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Long.range migratory travel of a green turtle tracked by satellite: evidence for navigational ability in the open sea

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Abstract A female of *Chelonia mydas* was tracked by satellite in the South China Sea in 1993 from the nesting beach to the resident foraging grounds more than 600 km away. The final leg of the journey, 475 km long, directly pinpointed the goal, with the turtle maintaining a constant speed and direction both night and day. This provides clues about the navigational mechanism used.

Introduction

Some species of sea turtles are known to be long-distance migrants, whose amazing navigational performances are very poorly understood. Most of the available information about turtles' migratory patterns derives from tagging projects on nesting adult females. These studies have shown that females periodically come back to the same nesting beach, moving away from the resident feeding grounds, which can be hundreds or thousands of kilometres away. In some cases, in addition to fidelity to the nesting beach, fidelity to the feeding grounds has also been demonstrated (Meylan 1982; Mortimer and Carr 1987; Limpus et al. 1992). This has supported the widespread opinion that, at least in some species, a 2-way migration occurs. The phenomenon is best documented for the green turtle, *Chelonia mydas,* whose nesting and foraging grounds are generally spatially separated (Balazs 1976; Meylan 1982; Green 1984). This implies a navigational capability, which is most

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highly developed in the case of the Brasilian green turtles migrating to Ascension Island, a small, isolated target in the ocean (Carr 1984; Mortimer and Carr 1987). Such a performance demonstrates goal navigation in the absence of guiding landmarks.

The mechanisms permitting such travel have been the object of a number of hypotheses, which have never been successfully verified. A first approach to the problem may consist of carefully tracking an open-sea migratory journey in order to infer from the characteristics of the path what cues could or could not be involved, thus providing the rationale for further experiments. We found that, for this purpose, the most suitable method is satellite tracking, which can provide reliable tracks (see Hays 1992; Renaud et al. 1993 for references), in spite of the fact that transmissions to the satellite are only possible during the short time intervals spent by the turtles on the surface.

The present paper reports results of interest for the field of animal navigation which we obtained by satellite tracking a green turtle from its nesting beach to its resident grounds about 600 km away. Our tracking study is a part of a research programme on the biology and migration of West Malaysian green turtles which is expected to contribute to the conservation of this endangered species.

Materials and methods

The female successfully tracked belongs to a population nesting on the Chagar Hutang beach of Pulau Redang, an island located 45 km off the coast of Terengganu, Peninsular Malaysia (Fig. 1). The internesting behaviour of the population was studied (Liew and Chan 1993) and its nesting activity throughout the breeding season was monitored. In summer 1993 we made three attempts to track the postnesting journey of females, but in only one case did we obtain useful results. The tracked turtle, whose carapace measured 88 cm in length, had been tagged earlier in the season. On 23 September she had just laid her sixth - and final - clutch of eggs when we glued a satellite transmitter (PTT, platform transmitter terminal) to her carapace (Beavers et al. 1992).

The transmitter was an ST-3 PTT manufactured by Telonics (Mesa, AZ, USA), which was provided with a salt-water switch suppressing transmissions under water; its repetition frequency was 50 s.

Fig. 1 *Chelonia mydas.* Track of the sea turtle migratory journey in the South China Sea. $(\odot$: Class 1-3 fixes; +: Class 0 fixes.) Seven Class 0 fixes, which were considered erroneous, are indicated with A. Class 0 locations obtained after 5 October not reported

Table 1 *Chelonia mydas.* Class 1-3 locations obtained during tracking experiment. *(L.C.* location class, see "Materials and methods".) Values of distance, time, speed and direction after the last fix of the migratory journey (No. 20) reported in parentheses

The emissions were received and processed by the Argos system (see Taillade 1992 for further information). The locations (or "fixes") obtained were assigned by Argos to four main classes. For the Classes 1-3 the Argos system gives the following degree of accuracy (for 1 SD): Class 3, accuracy 150 m; Class 2,350 m; Class 1, 1 km (Taillade 1992, but see also Weimerskirch et al. 1992). The accuracy of Class 0 locations should be determined by the user; they are subdivided into a further 11 subclasses, of which only the best six were taken into account in our analysis and reported in Fig. 1. From the other two PTTs applied (which were both made by a different manufacturer), only a few messages were received and no reliable location was obtained.

