PINPOINTING 'ISLA META': THE CASE OF SEA TURTLES AND ALBATROSSES

F. PAPI[1] AND P. LUSCHI[2]

[1]*Dipartimento di Scienze del Comportamento Animale e dell'Uomo, University of Pisa, Via A. Volta 6, I-56126 Pisa, Italy* and [2]*Centro di Studio per la Faunistica ed Ecologia Tropicali del CNR, Via Romana 17, I-50125 Florence, Italy*

Summary

Satellite tracking has recently shown that the very long open-sea journeys of sea turtles and albatrosses share several features, in spite of the different physiological and environmental constraints to which turtles and birds are subjected. The reviews of data obtained by tracking migration and feeding routes show that both sea turtles and albatrosses are able (i) to pinpoint small, isolated targets by following straight courses, (ii) to continue on a bearing at night even when the moon is not visible, (iii) to compensate for wind or current drift and (iv) to return home after experimental, long-distance displacements. Sea turtles and albatrosses seem to rely on a position-fixing capacity which cannot be explained by known navigational mechanisms but might be shared by other animals that display similar feats of open-sea guidance. Future research will further benefit from satellite telemetry and other new techniques applied to experimental investigations.

Key words: navigation, homing, satellite tracking, sea turtles, albatrosses.

Introduction

Research on animal navigation provides special reasons for comparing sea turtles, nature's heavily built marathon swimmers, which cross the seas using the strength of their flippers, with albatrosses, her swift acrobats, which glide over the waves. The first reason is that both sea turtles and albatrosses are genuine oceanic navigators; by undertaking journeys thousands of kilometres long, they are able to reach a small target, such as a tiny island in the middle of the ocean, or a specific site on a continental coast. This performance, like the reproductive migration of some fishes, is astonishing mainly on account of the uniformity of the environment within which it is achieved. By reducing the number of cues available for navigation, this environment eliminates the factor which is so disturbing in evaluating navigational performances, namely the presence of landmarks with their implicit capacity to guide, attract or repel.

The amazing performance of sea turtles was stressed by Archie Carr, who had been struck by the case of the Brazilian green turtles (*Chelonia mydas*) that migrate to Ascension Island, 2000 km or so distant, to lay their eggs. For these turtles, Ascension Island is the target island, the 'Isla Meta', to which Carr devoted an entire chapter of his book (Carr, 1984). He had also emphasized that other animal navigators, such as oceanic birds, which achieve similar performances, may have to rely on similar cues and mechanisms. Comparative studies may thus facilitate the discovery of the underlying navigational mechanisms.

To these reasons for comparing turtles and albatrosses one may add that satellite tracking has recently been applied to both, permitting reconstruction of the paths they follow even when very long distances are involved. This technique has considerably enhanced our knowledge and understanding of the navigational performances of these creatures.

The present review emphasizes the findings obtained using satellite tracking and briefly discusses the new perspectives it has opened up.

Sea turtles

Most of our knowledge about sea turtles' spatial behaviour derives from the recovery of tagged individuals (Meylan, 1982). Adult females are known to return regularly to the same nesting beach where they accomplish a series of egg-layings at intervals of several days, during which they wander in the surrounding waters. At the end of the nesting cycle, they may exhibit different forms of spatial behaviour; they may (i) remain in the same area, (ii) perform erratic movements or long-distance journeys not directed to resident grounds or (iii) undertake migrations towards spatially separate resident grounds. In the loggerhead turtle (*Caretta caretta*) and the green turtle, fidelity to the feeding grounds has been demonstrated (Limpus *et al.* 1992; Balazs, 1994), so that a regular migration between two specific areas can be said to occur, at least in some cases. These different behavioural patterns may be displayed not only by different species or demes but also by different members of the same deme (Carr *et al.* 1978; Green, 1984).

Obviously, tag recoveries can hardly permit reconstruction of the turtle journeys. Before the introduction of satellite telemetry, the previously available methods allowed only a

time-consuming reconstruction of short legs of journeys by the visual or radio tracking of turtles towing helium balloons or transmitting floats (Carr, 1963, 1972; Baldwin, 1972). The most interesting findings included the capacity for coastal navigation and straight movements off shore.

Pioneer experiments using satellite tracking were performed on the loggerhead turtle (Stoneburner, 1982; Timko and Kolz, 1982), and complete reconstructions of long-distance journeys became possible several years later.

