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Sea turtles are known to perform long-distance, oceanic migrations between disparate feeding areas and breeding sites, some of them located on isolated oceanic islands. These migrations demonstrate impressive navigational abilities, but the sensory mechanisms used are still largely unknown. Green turtles breeding at Ascension Island perform long oceanic migrations (> 2200 km) between foraging areas along the Brazilian coast and the isolated island. By performing displacement experiments of female green turtles tracked by satellite telemetry in the waters around Ascension Island we investigated which strategies most probably are used by the turtles in locating the island. In the present paper we analysed the search trajectories in relation to alternative navigation strategies including the use of global geomagnetic cues, ocean currents, celestial cues and wind. The results suggest that the turtles did not use chemical information transported with ocean currents. Neither did the results indicate that the turtles use true bi-coordinate geomagnetic navigation nor did they use indirect navigation with respect to any of the available magnetic gradients (total field intensity, horizontal field intensity, vertical field intensity, inclination and declination) or celestial cues. The female green turtles successfully locating Ascension Island seemed to use a combination of searching followed by beaconing, since they searched for sensory contact with the island until they reached positions NW and N of the Island and from there presumably used cues transported by wind to locate the island during the final stages of the search.

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Long-distance migrating sea turtles are known for their impressive navigational abilities, enabling them to successfully locate isolated breeding islands and to pinpoint specific locations on continental shores after migration through open oceans. Despite these impressive navigational performances, it is still largely unknown which cues they use for navigation and how they are able to locate these remote sites (Papi and Luschi 1996, Åkesson 1996).

Recent experiments with loggerhead turtles *Caretta caretta* show that hatchlings rely on an inherited program, which enable them to use a number of different cues to find their direction to open ocean (Lohmann and Lohmann 1996a, 1998). The program contains a sequence of behavioural responses that is triggered by first visual cues on the beach, then wave direction as the hatchlings enter the sea and later in the open ocean by geomagnetic cues (Lohmann and Lohmann 1994, 1996a, b, 1998). Loggerhead hatchlings have been shown to respond, by changing their preferred courses recorded in circular test arenas, when exposed to artificial magnetic fields simulating local combinations of

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total field intensity and angles of inclination (Lohmann et al. 2001), suggesting an ability to navigate by using geomagnetic information. These behavioural experiments support the idea that hatchlings are able to detect and respond to very small changes in the two parameters of the Earth's magnetic field: total field intensity and angle of inclination (Lohmann and Lohmann 1994, 1996a, b, 1998). Both these gradients vary over the Earth's surface (Skiles 1985), and can in theory be used in many areas to locate geographical sites (Lohmann and Lohmann 1996a, Phillips 1996, Åkesson 1996, Walker 1998). However, due to the secular variation of the geomagnetic parameters and alignment of geomagnetic gradients this possibility might be limited in some geographical areas (Courtillot et al. 1997, Åkesson and Alerstam 1998, Wallraff 1999). The ocean between Ascension Island and Brazil in the south Atlantic is one of these areas where magnetic bi-coordinate navigation has been suggested for sea turtles (Lohmann and Lohmann 1996a).

The population of green turtles *Chelonia mydas* breeding on the tiny and isolated Ascension Island in the south Atlantic Ocean (7°57′S, 14°22′W), migrate more than 2200 km to feeding areas in the coastal waters of Brazil (Carr 1984, Mortimer and Carr 1987, Luschi et al. 1998). Adult breeding turtles start to return to Ascension Island from foraging areas along the coast of Brazil in November and most turtles have left the breeding island by the end of June (Carr 1984, Mortimer and Carr 1987). The navigational abilities of Ascension Island green turtles have extensively been discussed (Carr 1984, Luschi et al. 1998, Papi and Mencacci 1999), and two main hypotheses have been proposed to explain the turtles' ability to pinpoint the island. The first hypothesis is based on chemosensory information transported westwards with the South Atlantic Equatorial Current (Koch et al. 1969, Carr 1972), while the second is based on geomagnetic field information forming a bi-coordinate gradient map (angle of inclination and total field intensity) in the area between Ascension Island and Brazil (Wallraff 1990, Lohmann and Lohmann 1996a, 1998). The magnetic grid around Ascension Island, provide optimal conditions for bi-coordinate magnetic navigation (Skiles 1985, Lohmann and Lohmann 1996a).

By performing displacements by ship and tracking the adult female green turtles by satellite telemetry (ARGOS) as they returned to Ascension Island during the breeding period we studied the turtles' ability to locate the island (Carr 1984, Mortimer and Carr 1987, Luschi et al. 1998). The aim of these experiments was to investigate alternative strategies used for homing, by releasing the turtles at eight different geographical sites between 60 and 450 km from the island. The turtles' search trajectories were later analysed with respect to alternative navigation strategies based on global geomagnetic gradients, celestial information, ocean currents and winds. Navigation by use of a bi-coordinate magnetic map, ocean currents and winds, have previously been discussed in Luschi et al. (2001). In the present paper we have extended the evaluations by also considering a number of alternative magnetic (indirect navigation and bi-coordinate map) and celestial navigation mechanisms available to the turtles, and given predictions of the turtles behaviour depending on which strategy is used. Furthermore, we have analysed the turtles' movements in detail in relation to global geomagnetic gradients.

