Open-sea migration of magnetically disturbed sea turtles

Papi, F; Luschi, P; Åkesson, Susanne; Capogrossi, S; Hays, G C

Published in:
Journal of Experimental Biology

2000

Citation for published version (APA):
Papi, F., Luschi, P., Åkesson, S., Capogrossi, S., & Hays, G. C. (2000). Open-sea migration of magnetically disturbed sea turtles. *Journal of Experimental Biology*, *203*(22), 3435-3443. http://jeb.biologists.org/cgi/content/abstract/203/22/3435

Total number of authors:
5

The Journal of Experimental Biology 203, 3435–3443 (2000)
Printed in Great Britain © The Company of Biologists Limited 2000
JEB2805

OPEN-SEA MIGRATION OF MAGNETICALLY DISTURBED SEA TURTLES

F. PAPI[1,*], P. LUSCHI[1], S. ÅKESSON[2], S. CAPOGROSSI[3] AND G. C. HAYS[4]

[1]*Dipartimento di Etologia, Ecologia, Evoluzione, University of Pisa, Via A. Volta 6, I-56126 Pisa, Italy,*
[2]*Department of Animal Ecology, Lund University, Ecology Building, SE-223 62 Lund, Sweden,*
[3]*Centro di Studio per la Faunistica ed Ecologia Tropicali del CNR, Via Romana 17, I-50125 Firenze, Italy* and
[4]*School of Biological Sciences, University of Wales Swansea, Singleton Park, Swansea SA2 8PP, UK*

*e-mail: papi@discau.unipi.it

Accepted 21 August; published on WWW 24 October 2000

Summary

Green turtles (*Chelonia mydas*) that shuttle between their Brazilian feeding grounds and nesting beaches at Ascension Island in the middle of the Atlantic Ocean are a paradigmatic case of long-distance oceanic migrants. It has been suggested that they calculate their position and the direction of their target areas by using the inclination and intensity of the earth's magnetic field. To test this hypothesis, we tracked, by satellite, green turtles during their postnesting migration from Ascension Island to the Brazilian coast more than 2000 km away. Seven turtles were each fitted with six powerful static magnets attached in such a way as to produce variable artificial fields around the turtle that made reliance on a geomagnetic map impossible. The reconstructed courses were very similar to those of eight turtles without magnets that were tracked over the same period and in the previous year, and no differences between magnetically disrupted and untreated turtles were found as regards navigational performance and course straightness. These findings show that magnetic cues are not essential to turtles making the return trip to the Brazilian coast. The navigational mechanisms used by these turtles remain enigmatic.

Key words: green turtle, *Chelonia mydas*, migration, geomagnetic map, navigation.

Introduction

Marine animals belonging to various groups are able to find their way to distant, remote targets in the apparently featureless homogeneity of the ocean (Baker, 1977; Papi, 1992a). Satellite telemetry has revealed many features of the routes followed, which are often straight and direct (Papi and Luschi, 1996; McConnell and Fedak, 1996), but the mechanism(s) underlying such performances remain speculative. Sea turtles are particularly suitable for investigation because they can carry powerful satellite-linked transmitters during long migratory trips. The green turtles that nest at Ascension Island (7°57′S, 14°22′W) have long attracted the attention of zoologists because they undertake a very long migration (a round trip of at least 4400 km) shuttling between this island and their feeding grounds on the Brazilian coast (Carr, 1984; Mortimer and Carr, 1987). They have recently been tracked during their postnesting migration and have been shown to follow fairly straight routes towards the easternmost part of Brazil, the so-called Brazilian bulge (Luschi et al., 1998). Their navigational ability needs to be even more acute during the migration to Ascension, since this island is a tiny target. Unfortunately, logistical difficulties have so far prevented tracking over this part of the migratory journey.

The navigational performance of Ascension turtles has been a matter of considerable discussion. Some authors argue that simple compass orientation cannot explain how these turtles reach their goal because they would then be unable to compensate for current drift and inaccuracy in course steering, which can result in large deviations over long distances (Carr, 1984; Papi and Luschi, 1996; Luschi et al., 1998). The involvement of more sophisticated mechanisms of navigation has therefore been proposed. According to a recent hypothesis, turtles may use a navigational map based on geomagnetic inclination and intensity. In the area crossed by Ascension turtles, the isoclinics and isodynamics of the earth's magnetic field form a grid that may provide the turtles with a bicoordinate position-fixing system (Lohmann and Lohmann, 1996a,b, 1998). Migrating adult turtles could use this system if they retain the sensitivity to magnetic field variables shown by hatchlings in laboratory tests (Lohmann and Lohmann, 1994, 1996a). A concurrent chemosensory hypothesis assumes that turtles would be guided by the perception of substances originating from Ascension and transported westwards by the South Atlantic Equatorial Current (Koch et al., 1969; Carr, 1972), forming a plume that establishes a chemical link between the island and the easternmost part of Brazil. Turtles would use their chemical sense to swim within the plume on the way to the island and back (Luschi et al., 1998).

