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The Ecology and Migrations of Sea Turtles, 6 The Hawksbill Turtle in the Caribbean Sea

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Although the sea-turtle research being carried out at Tortuguero, Costa Rica, has been concerned mainly with the green turtle, *Chelonia mydas,* information on other marine turtles has accumulated. A recent change in the survival outlook for the hawksbill, *Eretmochelys imbricata,* has suggested the desirability of bringing together data bearing on the natural history of that neglected species. During the years from 1956 through 1964, 70 hawksbills have been tagged at Tortuguero, mostly during the period from July 7 to September 15. Twenty-five others, including eight mature males, were examined after having been harpooned by turtle fishermen offshore. Although the information from this limited contact with the Caribbean population is meager, it nevertheless furnishes the first insight into several aspects of the life history of *Eretmochelys.*

The chief physical and biological features of Tortuguero Beach, a 22-mile section of the Caribbean coast of Costa Rica, have been described by Carr and Ogren (1960) and by Hirth (1963). Tortuguero is the only remaining site of mass nesting by the green turtle in the western Carib-

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bean, and from all parts of this region periodic migration to Costa Rica occurs. Besides the green-turtle colony, the beach is annually visited by a few nesting leatherbacks (*Dermochelys;* see Carr and Ogren, 1959), which come mainly in March, April, and May; and by a somewhat greater number of hawksbills. We have two records of the emergence of the loggerhead (*Caretta caretta*) during the nine seasons that we have patrolled the beach there. The ridley (*Lepidochelys kempi*) has never been seen at Tortuguero, nor has it been recorded anywhere else in the Caribbean.

NESTING RANGE AND SEASON

The nesting of *Eretmochelys* is less concentrated, geographically as well as seasonally, than that of *Chelonia.* A great many records and word-of-mouth reports of individually emerging hawksbills have accumulated, and it seems clear that nesting takes place periodically or sporadically on all undisturbed Caribbean shores, both insular and mainland, wherever there is suitable sand beach. The nesting range thus includes, or once included, the tropical Gulf coast of Mexico and its islands, and the whole of the West Indies to the northern coast of Cuba and throughout the Bahamas. The northernmost limits of nesting are southern Florida and Bermuda, and along the Atlantic coast of South America nesting occurs in Venezuela and the Guianas and into southern Brazil.

Word-of-mouth records of hawksbills nesting in Florida have circulated for decades. These have become rare in recent years, and only one has ever been substantiated, that of Mr. Julian Ryder of West Palm Beach, who found a hawksbill nesting near Juno, Florida, in August, 1959. Thinking that it was a green turtle, he called the nest to the attention of Conservation Officer Roland Bird, who took the 172 eggs to the House of Refuge Museum at Stuart, Florida, for incubation in an artificial nest. Fifty of the eggs hatched. The young were seen and identified as hawksbills by Mr. Ross Witham of the Florida Board of Conservation. This is the only nesting record for the hawksbill in the continental United States.

From what now is known of the five genera of sea turtles, there appear to be three general patterns of ecological geography. One is the markedly aberrant one of the Atlantic ridley, which for some unknown reason forms reproductive aggregations so huge that virtually the whole generative function of the species may be carried out at one place and time (Hildebrand, 1963; Carr, 1963). Another is the green-turtle pattern, in which the herbivorous habit of the animal concentrates populations in particularly rich pasturage of marine plants. These feeding grounds may

or may not lie near suitable nesting shore. Accordingly, some of the larger feeding colonies make mass reproductive migrations, while turtles inhabiting less extensive or less densely grazed pasturage go ashore wherever there is a stretch of suitable beach. A less-specialized pattern is that of *Dermochelys, Caretta,* and, apparently, the Pacific ridley, *L. olivacea.* All these are omnivorous but heavily dependent on animal food, so tend either to establish individual feeding territories or to wander in foraging.

Although most hawksbill nesting beaches were depleted by *careyeros* (tortoiseshell hunters) early in the history of Caribbean colonization, some are still visited by nesting hawksbills in numbers that appear to be disproportionately greater than those of resident populations in adjacent waters. The same can be said of the loggerhead and the leatherback. This fact suggests that some migratory convergence takes place. The salient aspect of the nesting range of all three of these is, however, that it tends to be diffuse rather than nodal. Nearly any undisturbed reef or rock bank in the tropics has a few hawksbills, and in the nesting season nearly every deep-sand beach free of human activity may be visited by nesting females, either alone or in small bands.

At Tortuguero the nesting season of the hawksbill is essentially the months from May through November. Because we have kept systematic records there only during the green-turtle season (July to October), we have had to rely on observations made during irregular off-season visits and on reports of residents of the beach for information on conditions during other parts of the year. All observations seem to indicate that at Tortuguero and elsewhere in the Caribbean May and June are the principal nesting months. Whether by chance or by adaptive evolution this schedule gives the hawksbills access to nesting beaches at a time when green turtles are not there. A similar situation appears to prevail in the Seychelles Islands, where, according to Hornell (1927), *Eretmochelys* nests from September through November, whereas the season of the green turtle is February through June. On much of the tropical seashore of the world *Chelonia* and *Eretmochelys* emerge to nest in the same places. One evident advantage in the hawksbill's spreading its nesting season would thus be the avoiding of the traffic wherever its breeding range overlaps the sites of more heavily aggregated breeding of the green turtle.

Although the May emergences of *Eretmochelys* come prior to the big immigrations of green turtles (which in time of primitive abundance were, and in a very few places still are, so heavy that nesting turtles dig up one another's eggs), they place the hawksbill in the company of the nesting leatherback, crocodile, and iguana, all of which at one place or another choose the same beaches. All these, however, are solitary nesters. Carr

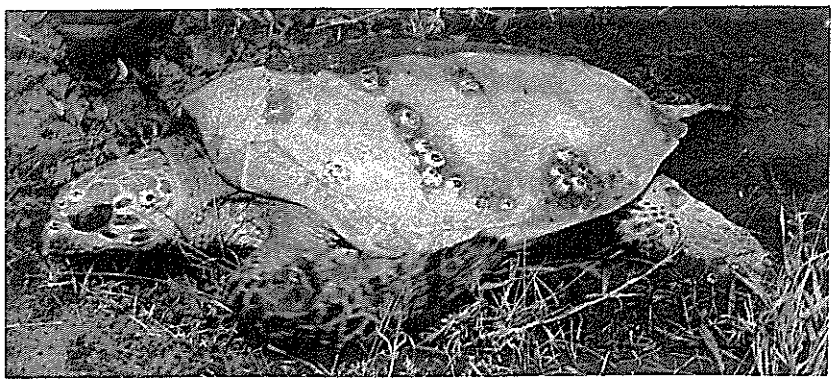

FIG. 1. Mature female hawksbill; Tortuguero, Costa Rica. The numerous big barnacles on the carapace are typical of Tortuguero hawksbills, but not of *Chelonia.*

(1956) found the nest of an iguana built directly above that of a hawksbill, but the frequency of such interspecific crowding is evidently low.

SIZE AND MEASUREMENTS

Because of the incomplete knowledge of the life cycle of the hawksbill,

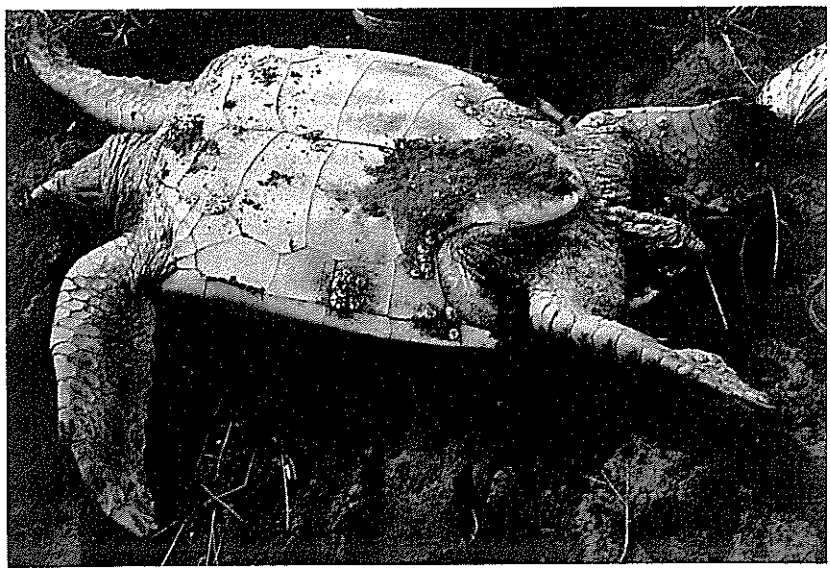

FIG. 2. Ventral view of the turtle shown in figure 1, showing barnacles on the plastron.

