

1960

THE ECOLOGY AND MIGRATIONS
OF SEA TURTLES, 4

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THE GREEN TURTLE IN THE CARIBBEAN SEA

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BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 121 : ARTICLE 1
NEW YORK : 1960

INTRODUCTION

EXCEPT FOR CASUAL REFERENCES (Carr and Ingle, 1959; Carr and Ogren, 1959; Caldwell, Carr, and others, 1959) to some of its findings, no account of results of the green turtle investigation being carried out with National Science Foundation support at Tortuguero, Costa Rica, has appeared in print since Carr and Giovannoli (1957) summarized information from the first year's work in 1955. While we are still far from understanding the life cycle of the green turtle, even as it is lived by the populations of the western Caribbean, the advances that have been made, and the new basis for comparative interpretation that has been furnished by the recent studies of Hendrickson (1958) and of Harrisson (1956) in the

China Sea, make the time seem propitious for a summary of results to date.

The data and observations presented here have come from a tagging program centered upon the nesting colony of the green turtle at Tortuguero, 50 miles north of the Caribbean port of Limon, Costa Rica, and from field reconnaissance and aerial surveys and tallies throughout the Caribbean. Morphometric data collected during the course of the study, and miscellaneous additional observations, will be published elsewhere, as will results of some work with the hawksbill (*Eretmochelys*), which also nests at Tortuguero in small numbers.

ACKNOWLEDGMENTS

For much of our data for the 1959 season, we are indebted to Mr. Harry Hirth who was in residence at the research camp from late June until September 15. During this period the work has profited from a sharing of facilities, including the services of our friend Sr. Leo Martinez, with the Caribbean Conservation Corporation. The Minister of Agriculture and Industry of Costa Rica, Sr. Jorge Borbón Castro, has furthered the research by renewing the allotment of an inviolate section of the nesting beach for joint use in the research and conservation programs. As from

the beginning of the tagging program, Capt. Allie Ebanks of West Bay, Grand Cayman, has been our main reliance for well-documented tag recoveries. We are grateful to Miss Esther Coogle, Staff Artist, Department of Biology, University of Florida, for illustrations, and to Mrs. Marge Tondo for patience and skill in typing from poor copy.

The research work of the junior author was done while he was a Research Assistant in the Department of Biology of the University of Florida.

THE TORTUGUERO COLONY

RANGE IN SIZE IN MATURE FEMALE

THE NESTING COLONY of the green turtle at Tortuguero, representing populations evidently recruited from throughout the western Caribbean (see following section), comprises mature females ranging in over-all length of the shell (that is, the length in a straight line from anteriormost to posteriormost projections of the shell) between 27.25 and 46.25 inches, with an average, for 1146 individuals, of 39.40 inches (see figs. 1 and 2). Carr and Giovannoli (1957) found slight indication of differential seasonal frequency of size groups (see their fig. 8). Figures 3 and 4 of the present paper similarly plot size against arbitrarily delimited periods of time. Figure 3 shows only that medium-sized turtles predominate at all times of the season (except in the first

period, when the sample is too small to show anything). Figure 4, however, although also based on an inadequate sample, seems to corroborate the impression one gets, in going from place to place and from week to week on the nesting grounds, that size distribution is weakly nodal, which is what would be expected in a nesting aggregation recruited from widely separated points of origin, and with some individuals or demes operating on a three-year reproductive cycle (see section on Reproductive Cycle) and some on a two-year schedule.

A number of counts and measurements, made during two or more years of the investigation and to be published elsewhere, seem to show no differential seasonal frequencies

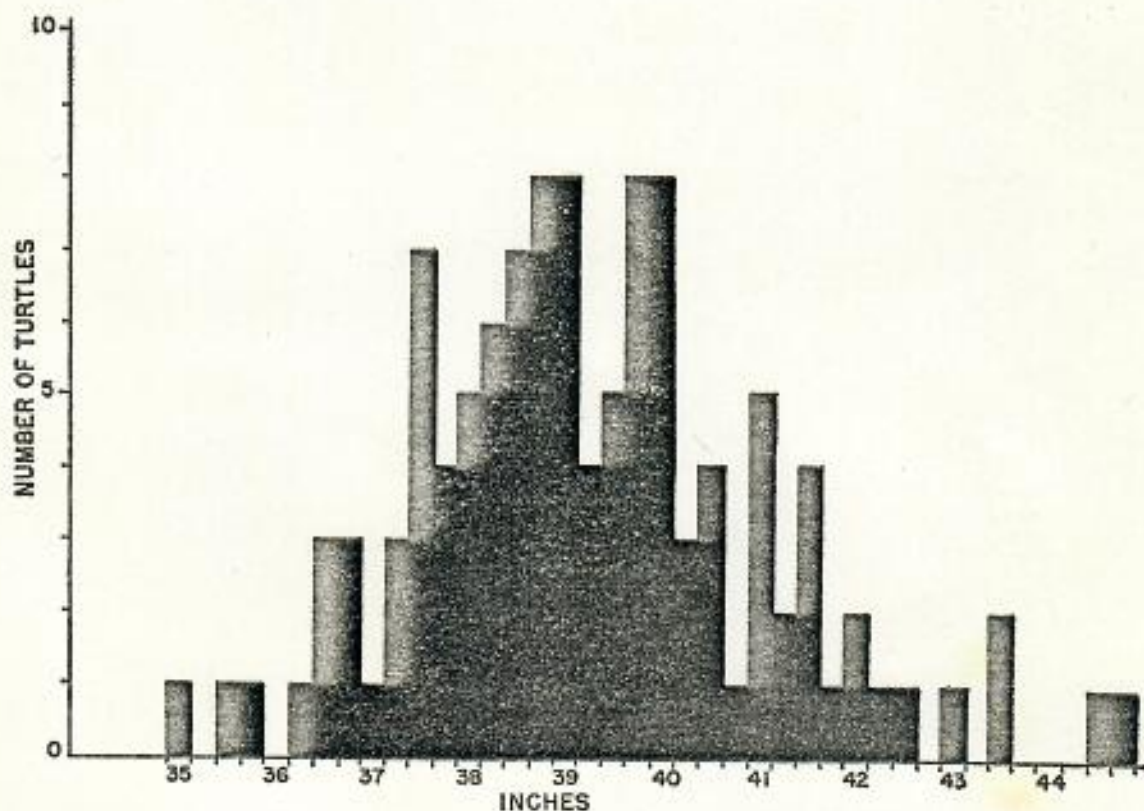


FIG. 1. Frequency of over-all shell lengths in mature female green turtles at Tortuguero, Costa Rica, July, August, and September, 1956.

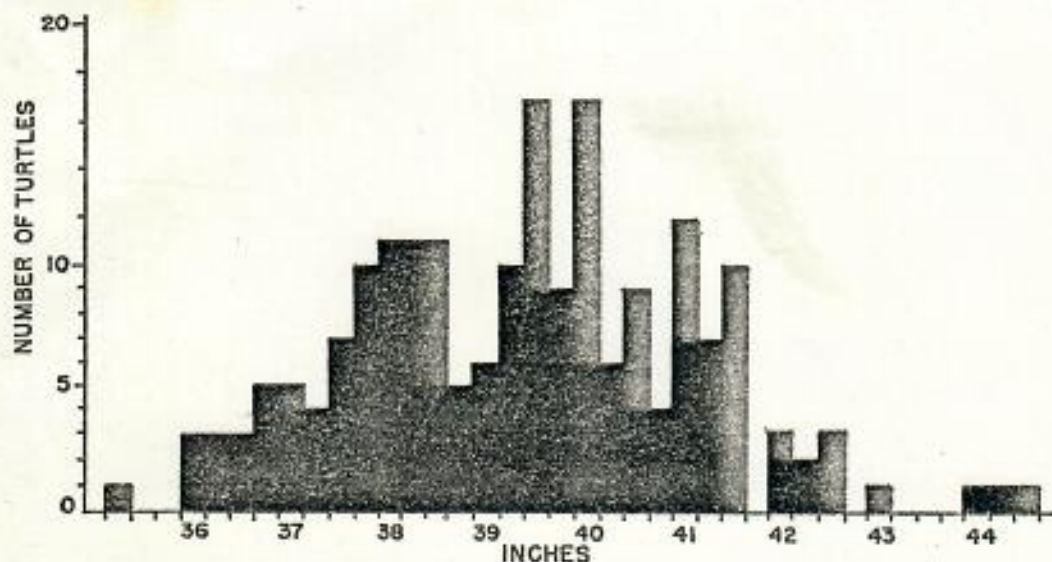


FIG. 2. Frequency of over-all shell lengths in mature female green turtles at Tortuguero, Costa Rica, July, August, and September, 1957.

either during different years or during different parts of a single season. One trait alone appeared to be seasonal in its frequency; that was the two-year-versus-three-year scheduling of the nesting migration (see section on Reproductive Cycle). Whether this repre-

sents physiologic divergence of geographically isolated stocks, or endocrinological demes within populations, or merely random variation in the Caribbean population as a whole remains to be determined.

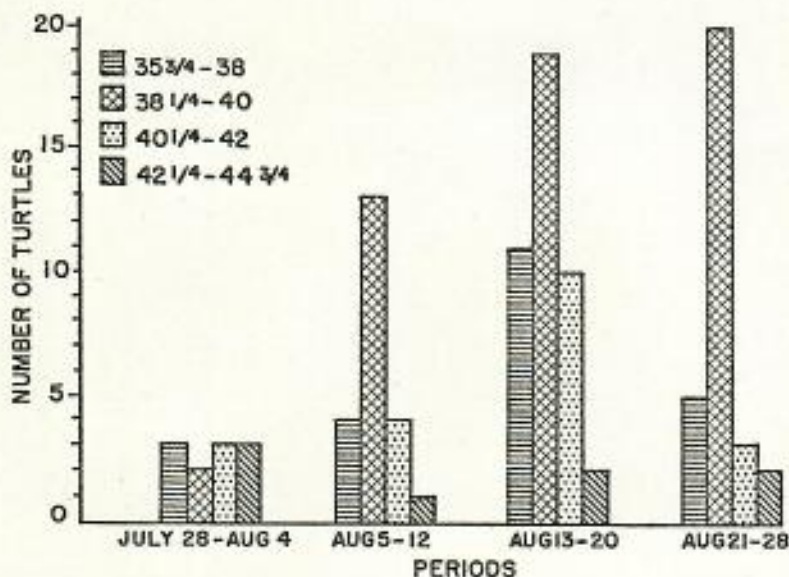


FIG. 3. Periodic frequency of over-all shell lengths in mature female green turtles at Tortuguero, Costa Rica, July-August, 1956.