The present study reports the results of an experiment aimed

Table 1. *Performance of turtles tracked in 1997 and 1998*

Turtle	Transmitter model	CCL (cm)	Deployment date	Departure date	Migration duration (days)	Distance covered (km)	Mean travel speed (km h^{-1})	Straightness index
C1	ST-10	121	30 May 1998	29 June 1998	32.5	2358.8	3.02	0.973
C2	ST-10	117	2 June1998	3 June 1998	45.5	2896.0	2.65	0.948
C3	ST-6	105	3 June 1998	4 June 1998	42.1	2374.7	2.35	0.945
C4	ST-14	120	12 May 1997	13 May 1997	34.6	2315.2	2.79	0.959
C5	ST-14	112	22 June 1997	23 June 1997	37.6	2328.5	2.58	0.953
C6	ST-14	110	24 June 1997	25 June 1997	32.5	1785.3	2.29	0.947
C7	ST-14	117	1 July 1997	2 July 1997	35.8	2284.8	2.66	0.946
C8	ST-14	107	28 June 1997	28 June 1997	46.3	2091.6	1.88	0.969
Mean C1–C8	–	–	–	–	38.4±2.0	2304.4±109.7	2.53±0.12	0.955±0.004
E1	ST-6	113	27 May 1998	28 May 1998	14.1	961.9	2.84	0.969
E2	ST-14	109	30 May 1998	30 May 1998	39.9	2424.0	2.53	0.958
E3	ST-14	107	2 June 1998	3 June 1998	36.7	2299.1	2.61	0.967
E4	ST-6	111	2 June 1998	3 June 1998	37.5	2508.1	2.79	0.946
E5	ST-6	119	3 June 1998	7 June 1998	36.4	2359.5	2.70	0.943
E6	ST-14	113	5 June 1998	5 June 1998	20.6	1436.7	2.90	0.950
E7	ST-6	118	12 June 1998	19 June 1998	32.7	2370.3	3.02	0.965
Mean E1–E7	–	–	–	–	31.1±3.7	2051.4±227.3	2.77±0.06	0.957±0.004
						t-test (C *versus* E)	*P*=0.12	*P*=0.74

Migration was considered to start with the first fix followed by a consistent movement away from the island (departure date). After transmitter attachment, turtle C1 performed two successive egg-layings. Turtle E7 did not lay eggs on the night of transmitter attachment, but returned to the beach to nest the following night. For turtles C2 and C3, which were also tracked during their stay at the feeding grounds, we considered the end point of the migration to be the first fix inside the area where the turtles remained for some days.

Distance covered was computed by adding the distances between successive valid fixes obtained during the migration (see text for details).

The straightness index was calculated as the ratio between the direct-line distance between Ascension Island and the last fix of a turtle's route and the total length of the route (Batschelet, 1981).

CCL, curved carapace length.

Probability levels were calculated using a *t*-test for the comparisons between control (C) and experimental (E) mean travel speed and straightness index.

Mean values ± S.E.M. are given.

to test the geomagnetic hypothesis by applying a magnetic disturbance to Ascension turtles returning to Brazil. If this disturbance were to impair the orientation of the turtles, this interesting hypothesis would receive its first experimental support. However, the contrary result would show that magnetic cues are not essential for oceanic navigation by adult turtles. The latter finding should not be trivialised by arguing that the animal navigational cues are redundant (Keeton, 1979; Wehner, 1998), as it would represent the first experimental evidence for the involvement of so-far unknown non-magnetic cues in long-distance navigation in the ocean.

Materials and methods

Between 27 May and 12 June 1998, ten female turtles (*Chelonia mydas* L.) were located on beaches of Ascension Island and equipped with Telonics satellite transmitters (model ST-6, ST-10 or ST-14; Table 1) linked to the Argos system. Seven turtles were chosen as experimental animals (E1–E7) and three as controls (C1–C3), but comparisons were extended to five turtles tracked in the same period of 1997 (C4–C8; for details, see Luschi et al., 1998). We attached ST-6 and ST-14 transmitters to the top of the carapace using standard methods (Balazs et al., 1996), whereas the ST-10 units were fitted onto the head using Isopon P40 (W. David & Sons Ltd, Northants, UK) as a glue. The glue was shaped in such a way as to form a base onto which the transmitter was pressed: as a result, the transmitter was approximately 1 cm above the surface of the turtle's head. Six magnets were applied to each experimental turtle, one on the central scale of the head and five on the carapace, of which two were attached on the anterior part of the first lateral scutes, two on the posterior part of the fourth lateral scutes and one on the border between the third and the fourth central scute (Fig. 1A,B). In turtles E1–E6, the disk-shaped magnets were placed in a plastic bag and linked to a rubber plate by means of a galvanic timed releaser made of two pieces of copper wire twisted around a ring of magnesium (Fig. 1C). The rubber plate was glued to the turtle's body using Isopon P40. This arrangement ensured a nearly random oscillation of the magnet as the turtle moved; the corrosion of the magnesium ring was expected to produce detachment of the magnets in approximately 4 weeks, as shown by tests performed in