Apart from preliminary reports that are often hard to classify (e.g. Eagleson et al. 1978; Renaud, 1990; Byles and Swimmer, 1994; Renaud et al. 1994), the types of movement that have been studied by satellite tracking can be grouped as follows. (1) Short segments of migratory journeys or similar movements: loggerhead turtle (Hays et al. 1991). (2) Tracks showing wandering activity in feeding grounds: loggerhead turtle (adults and subadults, Renaud and Carpenter, 1994); Kemp's ridley turtle (*Lepidochelys kempi*, juveniles, Renaud, 1994). (3) Long-distance movements apparently not directed at specific resident grounds: loggerhead turtle (Timko and Kolz, 1982; Stoneburner, 1982; Byles and Dodd, 1989; Keinath et al. 1989); olive ridley turtle (*Lepidochelys olivacea*, Byles and Plotkin, 1994). (4) Incomplete long-distance migratory journeys: this description is adopted when there is no evidence of arrival at the resident grounds. Sometimes it is difficult to distinguish between cases to be assigned to this or the previous group: green turtle (Spring, 1990; Liew et al. 1995); hawksbill turtle (*Eretmochelys imbricata*, Groshens and Vaughan, 1994); Kemp's ridley turtle (Byles, 1989); olive ridley turtle (Plotkin et al. 1995); leatherback turtle (*Dermochelys coriacea*, Duron-Dufrenne, 1987; see also Keinath and Musick, 1993, for movements in the interesting period). (5) Entirely reconstructed migratory journeys to the feeding grounds (Fig. 1). They can be subdivided into: (5a) journeys mostly swum along the coast (green turtle, Liew et al. 1995: Fig. 1C, track e; hawksbill turtle, Groshens and Vaughan, 1994; Byles and Swimmer, 1994; Kemp's ridley turtle, Byles and Plotkin, 1994; Plotkin et al. 1995) and (5b) journeys mainly carried out in open seas (green turtle, Balazs, 1994; Balazs et al. 1994; Papi et al. 1995; Liew et al. 1995).

Besides the ability to maintain straight courses, which is a frequent feature in tracked journeys, the cases illustrated in 5b also reveal that these turtles have a surprising capacity to pinpoint specific targets during a long-distance journey in open seas, without movements indicating a random or systematic search. This behaviour is particularly striking in track a in Fig. 1C: this turtle was able to take a route which led her straight to the strait through which she had to pass to reach the feeding grounds. In the cases illustrated in Fig. 1, the ratio between the 'beeline' distance from nesting to resident grounds and the distance actually travelled (straightness index, Batschelet, 1981) ranges between 0.71 and 0.98.

Tracks of naturally occurring journeys can certainly allow inferences to be drawn about turtle navigational mechanisms, but further progress is only possible using an experimental approach. In this connection, experimental displacement from
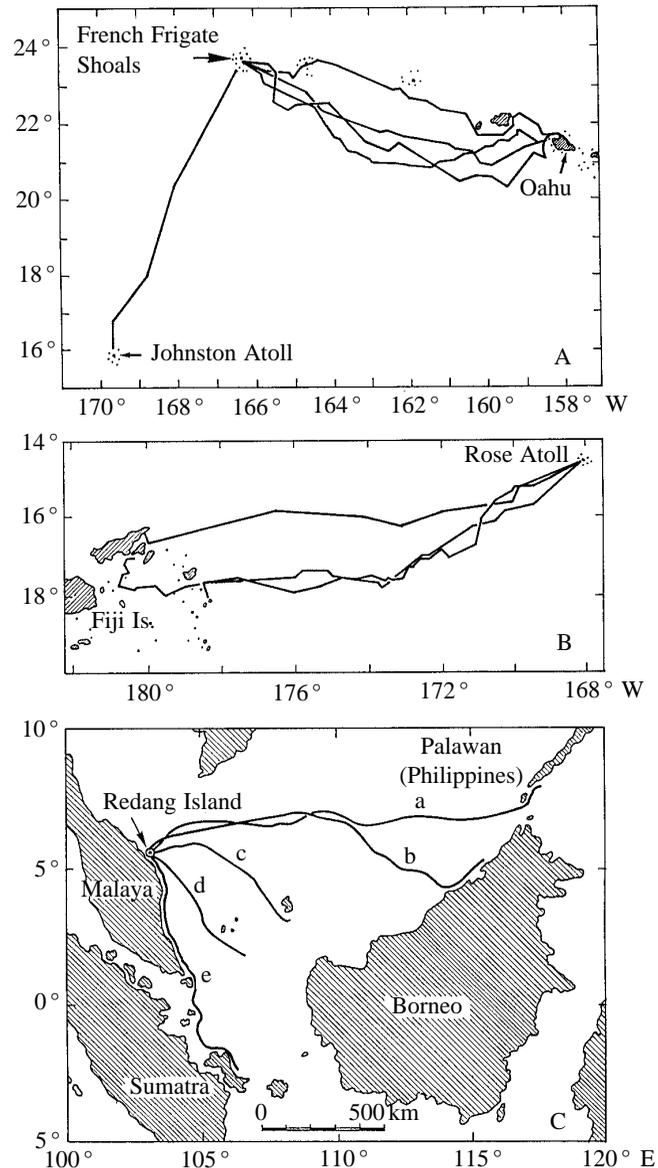

Fig. 1. Examples of migratory journeys of green turtles tracked by satellite. (A) Tracks recorded in the Hawaii region (from Balazs, 1994; Balazs et al. 1994, modified). (B) Tracks of turtles migrating from Rose Atoll, American Samoa, to Fiji Islands (from Balazs et al. 1994, modified). (C) Tracks of turtles migrating from Redang Island, West Malaysia (from Papi et al. 1995; Liew et al. 1995, modified): track d is not complete, as the transmitter stopped emissions before the resident grounds were reached. Track e is an example of navigation along a coastline. The turtle in track c stopped in the waters near the island.

the nesting grounds or *en route* seems to be a promising method. Only a few long-distance experiments have so far been attempted, and not all of these have led to meaningful outcomes.

