

The Case for Long-Range Chemoreceptive Piloting in

Chelonia in Animal Orientation and Navigation *?* (editor)

National Aeronautics and Space Administration, NASA, SP-262,

ARCHIE F. CARR, JR.
University of Florida

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THE RECENT SUGGESTION that chemoreception may provide the latitudinal component of the open-sea guidance mechanism of the South Atlantic green turtle (ref. 1) has not been subjected to test. The straightforward way to test the assumption would be to monitor sensory responses of migrating turtles through electronically tracked and telemetered journeys to the island breeding ground (fig. 1). Efforts to do this have not yet been successful, and the case for piloting by chemical cues still rests on circumstantial evidence. This paper considers some aspects of that evidence and suggests ways in which the known ecology of the species bears upon the search for a theory of island-finding navigation by an aquatic, airbreathing animal.

OCEAN CURRENTS AND THE ECOLOGICAL GEOGRAPHY OF THE GREEN TURTLE

Three problems in the reproductive ecology of sea turtles, under scrutiny since the program of marine turtle research at the University of Florida began, are (1) to explain why certain small islands or restricted

sections of mainland shore are chosen by *Chelonia* as nesting grounds, even when located a thousand miles or more from the year-around feeding ground of the population (figs. 1 and 2); (2) to identify guidance mechanisms used by the migrants in their periodic open-ocean travel to those places; and (3) to account for the so-called "lost-year"—the virtually complete disappearance of young sea turtles during their first several months of life. It seems increasingly clear that the three problems are closely related.

In the search for an answer to the site-choice question, beach topography, the physical character of the nesting medium (refs. 2 to 4), differential immunity to predation and to past human depredations, and even paleogeographic changes (ref. 5) have all been considered as possible factors, but many cases of breeding-site selection remain wholly anomalous. It now seems possible that these will be explained only if answers to the second and third questions listed above can be found.

As information from tagging and field surveys accumulates, it appears increasingly likely that ocean currents are fundamentally

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Edited by
SIDNEY R. GALLER, KLAUS SCHMIDT-KOENIG,
GEORGE J. JACOBS, AND RICHARD E. BELLEVILLE



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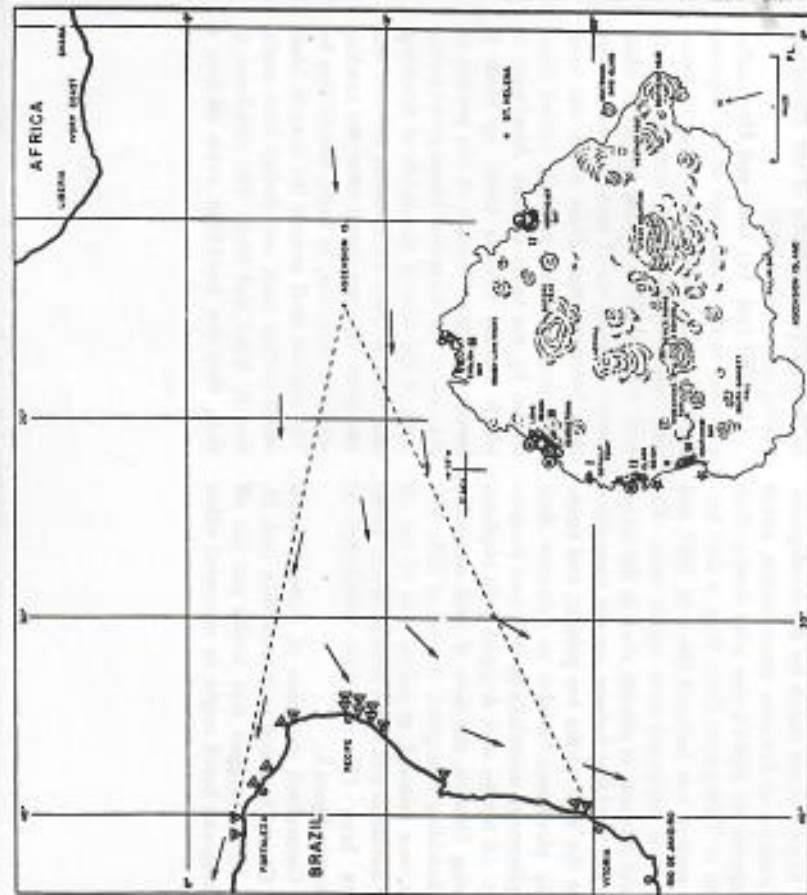