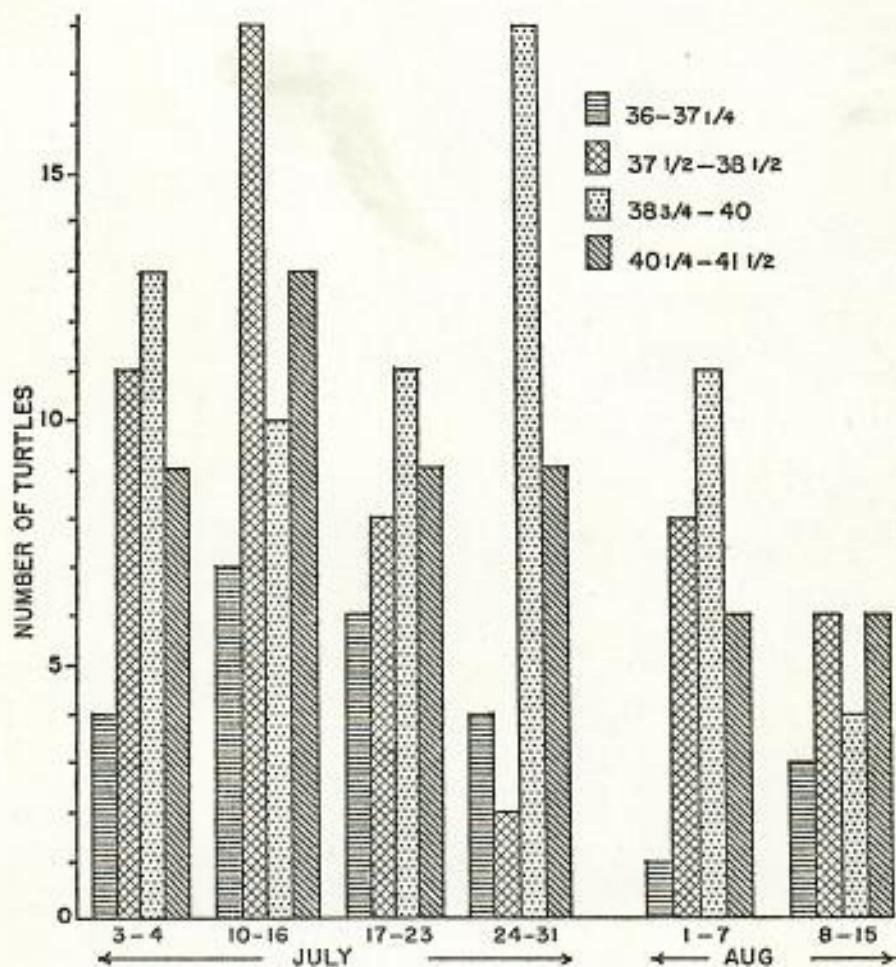


FIG. 4. Periodic frequency of over-all shell lengths in mature female green turtles at Tortuguero, Costa Rica, July-August, 1957.

RECRUITMENT: INTERNATIONAL TAG RECOVERIES

When Carr and Giovannoli (1957) summarized results of the tagging program of 1955 at Tortuguero, they had 10 international recoveries. Of these, seven were from the Miskito Cays area and three from Colon Province, Panama—localities lying, respectively, to the north and to the south of the tagging camp, and within distances of between 200 and 300 miles from it.

During the first season, it began to be apparent that the shell tag in use was not satisfactory. The scraping and scratching ac-

tion of the male during the mating process evidently made it impracticable to fasten anything to the shell of the female during the courting and mating season, which roughly corresponds with the first half of the nesting period. We did not realize this fully until the end of the 1955 season, when some 500 turtles had been tagged with the shell plaques. Fortunately all the tags put on were fastened through a pair of holes located in a restricted section of the after margin of the shell. It was thus possible to identify a turtle

all engaged in mating after tagging

marked at Tortuguero, if seen by someone familiar with our tagging method, even when the tag had been lost.

Since the first year, the shell tag has been replaced in our work by a cow-ear tag of monel metal (adapted to use with turtles by Dr. Tom Harrison of the Sarawak Museum and Dr. John R. Hendrickson of the University of Malaya) clamped to the thin, tough, hind, proximal edge of the fore flipper. As a safeguard in case the tag should be lost, we have continued to bore two holes in the shell margin. These holes have been made in different pairs of marginals in each successive season. As have the tags, they have proved to be readily discernible after three years. Although they are of no value as marks for long-range recovery by persons not familiar with the project, they have proved important as a source of information on the triennial and biennial returns to Tortuguero itself (see section on Reproductive Cycle).

Although the impermanency of the shell plaque was proved by the numerous 1955 re-nesting returns of tagless females that had been marked that same season, the fact that the loss of the tags was not 100 per cent was shown by the recovery of two turtles with shell tags in the Miskito Cays area and Bocas del Toro, over a year after they had been marked.

At the present writing, the total number of green turtles marked at the Tortuguero camp is 1178. There were 35 international returns (see table 1 and pl. 1). Of these the majority came from the Miskito Cays region, as at the end of the first season. Two have been added to the original three Panamanian recoveries; three came from Colombia; and there was one each from Mexico, British Honduras, Cuba, and Jamaica (Morant Cays). This total gives a spread of recoveries representing the extreme reaches of the western Caribbean. It is important to note that not a single post-season recovery of a turtle marked at Tortuguero was made in Costa Rican waters. That is to say, although returns to Tortuguero itself totaling about 200 have been recorded, these were all females returning to complete the series of laying emergences of the current season. Once the season was over, no tagged turtles were ever taken at Tortuguero or elsewhere in Costa Rica.

A steady trickle of information has come in to support the original assumptions of the investigation: that the big Miskito Cays population is derived from the Tortuguero breeding ground, and that Tortuguero is also the reproductive center for turtles from a great area.

Throughout the circumtropical range of *Chelonia*, the standard pattern of habitat occupancy seems to involve more or less widely separated feeding and nesting grounds. One need look no farther than the famous turtle island of Ascension to see an example of what appears to be the most usual arrangement: an insular rookery beach, with recruiting from distant, year-around pastures, in this case probably located on the African coast. It is easy to see why none of the turtles remains at Ascension after the nesting season is over. The shore waters about the island slope abruptly, and there are none of the shallow *Thalassia* flats that seem necessary for the maintenance of stable green turtle populations. We hope to corroborate the supposed African origin of the Ascension breeding colony by means of a tagging program carried out at the island. It is not clear why the turtles should make the long trip out to this pin-point of an oceanic island when a large extent of the coast of the African bulge seems to an observer to offer suitable nesting conditions. But throughout the world this arrangement of island rookery and mainland pasture ground seems to be the one most frequently met. Tortuguero, a mainland beach, drawing its breeding colony principally from island sources (although to some extent from all about the littoral), seems in this regard exceptional, although by no means without counterpart.

In the eastern Caribbean the only known center of aggregated breeding is the tiny island *Isla de Aves*, 140 miles west-northwest of the island of Dominica. There is some evidence that this island has greatly diminished in size within recent decades (Zuloaga, 1955; Phelps and Phelps, 1957). One wonders about the eventual fate of the Aves-oriented nesting flotillas, presumably comprising most of the green turtles of the eastern Caribbean, when the island finally becomes wholly awash.

From what we have learned to date, it

TABLE 1
INTERNATIONAL RECOVERIES OF GREEN TURTLES TAGGED AT TORTUGUERO,
COSTA RICA, 1955-1959

Tag No.	Date Tagged	Place of Recovery	Date of Recovery	Distance Traveled (Statute Miles)
483	Aug. 17, 1955	Colon Province, Panama, 1½ m. W. of mouth of Palmilla R.	Sept. 21, 1955	218
133	Aug. 3, 1955	5 m. N. of Puerto Cabezas, Nicaragua	Oct. 26, 1955	240
316	Aug. 5, 1955	Near Palmilla, Colon Province, Panama	Sept. 3, 1955	218
213	Aug. 26, 1955	Near Palmilla, Colon Province, Panama	Sept. 3, 1955	218
363	Aug. 11, 1955	Puerto Cabezas, Nicaragua	Sept., 1955	270
247	Aug. 25, 1955	14 m. SSE. of Miskito Cays	Mar. 14, 1956	230
219	Aug. 25, 1955	Barra del Rio Grande, Nicaragua	May 1, 1956	120
240	Aug. 24, 1955	Southeast Rock, Miskito Cays	Mar. 3, 1956	270
lost	July-Sept., 1955	Miskito Cays area	Feb. 14- Apr. 3, 1956	240±
324	Aug. 5, 1955	Bocas del Toro, Panama; 5 m. off Bastimento I.	Oct. 29, 1956	120
369	Aug. 25, 1956	Isla de Mujeres, Quintana Roo, Mexico	Aug. 20, 1958	775
732	Aug. 6, 1958	Arastro, 12 m. N. of Puerto Cabezas, Nicaragua	Oct. 2, 1958	247
374	Aug. 25, 1956	Morant Cays, near Jamaica	May 29, 1957	684
380	Aug. 28, 1956	Edinburgh Reef (Miskito Cays area)	Sept. 1, 1957	295
611	Aug. 13, 1957	Bluefields, Nicaragua	Oct. 16, 1957	98
615	Aug. 14, 1957	Colon Province, Panama	Sept. 27, 1957	218
295	Aug. 12, 1956	Southeast Rock (Miskito Cays area)	Jan. 30, 1958	270
349	Aug. 21, 1956	Porgee Reef (Miskito Cays area)	Jan. 9, 1958	284
366	Aug. 24, 1956	Miskito Cays area; lat. 14° 02' N., long. 82° 37' W.	Mar. 8, 1958	260
523	July 24, 1957	Near Tingo Reef (Miskito Cays area)	Apr. 15, 1958	235
628	Sept. 5, 1957	Miskito Cays area	Jan. 24, 1958	270
761	Aug. 18, 1958	Awastara, 20 m. N. of Puerto Cabezas, Nicaragua	Nov. 1, 1958	290
239	Aug. 24, 1955	Deutman Bar, Miskito Cays	Sept., 1958	240±
694	July 22, 1958	35 m. E. of Placencia, British Honduras	Dec. 8, 1958	705
594	Aug. 19, 1956	Tinkham Rock, Miskito Cays	Feb. 15, 1958	265
336	July 24, 1957	Tinkham Rock, Miskito Cays	Mar. 7, 1959	265
539	Aug. 6, 1957	Edinburgh Reef, Miskito Cays area	Apr. 10, 1959	295
755	Aug. 10, 1958	Cayos de Las Doce Leguas, S. coast of Cuba, between Isle of Pines and Manzanillo	Mar. 20, 1959	793
734	Aug. 6, 1958	Miskito Cays area; lat. 14° 10' N., long. 82° 23' W.	May 10, 1959	278
703	July 31, 1958	Miskito Cays area; lat. 14° 21' N., long. 82° 44' W.	Apr. 25, 1959	276
436	July 10, 1957	Southeast of Southeast Rock (Miskito Cays area)	Apr. 12, 1959	275
909	July 8, 1959	6 m. N. of Cartagena, Colombia; caught at depth of 10 fathoms	Aug. 10, 1959	535
1074	July 18, 1959	6 m. N. of Cartagena, Colombia	Sept. 23, 1959	535
954	July 21, 1959	6 m. N. of Cartagena, Colombia	Nov. 16, 1959	535

seems reasonable to conclude that there are in the Caribbean only two remaining centers of mass reproduction by the green turtle: Isla de Aves in the east and our study area, Turtle Bogue, in the west.