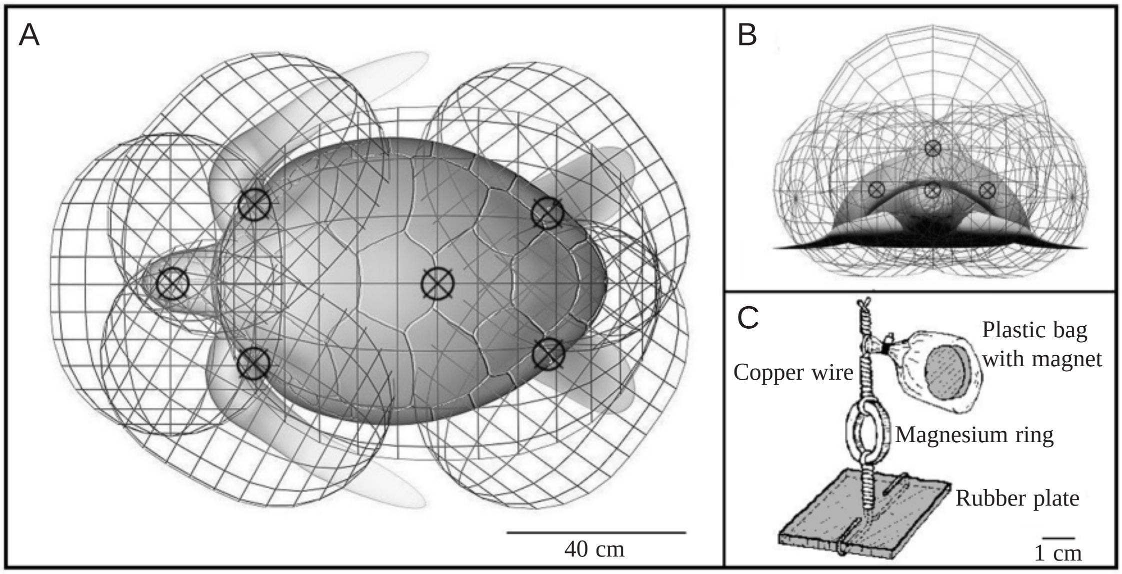

Fig. 1. (A,B) Pictorial views of the fields produced by the six magnets glued to the head and body of turtles E1–E6. (A) View from above. (B) Frontal view. The position of each magnet is indicated by a cross. For each magnetic field, the isodynamic surface at 5000 nT is represented. Calculation of the shape and dimensions of the magnetic perturbation was made using the equation: $r=10\sqrt[3]{(m/B)}\sqrt[6]{(3\cos^2\theta+1)}$, where r is the distance from the magnet in cm, m is the magnetic moment of the magnet in A m^2, B is the intensity of the field (5000 nT, in this case) expressed in gauss and θ is the colatitude angle (Tipler, 1976). Magnets were approximated to dipoles, and the effect of marine water magnetic permeability was neglected (both approximations were found to produce a negligible discrepancy in field values). The nominal residual induction of the magnets as provided by the manufacturer was between 11 700 and 12 200 G; the actual field generated by the magnets (measured by a THM 7025 magnetometer, Metrolab Instruments, Geneva, Switzerland) was found to be in accordance with these values. (C) Sketch of the arrangement carrying the magnets that was glued to the turtles.

laboratory aquaria and in Ascension waters. The magnets applied to experimental animal E7 were placed inside small cylindrical plastic boxes, which allowed the magnets to slide when the turtle pitched or rolled. The boxes were glued directly to the turtle by Isopon P40 without any release arrangement.

We used cylindrical magnets made of neodymium (type Neo 35, Calamit Trading, Milan, Italy) of two different sizes. The larger ones measured 22.5 mm in diameter and 10 mm in height, the smaller ones 18 mm in diameter and 5 mm in height (for the fields generated, see Fig. 1A,B). Only one large magnet was attached to each experimental turtle, on the central position of the carapace in turtles E1–E6 and on the head in turtle E7. Instead of magnets, controls C1–C3 carried brass bars of the same size as the magnets, attached in the same way as to experimentals E1–E6. The brass bars were not detachable since the magnesium ring was replaced by a brass ring. Controls released in 1997 did not carry any device apart from the transmitter. The transmitter of turtles C1 and C2, which was glued onto the head, produced a non-oscillating static magnetic field. Successive measurements (using a MPU-ST magnetic field meter, Namicon, Varese, Italy) showed that the maximum intensity of the field produced was 40 000 nT at 3 cm below the transmitter (i.e. just below the top of the turtle's skull), 20 000 nT at 6 cm and less than 10 000 nT at 8 cm. For comparison, the fields produced by the small magnets placed on the head of turtles E1–E6 were approximately 6 500 000, 1 030 000 and 450 000 nT at 3, 6 and 8 cm, respectively. During turtle surfacings, the emissions also produced a static field of approximately 720 000 nT at 3 cm below the transmitter for 360 ms every 50 s, together with a dynamic field at 401.650 MHz. This radio frequency field could potentially influence the turtles by producing a thermal effect on the brain tissues, but the maximum electric field produced (25 V m^{-1}; average over 6 min; ICNIRP, 1998) was much lower than that known to be associated with a temperature rise of 1 °C in animal tissues (ICNIRP, 1998). In any case, since there are indications that the putative vertebrate magnetic receptor is in the head (see Walker et al., 1997; Diebel et al., 2000), the results from these two turtles will be considered with caution (see below).

Turtles were localised by the Argos satellite system, which classifies locations into six classes of decreasing accuracy. Filled symbols in Fig. 2 represent fixes of the three most accurate classes (typically within 1 km of the true location), while open symbols represent the less accurate fixes. The routes followed by the turtles were reconstructed disregarding those fixes that were considered erroneous (250 out of 1770), either because they inferred a swimming speed exceeding 5 km h^{-1} (a threshold value estimated from speeds calculated from high-accuracy localisation only) or because they led to a change in direction that was inconsistent with the direction of previous and successive movements (see also Luschi et al., 1998).

Results

Comparison of the migratory courses revealed no difference between the experimental turtles and the two control groups in

