

DRO

Deakin University's Research Repository

This is the published version:

Akesson, S., Luschi, P., Papi, F., Broderick, A.C., Glen, F., Godley, B.J. and Hays, G.C. 2001, Oceanic long-distance navigation : do experienced migrants use the earth's magnetic field?, *Journal of navigation*, vol. 54, no. 3, pp. 419-427.

Available from Deakin Research Online:

<http://hdl.handle.net/10536/DRO/DU:30058252>

Reproduced with the kind permission of the copyright owner.

Copyright : 2001, Cambridge University Press

Oceanic Long-distance Navigation: Do Experienced Migrants use the Earth's Magnetic Field?

S. Åkesson

(Lund University, Sweden)

P. Luschi and F. Papi

(University of Pisa, Italy) and

A. C. Broderick, F. Glen, B. J. Godley and G. C. Hays

(University of Wales, Swansea)

Albatrosses and sea turtles are known to perform extremely long-distance journeys between disparate feeding areas and breeding sites located on small, isolated, oceanic islands or at specific coastal sites. These oceanic journeys, performed mainly over or through apparently featureless mediums, indicate impressive navigational abilities, and the sensory mechanisms used are still largely unknown. This research used three different approaches to investigate whether bi-coordinate navigation based on magnetic field gradients is likely to explain the navigational performance of wandering albatrosses in the South Atlantic and Indian Oceans and of green turtles breeding on Ascension Island in the South Atlantic Ocean. The possibility that magnetic field parameters can potentially be used in a bi-coordinate magnetic map by wandering albatrosses in their foraging area was investigated by analysing satellite telemetry data published in the literature. The possibilities for using bi-coordinate magnetic navigation varied widely between different areas of the Southern Oceans, indicating that a common mechanism, based on a bi-coordinate geomagnetic map alone, was unlikely for navigation in these areas. In the second approach, satellite telemetry was used to investigate whether Ascension Island green turtles use magnetic information for navigation during migration from their breeding island to foraging areas in Brazilian coastal waters. Disturbing magnets were applied to the heads and carapaces of the turtles, but these appeared to have little effect on their ability to navigate. The only possible effect observed was that some of the turtles with magnets attached were heading for foraging areas slightly south of the control turtles along the Brazilian coast. In the third approach, breeding female green turtles were deliberately displaced in the waters around Ascension Island to investigate which cues these turtles might use to locate and return to the island; the results suggested that cues transported by wind might be involved in the final stages of navigation.

KEY WORDS

1. Animal Navigation. 2. Migration. 3. Orientation.

1. INTRODUCTION. Albatrosses and sea turtles are known for their impressive navigational abilities, enabling them to locate isolated breeding islands or to pinpoint specific locations on continental shores successfully after long oceanic migrations.

They exemplify the most enigmatic masterpieces of long-distance navigation performed by any animal. Despite these impressive navigational performances, it is still largely unknown which cues they use for navigation in open oceans and how they are able to locate remote islands (cf. Åkesson, 1996; Papi and Luschi, 1996).

Recent experiments with loggerhead turtles *Caretta caretta* show that hatchlings rely on an inherited programme that enables them to use a number of different cues to find a direction to the open ocean. A sequence of behavioural responses is triggered by first visual cues on the beach, then wave direction as the hatchlings enter the sea and later geomagnetic cues become predominant in the ocean (Lohmann and Lohmann, 1996a and 1998). Hatchlings of loggerhead turtles have been shown to respond, by changing their preferred courses recorded in circular test arenas, when exposed to artificial magnetic fields of increased field strength and decreased steepness of the inclination angle (Lohmann and Lohmann, 1994 and 1996). These results suggest that hatchlings have an inherited tendency to change their migratory course on the basis of 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, 1996b and 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 (Wallraff, 1990; see also Lohmann and Lohmann 1996a).