Obviously all that these recoveries of turtles marked at Tortuguero actually prove is that the turtles, after being tagged, traveled (or were carried by currents) to the localities in which they were retaken. Their turning up in those places could conceivably be attributed to random wandering. The uneven character of the sampling that produced the recoveries makes it pointless to try to test the results statistically. Final proof of periodic guided migration will await a difficult maneuver: the recapture in Cuba, say, of a turtle tagged in Tortuguero; the release of this turtle; and a second recapture back in Tortuguero during another nesting venture three (or, less likely, two) years after the first. Meantime, however, in spite of the gap in the circle of direct evidence, there remains in our minds little doubt that the tag-return data, plus such suggestive circumstances as (A) the lack of turtles in Costa Rican waters after the end of the breeding season, (B) their abundant occurrence in and periodic disappearance from certain areas of good pasturage (most notably the Miskito Cays region), and (C) the seasonal appearance of schools in areas between Tortuguero and the feeding grounds, are adding substance to the folk beliefs on which the original assumptions of this study were based.

Several factors detract from the usability of our data for quantitative assessment and census. Perhaps the most important is the fact that the Miskito Cays area, from which most (65.7%) of our recoveries have come, is more heavily sampled than any other part of the Caribbean—is, in fact, probably the most heavily "turtled" area of comparable size in the world. This uneven sampling precludes the making of simple calculations of population sizes, and the fact that the Miskito Cays region attracts the most turtle schooners because there are more turtles there than anywhere else in the Caribbean further complicates the picture. Still another factor detracting from the statistical value of the data is the loss of tags, referred to above. It is even impossible to calculate useful recovery percent-

ages, because the size of the tagged sample is not known, as some of the tagged animals failed to carry their tags away from the breeding ground. Another source of quantitative uncertainty is the unknown proportion of turtles tagged by us and then retaken, during subsequent nesting emergences of the same season, by professional turtle hunters on the unprotected beach to the south of our camp. During the first two or three seasons such loss was surely heavy. Lately, restrictions have been placed by the government on the industry, fewer females have been turned on the very heavily visited Miles 7-11, and perhaps more of the tagged turtles have survived the season.

The total for the five seasons of tagging is 1178, and the percentage of international post-season returns is 2.9 per cent. With the use of only turtles marked with fin tags (723), the percentage was 3.5 per cent. One of the most productive groups within this latter contingent was the series of individuals tagged during the last of the 1955 season (the first to be marked with the fin tag). Of these, five, or 12.5 per cent, have been retaken.

A surprising recovery is that from Isla de Mujeres, itself a site of some nesting activity, although much less important in this respect than Tortuguero. This recovery may reinforce the inference from other evidence, that green turtle populations include both resident and migratory components.

Most of our recoveries have been made too long after the date of tagging to have any clear relevance to the question of speed of travel in the species. A recapture in Panama giving a speed of about 23 miles per day over a nine-day period is shown in table 1 and was noted by Carr and Giovannoli (1957). The only cases among later returns that are noteworthy in this respect are Nos. 909 and 1074 (see table 1), both 1959 recoveries from Cartagena, Colombia, 500 miles by shortest route from Tortuguero. The turtles were caught in the same place, No. 909 having been tagged July 8 and recovered August 10, and No. 1074 tagged August 18 and recovered September 23. Both were taken in nets and at considerable depth, No. 909 at 10 fathoms. Green turtles are so seldom seen at the locality that the captures were described there in a front-page news story, and the turtles, al-

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though of only average size for the species, were referred to as "gigantic animals" of unknown kind. These recoveries allow the calculating of a minimum speed of travel of 14.7 miles a day for the 34-day period and of 13.5 miles per day for the period of 37 days. After Nos. 909 and 1094 were retaken, a third Colombian recovery was made. Number 954, tagged July 21, 1959, was retaken November 16, 1959, at a depth of 6 meters at Punta Canoas, in the same general area as were the other two. That the taking of these turtles astonished people in the area suggests that they were on the way to other parts. The recapture, in one season, of three turtles marked at Tortuguero, and representing the

first South American returns for the four years of the study, may be taken as further support for the assumption that the breeding colony at Tortuguero is made up of contingents from widely separated points of origin, and that these start their journeys to the rookery on staggered schedules. How tight the organization of the migrating groups is remains to be determined. It is tempting to suppose that the Colombian turtles represented a flotilla returning to the Trinidad-Venezuela area, where green turtles occur in fair numbers and where Carr has been told by fishermen that they go somewhere to the north to nest.

REPRODUCTIVE CYCLE

Harrison (1956), in his studies of nesting colonies of Pacific green turtles in Sarawak, found surprising evidence of a three-year breeding cycle in the populations nesting on the turtle islands of the China Sea. In early 1956, the second year of our work at Tortuguero, Carr heard from Harrison that none of the turtles he had marked during the previous two years had returned to nest on the islands where they were tagged. Similarly, in 1956, none of the Tortuguero females tagged in 1955 came back, but later that season we learned that Harrison was finding turtles tagged in 1953 returning to his beaches again. We thus awaited the outcome of the 1958 season in Costa Rica with great interest. The results, together with those of the 1959 season, are given in table 2. The noteworthy aspects of the data are as follows:

1. There is no case of a turtle returning to nest during a season following one in which it had nested before.

2. There is a strong three-year cycle shown in the nesting returns.

3. There is a minority of cases in which nesting is carried out on a two-year schedule.

4. None of the two-year nesters was represented among the females tagged during 1955. That is, none of the turtles that nested in 1957 had previously been tagged in 1955 in spite of the fact that the 1955 group was much the largest yet tagged by us.

What periodic influences might control a three-year reproductive cycle are by no means clear. That they should in the same species permit a two-year cyclical undercurrent is also puzzling. That this undercurrent should be missing among members of one of

TABLE 2
RETURNS OF TAGGED TURTLES TO THE NESTING BEACH AT TORTUGUERO, COSTA RICA,
IN SUCCESSIVE SEASONS

Year	No. Tagged	Returns from Previous Years	
		Year	No. of Returns
1955	495	—	—
1956	114	—	—
1957	248	—	—
1958	131	1955	16
		1956	7
1959	190	1956	6
		1957	4

the year groups at Tortuguero is still less easily explained. Apparently such superimposition of nesting schedules does not occur in the Pacific form, because Harrison found no individuals nesting on a two-year cycle,

despite the fact that his sample is far larger than ours and that he maintains contact with entire breeding colonies, the members of which show extraordinary tenacity in returning to specific islands to nest.

MATING

We can add little to what Carr and Giovannoli (1957) said of mating in the Tortuguero colony. Copulation occurs (as Harrison, 1954, found to be the case in the populations he studied in the China Sea) at the nesting beach and, as far as we have been able to determine, nowhere else. Whether it takes place before, or after, the first or some other one of the nesting emergences is still not known. The nesting season is, however, much longer than the mating season, as we rarely saw any courtship or mating after August 1, and never after August 15.

In figure 2 of plate 5 note the deep notches at the third intermarginal seam on the fore edge of the shell of the female shown. These were made by the enlarged grappling nails of the male (pl. 7), which, together with the

strong horn at the tip of the prehensile tail, provide an effective three-point coupling rig for coping with the coyness of the female and the throw of the waves. Females often come ashore with such notches raw and bleeding and cut symmetrically back into bone half an inch thick. This phenomenon has bearing on the still unknown fertilization schedule of sea turtles. Finding a nesting female in this condition proves that she was attended by a male before she laid, on this particular occasion. But she may have laid one or more times previously, during the same season, and copulation may have occurred after those times. Thus all that we know at the present time is that copulation occurs at the rookery and is not restricted to the period after all the layings of the season have been completed.

NESTING SEASON

The nesting of green turtles at Tortuguero is strongly seasonal (cf. Moorhouse, 1933, who worked with a similarly seasonal colony at Heron Island; Harrison, 1951; and Henrikson, 1958, whose work with the green turtle in Sarawak shows that it nests throughout the year). At Tortuguero the bulk of the year's eggs are laid in July, August, and September. The peak comes in August, although during the last two weeks of July and the first two of September there may be several nights when as many turtles come out as on any August night. Throughout June, even towards the end of the month, several nights may pass without the emergence of a single turtle, even to leave a trail halfmoon trail. We have no record for May. The beginning of the season is thus quite abrupt. The ending is more gradual, emergences usually beginning to taper off in mid-September and coming to a virtual stop by the end of October. Members of the Martinez family, old residents of

Tortuguero, tell us that they have seen nests in November but that they are infrequent.

In 1959 the first turtle found on the 2 miles that were patrolled came up the night of June 16, the second on June 25, and the third on July 6. The greatest activity took place between July 9 and August 1. After August 28 activity diminished rapidly, although two or three turtles were still emerging nearly every night by September 17 when we left the camp.

That the season begins more abruptly than it ends may be owing simply to the fact that the turtles arrive in schools (the "fleets" of the Spanish-speaking turtlers), which gather at the pasture ground, and which partly break up as events at the nesting ground proceed on divergent schedules for different individuals of the school. A turtle frightened back into the sea, say, at the beginning of a nesting emergence, might be thrown off schedule in her suite of nestings, and her

eventual return to home ground might be made in company different from that with which she came. In any event, the impression one gets in watching tracks on the beach and turtles loafing outside the surf line is that they arrive *en masse* but tend to trickle away at the end of the season.

The fact that the trunkback season ends as the green turtle season begins is probably significant. There is not enough nesting by trunkbacks at Tortuguero to offer any important competition for the green turtles at any time, or *vice versa*. The periodicities of the

two animals were developed elsewhere, however, through a long period of geological time and no doubt were conditioned by the fact that a tendency for two big, active reptiles inhabiting the same geographic areas to aggregate at the same time and at the same nesting beaches resulted in injurious competition. It is worth noting that at the nearest site of aggregated nesting by the trunkback (Matina Beach, 30 miles to the southward) hardly any nesting by green turtles takes place.

