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Adaptive Aspects of the Scheduled Travel of *Chelonia*

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RESEARCH IN ANIMAL navigation has kept pace neither with advances in sensory physiology nor with progress in field studies of patterns of animal migration. Ten years ago it seemed that a general theory of bicoordinate celestial navigation might soon explain the long-range guidance feats of most migratory animals. The last five years have seen a marked decline in celestial navigation research and a concurrent resurgence of older theories.

An initial setback was the death of the German student Gustav Kramer, a gifted pioneer in the field. A continuously refractory obstacle has been the difficulty of plotting the travel paths of navigating animals. In no case has anyone traced the course of an animal migrating to an island or even plotted any considerable segment of such a course. This appears to be a fundamental obstacle to development of theories of animal navigation. It seems futile to try to understand a complicated, probably composite, guidance system when the environment in which the system is used remains unknown.

This does not mean that navigation research must stop and await the development of tracking techniques. In the case of the island-finding capacity of the green turtle, *Chelonia mydas*, there are various ways in which to lay groundwork, as follows: (1) to determine the acuity and versatility of senses that might be involved in the navigation process; (2) to plot the world distribution of island-finding patterns—that is, of seasonal high-seas travel between a pasture and an oceanic island nesting ground; (3) to try to determine the chief adaptive utility of each pattern; (4) to collate evidence bearing on probable paleogeographic conditions at the time of origin, or of refinement, of each pattern; and (5) to investigate the character and flexibility of short-range guidance feats where visual contact can be maintained.

This paper is a report on progress and problems in the green turtle research now being carried out at the University of Florida.

The Reproductive Cycle of *Chelonia*

Much of what has been learned about green turtle migration has been pieced together from results of tagging projects. The number of mature female green turtles that now have been tagged in the Tortuguero and Ascension Island projects is 4,264, and 189 have been recovered at a distance from the tagging site. Such data are useful, but they leave important gaps in the life cycle and tell little about the paths and periodicity of migratory travel.

Tagging sea turtles is much less enlightening than tagging colonial marine birds. Because birds are banded as nestlings, a tag affords potential contact with both sexes and with all stages of the life of the individual. With green turtles, only the mature nesting female can be marked satisfactorily in statistically useful numbers. From such results, one might assume that the population involved has a regimen of scheduled travel between a feeding ground and an ancestral nesting beach, but that conclusion would be a serious oversimplification. Nothing is known, for instance, of the periodicity of the male, or of the movements of the young turtles, which for at least a year after entering the sea remain completely hidden from view and thereafter only turn up seasonally as itinerants of unknown origin and with unknown destination.

In spite of the gaps, however, our tagging of *Chelonia* continues to furnish new information on the reproductive and migratory cycles. Table 1 shows all international returns of the tagging program at

Table 1. International Returns of Turtles Tagged at Tortuguero, Costa Rica

Country	Year tagged										
	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965
Nicaragua	6	8	11	9	14	10	18	9	19	3	2
Colombia	0	0	1	0	5	1	7	0	3	1	0
Panama	3	1	1	0	0	1	3	0	0	0	0
Mexico	0	1	0	0	0	7	0	0	1	1	0
Cuba	0	0	2	1	2	0	0	0	0	0	0
Venezuela	0	0	0	0	0	0	2	0	0	1	0
Grand Cayman	0	0	0	0	0	0	0	1	0	0	0
Jamaica	0	1	0	0	0	0	0	0	0	0	0
British Honduras	0	0	0	1	0	0	0	0	0	0	0

Tortuguero, Costa Rica. While there seems to be some indication of differential recruitment, the sample is too small to override shifts in the habits of the fishermen who make most of the recoveries. Figure 1 shows frequency of intervals between emergences of turtles tagged at

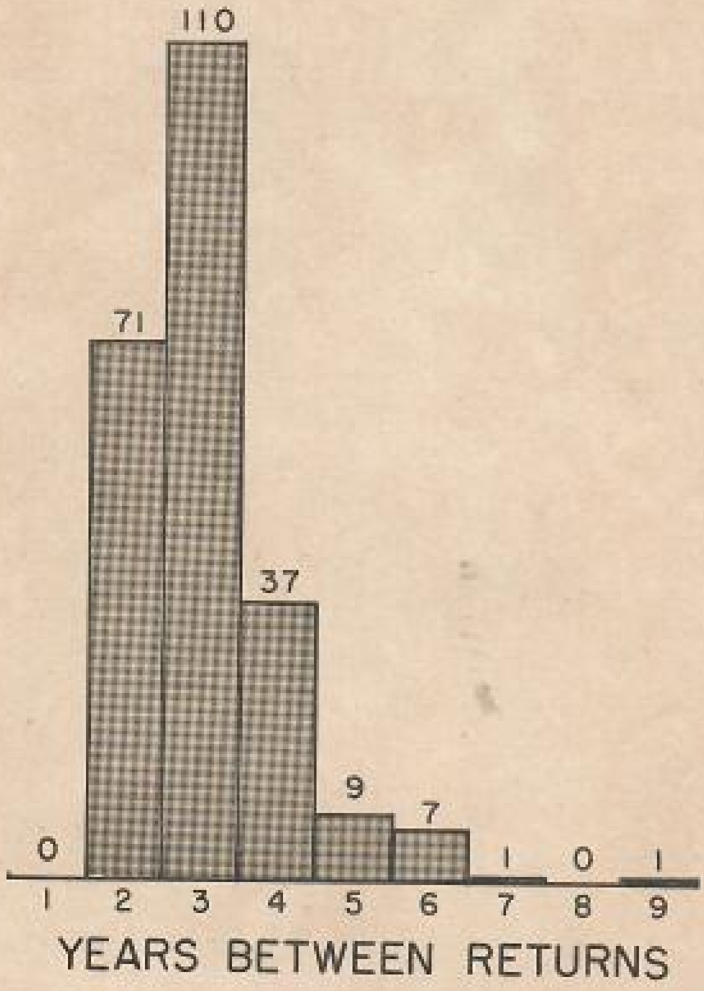

FIGURE 1. Interval frequency between emergences of green turtles tagged at Tortuguero Beach, Costa Rica, and retaken in later seasons, 1956-1966.

