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ORIGINAL ARTICLE

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Testing the navigational abilities of ocean migrants: displacement experiments on green sea turtles (*Chelonia mydas*)

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Abstract Like many animals migrating through the oceans, sea turtles face difficult navigational tasks when they have to reach distant, specific sites. The paradigmatic case of Brazilian green turtles (*Chelonia mydas*), which nest on the tiny Ascension Island in the middle of the Atlantic Ocean, has often been the subject of hypotheses concerning their navigational mechanisms. To investigate their nature, we displaced 18 females from Ascension and tracked them by satellite after release from eight different points in the ocean, 60–450 km away from the island. Four turtles moved to Brazil soon after the release, 4 moved in various directions before heading to Brazil, and 10 reached the island. All the successful trips, bar 1, were winding but ended with a final straight segment of variable length, as if the turtles were searching for a sensory contact with the island which they obtained at various distances. The approach to Ascension mostly occurred from the direction opposite to the trade wind, suggesting a navigational role of wind-borne information originating from the island.

Keywords Navigation · Turtles · Magnetic map · Chemosensory hypothesis · Ascension Island

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Introduction

The experimental displacement of animals and the successive monitoring of their behaviour is a classic method to investigate the navigational mechanisms employed (Papi 1992). If a displaced animal compensates for passive displacement in every direction, one can conclude either that it possesses a map of the area extended at least up to the release site, or that it has been able to establish the direction of the displacement. In the former case, the animal can be said to rely on a system of true navigation, that allows position fixing on the basis of local environmental cues which are compared with those of the target (Wallraff 1991).

Such an experimental approach appeared to be most suited to investigate the sophisticated guidance system used by green sea turtles (*Chelonia mydas*) living on the Brazilian coasts, which migrate to the 2,200-km distant Ascension Island (7°57′ S, 14°22′ W) to nest (Carr 1972, 1984; Mortimer and Carr 1987; Papi and Luschi 1996). In previous experiments, satellite tracking of their return trips to Brazil showed that turtles headed to the easternmost part of Brazil with fairly straight courses, which were not disturbed by the application of powerful magnets on the turtle's body (Luschi et al. 1998; Papi et al. 2000).

The main purpose of the present experiments was to obtain insight into the turtles' navigational mechanism, which is possibly shared by other animals able to reach distant, specific targets in the featureless vastness of the ocean (Carr 1984; Papi and Luschi 1996). In addition, we aimed to test the two hypotheses so far put forward specifically for Ascension turtles. According to a first, chemosensory hypothesis, turtles would be guided to Ascension by a chemical plume made up of substances originating from the island and transported roughly westwards by the South Atlantic Equatorial Current (Carr 1972; Koch et al. 1969). A second, magnetic hypothesis proposes that turtles make use of a navigational map based on the values of geomagnetic inclination and intensity, that would allow bi-coordinate true navigation in the area crossed (Lohmann and Lohmann 1996;

Lohmann et al. 1999). Both these hypotheses are burdened with a number of objectionable points, mainly regarding their (geo-)physical soundness and their assumptions about the turtles' sensory abilities (Brown 1990; Koch et al. 1969; Lohmann and Lohmann 1996); nonetheless, they presently constitute the only attempt to provide an explanation for the remarkable navigational feats of Ascension turtles.

Displacing nesting females in different directions allows a direct testing of both hypotheses. In the case of reliance on the current-borne plume, direct return to the island after displacement would only be possible when turtles are released within the plume, while if turtles rely on a magnetic map they would be able to return from any direction, possibly with courses influenced by the local pattern of geomagnetic parameters.

