EVIDENCE THAT FIN WHALES RESPOND TO THE GEOMAGNETIC FIELD DURING MIGRATION

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Summary

We challenge the hypothesis that fin whales use a magnetic sense to guide migration by testing for associations between geophysical parameters and the positions where fin whales were observed over the continental shelf off the northeastern United States. Monte Carlo simulations estimated the probability that the distribution of fin whale sightings was random with respect to bottom depth, bottom slope and the intensity and gradient of the geomagnetic field. The simulations demonstrated no overall association of sighting positions with any of these four geophysical parameters. Analysis of the data by season, however, demonstrated statistically reliable associations of sighting positions with areas of low geomagnetic intensity and gradient in winter and fall, respectively, but no association of sighting positions with bathymetric parameters in any season. An attempt to focus on migrating animals by excluding those observed feeding confirmed the associations of sighting positions with low geomagnetic intensity and gradient in winter and fall, respectively, and revealed additional associations with low geomagnetic gradients in winter and spring. These results are consistent with the hypothesis that fin whales, and perhaps other mysticete species, possess a magnetic sense that they use to guide migration.

Introduction

Because little is known about how some marine animals navigate over long distances, it is necessary to identify environmental stimuli that animals might use to guide their movements in the deep ocean (Harden Jones, 1968). Many of the stimuli commonly considered to provide directional and positional information are unavailable to marine animals travelling in the deep ocean because (1) the animals

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do not possess the necessary sensory modality (e.g. olfaction in cetaceans), (2) the sensory modality exists but does not exhibit the sensitivity necessary to provide useful information to the animal [e.g. temperature sensitivity in tuna (Steffel et al. 1976)], or (3) the stimulus is out of sensory contact (e.g. bottom topography in the deep ocean). One possible stimulus is the geomagnetic field, which provides a great deal of stable positional and directional information (Skiles, 1985), although behavioral evidence for any ability of animals to detect the geomagnetic field has been sparse and poorly documented until only recently.

During the last twenty years, laboratory orientation and conditioning experiments have demonstrated that many migratory and homing animals respond to the direction or some feature related to the intensity of the geomagnetic field, or to both of these parameters. For example, migratory birds placed in featureless arenas exhibit preferences for orientation in seasonally appropriate directions that can be controlled experimentally by systematic variation of magnetic field direction (Wiltschko, 1972; Emlen, 1975), and fish (Kalmijn, 1981; Walker, 1984) and honeybees (Walker and Bitterman, 1985, 1989a,b; Walker et al. 1989) have been conditioned to respond to a variety of different magnetic field stimuli. In addition, involvement of magnetic field stimuli in pigeon homing has been demonstrated by comparing the homing performance of pigeons with magnets or coils mounted on their heads with that of control birds (Keeton, 1971, 1972; Walcott and Green, 1974) or by releasing the birds at local geomagnetic field anomalies (Walcott, 1978). These results have led to renewed interest in the hypothesis that animals use the geomagnetic field to guide their long-distance movements, particularly where they cannot use other stimuli.

An important step towards indirectly demonstrating the operation of a magnetic sense in cetaceans was taken by Klinowska (1985), who reasoned that otherwise healthy whales that strand themselves alive must have made a serious navigational mistake and that analyzing the circumstances surrounding such strandings might identify the sensory modality responsible for the error. After she had plotted live stranding positions on magnetic field maps of the coast of Great Britain, Klinowska (1985) observed an association between stranding positions and areas where magnetic minima intersect the coast, and suggested that cetaceans possess a magnetic sensory system. Kirschvink and his colleagues (Kirschvink et al. 1986; Kirschvink, 1990) extended Klinowska's work. They mapped stranding positions from a computerized data set onto digital aeromagnetic data for the east coast of the United States and then developed procedures that demonstrated statistically reliable associations of stranding sites with locations where magnetic minima intersected the coast. Total intensity variations of as little as 50 nanoTesla (nT; 0.1 % of the total field) were sufficient to influence stranding location (Kirschvink et al. 1986; Kirschvink, 1990).

If a magnetic sense is used by whales at sea to guide their migrations, it should be possible to demonstrate evidence of differential responses to the geomagnetic field. The assumption of such correlative studies is that responses by the animals to important environmental stimuli, including the geomagnetic field, should be

detectable as statistical associations of sighting positions with spatial variations in the properties of the stimuli. It is necessary to use a statistical approach in order to overcome the difficulty that the geomagnetic field is but one of many physical and biological stimuli, and there is no way to recognize or measure behavioral responses to the field by individual animals.