Theoretical predictions

There are in theory at least five different homing strategies (Wallraff 1990, Dusenbery 1992, Åkesson 2003) adult green turtles might use alone or in combination to navigate to the isolated Ascension Island after displacement. Below we have listed the alternative homing strategies and the corresponding predictions of the turtles' homing behaviour generated by each model.

Hypothesis 1. Bi-coordinate geomagnetic navigation has been proposed for sea turtles and should, in theory, be possible to use around Ascension Island (Wallraff 1990, Lohmann and Lohmann 1996a). By combining two geomagnetic gradients varying in different directions (i.e. total field intensity and inclination; Skiles 1985) the turtle should be able to locate its position relative to the goal, and reach the island by a relatively direct route from any geographical direction around Ascension Island. To fulfil this assumption, displaced turtles should have access to magnetic cues, and be released within the appropriate range of distances over which magnetic cues can be used for navigation. Aeromagnetic surveys suggest that because of local irregularities the geomagnetic field could be used for map information over long (>50–70 km) and at least for some areas over short (<5–10 km) distances (Phillips 1996). At intermediate distances (5–50 km) the local and regional gradients are likely to be of the same magnitude, but vary in relative direction, resulting in difficulties to use the magnetic field for navigation.

Hypothesis 2. Instead of combining two gradients and following a direct route to the goal (see above), in theory the turtle would be able to use indirect navigation (Dusenbery 1992) to locate a distant goal by either using a global geomagnetic gradient (*Hypothesis 2a.* Skiles 1985) or celestial information providing the value of a gradient, presumably the latitude (*Hypothesis 2b.* Dusenbery 1992). By locating and follow one of the five geomagnetic gradients to the goal the turtle will be expected to arrive at the island from two alternative geographical directions. A celestial compass or other cues may give the geographical direction of approach. By either method the turtle can be expected to move in more or less circuitous routes or perpendicular to the gradient (direction of increase or decrease) until it experiences the correct "home value" of the gradient and thereafter follow the isocline for this value of the gradient to the island by a direct route along the isocline. By this way of arguing any geomagnetic gradient can in theory be used for indirect navigation in combination with either celestial cues or a second geomagnetic gradient to define the direction of movement, and given the geographical distribution of the gradient, two directions of approach to the isolated Ascension Island are available for each gradient (Fig. 1). The distances over which the strategies are applicable are in principle unlimited, depending on the distribution of the gradient used (geomagnetic gradients given in Fig. 1). For indirect navigation based on celestial information (as defined above), we expect that the turtles locate the correct latitude and home to Ascension Island from E or W. We disregard the possibility that the turtles alternatively fix the longitude, as this would require a clock with accuracy and stability not yet found in any organism (Dusenbery 1992, see also Wehner 1998).

Hypothesis 3. A search strategy, with random or systematic components, might be applied to search for a target when any useful information is lacking (Papi 1992). Systematic search could in theory be performed by using path integration, by performing range excursions in different directions each excursion being fol-