Methods

The experiments were carried out during the Ascension turtles' nesting season, which runs from December to July (Table 1; Mortimer and Carr 1987; Godley et al. 2001). Eighteen turtles were captured on Ascension beaches after having laid a clutch of eggs, and immediately confined singly in open-topped, padded wooden crates (2×1×1 m) covered in a dark tarpaulin keeping out all sunlight. They were then transported by truck to the nearby Georgetown pierhead (<1 km) and were loaded using a forklift truck, cranes and barges onto a ship, the "M/V Ascension", or, for release B, the "RMS St Helena". Satellite transmitters (model ST-18; Telonics, Mesa, Ariz.) linked to the Argos system were attached on the turtles' head (Papi et al. 2000) using Foilfast (SFS Components, Cheltenham, UK) as a glue, except for turtle B2, whose transmitter was glued on the carapace. During transportation to the release site, the turtles stayed in their crates on the ship's deck and were moistened in seawater every hour. At the release site, they were released overboard by using a crane.

Eight different releases (A–H) were performed, at various distances from the island (Table 1). Releases C–E aimed to test the turtles' reliance on the hypothetical, current-borne chemical plume possibly guiding Ascension turtles (Carr 1972; Koch et al. 1969), and were WSW of the island, since the main ocean current in the Ascension area (the constant, shallow South Atlantic Equatorial Current) flows WSW (see Luschi et al. 1998 for a detailed discussion). The most likely location of the plume was estimated by referring to the corridor-like area where turtles were observed to pass at the beginning of their return trip to Brazil (Fig. 1), and which has been thought to be determined by the hypothetical plume (Luschi et al. 1998; Papi et al. 2000).

Table 1 Performances of turtles which did not move immediately towards Brazil but searched for Ascension Island. Distance covered was computed by adding the distances between successive valid fixes obtained (see text for details). The straightness index was calculated as the ratio between the bee-line distance from Ascension to the last fix of a turtle's route and the total length of the route (Batschelet 1981)

Turtle	Capture date	Release date/time (UT)	Time to first fix (h:mm)	Homing trip duration (days)[a]	Mean travel speed (km/h)[a]	Distance covered (km)[a]	Straightness index
Release A (distance 450 km, home direction 116°)							
A1	20 Feb. 1999	22 Feb. 8:12	1:34	19.4	2.44	1,131.8	0.40
A2	20 Feb. 1999	22 Feb. 8:06	1:45	44.8	1.97	2,120.6	0.21
A3	20 Feb. 1999	22 Feb. 8:19	8:20	26.4	1.16	632.6	
Release B (distance 340 km, home direction 313°)							
B1	15 Mar. 1999	17 Mar. 7.00	10:24	15.9	2.98	380.4	–
Release C (distance 340 km, home direction 84°)							
C1	25 Apr. 1999	26 Apr. 14.10	2:28[b]	19.3	2.00	464.0	–
Release D (distance 200 km, home direction 82°)							
D1	18 Dec. 1999	21 Dec. 3:15	0:55	9.7	2.14	499.8	0.39
D2	19 Dec. 1999	21 Dec. 3:21	0:47	12.2	2.25	660.6	0.30
Release E (distance 270 km, home direction 82°)							
E1	19 Dec. 1999	21 Dec. 5:55	2:28	63.7	2.50	3,820.1	–
E2	20 Dec. 1999	21 Dec. 6:00	2:23	7.1	2.33	395.2	0.68
Release F (distance 60 km, home direction 350°)							
F1	19 Feb. 2000	21 Feb. 18:30	2:43	13.6	0.94	307.2	0.19
Release G (distance 60 km, home direction 219°)							
G1	19 Feb. 2000	21 Feb. 23:00	4:54	2.4	1.97	111.8	0.54
G2	19 Feb. 2000	21 Feb. 23:07	0:42	3.9	1.70	160.0	0.38
Release H (distance 60 km, home direction 120°)							
H1	19 Feb. 2000	22 Feb. 2:57	2:41	2.2	1.63	86.1	0.68
H2	19 Feb. 2000	22 Feb. 3:05	4:49	7.3	1.35	234.1	0.25

[a] For the turtles that did not home, data refer to the tracking period considered
[b] Fix discarded in the filtering process

