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## **Notes on the Behavioral Ecology of Sea Turtles**

### **ABSTRACT**

Knowledge of the behavioral ecology of sea turtles, though still riddled with gaps, has progressed to the point where a short review is bound to be inadequate. This summary calls attention to features of sea turtle behavior that seem especially noteworthy, and to the major imperfections in knowledge of the group. As an example of the degree to which innate patterns of response govern sea turtle behavior, the peculiarly stereotyped process by which the egg-cavity is dug is described. This one behavioral trait distinguishes all sea turtles from all the terrestrial and freshwater species. Stages in the behavioral development of sea turtles are rapidly reviewed, as follows: ascent of hatchlings from nest to surface; traversal of the beach; traversal of the surf; orientation behavior after passing the breakers. The bearing of the last on the lost year puzzle and on the sargassum raft theory of hatchling refuging is discussed and the status of our knowledge of orientated movements within developmental habitats and in reproductive travel is assessed. The probable existence of nonmigratory populations or population segments is pointed out; and basking and hibernation as possible alternatives to migration are discussed.

The natural history of marine turtles has received growing attention during the last 20 years, and much has been learned. Much remains to be learned, however, and the gaps are both an intellectual challenge and an obstacle to conservation. My aim in the present paper is to point out what seem to me high points in the behavioral ecology of the group, and to call attention to conspicuous gaps in our knowledge.

The ecology of an air-breathing vertebrate in the ocean is bound to be complicated. The Cetacea have solved the problems through cerebration, sociality, and parental care. The sea turtles show little of these—none of the last—and instead have evolved a remark-

ably successful repertoire of purely inherent responses to the demands of a changing suite of environments.

A trait that epitomizes the role of machinelike instinctive patterns in sea turtle behavior is the technique used in digging the cavity in which the eggs are laid. For a long time I have found this hard to explain and impossible to ignore. Many years ago, in an effort to make sense out of the confused taxonomy of sea turtles, I tabulated some osteological characters of the four thecophoran (hardshelled) genera and concluded that, while it was probably best to keep them all in a single family (Cheloniidae), a case could be made for giving separate familial recognition to *Chelonia* and placing *Lepidochelys*, *Eretmochelys* and *Caretta* together in another family (Carr 1942). Dr. Rainer Zangerl pointed out that my assessment gave undue weight to certain characters that were all just expressions of the same structural adaptation (Zangerl and Turnbull 1955). In his view, *Chelonia* and *Eretmochelys* seemed clearly allied, on the one hand, and *Caretta* and *Lepidochelys* on the other; although he saw no reason to recognize separate families for any of the group. Dr. Zangerl is a distinguished paleontologist, and I bowed to his pronouncement; but only insofar as his criticism of my skull characters was concerned. I reserved judgment on the relationships of *Chelonia*.

Later on I turned to behavioral characters that I hoped might provide criteria for judging relationships among the genera, including those of the aberrant *Dermochelys*. One aspect of sea turtle behavior which, because of its stereotyped complexity, might be expected to show relationships, is the activity of the nesting female. During the first years of our sea turtle program at the University of Florida, we accumulated films and photographic records of nesting behavior, as material for such comparisons. Almost at once it became clear that nesting behavior was a somewhat unreliable source of taxonomic criteria.

There are differences among the genera, to be sure. John Hendrickson has listed some of them in a paper in this volume. For example, a ridley compresses the sand over her finished nest by rocking laterally and slapping the sand with alternate sides of the plastron. With much diminished emphasis, this can be seen in *Eretmochelys*, and to even less degree in *Caretta*, so it might be interpreted as evidence of affinity among the three. On the other hand, the fact that *Chelonia* and the leatherback do no pounding may simply reflect their greater body weight—as may also the marked difference in gait between the same two sets of genera. Other variations in the behavior of sea turtles on shore may be merely phenotypical responses to environmental differences. For example, most Tortuguero green turtles make no trial egg-holes before completing one; on Ascension Island this task may be begun and aban-

doned many times during one emergence (Jeanne Mortimer, personal communication). Also, a Tortuguero green turtle almost always turns quickly back into the sea if a light is shined on her when she emerges from the surf; Ascension Island turtles seem usually unperturbed by lights. Detailed attention to each stage of the nesting process reveals minor differences that may be genetically controlled, and thus of taxonomic utility. The salient feature, however, is an astonishing conservatism.