Åkesson and Alerstam (1998) approached this possible use of geomagnetic information by analysing satellite telemetry data recorded and published in the literature for foraging wandering albatrosses *Diomedea exulans* breeding in South Georgia, in the south-western Atlantic Ocean (Prince *et al.*, 1992) and on the Crozet islands, in the south-western Indian Ocean (e.g. Jouventin and Weimerskirch 1990, Weimerskirch *et al.*, 1993). The objective was to analyse whether any combination of the five geomagnetic field parameters, i.e. inclination, declination, horizontal, vertical and total field intensity, could explain the birds' navigation performances in the two oceanic foraging areas. Other approaches adopted were to perform experiments with green turtles *Chelonia mydas* breeding on Ascension Island in the South Atlantic, by temporarily applying disturbing magnets and by performing displacements (Carr, 1984; Mortimer and Carr, 1987 and Luschi *et al.*, 1998) and studying the subsequent movements of the turtles recorded by satellite telemetry (ARGOS).

2. METHODS AND STUDY SPECIES.

2.1. *Wandering albatrosses.* Long-distance foraging flights of wandering albatrosses breeding on South Georgia (54°00'S, 38°36'W; 3 tracks) and Crozet Islands (46°26'S, 51°52'W; 8 tracks) recorded by satellite telemetry (Jouventin and Weimerskirch, 1990; Prince *et al.*, 1992 and Weimerskirch *et al.*, 1993) were selected for further analyses of the geomagnetic field parameters encountered (Åkesson and Alerstam, 1998). The foraging trips lasted between 3 and 33 days and covered distances of 3664 to 15200 km mainly to the northwest (South Georgia) and north to east (Crozet) of the breeding islands (Jouventin and Weimerskirch, 1990; Prince *et al.*, 1992 and Weimerskirch *et al.*, 1993). Information on total field intensity, horizontal and vertical field intensity, inclination and declination in the area of foraging were extracted from geomagnetic maps published by the US Geological Survey (Peddie, 1993; for further details of method see Åkesson and Alerstam, 1998). From these values, the extent to which different combinations of magnetic field parameters give

unique combinations of values useful for bi-coordinate navigation in the two foraging areas was evaluated (Figure 1; cf. Åkesson and Alerstam, 1998).

2.2. *Experiments with green turtles breeding on Ascension Island.* The navigational abilities of green turtles breeding on Ascension Island (7°57'S, 14°22'W) and migrating to coastal waters of Brazil has been a matter of considerable discussion (Carr, 1984; Mortimer and Carr, 1987 and Luschi *et al.*, 1998). Two main hypotheses have been suggested to explain the turtles' ability to pinpoint the island, based on chemosensory information transported westwards with the South Atlantic Equatorial Current (Koch *et al.*, 1969 and Carr, 1972) and geomagnetic field information forming a bi-coordinate gradient map, based on angle of inclination and total field intensity (Lohmann and Lohmann, 1996a and 1998). The magnetic grid around Ascension Island provides optimal conditions for bi-coordinate magnetic navigation (Skiles, 1985; Lohmann and Lohmann, 1996b) and, therefore, the research investigated this possibility by applying disturbing magnets to sea turtles to be tracked by satellite telemetry during ocean migration, with particular interest in recording the turtles' orientation during natural migration (Papi *et al.*, 2000).

Female green turtles were equipped with satellite transmitters (Telonics), eight as controls and seven also with magnets as experimentals. Six cylindrical magnets of neodymium (type Neo 35, Calamit Trading, Milan, Italy) were attached at positions on the carapace and head of the experimental turtles, with a galvanic-timed mechanism to release the magnets after approximately four weeks. No point on the head of each turtle was more than 20 cm from the magnet, resulting in magnetic field exposures of at least 15000 nT; for the rest of the body, the artificial magnetic field was increased by at least 6000 nT. The magnets were attached so that a nearly random oscillation of the magnets was assured as the turtle moved in water (for details on methods see Papi *et al.*, 2000). The migration direction, mean speed of migration, and straightness index recorded from satellite telemetry for experimental turtles was later compared with the migration routes taken by the control turtles without magnets. Mardia's one-way classification test ($F_{1,df}$) was used to examine whether the mean orientation differed between turtles with and without magnets, based on the time passed (2, 5 or 10 days) after deployment with satellite transmitters (Mardia, 1972). One additional turtle was released without magnets, but she followed a winding route around the Island before departure to Brazil, and was therefore excluded from further analysis.