Tortuguero in different seasons. Table 2 shows all cases in which turtles have been retaken on the nesting beach at Tortuguero two or more times in different seasons. These data give some indication of the proportions of two-year and three-year reproductive cycles. Whether this periodicity is in any way related to the length of the migratory journey is not known. Whatever the adaptive reason for the dichotomy in cycle, each resident population appears to have both. A question that arose early in the study was whether an individual green turtle may experience an ontogenetic shift in reproductive period. Table 2 shows a clear case of a change from a two-year to a three-year period. It leaves uncertain whether the turtles retaken after four years breed on a four-year cycle, or were simply missed when they came back for the first of two two-year returns. The five-year returns shown in the table could represent either a five-year cycle, which seems unlikely, or shifts from two-year to three-year cycles, or *vice versa*. Only continued tagging will provide the samples needed to clear up these points. Meanwhile, there seems no evidence that a relation exists between length of cycle and distance between endpoints of migratory travel.

Table 2. Repeated Returns of Green Turtles to Tortuguero, Costa Rica, 1956-1965

Tag No.	Year	Mile	Year	Mile	Year	Mile	Interval sequence
377	1956	3/8	1959	1	1962	1/2	3,3
730	1958	1/2	1961	1 1/2	1964	0	3,3
952	1959	1 1/2	1962	1	1965	4	3,3
1024	1959	3/4	1962	2 3/4	1965	3 1/2	3,3
1344	1960	2 1/2	1962	3/4	1964	1 1/2	2,2
1386	1960	2 1/4	1962	1	1965	1 1/4	2,3
1429	1960	2 1/4	1962	3 3/4	1964	2 3/4	2,2
1671	1961	1	1963	1 1/4	1965	2 3/8	2,2
1755	1961	1 3/4	1963	1 1/4	1965	1	2,2
1928	1961	1	1963	3	1965	3 5/8	2,2
1969	1961	3/4	1963	1	1965	3/4	2,2

Disappearance of the First-Year Green Turtle

One of the fundamental troubles in studying the life cycle of the green turtle is the disappearance of the first-year young. It is not known how long the infantile tendency to swim violently and constantly continues after the hatchlings enter the ocean, nor is it known when a compass sense or navigation process may replace the initial tendency to swim toward the open sea. It is therefore not possible to say whether hatchlings, upon entering the ocean, remain wholly at the mercy of longshore currents or to some extent assume control of their early movements.

To furnish clues in the search for the first-year turtles we have for three years been releasing drift bottles off the Costa Rica nesting beach at the season when hatchlings are emerging in peak abundance. The thirty-eight bottle recoveries to date show that October currents off Tortuguero lead to places where green turtles have resident colonies both to the north and to the south of the breeding ground. The value of this information is not clear, however, because no young turtles are ever found on the resident feeding ground of the mature green turtles.

The need to trace the movements of the young, therefore, is as urgent as the need to track the mature turtles, and following them will probably prove an even more refractory problem. The least unacceptable theory is that they are pelagic. If so, the only conceivable way they could find food and shelter at the surface in the open sea is in drifting sargasso weed or other debris. A project to sample sargasso raft fauna and to plot the distribution of sargasso weed outside the Sargasso Sea is being planned.

Site Discrimination

Beginning with the original urge to leave the pasture ground on a reproductive migration, and culminating in the final selection of the nest site on the shore, the nesting migration is a complex orientation process that almost certainly involves repeated changes in the guidance mechanisms used. One of the clearly separate operations in this chain of events is that by which the turtle chooses the section of beach on which she will strand and emerge. Whatever navigatory process may have brought her to the nesting beach, the final landing-site discrimination is surely a distinct process, and one that so far remains as little understood as the high-seas navigation itself.

Figure 2 shows distances between places on Tortuguero Beach at which 232 turtles were tagged and retaken two or more years later. Although extraneous factors confuse the analysis somewhat, the data probably are a fairly valid representation of the degree of site tenacity involved. The turtles had converged upon a 22-mile stretch of beach from places as far as 800 miles away. Almost no nesting occurs on Costa Rican shores to the south of Tortuguero Beach, and very little on those to the north of it. In spite of various distracting factors, there seems a significant tendency for the turtles to emerge at distances of half a mile or less away from points of previous emergence. The