This impression reaches a peak in the process by which a sea turtle—any sea turtle, anywhere on earth—uses the hind feet to form the flask-shaped cavity in which her eggs will be deposited. In this operation the digging is done by the back flippers. Their work is inflexibly stereotyped. The feet work alternately. A foot is brought in beneath the hind edge of the shell, and its edge is pressed against the ground and curled to pick up a small amount of sand. The cupped foot is then lifted and swung laterally, and the sand falls; and instantly, the other hind foot, which until then has rested on the sand by the rim of the egg cavity, snaps sharply forward, throwing sand from beside the hole to the front and side. This sequence is then precisely repeated in reverse. The nest-digging process is an unvarying series of these reciprocating actions of the hind feet. It continues until the nest grows to a depth equal to the reach of the hind leg. If this ritual were confined to a single species it would be arresting, because the rigidly stereotyped behavior seems to go beyond ecologic utility. When one finds it in almost unmodified form in each of the five genera of sea turtles, one longs for a logical explanation. At least I do.

No other kind of turtle appears to be bound by such discipline. I have watched the nesting of soft-shells, snapping turtles, box turtles and several species of *Pseudemys*, and can clear them of any such hidebound behavior. According to Eglis (1963) a parrot-beaked tortoise that he observed "scooped small amounts of earth 8 to 12 times with the near side of the left heel and deposited them near the right foot . . ." sometimes resting a few seconds before completing the sequence. That side-neck turtles practice no such strict manual of arms as sea turtles is clear from Vanzolini's observation (1967) of the nest digging of *Podocnemis expansa*. A female that he watched "started scooping vigorously with the (left) hind foot . . . throwing the sand toward the opposite side of the body. After 4 to 10 scoops she would stop for 15 to 30 seconds, then start another, usually shorter, series of movements with the same foot."

There is no such laxity in a sea turtle. She scoops and drops sand with the left foot, then kicks sand forward with the right foot, then invariably puts the right foot in the nest, then repeats the process in reverse. If this were the only way, or even clearly the best way,

to dig a hole in sand, the machinelike rigidity of the drill would seem reasonable. When one finds that all the other kinds of sea turtles make precisely the same ritualistic approach to nesting, puzzlement is compounded. Sea turtles dig nests in material that ranges from fine siliceous particles to spherical pellets of calcareous algae. The density, friability, and angle of repose of the nesting media vary widely, and suggest nothing that explains why sea turtles, as compared with turtles of land or fresh water, have so consistently stereotyped their technique of shaping an egg chamber.

When I watch film clips showing, in succession, nest digging by each of the five genera only one, very slight divergence is revealed. This occurs in the forward sandkick of the back flipper of the leatherback. In all the others the fin that kicks returns in one smooth motion to take its turn in digging. In *Dermochelys*, immediately after slapping forward the foot swings part way back, then very weakly repeats the kick before returning to its place in the egg-hole.

Minimum chronologic separation of modern sea-turtle lines is probably no less than 30 million years. That leading to *Dermochelys* is probably at least 50 million years old. It seems almost irrational to believe that the slavish concordance of the five genera in their identical technique of digging a hole is convergent. The only alternative is that it has been inherited from a common ancestor. Zangerl (1980) believes that *Dermochelys* belongs in the same family as the other sea turtles. There is evidence from both immunological criteria (Frair, 1979) and chromosome morphology (Bickham, 1979) that supports this view. However, the two lines may have been separate since at least the Late Cretaceous; and this seems an unconscionable length of time to retain a pattern of behavior the stereotyped detail of which appears to go so far beyond adaptive demand.

Nevertheless, a person asked what a sea turtle is, might truthfully reply: "A sea turtle is a kind of turtle that never puts the same back foot into its egg-hole twice in succession."

Two fundamental features of the life cycles of sea turtles complicate their ecology. One is their adherence to the ancestral habit of laying eggs in holes in the ground. This obligation draws them to land, often from distant foraging grounds, and introduces severe ecologic problems for both the female turtle and her offspring. The other complicating factor is their large size. The advantages of being big are obvious; but in sea turtles the change from hatchling-size to ponderous maturity is accompanied by repeated shifts in foraging requirements, and thus in habitat.

The burden of being born on land rests heavily upon the hatchlings; and they have responded with dramatic adaptations. They begin coping with their environment a meter down in the sand of the sea beach. Any overview of sea turtle ecology, however cursory, should

signalize the proto cooperative activity by which newly hatched young turtles, imprisoned in a hat-sized chamber far down under settled sand, move up *en masse* to the surface. The process is apparently not mediated by geotactic stimuli. The hatchlings are not striving toward the surface as a goal, but merely reacting to local stimuli in ways that take them toward the surface. They do not dig upward; they merely thrash about.