A first unplanned experiment, reported by Cornelius (1865), involved a green turtle caught at Ascension and transported by ship as far as the English Channel, where the animal looked unhealthy and was thrown overboard. This turtle, which was

recognisable because it had been branded, was caught again at Ascension 2 years later. This finding appears even more remarkable now, after the discovery that all Ascension turtles have their resident feeding grounds on the Brazilian coast (Carr and Mortimer, 1987). Thus, this unlucky turtle succeeded in finding its way back to Ascension, probably after a stay at its Brazilian feeding grounds, starting from a distant site well away from its migratory route.

Carr (1972) interrupted the nesting of an Ascension green turtle and displaced her 187 km north from what should have been her course to Brazil. After an initial zigzag, the female headed straight in one direction, only deflecting 15° from Ascension. Unfortunately, visual tracking was interrupted after about 9 km.

Liew *et al.* (1995) transported a green turtle caught at Redang Island, Malaya, 280 km south and released her on the east continental coast. The turtle, equipped with a satellite transmitter, quickly returned to Redang, following a course along the coast.

According to a preliminary report by Renaud (1994), a juvenile Kemp's ridley turtle, tracked by satellite, homed after a 110 km displacement along the Texas coast. Other experiments have involved green turtles displaced over short distances: Baldwin (1972) tracked target-directed movements, whereas Ireland (1980), Renaud and Carpenter (1994) and Luschi *et al.* (1995) followed complete return paths.

Albatrosses

A great number of field and at-sea observations and one crucial displacement experiment (Kenyon and Rice, 1958) have for quite a time earned albatrosses a reputation as skilful oceanic navigators. They have developed a technique of slope-soaring along waves which allows them to proceed over the ocean at an extremely low cost in terms of energy and to wander in search of food at enormous distances from lands. There is circumstantial evidence that some albatrosses, such as the related giant petrel (*Macronectes giganteus*), perform circumpolar journeys over the Southern Ocean (Tickell and Scotland, 1961; Robertson and Kinsky, 1972), moving eastwards with the aid of the prevailing winds. However, albatrosses periodically return to nest in their natal colony, thus showing their excellent ability to rediscover a specific remote island (see Gibson, 1967; Fisher, 1971, for references). A similar performance is displayed when they home from long foraging flights during the nesting season. Definitive evidence of albatrosses' mastery of navigation derives from the classic displacement experiment of Kenyon and Rice (1958), who reported that 14 out of a group of 18 nesting Laysan albatrosses (*Diomedea immutabilis*), which had been moved 2116–6629 km in the Pacific area, managed to return to their nests in a relatively short time.

As with turtles, satellite telemetry has provided the basis upon which reasonable hypotheses about albatross navigational mechanisms can be formulated. In these experiments, the transmitters are usually attached to nesting birds in order to track their foraging trips. Following a pioneer study on the southern giant petrel (Strikwerda *et al.* 1986), French authors have provided a large quantity of useful tracks and data on the wandering albatross (*Diomedea exulans*) nesting at the Crozet Islands and, to a lesser extent, on the light-mantled sooty albatross (*Phoebetria palpebrata*) breeding at Macquarie Island (Jouventin and Weimerskirch, 1990; Weimerskirch *et al.* 1993, 1994; Weimerskirch and Robertson, 1994). Further tracks were recorded for wandering albatrosses by Prince *et al.* (1992) in South Georgia and by Nicholls *et al.* (1992) in southern Australia.

The albatrosses may forage in the surroundings of their nesting island or perform long journeys, which are clearly of greater interest to navigation. The evaluation of their routes is made difficult by two main factors. Albatrosses forage in different areas and also *en route*, so that the destination of their flights cannot be predicted. Moreover, their routes depend on wind direction and intensity; hence, a larger number of tracks, together with the pertaining wind data, are necessary to assess how the wind pattern actually influences their directional options.