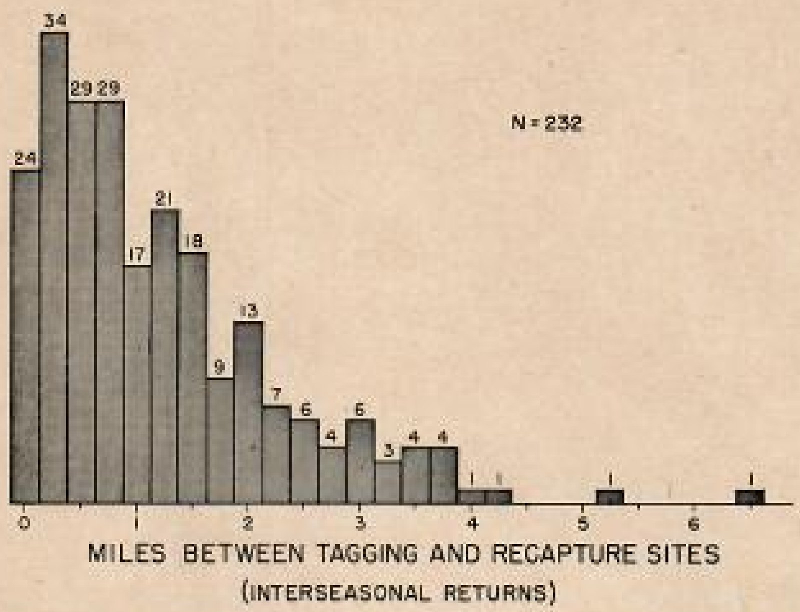

Figure 2. Distance between sites of tagging and recapture of green turtles tagged at Tortuguero, Costa Rica, and retaken in later seasons between 1956 and 1966.

figure shows twenty-four pairs of emergence points so near each other that our grid of the beach fails to separate them. This means they came out on the same one-eighth mile on which they had appeared earlier. There was no way to determine whether the two sites were even closer together.

The decreasing number of emergences at distances of two and three miles, and on out to the right of the histogram is not necessarily a reliable representation, because tagging is regularly done only in the five miles of the northernmost end of the beach. Fewer turtles may have been so undiscriminating; but also, fewer man-hours were spent patrolling the northern reaches of the shore.

Another obstacle to quantitative analysis has been seasonal changes in the shore. As Hirth (1963) pointed out, the Tortuguero shore is a scalloped series of little spits and embayments. The spits are on the average about one hundred yards apart. This pattern changes constantly; other changes in the shore are brought about by shifts in the positions of tidal channels and bars; and storm-wave deposition and erosion may drastically modify even the higher beach. The combined effects of these factors remodel the whole foreshore from season to season and would completely forestall any discriminatory process that depended upon either the structure of the beach or a stable sand surface.

One theory of stranding-site selection is that olfaction may be the sense that determines it. The "sand-smelling" mannerism of the emerging turtles invites this interpretation (Carr and Ogren, 1960). It now seems clear that, although olfaction may be involved, the sense of smell could at the most serve only to assess and recognize a general region of the coast or coastal waters. It could not possibly locate a spot where emergence occurred three years before, because there would always be a different sand surface at that spot. In spite of this reasoning, however, arriving turtles continue to make what appears to be an olfactory appraisal of the sand of the nesting shore, and it would be very interesting to know why. As to the sense by which site discriminations as accurate as those suggested by Table 2 and Figure 2 are made, the only reasonable possibility would seem to be visual appraisal of background topography or of the pattern of light and shadow that the inland horizon makes.

Time and Distance in Tag Recoveries

Carr and Hirth (1962) pointed out that among fifty-four tag returns from the first five years of the program at Tortuguero, there was no correlation between the length of the interval between tagging and recovery and the distance between tagging and recovery sites. This was interpreted to mean that the turtles were not wanderers that tended to move farther from their nesting ground with passing time, but were scheduled migrants commuting between the nest beach and a definite home feeding ground.

Table 1 shows what appears to be a disproportionate increase in the numbers of recent long-distance recoveries. One of the most recent of these, for example, was by far the most important to date. The turtle involved was retaken near Isla de Coche off the coast of Venezuela, far over into the eastern Caribbean. The interval between tagging and recapture, however, was only fourteen months, so the occurrence of the recapture late in the period has no bearing on the question of wandering. It is the same with the other recent long-range recoveries. If significant, the recent rise in the rate of long-distance recaptures may mean that protection of the Tortuguero rookery is increasing population pressure on distant feeding grounds and stimulating colonies there to spread into new feeding areas. Unfortunately, nothing at all is known about the factors that produce colony proliferation in *Chelonia*. Our ignorance here combines with the hidden routes of migratory travel and the disappearance of the first-year young to aggravate the difficulty of studying navigation mechanisms. It also emphasizes the need for accurate tracking.

The Problem of Open-Sea Migration

There is a worldwide tendency among green turtle populations to go to small, remote islands for their aggregated nesting. They share this peculiar ecologic tendency with various other colonial animals, most intimately with the sooty tern. The original adaptive utility involved would appear to be the relative freedom from terrestrial predation offered by islands, which, since they get their faunas as flotsam and jetsam, lack many of the predators that raid sea turtle colonies on mainland beaches. Thus, the seemingly bizarre habit of crossing open ocean to nest on an island would appear to be instigated by the same factor responsible for the generally depauperate biota of oceanic islands.

The most clearly documented island-finding feat of *Chelonia* is the travel between Brazil and Ascension Island in the South Atlantic. The high-seas distance is at least a thousand miles; the target for the outbound journey is only five miles across. The island lies in the westward flow of the Equatorial Current, directly upstream from the Bulge of Brazil. Before this current strikes the mainland, it splits—part moves up to the West Indies and Caribbean and becomes the Gulf Stream, part turns southward along the coast as the Brazil Current. Results of our tagging program on Ascension (Figure 3) indicate that the island nesting colony is derived from both north and south of the point on the Bulge opposite which the current splits.