TABLE 1

MEASUREMENTS (IN INCHES) OF HAWKSBILL TURTLES AT TORTUGUERO BEACH, COSTA RICA

	Length of Carapace	Width of Carapace	Length of Plastron	Width of Head
Mature females				
Range	29.50–36.00	19.00–31.00	22.00–29.00	3.50–5.75
Mean	32.72	23.44	24.30	4.46
Number	62	62	62	61
Newly emerged young				
Range	1.54–1.81	1.06–1.38	1.22–1.46	0.57–0.59
Mean	1.67	1.23	1.34	0.57
Number	41	41	41	41
Mature males				
Range	31.25–32.00	22.25–22.75	22.75–25.00	4.00–4.50
Mean	31.56	22.75	23.75	4.25
Number	3	3	3	3

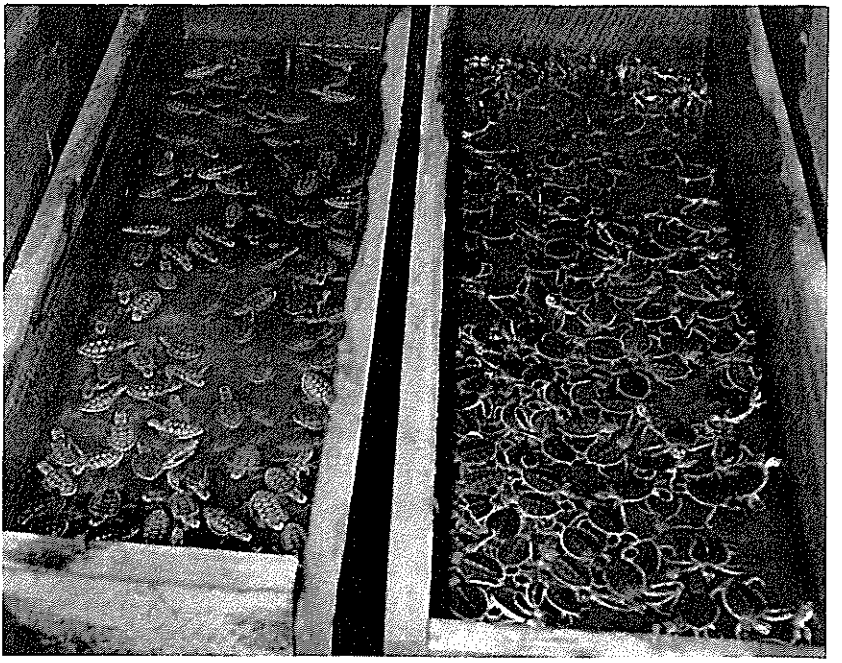

FIG. 3. Newly hatched hawksbills (left) and green turtles (right) in tank shed of the Caribbean Conservation Corporation, awaiting distribution in a restoration project.

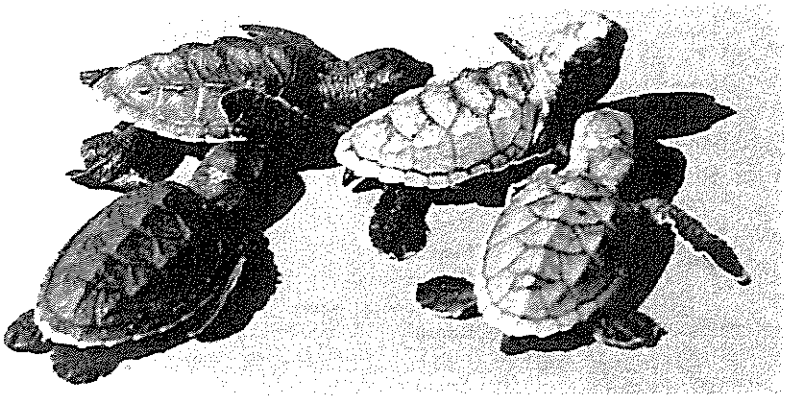

FIG. 4. Hatchling Tortuguero hawksbills, showing the extremes of color variation that occur in the Caribbean form.

published data have not correctly indicated the size of the adult animal. Figures 1 and 2 show a mature Tortuguero female of average size, and table 1 gives measurements of 62 mature female hawksbills at the Tortuguero nesting ground and of four adult males harpooned on Tortuguero Bank. These figures show the hawksbill to be not the smallest of the sea turtles, as was once thought, but considerably larger than *Lepidochelys,* neither sex of which reaches lengths much greater than 28 inches. It is thus necessary to revise the estimate cited by Carr (1952) that the hawksbill may reach sexual maturity at weights as low as 30 pounds. Al-

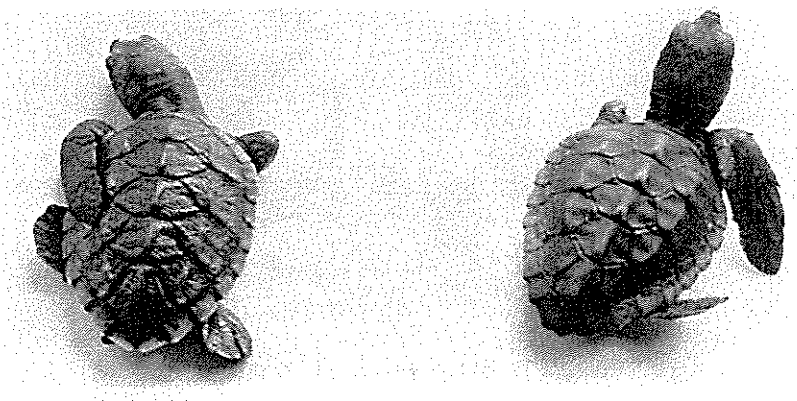

FIG. 5. Hatchling hawksbill (left) compared with an Atlantic loggerhead of about the same age.

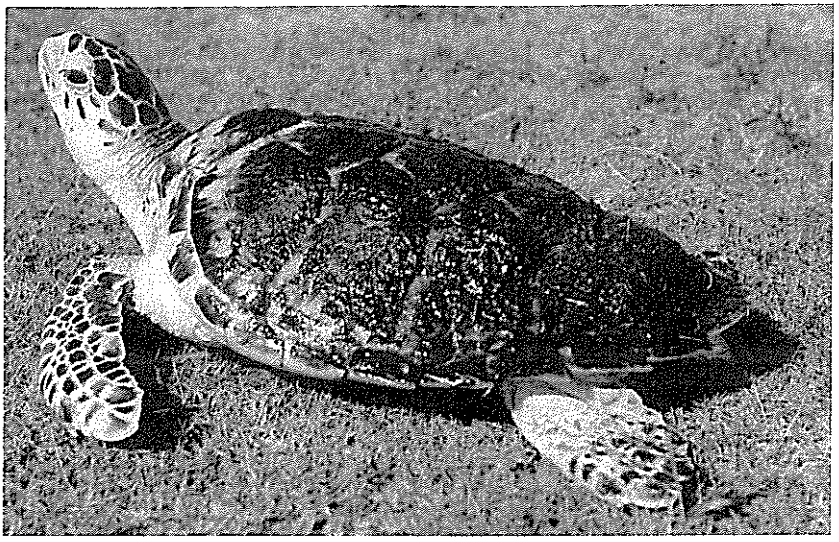

FIG. 6. Year-old hawksbill, hatched at Tortuguero, Costa Rica, and reared in a tank at the Lerner Marine Laboratory, Bimini, Bahamas.

though no weights of hawksbills of known length are available, it seems clear that they mature at weights of not less than 80 pounds. Table 1 also gives measurements of a sample of Tortuguero hatchlings (see also figs. 3, 4, 5, and 8). Figure 6 shows a hand-reared Tortuguero yearling.