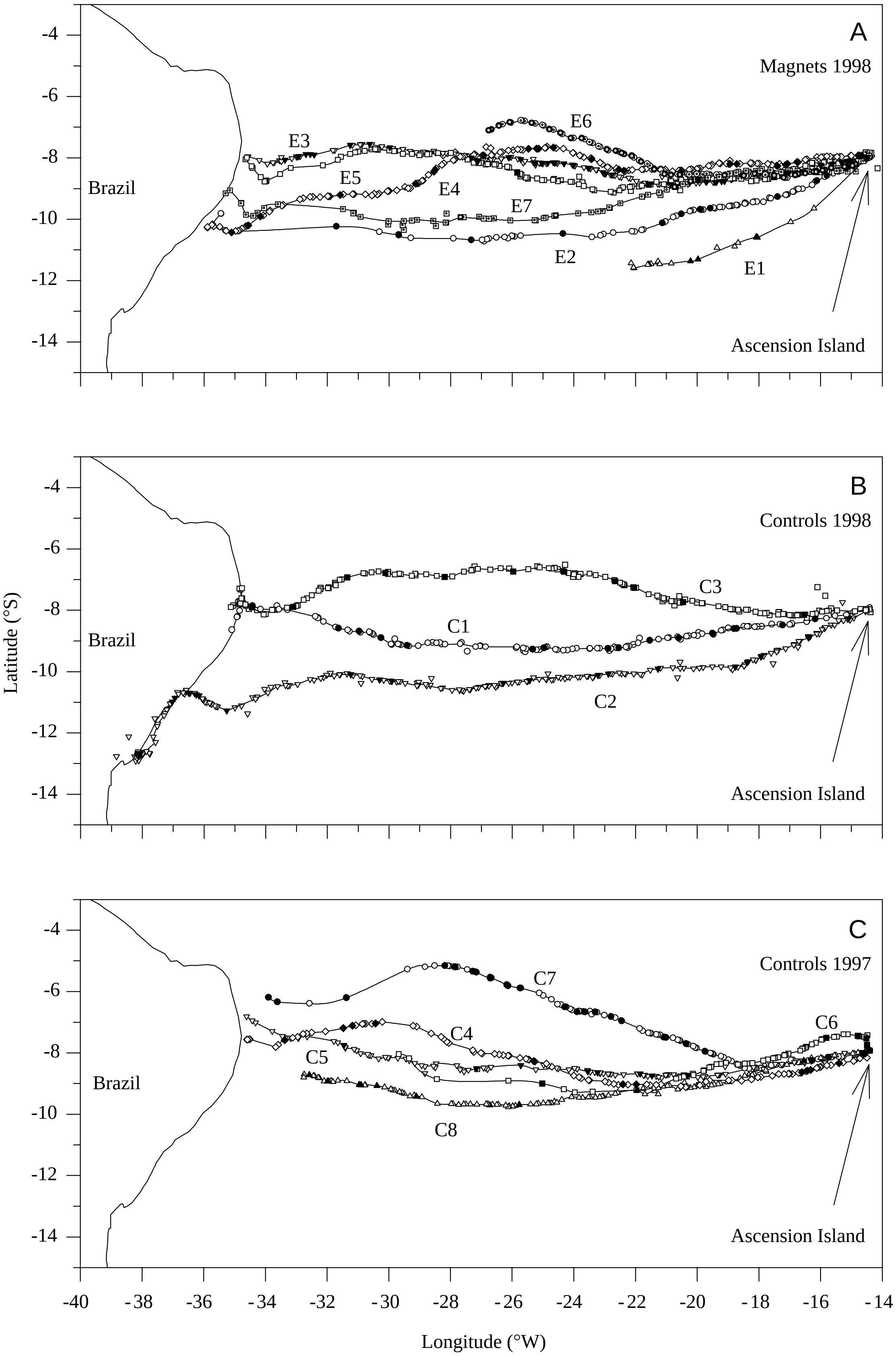

Fig. 2. Migratory routes of tracked turtles. (A) Magnetically treated turtles released in 1998 (E1–E7), (B) control turtles released in 1998 (C1–C3) and (C) control turtles released in 1997 (C4–C8). Fixes disregarded in the reconstruction of the routes (see text) are shown, but not joined by lines. Filled symbols, fixes in the three most accurate classes; open symbols, less accurate fixes (see text).

Table 2. *Turtle speed in segments between successive valid fixes covered under different conditions*

Turtle	N	Daytime speed (km h^{-1})	N	Night-time speed (km h^{-1})	t-test, day *versus* night	N	Moonlit speed (km h^{-1})	N	Moonless speed (km h^{-1})	t-test, moon *versus* moonless
C1	22	3.26±0.11	14	2.82±0.10	P=0.011	6	3.01±0.16	5	2.78±0.18	P=0.35
C2	31	2.86±0.12	21	2.53±0.13	P=0.066	7	2.28±0.13	7	2.73±0.31	P=0.21
C3	22	2.87±0.16	13	2.12±0.20	P=0.005	5	1.84±0.39	2	2.90±0.32	P=0.18
C4	21	3.13±0.09	19	2.80±0.08	P=0.012	7	2.83±0.10	7	2.96±0.22	P=0.61
C5	19	2.91±0.17	20	2.37±0.18	P=0.033	9	2.28±0.30	7	2.23±0.30	P=0.92
C6	11	2.73±0.17	7	2.93±0.17	P=0.454	2	3.47±0.05	5	2.82±0.21	P=0.12
C7	22	2.75±0.15	20	2.30±0.11	P=0.023	3	2.39±0.53	4	1.19±0.24	P=0.07
C8	30	2.37±0.12	19	1.61±0.16	P=0.0003	10	2.06±0.15	9	2.82±0.11	P=0.0009
Mean C1–C8	8	2.86±0.09†	8	2.44±0.15†	P=0.034‡	8	2.52±0.19†	8	2.55±0.21†	P=0.91‡
E2	14	2.71±0.16	13	2.68±0.09	P=0.874	7	2.84±0.13	2	2.51±0.30	P=0.27
E3	34	2.88±0.09	28	2.39±0.11	P=0.001	10	2.49±0.19	5	2.04±0.25	P=0.19
E4	32	2.79±0.13	24	2.60±0.14	P=0.310	10	2.47±0.23	10	3.14±0.16	P=0.027
E5	24	2.91±0.14	18	2.45±0.19	P=0.058	6	2.19±0.35	7	2.57±0.31	P=0.43
E6	19	3.13±0.09	17	2.74±0.12	P=0.012	7	2.67±0.10	5	2.67±0.31	P=0.99
E7	13	2.81±0.19	9	2.65±0.31	P=0.649	2	1.97±1.39	4	3.01±0.15	P=0.30
Mean E2–E7	6	2.87±0.06†	6	2.59±0.06†	P=0.006‡	6	2.44±0.13†	6	2.66±0.16†	P=0.31‡
t-test (C *versus* E)		P=0.93		P=0.44			P=0.75		P=0.72	

Values are means ± S.E.M.