If instead of searching for a general theory of island finding, one examines each case for special factors that appear to ease orientation and travel problems, two such advantages are at once apparent in the Brazil-Ascension migration. One is the current that comes directly from the island toward the nesting grounds. The other is the position of Ascension on the same parallel of latitude as the nearest point on the mainland. While these special features may have favored development of the Ascension-seeking pattern, in a way they increase the difficulty of reasoning out the mechanics of the guidance process. This is because they seem to favor no one navigation process over another. Celestial, inertial, magnetic-field, and Coriolis Force guidance would all to some extent be simplified by the geography of the situation. In addition, the oddly propitious relationship between the current direction

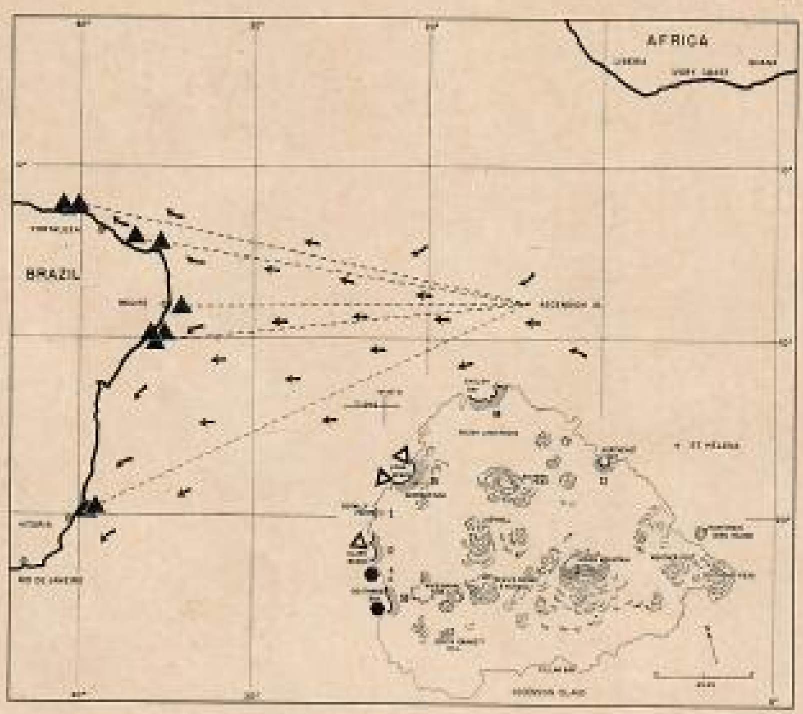

FIGURE 3. History of a tagging project at Ascension Island. The figure next to each nesting beach is the number of turtles tagged there. Solid triangles indicate locations on mainland where turtles were recovered. Hollow triangles indicate points to which turtles returned to nest after a three-year interval. Solid hexagons represent areas to which turtles returned after four years, presumably for a second time, after two round trips to Brazil. All but one of the turtles recovered on Ascension had gone back to the original tagging site. The one that failed to home precisely came out on a closely adjacent beach formed by recent wave action. Arrows represent trends of ocean currents.

and that of the nearest course between the island and mainland makes it impossible to rule out a fifth possibility: landmark piloting by an olfactory emanation from the island, possibly detectable from far out at sea. Physiologists are not willing to admit that a smell gradient can be followed in its direction of increasing strength, but a zigzag, upstream course along the shear line at the edge of the triangle made by dissolved substances on the ocean surface might possibly accomplish the same purpose.

Ten years ago it seemed quixotic to consider any theory of long-range navigation other than a celestial one. Now, interest in the older theories appears to be reawakening. Yeagley (1947-1951) put magnets on pigeons, found them able to come home unhindered, and concluded that the earth's magnetic field is not used by pigeons for guidance. In 1964, however, Talkington, at the Montreal meeting of AAAB, read a paper proposing rehabilitation of the magnetic guidance theory. In 1965 Markel and Wiltschko reported finding that robins placed in a steel-walled room assumed appropriate (SW or NE) migratory directions with no celestial bodies in view, and that these preferred directions were significantly influenced by subjecting the robins to a magnetic field generated by two Helmholtz coils. In 1964, Barlow published a long article exhaustively exploring the possibility that an inertial recording system may be used in animal navigation. In 1965, Groot found salmon smolts able to assume constant preferred directions that corresponded to courses that would have taken them across their natal lakes to the outlet stream on the far shore. They were able to do this in the laboratory, both with the sun in view and with the experimental tank covered. Groot's conclusion was that the smolts were probably capable of both celestial and inertial orientation.

And so it goes. As progress in research in celestial navigation slows down, the other theories, once considered practically obsolete, get increasing attention.

The guidance system of the Ascension green turtle migrants is still wholly unknown. It will surely remain unknown until long-range tracking techniques are available. Since radio tracking first loomed as a possible means of maintaining contact with migrating animals, a great deal of time has been spent in fruitless attempts to apply it in turtle research.

The system used was tested with transmitters elevated to 50 feet by balloons and with receiving antennas located at various elevations on shore and on the cabin roof of a 35-foot launch. In repeated trials, the maximum range proved to be nine miles, and the sensitivity of the directional antenna was about five degrees. The final conclusion was that at the frequency of the original equipment, there is no advantage in radio tracking of an animal swimming at the surface of the sea, as compared with visual techniques.