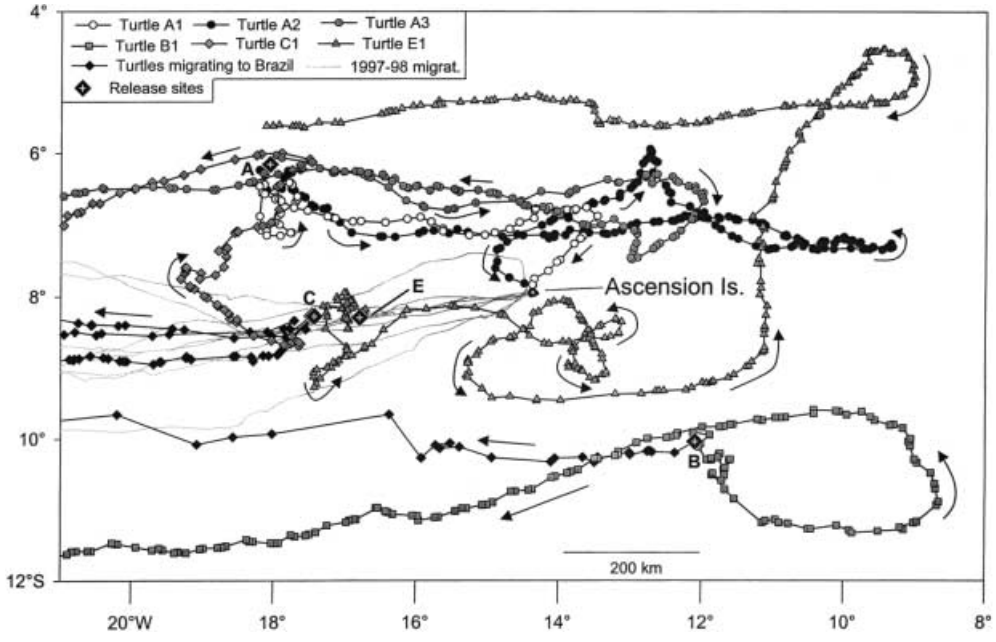

Fig. 1 Reconstructed routes of turtles displaced in experiments A–C and of turtle E1, including those that started their post-nesting migration towards Brazil (first part of the track only shown). *Thin lines* show the initial part of the routes of turtles tracked in 1997 and 1998 during their post-nesting migratory trip towards Brazil (Luschi et al. 1998; Papi et al. 2000), indicating the most likely location of the hypothetical, current-borne chemical plume (Carr 1972; Koch et al. 1969). The chart is constructed on equatorial Mercator's projection. See text for further details

Ascension green turtles are known to spend the period between successive egg-layings (roughly 14 days; Mortimer and Carr 1987) in the waters close to shore (Hays et al. 1999; Mortimer and Portier 1989), where they mostly rest and possibly mate (Carr 1975; Hays et al. 1999). Displaced females that had not completed the nesting cycle were therefore motivated to return to the island, which can then be considered the target of a homing behaviour. Four turtles (one in release B and three in release C) started, instead, their post-nesting migration towards Brazil immediately after release (Fig. 1), without showing any attempt to swim back to the island. They will not be considered further.

Turtles were localised by the Argos satellite system that classifies locations into six classes of decreasing accuracy (typically within 1 km of the true location for the three most accurate classes). The routes followed by the turtles were reconstructed disregarding those fixes which were considered erroneous (278 out of 1,788), either because they inferred a swimming speed exceeding 5 km/h (a threshold value estimated from speed values calculated from high-accuracy localisations only) or because they were on land (see also Luschi et al. 1998; Papi et al. 2000).

For the analysis of the turtles' performances after release, we determined for each turtle the temporally closest fix to the chosen times (48, 72, 96 and 120 h after release), and calculated the distance and the direction to Ascension from each fix. The circular distributions of turtles' successive headings and direction of approach to the island were processed using standard methods of circular statistics and tested for randomness by the Rayleigh test (Batschelet 1981). Each turtle's direction of approach to the island was calculated by referring to the first fix of the final, island-directed leg of each turtle's route (asterisks in Figs. 2, 3).

Results

Figure 1 shows the results of the first two releases (A and B), which were performed from the most distant sites. All four turtles performed long-distance, winding movements and only turtles A1 and A2 eventually managed to relocate Ascension. Turtles A3 and B1 returned to the vicinity of the release site before heading to Brazil, B1 after completing a 1,100-km-long loop in a SE direction.