To test for geomagnetic sensitivity in whales, we needed rigorously collected sighting position data for a species that undertakes regular migrations in an area for which there are sufficient magnetic and bathymetric data. We obtained a computerized data set recording the positions where fin whales were observed at sea during dedicated aerial surveys together with digital geomagnetic and bathymetric data for the coast and continental shelf of the northeastern United States. We then did Monte Carlo simulations to test the null hypothesis that the whale positions were random with respect to geomagnetic and bathymetric parameters. Subsequent simulations tested whether there was any temporal pattern to the associations that could be related to known migratory behavior. Our results suggest that fin whales recognize and associate with geomagnetic field features independently of other geophysical stimuli and that their association with geomagnetic field features is correlated with seasonal migration patterns.

Data and methods

Sighting data

The Cetacean and Turtle Assessment Program (CETAP) was sponsored by the Bureau of Land Management and conducted between October 1978 and January 1982 by the University of Rhode Island in outer continental shelf (OCS) waters of the northeastern United States from Cape Hatteras, North Carolina, to the Gulf of Maine and from shore to 9.3 km (5 nautical miles) seaward of the 1829 m (1000 fathoms) isobath. Population surveys were conducted by CETAP to assess the distribution and abundance of whales, dolphins and sea turtles inhabiting the OCS. Each survey flew a series of parallel aerial transects selected randomly from a pool of lines running northwest–southeast and spaced at 3.7 km (2 nautical mile) intervals. Observers on the surveys collected both meteorological and behavioral observations, the latter involving identifying, counting and recording positions and making notes on the behavior of the whales and other animals observed during the flights. The entire CETAP data base included nearly 70000 entries and 112 variables. (For a more complete description of the data and methods of collection employed see Kenney and Winn, 1986.)

Geophysical data

The magnetic anomaly data were obtained in high-density gridded digital format from the Geological Society of North America's Decade of North American Geology (DNAG) program. The DNAG data set, which is distributed by the NOAA Geophysical Data Center, includes all the CETAP study area. The survey also covers most of the North American continent and extends over the Atlantic

and Pacific Oceans. Using the new Definitive Geomagnetic Reference Field, the data were compiled and merged at different levels from the following sources: original shiptrack data, flight line data, gridded data and compiled regional maps. All data are in Universal Transverse Mercator coordinates and are gridded at 2 km intervals. All the magnetic intensity data were given a positive offset to produce net values of field intensity that were positive and would fit in two bytes of memory (integer×2) on a micro-VAX II computer system.

The intensity data then were mapped onto a 512×512 array of picture elements (pixels). The field gradient at each point in the array was determined by calculating the mean difference between the field intensity at each pixel and the intensity at each of the eight adjacent pixels. The gradient data were then mapped onto the array and plotted as the image shown in Fig. 1, with the gradient at each pixel being assigned a color shade ranging from blue (lowest) to yellow (highest).

A similar procedure was followed with bathymetric data for the region taken from the Digital Bathymetric Data Base, which we obtained from the National Geophysical Data Center. Using this data set, which contains over 7.8×10^6 data values on a 5' (0.083°) grid, we were able to assign a value for the bottom depth to each pixel in the array. The bottom slope at each pixel was calculated in the same way as the magnetic field gradient was calculated from the magnetic intensity data. We were thus able to produce pixel by pixel matches to the geomagnetic data for two bathymetric parameters over the CETAP study area and to prepare images of bathymetric parameters like those produced for the magnetic data (Fig. 1; Kirschvink et al. 1986).

Biological and geophysical constraints on the study area

The key conclusions of the CETAP study for our work were that the Gulf of Maine is an important summer feeding area for mysticete whales, and that several mysticete species migrate there during spring from winter habitats in the deep ocean or to the south of the Gulf of Maine (Kenney and Winn, 1986). Little is known about mysticete migration patterns except that the whales generally spend winter in breeding grounds in low latitudes, move north (in the northern hemisphere) to higher latitudes during spring and summer to enter feeding grounds, and return south to lower latitudes during fall (Gaskin, 1976). Of species observed in the CETAP surveys, only the fin whales were observed outside the Gulf of Maine in numbers large enough for analysis. Migration through the area south of the Gulf of Maine could be inferred only from latitudinal shifts in peak abundance of sightings in different seasons (Winn and Edel, 1982). Other mysticete species were usually first seen entering the Gulf of Maine and made little use of the continental shelf and slope between Cape Hatteras and Cape Cod (Kenney and Winn, 1986). A variety of odontocete species, such as pilot whales, that were common in the CETAP area were excluded from the study because they gave no evidence of migration (Winn and Edel, 1982) or were associated primarily with the continental margin and slope rather than with the continental shelf (see below).