Meanwhile, a series of optical tracking experiments was begun and will be continued. Figure 4 shows results of two tracking tests made with mature female green turtles at Tortuguero, Costa Rica. At the Tortuguero nesting ground, a lone mass of volcanic rock rises to an elevation of 500 feet on the shore just behind the research station. A tracking position on the summit of this mass commands a view

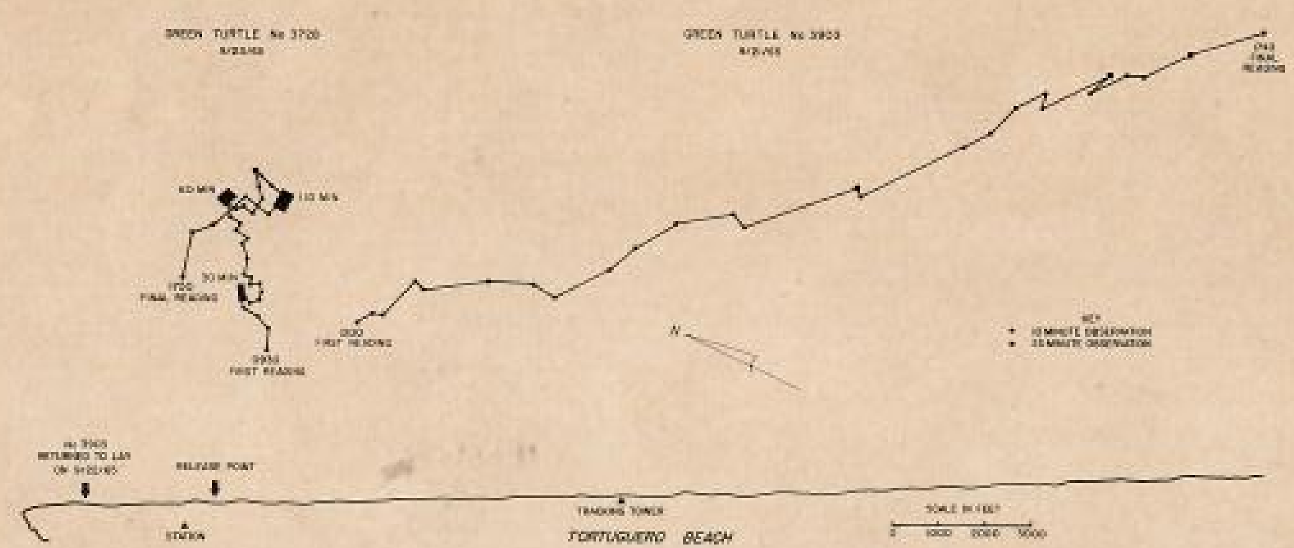

FIGURE 4. Movements of two mature female green turtles tracked by alidades off the nesting beach at Tortuguero, Costa Rica. Azimuths were recorded from the station and from the tracking tower, the positions of which are shown. Each turtle towed a float from which a helium balloon rose on a 40-foot line. Turtle No. 3728 had laid her eggs; No. 3903 was released without being allowed to nest. That No. 3728 loafed offshore for eight hours, while No. 3903 struck out, seemingly, for Colombia, violates expectations and illustrates the need for much more short-range tracking of this kind.

far out to sea and along the coast in both directions. A 35-foot tracking tower was built on the beach in front of the tagging camp, 3½ miles south of the mountain station. A turtle that is towing a float from which a balloon rises on a 50-foot line can usually be followed for a distance of about 10 miles by use of these two sighting stations. Precise plots of the travel can be made by triangulation. With this system, information on inshore movements and clues to possible landmark reference in site selection may be gained. When suitable radio-tracking equipment has been devised, it will be put into operation at Tortuguero, using the facilities already developed for visual tracking.

The ideal for long-range studies is to be able to follow the entire course of a navigating animal in the open sea. If the proper equipment becomes available, it is hoped that another tracking station can be installed on Green Mountain on Ascension Island. With this single point of contact, however, it will not be possible to get precise long-range plots. These may have to await the facilities of an orbiting satellite, and we have applied to NASA for such assistance.

Meanwhile, accurate plots of shorter sections of the courses of orienting turtles are being made, with the following aims: (1) To study ability to hold a constant heading in the absence of fixed landmarks; (2) to reveal any statistically significant tendency to head in a particular direction; (3) to reveal any statistically significant tendency for the preferred heading to correspond with a "goal" assumed by the observer; (4) to test the frequence and appropriateness of initial headings of turtles departing for the year-around feeding ground at the end of the nesting season; and (5) to learn more of the movements and behavior of turtles along the nesting shore, during the twelve-day interval between the nesting emergences.

Besides these short-range tracking tests, a series of homing experiments that may ameliorate the lack of long-distance tracking data are planned. In these, systematically displaced females, taken just before they have nested and thus presumably motivated to go to the nesting beach, will be tagged and released. The sites of release will be arranged so as to show the relation of homing success to identifiable geographic or hydrographic landmarks, if any. The time that elapses before the return to the nesting beach will in some cases represent true travel time. From such cases, courses and schedules can be roughly plotted. The aim of these experiments is to get evidence that can be brought to bear on the problem of distinguishing landmark guidance from other more complex forms of travel orientation.

Studies of the Sea-Finding Sense

A part of the research effort at the Tortuguero camp has been to investigate the character of the light cues involved in the seaward orientation of newly emerged hatchlings and of the female after nesting, when the water is not in view. Two separate but related attempts to identify the signals were begun during the summer of 1965, one by Dr. David Ehrenfeld of the University of Florida, the other by Dr. Nicholas Mrosovsky of the University of London.