Calculations of distance, speed, and direction (Table 1, Fig. 2) are all based on Class 1-3 locations. Note that the values relative to small stretches may have been more heavily biased by the approximation of the localizations. Time has been calculated as mean solar time of the 106°E meridian.

Results

The locations plotted on Fig. 1 show the complete migratory travel of the tracked female from her nesting beach at Pulau Redang to her resident grounds in the waters of North Natuna Archipelago.

The first fix was obtained on 23 September, during the period in which the turtle was held on the beach for the attachment of the transmitter. From 23 September to 5 October we obtained 40 more fixes, 21 of which belonging to Class 0 (Fig. 1). Seven Class 0 fixes are indicated as probably erroneous, as they entailed speed values out of the normal range (see Fig. 1). From 6 October to 22 NovemFig. 2 *Chelonia mydas,* a Direction and b speed recorded between successive fixes during second leg of the journey given by the horizontal lines. Cross-hatched columns represent nights. Arrow and the dashed line in a indicate direction from the starting point of the leg (Fix No. 2) to the final point (Fix No. 20)

ber, which was the date of the last location, we received 31 more fixes, only two of which were of Class 1 and reported in Fig. 1. The others, which are not given in the figure, indicated a wandering activity in the southeastern waters of the North Natnna Archipelago. Therefore, we consider the migration to have been concluded on 5 October.

The migratory path consisted of two legs. According to Fixes 1 and 2 (Table 1), the turtle first moved eastwards, covering 193.3 km in ca. 97 h at a speed of 2.0 km h⁻¹. From 27 September onward, she switched to a southeasterly course, which was held for the rest of the migration period (Table 1).

This second leg, which was more precisely tracked thanks to a large number of fixes, shows a slightly curved course, with only minor deflections (Fig. 1). In fact, the distance covered from Fix 2 to 20, calculated as a sum of the distances between successive fixes, is 475.7 km, while the bee-line course would be 461.1 km. The straightness index r (Batschelet 1981), which varies between 0 and 1, is therefore ca. 0.97. The average speed in this second segment was 2.4 km h^{-1} .

Turtle behaviour varied very little between night and day, as regards both heading and speed (Table 1, Fig. 2).

Discussion

tn recent years, a number of studies have been published about the movements of sea turtles tracked by satellite (Stoneburner 1982; Timko and Kolz 1982; Byles and Dodd

1989; Keinath et al. 1989; Hays et al. 1991). However, a complete reconstruction of a high-seas migratory journey is only known through the reports of G. Balazs' research on Hawaiian green turtles (1994 b) and the present paper.

Our findings confirm that *Chelonia mydas* is a longrange migrant which moves between separated nesting and resident foraging grounds. Since green turtles display sitefidelity to both grounds (see "Introduction"), we can assume that the Natuna Besar waters are the resident foraging grounds of our turtle, the first ones to be known for turtles nesting at Pulau Redang. The alternative hypothesis that Natuna Besar waters were only a resting site on the way home is improbable, as a rest of one and half months (at least) after a leg of only a dozen days seems to be too long for a turtle species which is known to perform very long postreproductive no-stop journeys. Therefore, the migration we recorded can be considered goal-oriented travel towards home.

We have no explanation for the fact that our turtle steered directly towards the goal only after an eastward segment of her trip. The most relevant finding is that the second leg of the journey, ca. 470 km long, was almost straight and was covered in the absence of any landmark. The turtle was able to pinpoint its goal, the Natuna Besar Island, which has a maximal length of ca. 70 km and is more than 200 km away from the Borneo coast. A similar goal directedness was also found in Balazs' studies (Balazs 1994b).