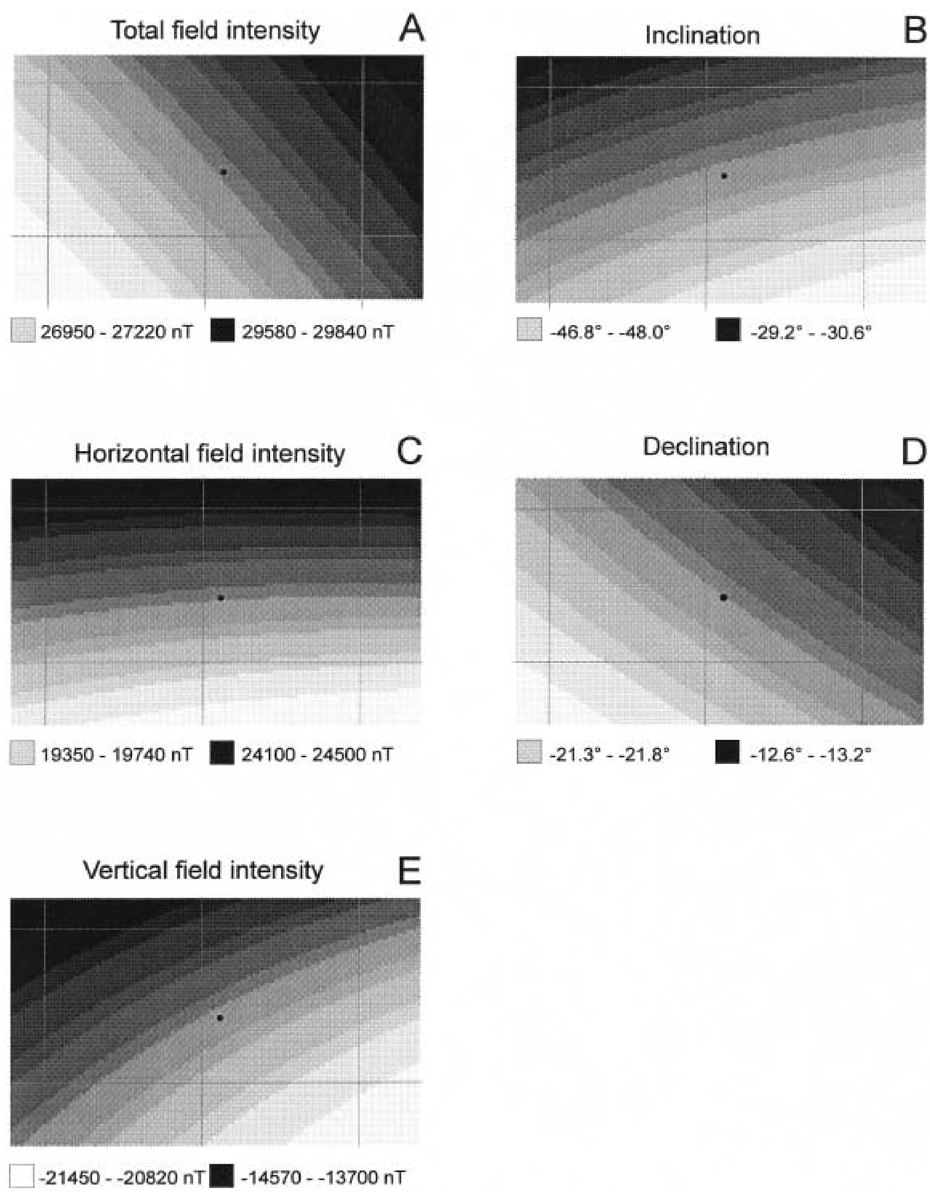

Fig. 1. The gradients of the global geomagnetic field based on the world magnetic model (WMM-95) for (A) total field intensity, (B) inclination, (C) horizontal field intensity, (D) declination and (E) vertical field intensity are given for the area around Ascension Island in the south Atlantic Ocean. Gradient values are given below each graph.

lowed by a return to the starting point (Bovet 1992, Müller and Wehner 1994). These strategies would increase the chance to find the island by, for example, visual contact, and thereby recognition of local cues connected to the goal. According to this hypothesis the probability of finding Ascension Island, should be related to the distance to the release site, i.e. starting point of the search, and not necessarily to the direction of release. Thus, by chance the turtles should be able to find the island from any direction, presumably after circuitous routes of searching.

Hypothesis 4. Beaconing by using chemical information transported by ocean currents, concerns the use of chemical information transported WSW to W with the South Equatorial Current (Koch et al. 1969, Carr 1972, Luschi et al. 1998, 2001). According to this hypothesis we expect the turtles to be able to find Ascension Island by approach within a hypothetical plume from a generally westerly direction.

Hypothesis 5. Beaconing, by using local information from the island transported or caused by wind, such as odours (Dusenbery 1992, Able 2001, Luschi et al. 2001), or surface wave patterns, which are expected to be different on the leeside of the island compared to in open ocean is also an option for the turtles. Successful homing by a direct route is expected from positions downwind from Ascension Island, in which direction the information of importance is transported. The distance from where the animals can home by beaconing, are defined by the level of perception and the mode of transport of the information used. Thus, we expect turtles to be able to home mainly from NW, as southeasterly winds dominate at Ascension Island (Luschi et al. 2001).

Methods

Experimental displacements

We investigated the turtles' ability to find the breeding site on Ascension Island after experimental displacements by ship. For these displacements we used adult female green turtles captured immediately after laying eggs at the beaches of Ascension Island and displaced primarily during the early to middle part of the breeding season (December–April; Godley et al. 2001) in 1999 and 2000. Experimental females were transported between 60 and 450 km by ship and released at sea at 8 sites in different compass directions NE, SE, W and NW of the breeding island (for detailed description of procedure see Luschi et al. 2001). Female green turtles breeding on Ascension Island return every 3–4 years and lay several clutches each time they return. They are known to spend the period between egg-laying, lasting approximately 11–13 days (Mortimer and Carr 1987), in waters close to the shores of Ascension Island (Carr 1975, Hays et al. 1999). Hence, we expect females at least displaced early in the breeding season, to have high motivation to return for a second clutch.

By analysing the turtles' search trajectories recorded by satellite telemetry we investigated if any of the alternative hypotheses given above could explain the turtles' ability to locate Ascension Island after displacement.

The geomagnetic field, ocean currents and wind

The geomagnetic parameters, i.e. total field intensity, inclination and declination, were calculated based on the World Magnetic Model 1995 (WMM-95) by the program GEOMAGIX (Interplex Limited 1990). The precision of this model is approximately 0.5° for both angles of inclination and declination, and 280 nT for the total field intensity. Other geomagnetic components that can be derived from these values show the following precision for oceanic areas: X (140 nT, north-south component), Y (140 nT, east-west), Z (200 nT, vertical) and H (200 nT, horizontal).