THE REPRODUCTIVE CYCLE

The literature contains no information on the major reproductive cycle of *Eretmochelys*. It is not known whether nesting occurs each year, or, as in *Chelonia,* at intervals of more than a year. Our small tagged sample provides some evidence but not grounds for any definite conclusions. Of the 70 hawksbills tagged, none has come back to Tortuguero beach to nest after an absence of one year, and none has ever been found nesting on any other beach. The only two long-term nesting returns to Tortuguero (see table 2 and fig. 7) occurred, respectively, three years and six years after the turtles were tagged. With the lack of other data, these cases should be considered in the light of what is known about the green turtle. In the Atlantic and Caribbean *Chelonia* nests each three or, less frequently, each two years. Among the more than 3000 green turtles tagged, there is no record of a one-year return, and no tagged green turtle has ever returned to nest on any beach other than that on which she was tagged.

The return of a hawksbill after a three-year absence (shown in table 2)

TABLE 2
DETAILS OF TWO LONG-TERM NESTING RETURNS OF HAWKSBILL TURTLES TO TORTUGUERO BEACH

Tag No.	Date Tagged	Place Tagged	Place Retaken	Date Retaken
306	August 15, 1956	Mile ⅝	Mile ½	June 18, 1959
783	August 25, 1958	Mile ½	Mile ½	August 6, 1964

may thus actually have been the first nesting emergence of that turtle after she was tagged; and the six-year interval could represent two cycles, with one return simply having been missed by our beach patrol. Obviously, however, both of the periods involved could be factored differently.

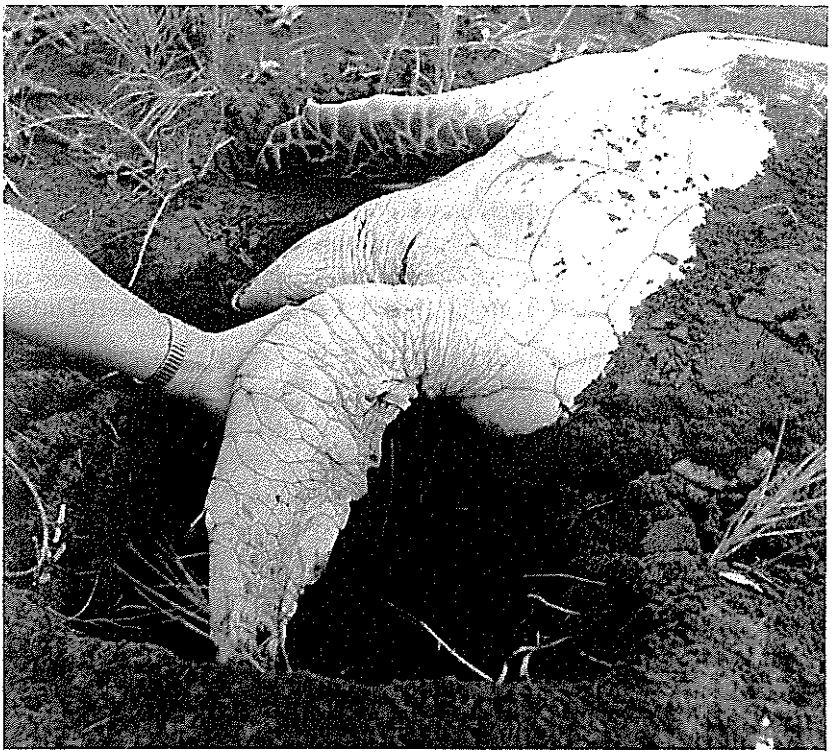

FIG. 7. Hawksbill turtle taken nesting on Tortuguero Beach six years after the date on which she had originally been tagged (see table 2). The six-year-old tag, shown in the center of the picture, was in good condition.

It seems unlikely, nevertheless, that the reproductive cycle of the hawksbill is an annual one.

RENESTING

It is generally believed by people of the Caribbean shores that the hawksbill nests more than once during its nesting season, and that renestings occur at intervals of about two weeks. It is of interest that the same curiously accurate bit of ethnozoology is widely prevalent among local folk of the Indo-Pacific. Hornell (1927) cited "various trustworthy observers" in the Seychelles as having found that females marked while nesting came back to nest again after 13 to 15 days. Our only data on renesting appear in table 3. Of the three cases of renesting, one occurred

TABLE 3
OBSERVED RENESTING RETURNS OF FEMALE HAWKSBILL TURTLES AT TORTUGUERO BEACH

Tag No.	First Observed Emergence		Return	
	Date and Time	Mile	Date and Time	Mile
348	August 20, 1956, P.M.	0	September 8, 1956, P.M.	1⅛
1167	July 1, 1960, P.M.	2¾	August 1, 1960, P.M.	¾
2149	July 17, 1962, P.M.	1½	August 4, 1962, P.M.	1

after 18 days, another after 30 days, and the other after 17 days. The 30-day period could, of course, represent a return after two previous nestings at two-week intervals, with one of these simply not having been observed. It is not possible to say whether the other two represent normal intervals or whether, as often occurs, the periods were extended a day or two because the emerging female was frightened by lights used during the tagging of green turtles. Because our observations have been restricted to the months of the green-turtle season at Tortuguero, they do not cover the full season of the hawksbill, and this fact has hindered progress in the determining of periodicities. In the future, patroling of the Tortuguero beach will be extended to include May, June, and November, in order to determine the usual and maximum number of times a turtle nests during a season, and to provide more accurate averages of the intervals in both internesting and postseason returns.

EGGS AND INCUBATION

The hawksbill lays more eggs than the green turtle. The average number of eggs in 57 nests was 161.10 (range, 53–206).

The eggs are spherical in shape, although a few in each clutch may be slightly elongate. A variable number of very small yolkless eggs may be laid. In July and August a series of eggs was measured from five different nests, 20 being taken from the top, and 20 from the bottom, of each nest. The average diameter of the 200 eggs was 38.0 mm. (range, 35.8–42.0).

The average incubation period of 13 clutches of eggs moved to artificial nests (that is, simply reburied at an appropriate depth in sand in a nearby area protected by a fence) was 58.6 days (range, 52–74 days). These nine nests represented a total of 2193 eggs, and 46.7 per cent (range in the individual nests, 12% to 80%) of these hatched. Whether such mortality is normal in nests of the hawksbill or was caused by the moving is not known.

Hawksbills dig shallower nests than green turtles (see fig. 15). In four nests the distance from the surface of the ground to the top of the egg clutch, and that to the bottom of the egg hole, were measured. The average depth to the uppermost eggs was 10.0 inches (range, 9–12 inches) and that to the bottom of the nest 17.1 inches (range 17.0–17.5 inches). The size of the egg chamber in the four nests averaged 9 inches by 11 inches, with no nest varying from this average more than 2 inches in either measurement.

HABITAT AND FOOD

All available evidence indicates that the hawksbill is characteristically an inhabitant of rocky places. On coral reefs it is the turtle most often seen, in both its adult and immature stages. As with all other sea turtles, there is a conspicuous gap in the known natural history of *Eretmochelys* during its first year of life. The few very young Caribbean hawksbills that have been found, however, have been taken mostly about coral reefs. In the Tortuguero area the only important hawksbill habitat is Tortuguero Bank, two patches of rock separated by a few hundred yards and lying about half a mile off the mouth of the Tortuguero River; and Greytown Bank, a series of 11 separate rocks some 12 miles off Greytown, Nicaragua, under water 10 to 15 fathoms deep. During good weather Tortuguero Bank may be visited by as many as a dozen boats, mostly from a seasonal camp of *careyeros* just north of the mouth of the river (see figs. 18–20), but also including boats from Tortuguero Settlement, from Barra del Colorado, 16 miles to the north, and even from Limon, 50 miles to the south. In times of good tortoiseshell prices, the Greytown banks were fished by as many as 60 boats, nearly all of them from Bluefields. When the prices declined 20 years ago, this fishery disappeared but now is building up again. These two banks appear to be the only populous feed-

ing ground of the hawksbill between Bluefields, Nicaragua, and Bocas del Toro, Panama.