Although the relation of the sea-finding senses to those by which the same animals later navigate is not known, the two phenomena clearly overlap in various ways. Both probably depend upon visual cues, for example, and phototaxis is evidently involved in each. Both are nevertheless composite processes in which various subsidiary environmental cues probably supplement the information furnished by illumination. Finally, both hatchling and mature green turtles evidently share both the sea-finding sense and a light-compass sense, and the adult almost certainly uses in addition some more sophisticated form of navigation. Whether the hatchling is capable of the latter is not known. Because of the obvious duplication and interdigitation of the sea-finding and island-finding capacities, it has seemed logical to undertake investigations of both, attacking aspects of the problems that may seem most feasible at any given time, with the expectation that any information gained will bear upon the central phenomenon of island-finding in the open sea.

In the summer and fall of 1965, Dr. David Ehrenfeld began an experimental investigation of the visual cues used in sea-finding orientation. In his first tests, 143 mature females were used. Adjustable spectacles that did not hamper the movements of the turtles and seemed well tolerated were used for the systematic elimination of components of the total visual input, while the sea-finding performance was monitored. In this way the effects of colored, neutral-density, depolarizing, and diffusing filters upon green turtle orientation under controlled conditions could be quantitatively compared.

In another series of experiments, a total of 525 hatchling turtles were placed in a circular arena at various times of the day and night. The horizon was blocked in some tests and unblocked in others. Seaward orientation success was recorded in a way that lent itself to quantitative analysis. At the same time, the relative intensities of polarized and nonpolarized incident light and of selected wavelengths from a number of directions were measured with a portable photometer.

The experiments begun by Dr. Nicholas Mrosovsky were designed to determine color or brightness preferences of hatchling green turtles. In one group of tests, a circular arena was used to determine the distracting effect of light of different wavelengths on hatchlings heading seaward. In another group of trials, the turtles were allowed to choose between paths leading to panels reflecting light of different wavelengths. In all cases, both wavelength and intensity of the light were carefully controlled.

These experiments represent a successful attempt to use rigorous laboratory techniques in the field, where sea-turtle orientation may be studied to best advantage (Ehrenfeld and Carr, 1967; Ehrenfeld and Koch, 1967; Mrosovsky and Carr, 1967).

The Evolution of Island-Finding

It is as hard to account for the evolution of the Ascension migration as it is to explain the navigation mechanisms involved. It seems to be asking too much of either selection or preadaptive imprint-behavior to suggest that the pattern could have originated under present geographic conditions. The same is true of migratory patterns of *Chelonia* in some other parts of the world.

It seems probable that the Ascension migration is partly a vestigial behavior pattern, a trait that once imparted strong survival value which now is waning. What may serve as reinforcement for this idea is the situation at Aves Island, in the eastern Caribbean southwest of Guadalupe. This tiny bit of exposed sand is the site of the only mass nesting by green turtles in the eastern half of the Caribbean. Nesting is injuriously heavy there, and the cause of the crowding seems to be an apparently extraordinarily rapid rate of subsidence of the bank on which Aves is the highest point. In August the Aves green turtles actually dig up each other's eggs. The problem at Aves Island is not just to explain the scheduled seasonal arrival of turtles at such a tiny speck of land, but also to explain the fact that they arrive there in such disadvantageous numbers. The shrinking of the island would furnish an explanation, and in this case the evidence seems to be available. Successive visitors to Aves have reported progressive decrease in the size of the island during the past two centuries (Zuloaga, 1955). While the time scales involved are, of course, vastly different, the Aves and Ascension migrations both make sense only if subsidence or some other drastic physiographic change can be assumed.

It is not known where the Aves nesting colony is recruited. Certainly it is not wholly derived from the nearby islands—Monserrat, Martinique, Guadalupe, and Dominica. The turtles probably converge on Aves from all along the Leeward and Windward archipelagos. Like most green turtles, they appear to go far beyond practical necessity in their reproductive travel, making breeding journeys that take them past great expanses of beach which to a human judge meet all of the requirements of nesting grounds. While admittedly a green turtle is a more astute judge of nesting beaches than a man, it nevertheless seems evident that some of the present-day migratory habits of *Chelonia* are to a degree vestigial behavior, once of prime survival value but now operative simply because adverse selection has not had time to delete them.

In explaining any migratory pattern, one is tempted to say that a species travels to get to a more favorable environment. A safer pronouncement, however, would be that it travels because it inherits the tendency and capacity to do so. The tendency and capacity may not have been built into the strain in the immediate past, but at some much earlier date. In many cases, as in the Ascension and Aves green turtle migrations, it seems evident that the physical setting at the time of origin of the trait, or through the time of its maximum utility, must have been different from that of today.

The original instigation of a migratory habit in ancestors of the herbivorous green turtle was no doubt the separation of habitat that the grazing habit imposed. Good grazing grounds occur in shallow, protected places, and these usually are located far away from the high surf-built beaches that *Chelonia* requires for nesting.

With this background, the evolution of an island-seeking nesting habit might be reconstructed as follows: In the beginning, say, a population of turtles begins moving a short distance from its pasture on a mainland shore to a nearby island to nest. The tendency to do this favors the survival of strains so included, because the island has better beaches where predation is less or where the incubation medium is for some reason more suitable than on the mainland. Each generation, mainland nests are flooded or the eggs and young are extensively dug out and eaten. Any female with the urge and capacity to go out to the island will contribute more genes to reinforce the island-breeding pattern in the race. Each generation, more turtles go out to the island simply because their genotype was made more prevalent by the island-seeking tendency of the preceding generation. The island-seeking migration is thus a successful evolutionary venture, and it becomes the established regimen for the population.