RENESTING

Carr and Giovannoli (1957) showed by indirect evidence that, as all sea turtles probably do, turtles of the Tortuguero colony nest more than once during the season that they visit the rookery. During the 1956 season, when for the first time we began tagging only turtles known to have just nested, it quickly became evident that Carr and Giovannoli's inferences had been correct. Of 683 green turtles tagged during 1956, 1957, 1958, and 1959, 92 were retaken while laying a second time and 12 on a third occasion. In none of these cases did we have any way of knowing how many layings had occurred prior to, or took place after, the date of our contact with the animal. But from the aggregate of our recapture data, an interval of 12-14 days (average 12.5) between nestings was calculated, and with this average as a divisor we find six nestings to be the maximum for the Tortuguero colony. This figure may be short of the real maximum, because desultory nesting occurred before and after the period of our residence in the camp. The opinions of fishermen support the figure, however, and to some extent it is substantiated by measurements of oviducal eggs. Data on recaptures are given in tables 3-6. In these tables the very short intervals represent returns after some inter-

ruption (a flashlight beam, for instance, or a barking, snapping dog) had sent the female back into the sea without laying. The longest such interval may be seen in the case of No. 341, which returned to lay five days after having been interrupted in her emergence. More usually a return is made either on the same night as the interruption or on the following night. Intervals well over the 12.5-day mean are interpreted as multiples of the actual renesting interval, or these plus one or more of the periods of recovery after abortive emergences.

A noteworthy difference between our colony and the colonies of the China Sea is the evidently shorter internesting period in the latter (12.5 at Tortuguero and 10.5 in the colony studied by Hendrickson at Sarawak). It would be of interest to calculate maximum chronological spread for rookery-residence periods in the Sarawak colony, to learn whether the greater number of nestings by those turtles is attributable to a longer season, or to the shorter time between emergences. Even in the three-month season at Tortuguero, a female turtle laying on a 10.5-day interval might squeeze eight or nine nestings into her season at the beach.

TABLE 3

OBSERVED RENESTING RETURNS OF FEMALE GREEN TURTLES TO TORTUGUERO,
COSTA RICA, DURING THE SEASON OF 1956

(The beach sections are counted in eighths of a mile from the river mouth southward.)

Tag No.	First Observed Emergence		First Return		Second Return	
	Date and Time	Mile	Date and Time	Mile	Date and Time	Mile
254	July 13, P.M.	1½	July 28, P.M.	1½	Aug. 11, A.M.	½
269	Aug. 4, P.M.	¾	Aug. 5, P.M.	—	—	—
270	Aug. 4, P.M.	¼	Aug. 5, P.M.	1½	Aug. 16, P.M.	¾
260	July 24, P.M.	½	Aug. 8, A.M.	¾	—	—
373 (267)	Aug. 4, P.M.	1½	Aug. 8, A.M.	½	Aug. 24, P.M.	½
309 ^a	Aug. 15, A.M.	½	Aug. 16, A.M.	½	Aug. 27, A.M.	½
302	Aug. 13, P.M.	2¾	Aug. 16, P.M.	2½	—	—
272	Aug. 5, P.M.	1½	Aug. 18, P.M.	1½	—	—
323	Aug. 17, A.M.	½	Aug. 19, P.M.	¼	—	—
299	Aug. 12, P.M.	1½	Aug. 20, P.M.	1½	—	—
333	Aug. 18, P.M.	¼	Aug. 20, P.M.	¾	—	—
285	Aug. 9, P.M.	2¾	Aug. 20, P.M.	¼	Sept. 4, A.M.	¾
279 ^b	Aug. 7, P.M.	¼	Aug. 20, P.M.	½	Aug. 22, P.M.	¾
292	Aug. 11, A.M.	0	Aug. 21, P.M.	¾	Sept. 3, A.M.	½
259	Aug. 11, A.M.	1½	Aug. 22, P.M.	1½	—	—
363 (328)	Aug. 17, P.M.	¾	Aug. 23, P.M.	1	—	—
282	Aug. 10, A.M.	½	Aug. 23, P.M.	½	Sept. 6, P.M.	0
290	Aug. 11, A.M.	½	Aug. 23, P.M.	½	—	—
289	Aug. 11, A.M.	½	Aug. 24, P.M.	0	—	—
294	Aug. 12, A.M.	¾	Aug. 24, P.M.	½	—	—
295	Aug. 12, A.M.	¾	Aug. 24, P.M.	½	—	—
304	Aug. 14, A.M.	½	Aug. 25, P.M.	1	—	—
341	Aug. 20, P.M.	1½	Aug. 25, P.M.	½	—	—
317 ^c	Aug. 16, A.M.	½	Aug. 27, A.M.	¾	—	—
320	Aug. 16, P.M.	1½	Aug. 27, P.M.	¾	—	—
313	Aug. 16, A.M.	½	Aug. 30, A.M.	¾	—	—
322	Aug. 16, P.M.	¾	Aug. 30, A.M.	¾	—	—
385 (265)	Aug. 4, A.M.	1½	Aug. 31, A.M.	½	—	—
336	Aug. 19, P.M.	¾	Sept. 2, P.M.	1	—	—
358	Aug. 22, P.M.	½	Sept. 5, P.M.	½	—	—
336	Aug. 23, P.M.	½	Sept. 5, P.M.	¾	—	—
378	Aug. 25, P.M.	¾	Sept. 5, P.M.	½	Sept. 6, P.M.	½

^a No. 309 made a third return Sept. 6, P.M., at Mile 0.^b No. 279 made a third return Sept. 5, P.M., at Mile ¾+.^c No. 317 made a third return Aug. 31, A.M., at Mile ¼.

TABLE 4

OBSERVED RENESTING RETURNS OF FEMALE GREEN TURTLES TO TORTUGUERO,
COSTA RICA, DURING THE SEASON OF 1957

(The quarter-mile beach sections are numbered from the river mouth southward.)

Tag No.	First Observed Emergence Date and Time	Mile	First Return Date and Time	Mile
392	July 3, P.M.	1 $\frac{1}{4}$	July 17, P.M.	1 $\frac{1}{4}$
396	July 3, P.M.	$\frac{1}{2}$	Sept. 3, P.M.	$\frac{1}{2}$
461	July 3, P.M.	$\frac{1}{4}$	July 14, A.M.	1
404	July 5, A.M.	1 $\frac{1}{4}$	July 16, P.M.	$\frac{1}{2}$
410	July 4, P.M.	$\frac{1}{2}$	July 18, P.M.	1 $\frac{1}{2}$
493	July 5, P.M.	1 $\frac{1}{4}$	July 18, P.M.	1
414	July 5, P.M.	1	July 16, P.M.	$\frac{1}{2}$
417	July 6, P.M.	$\frac{1}{2}$	Sept. 4, P.M.	1
421	July 6, P.M.	$\frac{1}{2}$	July 20, P.M.	$\frac{1}{2}$
424	July 7, P.M.	1	Aug. 9, P.M.	$\frac{1}{4}$
430	July 9, P.M.	$\frac{3}{4}$	Aug. 1, P.M.	0
440	July 10, P.M.	1 $\frac{1}{2}$	July 22, P.M.	1
444	July 12, A.M.	0	Aug. 6, P.M.	$\frac{1}{4}$
446	July 11, P.M.	$\frac{1}{2}$	Aug. 7, P.M.	$\frac{1}{2}$
448	July 12, A.M.	$\frac{1}{2}$	July 23, P.M.	$\frac{1}{2}$
454	July 11, P.M.	1 $\frac{1}{4}$	July 23, P.M.	1
470*	July 14, P.M.	$\frac{3}{4}$	July 17, P.M.	$\frac{1}{2}$
473	July 14, P.M.	$\frac{1}{2}$	July 26, P.M.	$\frac{3}{4}$
474	July 14, P.M.	$\frac{1}{2}$	Aug. 30, P.M.	$\frac{1}{2}$
480	July 15, P.M.	$\frac{3}{4}$	Sept. 3, P.M.	$\frac{1}{2}$
511	July 21, P.M.	1	Aug. 4, P.M.	$\frac{1}{2}$
513	July 22, P.M.	1 $\frac{1}{2}$	Aug. 6, P.M.	$\frac{3}{4}$
526	July 23, P.M.	$\frac{3}{4}$	Aug. 4, P.M.	1
527 ^b	July 23, P.M.	$\frac{1}{2}$	Aug. 4, P.M.	$\frac{1}{2}$
529	July 23, P.M.	$\frac{1}{2}$	Aug. 14, P.M.	1
558	July 26, P.M.	1 $\frac{1}{2}$	Aug. 7, P.M.	1 $\frac{1}{2}$
560	July 26, P.M.	1 $\frac{1}{2}$	Aug. 8, P.M.	$\frac{3}{4}$
569	Aug. 1, A.M.	1	Sept. 3, P.M.	$\frac{1}{4}$
570	Aug. 1, P.M.	$\frac{3}{4}$	Sept. 6, P.M.	$\frac{1}{4}$
580	Aug. 3, A.M.	$\frac{1}{2}$	Sept. 6, P.M.	$\frac{1}{2}$
586	Aug. 4, A.M.	1 $\frac{1}{4}$	Sept. 7, P.M.	$\frac{1}{4}$
604	Aug. 9, P.M.	$\frac{1}{2}$	Sept. 3, P.M.	1
615	Aug. 13, P.M.	1	Sept. 6, P.M.	$\frac{1}{2}$
450	July 12, A.M.	1	Aug. 6, P.M.	2

* No. 470 made a second return Aug. 17, P.M., at Mile 2.

^b No. 527 made a second return Sept. 7, P.M., at Mile $\frac{1}{4}$.

TABLE 5

OBSERVED RENEWING RETURNS OF FEMALE GREEN TURTLES TO TORTUGUERO, COSTA RICA, 1958
(The quarter-mile beach sections are numbered from the mouth of the river southward.)

Tag No.	First Observed Emergence Date and Time	Mile	First Return Date and Time	Mile	Second Return Date and Time	Mile	Third Return Date and Time	Mile
653	June 25, 2100	$\frac{1}{4}$	Aug. 7, P.M.	$\frac{1}{4}$	Aug. 28, 2100	$\frac{1}{2}$	—	—
654	June 26, 2200	$1\frac{1}{2}$	July 28, 2230	$\frac{1}{4}$	—	—	—	—
657*	July 3, P.M.	$1\frac{1}{2}$	July 28, 2200	$\frac{1}{4}$	July 29, 2000	$1\frac{1}{2}$	July 30, 2300	$\frac{1}{4}$
664	July 11, 2200	$1\frac{1}{2}$	July 6, 2400	$\frac{1}{4}$	Aug. 17, 2245	$\frac{1}{4}$	Aug. 17, 2300	1
668	July 15, 2200	$\frac{1}{2}$	Aug. 6, 2100	$\frac{1}{4}$	—	—	—	—
669	July 16, 2100	1	July 30, 2100	$\frac{1}{4}$	July 31, P.M.	$\frac{1}{4}$	—	—
674	July 18, 2200	$\frac{1}{2}$	Aug. 22, P.M.	10	—	—	—	—
679	July 20, 2000	$1\frac{1}{2}$	Aug. 1, 2000	$1\frac{1}{2}$	Aug. 2, P.M.	$\frac{1}{4}$	—	—
680	July 20, 2200	$1\frac{1}{2}$	July 30, P.M.	$\frac{1}{4}$	—	—	—	—
687	July 24, 2000	$1\frac{1}{2}$	Aug. 5, 2200	$\frac{1}{4}$	—	—	—	—
691	July 24, 2300	$\frac{1}{4}$	Aug. 7, P.M.	$\frac{1}{4}$	—	—	—	—
695	July 28, 2230	$1\frac{1}{2}$	Aug. 7, P.M.	$\frac{1}{4}$	—	—	—	—
696	July 28, 2200	$1\frac{1}{2}$	Sept. 1, 2100	$\frac{1}{4}$	—	—	—	—
697	July 28, 2130	$1\frac{1}{4}$	Aug. 19, 2200	$\frac{1}{4}$	—	—	—	—
705	July 30, 2400	$\frac{1}{2}$	Aug. 22, P.M.	$\frac{1}{4}$	—	—	—	—
707	July 30, 2100	$\frac{1}{2}$	Aug. 11, 2020	1	Aug. 11, 2020	1	Aug. 22, P.M.	$\frac{1}{4}$
711	July 31, P.M.	$\frac{1}{2}$	Aug. 22, P.M.	$\frac{1}{4}$	—	—	—	—
721	Aug. 2, 2100	$1\frac{1}{2}$	Aug. 25, P.M.	$\frac{1}{4}$	—	—	—	—
729	Aug. 4, P.M.	$\frac{1}{4}$	Aug. 24, P.M.	$\frac{1}{4}$	—	—	—	—
750	Aug. 7, P.M.	$\frac{1}{2}$	Aug. 18, P.M.	$\frac{1}{4}$	—	—	—	—
758	Aug. 9, P.M.	$\frac{1}{2}$	Aug. 22, P.M.	$\frac{1}{4}$	—	—	—	—
771	Aug. 22, 2230	1	Sept. 3, 2100	$1\frac{1}{2}$	—	—	—	—