Although little is known of the habits of *Eretmochelys* in its year-around habitat, the association with rocks is evidently related to both food and protection. All *careyeros* agree that the hawksbill, though omnivorous, feeds mostly on invertebrate animals. The stomach of one of two mature males taken on Tortuguero Bank during August, 1964, contained only large amounts of a sponge, said by Dr. Frank Maturo to be probably *Geodia gibberosa.* In the other stomach there were the following items (also identified by Dr. Maturo): (1) a sponge, apparently the same as the foregoing; (2) ectoprocts of the genera *Amthia* and *Steganoporella,* and an unidentified calcareous species; (3) a hydroid, like *Sertularia;* and (4) two sea-urchin spines. The most striking feature of the skull of *Eretmochelys* is the narrowness of the snout, the beaklike look responsible for the not very accurate figurative name "hawksbill." Watching a hawksbill on a reef, one gets the impression that this narrow beak is primarily an adaptation for prying and probing for food in crevices and cavities among rocks and coral.

A characteristic of the hawksbill that no doubt reflects its habits and habitat is the tendency to have large barnacles on the plastron and carapace (see figs. 1, 2, and 8). In this respect, *Eretmochelys* contrasts strongly with *Chelonia,* which usually has only small barnacles grouped on hydrodynamically uncritical regions of the shell, where they cause little disruption of the streamline. The prevalence of barnacles on the hawksbill probably attests to a relatively sedentary life. *Chelonia,* a high-speed swimmer and long-distance migrant, would be seriously impeded by such fouling. How it keeps its shell so clean is not known. It is in this way comparable to the clean-shelled *Lepidochelys,* while *Caretta* is like the hawksbill in being often encrusted with big barnacles and other invertebrates or vegetation.

NESTING BEHAVIOR

No account of the nesting habits of the Atlantic hawksbill has been published. Deraniyagala (1939) described the nesting of a female of the Pacific form on a Ceylon beach, but his account was generalized and lacked some of the detail that we have found of special value in comparing behavior of the five genera of sea turtles.

The complete nesting process of the hawksbill has been observed repeatedly by each of the writers. During the 1964 season Carr began recording the nesting behavior of sea turtles on 16-mm. moving-picture film, as a basis for an eventual detailed ethologic comparison of the five

genera. Approximately half of the nesting process of the hawksbill has to date been filmed.

In sea turtles the events leading up to and following oviposition constitute a predictable sequence of stereotyped acts of orientation, locomotion, and excavation, which are fundamentally similar in all the genera, and, in fact, surprisingly homogeneous throughout the Testudinata. Carr and Ogren (1960) subdivided the nesting process of the green turtle into 11 stages. These have proved to be characteristic of the other genera of sea

TABLE 4

BEHAVIORAL DIFFERENCES IN THE NESTING OF *Eretmochelys* AND *Chelonia*

Trait, Stage, or Feature	*Eretmochelys*	*Chelonia*
Gait	Diagonal legs move together	Paired legs move together
Oviposition	Edge of back flippers curl as eggs are extruded	Flippers remain at rest as eggs are extruded
Oviposition	Flippers spread beside nest during oviposition	Flippers spread together over nest during oviposition
Filling of nest	Sand dropped into egg cavity by separate flipperfuls	Sand scraped into nest by alternate hind flippers
"Sand smelling"	Muzzle repeatedly pressed against the sand throughout nesting emergence	Pressing of muzzle against sand mostly confined to initial stage of emergence
Visual appraisal of shore situation	More constant peering and craning of neck	More mechanical, dragging locomotion, with little peering or craning
Character of body pit	Body pit shallow, or desultory, or lacking	Body pit usually deep, often deeper than height of shell of turtle
Timing	Longer period of prospecting and filling	Longer period of digging pit and nest

turtles as well and are here used as framework for an analysis of nesting in *Eretmochelys*. The account below is a composite of observations made by the three of us during the past eight years.

LANDFALL, STRANDING, AND EMERGENCE FROM THE SURF

The responses that cause the female to come to land at a given place are, as in the case of each of the other sea turtles, wholly unknown, as is the nature of the sense by which the exact point of emergence is selected. The first contact that an observer has with an emerging turtle comes when she is stranded by the wave wash. At this point, as during the whole trip up the beach, the hawksbill is exceptionally wary. If a light is played on her, she usually turns and goes rapidly back to the sea. On

moonlight nights, or even in strong starlight, if the shell of the turtle is not heavily fouled with algae and barnacles it glints with reflections and even without artificial light sometimes attracts the attention of a watcher. If it does, one may sometimes crawl close to the emerging turtle and watch as she appraises the stranding site. The process is essentially the "sand-smelling" described by Carr and Ogren (1960) for *Chelonia.* The muzzle is pressed against the sand and held there a second or more, then the head is lifted, and the turtle peers about the foreground and back and forth into the gloom of the upper beach. This process is kept up both

FIG. 8. Female hawksbill nesting at Tortuguero, Costa Rica, July 26, 1960. The picture shows the typical position held while the eggs, which in this case numbered 130, are being laid.

while she rests in the wave wash and after her emergence onto dry beach. Whether it is actually an olfactory assessment or merely a tactile one is not known. In any case the habit is much more strongly developed in the hawksbill than in the green turtle and is usually continued all the way up to the site the turtle finally chooses for nesting. Besides this nuzzling of the sand, the turtle cranes her neck and peers about warily, presumably assessing the topography and security of the situation. At this stage, when a dog or man moves near a turtle she still is likely to return to the sea.

TRAVEL FROM SURF TO HIGH BEACH

The gait of the hawksbill involves little of the breast stroke of *Chelonia* —the labored dragging forward of the body by simultaneous movements of all the legs. *Eretmochelys* uses a more reptilian style of walking, with di-

agonal limbs working together. When the turtle is tired, a few breast strokes may be made, but the alternating style is usually quickly resumed. This marked difference in gait, combined with the active peering and neck craning and more frequent sand smelling of the hawksbill, makes her journey up the beach strikingly different from the machine-like locomotion of *Chelonia.*

The orientation processes that guide the turtle inland are not understood, nor are those by which she returns to the sea. It is clear, however, that more than sand smelling and direct topical appraisal of the landscape is involved. The orientation of the mature female in going from a nest back to the sea seems identical with that in the sea-finding feats of neonate hatchlings, and, as in them, it is probably a composite process dominated by a response to illumination and not a compass sense (Carr and Ogren, 1960). Like hatchlings, the female has no trouble turning directly toward the ocean from any nest site, even when view of the water is blocked. Whatever the nature of the process, the back-azimuth orientation that takes the turtle from the water to the upper beach must be the converse of it. Dr. David Ehrenfeld of the University of Florida has just begun an experimental study of this problem.

Selection of Nest Site

As the turtle approaches the dry, tumbled sand above the tidal zone she starts making trial sweeps with the fore fins, and lowers her snout against the ground more frequently. She may move directly inland on a more or less zigzag course, but sometimes for no evident reason will crawl long distances up or down the upper beach before finally stopping, crossing broad expanses of territory that, to the observer, appears suitable nesting ground. The prenesting prospecting of the hawksbill seems on the average to be more protracted than that of *Chelonia.* One hawksbill trail that we paced off was 450 paces long, with the nest situated about 400 paces along the trail from the point of emergence. To the observer, the process of selection of the nest site seems to be a direct visual assessment of the terrain, augmented by tactile and possibly olfactory corrections. Even on the darkest nights obstacles appear to be avoided visually. Nests are rarely made in wave-washed, hard-surfaced, or turf-grown ground. The discrimination by which these are avoided seems to involve trial scraping with the flippers, supplemented by more of the sand-smelling maneuver. When a satisfactory site is finally reached, the turtle makes a few sweeps with the fore flippers, used singly; then the back feet are brought into play and the actual digging begins.