The process has been watched and photographed in nests of *Chelonia*, *Dermochelys*, *Eretmochelys*, and *Caretta*, behind glass panes, both in the laboratory and in natural nests in the field. In all cases, the rise to the surface has been achieved by sporadic outbursts of thrashing, usually triggered by one turtle and quickly spreading through the clutch. This activity automatically dislodges sand from the walls and ceiling, builds up the floor of the chamber, and carries the group to within a few inches of the surface. There the sand often sinks in a circular area above the hatchlings. They remain quiet there for a while, evidently awaiting the propitious temperature change that usually occurs near dawn (Bustard 1967; Mrosovsky 1968).

This example of group facilitation (Carr and Hirth 1961) is particularly noteworthy because from there on, the social organization of sea turtles is weak. There is fleeting social intercourse during courtship and mating, and in *Lepidochelys* the fantastic reproductive aggregations variously known as *arribadas*, *arribazones*, *morriñas*, and *flotas* must be adaptive. Otherwise, little sociality has been observed.

As soon as the hatchlings are out of the nest and on the surface of the beach, each separately faces the problem of finding the sea. A voluminous literature, summarized by Ehrenfeld (1968) and Mrosovsky (1978), describes and seeks to explain their remarkable sea-finding ability. A mechanism that will account for its full versatility has not yet been identified. Hatchlings of all the genera are able to take accurate seaward headings from most nest sites even when the surf is not in view. They can do this even when the emergence site is experimentally moved to a shore with diametrically opposite exposure (Carr and Ogren 1960). That means that the guiding sense is not a combined, genetically represented, compass sense and regional map sense. Light is clearly important in the guidance process, but the exact way in which light guides the turtles is not clear. Recent results of a series of experiments with green turtle hatchlings, in which hoods were used to interfere with vision, lead Van Rhijn (1979) to the conclusion that a mechanism drawing the turtle toward maximum brightness is inadequate. He suggested that a multiple input system, as defined by Schone (1975), must be involved, perhaps with some reference to silhouette patterns and to substrate inclination as well. His conclusions seem sound, but they still do not provide a complete model for the versatile sea-finding

abilities of newly hatched sea turtles.

The next stage in the behavioral ontogeny of marine turtles is the sudden, short, violent encounter of the hatchling with the surf. The passing of newly hatched turtles through breakers is a striking manifestation of compressed behavioral ontogeny. The surf line is an extremely dynamic environment. There could be no more dramatic example of instant response to environmental releasers than the ability of the little turtles, only minutes out of the nest, to react appropriately before the jolting suite of forces inside a breaking wave. Any hatchling which, on reaching the water, merely tried to swim doggedly away from the beach would usually not get beyond the surfline. Their performance involves instantaneous responses to a chain of cues encountered for the first time and in rapid sequence.

I once spent some hours releasing hatchlings on a Pacific beach in very clear water and watching their encounters with the surf. I published a brief description of these observations (Carr 1963). From the standpoint of both developmental behavior and orientation ecology, the interlude would repay a more systematic analysis. The first bit of ocean that the hatchling encounters is the shallow sheet flow of a spent wave. This lifts the turtle slightly, and instantly the crawling locomotion is replaced by winglike swimming strokes. The seaward bearing is maintained, but now positive rheotaxis appears to be the response; and when the backwash starts sliding seaward the polarity of the current cue must reverse because the heading of the hatchling remains the same. As the next breaker looms, the turtle dives to the bottom and rides the undertow, avoiding the breaking wave, which otherwise would carry it back on the beach, and reappearing on the surface in the relatively calm water beyond.

That appears to be the sequence of events in its simplest form. I have been able to watch it closely only in low, long-period Pacific surf. In multiphase breakers, or where a strong longshore current prevails, the process must be much more complicated. The trip through the surf may be completed in a minute or two, and when one considers that the hatchling may have broken through its nest roof only 3 or 4 minutes before, the fact seems a spectacular example of the releaser effect in behavioral ecology.