FIGURE 1. Results of four seasons' tagging at Ascension Island, where 660 mature female green turtles have been tagged. Triangles represent recoveries along Brazil coast. Hollow circles show recoveries of turtles that had been tagged and returned to nest after 2 year' absence. Circles with dots show turtles that were tagged at Ascension and returned to nest after 5 year' absence, presumably in Brazil. Stars represent turtles that returned to nest 4 years after they were tagged and presumably after having made two round trips to Brazil. Turtles recovered at Ascension had gone back to original nesting sites. Arrows suggest current trends.

involved in the ecological geography of at least some populations of *Chelonia*, both in the transporting of the hatchlings into their presumably pelagic first-year habitat, and as a vehicle for the olfactory guidance cues that may be used by the migrating adults in their travel to the breeding ground. When Koch, Carr and Ehrenfeld (ref. 1) suggested a dual olfaction-and-Sun-compass mechanism to explain the ability of Brazilian green turtles to locate their Ascension Island breeding ground (fig. 1), they considered this a special case in which the westward flow of the South Equatorial Current affords a unique sensory



FIGURE 2. Distribution of recoveries of mature female green turtles tagged at Tortuguero, Costa Rica, 1955-1969. Circled figures indicate numbers of recoveries. Arrows show general trend and strength of currents in the Western Caribbean for July (data from Wilst, ref. 13), (the arrival time of the nesting schools at Tortuguero.

link between the island rookery and the resident grounds along the coast of Brazil. The relative shallowness of the surface current was seen as an additional special advantage that would not only limit diffusion of any dissolved substances given off by the island, but also might allow the migrants to dive below the thermal discontinuity for rest. This would not only avoid the setbacks that would be imposed by rest in the contrary surface current, but also would allow the sensory recuperation considered necessary for prolonged olfactory appraisal of changes in strength of the Ascension emanation.

That suggestion was made before the authors were aware of the existence and appar-

ently widespread occurrence of equatorial counter currents. Since the first subsurface equatorial current was detected by Buchanan (refs. 6 and 7) in the Central Atlantic, there has been growing evidence (refs. 8 to 11) that equatorial counter currents flow beneath the global surface currents of the Atlantic, Pacific, and Indian oceans. The accumulating data on these currents not only reinforce the possibility that dissolved chemicals may serve as long-range beacons guiding the migration of South Atlantic *Chelonia* but also suggest that currents may be widely involved in molding the ecological geography of sea turtles. Although information on seasonal variations in the depth and velocity of the

counter-currents is limited, there are indications that they flow at depths within the diving range of a green turtle. Jones (ref. 12) even found that the Pacific Equatorial Undercurrent sometimes rises to the surface of the sea. The counter-currents might therefore serve both as an asylum for olfactory recuperation and as a means of continuing progress in the general direction of the goal during periods of rest.

It has only recently occurred to the author that horizontally juxtaposed surface currents might afford some of the same advantages for long-range migratory guidance postulated for the vertically juxtaposed equatorial currents. Data from drift-bottle releases on the Caribbean coast of Costa Rica, and other information on local currents there, suggest that a modification of the chemoreceptive piloting theory might be equally applicable to this migration, in which the goal is a mainland beach.

As part of our search for the development of first-year green turtles, which disappear for about a year after leaving their nests at Tortuguero, Costa Rica, a drift bottle project was initiated there in 1963 and has been continued each season since. The initial aim was to provide clues in the search for the hatchling habitat, on the assumption that the little turtles are pelagic, and essentially planktonic—unable to influence their displacement materially by their own locomotion. All bottles were dropped from airplanes during October, the time of peak frequency of hatchling emergence. A total of 5351 bottles were released, at points 1 to 19 km off the northeast end of the nesting beach. There have been 175 recoveries distributed as shown in figure 3.

Generalized diagrams of current trends off Costa Rica, such as that of Wüst (ref. 13, see fig. 3), suggest that bottles put out off Tortuguero beach might be recovered either

to the south or to the north of the release point, depending on whether they lodged in the north-trending Equatorial Current or in a south-trending inshore current that is perhaps a segment of the gyre shown in Wüst's chart. Our 15 years' observations at Tortuguero have shown that, throughout the turtle season, floating islands and rafts of water hyacinths from the rivermouths of the region move consistently southward when close enough to shore to be seen from the beach. The speed and width of the inshore current appear to vary both seasonally and sporadically, and occasionally the flow may even turn northward for a while. Nevertheless, both Wüst's data and observed movements of floats show that a buoyant object dropped off the turtle beach might go either northward or southward, depending upon the distance offshore of the point of release, and on the width of the longshore current at the time. That this hydrologic pattern is involved in the ecologic geography of the Tortuguero nesting colony seems likely.