* No. 657 made a fourth return Aug. 13, P.M., at Mile $\frac{1}{4}$.

TABLE 6

OBSERVED RENEWING RETURNS OF FEMALE GREEN TURTLES AT TORTUGUERO, COSTA RICA, DURING THE SEASON OF 1959

(The quarter-mile beach sections are numbered from the mouth of the river southward.)

Tag No.	First Observed Emergence Date and Time	Mile	First Return Date and Time	Mile
910	July 9, 2300	1	July 23, 2230	1
912	July 10, 2245	1	July 23, 2230	1
915	July 10, 2330	1	July 23, 2200	$1\frac{1}{2}$
917	July 10, 2350	1	July 23, 2330	1
920	July 10, 0100	1	Aug. 2, 2100	1
934 ^a	July 13, 2400	$1\frac{1}{2}$	Aug. 4, 2300	$\frac{1}{2}$
938	July 15, 2000	$\frac{1}{2}$	Aug. 7, 2100	1
950	July 17, 0200	1	Aug. 7, 2300	1
953	July 20, 2330	$\frac{1}{2}$	Aug. 10, 2045	1
957	July 22, 2200	$1\frac{1}{2}$	Aug. 29, 2100	1
966	July 23, 0330	$1\frac{1}{2}$	Aug. 14, 2400	1
973	July 23, 2330	$1\frac{1}{2}$	Aug. 28, 2000	1
990	July 27, 0130	$\frac{1}{2}$	Aug. 19, 2400	$\frac{1}{2}$
996 ^b	July 27, 2200	1	Aug. 7, 2030	1
1010	July 29, 2300	$1\frac{1}{2}$	July 19, 2230	1
1013	July 30, 2300	$1\frac{1}{2}$	Aug. 11, 2400	1
1053	Aug. 11, 2330	$\frac{1}{2}$	Sept. 13, 2100	$\frac{1}{4}$
1057	Aug. 12, 2345	1	Aug. 23, 0130	$1\frac{1}{2}$
1070	Aug. 18, 2300	$1\frac{1}{2}$	Aug. 29, 2315	$\frac{1}{2}$

^a No. 934 made a second return Aug. 14, at 2300 hours, at Mile $\frac{1}{4}$.

^b No. 996 made a second return Aug. 19, at 2330 hours, at Mile $1\frac{1}{2}$.

INCUBATION PERIOD

During the seasons from 1956 to 1959, the average incubation period (defined as the period between oviposition and the time of appearance on the surface of the beach of the largest number of hatchlings for that batch) for 117 nests (including both undisturbed and hatchery-incubated complements) was 57.5 days, with a range of from 48 to 70 days. Hendrickson found the average period for the

Sarawak colony to be about 65 days during the monsoon season, and about 55 days for the rest of the year, with year-around extremes of 48 and 80 days. Baldwin and Lofton (in Caldwell, Carr, and others, 1959) found the average incubation period for 55 nests of the loggerhead (*Caretta*) at Cape Romain, North Carolina, to be 55 days (49 to 62 days).

NESTING BEHAVIOR

The nesting behavior of the Atlantic green turtle was described in general terms by Carr and Giovannoli (1957). Continued observation of nesting females suggests that the behavioral study of sea turtles may be given a helpful comparative basis by breaking the emergence venture down into 11 stages, as follows:

1. Stranding, testing of stranding site, and emergence from wave wash.
2. Selecting of course and crawling from surf to nest site.
3. Selecting of nest site.
4. Clearing of nest premises.
5. Excavating of body pit.
6. Excavating of nest hole.
7. Oviposition.
8. Filling, covering, and packing of nest hole.
9. Filling of body pit and concealing of site of nesting.
10. Selecting of course, and locomotion back to the sea.
11. Re-entering of wave wash and traversal of the surf.

Each of the above operations is obviously a complex chain of responses, offering considerable opportunity for ethologic comparison, although in some cases quite hard to observe or interpret. If differences in the point of view of the observer be allowed for, the behavior of the Tortuguero turtles seems very similar to that of the Pacific form (see the excellent detailed account of Hendrickson, 1958), and indeed to the sea-turtle nesting pattern generally. As suggested by Carr and Ogren (1959), two explanations for such extreme behavioral stability suggest themselves. It may be because the terrestrial interlude comes just before or just after fertilization has occurred, obviating any need for iso-

lating mechanisms at this time. Or, one might suggest that the operations are carried out in more or less the same way by all the unequally divergent blood lines of sea turtles simple because this is the one best way to do them. Animals regularly fall short of maximum behavioral efficiency, however, if departing from it helps maintain their genic integrity. In any event, the degree to which the green turtle, hawksbill, loggerhead, and ridley, and even the very divergent trunkback, duplicate the mannerisms of one another in each of the 11 stages of the emergence venture is remarkable. With this ethologic conservatism added to the convergent morphologic sculpturing by the marine habitat, it is no wonder relationships among sea turtles are so difficult to assess.

The hazard of interspecific crowding and competition for space at the rookeries is avoided by slight differences in breeding season and in location of nodes of aggregate nesting. The loggerhead nests chiefly along the margins of the tropics, well out of the main breeding range of the other genera. The trunkback comes out in April and May, and, although individuals may choose a beach frequented by other kinds of sea turtles, the nesting colonies seem to be always located away from sites of mass emergence of green turtles, which in the Caribbean nest mainly in July and August. On beaches such as that at Tortuguero, where green turtles nest heavily, trunkbacks and hawksbills occasionally, and loggerheads sporadically, the trunkbacks are the first to come out, the hawksbills are next, and then the big flotillas of *Chelonia* follow. The loggerhead visitors seem to be fortuitous stragglers. It is of in-

terest that fishermen along the Central American coast say that after the green turtles have gone in October a few hawksbills may be seen again in November. Such an occurrence, if true, represents a split season for *Eretmochelys*, and this might be regarded as an adaptive response to the overpoweringly heavy green-turtle activity that takes place in midsummer.

Although we are by no means ready to fill out details of the above outline of emergence and nesting behavior, even for the green turtle, plates 2 to 6 herein show the stages of the nesting process and some of the behavioral stereotypes that appear to be promising ethologic criteria.

Plate 2 (fig. 1) shows a turtle thrashing out the concealing pit in which she lies during the laying process. Besides the protection that it offers, this depression adds 9 to 18 inches to the depth of the nest proper, which is dug in its bottom. A nest begun at the general sand surface would often be too shallow to maintain an even temperature and moisture throughout the incubation period. The first digging is done by the fore fins working together; then one hind foot starts kicking, then the other, and finally kicking by the back fins alternates with the sweeping by the fore flippers. The body pit of the green turtle is deeper than that made by the other thecophoran sea turtles. An hour may be consumed in digging it, and when finished it often lets the turtle rest with the top of her shell level with the ground. The digging of this pit grades into the work of digging the nest. The forefeet slowly decrease the pace of their thrashing, and the hind fins change over from a backward kick to a scooping push at the ground directly under the back of the shell.

In excavating the egg cavity the turtle pushes the edge of a hind flipper into the sand just under the hind angle of the shell (pl. 2, fig. 2), picks up a small amount of sand and drops it at one side (pl. 3, figs. 1-2). As this happens, the right hind foot, until now anchoring the body posteriorly for the digging work, jerks quickly forward, kicking away any loose sand that might slump into the hole on that side (see Carr and Giovan-

noli, 1957; Carr and Ogren, 1959). Excavation proceeds in a series of such alternating actions by the hind feet, except when some obstruction such as the root shown in plate 4, figure 1, is met and the rhythm is temporarily broken.

In figure 2 of plate 5 note the sand caked beneath the eye. Green turtles "cry" while nesting, as other sea turtles do. The discovery, by Schmidt-Nielsen and Ragnär (1958), that this crying is associated with salt regulation should not distract attention from the fact that it is a useful adaptation in another way. Sand is bound to get into a turtle's eye while she is digging her nest. A simply moist eye would go blind on shore from the sand stuck on it. A dry eye such as that of the snakes might serve but turtles do not possess such an eye. The wetting of the adhering sand by copious tear flow causes it to cake into masses that keep falling away repeatedly and leaving the eye clean. It thus seems clear that the tear secretion by sea turtles is a dual adaptation, with one use in the sea and another on land.

When laying is finished (pl. 6, fig. 1), the two hind feet scrape and push in sand from the sides, working separately or together, until the hole is full, and a mound rises where it was. The turtle kneads this mound and pushes at it with the inner edges of the flippers in short, chopping strokes. This stage ends when, after a few short kicks with the hind feet, first one and then the other of the fore fins slings sand backward, beginning the work of covering and concealing the body pit and nest site (pl. 6, fig. 2). Resumption of work by the fore flippers throws sand into and around the pit, and occasional spurts of kicking by the hind feet help fill the basin. After a while the turtle starts inching forward as the sand is slung backward. She continues this motion until a broad strip has been ploughed for a variable distance away from the nest, quite clearly as a concealing maneuver. As in *Dermochelys* (see Carr and Ogren, 1959) this slow, jerky progress builds gradually into full-pace locomotion towards the sea. The turtle shown in figure 2 of plate 6 is approximately 6 feet from her covered nest, and she is still throwing sand.