Considering the major source of information available, namely the tracks of Crozet wandering albatrosses (Jouventin and Weimerskirch, 1990; Weimerskirch *et al.* 1993, 1994), some general features can be deduced. (1) The birds may forage in all quadrants (Fig. 2), even if prevailing winds blow from only one direction (west in the case considered). (2) The shape of the entire trip varies substantially; the outbound and inbound legs may be more or less widely separated, thus forming loops of different shape (Fig. 2A–C). Alternatively, they may intersect (Fig. 2D–F) or nearly coincide (Fig. 2G–I). Tracks of all these types have also been recorded in sooty albatrosses (Weimerskirch and Robertson, 1994; H. Weimerskirch, unpublished data). (3) The birds' return flights do not reveal reliance on search mechanisms, and they mostly approach the home island along a straight course. Such straight approaches can occur with crosswinds (Fig. 2A,B).

Besides the displacement experiment of Kenyon and Rice mentioned above, only one other experiment of this kind has been performed. Fisher (1971) displaced chicks and fledglings of Laysan albatrosses from their natal site to different islands. Only the fledglings were later able to rediscover the natal colony, whereas the chicks were only recovered at the site of the foster colony. This result indicates that the cues required to recognise the mother colony may be acquired between the ages of 1 and 5.5 months.

Experiments on species of procellariformes other than albatrosses confirm excellent homing abilities in this order (see references in Matthews, 1968; Dall'Antonia *et al.* 1995). In Cory's shearwater (*Calonectris diomedea*), homing paths of displaced individuals were recently reconstructed by means of a direction-recording data-logger (Dall'Antonia *et al.* 1995).

Discussion and conclusions

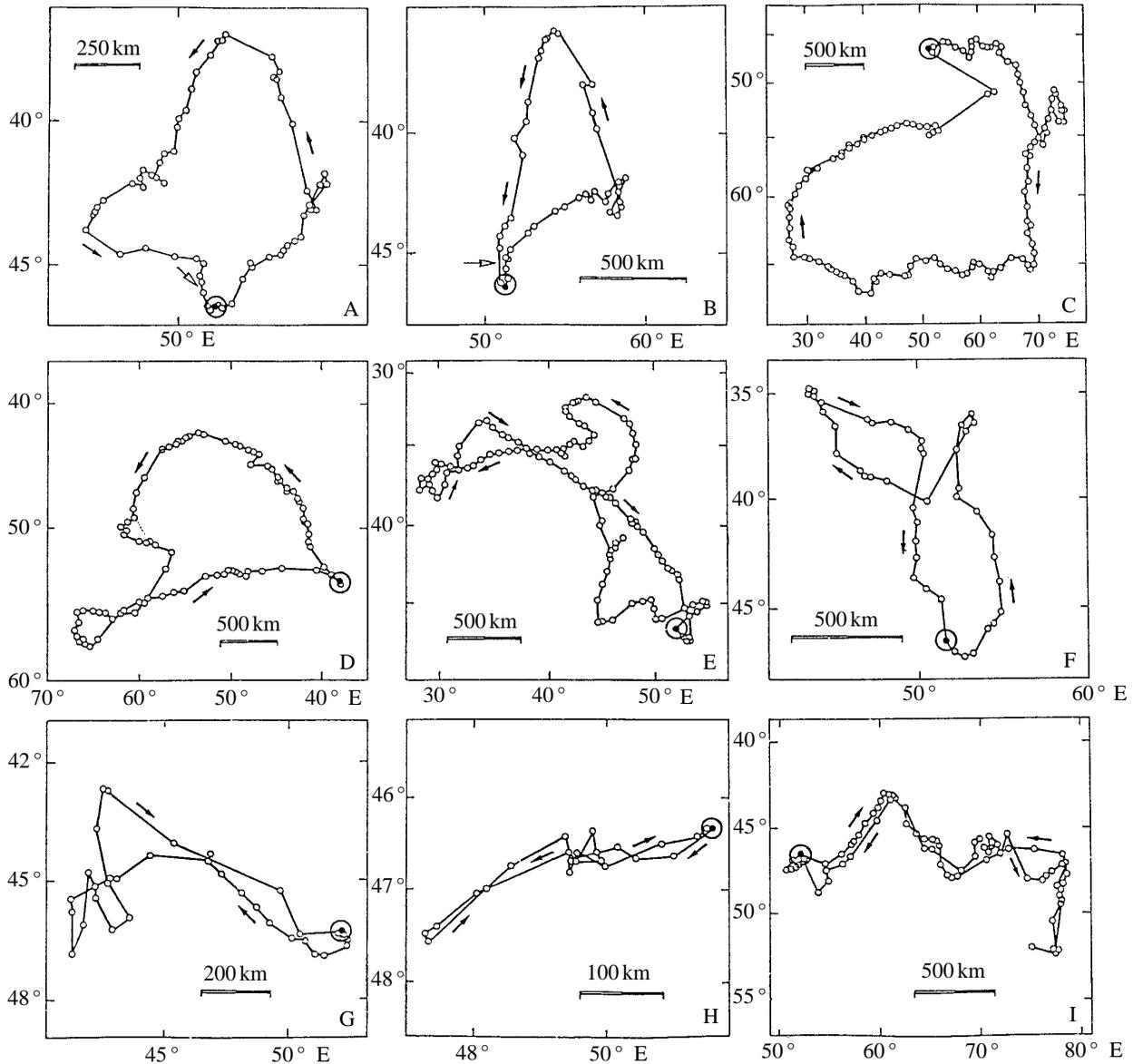Satellite tracking has shown that sea turtles and albatrosses