The next stage in the ecologic ontogeny of sea turtles is the so-called "lost year." After entering the sea, young turtles of all kinds stay out of human view for from several to many months. Until lately this gap in the record of the life cycle began just after breakers were passed. What hatchlings did then was almost wholly unknown. Did they merely relax or paddle around at random, beginning their journey into the limbo of the lost year as totally passive plankton? It now is known that, for the green turtle, at least, this is not the case. The single-minded, oriented, seaward drive that the

hatchling shows in crossing the beach and during the hectic trip through the surf, is sustained, for a while at least, in the open water beyond. In some ingenious tracking experiments, involving direct visual contact with swimming turtles that had just emerged from nests on an adjacent shore, Frick (1976) showed that the sea-finding sense, or something apparently identical, is maintained as a clearly oriented open-sea heading. Her tests were made both at Tortuguero, and at Bermuda with Tortuguero hatchlings. Later experiments, in which sonic tracking techniques were used, produced similar results (Ireland et al. 1978). In still other trials, results of which are unpublished, Frick found that when hatchlings were allowed to enter the sea, then caught and released far offshore, they assumed and maintained nonrandom, open-sea courses up to 50 miles out from an invisible shoreline.

This research did not solve the lost-year puzzle, but it was a step in that direction. For one thing, the results lent meaning to the frantic swimming urge displayed by new hatchlings: which, if confined in a tank swim frenziedly against the walls, sometimes for days. This is evidently a behavioral adaptation to take them into their juvenile habitat—whatever that may be; and the yolk remnant that they take with them would seem to be a travel ration for the often foodless early stages of the journey. Most turtle students are satisfied that the lost year is not passed in littoral or estuarine environments. The alternative is a pelagic existence; and the Frick experiments reinforce the assumption that the swim frenzy and yolk store are equipment for a period of long-range travel toward an open-ocean lost-year habitat.

At most nesting grounds in the West Atlantic system, an open-sea heading would sooner or later take a swimmer either into the regional segment of the Equatorial Current or into an inshore gyre or counter-current. At Tortuguero, Frick's hatchlings left on headings that would have led them into the Southwest Caribbean Gyre, an eddy of the North Equatorial Current. In the near edge of this eddy sargassum rafts go by 20 to 50 miles off the coast, sometimes aligned in long bands. Carr and Meylan (1980) record finding green turtle hatchlings in a sargassum drift-line off Panama, about 20 miles offshore and more than a hundred miles south of Tortuguero. The locality corresponded closely with the position predictable from current set and a constant seaward heading; moreover, huge numbers of hatchlings were entering the sea at Tortuguero at the time, and only very desultory nesting occurs south of there. The Panama hatchlings thus were almost surely derived from Tortuguero. Further tracking will be required to reveal whether Tortuguero hatchlings show any tendency to correct for current set and, thus, to intercept the sargassum rafts on the shortest possible course. Frick's unpublished results show no such cor-

rection.

The possibility that the West Caribbean Gyre may be a closed-circuit lost-year habitat is now being investigated. It seems at least possible that hatchlings could pass the whole cryptic first period of their lives cycling in rafts within the eddy, moving out of it onto the contiguous reefs and flats of the Miskito Bank after reaching an age and size appropriate to those habitats.

While this may be one model for the lost-year, it clearly is not universally applicable; because at some nesting grounds long-range global currents flow close to shore, and the history of hatchlings that enter these seems for the moment imponderable. Moreover, drift bottles set out at Tortuguero (Carr 1972) show that even in the case of the West Caribbean population, an unknown percentage of the hatchlings that enter the southerly current would not continue drifting within the gyre but would be carried into the main stream of the Equatorial Current and thus to a wholly unpredictable lost-year destination. In any case, it now seems clear that a sargassum raft refuge for hatchlings is a reality—that some do enter and stay in the rafts. However, it also seems probable that the young of other colonies do not join rafts, simply because there are none where their natal shore is located.

In any case, the migrations of sea turtles begin at the hatchling stage and continue throughout life. Their travels range in scope from daily commuting between feeding and sleeping places to periodic reproductive journeys that may take them across a thousand miles or more of ocean. In a paper included in this volume, Anne Meylan has assessed current knowledge of the patterns of the reproductive migrations of sea turtles, about which has come nearly everything known from tag-recovery data accumulated slowly during the last 25 years. Because the turtles tagged are almost all nesting females, the cycles of breeding-ground, feeding-ground commutation must be closed by deduction and their details pieced out by the scant data on the non-breeding stages of the life cycle. Nevertheless, enough information is at hand to reveal some of the spatial and temporal outlines of the reproductive travel of the five genera.