EMERGENCE OF HATCHLINGS FROM NEST

It is usual to dismiss the process by which turtle hatchlings climb out of the earth at the nest site as "negative geotropism." An excellent and detailed account of the actually complex series of activities, and the changing space relations, that attend the emergence process was given by Hendrickson (*loc. cit.*). Baldwin and Lofton (*in* Caldwell, Carr, and others, 1959) mentioned the role of group action in the escape of young loggerheads from the nest. Carr and Ogren (1959) called attention to survival values presumably involved in this activity and stressed the evolutionary importance of group behavior at this time. Results of preliminary experiments aimed at evaluating the selective importance of group emergence will appear in another paper (Carr and Hirth, in press).

To study more closely the emergence responses of a group of green turtle siblings, a late-stage clutch of eggs was removed to an artificial nest, and a glass pane was substituted for one side of the nest cavity. The eggs were laid July 1, 1958, and were removed August 19. The outer part of the shell had started to flake off and the eggs to lose turgor, and the fully formed young could be readily felt through the wrinkling shell. In the new nest the bottom of the mass of eggs was 22 inches below the surface of the beach and the top of the mass 17 inches deep. The sequence of events that ensued is outlined in the notes below.

AUGUST 23: The surface of the sand directly over the nest has been lowered about an inch. Inspection through the pane shows that the eggs have mostly hatched, probably last night. The surface slumping is due to the dropping of the nest plug to fill the space left at hatching. The loss of this space as working room between the bottom of the plug and the top of the mass of hatchlings presents an abnormal factor, perhaps obviated in nature by the careful pressing and kneading the female does as she fills the nest.

AUGUST 24: Ceiling of nest cavity still 17 inches from the general surface of the sand, the hatchlings having regained the inch or so of free space lost the day before when the plug dropped.

AUGUST 25: Ceiling now 16 inches from

surface. The floor level has been built up 3½ inches by fallen sand and trampled eggshells.

AUGUST 26: Ceiling 15½ inches from surface at 1300 hours; at 1830 hours, 14 inches from surface.

AUGUST 27: Ceiling 13½ inches below surface, with ½ inch of space between ceiling and topmost hatchlings in the mass.

AUGUST 28: At 0700 hours ceiling irregularly sapped out, with highest point only 1 inch below surface. Topmost turtles now about 5 inches from ceiling. A heavy rain during the night may have helped to collapse the lower end of the nest plug, hastening the ascent of the turtles in the hatchling chamber. By 1800 hours, more of the ceiling has fallen, without, however, raising the level of the hatchling group appreciably. Digging is evidently much more active at night; in the present test it seems possible that light entering through the glass pane during the daytime may inhibit activity. At 1910 hours there is more horizontal movement by the individual turtles, causing an undercutting of the lateral walls and a continued raising of the floor by the sand produced.

AUGUST 29: At 0600 hours the nest roof is only an inch thick, and the top turtles are 4½ inches below it and resting horizontally. At 1830 hours most of the turtles have assumed vertically oriented positions (as they had for brief periods previously) and are only 2 inches from the ceiling and only 3 inches below the surface of the beach. Their flurries of activity are intermittent and short and always stop abruptly when the rays of the flashlight pass across them.

AUGUST 30: The hatchlings emerged unobserved during early morning hours.

Observation of the above nest, and of numerous others dug out at various stages of the emergence process, suggests that it is not adequate to attribute the emergence feat to negative geotropism alone. In our observations, while the result of group activity was vertical displacement of the group, the emergence process was not by any means a simple upward climb by each separate individual. The work that caused the raising of the common chamber was a series of outbursts of thrashing and twisting, during each of which

the topmost turtles sapped the ceiling, those at the sides dislodged sand from the walls, and those on the bottom of the mass shifted jerkily about, allowing the sand from ceiling and walls to settle and be packed into a new, higher floor. Such group spasms were followed by periods of complete quiescence. The stimulus for renewed movement seemed to come, not from the individuals on top, where the most effective sapping could be done, but from among the uncomfortably situated lower layer of hatchlings. That is to say, the group effort is instigated by the bottom tier of turtles when the group weight of their siblings above irritates them. An onset of restlessness by any one of these is sufficient to plunge the whole group into another convulsion of work. The emergence process thus appears to be a strongly cooperative undertaking. Besides the teamwork and division of labor involved in the actual sapping and packing, the onset of the successive bursts of digging seems also to some extent dependent upon crowding.

Hendrickson (1958) and Carr and Ogren (1959) observed that hatchlings often emerge in small lots, at intervals, instead of all together, owing to subdivision of the group by slight differences in hatching schedule. In most of our nests emergence by such subgroups of siblings usually occurred at intervals of 24 hours. As has been found to be the case with most sea turtles, nests at Tortu-

guero seem to erupt usually at night, the hatchlings probably being inhibited in their digging, if near the surface, during the daytime, by the heated upper layers, as was suggested by Hendrickson (1958). He found that most emergences occurred between midnight and dawn, while at Tortuguero they seem to take place mostly before 2000 hours. The blackness of the sand at Tortuguero must have considerable bearing on its properties as an incubating medium, causing it to heat up faster and to reach higher daytime temperatures than beaches of the usual shades of tan or white. We had formerly assumed that, in accordance with the physics of black bodies, it should cool off more rapidly at night than the usual beach and that such cooling, if it occurred, might explain the earlier emergence of hatchlings there. But in a letter (February 10, 1957) Dr. Charles F. Brooks has corrected this misapprehension, saying: "Tortuguero's black sand must indeed make it get hotter by day than white or yellow sand. Its blackness, however, would not make it cool more rapidly at night than white or yellow, for all non-metallic surfaces are virtually like black bodies when it comes to long-wave radiation." Certainly the budget of absorbed heat is greater for each period of insolation than in most places, but the bearing of this upon the timing of nest eruptions is not evident.

ORIENTATION

The dual, land and water life cycle of aquatic turtles imposes extraordinary orientation demands, and, in the case of *Chelonia*, the great distances that separate feeding and nesting grounds almost surely make true navigation necessary. From the time the hatchling green turtle breaks out of the egg and begins its vertical climb to the surface of the beach until the mature female comes back to shore to nest, sea turtles are presumably guided towards genetically represented "goals" by information, or cues, about which biologists know very little. These orientation events may be arranged in a number of stages, corresponding to ontogenetic and periodic stages in the life cycle, as outlined below.

MOVEMENTS OF HATCHLINGS

FROM NEST TO SURFACE: The goal in this case is the surface of the beach. Geotaxis is the sense usually suggested as guiding the emerging hatchlings. The process is actually quite complex. Details are discussed in another section (see above).

FROM NEST TO WAVE-WET SAND: The general goal here is of course the sea, which the animal has not seen before, and the location of which may be hidden behind obstacles of various sorts. The kinds of stimuli involved and the complexity of the problem faced by the hatchling are discussed in our section on field tests of sea-seeking orientation.

ACROSS WAVE-WET SAND: The abrupt quickening of gait and mounting "enthu-

siasm" of the hatchling on reaching the wave-smoothed lower beach suggest that a change of cue takes place at this point. Perhaps the feel of the smooth wet substrate serves to heighten drive as the water goal is approached, and to condition the hatchling for changes in responses and for the increased exertion to be required of it in going through the surf.

TROUGH WAVE WASH: At the instant the hatchling is lifted by the wash of the first wave, its gait changes from a crawling to a swimming stroke. Although no break in the continuity of locomotion can be noted, it seems likely that current sense must take over as the dominant orienting factor during the energetic (sometimes almost frantic) approach to the breaker line.

THROUGH BREAKERS: On approaching the outermost, more or less rhythmically breaking surf, the hatchling dives as each comber approaches, clearly taking a visual cue in timing its dive to get under the shoreward push of the wave and to ride the undertow through the breaker line. During the half minute or so of this dive, current sense is also probably still in operation. This would not be simple rheotaxy, as it involves fighting the current at one moment and running a downstream course the next. The reaction would appear to be one of simply maintaining axial alignment with any current, positive or negative.

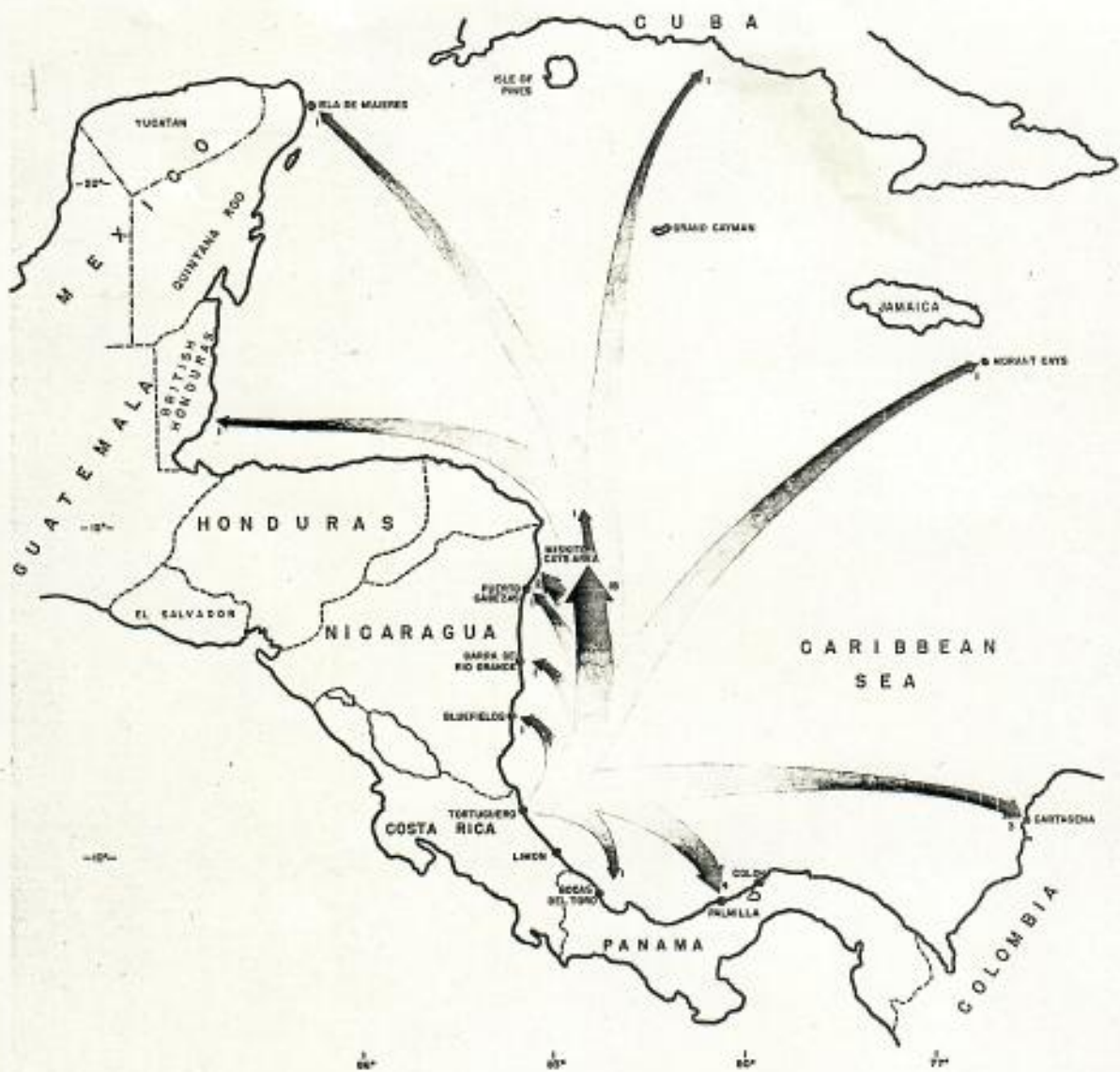
TRAVEL BY HATCHLINGS AND IMMATURE STAGES: Once the quiet swells beyond the surf are reached, the hatchling floats for a bit, with head held high, and then, alternately paddling and craning its neck to "inspect" the horizon, makes off to sea and disappears from view. During the stages of development that follow, until the nesting female comes ashore to lay, little or nothing is known of the life of the green turtle. It is known that food habits shift from largely carnivorous tendencies in the young to mainly herbivorous feeding in the adult. It may be that this change involves a number of steps, requiring that the developing turtle be in different places at different times to find animal food of appropriate size and abundance. Possibly this feeding ontogeny has resulted in long-distance travel by the developing animal, with age groups (feeding stages) distributed in different stations along a route of active