Fig. 2. Tracks of foraging trips of wandering albatrosses as revealed by satellite telemetry. The small circles indicate the localizations obtained, the larger circle indicates the position of the home island. (A–C, E–I) Tracks of birds nesting at Crozet Islands (from Jouventin and Weimerskirch, 1990; Weimerskirch *et al.* 1993, modified). (D) Track of a bird moving from South Georgia (from Prince *et al.* 1992, modified). The open arrows in A and B indicate wind direction during the birds' arrival at the island. The small filled arrows show the direction taken by the birds.

succeed in covering long legs of oceanic journeys maintaining straight courses and heading for specific targets from hundreds of kilometres away, compensating for wind or current drift. Homing experiments have demonstrated that these animals are able to reach home after a displacement to an unfamiliar area.

The navigational mechanisms described for other animals can only partly explain these performances. In the absence of drift, straight courses could be maintained by a compass orientation mechanisms. Besides a sun compass, both turtles and albatrosses have to rely on a star or a magnetic compass to keep straight courses, even on moonless nights (Prince *et al.* 1992; Luschi *et al.* 1995). Turtles, which are myopic out of water and thus unable to see stars, must, however, rely on the magnetic compass alone. The wave direction may also be used

for compass orientation. This has been proposed for birds for a long time, and Lohmann *et al.* (1995) have found that wave direction is the primary orientation cue used by turtle hatchlings after entering the sea. So, the wave direction might be utilized by adults in navigation, provided that they are able to calibrate their direction with a true compass. However, compass orientation cannot by itself account for the compensation of drift and experimental displacement.

The orientation mechanism may be based on sensory contact with the target; one possibility to be considered is reliance on chemical cues originating from the target (for Ascension green turtles, see Koch *et al.* 1969). The tracked routes of turtles and albatrosses fail to show the zigzag movements to be expected in the case of a gradient appraisal. Moreover, the migrations

of green turtles in the South China Sea may occur in the presence of cross currents (Papi *et al.* 1995), and wandering albatrosses may reach the nesting island when a side wind is blowing. When turtles migrate over shallow waters, cues of any nature originating from the sea bottom may play a role. The tracks of two green turtles reported in Fig. 1C, which migrated separately towards different feeding grounds, almost coincide over a long leg, as there were local guiding stimuli. However, a similar coincidence between the routes of two individuals also occurred over deep waters (see Fig. 1B); in this case, cues perceived from the sea bottom could hardly have been involved.

Information that is used in navigation may originate from an outward or previous journey (route-based navigation). Reliance on such information, however, could not explain pinpointing navigation in animals subjected to the drift of winds and currents and able to compensate for passive displacement. For the same reason, journeys based on endogenous spatio-temporal programmes (vectorial navigation) are to be excluded.

On the whole, the available data indicate that turtles and albatrosses take advantage of a position-fixing mechanism that is operative over the entire journey and can still be used far from familiar areas and the customary routes. This mechanism would allow drift compensation *en route*, homing from unfamiliar areas and other remarkable performances such as those illustrated in Fig. 2I. Here, the albatross flies home by almost exactly retracing a zigzag outward leg, a behaviour pattern which, in the presence of trails or landmarks, could be classified as trail following or route reversal. On the windy Southern Ocean, this performance can be explained only by assuming that a series of fixes is made, memorised and used to relocate the outbound track.

The position-fixing mechanisms of animals (map-based and grid-based navigation, Papi, 1992) have only rarely been investigated, except in the case of the homing pigeon, which has been shown to possess an olfactory map allowing homing from unfamiliar sites (Papi and Wallraff, 1992). It is hard to imagine that a map of this kind can operate over long distances in open seas. Among other things, the Southern Ocean, with its violent winds, which blow mostly in one direction, seems to lack the requirements needed for the acquisition and use of an olfactory map.

Grid-based (bicoordinate) mechanisms of navigation, which might explain these performances, have been hypothesised but not yet demonstrated. It is often assumed that one of the coordinates is obtained by calculating the astronomical or magnetic latitude. Since turtle hatchlings and birds have been found to be responsive to variations in the inclination of the magnetic field (Lohmann and Lohmann, 1994; Wiltschko and Wiltschko, 1972), magnetic reckoning, which also has the advantage of being ever present, seems to be the best candidate for our animals.