Data are given for four different types of segments: those covered mostly (>90 %) during the day or the night, and those covered at night when the moon was mostly (>90 %) above (moonlit segments) or below (moonless segments) the horizon.

Data from segments covered in less than 120 min were excluded.

†Mean ± S.E.M. of the above means.

‡Result of the comparison between the two sets of individual means for control and experimental turtles.

Probability levels were calculated using t-tests for the comparisons between control (C) and experimental (E) speed in the different types of segments.

their general pattern (Fig. 2). All the turtles left Ascension with a small southward deflection with respect to the shortest course to Brazil and later corrected their route more to due west, thus roughly converging on the easternmost part of Brazil. Of particular note is the coincidence of most routes in the first leg of the journey, even though they were covered in different days or years. Most transmitters stopped emissions just after the turtles had reached the shelf waters off Brazil, except for controls C2 and C3, which could be followed within their feeding grounds (Fig. 2; Table 1). Experimentals E1 and E6 and control C6 stopped emissions some distance from the Brazilian coast.

A comparison of turtle performance failed to reveal any difference between experimentals and controls regarding mean travel speed and course straightness index (Table 1). The experimentals and controls also corrected their courses in a similar way, thus progressively converging on the easternmost part of Brazil (Fig. 3). The turtles of both treatment groups travelled significantly faster during the day than at night; intra-individual differences were significant in two experimental and six control turtles (Table 2). No significant differences were found between the mean speeds of controls and experimentals either during the day or at night. Similarly, no differences were found between the swimming speeds recorded in segments covered at night whether or not the moon was above the horizon, experimental and control turtles performing similarly under both conditions (Table 2).

Since the Argos transmitter was glued onto the head of turtles C1 and C2, producing a magnetic field, these two individuals might be considered as having been magnetically disturbed, although the field applied was not mobile and was much smaller than that produced in the experimental turtles. The routes of turtles C1 and C2 were, however, very similar to those of the other controls (Fig. 2). The route of turtle C1was very similar to that of turtle C3 and ended exactly on the easternmost point of Brazil. Turtle C2 reached Brazilian waters further south, but this was in accordance with the southern location of her coastal feeding grounds. To err on the side of caution, however, we repeated the statistical comparisons of the speed and straightness index of the turtles, considering C1 and C2 as experimentals. A t-test showed no differences between the two groups of turtles in any of the variables taken into account, except for the mean travel speed, which turned out to be higher for the 'experimental' group than for the controls (t-test, $P<0.05$). In addition, we compared the positions where the individual turtles were expected to cross the 35°W meridian or actually reached the coast in successive steps of the journey (Fig. 3). Considering C1 and C2 either as controls or as experimentals, no significant differences in the arrival latitudes were found in the first three steps considered

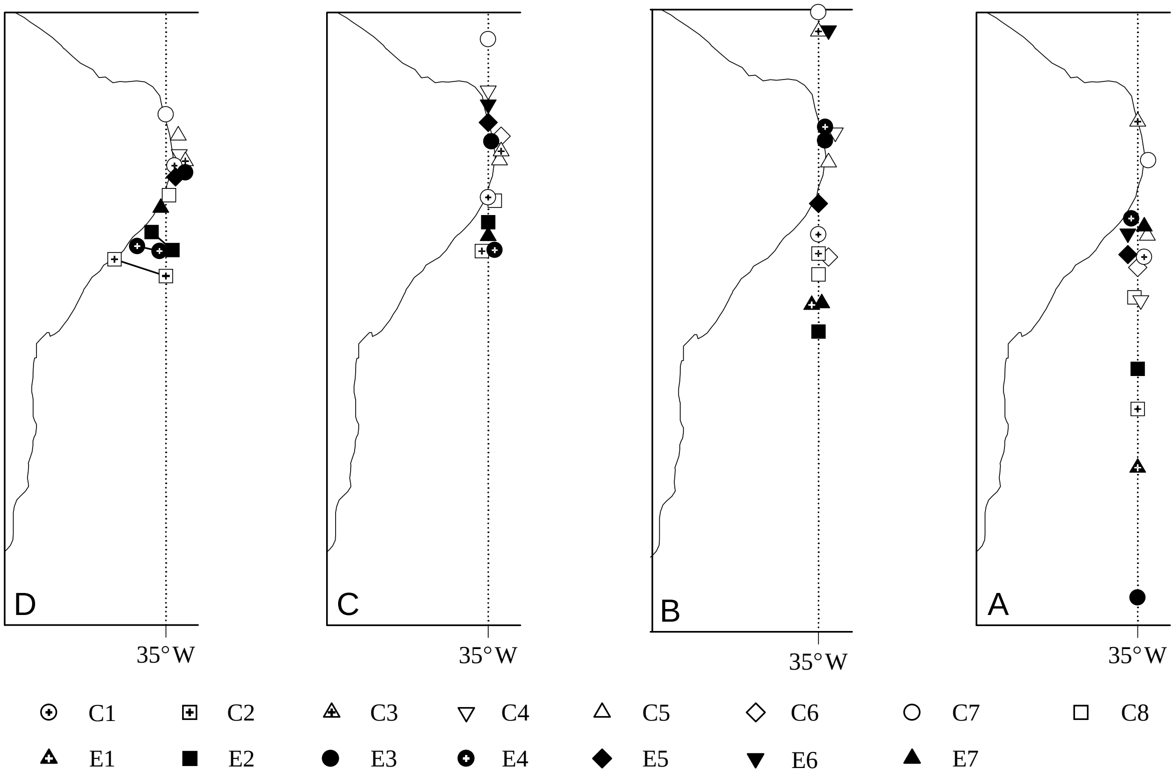

Fig. 3. Charts showing how the turtles progressively corrected their course while migrating towards Brazil. Symbols on the charts represent the site where an individual turtle was expected to cross the 35°W meridian or to reach the coast (when the coast is east of 35°W). Individuals are identified by different symbols. Estimations were made according to the mean directions held (A) before 20°W, (B) between 20 and 25°W, (C) between 25 and 30°W and (D) after 30°W. For turtles C6, E1 and E6, whose course reconstruction was incomplete (see Fig. 2), symbols are not shown in C and/or D. For the turtles that were tracked up to the coast, the symbols in D show their last fix; for turtles C2, E2 and E4, the site of crossing the 35°W meridian is represented by a second symbol, joined by a line.