Releases C–E were within the migratory corridor WSW of the island and thus in an area where the hypothetical chemical plume most likely lies (Luschi et al. 1998; Papi et al. 2000). Two of the five turtles (C1 and E1) were unable to reach Ascension (Fig. 1). Turtle C1 wandered mostly north of the release site, and turtle E1 missed the island even though she swam for a long time within the corridor and then passed as close as 23 km SE of her target. Turtles D1, D2 and E2 (Fig. 2) did not swim directly to the island within the corridor, and displayed northward curved routes before reaching Ascension from WNW or NW.

All five turtles released from three closer sites symmetrically arranged around Ascension homed (releases F–H: Fig. 3). Turtle H1 did so with a straight, direct route from the NW, while the other four made circuitous routes and only moved toward the island when NW or N of it.

The mean distance of displaced turtles from Ascension 48, 72, 96 and 120 h after release was not significantly lower than that of the release sites (Friedman repeated-measures ANOVA, χ^2=5.75, P>0.05) and the circular distributions of their heading with respect to home direction were never different from random (r=0.11, 0.10, 0.20 and 0.38; Rayleigh test, P>0.05 in all cases). The turtles that homed (10 out of 14; 71%), reached the island with winding routes, with the distance covered to reach the target being on average 2.5 longer than the bee-line from the release site to Ascension. In fact, the mean straightness index was 0.40, and the single values ranged between 0.19 and 0.68 (Table 1).

Most of these turtles reached Ascension approaching from the NW, the only exception being turtles A1 and G1 that homed from N or NE (Figs. 2, 3). Turtles D2 and E2 reached Ascension with a direct route from about 170 km NW of the island (Fig. 2), while in some other

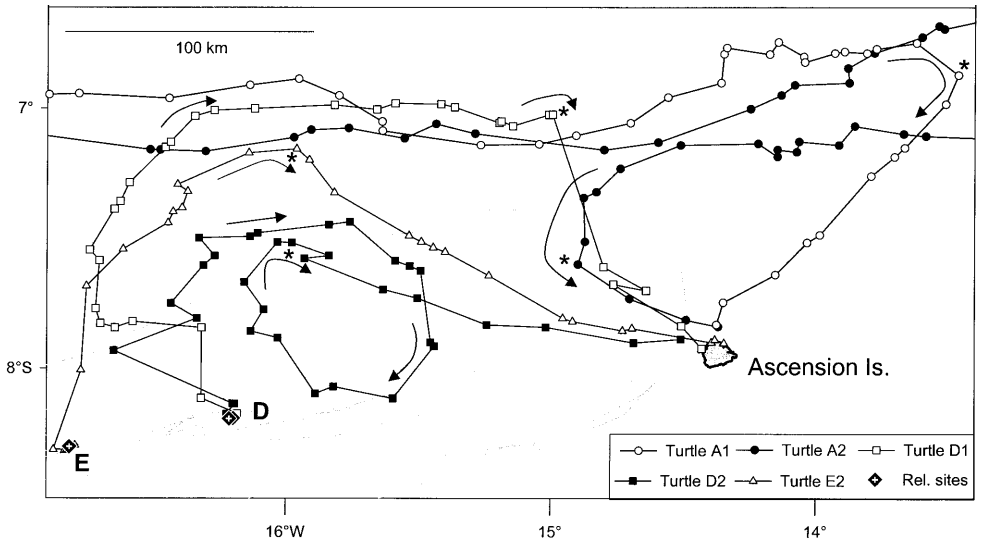

Fig. 2 Reconstructed routes of turtles displaced in experiments D and E (excluding turtle E1), together with the final part of the course of turtles A1 and A2. *Thin lines* show the initial part of the routes of the turtles previously tracked. *Asterisks* indicate the first fix of the island-directed leg of the courses. For further information see legend to Fig. 1