Clearing the Site and Excavating the Body Pit

The whole site-clearing, pit-thrashing, nest-digging operation is a sequence of intergrading stereotyped movements. The hawksbill makes no such deep basin as that in which the green turtle and trunkback rest while nesting. The process of site clearing, in which sand is thrown back by first the front and then the back fins, is sometimes continued until a shallow excavation is formed, but in other cases only a few scratches that do little more than clear the vines or debris away from the site may be made. The fore fins start to work first, then hesitantly the hind feet begin, working alternately, and alternating also with front fins. During this action the body may inch forward slightly and may shift back and forth, to right or to left. After several minutes the action of the fore flippers stops, and that of the back foot changes gradually from a kick to a scraping stroke applied to the sand just beneath the tail, and then becomes the scooping action used in digging the nest.

Excavation of the Egg Cavity

Figures 9–12

The egg cavity is a flask-shaped hole. It is dug by the hind feet only, working alternately. The 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 is dropped several inches out from the rear margin of the shell. As the sand falls, the other hind foot, which until then has rested on the sand beside the beginning of the egg cavity, snaps sharply forward, throwing sand from beside the hole to the front and side. This whole operation is then repeated in reverse. The entire nest-digging process is a series of these reciprocating actions of the hind feet. As they continue, the nest grows to a depth that finally is equal to the reach of the hind leg. This depth usually is about 19 (18–22) inches. The nest is neatly urn-shaped, its diameter slightly smaller toward the top than near the bottom. The front-to-back diameter of the lower cavity tends to be a little greater than its side-to-side diameter.

Oviposition

Figures 8, 13–16

The nest-digging stage tapers off in a series of light, unproductive scrapes at the interior of the nest. Finally these stop, and both back fins come to rest, palm down, several inches on each side of the nest opening. The tail is then dropped low into the cavity, the cloacal opening is everted slightly, and extrusion of the eggs begins.

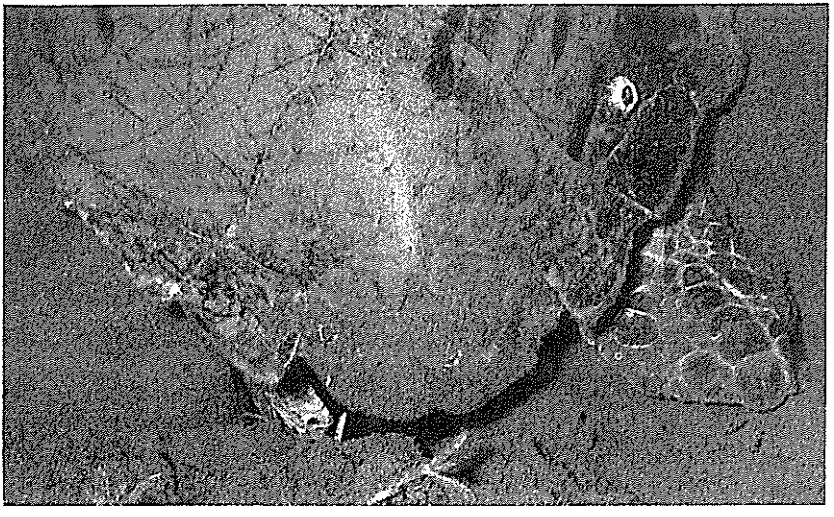

FIG. 9. Digging the nest cavity. The left flipper is being pushed down into the deepening hole, to scrape out and remove sand.

Throughout oviposition the hind legs keep their position at the right and left of the nest, and the fore fins rest half folded against the body and partly embedded in the sand. The first eggs may fall as far as 14 inches to the bottom of the nest. The whole clutch generally fills the cavity to within 5 to 8 inches of the level of the opening. Mucus is frequently secreted between the extrusions of eggs, but there is no wetting by other liquid from the cloaca.

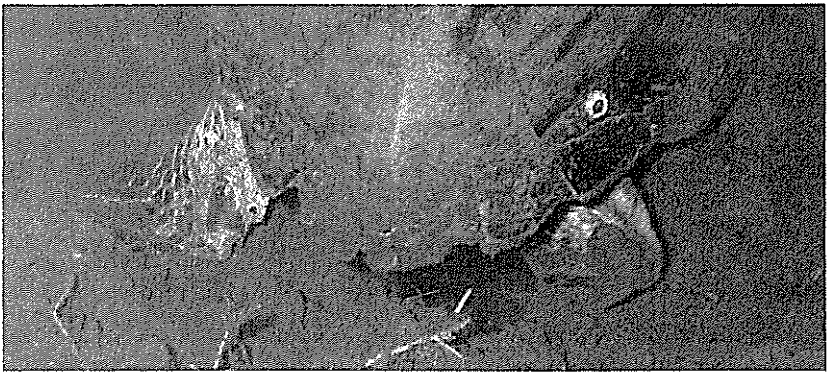

FIG. 10. Digging the egg cavity. The right flipper has scraped a palmful of sand from the hole and is moving it out to the side to be dropped.

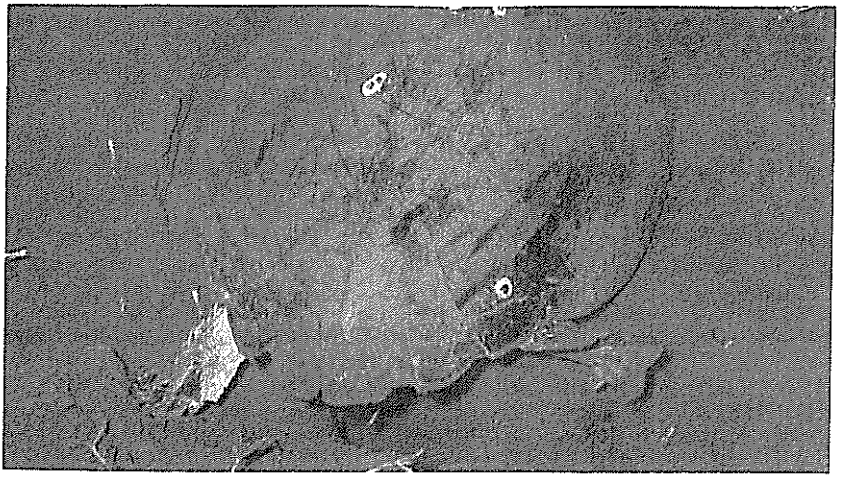

FIG. 11. Digging the egg cavity. The right flipper has just dropped a flipperful of sand from the nest.

As eggs emerge, the spread hind fins usually curl up sharply at the edges, and then relax as the eggs drop. In the hawksbill, as in all the other sea turtles, each extrusion of eggs is also accompanied by regular movements of the neck and head, evidently produced by contractions

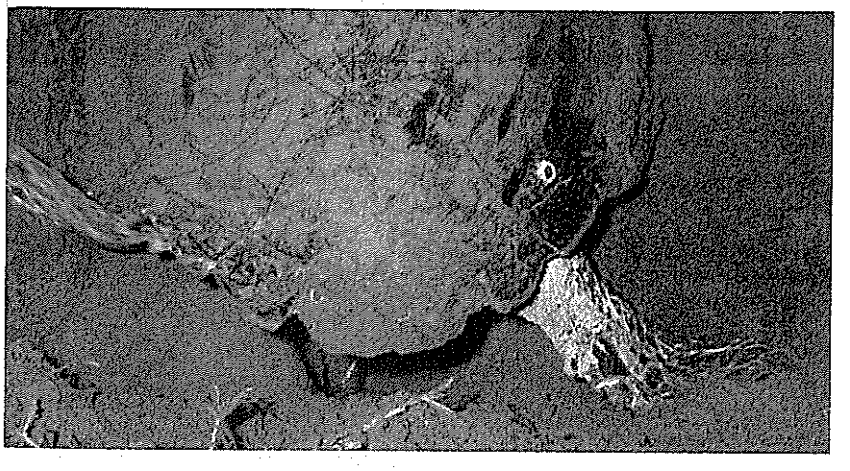

FIG. 12. Digging the egg cavity. The right flipper has dropped sand, and at the same time the left flipper is kicked straight forward with a backhand stroke, here shown in its extreme forward position. This odd combination of movements is for some reason characteristic of all marine turtles.