Fig. 1. Sighting positions (all seasons) for fin whales superimposed on an image of magnetic field intensity gradients over the outer continental shelf off the northeastern United States. Magnetic data are from the DNAG data set. Sighting positions from the CETAP dedicated aerial surveys are indicated by red crosses. Magnetic field gradients are indicated by shading, with 256 steps between minimum (blue) and maximum (yellow) gradients. The dark east–west line indicates latitude 41°N.

The areas covered by the geophysical and sighting data sets and the uses made by fin whales of different parts of the CETAP study area placed two important constraints on our study. First, magnetic and bathymetric data are correlated where the continental margin (indicated by the East Coast Magnetic Anomaly running parallel to the coastline in Fig. 1; see also Fig. 1 of Kirschvink *et al.* 1986) and continental slope (182.9–1829 m depth) coincide. Second, the Gulf of Maine is a summer feeding ground for mysticete whales (Kenney and Winn, 1986), which means that the distribution of sightings was highly likely to be controlled by the distribution of prey organisms. Fin whale sightings in the Gulf of Maine were aggregated and the animals were often observed feeding. By contrast, sightings in the area south of the Gulf of Maine could be treated as independent of each other because the observed frequencies of sightings per pixel gave a variance to mean ratio of 1.062 and fitted expected Poisson frequencies (goodness of fit $\chi_2^2=3.47$, $P>0.1$; Pielou, 1969). Feeding by fin whales was observed only rarely outside the Gulf of Maine. We therefore restricted our analyses to testing for associations of sightings with geomagnetic and bathymetric parameters over the continental shelf (<182.9 m depth) south of 41°N, which we used to mark the southern limit of the Gulf of Maine.

Monte Carlo simulations

We did Monte Carlo simulations to test the hypothesis that fin whale sighting positions in the southern region of the CETAP study area were associated with one or more of the geophysical parameters (geomagnetic field intensity and gradient; bottom depth and slope). The simulations were made by generating a set of random sighting positions along each CETAP flight track. Each track received the same number of observations as was present in the original CETAP survey and, where flight tracks passed outside the boundaries of the study area, the number of positions assigned was reduced to match the number of real positions found within the study area. The means and variances of magnetic field intensity, magnetic field gradient, depth and bottom slope for the simulated positions were then computed and the results from 1000 or more such simulations compared with those obtained from the original data. A mean value for any of the geophysical parameters at real sighting positions that was greater (or less) than 975 out of 1000 mean values for simulated positions gave a two-tailed probability of 0.05 that the sighting positions were non-randomly associated with the geophysical parameter.

In subsequent simulations, we partitioned the sighting data to test for the influence of season and behavior on associations of sighting positions with geophysical parameters. We did simulations after sorting the data by calendar months (trimesters) corresponding to the seasons: winter was December–February, spring was March–May, summer was June–August and fall was September–November. We then did simulations in which the data were sorted by season and behavior. Animals observed feeding or in behavior associated with feeding were excluded from the simulations on the assumption that the positions where such animals were observed would be controlled by the distribution of their

prey organisms. Final sample sizes resulting from these treatments ranged from 7 (fall) to 31 (spring) per trimester for fin whales sighted in the study area.

Results

The Monte Carlo simulations made with all sightings included (summarized in Table 1) demonstrated no overall association of fin whale sighting positions with any geophysical parameter tested. Monte Carlo simulations (summarized in Table 2A) testing for the influence of season on the distribution of sighting positions with respect to the four geophysical parameters, however, demonstrated a series of associations of fin whale sighting positions with geomagnetic but not with bathymetric parameters. Sighting positions were associated with areas of high geomagnetic field gradient ($P=0.02$) during summer but low intensity in winter ($P=0.02$) and low gradient in fall ($P=0.008$).