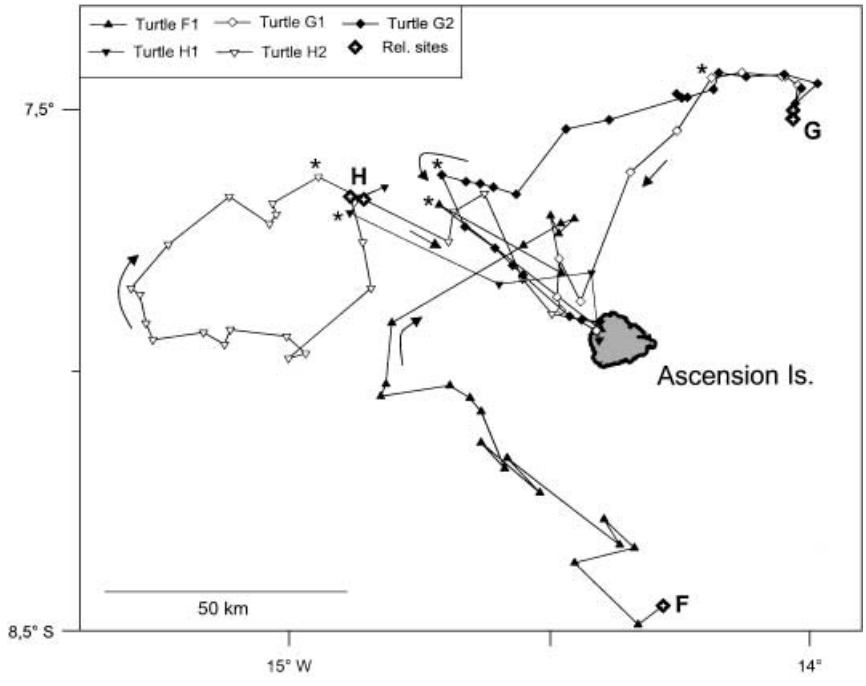

Fig. 3 Reconstructed routes of turtles displaced in experiments F–H. Further explanations given in legends to Figs. 1, 2

cases homing was possible only after wandering movements had led the turtles into the NW sector (e.g. turtles A2, D1, F1 and G2). The circular distribution of the directions of approach to the island (Fig. 4) is significantly different from random and is centred from the NW.

Discussion

Since 14 of the 18 displaced turtles made prolonged attempts to relocate the island, we can conclude that the treatments involved in the displacements did not substantially disrupt their motivation to swim back to the island for further egg-laying. Each turtle's motivation to home was most probably dependent on her willingness to lay further clutches of eggs and thus on the stage of the nesting season at which experiments were performed. Although the number of previous egg-layings of the single turtles was not known, turtles displaced later in the season are more likely to have completed their nesting cycle, and thus more motivated to migrate to their Brazilian feeding areas than to returning to the island (where they do not feed; Carr 1975). In fact, the turtles that headed directly to Brazil (releases B and C) were displaced in the second part of the season (Table 1). Even those motivated to home, however, usually gave up searching after some time and headed back to Brazil, as was the case for turtles A3, B1, C1 and E1. In these cases too, the turtles released early in the season (A3 and E1) spent more time than the others searching for the island.