migration, or of passive drifting, or of both. Evidence (such as the absence of young turtles on the *Thalassia* pastures of the adult, and the lack of hatchlings off the nesting beach after the nesting season) is mostly negative, the only possibly relevant fact available being the regular yearly appearance in Florida of an itinerant population of immature green turtles evidently derived from some distant nesting ground (Carr and Caldwell, 1956).

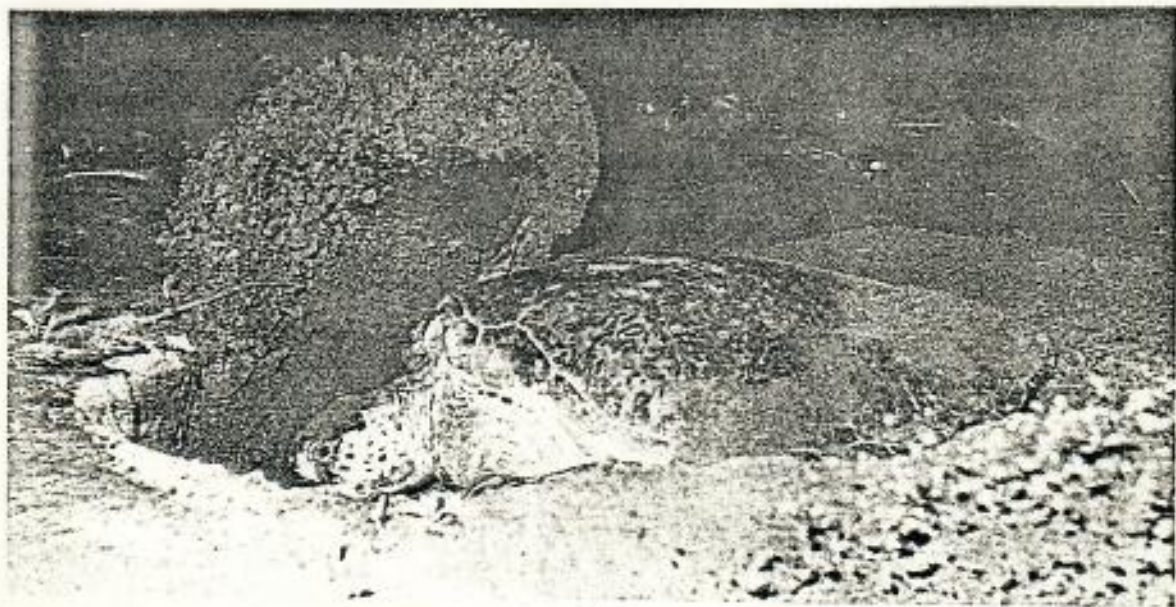
MOVEMENTS OF SEXUALLY MATURE TURTLES

DIEL COMMUTING: Green turtles in the Caribbean appear usually to spend the night on the bottom, or among rocks or coral crags. Suitable sleeping sites may be located some distance away from the turtle-grass pastures. While not proved by tagging data, it is widely believed by people in the turtle fishery that strong site tenacity is shown by the green turtle returning to its sleeping place. The senses and information used by the animal in these homing feats are unknown. The trips take place in shallow water, and it seems possible that landmarks or bottom topography are used. Cases of homing by young Florida green turtles over some 30 miles of shore water, after having been carried away overland by truck, suggest (but do not prove) that something less simple than landmark guidance may be involved (see Carr and Caldwell, 1956).

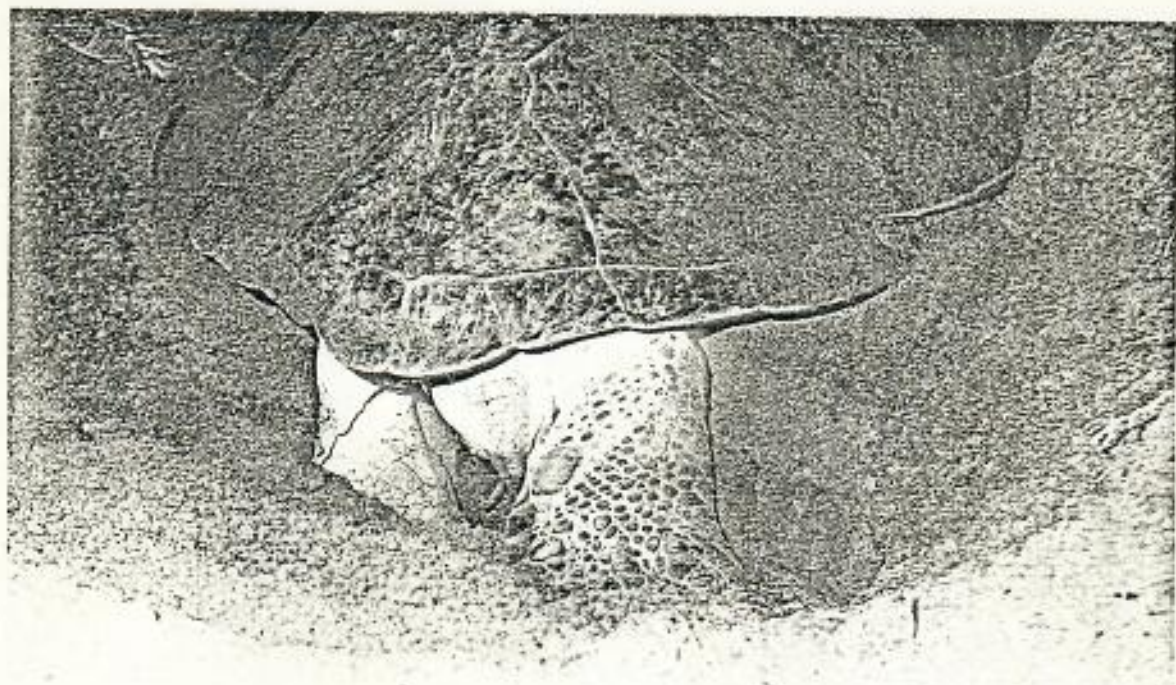
PERIODIC REPRODUCTIVE TRAVEL: The evidence that high-seas travel to distant rookeries actually occurs is discussed in another section. If our interpretation of those results and of supporting observations is correct, it appears likely that the reproductive travel involves true navigation. Recent experiments demonstrating a light-compass sense in birds and arthropods, the work of Hasler and his co-authors (1958) describing sun orientation in fishes, and Gould's studies (1950) of homing in box turtles all make it easier to suppose that green turtles use the heavens for guidance (as the turtle men say they do) and have the same spectacular guidance equipment (an inherent goal sense, a light-compass sense, a time correction sense, and a displacement sense or map sense) that other animals have been found to have.



Distribution of international recoveries of tags from green turtles marked at Tortuguero, Costa Rica, 1955-1959. The arrows show only spread from the tagging locality, not routes. The figure near the head of each arrow indicates the number of recoveries at that place