(Fig. 3A–C). In the fourth step (Fig. 3D), a significant difference emerged only when C1 and C2 were considered as experimentals, with the ‘experimental’ turtles making landfall at a significantly more southerly position than the remaining control turtles (*t*-test, $P<0.05$).

Discussion

Validity of the methods used

The migratory behaviour of the turtles failed to reveal any difference between those carrying magnets and the controls. Even when turtles C1 and C2 were considered as experimentals, no consistent significant differences between the two groups arose. The only two significant differences we found in this case (a higher travel speed and a more southerly arrival position of the extended experimental group) are unlikely to be due to the influence of the magnets on the navigational ability of the turtles. Was turtle magnetoreception actually disturbed by the treatment? Laboratory experiments have shown that turtle hatchlings orientate using magnetic information (Lohmann and Lohmann, 1996b), and magnetite has been found in the head of adult green turtles (Perry et al., 1985). However, since the presence of magnetite is not *per se* evidence of magnetoreception at that site, we arranged the permanent magnets over the entire body of the turtles in such a way as to prevent them from picking up accurate geomagnetic information, wherever a magnetoreceptor was located. Moreover, since nothing is known about the transduction mechanism, we used mobile magnets that produced variable fields as the turtle swam, thus preventing magnetoreception based on induction (see Wiltschko and Wiltschko, 1995). The strength of the field produced by the magnets was different in different regions of the body (Fig. 1). In turtles E1–E6, no point on the head was more than 20 cm from the head magnet and thus all points were exposed to an artificial field of at least 15 000 nT; in the rest of the body, the areas least influenced were exposed to a field of at least 6000 nT. In turtle E7, the weakest fields were approximately 49 000 nT on the head and 1500 nT over the rest of the body. In all the experimental turtles, the tips of the front flippers were exposed to a variable field ranging from approximately 1000 to 15 000 nT depending on their position during swimming. These artificial fields were superimposed on the natural field which, in the area crossed by the turtles, varies between approximately 26 000 and 29 000 nT.

Navigation based on a magnetic map requires the evaluation of subtle differences in values of geomagnetic parameters. For instance, total magnetic intensity decreases by approximately 110 nT (0.004 % of the Earth's field intensity) every 100 km moving from Ascension to Recife, Brazil, so that the threshold for magnetic intensity variations of turtles navigating in this area should be only a few tens of nanotesla (Lohmann and Lohmann, 1996a), a range in accordance with the theoretical requirements of a bicoordinate magnetic navigation system (Wiltschko and Wiltschko, 1995; Walker and Bitterman, 1989; Walker et al., 1997). Since these values are considerably lower than those of the weakest artificial field produced by our magnets, it is unlikely that the experimental turtles could have read the magnetic map of the area unless the magnets had become detached before exerting a detectable influence on the course of the turtle. However, this latter possibility can be excluded. All the experimental turtles left Ascension shortly after the magnets were attached (Table 1), and their courses were indistinguishable from those of controls even in the very early stages. It is unlikely that the magnets would have become detached in a very short time from all the turtles (i) because in other unpublished experiments, time/depth recorders attached to turtles using the same procedure and the same glue were recovered still in place after 12 days and (ii) because the transmitters of controls C1 and C2 were attached on the head using the same glue and remained in place for at least 61 and 78 days, respectively. It is therefore likely that the magnets remained attached for most of the migratory journey.

Which compasses were used by the turtles?

While migrating towards Brazil, experimental turtles covered lengthy straight paths. In the open ocean, a constant heading can be held using any of the animal biological compasses, which are based either on astronomical cues (the sun and the related pattern of skylight polarisation, moon and stars) or on the direction of the earth's magnetic field (Papi, 1992b). Since sea turtles seem to be unable to distinguish stars (Ehrenfeld and Koch, 1967), they would need to rely on a magnetic compass on moonless nights and under totally overcast conditions. However, the navigational performance of the experimental turtles, whose detection of magnetic north was certainly disturbed by the magnets to some extent, was not inferior to that of controls, even on moonless nights. We must conclude that the magnetic compass played a minor role, if any, in directing the turtles during their migration. It is possible that the direction of the waves, which is fairly constant in the open ocean, is used by turtles when other cues are absent, an idea supported by the finding that hatchlings are able to detect wave direction (Lohmann et al., 1995). To use waves, however, migrating turtles should repeatedly calibrate the wave direction using one of the astronomical compasses (Papi and Luschi, 1996).

Navigational requirements of turtles crossing the ocean

The main conclusion to be drawn from our experiments is that experimental turtles reached the Brazilian coast without resorting to a magnetic map. Since their performance in terms of directedness and route shape was indistinguishable from that of controls, two alternative possibilities arise. The first is that neither the control nor the experimental turtles used a magnetic map; the second is that the experimental turtles resorted to an alternative mechanism of equal effectiveness. In any case, magnetic cues were not essential for the turtles to display a normal performance on their return trip to Brazil.

