<sup>26</sup> Each dataset contained comparisons within and between distinct geographic/genetic regions; we restricted our analysis to comparisons within regions, as divergence saturation becomes problematic across hierarchically structured populations at large geographic scales. We retained comparisons between Belize and Panama<sup>23</sup> and Campeche, MX and Tabasco, MX<sup>24,26</sup> as these comparisons were considered within region. Given the sensitivity of inferred genetic relationships to geographic sampling and the portion of the genome analyzed, we considered each dataset separately. Genetic distances between geographic locations (from reported  $F_{ST}$  values for nDNA and  $\Phi_{ST}$  values for mtDNA) were compared against pairwise differences in temperature, coastal distance, and the magnetic field. Any reported value of  $F_{ST}$  or  $\Phi_{ST}$  that was negative (indicating no population differentiation) was changed to 0.

Temperature is directly related to the physiology (e.g., metabolism and growth) and ecology (e.g., timing of migration and duration of residency) of sharks and is correlated with a suite of environmental variables.<sup>38</sup> Thus, we used mean sea surface temperature (SST) calculated between 1982 and 2019 (<https://www.ncdc.noaa.gov/oisst/optimum-interpolation-sea-surface-temperature-oisst-v20>) at each site as a proxy for oceanographic conditions that could relate to population structure in Bonnetheads. To assess pairwise differences between geographic locations we took the absolute value of the temperature difference between sites and divided it by the mean temperature of all sites. Geographic distances along the coastline (referred to as coastal distance) between each pair of sites were estimated using the "path tool" in Google Earth (<https://www.google.com/earth/>). Distances between the north-eastern sites (e.g., North Carolina, South Carolina, Florida) and the Caribbean sites (e.g., Belize, Panama) were measured assuming the animals swam along the coastline up to the Florida Keys, USA or Cancun, Mexico and then took a direct overwater path that crossed the Straits of Florida and Yucatan Channel. Distance between Grand Bahama and other sites was calculated assuming the sharks swam the shortest possible path over the Gulf Stream and then up or down the Florida coastline accordingly. To determine differences in the magnetic field between each pair of sites, we first calculated the mean total field intensity and the mean inclination angle for the years 1590–1990 at 50-year intervals for each location using the gufm1 and IGRF models (<https://www.ngdc.noaa.gov/geomag/>). We then took the absolute value of the difference in intensity and inclination for each pair of sites and divided it by the mean intensity and inclination for all sites to determine the percent difference in magnetic intensity and the percent difference in magnetic inclination. Given that loggerhead sea turtles, Chinook Salmon, and European Eels are known to independently detect intensity and inclination,<sup>2</sup> we assumed that locations could be differentiated by either of these magnetic parameters and thus selected the magnetic parameter with the higher percent difference as the value for comparison to  $\Phi_{ST}$  or  $F_{ST}$ .

We then separately analyzed each of the datasets using standard multiple linear regression and variance partitioning procedures to determine how well temperature differences, coastal distance, and magnetic differences between sites predicted genetic distance in Bonnetheads. As the nuclear and mitochondrial genomes may be influenced by different selective and demographic processes,<sup>42</sup> we present the results for these separately (Table S2). To summarize findings across the three mtDNA datasets we calculated a weighted average of the adjusted  $R^2$  values obtained for each independent variable and all/some combinations of them (Table S2). Likewise, we calculated the variation uniquely attributable to these three variables as well as that attributable to their combined interaction for each study (Tables S4 and S5). Weighting was based on the number of pairwise comparisons (datasets with more geographic sites received a greater weight; Tables S4 and S5).