FIG. 13. Laying. The head is raised just prior to the contraction that will expel one or more eggs. Notice the tear-soaked sand around the eye.

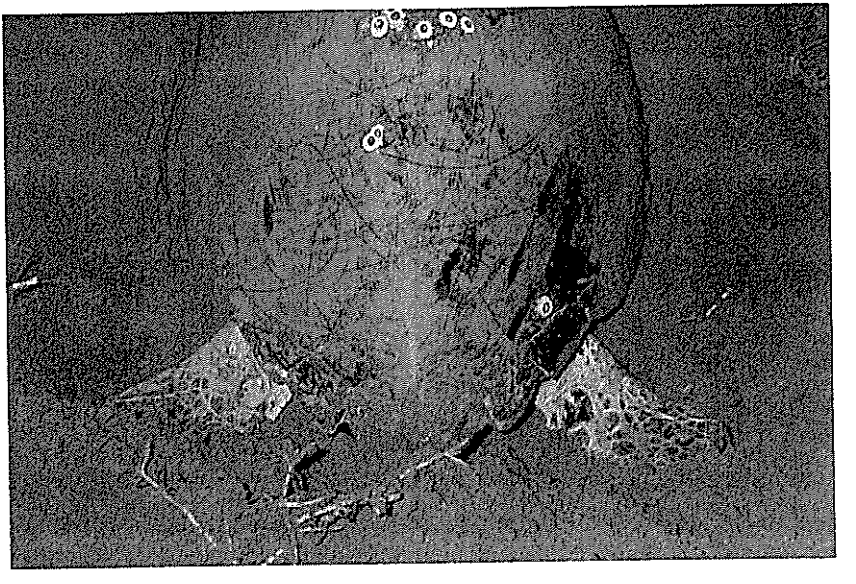

FIG. 14. Laying. The position of the hind flippers at same distance out to each side of the next cavity is typical.

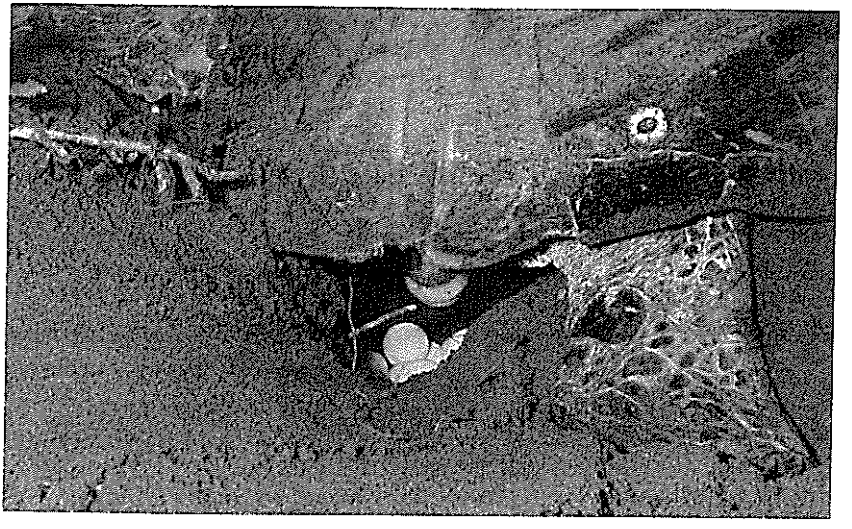

FIG. 15. Laying. The back wall of the egg cavity has been scraped away to show the top of the nearly complete clutch of eggs.

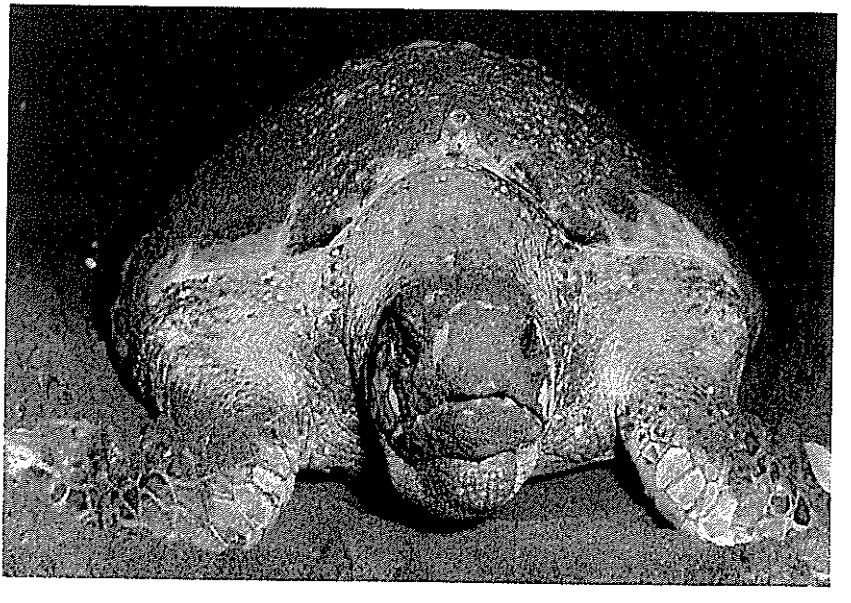

FIG. 16. Front view of hawksbill nesting at Tortuguero, July 6, 1962. The photograph shows the typical position of the fore flippers during oviposition, and elevation of head just before an extrusion of eggs.

that help push the eggs down the oviduct and out of the cloaca. After each extrusion the neck extends horizontally and the chin rests in a shallow recess in the sand, or in the wall of the body pit if one has been made. Just before the eggs are expelled, the neck is retracted and bent downward and the chin is pushed against the sand. It is at this moment that the eggs are pushed out, and, as they fall, the neck stretches horizontally forward again until the chin again rests in its mold in the sand. The first extrusion is usually a single egg, while the main complement drops mostly in two's or three's, and the last eggs appear singly. The oviposition of the turtle tagged as number 3231 terminated with the extrusion of five single eggs; then the head movements associated with extrusion were executed, with no eggs appearing; then the covering of the nest began abruptly.

Filling Nest

When the last egg has been laid, filling begins immediately. Sand is not scraped into the hole, as in *Chelonia*. Instead, the flippers, working alternately, reach far out beside the opening, pick up sand, and carry it in over the hole and drop it. As this process continues, two excavations grow beside the nest and a mound rises where the filled mouth was situated. The tail is repeatedly thrust into the sand of this pile, as if to determine its height. When the mound has reached a certain, somewhat variable, elevation, filling stops and the turtle begins to knead and press the sand of the fill with the leading edges of her back flippers. This process is long and fussy. The tail is constantly manipulated in its seemingly tactile role, and more sand is brought in from time to time as the fill is compacted. The stage ends when the filling action begins to lag and the front fins, until this time quietly bracing the body of the turtle, gradually make the jerky motions that are a prelude to the concealment tactics.

Filling the Body Pit and Concealing the Site

This stage begins when the front flippers start throwing sand backward, working at first alternately, then together, and when the pressing action of the hind feet is gradually converted into kicking strokes. This work of the four limbs not only obliterates all signs of the nest but pushes the turtle slowly forward away from its location. The slow advance may carry her 6 or 8 feet away from the place where her eggs are buried, leaving behind a broad zone of thrown and harrowed sand. The concealment operation ends when the work of the fore fins becomes desultory, and they begin to work separately instead of in unison, and with increasing intervals between periods of activity.