Further simulations (summarized in Table 2B) in which animals observed feeding were excluded from the analysis demonstrated associations of sighting positions only with low geomagnetic gradients and intensity. The simulations for the fall trimester were not affected because no animals were observed feeding. The new simulations also had little effect on the result for geomagnetic intensity in winter ($P=0.034$) as only one animal had been excluded. After exclusion of feeding animals, the simulations demonstrated further associations of sightings with low geomagnetic field gradients in the spring ($P=0.024$) and winter ($P=0.038$) trimesters but, again, no association of sighting positions with bathymetric parameters. In contrast, exclusion of a single observation of feeding removed the significant association of sighting positions with areas of high geomagnetic field gradient during summer.

Table 1. *Results of Monte Carlo simulations used in two-tailed tests of the hypothesis that the mean values of the geophysical parameters at positions where fin whales were sighted were significantly different from the mean values of the parameters at simulated sighting positions on the CETAP flight tracks*

Parameter	N	Mean actual positions	Mean simulated positions	P
Bottom depth	94	58.4	58.5	0.638
Bottom slope	94	298.6	316.5	0.346
Field intensity	94	1841.1	1858.8	0.068
Field gradient	94	110.7	120.7	0.700

Mean values for each parameter at actual and simulated sighting positions are shown in the middle columns of the table.

N, number of sightings.

Probabilities (P) given in the right-hand column of the table are that the mean values of the geophysical parameters for the simulated positions that are equal to or lower than the mean values for the parameters at actual sighting positions could be obtained by chance.

Table 2A. *Results of Monte Carlo simulations used in two-tailed tests of the hypothesis that the mean values of the geophysical parameters at positions where fin whales were sighted in different seasons were significantly different from the mean values of the parameters at simulated sighting positions on the CETAP flight tracks*

Parameter	All	Winter	Spring	Summer	Fall
Number of sightings	94	16	41	30	7
Bottom depth	0.638	>0.1	>0.1	>0.1	>0.1
Bottom slope	0.346	>0.1	>0.1	>0.1	>0.1
Field intensity	0.068	0.020	>0.1	>0.1	>0.1
Field gradient	0.700	0.092	0.088	>0.1*	0.008

*The mean value for magnetic field gradient at sighting positions in summer was higher than would have been expected from chance ($P=0.02$).

The probabilities for all seasons combined are the same as those in the last column of Table 1.

B. *Results of simulations made with animals observed feeding or in behavior associated with feeding excluded from the analysis*

Parameter	All	Winter	Spring	Summer	Fall
Number of sightings	82	15	31	29	7
Bottom depth	>0.1	>0.1	>0.1	>0.1	>0.1
Bottom slope	>0.1	>0.1	>0.1	>0.1	>0.1
Field intensity	>0.1	0.034	>0.1	>0.1	>0.1
Field gradient	>0.1	0.038	0.024	>0.1	0.008

Cells in the table contain estimates of the probabilities that the mean values of the geophysical parameters for the simulated positions that are equal to or lower than the mean values for the parameters at actual sighting positions could be obtained by chance.

Frequency histograms of the values for the magnetic field intensity and magnetic field gradient at pixels on the tracks flown by the CETAP in the winter, spring and fall are plotted in Fig. 2A–D. Pixels in which fin whales were sighted are indicated by the shaded portions of the histograms and represent only a very small proportion (1–2%) of the total sample of pixels in all seasons except for the fall. Evidence that pixels containing whale sightings comprise a non-random subset of the pixels on the flight tracks would be expected to appear as a displacement of each distribution above or below the distribution for all pixels.