In 1962 (ref. 14) Carr and Hirth called attention to the consonance of the migratory pattern of the green turtle colony of Ascension Island in the South Atlantic (fig. 1) with those of other marine species in which mature animals travel upstream in a current to a breeding place from which the weak, naive young are then passively carried downstream by the same current. Anadromy, in which marine animals travel up rivers to breed, is a special variant of this pattern. In the case of the Ascension Island green turtles, none of the tens of thousands of hatchlings that emerge there each season are ever seen anywhere near the island after the hatching season is over; nor, by logic, should they be. The narrow shelf around the oceanic island offers neither food, nor shelter from predation by fishes and birds. The conclusion is, thus, that the hatchlings swim offshore a

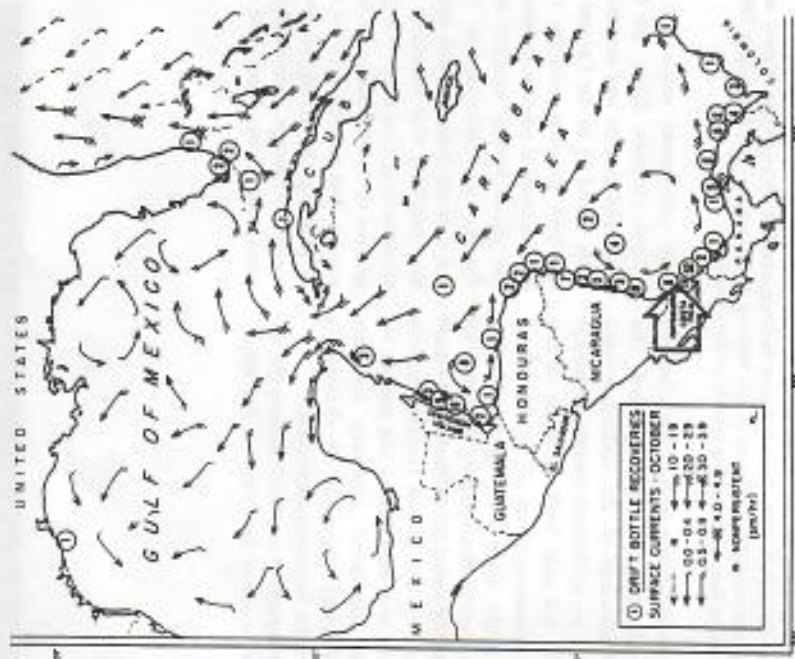


FIGURE 3. Recoveries of drift bottles (circles) released at Tortuguero, 1963 through 1969, in October, the time when most of the hatchlings enter the sea at the Tortuguero nesting ground. Arrows indicate trend and strength of currents for October (data from Wüst, ref. 13).

short way and are picked up and carried away by the Equatorial Current, which at that place and season flows westward at a speed of about one knot.

Where the current takes them is a part of the "lost-year" puzzle. It is of interest, however, that at both Ascension and Tortuguero the only overt move required of a hatchling, in order to initiate its passive dispersal to distant places, would be strong, oriented locomotion immediately after it enters the sea, to

move itself beyond the hazards of the surf and shore-water and into a medium of long-range transport.

Appropriate responses are innate in hatchlings. The tendency of young sea turtles of all kinds to swim furiously against the walls of a container has been repeatedly noted. Under natural conditions this swim-frenzy is coincident with a strong motivation to move away from the shore; and this, in turn, seems to be an extrapolation of the

directional sense that guides young turtles across the beach from the nest to the sea on a course normal to the surf-line. Observations of hatchlings immediately after they have passed through the surf suggest that they continue to move directly away from land for some time. That this oriented swimming could disperse them into their unknown but clearly remote first-year habitat, or series of habitats, seems unlikely. There can be little doubt that currents are the main long-range dispersal agent and that the swim-frenzy is merely a mechanism to get the young turtles away from the coast and into the current. In any evaluation of the probability that the migrating adults find chemical cues in the same current, this advantage to the hatchling should be considered.

The possibility that olfaction is a component of the guidance mechanism seems further reinforced when Ascension Island and Tortuguero are compared, with respect to their relation to the places of origin of the colonies that nest there and to the current systems of the areas. As figure 1 shows, Ascension Island receives migrants from both north and south of the bulge of Brazil. Results of the 15-year tagging program at Tortuguero show that there, too, females that nest each year, between July and October, comprise a northern contingent, mainly from the Miskito Cays off Nicaragua, with smaller groups derived from more distant resident grounds as far away as Cuba and Florida; and a southern element, from Panama, Colombia and Venezuela (fig. 3).