In the second experiment, the turtles' ability to find the breeding site on Ascension Island after deliberate displacement was investigated. For these displacements, female green turtles were captured after egg laying at the beaches of Ascension during the early phase of the breeding cycle. They were transported between 60 and 450 km by ship and released at sea at 8 sites in different compass directions from the breeding island (Luschi *et al.*, in press). By analyzing the turtles' search trajectories, the two alternative hypotheses, based on chemosensory cues transported by ocean currents (Koch *et al.*, 1969 and Carr, 1984) and geomagnetic bi-coordinate navigation (Lohmann and Lohmann, 1996a and b, see also Wallraff, 1990), were investigated to see if they explain the turtles' ability to locate the island, or if the navigational performances could be explained by other cues.

3. RESULTS.

3.1. *Foraging wandering albatrosses: are reliable bi-coordinate magnetic maps*

available in the ocean? The two longest foraging tracks from South Georgia (7478 km) and Crozet Islands (15200 km) were selected and plotted in the parameter space of total field intensity and angle of inclination in Figure 1 (from Åkesson and

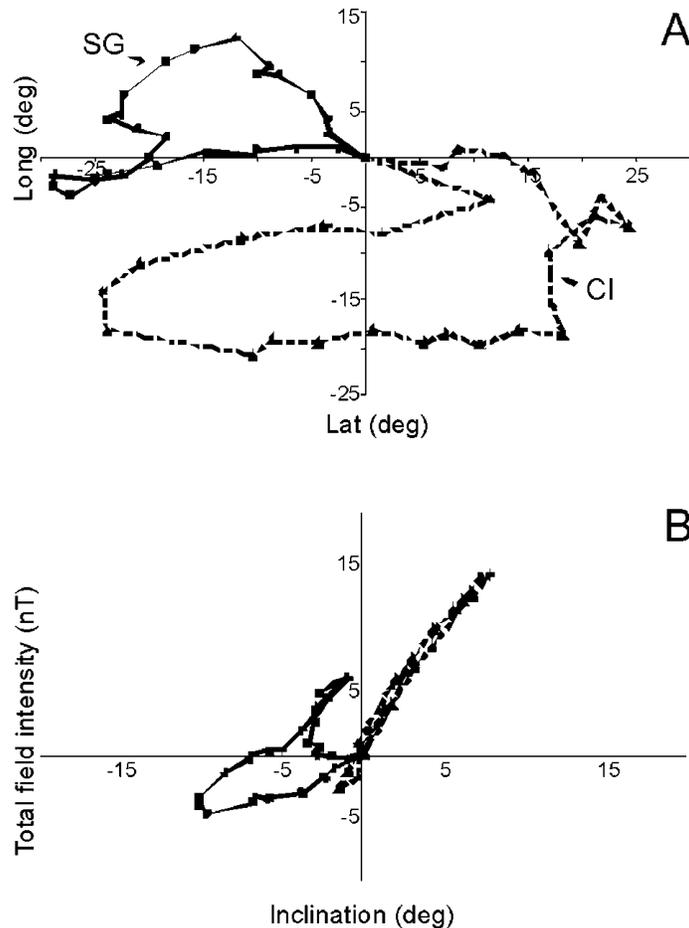


Figure 1. (A) Trajectories of the two longest foraging tracks for wandering albatrosses breeding at South Georgia (SG, from Prince *et al.*, 1992) and Crozet Islands (CI, from Jouventin and Weimerskirch, 1990). (B) Total field intensity and angle of inclination for the foraging trajectories given in A (unbroken line: SG, broken line: CI). The values are plotted as deviations from values at the starting point (origin for track SG: inclination = 53.4° and total field intensity = $29.6 \mu\text{T}$; origin for track CI: inclination = 62.2° and total field intensity = $37.6 \mu\text{T}$). Modified after Åkesson and Alerstam (1998).