Return to the Sea

After the last sand-slinging stroke the turtle usually hesitates only a second or two before moving off in her return to the water. Unless lights are shone upon her, the very first shift in the axis of her body is nearly always a seaward correction of heading. While the return is rarely a straight perpendicular to the surf, it is always a clearly oriented course that is maintained even when elevations or brush completely hide the sea. The gait is mostly a lizard-like diagonal action of the four legs, with only occasional breast strokes like those of the green turtle. As in the coming in to nest, there is much more peering from side to side and more lowering of the muzzle against the sand than are characteristic of *Chelonia*. The return to the surf is nearly always far less protracted than the journey prospecting for the nest site. One Tortuguero hawksbill traveled half an hour before stopping to nest, while her return trip was made in four and a half minutes.

In general the hawksbill on shore gives the impression of being more typically reptilian in its behavior than the green turtle—more furtive, aware, and active. Much of the contrast is no doubt due to the more ponderous body of *Chelonia* and to the greater effort required to drag it forward. Moreover, the shorter, stiffer neck of the green turtle perhaps precludes the lizard-like peering about characteristic of the hawksbill on shore.

Throughout the entire interlude on shore, which may last as much as two hours, there is a constant slight secretion of tears from the eyes.

Traversal of the Surf

The last stage of the nesting emergence is the return through the breakers, a process that remains wholly unobserved, as is also the case with hatchlings entering the sea (see Carr, 1962). The relatively weaker swimming ability of *Eretmochelys* as compared to *Chelonia* may partly account for its tendency to frequent the less heavily wave-pounded beaches throughout the shared range of the two genera.

NESTING-SITE TENACITY

Except for casual observations that individuals are sometimes seen repeatedly about certain rocks or reefs, nothing is known of home range, territoriality, or homing tendencies of the hawksbill in its foraging habitat. The diffuse nature of the nesting range of the species might suggest that the site fixity of the ovigerous female is less well developed than that of *Chelonia,* although such does not necessarily follow. The classic case of homing in reptiles, cited in the literature for more than 100 years, is that

of a hawksbill said to have been marked with a ring fixed to one of its flippers by a Dutch officer in 1794 on the southern coast of Ceylon and recovered on the same beach 30 years later (Tennent, 1861). Throughout the worldwide range of *Eretmochelys*, coastal people believe it to have a strong homing urge and ability. There seems no reason to doubt that the female hawksbill that nests alone on some isolated bit of beach returns to her nesting place with the same persistence and discrimination shown by members of a more populous nesting colony.

Our only data bearing on this point are shown in tables 2 and 3. The case of turtle number 783 in table 2, considered separately, seems striking evidence of homing. The female involved was recovered after an absence of six years, at a spot so near the place where she had originally been tagged that our grid of the beach shows no separation at all. The case of number 306 is almost as imposing; the separation of her points of emergence before and after a three-year interval was not more than 300 yards, and perhaps less. The few records of renesting emergence during one season (table 3) show less fine-scale site fixity, however, and suggest that the impressive performance in table 2 may simply reflect inadequate sampling. It should, nevertheless, be kept in mind that successive nesting emergences of a hawksbill have never been found at localities more than 2 miles apart.

MIGRATION

Although no such clear-cut migratory pattern as that of *Chelonia* has been revealed for the hawksbill, there are indications that some kind and degree of migratory travel occur. The evidence, all circumstantial, is as follows:

1. As in *Chelonia,* young hawksbills disappear from view when they enter the sea after hatching and are rarely seen again until they reach shell lengths of 5 or 6 inches. On the assumption that green turtles might simply swim out from the beach on which they hatch, and be picked up by along-shore currents, we initiated a drift-bottle project at Tortuguero to determine the character of the currents off the nesting shore during late September and early October, when hatchlings enter the sea in abundance. Bottle returns to date show that if young turtles are essentially plankton, that is, if they behave like drift bottles, their net displacement may be either to the southward or to the northward of Tortuguero. Our bottles have been recovered as far away as the coast of Colombia and the northern coast of western Cuba. Just what bearing the postulated current transportation of hatchlings, if fully demonstrated, would have as a clue in the problem of migration patterns is not yet clear. So far, all that can be said is that no very young turtles are ever caught anywhere near Tor-

TABLE 5
INTERNATIONAL RECOVERIES OF HAWKSBILL TURTLES TAGGED AT TORTUGUERO, COSTA RICA, 1956–1961

Tag No.	Date Turtle Tagged	Place of Recovery	Date of Recovery	Distance Traveled (Statute Miles)
330	Aug. 18, 1956	Miskito coast, near Awastara, 15 miles north of Puerto Cabezas, Nicaragua	Before Oct. 18, 1956	285
903	June 17, 1959	Mouth of Matina River, Costa Rica	Sept. 6, 1959	37
984	July 27, 1959	Miskito Cays, Nicaragua, latitude 14° 35′ N., longitude 82° 35′ W.	July 25, 1960	325
1627	July 16, 1961	Barra del Colorado, Costa Rica	Aug. 9, 1961	14

tuguero and that drift bottles dropped inshore may be carried hundreds of miles away, to either the north or the south, and to places inhabited by hawksbills. It remains to be determined whether this expatriation actually happens to the hatchlings, whether they make regular return migrations to Tortuguero to nest when they reach maturity, and where the interim is passed.

2. Hawksbills decrease in numbers on Tortuguero Bank (see section on habitat, above) during the period from November to April. The withdrawal is so complete that the settlement of tortoiseshell hunters on the coast opposite Tortuguero Bank is abandoned in October, and the men go away to other work until April or May. Although the seasonal reduction in the colony at Tortuguero Bank is marked, it is not complete. A few hawksbills can be seen there throughout the year. Elsewhere, other rocks and reefs appear to be regularly inhabited by hawksbills, which may be seen there through considerable periods of time.

3. The hawksbill, like all the other sea turtles, is known as a stray along the coast of the United States far north of its regular feeding and breeding habitat. Individuals, evidently derived from America, are even taken in the British Isles and Europe. While it seems unlikely that these are migrants in any meaningful sense, they may be evidence of a tendency to travel in the open sea, where the major currents could catch them up. Such travel, however, could be sporadic casual wandering.

4. A somewhat more tangible but still indirect sort of evidence of long-distance travel is furnished by the results of tag returns. Even these, however, prove only that a recovered turtle moved from the place where it was tagged to the place where it was caught. If a tag should be taken from a hawksbill caught on the Irish coast, for example, it would prove nothing at all with respect to the cyclical migrations of the species. However, the turtles that we tag at Tortuguero are not planktonic hatchlings, but mature females, presumably able to go and come in or in spite of the along-shore currents. When one of these females is tagged at her nest and then recaught at a distant locality, the most probable explanation would seem to be that she had traveled from there to the nesting beach in the first place.

Recoveries of tags at other than the nesting shore are shown in table 5. There have been only four of these, out of the 70 hawksbills that have been tagged. The most distant recovery was made in the Miskito Keys, 325 miles away. Hawksbills occur throughout these keys, although nowhere in abundance. The other Nicaraguan recovery gives a little evidence on the speed of travel, the turtle involved having gone 285 statute miles in not more than 60 days. This point-to-point movement seems too fast to have been achieved in random wandering. Moreover, the speed may have been even greater, because the tag was returned, just two months after it had been put on the turtle, by a Nicaraguan who unfortunately failed to provide the exact date of the recovery and has now forgotten it.

HATCHLING ORIENTATION

In a series of simple field tests, similar to those made by Carr and Ogren (1960), the ability of little hawksbills to find the sea from whatever site on which the female might have nested was investigated. Results of these suggest that the sea-finding cues and senses used by *Eretmochelys* are probably the same as those used by *Chelonia* and *Dermochelys*. They do not, however, satisfactorily reveal the character of the fundamental guidance process.