Regardless of whether only the experimentals or both groups of turtles used a non-magnetic mechanism, the nature of this unknown guidance system and the cues involved deserve to be discussed. Some hypotheses can be examined in the light of the recorded tracks. First, we note that Ascension turtles, or at least most of them, did not head directly to their feeding grounds, which are widely spread along the Brazilian coast, but instead tried first to reach the Brazilian bulge. The tracks we recorded indicate that turtles headed to this area, and this is in agreement with the fact that most of the recoveries of turtles tagged at Ascension are concentrated there (Mortimer and Carr, 1987). Moreover, it is reasonable that, after a long, energetically expensive journey, herbivorous animals such as green turtles would try to reach the continental coast as soon as possible to start to replenish their fat reserves (Hays et al., 1999). The residential feeding grounds would then be reached by successive movements along the coast, as clearly shown by turtle C2.

The simplest hypothesis is that the turtles relied on a simple compass orientation to reach the Brazilian bulge. Given the information – no matter how it has been obtained – that the closest point on the South American continent lies due west, turtles leaving Ascension may only have to steer in this direction using a biological compass. In this case, one would expect a steady increase in course error during the trip because of inaccuracy in course steering or the temporary unavailability of orienting cues. However, a progressive convergence of the courses of the turtles towards the Brazilian bulge obtained by means of course changes was observed in the second half of the journey (Fig. 3), in agreement with previous results (Luschi et al., 1998). The observed course changes are difficult to explain in terms of current drift because the pattern of the currents in the area (see Fig. 4 in Luschi et al., 1998) suggests that drift may have been rather more effective in increasing than in decreasing course error.

Thus, the mechanism used by the turtles must be more sophisticated than a simple compass orientation. More complex mechanisms are thought to be necessary to pinpoint Ascension at the end of the outward journey (Koch et al., 1969; Carr, 1984), and it seems strange that turtles, possessing a more sophisticated mechanism, give up its advantages during the return trip. An involvement of chemical cues operating in conjunction with compass orientation has been proposed by Koch et al. (1969). According to this hypothesis, turtles would be guided to Ascension by a chemical plume made up of substances from the island transported in a westsouthwesterly direction by the South Atlantic Equatorial Current (Carr, 1972; Luschi et al., 1998). The initial overlap of the turtle's courses in the present study and their alignment with the current direction (Luschi et al., 1998), observed in two successive years, are also consistent with the idea that they rely on a chemical plume on the return trip. However, such an explanation does not explain the shape of their courses during the last part of the trip since turtles guided to Brazil by an Ascension-derived plume would progressively increase their divergence. The convergence of the courses towards the Brazilian bulge suggests long-distance sensory contact with the goal. Although very speculative, this hypothesis of guiding stimuli originating from the bulge, such as odorants or infrasound, has considerable appeal.

The same degree of uncertainty applies to any non-magnetic mechanism of true navigation. Over the continents, map-and-compass mechanisms have been described, such as the maps used by pigeons based on the distribution of familiar landmarks and of chemical components dispersed in the atmosphere (Papi and Wallraff, 1992; Wallraff and Andreae, 2000). In the apparent uniformity of the ocean, however, the use of landmark- or odour-based maps seems highly improbable (Papi and Luschi, 1996), and no trustworthy alternatives exist. The claim that Coriolis forces or subtle differences in the sun's position could represent navigational cues is not supported by experimental evidence (Wallraff, 1990; Wehner, 1998).

Perspectives

The demonstration that turtles can cross the ocean disregarding magnetic information does not exclude the possibility that adult turtles retain the capacity of hatchlings to evaluate geomagnetic field features (Lohmann and Lohmann, 1994, 1996a). In particular, pinpointing Ascension on the pre-nesting migration is a difficult navigational task that may require additional cues (for example, those derived from the earth's magnetic field or of a different, still unknown, nature) compared with those used on the post-nesting trip. In any case, experiments on turtles migrating from Brazil to Ascension could produce substantial progress towards a solution to the problem. More generally, the present results call for new hypotheses about the navigational tools and mechanisms of marine animals. So far, research in the field has been influenced by two recurrent assumptions. The first is that the earth's magnetic field, being a potential source of positional information, is actually used by animals as a navigational map (e.g. Walker et al., 1997). This hypothesis, suggested in its original form long ago (Viguier, 1882; Gould, 1985), faces a burden of theoretical problems (Wiltschko and Wiltschko, 1995; Wallraff, 1999) and has received very little support from the many experiments prompted by the enthusiasm for the findings demonstrating magnetic orientation (but not navigation) in many animals (Wiltschko and Wiltschko, 1995; Åkesson and Alerstam, 1998). The second assumption is that the oceans are featureless voids with few navigational cues, a view that has led to a disregard for the many types of information that can be conveyed to navigators by the physical and chemical features of the oceanic environment, especially those provided by winds and currents. New lines of research paying attention to these issues may be rewarding.

We are especially grateful to H. H. R. C. Huxley, Administrator of Ascension Island, and to W. Wilkie, vice-administrator, for permission to work at the island and for their encouragement and welcome during our stay. We also wish to thank Professor G. Alzetta (University of Pisa) for his suggestions about the magnetic disturbance to be used and to an anonymous referee who suggested that we check the magnetic disturbance of the transmitter glued to the head of two controls. The measurements of this field were performed by Dr F. Francia of the agency ARPAT (Livorno, Italy). Drs A. Cordelli and D. Giannini prepared Fig. 1. This research was supported by the Italian CNR and MURST, the Swedish Natural Science Research Council (NFR; to S.Å.), the NERC (UK), the Darwin Initiative (DETR, UK), the Italian Space Agency and the Accademia Nazionale dei Lincei.

References

Åkesson, S. and Alerstam, T. (1998). Oceanic navigation: are there any feasible geomagnetic bi-coordinate combinations for albatrosses? *J. Avian Biol.* **29**, 618–625.

Baker, R. R. (1977). *The Evolutionary Ecology of Animal Migration.* London: Hodder & Staughton.