It seems unlikely that any form of visible-landmark piloting could be the guidance mechanism for any except the last stages of the periodic, mass arrivals of green turtles at Tortuguero and appears reasonable that chemoreception may be involved in this case, also, even though the goal is a section of mainland shore. From both Ascension and

Tortuguero, dissolved marker chemicals might be carried northward for great distances by the Equatorial Current and its branches. Moreover, Brazilian turtles from home grounds south of the bulge could be led into the South Equatorial Current by its branch, the south-trending Brazil Current. As our drift bottle returns show, the inshore current at Tortuguero could carry chemical cues to resident colonies on pastures as far south as Panama and Colombia. If the latter made their breeding migration in coastal water, they could overcome sensory fatigue, if this actually is necessary, by moving periodically out of the longshore current and into offshore water, just as the Ascension migrants are assumed to move vertically into the subtropical counter current.

It at first seems another striking point of agreement in the Ascension and Tortuguero patterns that hatchlings entering the sea in either place might be transported directly to the parental residence grounds. This suggests that the same current that guides the migrating adult transports the offspring back to the home territory of the parents. Such a possibility, however, would be based on an assumption that hatchlings emerge with a genetically controlled racial tendency to control the direction of their passive transportation by varying the duration of their swimming toward the open sea. That is, Colombian hatchlings might relax their swim frenzy only a few hundred meters off shore, and so be swept southward, while Mexican hatchlings would continue to swim seaward long enough to be picked up by the northerly Equatorial Current. In order for such dichotomy to evolve as an adaptation, however, segregation of mating pairs at the breeding ground would have to be ensured, with Colombian and Panamanian males mating only with Colombian and Panamanian females, and so on. There is no evidence, either positive or negative, that

such selection occurs. In any case, however, the idea of bipolarity in the dispersal of the hatchlings may be a red herring, because young green turtles are never found anywhere near the parental residence pastures. The least objectionable assumption to explain their lost year appears to be that they take asylum in sargasso rafts in open ocean. Nevertheless, it must be significant that at both Tortuguero and Ascension hatchlings have quick access to currents that could serve as the agent of their hidden developmental travel.

Thus, in the two best-known migration patterns of marine turtles—those of the Ascension Island and Tortuguero colonies—the dispersal of regional currents could aid both the dispersal of the young and the navigation of the migrating adult returning to her hatching place, with only a chemoreceptive imprint and a Sun-compass sense to guide her. That conditions at both a mainland nesting beach and a small oceanic island afford this dual advantage suggests that the pattern may be a widespread one, and this possibility seems strengthened by recent oceanographic data. Further testing of the idea may reveal that, other things being equal, a good nesting beach, in the eyes of *Chelonia*, is one that lies near a current system capable of providing (1) olfactory guidance for the nesting migrations and (2) appropriate transportation for the newly hatched young.

THE ROLE OF TRACKING AND TELEMETRY

The most important obstacle to investigation of this and other aspects of the ecology and migrations of the five genera of marine turtles is the difficulty of keeping in touch with them in the open sea. Most of what has been learned of sea turtle ecology has come from tagging-and-recovery data, and while a

good deal can be deduced from such point-to-point contacts, the data leave fundamental aspects of the life cycle completely obscure. Although all the genera appear to be at least partly migratory, their routes of travel have in no case been adequately traced.

Caretta is sometimes sighted on the high seas and is also seen in estuaries or even in little creeks in salt marsh. *Chelonia*, being herbivorous, comes under observation by turtles on its shallow-water pasture grounds. Divers find hawksbills about submerged rocks and reefs. The Atlantic ridley is accidentally taken off the coasts of Florida by shrimp trawlers or in green turtle nets, and seamen and hide hunters intercept schools of Pacific ridleys in deep waters off Mexico and Central America. Leatherbacks are frequently harpooned by fishermen off New England and Nova Scotia and in the Sea of Japan. Such sightings as these, however, are usually so fleeting that little is learned from them. Often even a firm identification is impossible. For instance, the Airborne Radiation Thermometer Program of the U. S. Coast Guard has compiled a massive record of sightings of sea turtles along the inner edge of the Gulf Stream; and while the turtles recorded are no doubt mostly loggerheads, the admixture of other species cannot always be detected, and this defect obviously lowers the value of the data.

During the past 8 years, one aspect of the program of sea turtle research at the University of Florida has been a series of attempts to track sea turtles in their local and long-range travel. Although this work has never advanced beyond the equipment-testing stage, a few partly successful tracking runs have been made. The desultory data that have accumulated—some of which have appeared in previous publications—are plotted in figures 4 to 10. The tests were carried out in Florida, Costa Rica, and in the South Atlantic off