The patterns of the distributions shown in Fig. 2 are consistent with the results of the Monte Carlo simulations. The medians and arithmetic means of the distributions of pixels with whales all occurred at lower values than did those of the distributions for pixels on the flight tracks. For example, the arithmetic mean value for magnetic intensity for pixels with whales was approximately 100 nT lower than for all pixels on the flight tracks in winter (Fig. 2A). Similarly, the arithmetic mean values for magnetic gradient for pixels with whales were between 25 % and 45 % (30–40 units) below the mean gradient values for all pixels on the flight tracks
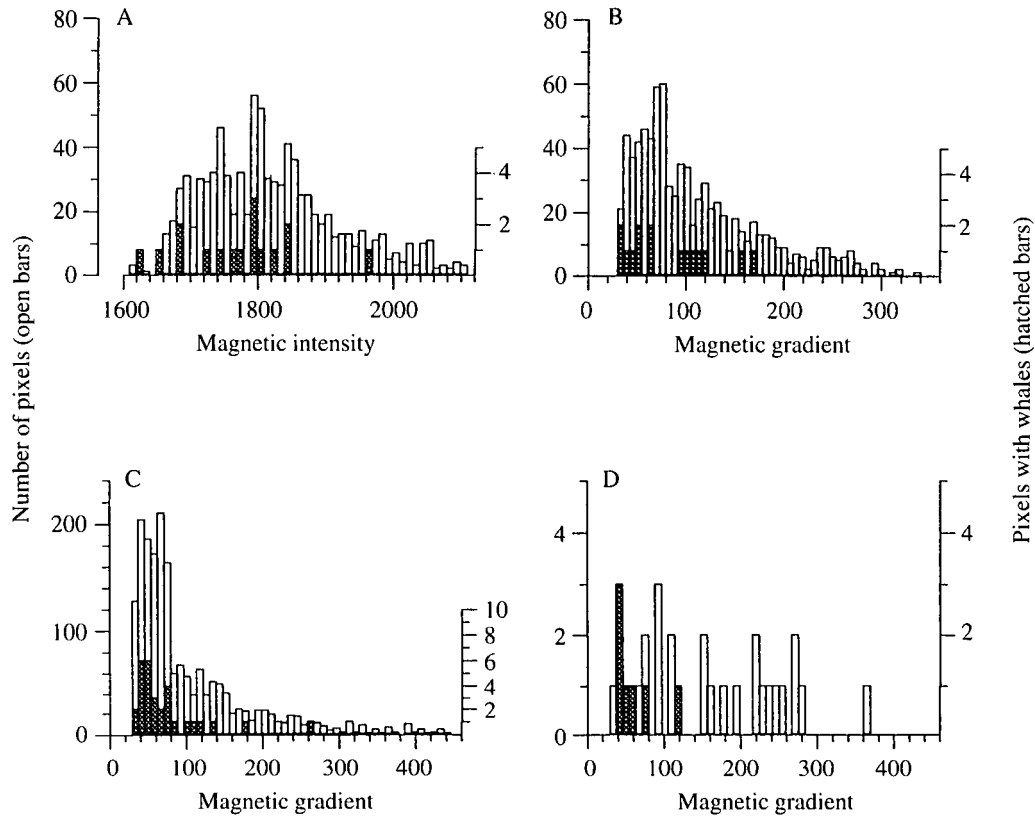
Fig. 2. Frequency distributions of (A) geomagnetic field intensity at pixels lying along all the tracks flown in winter in the study area; (B–D) geomagnetic field gradient at pixels lying along all the tracks flown in winter (B), spring (C) and fall (D) in the study area. The shaded portions of the histograms indicate (on the scale shown on the right-hand ordinate) the distribution of values of the parameters at the pixels in which non-feeding fin whales were observed.

in winter, spring and fall (Fig. 2B–D). As might be expected from the results of the simulations, the distributions of the pixels containing whales were also truncated at high values. In the four frequency histograms in Fig. 2, no more than one pixel with whales was observed in the upper half of the range of each histogram where at least 2–5 would have been expected if sightings had been randomly distributed with regard to the geomagnetic parameters.

Discussion

Although there was no previous experimental evidence for magnetic sensitivity in whales, our results are consistent with the hypothesis that fin whales possess a magnetic sense and that they use it to travel in areas of low geomagnetic field gradient and possibly low magnetic intensity during migration. We began our

study with the most straightforward analysis possible with our data – using all sightings of fin whales made by the CETAP in the area south of 41°N – and proceeded to more complex analyses in which we sorted the sighting data by season and behavior. The study showed (1) that the positions in the study area for fin whales not seen actively feeding were associated statistically with areas of low geomagnetic field gradient and (2) that these associations were correlated with the general pattern of the northward and southward migrations undertaken during spring and fall, respectively, by mysticete whales (Gaskin, 1976; Winn and Edel, 1982). Additional associations of the sightings with areas of low magnetic field intensity and gradient were demonstrated in winter. Taken together, these findings are consistent with earlier analyses of live strandings of whales, which showed that strandings occur most often in areas where magnetic minima – areas characterized by low magnetic field gradients and intensities – intersect the coast (Klinowska, 1985; Kirschvink, 1990; Kirschvink *et al.* 1986). The data used in this study, however, were free of the sampling biases to which the stranding data were subject (Mead, 1979) and reflected behavior in normal, rather than abnormal, situations.