But sea turtles are much older than present configurations of lands and seas. At some time in the history of some of them, the nesting islands have slowly sunk or have grown or have otherwise changed in size. When that happened, there were two disadvantages to be weighed against the original advantages of going out to the island. It got harder to find, and this killed off growing numbers of mature migrants; and the increasing distance lengthened the journey the hatchlings had to make back to the residence ground. Even though this trip was probably, as now, made downstream in a major current, the young would be subjected to longer exposure to the hazards of the open sea. This might have been no disadvantage; perhaps the open sea is where all hatchlings are when we are unable to find them. But in any case, as the island got smaller and more distant, the ratio of advantage to disadvantage—the net survival value—in going to it would have grown less. Eventually the pattern, though still for a while adhered to, would be actually disadvantageous. This is the only way I can explain the existence of the Aves turtle colony; and I suggest that it may in some way explain the nesting of the Brazilian population of *Chelonia* on Ascension Island.

That idea evokes the objection that there is no evidence that any diminution of land area occurred in the Ascension region of the Mid-Atlantic during the Tertiary, through either subsidence or eustatic change in sea level. With shrinking of the island ruled out, one looks for other paleogeographic changes that might have allowed the slow evolutionary refinement of the Ascension-finding system under conditions combining gradually diminishing advantage and gradual selective improvement of the necessary navigation capacity.

One conceivably relevant event is the growth of the Atlantic Ocean through continental drift. If it is postulated that green turtles once migrated a short distance from South America to a nearby African beach to nest, and that later on the way grew longer because the continents moved apart, the problem of accounting for the development of the navigational equipment needed to find a point on the Atlantic Ridge between the two seems a little less overpowering.

A few years ago this would have been a completely outrageous proposal because, for one thing, continental drift was in virtual eclipse as a theory. Today, however, among geologists and geophysicists at least, the drift theory is by no means dead. There now seems no real basis for doubt that the Atlantic is a relatively new ocean.

A possible relation between drift and some of the more elaborate routes of bird migration was suggested by Wolfson (1948). His theory was overridden by the instability of the drift theory itself and by the seeming anachronism in relating the evolution of modern birds to the fragmentation of Gondwanaland.

The new evidence for drift, brought together in Runcorn (1962) and in papers in *A Symposium on Continental Drift* (1965) comes mainly from paleomagnetic studies of rocks. These show that the ancient positions of land masses were different from their present positions. If it is assumed that the earth's magnetic field has remained an axial dipole, when it is found that the directions of magnetization of rocks of the same age on different land masses do not agree, it must be concluded that the continents have moved, relative to each other. Unfortunately, such measurements give only latitude and orientation—not longitude—for the continents on which they are found. They nevertheless have brought a marked reawakening of confidence in the theory of continental drift. The cause of drift is now thought most probably to be not just a floating apart of land masses, but a complex convectional movement in the whole material of the mantle.

If the new views on continental drift are accepted, there remains the question whether the increase in distances brought about by the drift occurred too long ago to have influenced the evolution of the migration patterns of modern animals. In the case of the Ascension green turtles, a reasonable background for evolution would have been provided equally well by the moving apart of Africa and Brazil or by a growing separation of Brazil and Ascension Island. That the latter has not happened seems indicated by current opinion that the Atlantic Ridge, of which Ascension is a high point, was formed by uprise caused by (and thus concurrent with) the same convectional movements of the mantle that created the Atlantic Ocean. The island itself is a volcanic structure on the ridge. Its emergence, therefore, must have been later than the growth of the ocean that separated the continents.

The only other possibly relevant paleogeographic change that geologists will admit is the moving apart of the continents themselves. If this has occurred during a time when the genus *Chelonia*, or an ancestor, was evolving patterns that were to last into present time, then it seems logical to suppose that the original commuting was done between Brazil and Africa, and that the slow growth of the distance allowed a slow selection of the navigatory capacities required to hold an accurate east-west course along the tenth parallel of latitude. The Ascension rendezvous could in that case have been an old way-stop, with the island later and by slow degrees becoming the main target of the eastward migration.

The trouble with this idea is that the spread of the Atlantic Ocean is supposed to have been virtually completed before the beginning of the Tertiary. Modernization of the sea turtles began in the Cretaceous, but *Chelonia* is known to paleontology from no earlier than the Miocene. This gap makes it necessary to assume either that *Chelonia* has simply been missed as a fossil in earlier rocks or that the Ascension-finding trait comes down from an ancestor older than the genus. Both are troublesome thoughts, but either seems more acceptable than to assume that Brazilian green turtles got their Ascension-finding urge and ability under geographic conditions like those of today.

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DISCUSSION

QUESTION: Would you care to comment on the probable abundance of turtles 200 to 400 years ago, before the time or about the time of the European discovery of the American continent?

DR. CARR: They were extremely abundant. It is not known how many nesting colonies in the western Caribbean there were at that time, but certainly there were many and certainly the green turtle did constitute an important source of food for both the aboriginal inhabitants of the place and latecomers from Europe. The British Navy, as you probably have heard, used to have scheduled stops to take on turtles, to prolong its stays in the colonies, and the buccaneers and pirates did the same thing. Sea turtles were far more abundant then, and now they are all threatened. I regard them all as endangered species, not because they are just on the verge of disappearing tomorrow, but because of the terrible trend of loss of seashore areas to human development. Land is areal in extent but coast is linear, and because of this the encroachments of people mount up much faster. The loggerhead is really beginning to have a very narrow foothold on the North American continent. The Germans have created a large demand for turtle soup, utilizing any kind of sea turtle, including the ridley. They offer fantastic prices to the Mexicans for the dried-up lower shell of these turtles. Once they get to the point of knowing how to exploit them, they can kill the ridley out in two or three years. They can kill it out in the span of its sexual cycle; they cannot kill any turtle out in one year. If they make the clean sweep that they could make on the Mexican beach there, this year, next year, and the year after, there would be no ridleys left except the backlog of maturing ones.