During the migration, our turtle swam for at least 669 km to reach the feeding grounds, which were 607 km away (bee-line). Her average speed was 2.23 km h^{-1} , and

on some stretches the speed was ca. 3.5 $km h^{-1}$. Most travel speed values reported by various authors for the green turtle, though calculated for bee-line travel, are lower, as they usually derive from tag-return data (Meylan 1982; Limpus et al. 1992). In satellite recorded journeys exceeding 1000 km, Balazs (1994b) recorded average speeds ranging from 1.6 to 2.0 kmh^{-1} . Our study adds the noteworthy finding that speed remained quite constant throughout the 24-h period.

The travel path of our turtle allows a discussion of the underlying navigational mechanisms. The simplest one may consist of a sort of vectorial orientation based on a compass and derived from a bearing-and-distance programme, similar to that used by young birds (Berthold 1991). Such a possibility, however, has already been discarded by Carr (1984), as it would seem difficult for a turtle to keep a constant bearing over long distances by means of a compass only, even in the absence of any current drift.

Ithas beenproposed (Koch et al. 1969; Carr 1972, 1984) that odorants originating from the target may contribute to turtle navigation. In the case of migration to Ascension, a chemical gradient would originate in the westward flow of the South Equatorial Current reaching the Brasilian coasts, which the turtle would use in association with the sun compass (see, however, Brown 1990 for arguments against this idea). The flow of the currents, however, is quite different in the area crossed by our turtle. In September a current with an average speed of 1 knot flows northeasterly while in October the direction is reversed, the speed remaining unchanged (Shaw and Chao in preparation). Because in both cases the flow is thus roughly perpendicular to the course, the situation seems to be unsuitable to provide a stable gradient of odorants spreading from Natuna Besar Island.

The observed path of the turtle may be better explained by a system providing for the possibility of position fixing with respect to the goal and thus permitting frequent or continuous course corrections. This implies reliance on some kind of bicoordinate grid or map to be used in combination with a compass (map-and-compass mechanism). We are unable to propose any convincing sort of map which would work in high seas. However, some considerations are possible about the nature of the hypothetical compass. Since our turtle kept speed and direction quite constant both night and day, she could not have relied on the sun compass alone. Sea turtles, being extremely myopic when out of water (Ehrenfeld and Koch 1967), are unable to see stars. During the migration of our turtle, moon orientation could have been possible as there was a full moon during the central part of the journey. Reliance on the moon compass, however, would limit the possibility of straight courses to the moonlight nights. All in all, the best candidate for compass orientation seems to be the magnetic compass, the occurrence of which has been recently reported in hatchlings of two sea turtle species (Lohmann 1991; Lohmann and Lohmann 1993).

As the present findings have shown that sea turtles migrating in the open sea are able to maintain a constant speed and direction both night and day and to pinpoint their goal from hundreds of kilometres away, the range of explanations for their mysterious navigational ability is further reduced. While an explanation of the turtle's map remains elusive, research aimed at testing magnetic orientation in adults appears to be both feasible and potentially rewarding.