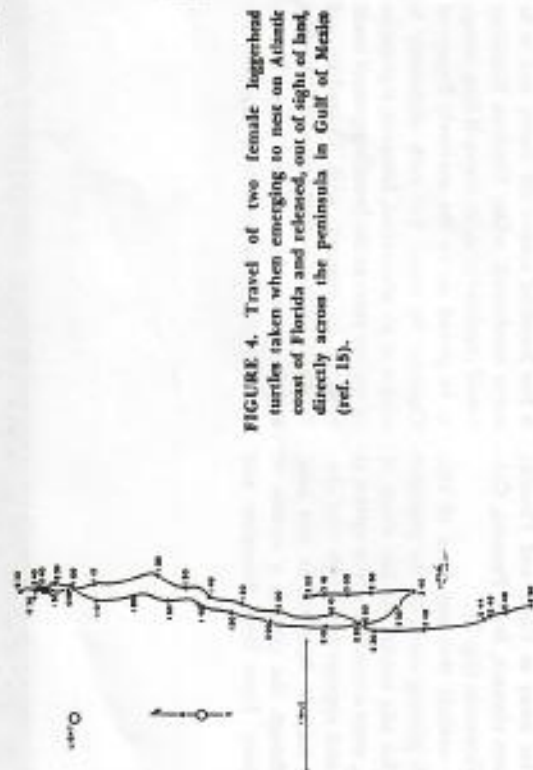


FIGURE 4. Travel of two female loggerhead turtles taken when emerging to nest on Atlantic coast of Florida and released, out of sight of land, directly across the peninsula in Gulf of Mexico (ref. 15).



FIGURE 5. Plots of movements of two female green turtles visually tracked off Tortuguero, Costa Rica. Tracking allidades were located at the Station and tracking tower on the beach. One turtle (no. 3728) had been allowed to nest before being fitted with a tow-float and helium balloon and released off the nesting beach. The other (no. 3903) was rigged and released before nesting. No. 3728 had evidently not finished her suite of renestings for the season. The motivation of the purposeful and seemingly well-oriented course of no. 3903 is not apparent, since she returned to the beach the following night and nested at point indicated (ref. 5).

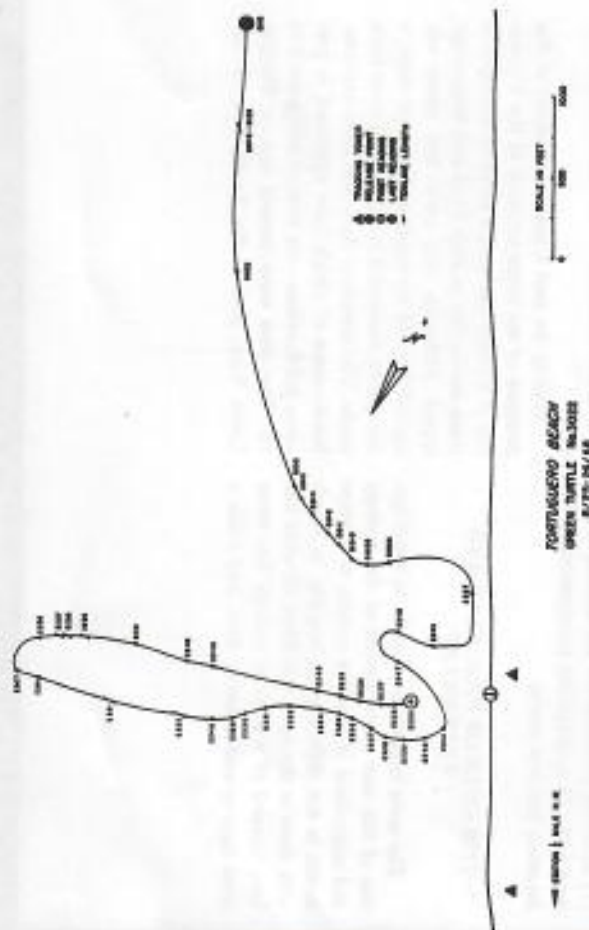


FIGURE 6. Plot of movements of mature female turtle visually tracked at night at Tortuguero, Costa Rica. The turtle was taken just before nesting and rigged with a tow-float bearing a single flashlight bulb at top of 1-meter mast. Bearings were recorded by allidades located at two tracking towers a half-mile apart on the fore-shore.

Ascension Island. In an effort to learn where a female sea turtle goes and what she does during the 12-to-14 day intervals between her nesting emergencies at the rookery, tow-floats and helium balloons have been used in daytime tracking (figs. 5 and 8) and lighted floats at night (figs. 6 and 7).

There has also been a series of largely unsuccessful efforts at tracking by radio. The first of these were made with transmitters fastened to the carapace of the travelling turtle. Of various defects in this system, the most fundamental was the limitation of the transmission period to the time when the turtle emerged to breathe and exposed the whip antenna that rose from its back. More recently, in collaboration with Sensory Systems Labo-

ratory, transmitters, and in some cases sensors capable of telemetering heading and velocity, have been installed in floats and attached to experimental turtles by long lines. Although both green turtles and loggerheads have shown themselves to be amenable to such manipulation, electronic troubles have plagued these efforts too.