We used the Global Isopycnic Model (GIM, Marsh et al. 2000) to assess the prevailing ocean currents around Ascension Island. The model provides estimations of the mean direction and strength of the ocean currents in the mixed surface layer for different months. The approximate direction of the South Equatorial Current in the area of Ascension is towards WSW (Koch et al. 1969, Carr 1972, Luschi et al. 1998). The wind directions measured during the month preceding the return of the turtles were recorded between 110° and 150° at Ascension Island (Wideawake Field Meteorological Observatory; Luschi et al. 2001). Trade winds in the Ascension Island area are very constant throughout the year blowing towards NW (Comprehensive Ocean Atmospheric Data Set; Luschi et al. 2001).

Data reduction and statistics

The locations provided by the ARGOS satellite telemetry system are classified according to six grades of varying accuracy. The classes with the highest precision are typically located within 1 km of the true location. We have based the analyses on locations that were considered as non-erroneous (278 excluded out of 1788). We excluded locations that inferred unrealistically high migration speeds (>5 m/s; natural swimming speed of adult sea turtle recorded as 1.5–1.6 m/s; Prange 1976, Butler et al. 1984).

For each turtle we calculated the initial departure direction according to the shortest route between two sites, the great circle route, between the release site and the location recorded at 24 h and 48 h after release relative to Geographic North (Imboden and Imboden

1972). We used circular statistics to calculate the mean orientation of a group of turtles, and the Rayleigh test to analyse if the mean orientation differed from a random distribution (Batschelet 1981). We used Circular Correlation (Batschelet 1981) to analyse if the departure directions at 24 h and 48 h differed from the direction of the ocean current and wind direction.

Results

In total 10 of the 18 displaced green turtles were able to home to Ascension Island after more or less circuitous routes (Fig. 2, Table 1, Luschi et al. 2001). The mean homing speed for these displacements was 1.8 km/h (range 0.9–2.4 km/h, $N = 10$) and covered between 2 and 45 days (Table 1). After 24 h and 48 h the turtles' had moved to locations 28 ± 19 km (mean $\pm$ sd, $n = 14$) and 59 ± 29 km, respectively, from the release sites.

Homing behaviour

The majority of the turtles searched for the Island by following circuitous routes, making large loops, and sometimes returning to the site of release or to geographical locations already visited during the search (Fig. 2). Only one of the female green turtles returned to Ascension Island by following a direct route from the release site, while most individuals seemed to move along circuitous routes until they reached a geographical area from where they homed to the island by a direct route (Fig. 2). The mean distance from where the sea turtles initiated the direct return route was 95 km (sd = $\pm$ 59 km, range = 38–192 km; $N = 10$) from Ascension Island. Most turtles returned to Ascension Island from directions to the NW, while only two turtles approached the Island from NNE (Fig. 2, Luschi et al. 2001). We analysed the search and direction of approach to the Island for each turtle with respect to the five alternative geomagnetic gradients (arrows indicate the point where the turtle returned to Ascension Island by following a direct route; Fig. 3). The results suggest that the turtles did not follow any particular global geomagnetic gradient to locate the Island. The two geomagnetic gradients: total field intensity and declination coincide with geographic NW and SE (Fig. 1 and 4A). However, by using these gradients, we expect the turtles to also be able to locate Ascension Island from SE, which did not seem to be the case (Fig. 2), since two turtles were searching for the Island in this area, and did not succeed in locating it. Furthermore, the turtles searching for Ascension Island in waters to the north that did not succeed in locating the Island, did not seem to respond to the geomagnetic gradients of total field intensity and declination, and perform indirect navigation despite the potential possibility of using this information at these distances.