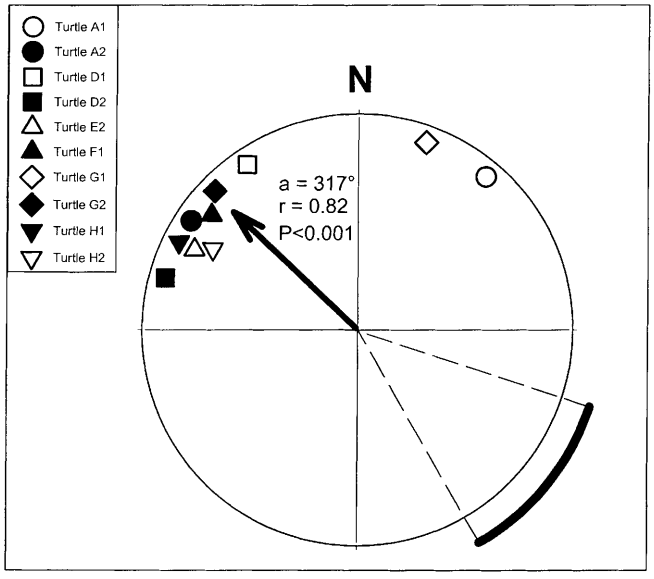

Fig. 4 Circular diagram of the directions of the first fix of the final leg of the routes of the turtles that returned to Ascension (*asterisks* in Figs. 2, 3) with respect to the island, together with their mean vector (*black arrow*). Mean vector length (*r*) and direction (*a*) and significance level according to the Rayleigh test are also reported. The range of wind directions recorded at Ascension in the month preceding the turtles' return is represented by the *black sector*

On the whole, the navigational performances of turtles motivated to return to Ascension were poor. Upon release, turtles failed to show any ability to compensate for the displacement and to head, even approximately, towards home. The straightness index values of the turtles that homed (0.19–0.68; Table 1) were very low if compared to those recorded in migrating turtles (always >0.94; Luschi et al. 1998; Papi et al. 2000). We interpret the winding pattern of these courses as an indication that displaced turtles had no reliable information on the location of their goal and were doing spatial explorations in search of a sensory contact with it. Such behaviour, comprising looping segments returning to a central start point, is similar to the systematic search done (albeit on a much smaller scale) by ants searching for the nest entrance (cf. Müller and Wehner 1994). These findings also show that turtles were not able to collect information on the direction of displacement during their transportation away from the island. Thus, the navigational skills of Ascension turtles turns out to be much worse than those known in birds, whose homing ability after long-distance displacement, either on land or in the open sea, is well known (Åkesson and Alerstam 1998; Papi and Wallraff 1992).

Five of the turtles (releases C–E) were released within the corridor where Ascension turtles migrating to Brazil were observed to pass (Figs. 1, 2; Luschi et al. 1998; Papi et al. 2000). Since the courses of these migrating turtles were found to be greatly overlapping and aligned with the WSW flow of the South Atlantic Equatorial Current (Luschi et al. 1998), this corridor has been thought to be determined by the hypothetical, current-borne chemical plume (Carr 1972; Koch et al. 1969; Luschi et al. 1998). Although determining the actual location of the plume is not possible, the five displaced turtles were therefore released in an area most probably exposed to the hypothetical plume. Even they, however, did not take advantage of this hypothetical cue. Only three of them reached the island, and did so with indirect courses and without swimming within the expected plume (Fig. 2). These turtles had been put in the same conditions in which, according to the chemosensory hypothesis, turtles migrating from Brazil either early in the season (releases D and E) or later (release C) would find themselves in the final leg of their journey towards Ascension, but their behaviour clearly disproves this hypothesis. In addition, the present results do not support the hypothesis of turtles' reliance on a magnetic map (Lohmann and Lohmann 1996) and, more generally, on any kind of spatial map that would allow them to acquire at least a crude estimate of their position (Åkesson and Alerstam 1998; Wallraff 1991; Wiltschko and Wiltschko 1995). On the basis of a true bi-coordinate navigation, turtles should be able to navigate directly to the island from any given site. However, this was not the case. After release, displaced turtles failed to show any tendency to orient towards the island, thus proving their inability to fix their position on the basis of local features. Any evidence of indirect navigation (cf. Dusenbery 1992) guided by the isodynamics or isoclinics of the geomagnetic field is also lacking. Since the Argos transmitter glued on the turtles' heads has been shown to produce a weak static magnetic field (Papi et al. 2000), this arrangement might have prevented turtles relying on a magnetic map. However, turtles with this kind of attachment have already been shown able to migrate from Ascension to Brazil with routes very similar to those of other turtles with the transmitter on the carapace (Papi et al. 2000).