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References

- Balazs GH (1976) Green turtle migrations in the Hawaiian Archipelago. Biol Conserv 9:125-140
- Balazs GH (1994a) Homeward bound: satellite tracking of Hawaiian green turtles from nesting beaches to foraging pastures. Proceedings of the Thirteenth Annual Symposium on Sea Turtle Biology and Conservation, NOAA tech Memo US Dep Commerce NMFS, NOAA-TM-NMFS-SEFCS-341:205-208
- Balazs GH (1994b). Satellite telemetry of green turtles nesting at French Frigate Shoals, Hawaii, and Rose Atoll, American Samoa. Proceedings of the Fourteenth Annual Symposium on Sea Turtle Biology and Conservation, NOAA tech Memo US Dep Commerce NMFS, NOAA-TM-NMFS-SEFCS-361:184-187
- Batschelet E (1981) Circular statistics in biology. Academic Press, London
- Beavers SC, Cassano ER, Byles RA (1992) Stuck on turtles: preliminary results from adhesive studies with satellite transmitters. Proceedings of the Eleventh Annual Workshop on Sea Turtle Biology and Conservation. NOAA tech Memo US Dep Commerce NMFS, NOAA-TM-NMFS-SEFCS-302:135-138
- Berthold P (1991) Spatiotemporal programmes and genetics of orientation. In: Berthold P (ed) Orientation in birds. Birkhäuser-Verlag, Basel, pp 86-105
- Brown CW (1990) The significance of the South Atlantic equatorial countercurrent to the ecology of the green turtle breeding population of Ascension Island. J Herpetol 24:81-84
- Byles RA, Dodd CK (1989) Satellite biotelemetry of a loggerhead sea turtle *(Caretta caretta)* from the east coast of Florida. In: Eckerr SA, Eckert KL, Richardson TH (eds) Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. NOAA tech Memo US Dep Commerce NMFS-SEFC-232:215-217
- Carr A (1972) The case for long-range, chemoreceptive piloting in Chelonia. In: Galler SR, Schmidt-Koenig K, Jacobs GJ, Belleville RE (eds) Animal orientation and navigation. NASA, Washington, DC, pp 469-483
- Carr A (1984) The sea turtle. So excellent a fish. University of Texas Press, Austin
- Ehrenfeld DW, Koch AL (1967) Visual accommodation in the green turtle. Science, NY 155:827-828
- Green D (1984) Long distance movements of Galapagos green turtles. J Herpetol 18:121-130
- Hays GC (1992) Assessing the nesting beach fidelity and clutch frequency of sea turtles by satellite tracking. In: Priede IG, Swift SM (eds) Wildlife Telemetry, Ellis Horwood Ltd., New York, pp 203-213
- Hays GC, Webb PI, Hayes JR Priede IG, French J (1991) Satellite tracking of a loggerhead turtle *(Caretta caretta)* in the Mediterranean. J mar biol Ass UK 71:743-746
- Keinath JA, Byles RA, Musick JA (1989) Satellite telemetry of loggerhead turtles in the western North Atlantic. In: Eckert SA, Eckert KL, Richardson TH (eds) Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. NOAA tech Memo US Dep Commerce NMFS-SEFC-232:75-76
- Liew HC, Chan EH (1993) Biotelemetry of green turtles *(Chelonia mydas)* in Pulau Redang, Malaysia, during the internesting period. In: Mancini P, Fioretti S, Cristalli C, Bedini R (eds) Biotelemetry XII. Litografia Felici, Pisa, pp 157-163
- Limpus CJ, Miller JD, Parmenter J, Reimer D, McLachlan N, Webb R (1992) Migration of green *(Chelonia mydas)* and loggerhead *(Caretta caretta)* turtles to and from eastern Australia rookeries. Wildl Res 19:347-358
- Lohmann KJ (1991) Magnetic orientation by hatchling loggerhead sea turtle *(Caretta caretta).* J exp Biol 155:37-49
- Lohmann KJ, Lohmann CMF (1993) A light-independent magnetic compass in the leatherback sea turtle. Biol Bull mar biol Lab, Woods Hole 185:145-151
- Meylan A (1982) Sea turtle migration-evidence from tag returns. In: Bjorndal KA (ed) Biology and conservation of sea turtles. Smithsonian Institution Press, Washington DC, pp 91-100
- Mortimer JA, Carr A (1987) Reproduction and migrations of the Ascension Island green turtle *(Chelonia mydas).* Copeia 1987: 103-113
- Renaud ML, Gitschlag GR, Hale JK (1993) Retention of imitation satellite transmitters fiberglassed to the carapace of sea turtles. Herpetol Rev 24:94-99
- Shaw P-T, Chao SY (submitted). Surface circulation in the South China Sea. Deep-Sea Res
- Stoneburner DL (1982) Satellite telemetry of loggerhead sea turtle movement in the Georgia Bight. Copeia 1982:400-408
- Taillade M (1992) Animal tracking by satellite. In: Priede IG, Swift SM (eds) Wildlife Telemetry, Ellis Horwood Ltd., New York, pp 149-160
- Timko RE, Kolz L (1982) Satellite sea turtle tracking. Mar Fish Rev 44:19-24
- Weimerskirch H, Salamolard M, Jouventin P (1992) Satellite telemetry of foraging movements in the wandering albatross. In: Priede IG, Swift SM (eds) Wildlife Telemetry, Ellis Horwood Ltd., New York, pp 184-198