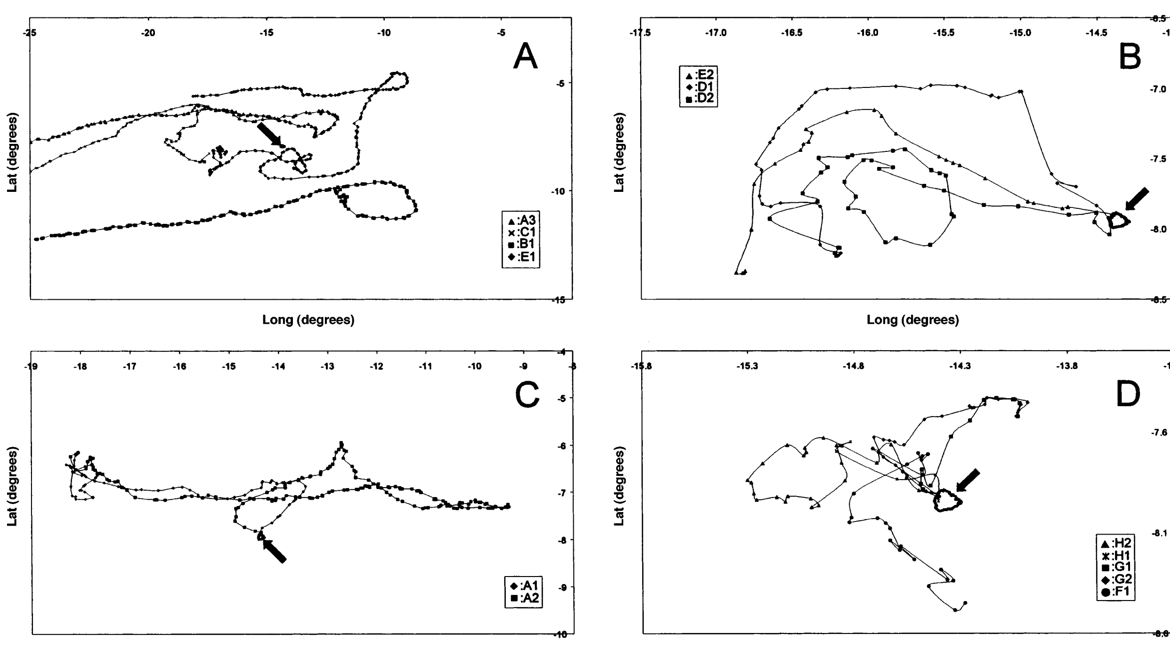

Fig. 2. Satellite tracks of adult female green turtles displaced by ship and released at sea at eight different sites around Ascension Island. (A) Female green turtles classified as searching for Ascension Island, but were not able to locate it, and (B–D) turtles successfully homing. Inlets denote the individual identification of the turtles and correspond to the numbers given in Table 1. Arrows indicate the position of Ascension Island.

Table 1. Homing time (days), mean speed of homing (km/h) and distance covered (km) for female green turtles displaced by ship to release sites around Ascension Island and tracked by satellite telemetry. The individual turtles were classified as successfully homing (Homing) or searching for Ascension Island (Searching). The location of the release sites, distance to Ascension Island and dates of release are given as well as distance and direction of locations from where direct return routes were initiated to Ascension Island

Individual	Site	Latitude (deg)	Longitude (deg)	Distance to Ascension (km)	Date of release	Homing time (days)	Mean speed (km/h)	Distance covered (km)	Direction of approach (degrees)	Distance of approach (km)
Homing										
A1	A	−6.145	−18.060	450	22 Feb 1999	19	2.4	1132	4	156
A2	A	−6.145	−18.060	450	22 Feb 1999	45	2.0	2121	303	65
D1	D	−8.191	−16.197	340	21 Dec 1999	10	2.1	500	296	192
D2	D	−8.193	−16.212	340	21 Dec 1999	12	2.2	661	282	173
E2	E	−8.300	−16.813	270	21 Dec 1999	7	2.3	395	326	120
F1	F	−8.450	−14.283	60	21 Feb 2000	14	0.9	307	253	50
G1	G	−7.525	−14.033	60	21 Feb 2000	2	2.0	112	25	57
G2	G	−7.508	−14.033	60	21 Feb 2000	4	1.7	160	315	46
H1	H	−7.673	−14.857	60	22 Feb 2000	2	1.6	86	294	58
H2	H	−7.668	−14.883	60	22 Feb 2000	7	1.4	234	317	38
Searching #										
A3	A	−6.145	−18.060	450	22 Feb 1999	57	2.6	3387	–	–
B1	B	−10.040	−12.092	340	16 Mar 1999	75	3.0	4671	–	–
C1	C	−8.275	−17.445	340	26 Apr 1999	90	2.2	3556	–	–
E1	E	−8.295	−16.792	270	21 Dec 1999	63	2.6	3820	–	–

Time (days), distance (km) and speed of migration (km/h) are given for the complete track, including the migration towards Brazil.

Direction of departure

The displaced turtles searching for Ascension Island departed in very different directions, resulting in distributions not significantly different from random (Fig. 2). We did not find a preferred geographical direction at departure, or that the turtles immediately headed towards home (Fig. 4A and B). Neither did they depart in a preferred direction relative to ocean currents or wind (Fig. 4C and D). There was no correlation between departure direction and direction of the current (24 h: $r = 0.30$, 48 h: $r = 0.25$, $N = 14$ and $P > 0.05$ for both cases, Circular correlation) or between departure direction and wind direction (24 h: $r = 0.28$, 48 h: $r = 0.21$, $N = 14$ and $P > 0.05$ for both cases). The mean directions of departure, recorded after 24 h and 48 h respectively, did not reveal any clear pattern of departures in relation to the five geomagnetic field gradients (Fig. 4A).