Sea turtles make breeding migrations because the ecologic systems in which successful feeding and successful nesting can occur are often by their nature widely separated. Turtles in a freshwater pond also come ashore periodically, but their nests are often dug on pond banks only meters away from their resident foraging habitat in the water. For turtles in the marine environment the only suitable incubation medium is a surf-built beach, where sand driven ashore by waves and wind is piled up to elevations at which it is free from flooding from above or below. Their food resources may be located far away from such beaches.

The problems of reproductive migration affect each

species differently because both the foraging habits, and to a lesser extent the nesting requirements, are different in each. Of the sea turtles, *Chelonia* most clearly illustrates why long range breeding travel has to occur. Being largely herbivorous, green turtles rarely find adequate plant food along the exposed coasts on which good nesting sand piles up. Some kinds of algae tolerate open-shore conditions and, where these abound as in the Galápagos Islands and parts of the Hawaiian Archipelago, the colonies of *Chelonia* may be at least partly nonmigratory (Dampier 1906; Green 1979; Balazs personal communication). Most of the submarine seed plants on which Atlantic green turtles feed, however, such as *Thalassia*, *Syringodium* and *Halodule*, form extensive stands only in relatively calm waters. Such conditions prevail in the western Caribbean, where green turtles that feed on the vast Miskito Bank off eastern Nicaragua go mainly to Tortuguero, Costa Rica to breed.

Where the range of a species lies entirely within the tropics, seasonal migration may be wholly dictated by the separation of nesting and foraging habitat. In the case of the West Caribbean green turtle colony, this separation appears to be sufficient to account for the travel. Within the temperate zone, or where seasonal or sporadic upwellings or shifts in cold currents occur, thermal factors may trigger major seasonal migration. Not many relevant data are available, but it seems reasonable to suppose that any sea turtle that invades waters destined to go down to 15° C must either emigrate or make appropriate physiological adjustments. One such recourse, resorted to by a few colonies of *Chelonia*, may be to go ashore and bask. The prevalence of basking among freshwater reptiles of all kinds attests to the ecologic utility of the habit, but what the utility of basking actually is in sea turtles has not been revealed. Escape from sharks may be one adaptive value involved (Whittow and Balazs 1979). Obviating the need to emigrate from a good foraging habitat may be another. Energetically, it is less costly to move onto the shore and raise body temperature in the sun than to swim away to a warmer climate. Nobody knows for sure that the basking of sea turtles is, in some cases, an adaptive alternative to emigration, but the possibility seems reasonable.

There is evidence that the prevalence of basking may have decreased during historic times. Today the only regions in which it is known to occur are the Galápagos Islands, the Pacific Coast of Mexico and the Hawaiian Archipelago. It is perhaps significant that two, and perhaps all three, of these regions have relatively sedentary colonies of *Chelonia*. Balazs (1980) believes that the Hawaiian population never leaves the Archipelago. A part of the Galápagos colony is apparently resident in the islands, but another segment goes away after nesting. In Mexico the range of East Pacific *Chelonia*

once extended northward along the coast to the U.S. frontier, and a few individuals have lately been turning up in San Diego Bay (Stinson, in litt.). It may be a straw in the wind that these regularly take refuge in warm water discharged from a power plant. Margie Stinson is studying the behavior of this interesting colony.

The other alternative to emigration is hibernation. It is sad for science that depletion of sea turtles will prevent adequate study of both basking and hibernation. Both are significant adaptations, investigation of which would enhance understanding of sea turtle ecology and the physiology of large reptiles. The distribution of both has been so reduced by the decline of temperate zone turtles, however, that the original prevalence and geography of the traits will never be determined.

In the case of hibernation this is particularly distressing to me, because in Florida many years ago I was party to neglecting what now seems to have been an opportunity to study the hibernation ecology of two species—the green turtle and Kemp's ridley. Carr and Caldwell (1956) recorded fishermen's reports that ridleys and green turtles went into winter dormancy in the mud off the west coast of the Florida peninsula. They gave the reports inadequate attention, however. After Felger, Clifton and Regal (1976) reported hibernation by *Chelonia agassizi* in the Gulf of California, I belatedly reinterviewed Florida fishermen old enough to remember times before the loss of the West Coast ridleys and green turtles. It now seems to me probable that the immature turtles which, each April in Florida in the Cedar Key-Wacasassa area, came partly in from the south as migrants, also came partly "up out of the mud," as informants consistently believed. I have recently learned from the manager of the University of Florida Marine Laboratory on Seahorse Key that as a boy he used to dive up turtles that he located from a boat, during winter months, as humps in the mud of the bottom. During the winter of 1978 we went out and searched for such humps and did exploratory trawling in the area. We found nothing. Both of these once populous colonies are nearly gone. Felger et al. (1976) gave their torpid black turtles a proper presentation in *Science*. At the time they discovered the colony, however, Mexican scuba divers were beginning to exploit the torpid turtles commercially. That drain, combined with incidental catches by trawlers is now thinning out the hibernating contingent dangerously (Clifton, personal communication).