Before speculating about the second element of the bicoordinate grid, we have to consider whether it is really required to explain the observed facts. Lohmann and Lohmann

(1994) propose that turtles might locate the nesting beach by relying only on magnetic latitude determination. This strategy would be more successful when the target is on a coast aligned north–south or an island to be reached from the east or west. There are, however, some cases of small islands that are reached from other directions (as in Fig. 1A); moreover, albatrosses approach their target island from all directions. Even if it is conceivable that the animals' task might be facilitated by stimuli deriving from the target and detectable at a certain distance, any auxiliary stimuli, if chemical in nature, could not be detected when the animals arrive with side or tail winds or currents.

If one supposes that a true bicoordinate grid is required, a difficult problem arises about the nature of the second coordinate. The history of human navigation shows that there are few cues accessible to living beings which can be used for fixing longitude; the method of determining it was solved only in the 18th century. A hypothesis worth testing is that of Lohmann and Lohmann (1996), who suggest that the entire map is magnetic and based on the inclination and intensity of the field. Over some areas, the isolines of these parameters actually intersect, forming a grid that could be used for position fixing.

The present survey has shown that sea turtles and albatrosses are excellent subjects for experimental research and that they could be used to make possible further achievements in the study of animal navigation. Their status as threatened species sets a limit to experimentation, which may yet provide information useful for conservation (Prince *et al.* 1992; Weimerskirch and Robertson, 1994). Interesting results may derive from systematic tracking experiments on displaced adult turtles and albatrosses, in some cases after treatments reducing or altering their perception of environmental stimuli. In this connection, tracking animals displaced over a limited distance with direction-recorder data-loggers may also provide meaningful results, as these devices allow continuous recordings of animal movements without the discontinuity of satellite fixing. Direction recorders carried by animals are nowadays reliable and are producing excellent reconstructions of animal journeys (Ioalè *et al.* 1994; Dall'Antonia *et al.* 1995; Wilson *et al.* 1993). In the near future, satellite transmitters, data-loggers and other devices which are being developed will provide the instrumental aid for the experimental strategies of the researcher.

References

Balazs, G. H. (1994). Homeward bound: satellite tracking of Hawaiian green turtles from nesting beaches to foraging pastures. In *Proceedings of the 13th Annual Symposium on Sea Turtle*

Biology and Conservation (ed. B. A. Schroeder and B. E. Witherington), pp. 205–208. U.S. Department of Commerce, NOAA Tech. Memo NMFS-SEFSC-341.

Balazs, G. H., Craig, P., Winton, B. R. and Miya, R. K. (1994). Satellite telemetry of green turtles nesting at French Frigate Shoals, Hawaii and Rose Atoll, American Samoa. In *Proceedings of the 14th Annual Symposium on Sea Turtle Biology and Conservation* (ed. K. A. Bjorndal, A. B. Bolten, D. A. Johnson and P. J. Eliazar), pp. 184–187. U.S. Department of Commerce, NOAA Tech. Memo NMFS-SEFSC-351.

Baldwin, H. A. (1972). Long-range radio tracking of sea turtles and polar bear: instrumentation and preliminary results. In *Animal Orientation and Navigation* (ed. S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs and R. E. Belleville), pp. 19–37. Washington, DC: NASA SP-262.

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

Byles, R. A. (1989). Satellite telemetry of Kemp's ridley sea turtle, *Lepidochelys kempi*, in the Gulf of Mexico. In *Proceedings of the 9th Annual Symposium on Sea Turtle Biology and Conservation* (ed. S. A. Eckert, K. L. Eckert and T. H. Richardson), pp. 25–26. U.S. Department of Commerce, NOAA Tech. Memo NMFS-SEFSC-232.

Byles, R. A. and Dodd, C. K. (1989). Satellite biotelemetry of a loggerhead sea turtle (*Caretta caretta*) from the east coast of Florida. In *Proceedings of the 9th Annual Workshop on Sea Turtle Biology and Conservation* (ed. S. A. Eckert, K. L. Eckert and T. H. Richardson), pp. 215–217. U.S. Department of Commerce, NOAA Tech. Memo NMFS-SEFSC-232.

Byles, R. A. and Plotkin, P. T. (1994). Comparison of the migratory behavior of the congeneric sea turtles *Lepidochelys olivacea* and *L. kempii*. In *Proceedings of the 13th Annual Symposium on Sea Turtle Biology and Conservation* (ed. B. A. Schroeder and B. E. Witherington), p. 39. U.S. Department of Commerce, NOAA Tech. Memo NMFS-SEFSC-341.

Byles, R. A. and Swimmer, Y. B. (1994). Post-nesting migration of *Eretmochelys imbricata* in the Yucatan Peninsula. In *Proceedings of the 14th Annual Symposium on Sea Turtle Biology and Conservation* (ed. K. A. Bjorndal, A. B. Bolten, D. A. Johnson and P. J. Eliazar), p. 202. U.S. Department of Commerce, NOAA Tech. Memo NMFS-SEFSC-351.