Discussion

The displacement experiment demonstrated that the female green turtles were not able to return to Ascension Island by following relatively direct routes from the release sites, but rather they searched for some sensory contact with the Island before being able to home successfully (see also discussion in Luschi et al. 2001). Only one of the female turtles homed by a direct route from a release site located NW of the island. One of the turtles was not able to locate Ascension Island from S to SE even though she was searching very close to the island for several days. A second female released SE of Ascension Island also failed to find the Island, but returned to Brazil after some loops of searching. These data suggest that both these turtles lacked important information for homing from this area of the ocean. Additional experiments with displaced turtles released 50 km NW and SE of Ascension Island (Hays et al. 2003), further strengthens this result, showing much longer homing speeds for turtles released SE (two females returned after 10 and 27 days, while one female failed to locate the island after 59 days when transmission ceased), compared to NW (successful homing after 1, 2 and 4 days).

Which strategy did the displaced green turtles use to locate the breeding Island? Below we discuss the alternative navigation strategies proposed, and evaluate the turtles' movements relative to the predictions generated by each hypothesis.

Navigation by using geomagnetic gradients

Bi-coordinate navigation

According to the hypothesis for bi-coordinate geomagnetic navigation (Hyp.1), we expected the turtles to home by more or less direct routes from any of the release sites around Ascension Island (Lohmann and Lohmann 1996a). Since only one of the displaced female green turtles was able to return following a direct route, it does not seem likely that they used geomagnetic bi-coordinate navigation to locate the island after

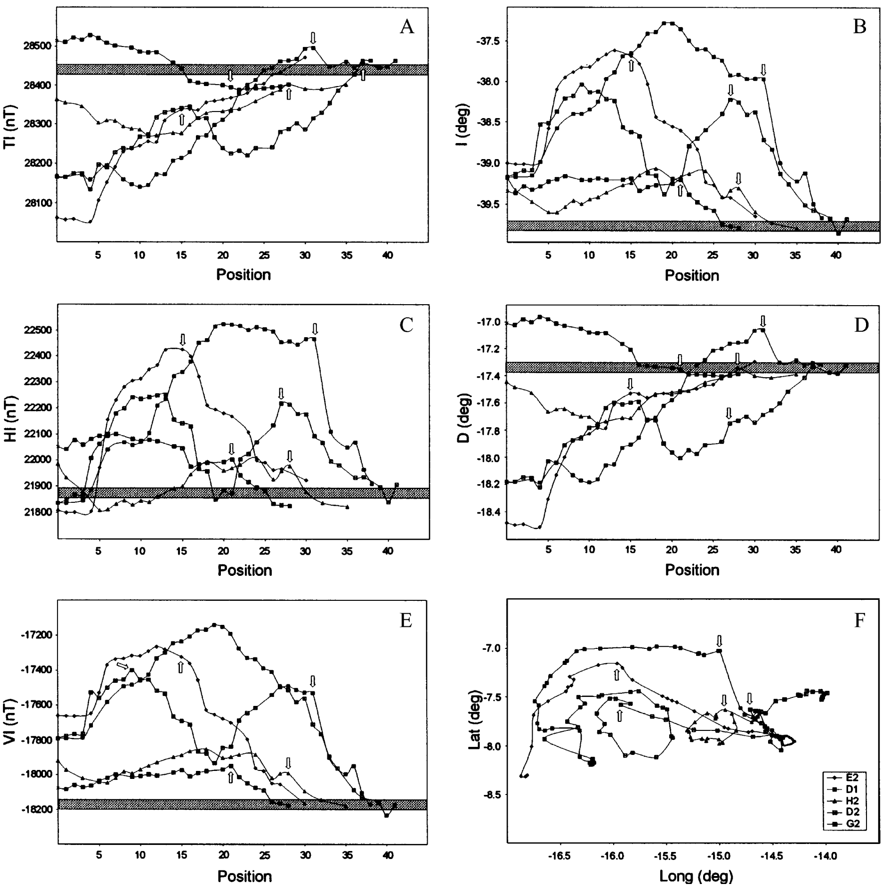

Fig. 3. The variation of geomagnetic field parameters (A) total field intensity, TI, (B) inclination, I, (C) horizontal field intensity, HI, (D) declination, D, (E) vertical intensity, VI, along the search trajectories for five female green turtles displaced by ship and homing to Ascension Island. Open arrows indicate the position along the track from where the female green turtle homed to the island by a direct route. Shaded (grey) horizontal bars indicate the geomagnetic parameter value recorded at Ascension Island. Inlet in (F) shows the turtles' individual numbers, for which geomagnetic field data are presented.

displacement. Bi-coordinate geomagnetic navigation does not seem to be used despite the fact that the geomagnetic gradients, total field intensity and inclination, available around Ascension Island, in contrast to other Oceanic areas (Åkesson and Alerstam 1998) seem to provide a very reliable bi-coordinate map (Skiles 1985, Lohmann and Lohmann 1996a, see further discussion below). Previous experiments with magnets attached with the intention of disturbing the magnetic field perceived by migrating Ascension Island green turtles, did not seem to affect the turtles navigational performance (Papi et al. 2000), suggesting that geomagnetic field information was not of crucial importance to select reasonable migration courses.