Alerstam, 1998). By observing the magnetic values for tracks, it could be seen that, for the track selected from South Georgia, each geographic location is represented by a unique combination of values on a grid that in theory could be used for bi-coordinate magnetic navigation (i.e. the lines do not overlap). However, the male wandering albatross departing on a foraging flight from Crozet Island, experienced a problem of parallel grids (magnetic field parameters varying in the same geographical direction) resulting in values plotted more or less along a straight line (Figure 1). In the foraging area used around South Georgia, all geomagnetic

Table 1. Departure directions for female green turtles migrating from Ascension Island to foraging areas along the Brazilian coast tracked by satellite telemetry. Mean angles of orientation (α), vector length (r), number of individuals (N) and significance level according to the Rayleigh test (Batschelet, 1981) are given for each category. ***: $p < 0.001$. For further information see Figure 2.

Category	Period	α	N	r
Control	2 days	254°	8	0.99***
Magnets	2 days	251°	7	0.99***
Control	5 days	259°	8	0.99***
Magnets	5 days	252°	7	0.99***
Control	10 days	261°	8	0.99***
Magnets	10 days	257°	7	0.99***

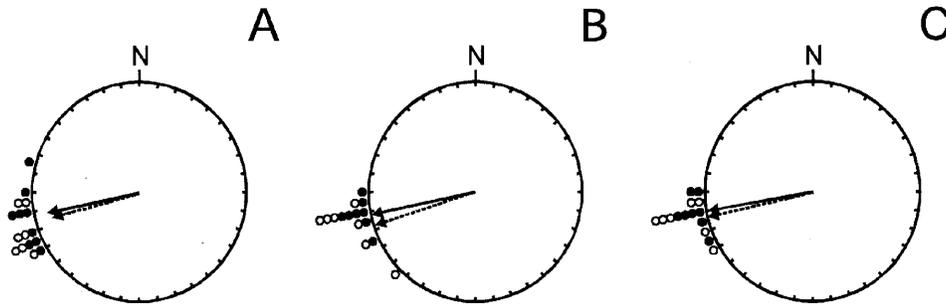


Figure 2. Mean angle of orientation for adult female green turtles departing with (open symbols, broken line) and without (filled symbols, filled line) disturbing magnets from Ascension Island to feeding waters along the Brazilian coast. (A) 2 days, (B) 5 days and (C) 10 days, after deployment with satellite transmitters on Ascension Island.

parameter combinations, except horizontal intensity and declination, were classified as feasible for bi-coordinate navigation (Table 1 in Åkesson and Alerstam, 1998). On the other hand, in the area of Crozet Island, it was observed that not a single pair of magnetic gradient combinations was free from complications (i.e. parallel isomagnetics, weak gradient, ridge or valley of gradient, curved isomagnetics giving the same coordinate values at two sites; for further information see Åkesson and Alerstam, 1998). There were only three parameter combinations for which at least 8 of the 11 tracks were classified as acceptable for geomagnetic navigation in both areas; these were total field intensity/declination, vertical field intensity/declination and inclination/declination (Åkesson and Alerstam, 1998). However, to record declination the birds need to be able to detect the direction towards the geographic North, and therefore a combination of information from the geomagnetic field and celestial cues are needed.