The turtles' searching behaviour for a sensory contact with the island allows insight into the nature of the cues signalling the island position to the turtles. The behaviour of turtle E1, that passed as close as 23 km SE of the island during daytime without moving towards it, indicates that vision plays little role. The highest peak on Ascension in the SE part of the island, is about 900 m high, and so its summit should be theoretically visible from at least 100 km (geometrical horizon), although island visibility would certainly vary with various atmospheric parameters (e.g. air turbidity, wind). At the site of release F (60 km S), the island was vaguely visible to a human eye from the deck of a ship (D. Haff, "MV Ascension" Captain, personal communication). In any case, green turtles are myopic when out of water (Ehrenfeldt and Koch 1967) and view the surroundings from the surface of the sea, so their ability to sight Ascension is probably limited to a few kilometres away from it.

Of major interest is the fact that nearly all of the turtles that homed approached Ascension from the NW

(Figs. 2, 3, and 4). This indicates that the sensory contact with the island is easier from the NW than from the other directions. While the main current flows WSW and there is no reason to suppose that Ascension should be visible from longer distances in this direction, the island is constantly exposed to SE trade winds (Fig. 4). The most likely explanation for the turtles' behaviour is that winds can convey island-derived cues in a NW direction and that these may act as a beacon indicating the position of the island to turtles well before visual contact with it is possible. While swimming in the open sea, green turtles dive for short periods and surface frequently to breathe (Hays et al. 1999), so they would be easily able to determine wind direction and to find their target by osmotaxis by swimming upwind. The maximum distance at which wind-borne cues are perceivable is hard to estimate: turtles D2 and E2 apparently headed towards the island from as far as 170 km, but turtles A1, A2 and D1 spent periods searching in areas downwind from the island closer than this without orienting towards it. Most probably, the perception range of wind-borne information varies according to wind strength and turbulence. Thus, sensory contact with the island at a given location will not be constantly available, and this might explain the behaviour of some displaced turtles (e.g. D2 or H2) that were apparently able to locate their target from a site they had previously visited but from which they had not oriented (Figs. 2, 3). Trade winds in the Ascension area are very constant throughout the year: 93.4% of wind directions recorded at sea in the years 1854–1997 were in the sector 100–170° (i.e. blowing NW; Comprehensive Ocean Atmosphere Data Set). The wind directions recorded at Ascension (Wideawake Field Meteorological Observatory) in the month preceding the turtles' returns were actually between 110–150° (Fig. 4).

The nature of the wind-borne cues used is not known, although an involvement of odours and/or sounds seems the most probable. Despite its aridity, Ascension is rich in odour sources such as the lush vegetation covering its main mountain or the deposits of guano in the nearby small Boatswain Bird Island, and marine turtles have been shown to possess a well-developed sense of smell (Owens et al. 1986). Distinctive sounds (especially in the low-frequency range) can also originate from the rocky island, for example as a result of waves breaking on it, and can propagate for long distances in the air with the help of winds. Involvement of infrasounds in avian navigation has often been proposed (Hagstrum 2000; Yodlowsky et al. 1977), and marine turtles have been shown to be sensitive to low-frequency sounds (O'Hara and Wilcox 1990; Bartol et al. 1999). Both kinds of cue could be perceived by swimming turtles when they surface to breathe.

The present results allow a tentative inference about the navigational system used by Brazilian turtles to reach Ascension. Having the knowledge (no matter how obtained) of the island distance and direction from a given point along the Brazilian coast, they could cover a programmed distance along this fixed direction (e.g. swimming for about 2,200 km towards the east). The correct heading could be selected and maintained by biological compasses (Luschi et al. 1998; Papi and Luschi 1996), while the distance travelled might be estimated subjectively (e.g. according to the swimming effort sustained) or be determined by endogenous activity programmes controlling the time spent migrating (Berthold 1991). The constant presence of the chemical beacon pointing towards NW (deriving from the inter-annual consistency of wind direction in the Ascension area) expands the target in this direction, and turtles would probably head somewhat north of Ascension to decrease the chance of missing their target. When such a spatiotemporal programme of vectorial navigation, similar to that known in migrating birds (Berthold 1991), is run successfully, the turtle should "automatically" arrive in sensory contact with Ascension and then reach it by direct orientation. If this strategy fails because of interfering influences (particularly current drift), far-ranging searching movements, similar to those we recorded after displacements, could be started until such contact is made.

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