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QUESTION: You mentioned interest in guidance by magnetism and inertial guidance as being on the up-swing now. Could you briefly review some of the new evidence of this?

DR. CARR: I can tell you what I know, which is almost nothing. I know that Yeagley put magnets on pigeons and that they successfully homed and this suggested to him that there was nothing to the theory of travel along magnetic lines of force. Then along comes Talkington, who read a paper referring to magnetic organs that I had never heard of, and giving an interesting account of aberrances in pigeon-homing flights corresponding to places where iron deposits produce aberrances in the earth's field.

Most recently, a paper by Merkel and Wiltschko reported putting robins in a steel chamber. They found that the robins were able to assume a southwest-northeast preferred azimuth both when the sky was visible and when the sky was not visible. They then occluded the sky and put Helmholz coils around the cage, and they were able to influence, in predictable ways, the orientation of this formerly southwest-northwest azimuth heading.

Until you get more people working in celestial navigation research with the sort of enthusiasm and excitement that there was ten years ago, you are bound to have people coming in with theories which I had thought had died down. Actually I am against eliminating any theory, because I could not agree more thoroughly with what the two speakers said this morning: namely, that an animal faced with the terrific demands of long-range travel is just bound to have evolved the tendency to take advantage of every scrap of environmental information he can possibly sense and use. I would not be at all surprised if we eventually find that there is a composite use of a lot of these different things. It is just that scientifically this is not a good way to investigate; it confuses experimentation. If you say that they are doing all of these things at once, how in the world do you ever test?

Groot, as Ferguson pointed out, worked with salmon smolts. He found that if you took them out of Babine Lake and put them in the laboratory in tanks where they could see only the sky, they assumed directions appropriate to take them from the shore on which they hatched, across the lake to the exit stream. Now, this was a circular lake. He then proceeded, unless I misinterpret him, to take smolts from a crooked lake where three changes in course were required. When they were placed in laboratory tanks, he found that for the first four days they assumed the northeast direction appropriate for the first leg of travel; for the second two days they changed to a different course appropriate for the second period of travel; and finally made a third proper choice of direction. If I did not think that Groot was an extremely reliable man, I just could not follow this. To make matters worse, when he covered up the smolts they still did the same thing. He not only found these amazingly sophisticated innate patterns bred into these salmon, but they apparently could follow them with either celestial information or with inertial means.

QUESTION: If it turned out that the turtles were feeding on pelagic animals, would this affect some of these migration patterns?

DR. CARR: I think it would. Young turtles cannot feed on the bottom; they can feed only four feet deep. They are not found in the Caribbean. The fishermen there use nets of all mesh. So once the turtles get away from the nesting ground, they would be caught by fishermen throughout the Gulf and the Caribbean, but they never are. On the other hand, they cannot feed at sea because they are unable to get to the bottom where they have to find the kinds of little invertebrates they use for food. So the only thing left is sargassy or something floating at the surface where they can get at it—where they can incorporate themselves into something and feed and get shelter.

If you mean the grown turtles, they have a home range, and I believe they are territorial creatures. They have a special sleeping rock; they live in groups on a grass flat; they live in areas of very dense spermatophyte pastures where they do not have to do anything but move out from the sleeping place each morning and slowly graze around on the bottom and then come back and sleep at night. For most of their lives, they lead a very sedentary life in water no more than 18 fathoms deep.

QUESTION: Have you happened to make any stomach-content analyses of these animals when they have been on the beach and have not been feeding over the last week or so? Just after their migration.

DR. CARR: They come in empty. One of the things we tried to get at with short-range tracking was to understand where they go during the twelve-and-a-half day interval between their nesting emergences. They nest three to five times, and some of them have come 800 miles or more to nest. They obviously do not go back where they came from. There is almost no food in the Costa Rican area for them, so that to know where the female green turtle goes during the twelve-and-a-half-day interval between her successive nesting emergences is an important thing for us to find out. We do not know, but we do know that when the villagers kill the turtles to eat once in a while, they have nothing, or just junk, in their stomachs, indicating that they pick up what they see. But there is actually nothing much to pick up.

QUESTION: (Student from Colombia, S. A.) Do you know of regulations as far as fishing for turtles is concerned and whether the Scientific Committee of the American States is protecting the turtles?

DR. CARR: Your own country is quite interested in the whole problem. They are doing mainly investigatory work, but they are also making recommendations in Bogota for regulations concerning turtles. The Caribbean country that has done the most so far is Costa Rica, because that is where the green turtles nest and that is when they are most vulnerable. A lot of our tags come back from Colombia, indicating that Costa Rican turtles go there to feed, and there are active turtle fisheries in Riohacha and in Cartagena. I think they are doing a fairly good job compared to some countries. As far as your question about the interest of world-wide bodies, the Survival Service Commission has taken sea turtles under its wing. They have written letters to all of the countries in which the nesting colonies are now located to urge some sort of patrolling of the beaches during the nesting season. This is extremely difficult to do. The Mexicans cannot really adequately patrol the 90 miles of beach on which tremendous emergences of ridleys occur; so anyone could go there and wipe them out quickly. It is an extremely difficult problem; poaching of sea turtles is very easy to do and very tough to regulate. There are many countries with laws regulating seasons at which they can be hunted on the pasture ground, and Colombia is one of them.