4. EXPERIMENTS WITH MAGNETS ON GREEN TURTLES. All female green turtles, with and without magnets, departing on migration from Ascension Island to Brazil selected very similar courses slightly south of west (Table 1 and Figure 2; Luschi *et al.*, 1998 and Papi *et al.*, 2000). There were no significant differences in mean angle of orientation between the control and experimental turtles for the three time periods analysed (2 days: $F_{1,13} = 0.3$; 5 days: $F_{1,13} = 1.5$; 10 days:

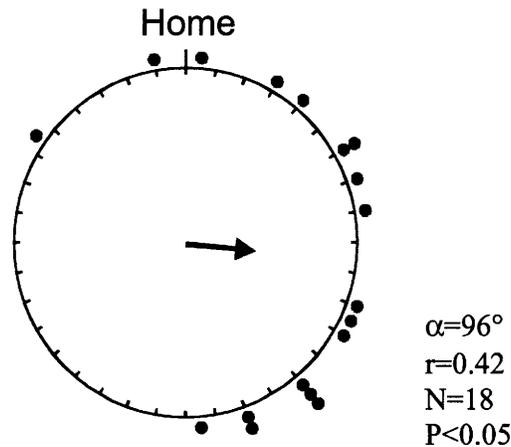


Figure 3. Departure directions recorded 24 hours after release for adult female green turtles displaced by ship from Ascension Island and released at sea during the breeding period. Departure directions are given relative to the direction to Ascension Island along a great circle route (up). Mean angle of orientation (α), vector length (r), number of individuals (N), and significance level (P) according to the Rayleigh test (Batchelet, 1981) are given.

$F_{1,13} = 0.8$; $p < 0.05$ in all cases, one-way classification test (Mardia, 1972)). The migration routes were compared with respect to mean travel speed and course straightness index, and no difference was found between the control and experimental turtles (statistics given in Papi *et al.*, 2000). The only difference found was that some of the experimental turtles with magnets were heading for foraging areas along the coast of Brazil slightly south of the controls. However, it is not clear if this was an effect of the magnets or if these individual turtles normally use these foraging areas, since foraging areas of green turtles are widely spread along the east coast of Brazil (Mortimer and Carr, 1987). Both groups of turtles travelled faster during the day than at night, and there was no difference in travel speed between the groups during the day or the night. Furthermore, no difference was found in the speed of migration with or without a visible moon at night. For further details on analyses, see Papi *et al.* (2000).

5. DISPLACEMENT EXPERIMENTS WITH BREEDING GREEN TURTLES. Turtles displaced by ship were released at eight different sites, to the south, west and north of Ascension Island. Of eighteen displaced turtles, ten were able to find their way back to the nesting beaches on Ascension Island (Luschi *et al.*, in press). Four immediately returned to Brazil when released at sea, while four others searched for the island without success, and later returned to Brazil (Luschi *et al.*, in press). The two sites to the west of the island were located within the hypothetical plume of chemical cues transported by the westerly ocean currents passing Ascension (cf. Koch *et al.*, 1969 and Carr, 1972). Five of the turtles were released at these sites and all of them moved off in different directions and initiated meandering movements suggestive of searching. Only three of these turtles were able to locate the island and only when, during their search, they were approaching from the north (Luschi *et al.*, in press). For all turtles, the mean departure direction, as calculated for 24 hours after

release, was not directed towards Ascension Island but east of the home direction (Figure 3), indicating that bi-coordinate magnetic navigation was not used by the turtles.

6. DISCUSSION.

6.1. *Do oceanic navigators use magnetic maps?* The recent findings by Lohmann and Lohmann (1996a, b), suggest that oceanic navigators such as sea turtles do indeed possess a sensory ability that can in theory be used for bi-coordinate magnetic navigation (cf. Wallraff, (1990). This possibility has resulted in the recent development of theoretical models (Phillips, 1996 and Walker, 1998) and in considerable discussion of behavioural data collected on magnetic navigation in animals (Wallraff, 1999; see also for example Gould, 1985 and Walcott, 1996). The analyses of satellite tracks of wandering albatrosses foraging in the Southern Ocean by Åkesson and Alerstam (1998) show that in some areas of the ocean, i.e. around Crozet Islands in south-western Indian Ocean, a reliable combination of magnetic gradients is not available for navigation, indicating against the possibility of bi-coordinate navigation in these areas. However, other geographical regions might provide useful magnetic bi-coordinate maps. Examples of such areas are currently found around South Georgia where wandering albatrosses forage (Åkesson and Alerstam, 1998) in the North Atlantic (cf. Lohmann and Lohmann, 1996a and b) and around Ascension Island (Luschi *et al.*, 1998 and Papi *et al.*, 2000) where sea turtles migrate as hatchlings or adults. However, due to secular variation, local values of magnetic field parameters change over time (Skiles, 1985; see also Courtillot *et al.*, 1997).