One of various applications of long-range tracking techniques to the study of sea-turtle natural history is in the gathering of information with which to test navigation theories. To theorize about the pathfinding mechanisms used by an animal when the paths it takes are unknown seems unpromising, if not simple-minded, when the process involved is as clearly complex as this one is. The slow

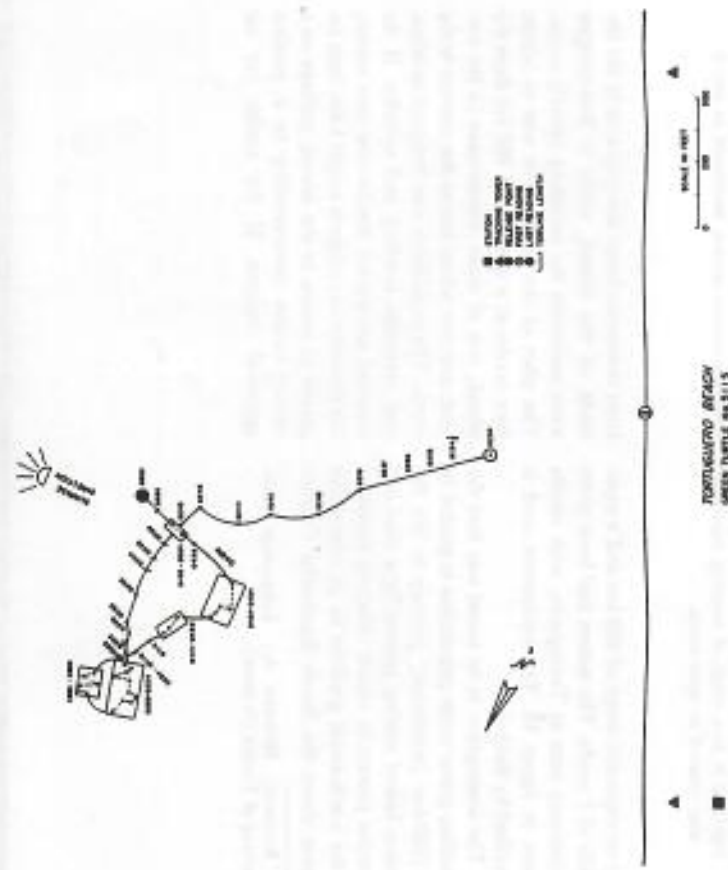


FIGURE 7. Movements of mature female green turtle visually tracked at night at Tortuguero, Costa Rica, after completing nesting emergence. Turtle was rigged with illuminated tow float, and bearings were taken with alidades located at tracking towers half-mile apart on the beach. Sudden resumption of activity at the moment sun showed above the horizon, after the long period of relative quiescence, was striking.

progress of animal navigation theory since its brief period of initial progress seems mainly attributable to the difficulty of tracking animals through significant segments of their long-range journeys in, on, or over the open sea.

The ideal is to trace whole migratory journeys in detail. Much can be learned from appropriate sample segments, however. Figure 9 suggests five ways in which such samples bear upon three fundamental questions

as the distance is increased. It should be stressed that in this trial the experimenter is not concerned with either the appropriateness of the course chosen or the frequency of a given guidance capacity in a population—only with the degree to which an individual migrant adheres to a nonrandom course. Thus the straight line is not drawn between end points of the segment but is put in as a trend-line to show mean performance. In trials B through E, on the contrary, the line that serves as the criterion for direction-holding capacity is the mean vector, drawn as shown, between endpoints in the timed travel-path.

In test B a single animal is used in repeated tracking runs. Sample size is augmented by increasing the number of trials. Such a test would logically be made after positive results had been obtained in experiment A, with the aim of determining whether the capacity for nonrandom travel is coupled with a tendency to choose the same direction in repeated trial runs. It is thus a test for both nonrandomness of travel and direction preference but not one for "goal" sense. In experiment C various animals are used in tests like those of B to learn whether a preferred direction trend is an individual or racial attribute. Sample size is increased by increasing the number of individuals.

A specific goal drive is assumed in test D. A turtle of the Ascension Island nesting colony, for example, is taken as she comes ashore to nest after a migratory journey from Brazil, carried back out the assumed line of her migratory travel, and released. The aim is to determine the success with which the migrant was able to repeat that segment of the Ascension travel. The test is designed to answer the question: How closely does the mean vector conform to the true course to the "goal" as assumed by the experimenter? Sample-size would be increased by repeating