Test groups of 10 young turtles of known age and history were selected on the basis of reactivity. In preliminary trials, hatchlings that failed to respond when released on the sand were discarded and replaced by siblings, until a group of 10 had accumulated. At the site of release the groups were placed in a shallow pit. This was briefly covered, then uncovered, to simulate unoriented emergence from the natural nest. Hatchlings with two different backgrounds were used. One set had emerged

from the nest eight to 15 hours before, and had subsequently been kept in a dry box. The others were 40 days old and had been kept in a tank of salt water during that period. Here, throughout their stay, they swam almost constantly during daylight hours, and at night slept floating at the surface with flippers folded back along the upper margin of the shell. They were fed chopped fish during their first 40 days, and were thus subjected to a regimen, swimming and feeding, which naturally would come only after the seaward orientation had served its adaptive purpose. The

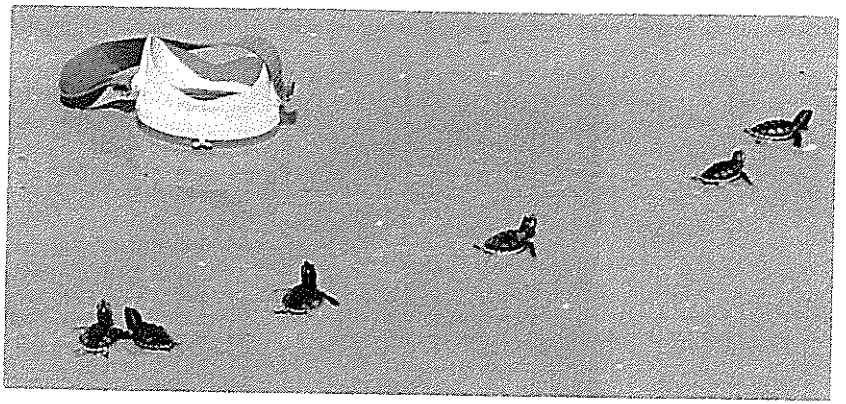

FIG. 17. Young hawksbills orienting toward the sea (which is closest toward the upper right) but momentarily diverted by a topical stimulus, evidently the white of the face mask. The figure epitomizes a problem awaiting experimental solution: precise definition of the character of the main beacon that draws hatchlings, as well as the spent female, from the upper beach back to the sea. (From Carr, 1962.)

reversal of the natural order of events had no discernible effect on the strength or appropriateness of the responses involved.

Thirteen such trials were carried out under essentially the same range of conditions as those arranged by Carr and Ogren with young green turtles, and with closely similar results. Although these field experiments added nothing to an understanding of the mechanism of sea-finding orientation, the results nevertheless seem worth reporting, if only to document the character of the phenomenon to be investigated. The results may be summarized as follows:

1. Neonate *Eretmochelys* were found to be able to find the sea from a wide range of release situations, including all conditions of topography and seaward outlook that occur at Tortuguero between the surf and the coconut-grove or shore-forest vegetation. The most immediate orientation

and most active locomotion occurred when the test nest was in sight of ocean surf and separated from it by beach that sloped toward the water. Orientation was successful, however, in rolling or cluttered ground, where the traveling turtle had to go over or around obstacles and climb long, blind, seaward slopes before the ocean came into view. Although most natural emergences are at night or at dawn, orientation success in the trials were equal by day and by night. The greatest single natural hazard, other than exceptional concentrations of predators, appeared to be the heat of the midday sun. This immobilized hatchlings within a

FIG. 18. Carey camp, a seasonal settlement of hawksbill fishermen on the northern shore of Tortuguero Estuary, Costa Rica. The camp is occupied from May through November.

few minutes, either killing them in the open or causing them to take refuge under debris, whence they rarely emerged.

2. The sea-finding feat was clearly shown to be, in most cases at least, not a single process, oriented by a single response, but a composite operation in which environmental information of diverse kinds is used. We conclude, however, as we and others have concluded after similar tests with other species of turtles, that the dominant cue is some aspect of the sky over the ocean. What aspect of exposure or illumination is involved has not been shown by our tests or by those of others working with other species of turtles. Further understanding of this aspect of the problem must now await controlled tests of the ability of turtles to discriminate among the several variable features of light on seashores.

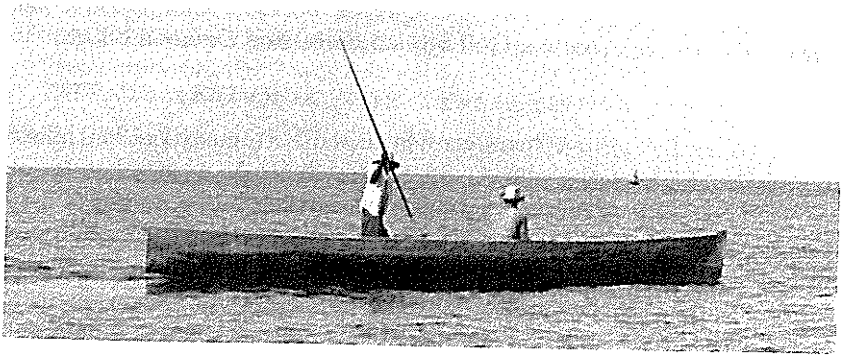

FIG. 19. Hawksbill fishermen on Tortuguero Bank, Costa Rica, October 2, 1964. A turtle has already been harpooned once. Another iron is now being thrown to anchor the second line needed to restrain the turtle while the boat closes with it.

3. The sea-finding senses and drive were found to be retained by hatchlings long after they had been placed in tanks of water. Tank-held turtles seemed less strongly motivated, however, and were easily confused by situations in which no indirect visual contact with the sea was available. One group of 40-day-old turtles unaccountably wandered in wide circles for 38 minutes, with none ever reaching the water.

4. When hatchlings were released on a spit or peninsula between the river and the sea, the seaward tendency dominated across much of the width of the land. At distances of a few yards from the river, however, where the river water was visible and the ocean was hidden, the turtles quickly entered the river. The significance in this result is the evidence that the orienting factors are topical and not an innate, compass-based direction tendency. Further evidence came from hatchlings released at sites distant from the home shore, and with different directions of the sea-

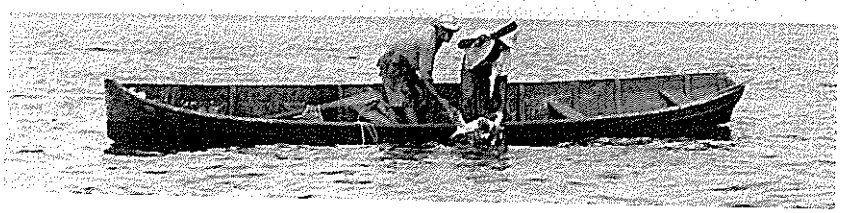

FIG. 20. Hawksbill fishermen dispatching a harpooned turtle with a club before hauling it into the boat. The hawksbill is extremely active when brought into a boat alive and sometimes bites furiously.

ward outlook: Quepos, on the Pacific coast of Costa Rica; Bimini, Bahamas, Gulf Stream shore; and Daytona Beach, Florida (see fig. 17).

SURVIVAL STATUS

When Carr first visited Tortuguero in 1954, plastic imitations had killed the market for tortoiseshell. A mature hawksbill had no commercial value, except as food for the small segment of the local population that eats the species. At the present time there is a resurging demand for genuine tortoiseshell, and this, along with a steady outlet for hawksbill calipee to the "green turtle" soup trade, and with the recent appearance of a strong market for turtle skins for making into leather, allows a fisherman to realize as much as $14 for a few pounds of easily prepared and transported products from a single hawksbill (see figs. 18–20). In a region in which this sum is more than the pay for a usual week's work, the motivation to kill hawksbills, legally or otherwise, is understandably strong. Add to these developments the general spread of seaside human populations and the perennial killing of hawksbill yearlings wherever they can be found, to be polished and mounted for the curio trade, and the survival outlook for *Eretmochelys* seems gloomy.

The localized character of the reef habitat and the attraction of reefs to fishermen and skin divers bring people into extensive contact with the hawksbill, perhaps more than with any other species; and its diffuse nesting range makes it hard to protect at breeding time. The future of all the sea turtles is obviously precarious. The hawksbill may at present be the most seriously threatened of the lot.

ACKNOWLEDGMENTS

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In Costa Rica Sr. Guillermo Cruz has for years smoothed the way for our field work, and at the University of Florida Mrs. Ruth Smith has given indispensable help with travel and shipping arrangements for the Tortuguero camp.

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