The experiments with green turtles using magnets to disturb their perception of the Earth's magnetic field resulted in only negligible negative effects on the turtles' migratory performance between Ascension Island and Brazil (Papi *et al.*, 2000). The turtles were able to navigate in the open ocean despite experiencing disturbed magnetic fields. They followed lengthy straight paths by day and night, suggesting that cues other than the magnetic field could provide reliable compass courses. In the open ocean, a constant heading can be held using any of the animal biological compasses, which are based on astronomical cues (the sun and the related pattern of skylight polarisation, moon and stars) or on the geomagnetic field (Papi, 1992). Sea turtles seem to be unable to see stars (Ehrenfeld and Koch, 1967) and therefore during moonless or overcast nights they would have to rely on geomagnetic field information. The experimental turtles with magnets, however, did not perform worse than the controls on moonless nights, suggesting that presumable cues other than the magnetic field might be used for keeping the course. It is possible that the direction of the waves, being fairly constant in open ocean, might be used for orientation. However, during the process of migration the wave direction would need to be repeatedly calibrated relative to, for example, astronomical compasses (Papi and Luschi, 1996 and Papi *et al.*, 2000) since the direction and speed of the currents might differ between geographical areas.

6.2. *What sensory cues do green turtles use to locate oceanic breeding islands?* Results from the displacement experiments suggest that the female green turtles did not use true bi-coordinate magnetic navigation to locate the island, nor did they swim against the ocean current passing Ascension, as was suggested by Koch *et al.* (1969) and Carr (1984). If the turtles had relied on geomagnetic field cues, they would be expected to home by direct routes to Ascension Island from any given location

around the breeding island. This was not the case, since on most occasions the sea turtles moved off in other directions and only later were able to find the island after searching for some time (Luschi *et al.*, in press). The ability to find the island from the west – that is, down-current from Ascension – was not – as expected – higher compared to other directions. Instead the turtles seemed to find Ascension Island successfully only from the north and northwest. This correlates with the downwind direction from Ascension, which suggests that cues transported by the wind are used (Luschi *et al.*, in press).

In conclusion, based on the different experimental and analytical approaches used to investigate the possibility that animals navigating in oceans use a bi-coordinate magnetic map, it must be concluded that there are areas of the ocean where the use of bi-coordinate magnetic navigation seems highly improbable (Åkesson and Alerstam, 1998). Furthermore, there is little support for the hypothesis that adult green turtles use geomagnetic cues for navigation during migration, but rather that visual cues and perhaps direction of waves provide compass information for orientation (Papi *et al.*, 2000). The displacement experiment with breeding green turtles suggests that windborne cues, rather than the geomagnetic field or cues transported by ocean currents, are used by the turtles to pinpoint the breeding island (Luschi *et al.*, in press).

ACKNOWLEDGEMENTS

We thank the crews of MV *Ascension* and RMS *St. Helena* and many island residents for invaluable help during fieldwork on Ascension Island. Thanks also to the Administrator of Ascension Island, H. H. Geoffrey Fairhurst, the First Ascension Scout Group, the United States Air Force, Merlin Communications, CRS, Sealift. Financial support was given by The Swedish Natural Science Research Council (NFR) and the Crafoord foundation (to S.Å.), from the Accademia Nazionale dei Lincei and the Italian Space Agency (to F.P.), and from the Natural Environmental Research Council of the UK (NERC) and from the Department of the Environment, Transport and Regions (DETR) through the Darwin Initiative program (to G.H.).