Carr, A. (1963). Orientation problems in the high seas travel and terrestrial movements of marine turtles. In *Bio-Telemetry* (ed. L. E. Slater), pp. 179–193. Oxford: Pergamon 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. 469–484. Washington, DC: NASA SP-262.

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

Carr, A., Carr, M. H. and Meylan, A. B. (1978). The ecology and migrations of sea turtles. 7. The West Caribbean green turtle colonies. *Bull. Am. Mus. nat. Hist.* **162**, 1–46.

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

Cornelius, C. (1865). *Die Zug- und Wander-Thiere aller Thierklassen*. Berlin: J. Springer.

Dall'Antonia, L., Dall'Antonia, P., Benvenuti, S., Ioalè, P., Massa, B. and Bonadonna, F. (1995). The homing behaviour of Cory's shearwaters (*Calonectris diomedea*) studied by means of a direction recorder. *J. exp. Biol.* **198**, 359–362.

Duron-Dufrenne, M. (1987). Premier suivi par satellite en Atlantique d'une tortue Luth *Dermochelys coriacea*. *C. R. Acad. Sci. Paris* **304**, 399–402.

Eagleson, K. W., Morgan, E. L., Stoneburner, D. L. and McCollough, N. (1978). Loggerhead sea turtle tracking by satellite, preliminary report. *ASB Bull.* **25**, 73.

Fisher, H. I. (1971). Experiments on homing in Laysan Albatrosses, *Diomedea immutabilis*. *Condor* **73**, 389–400.

Gibson, J. D. (1967). The wandering albatross (*Diomedea exulans*): results of banding and observations in New South Wales coastal waters and the Tasman Sea. *Notornis* **14**, 47–57.

Green, D. (1984). Long-distance movements of Galapagos green turtles. *J. Herpetol.* **18**, 121–130.

Groshens, E. B. and Vaughan, M. R. (1994). Post-nesting movements of hawksbill sea turtles from Buck Island Reef National Monument, St. Croix, USVI. In *Proceedings of the 13th Annual Symposium on Sea Turtle Biology and Conservation* (ed. B. A. Schroeder and B. E. Witherington), pp. 69–71. U.S. Department of Commerce, NOAA Tech. Memo NMFS-SEFSC-341.

Hays, G. C., Webb, P. I., Hayes, J. P., Priede, I. G. and French, J. (1991). Satellite tracking of a loggerhead turtle (*Caretta caretta*) in the Mediterranean. *J. mar. Biol. Ass. U.K.* **71**, 743–746.

Ioalè, P., Dall'Antonia, P., Dall'Antonia, L. and Benvenuti, S. (1994). Flight paths of homing pigeons studied by means of a direction recorder. *Ethol. Ecol. Evol.* **6**, 519–527.

Ireland, L. C. (1980). Homing behavior of juvenile green turtles, *Chelonia mydas*. In *A Handbook on Biotelemetry and Radio Tracking* (ed. C. J. Amlaner and D. W. MacDonald), pp. 761–764. Oxford, New York: Pergamon Press.

Jouventin, P. and Weimerskirch, H. (1990). Satellite tracking of wandering albatrosses. *Nature* **343**, 746–748.

Keinath, J. A., Byles, R. A. and Musick, J. A. (1989). Satellite telemetry of loggerhead turtles in the western north Atlantic. In *Proceedings of the 9th Annual Symposium on Sea Turtle Biology and Conservation* (ed. S. A. Eckert, K. L. Eckert and T. H. Richardson), pp. 75–76. U.S. Department of Commerce, NOAA Tech. Memo NMFS-SEFSC-232.

Keinath, J. A. and Musick, J. A. (1993). Movements and diving behavior of a leatherback turtle, *Dermochelys coriacea*. *Copeia* **1993**, 1010–1017.

Kenyon, K. W. and Rice, D. W. (1958). Homing of Laysan Albatrosses. *Condor* **60**, 3–6.

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.

Liew, H. C., Chan, E. H., Luschi, P. and Papi, F. (1995). Satellite tracking data on Malaysian Green Turtle migration. *Rend. Fis. Acc. Lincei* (in press).

Limpus, C. J., Miller, J. D., Parmenter, J., Reimer, D., McLachlan, N. and Webb, R. (1992). Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. *Wildl. Res.* **19**, 347–358.

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. (1996). Orientation and open-sea navigation in sea turtles. *J. exp. Biol.* **199**, 73–81.

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., Papi, F., Liew, H. C., Chan, E. H. and Bonadonna, F.

(1995). Long-distance migration and homing after displacement in the green turtle (*Chelonia mydas*): a satellite tracking study. *J. comp. Physiol.* (in press).

MATTHEWS, G. V. T. (1968). *Bird Navigation*. Cambridge: Cambridge University Press.

MEYLAN, A. (1982). Sea turtle migration – evidence from tag returns. In *Biology and Conservation of Sea Turtles* (ed. K. A. Bjorndal), pp. 91–100. Washington, DC: Smithsonian Institution Press.