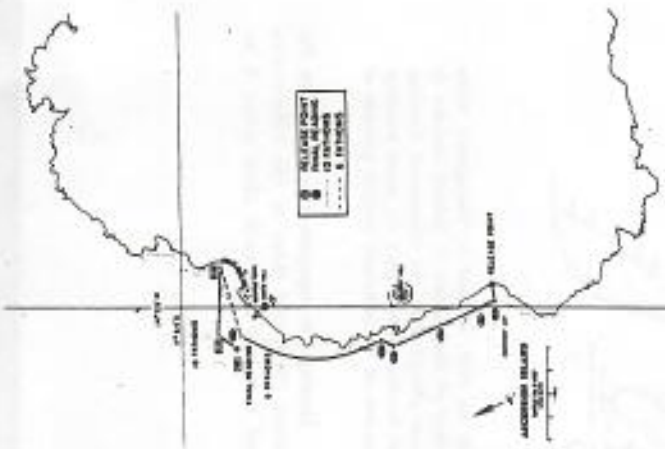


FIGURE 8. Movements of female green turtle (no. B 602), visually tracked after release at Southwest Bay, Ascension Island. Turtle had nested the night before. Close approach to the surf on Long Beach Cave was unexpected and unexplained.

runs. In experiment E, data from various goal-motivated animals, tested in the same area as that used in D would show how prevalent the goal-trend is in a population—that is, how widespread the tendency and capacity to hold a particular course are in the particular breeding colony from which the sample was taken.

During March 1969 an effort was made to carry out surface-to-surface tracking and telemetry using female Ascension Island green turtles displaced before completing their nesting venture. The plan involved four experimental animals. The transmitters to be used

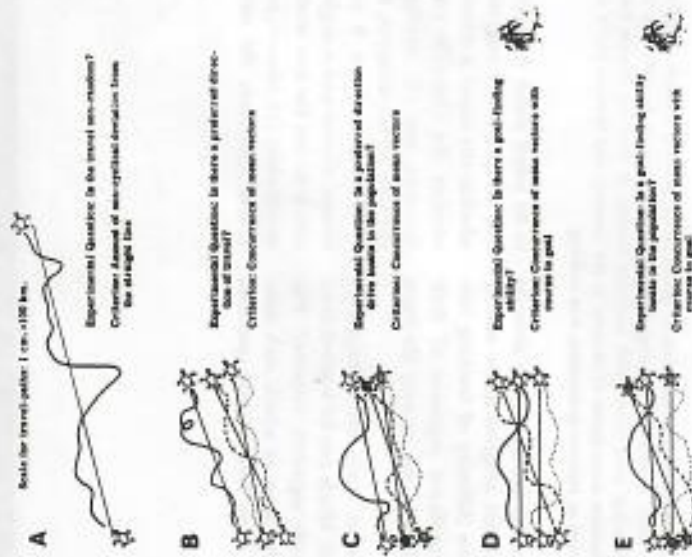


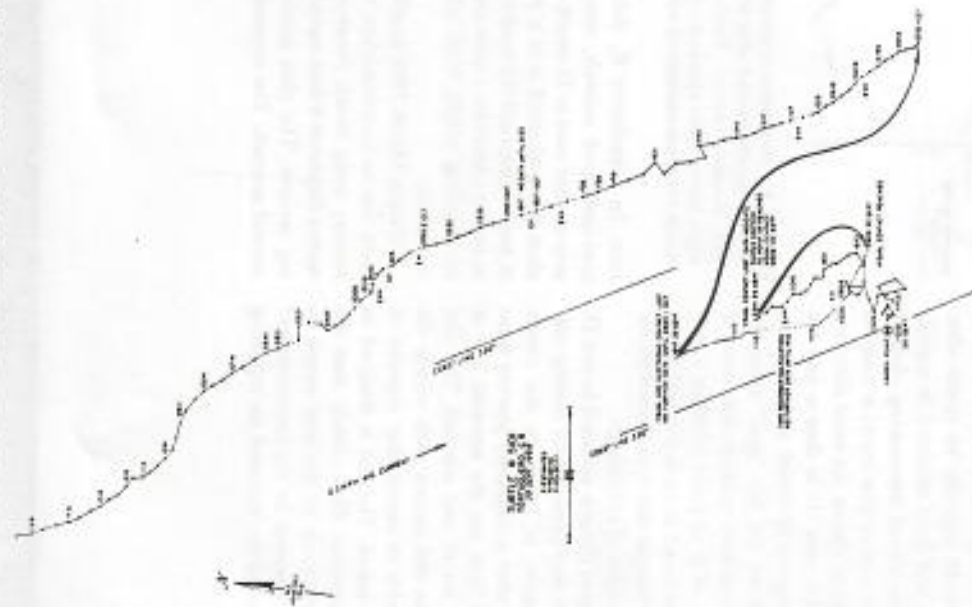
FIGURE 9. Five kinds of tracking experiments involving marine turtles, motivated to travel, and released in open ocean.