More recently Carr, McVea, and Ogren (1980) described an aggregation of loggerheads in a 6-mile, man-made channel leading into Port Canaveral on the eastern coast of Florida. At all seasons the concentration of turtles in the channel is extraordinary. When the colony was discovered in the winter of 1977 the water

off Florida had reached exceptionally low temperatures. Loggerheads taken by trawling in the channel during March of that year were mostly immature, and nearly all were torpid. Many showed unmistakable signs of having been dislodged by the trawl from the clay walls and bottom-mud of the cut. It has since been learned that loggerheads assemble in the channel at all seasons and that, during the winter, the colony is mainly composed of subadults while in summer it includes mature turtles some of which are females bearing tags that have been put on at nearby nesting beaches.

The ecologic attraction of the Canaveral channel has not been identified. It is not known whether its use as a hibernaculum is a wholly unique occurrence, evoked by some special feature of the artificial channel, or whether it reflects a prevalent habit of North American sea turtles that has just been overlooked (Ogren and McVea, this volume).

One of the most striking attributes of marine turtles is their ability to cross open ocean and make scheduled landfalls at ecologically necessary places, or to go back to such places if experimentally displaced. Like much of what we know about the group, this homing ability was widely known to seaside people before any zoologist ever put a tag on a turtle. When tagging projects began to develop, it was quickly corroborated, and eventually the ability of turtles to find little islands in the open sea was clearly revealed. This appears to require highly evolved guidance adaptations, comparable to those of terns, albatrosses, and other birds—and just as poorly understood.

Although usually thought of as a reproductive adaptation, homing orientation is not confined to breeding migrations. It is also clearly involved in the maintenance of home-range boundaries by nonbreeding individuals. It has long been known to professional turtle fishermen that when green turtles escape after being displaced great distances away from resident foraging or developmental range, they are capable of making quick, accurate returns. Carr and Caldwell (1956) recorded such returns by young Florida green turtles that had been displaced as far as 30 miles; and more recently Burnett-Herkes (1974) and Ireland (1979; 1980) reported an impressive series of homing performances at Bermuda. Balazs (1976, 1980) found strong feeding-site fidelity in Hawaiian green turtles, and Limpus (in litt.) has observed the same tendency in Australian loggerheads. It is widely believed by Florida fishermen that some loggerheads have home rock patches to which they return year after year. Striking corroboration of this is Norine Rouse's 6-year record (personal communication) of a male loggerhead that returns each fall to the same rock 15 meters down on a reef off Palm Beach. Nietschsmann (in press) records repeated territorial returns by displaced tagged hawksbills on Miskito Bank.

Animal orientation has received increasing attention in recent years. The proceedings of a recent symposium at Tubingen, Germany, (Schmidt-Koenig and Keeton 1978) reveal dramatic advances in defining homing capacities and revealing hitherto unknown ramifications of sensory physiology. One useful upshot of all this research is the evidence it provides that a broad palette of orienting cues is available to migrating animals. In any complex pathfinding feat, the migrant almost surely uses a number of different guidesigns. Despite the brilliant progress in both laboratory and field studies, however, we still have no idea how animals navigate. One reason for this may be that most of the field research has been done with birds traveling overland, where they are probably in touch with a number of different cues and where interpretation of field experiments is accordingly complicated. The ultimate refinement of animal navigation would seem to be the capacity of many species to make accurate landfalls after long journeys in the open sea. Such travel takes place in what must be the least cluttered theater for tracking experiments, and, if migratory paths could be accurately traced, carefully designed experiments would yield a wealth of circumstantial evidence by which navigation theories could be compared and assessed. In the case of the marine turtles, there seems no doubt that the experiments, though logistically difficult, through satellite telemetry are within the grasp of investigators. They are long overdue. The island-finding urge and ability rank among the most imposing behavioral adaptations that natural selection has produced. The lack of a satisfactory theory to explain the guidance mechanism is an embarrassment to science.

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