NICHOLLS, D., BATTAM, H., BROTHERS, N., BUTCHER, E., HILDEBRANDT, M., MOORS, P., MURRAY, D. AND ROBERTSON, G. (1992). Preliminary results of satellite tracking of the wandering albatross around and from Australia. *Corella* **16**, 134–136.

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

PAPI, F., LIEW, H. C., LUSCHI, P. AND CHAN, E. H. (1995). Long-range migratory travel of a green turtle tracked by satellite: evidence for navigational ability in the open sea. *Mar. Biol.* **122**, 171–175.

PAPI, F. AND WALLRAFF, H. G. (1992). Birds. In *Animal Homing* (ed. F. Papi), pp. 263–319. London: Chapman & Hall.

PLOTKIN, P. T., BYLES, R. A., ROSTAL, D. C. AND OWENS, D. W. (1995). Independent versus socially facilitated oceanic migrations of the olive ridley, *Lepidochelys olivacea. Mar. Biol.* **122**, 137–143.

PRINCE, P. A., WOOD, A. G., BARTON, T. AND CROXALL, J. P. (1992). Satellite tracking of wandering albatrosses (*Diomedea exulans*) in the South Atlantic. *Antarct. Sci.* **4**, 31–36.

RENAUD, M. L. (1990). Sea turtles and satellite tags: movements and dive patterns. In *Proceedings of the 10th Annual Symposium on Sea Turtle Biology and Conservation* (ed. T. H. Richardson, J. I. Richardson and M. Donnelly), p. 121. U.S. Department of Commerce, NOAA Tech. Memo NMFS-SEFSC-278.

RENAUD, M. L. (1994). Satellite tracking of juvenile Kemp's ridley sea turtles near Sabine Pass, Texas. In *Proceedings of the 13th Annual Symposium on Sea Turtle Biology and Conservation* (ed. B. A. Schroeder and B. E. Witherington), p. 147. U.S. Department of Commerce, NOAA Tech. Memo NMFS-SEFSC-341.

RENAUD, M. L. AND CARPENTER, J. A. (1994). Movements and submergence patterns of loggerhead turtles (*Caretta caretta*) in the Gulf of Mexico determined through satellite telemetry. *Bull. mar. Sci.* **55**, 1–15.

RENAUD, M. L., CARPENTER, J. A., WILLIAMS, J. A. AND MANZELLA-TIRPAK, S. (1994). Satellite tracking of juvenile Kemp's ridley sea turtles near Sabine Pass, Texas. In *Proceedings of the 14th Annual Symposium on Sea Turtle Biology and Conservation* (ed. B. A. Schroeder and B. E. Witherington), pp. 126–127. U.S. Department of Commerce, NOAA Tech. Memo NMFS-SEFSC-351.

ROBERTSON, C. J. R. AND KINSKY, F. C. (1972). The dispersal movements of the Royal Albatross *Diomedea epomophora. Notornis* **19**, 289–301.

SPRING, C. S. (1990). Satellite tracking of green turtles in Australia – Preliminary results. In *Proceedings of the Australian Marine Turtles Conservation Workshop* (ed. R. Jones), pp. 192–197.

STONEBURNER, D. L. (1982). Satellite telemetry of loggerhead sea turtle movement in the Georgia Bight. *Copeia* **1982**, 400–408.

STRIKWERDA, T. E., FULLER, M. R., SEEGAR, W. S., HOWEY, P. W. AND BLACK, H. D. (1986). Bird-borne satellite transmitter and location program. *Johns Hopkins APL Tech. Dig.* **7**, 203–208.

TICKELL, W. L. N. AND SCOTLAND, C. D. (1961). Recoveries of ringed giant petrels *Macronectes giganteus. Ibis* **103**A, 260–266.

TIMKO, R. E. AND KOLZ, L. (1982). Satellite sea turtle tracking. *Mar. Fish. Rev.* **44**, 19–24.

WEIMERSKIRCH, H., DONCASTER, C. P. AND CUENOT-CHAILLET, F. (1994). Pelagic seabirds and the marine environment: foraging patterns of wandering albatrosses in relation to prey availability and distribution. *Proc. R. Soc. Lond. B* **255**, 91–97.

WEIMERSKIRCH, H. AND ROBERTSON, G. (1994). Satellite tracking of light-mantled sooty albatrosses. *Polar Biol.* **14**, 123–126.

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.

WILSON, R. P., CULIK, B. M., BANNASH, R. AND DRIESEN, H. H. (1993). Monitoring penguins at sea using data loggers. In *Biotelemetry* XII (ed. P. Mancini, S. Fioretti, C. Cristalli and R. Bedini), pp. 205–214. Pisa: Litografia Felici.

WILTSCHKO, W. AND WILTSCHKO, R. (1972). Magnetic compass of European Robins. *Science* **176**, 62–64.