had an expected range of 480 km and a power-life of 2 weeks. The system had been given preliminary tests at Tortuguero, with results shown in figure 10. The equipment used is described by Baldwin.¹

The assumption to be tested was that the Brazilian green turtle population is guided in its 1920-km (minimum) journey to the Ascension Island nesting ground by a dual orientation process in which olfactory appraisal of the north-south gradient in an emanation stream down the South Equatorial Current

¹ BALDWIN, HOWARD A.: Long-range radio Tracking of Turtles (in press).

from Ascension keeps the migrants in the latitude of the island, while a Sun-compass sense maintains the necessary easterly course. The plan of the experiment was to release four turtles at a distance of 160 km from the island; two of them downstream in the current, and two others across the current to the north. The equipment was designed to telemeter magnetic heading and velocity. If the assumed navigation mechanism was correct, the downstream subjects might have been expected to return to the island, perhaps on a zig-zag course corresponding to a gradient appraisal regimen. If the turtles put out



FIGURES 10. Telemetered course of green turtle no. 5101, released at Tortuguero, Costa Rica, after nesting there the night before. Because of fluctuations of inshore currents at release site, it is unknown how closely the course plotted from the telemetered headings and velocities correspond to actual travel pattern; however, mean vector for travel headings closely approaches a true course to Miskito Cays, one of the principal resident grounds of Caribbean *Chelonia* (see fig. 2).

across the current had oriented successfully, the theory under test would automatically have been discredited. Damage to equipment in travel to the island eliminated three of the experiments and curtailed the fourth after about 2 hr.

Heading data from the single aborted run are shown in figure 11. These headings were taken by an animal orienting in open ocean where it was presumably isolated from all solid landmarks and, because of its position in the current, obviously not in olfactory contact with the island. Although nothing of significance is revealed by the degree of constancy of the course with the true course to Ascension, the travel of the subject was quite obviously non-random.

If this experiment had proceeded as planned, with continuous heading data coming in from both downstream and across-stream subjects, results would have permitted evaluation of navigation theories in various ways. If a Sun compass had actually been in use, for example, orientation should have failed at sunset. If the subject had slept at the surface, it would have been borne westward by the surface current during the night; if it had dived beneath the thermocline to rest, it would have remained stationary or been carried in an easterly direction by the counter-current. In neither case, however, would there have been evidence of orientation in the night-time heading-data. If all turtles released had returned successfully on direct courses, bicoordinate celestial navigation, or some equally complex mechanism, would have had to be reconsidered.

In spite of this setback in the effort to track the Ascension Island migrants, the colony remains a promising source of data for animal navigation theory. The relatively steady ocean current, moving directly along a parallel of latitude from the breeding island to the nearest projection of the mainland residence ground, suggests chemoreception as a guidance cue. Evolutionary feasibility favors the idea: back-tracking an imprinted stream to a tiny mid-ocean island seems a more evolvable adaptation than the Earth-map and star-almanac a migrant would need

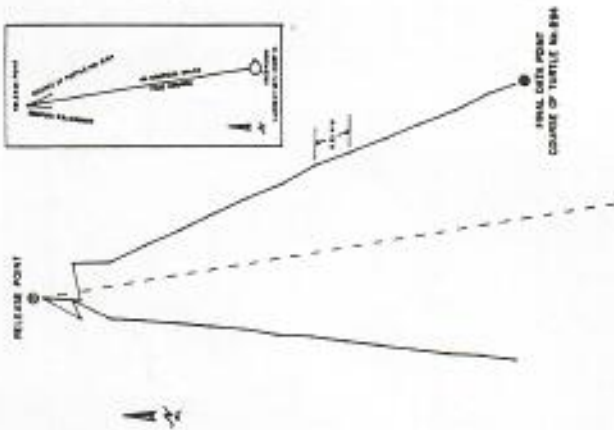


FIGURE 11. Course dead-reckoned from 13 headings telemetered by green turtle no. 94, rigged with tow-float after being interrupted in nothing at Ascension Island and released 101 nautical miles NW of the island ($06^{\circ}15'S$, $14^{\circ}41'W$). Velocity assumed was 0.83 nautical miles per duty-cycle interval. Course corrected for current set is the line at left.

in order to correct offcourse aberrations by celestial bicoordinate navigation. The weaknesses of the chemoreception theory are our ignorance of the migratory paths, the dearth of data on the sensory acuity of the species, and the regular mass arrivals at Ascension of 10 kinds of migratory sea-birds that surely have not smelled their way out there.

ACKNOWLEDGMENT

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DISCUSSION

QUESTION: Do you have plans, if the telemetry system works, for placing the turtles in different directions from the island?

CARR: Yes. The need is for a well-designed experiment in which a number of animals are set out at sites suggested as strategic by oceanographic and statistical considerations.

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