REFERENCES

- Åkesson, S. (1996). Geomagnetic map used for long-distance navigation? *Trends Ecol. Evol.* **11**, 398–400.
- Åkesson, S. and Alerstam, T. (1998). Oceanic navigation: are there any feasible geomagnetic bi-coordinate combinations for albatrosses? *J. Avian Biol.* **29**, 618–625.
- 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 Fish*. 2nd Ed. Austin: University of Texas Press.
- Courtilot, V., Hulot, G., Alexandrescu, M., Le Mouel, J.-L. and Kirschvink, J. L. (1997). Sensitivity and evolution of sea-turtle magnetoreception: observations, 27-9 modelling and constraints from geomagnetic secular variation. *Terra Nova*. **9**, 203–207.
- 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.
- Jouventin, P. and Weimerskirch, H. (1990). Satellite tracking of wandering albatrosses. *Nature*, **343**, 746–748.
- 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). Orientation and open-sea navigation in sea turtles. *J. Exp. Biol.* **199**, 73–81.
- Lohmann, K. J. and Lohmann, C. M. F. (1996b). Detection of magnetic field intensity by sea turtles. *Nature* **380**, 59–61.
- Lohmann, K. J. and Lohmann, C. M. F. (1998). Migratory guidance mechanisms in marine turtles. *J. Avian Biol.* **29**, 585–596.
- 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.
- Luschi, P., Åkesson, S., Broderick, A. C., Glen, F., Godley, B. J., Papi, F. and Hays, G. C. (in press). Testing the navigational abilities of oceanic migrants: displacement experiments on sea turtles (*Chelonia mydas*). *Behav. Ecol. Sociobiol.* in press.
- Mardia, K. V. (1972). *Statistics of Directional Data*. London: Academic Press.
- Mortimer, J. A. and Carr, A. (1987). Reproduction and migrations of the Ascension Island green turtle (*Chelonia mydas*). *Copeia* (1987), 103–113.
- Papi, F. (ed.) (1992). *Animal Homing*. London: Chapman and 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., Luschi, P., Åkesson, S., Capogrossi, S. and Hays, G. C. (2000). Open-sea migration of magnetically disturbed sea turtles. *J. Exp. Biol.* **203**, 3435–3443.
- Peddie, N. W. (1993). The magnetic field of the Earth, 1990. U.S. Geological Survey. Geophysical Investigation Maps GP-1004-I, D, F, H, Z.
- Phillips, J. B. (1996). Magnetic navigation. *J. Theor. Biol.* **180**, 309–319.
- Prince, P. A., Wood, A. G., Barton, T. and Coxhall, J. P. (1992). Satellite tracking of wandering albatrosses (*Diomedea exulans*) in the South Atlantic. *Antarctic Science*. **4**, 31–36.
- Skiles, D. D. (1985). The geomagnetic field; its nature, history and biological relevance. In: *Magnetite Biomineralization and Magnetoreception in Organisms* (Eds. J. L. Kirschvink, D. S. Jones and B. J. MacFadden), pp. 43–102. New York, Plenum Press.
- Walcott, C. (1996). Pigeon homing: observations, experiments and confusions. *J. Exp. Biol.* **199**, 21–27.
- Walker, M. M. (1998). On a wing and a vector: a model for magnetic navigation by homing pigeons. *J. Theor. Biol.* **192**, 341–349. 27–10.
- Wallraff, H. G. (1990). Conceptual approaches to avian navigation systems. *Experientia*. **46**, 379–388.
- Wallraff, H. G. (1999). The magnetic map of homing pigeons: an evergreen phantom. *J. Theor. Biol.* **197**, 265–269.
- Weimerskirch, H., Salamolard, M., Sarrazin, F. and Jouventin, P. (1993). Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk*. **110**, 325–342.
- Wiltschko, R. and Wiltschko, W. (1995). *Magnetic orientation in animals*. Springer-Verlag, Berlin, Heidelberg.