Balazs, G. H., Miya, R. K. and Beavers, S. C. (1996). Procedures to attach a satellite transmitter to the carapace of an adult of green turtle. In *Proceedings of the 15th Annual Symposium on Sea Turtle Biology and Conservation* (ed. J. A. Keinath, D. E. Barnard, J. A. Musick and B. A. Bell), pp. 21–26. National Oceanic and Atmospheric Administration, NOAA Tech. Mem. NMFS-SEFSC-387.

Batschelet, E. (1981). *Circular Statistics in Biology.* New York: Academic Press.

Carr, A. (1972). The case for long-range, chemoreceptive piloting in *Chelonia.* In *Animal Orientation and Navigation* (ed. S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs and R. E. Belleville), pp. 469–483. Washington, DC: NASA SP-262.

Carr, A. (1984). *The Sea Turtle. So Excellent a Fishe.* Second edition. Austin: University of Texas Press.

Diebel, C. E., Proksch, R., Green, C. R., Nielson, P. and Walker, M. M. (2000). Magnetite defines a vertebrate magnetoreceptor. *Nature* **406**, 299–302.

Ehrenfeld, D. W. and Koch, A. L. (1967). Visual accommodation in the green turtle. *Science* **155**, 827–828.

Gould, J. L. (1985). Are animal maps magnetic? In *Magnetite Biomineralization and Magnetoreception in Organisms* (ed. J. L. Kirschvink, D. S. Jones and B. J. MacFadden), pp. 257–268. New York: Plenum.

Hays, G. C., Luschi, P., Papi, F., Del Seppia, C. and Marsh, R. (1999). Changes in behaviour during the inter-nesting period and post-nesting migration for Ascension Island green turtles. *Mar. Ecol. Prog. Ser.* **189**, 263–273.

International Commission on Non-Ionizing Radiation Protection (ICNIRP) (1998). Guidelines for limiting exposure to time-varying electric, magnetic and electromagnetic fields (up to 300 GHz). *Health Physics* **74**, 494–522.

Keeton, W. T. (1979). Avian orientation and navigation. *Annu. Rev. Physiol.* **41**, 353–366.

Koch, A. L., Carr, A. and Ehrenfeld, D. W. (1969). The problem of open sea navigation: the migration of the green turtle to Ascension Island. *J. Theor. Biol.* **22**, 163–179.

Lohmann, K. J. and Lohmann, C. M. F. (1994). Detection of magnetic-inclination angle by sea-turtles: a possible mechanism for determining latitude. *J. Exp. Biol.* **194**, 23–32.

Lohmann, K. J. and Lohmann, C. M. F. (1996a). Detection of magnetic field intensity by sea turtles. *Nature* **380**, 59–61.

Lohmann, K. J. and Lohmann, C. M. F. (1996b). Orientation and open-sea navigation in sea turtles. *J. Exp. Biol.* **199**, 73–81.

Lohmann, K. J. and Lohmann, C. M. F. (1998). Sea turtle navigation and the detection of geomagnetic field features. *J. Navig.* **51**, 10–22.

Lohmann, K. J., Swartz, A. W. and Lohmann, C. M. F. (1995). Perception of ocean wave direction by sea turtles. *J. Exp. Biol.* **198**, 1079–1085.

Luschi, P., Hays, G. C., Del Seppia, C., Marsh, R. and Papi, F. (1998). The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. *Proc. R. Soc. Lond. B* **265**, 2279–2284.

McConnell, B. J. and Fedak, M. A. (1996). Movements of southern elephant seals. *Can. J. Zool.* **74**, 1485–1496.

Mortimer, J. A. and Carr, A. (1987). Reproduction and migrations of the Ascension Island green turtle (*Chelonia mydas*). *Copeia* **1987**, 103–113.

Papi, F. (1992a). (ed.) *Animal Homing.* London: Chapman & Hall.

Papi, F. (1992b). General aspects. In *Animal Homing* (ed. F. Papi), pp. 1–18. London: Chapman & Hall.

Papi, F. and Luschi, P. (1996). Pinpointing 'Isla Meta': the case of sea turtles and albatrosses. *J. Exp. Biol.* **199**, 65–71.

Papi, F. and Wallraff, H. G. (1992). Birds. In *Animal Homing* (ed. F. Papi), pp. 263–320. London: Chapman & Hall.

Perry, A., Bauer, G. B. and Dizon, A. E. (1985). Magnetoreception and biomineralization of magnetite in amphibians and reptiles. In *Magnetite Biomineralization and Magnetoreception in Organisms* (ed. J. L. Kirschvink, D. S. Jones and B. J. MacFadden), pp. 439–453. New York: Plenum.

Tipler, P. A. (1976). *Physics.* New York: Worth Publisher.

Viguier, C. (1882). Le sense de l'orientation et ses organes chez les animaux et chez l'homme. *Rev. Phil.* **14**, 1–36.

Walker, M. M. and Bitterman, M. E. (1989). Honeybees can be trained to respond to very small changes in geomagnetic field intensity. *J. Exp. Biol.* **145**, 489–494.

Walker, M. M., Diebel, C. E., Haugh, C. V., Pankhurst, P. M., Montgomery, J. C. and Green, C. R. (1997). Structure and functions of the vertebrate magnetic sense. *Nature* **390**, 371–376.

Wallraff, H. G. (1990). Navigation by homing pigeons. *Ethol. Ecol. Evol.* **2**, 81–115.

Wallraff, H. G. (1999). The magnetic map of homing pigeons: an evergreen phantom. *J. Theor. Biol.* **197**, 265–269.

Wallraff, H. G. and Andreae, M. O. (2000). Spatial gradients in ratios of atmospheric trace gases: a study stimulated by experiments on bird navigation. *Tellus B* **52**, 1138–1157.

Wehner, R. (1998). Navigation in context: grand theories and basic mechanisms. **J. Avian Biol. 29**, 370–386.

Wiltschko, R. and Wiltschko, W. (1995). *Magnetic Orientation in Animals.* Berlin: Springer Verlag.