Indirect navigation

The turtles' movements revealed no clear pattern of arrival from two alternative directions relative to the geomagnetic field, as was predicted for indirect navigation based on global geomagnetic gradients, indicating that the turtles did not follow any particular geomagnetic gradient to locate the breeding island. Neither did they seem to rely on celestial information for indirect navigation (Dusenbery 1992), as they did not show preferred arrival from either W or E. Most turtles returned to Ascension Island from directions to the NW, while only two turtles successfully approached the Island from NNE (see also Luschi et al. 2001). The two geomagnetic gradients total field intensity and declination coincide with geographic NW and SE (Fig. 1, Fig. 2A). However, by using these gradients, we expect the turtles to also be able to locate Ascension Island from SE, which did not seem to be possible by the two turtles searching for Ascension in this area of the ocean (Fig. 2). Therefore, we must conclude that the data on our searching green turtles do not support the hypothesis for indirect navigation by using global geomagnetic gradients or celestial information.

Why did the displaced turtles not use the geomagnetic field for navigation? There might be at least four explanations as to why the turtles did not follow any of the suggested strategies for geomagnetic navigation: 1) the turtles were not motivated to home immediately after release, but rather searched for food or alternative breeding sites before homing. Adult green turtles are mainly herbivores, feeding on sea grass in shallow coastal waters and are presumably not foraging in the waters of Ascension Island on migration (Carr 1984, Mortimer and Carr 1987). Furthermore, recordings of diving patterns of female green turtles during inter-

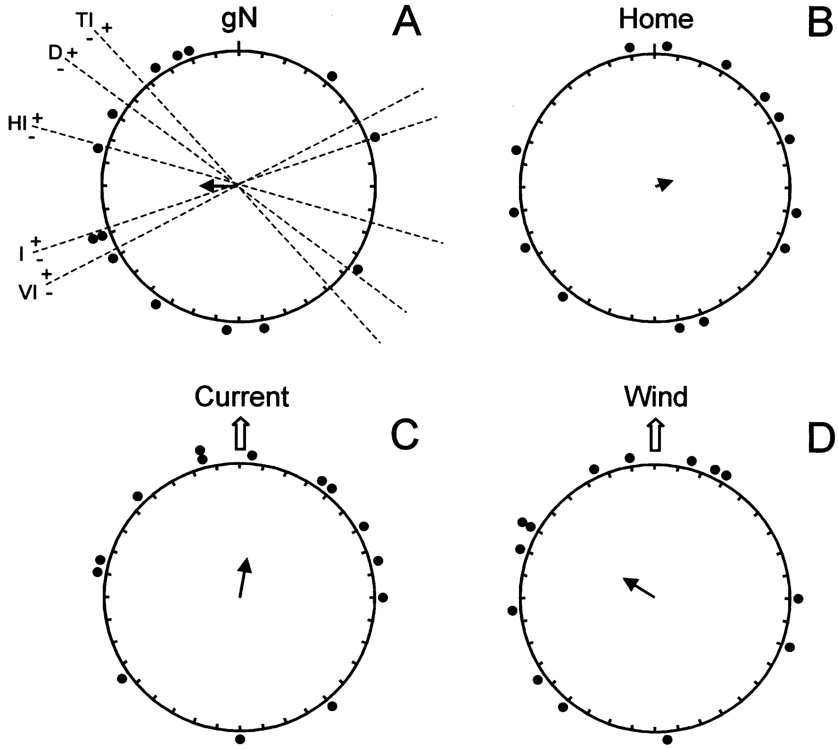

Fig. 4. Direction of departure from the release sites between 60 and 450 km from Ascension Island, and the position recorded 24 h after release. The mean direction of departure for the group of displaced female green turtles is indicated by an arrow and the individual departure directions (filled circles) have been plotted in relation to (A) geographical north (gN), (B) the direction towards home, as calculated from the release site (Home), (C) the direction of the ocean current (Current), and (D) the mean wind direction (Wind) measured at Ascension Island. Mean angles of orientation were not significantly different from random as calculated for time periods of 24 h and 48 h (range of r-values: 0.12–0.30, $p > 0.05$ in all cases, Rayleigh test, Batschelet 1981). The directions of current and wind are indicated by arrows. Broken lines indicate the orientation of the geomagnetic gradients (TI, HI, VI, I and D) given in Fig. 1. For further information see the methods section.