It is worth noting that five of the 32 simulations gave statistically reliable evidence of association of sightings with geophysical parameters where no more than two would have been expected from chance and that all of the associations demonstrated were with magnetic field parameters. All of the tests were two-tailed and were made on the only species observed in the CETAP surveys for which we were able to test the sighting data. These observations make it highly unlikely that the positive results from our simulations could be statistical artifacts or could have arisen through chance.

We consider it unlikely that similar analyses would have demonstrated significant associations of sightings with other environmental stimuli that might guide migration by fin whales. No associations between sightings of any species of mysticete whales and other environmental stimuli were found in early studies that would indicate use of the stimuli to guide migration (reviewed in Dawbin, 1966). Although Winn and Edel (1982) reported associations between bathymetric parameters and positions for mysticete whales sighted in the Gulf of Maine during the CETAP surveys, no such associations were detected outside this area.

Although there is still no experimental evidence for a magnetic sense in whales, our results are consistent with a variety of experimental results from other species. For example, Walcott (1978) released homing pigeons at local geomagnetic field anomalies and found that the more complex the pattern of magnetic field intensity gradients on the route home, the more scattered were the bearings at which the birds vanished from view at the release site. In addition, spatial variations or gradients in magnetic field intensity and a requirement that the animals be moving appeared to have been responsible for discrimination in recent magnetic conditioning experiments with both tuna (Walker, 1984) and honeybees (Walker and Bitterman, 1985, 1989*a,b*; Walker *et al.* 1989).

Several possibilities for experimental study arise from this work. First, although

the transduction mechanism for responses to geomagnetic fields has yet to be identified, an obvious candidate is the particles of single-domain magnetite detected in the anterior dura mater of the humpback whale, *Megaptera novaeangliae* (Fuller *et al.* 1985). A magnetite-based system is the only one yet proposed for cetaceans that could provide the sensitivity necessary to permit detection of fluctuations in the geomagnetic field as low as 100 nT (Kirschvink and Gould, 1981; Kirschvink and Walker, 1985; Yorke, 1981). Second, a number of species, such as pilot whales, which figured prominently in the stranding studies (Klinowska, 1985; Kirschvink, 1990; Kirschvink *et al.* 1986), can be maintained in captivity. Behavioral experiments testing for response to magnetic field stimuli therefore may be possible with these species.

Such studies present formidable obstacles. As a consequence, we expect that correlation studies will be the only practical means available in the near future to test the hypothesis that cetaceans respond to the geomagnetic field. Kirschvink (Kirschvink *et al.* 1986; Kirschvink, 1990) has advanced the hypothesis that following magnetic minima may be a useful strategy for guiding long-distance movements. A prediction of this hypothesis is that, during north–south migrations in the deep ocean, mysticete whales should be observed more frequently over the magnetic minima formed by seafloor spreading than elsewhere. This prediction could be tested by survey and tracking studies over the deep ocean along the paths between the summer feeding and wintering grounds used by mysticete whales. It may be possible also to investigate associations of sighting positions with the geomagnetic field for odontocete whales over the deep ocean or in areas where the continental slope is not marked by a salient magnetic anomaly. One such area is the continental slope and deep ocean off the Pacific coast of the United States. Problems for such a study will be the limited movements of most odontocete species and the difficulty of identifying feeding animals. Until such surveys are made, work similar to ours can be done using presently available geomagnetic and sighting data sets. Such studies need not be confined to whales as similar data exist for sea turtles, other marine mammals and birds and can benefit from the methods developed thus far.

There is, therefore, a developing body of evidence that cetaceans possess a magnetic sense that they use to guide movement. Our study differed from the earlier stranding studies because we were able to test whether point values of the geomagnetic field intensity and gradient influenced the distribution of sightings, whereas the stranding studies tested whether measures of the 'shape' of the field along the coast influenced the distribution of strandings. The results obtained using the two types of measure were, however, quite similar to each other and also to field experiments with homing pigeons and conditioning experiments with fish and honeybees. We suggest that our approach may be useful for studying the contribution of a magnetic sense to the guidance of homing and migration in a variety of species.

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