nesting periods (10–12 days) suggest that they spend a large proportion of the time engaged in resting dives (18–20 m) presumably not moving far away from Ascension Island, and probably mating with males near to the egg-laying sites (Hays et al. 2000). Therefore, we believe lack of motivation to home is not likely to explain the delayed homing and circuitous routes shown by some of the displaced turtles, at least not for the female turtles displaced early in the season. 2) The turtles might have been unable to perceive the geomagnetic field. We used satellite transmitters attached on the head or on the carapace of the turtles, and we cannot exclude that the transmission and static fields generated by the transmitters did not interfere with the perception of the geomagnetic field (locations of transmitters and measurements of magnetic fields given in Papi et al. 2000). Animals like, for example, insects, fish, salamanders and birds have been shown to possess very sensitive magnetic field detectors to react to very small changes in the external magnetic field (Wiltschko and Wiltschko 1995, Walker et al. 1997, Fischer et al. 2001, Åkesson et al. 2001), suggesting that also turtles might have this capability. We have displaced turtles with transmitters attached both to the head and carapace (this study, Hays et al. 2003). Until we know about the location and perceptive ability of a magnetic field sensor in turtles we cannot exclude that at least some of our turtles (Ptts attached to carapace or head) still were able to register the geomagnetic field and use it for navigation. 3) The turtles were not displaced within the range of distances where they use the geomagnetic field for navigation. Our turtles were displaced between 60 and 450 km to locations where the differences in total field intensity (TI) varied between −495 nT and +110 nT, compared to values at Ascension Island (TI: 28451 nT, I: −39.4°, D: −17.4°, calculations based on WMM 1995). At the same release sites angles of inclination (I) varied between −4.8° and +4.2° and declination (D) between −0.4° and +1.4°, compared to values at Ascension Island. Due to local irregularities of the geomagnetic field, magnetic navigation has been suggested to be possible only over larger geographical scales (> 50–75 km) or over short distances (< 5–10 km) but not for intermediate distances (Lednor 1982, Phillips 1996). Our turtles were displaced between 65 and 450 km, and following this reasoning at least from the sites with the longest homing distances (i.e. largest differences in magnetic values) the turtles should be expected to be able to locate their position and home by using geomagnetic information. 4) The displaced Ascension green turtles did not use geomagnetic field information for navigation (see discussion above).

Homing by using a search strategy

Two very typical features of the search trajectories by the female turtles were demonstrated. Firstly, there was considerable variation in initial departure directions, which did not seem to be correlated with any of the available orientation cues, currents and wind, or directions towards geomagnetic North or home. Secondly, all turtles undertook a pattern of large circuitous looping movements after departure; occasionally lasting for more than 30 days. Both features indicate that the female turtles, were searching for the island by a search strategy (Hyp. 3). Homing desert ants of the genus *Cataglyphis*, use a systematic search strategy when local information around their nest site (e.g. landmarks) are absent, and show a clear pattern of search by performing larger and larger loops directed in different geographical directions (Müller and Wehner 1994). The individual ant uses a path integration system during the search, continuously integrating its own movements by initiating each loop and thereafter return to the position where it started the search. Our searching green turtles were sometimes performing large loops in the open ocean, and occasionally returned to the vicinity of the release site or crossed an area where they had previously been (Bovet 1992). However, they did not seem to use the same strategy as desert ants, and it is not clear whether they used any position fixing mechanism.

Navigation using beaconing

Local information can be transported from Ascension Island by ocean currents and wind. The ocean currents are expected to transport chemical information in the water towards WSW to W (Hyp. 4; Koch et al. 1969, Carr 1972), while the prevailing and very stable winds will generally transport information NW (Hyp. 5; Luschi et al. 2001). Hence, depending on the alternative information used, successful homing is expected if the turtle enter the area from W (ocean currents) or NW (winds) relative to Ascension Island. Some of our turtles were released west of Ascension Island, within the expected chemical plume down-current, while others entered this area during the search, but without reacting to the hypothetical chemical plume by moving eastwards towards Ascension Island by a direct route. Rather the turtles continued their intended route crossing the hypothetical chemical plume as if they were not aware of the direction of the Island, suggesting that they did not react to any information transported by the ocean currents. Instead, the search patterns suggest that the turtles reacted to information transported with the wind, as most arrived from NW and had apparently located the direction of the Island at various distances before approaching the Island by a final direct route (Fig. 2; see also Luschi et al. 2001). Furthermore, two turtles searched SE of the Ascension Island without locating it, indicating that they were not able to detect the crucial information SE of Ascension (orientation in relation to geomagnetic gradients, Hyp. 1 and 2a above; Luschi et al. 2001).

In conclusion, we suggest that the displaced female green turtles tracked by satellite telemetry did not use true bi-coordinate geomagnetic navigation (Wallraff 1990, Lohmann and Lohmann 1996a) or chemical information transported with the ocean current (Koch et al. 1969, Carr 1972) to locate Ascension Island after passive displacement by ship. Neither did they seem to return by following any of the geomagnetic gradients or routes given by celestial information suggesting they used indirect navigation (Dusenbery 1992). Rather our satellite tracking data indicate that the turtles relied on a search strategy combined with beaconing to relocate the island (Åkesson 2003), where presumably information transported with the wind was the important cue finally guiding the turtles back to the breeding island (see also discussion in Luschi et al. 2001). Information available downwind from Ascension Island, might, for example, be odours and/or diffracted wave patterns. The use of a combination of navigation strategies is well known for homing insects (Wehner 1992, Wehner et al. 1996). However, if this combined strategy as we suggest above is used by green turtles returning from foraging areas in Brazil on natural migration, remains to be investigated.

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