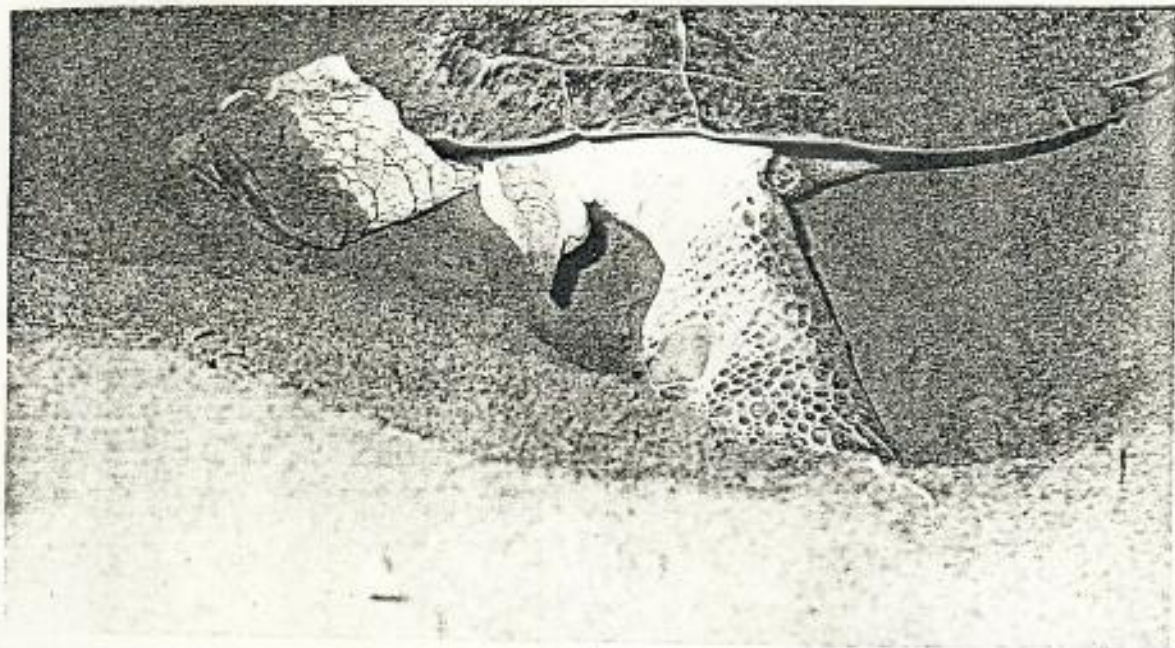


1

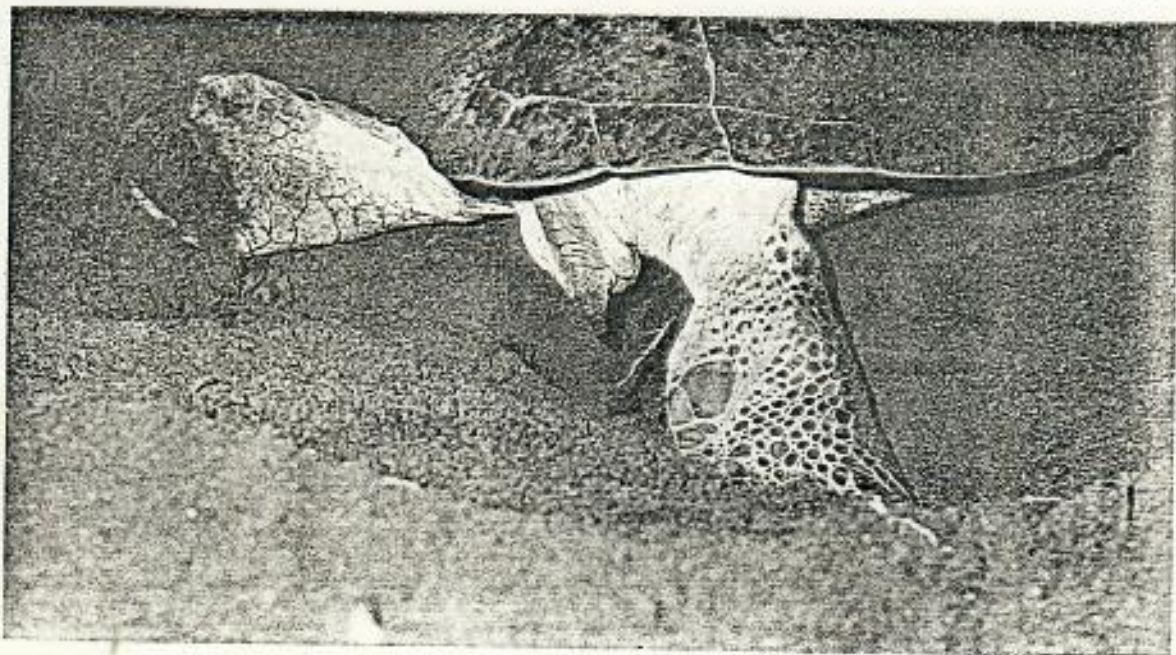


2

1. Tortuguero green turtle digging the concealing basin in which she rests while laying her eggs
2. Beginning to excavate the egg cavity — the nest proper

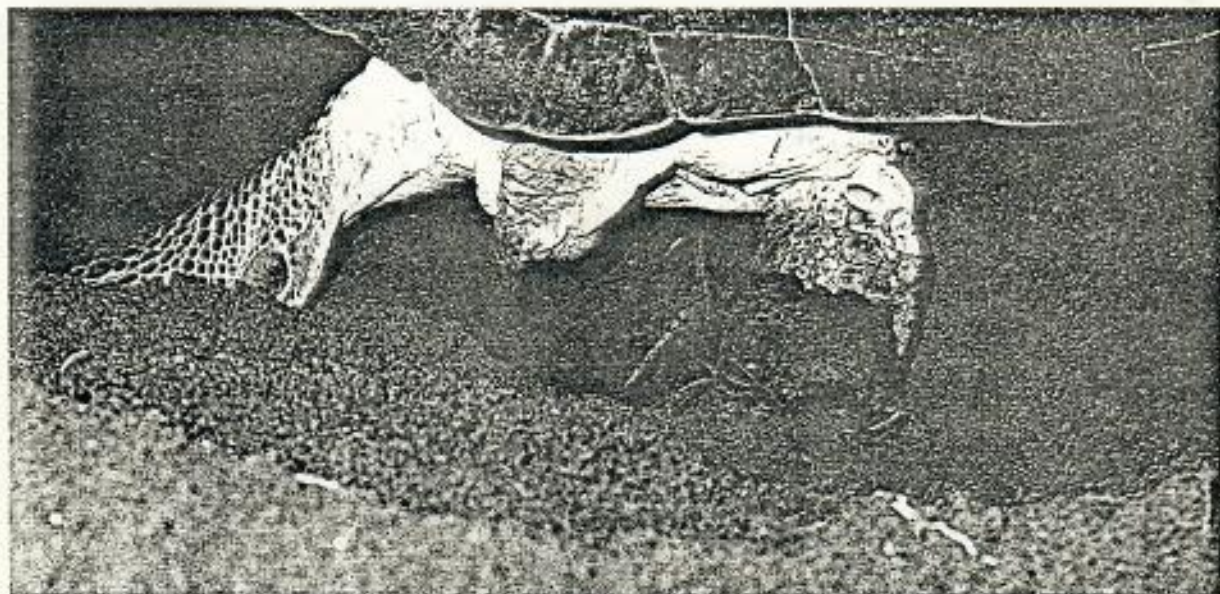


1

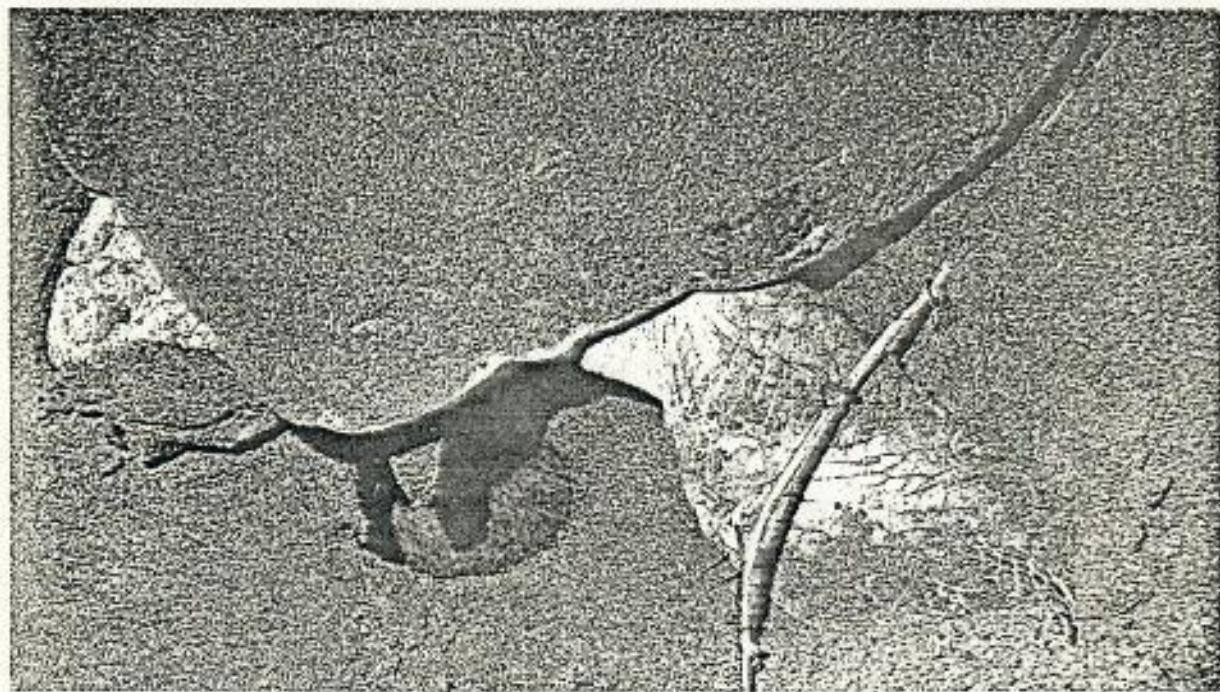


2

1. The left hind foot has removed a load of sand from the egg hole and is about to drop it at one side
2. The flipperful of sand is dropped, and the right hind foot will, in the next instant, kick sand forward

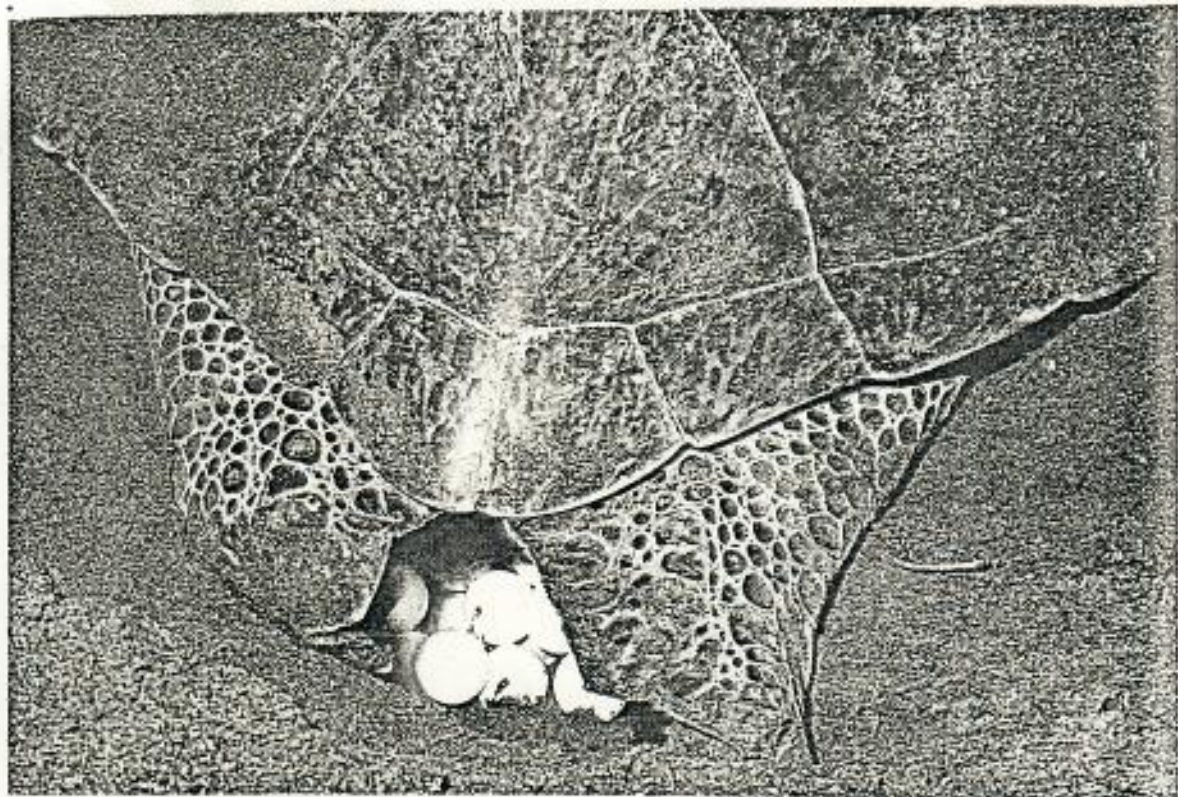


1

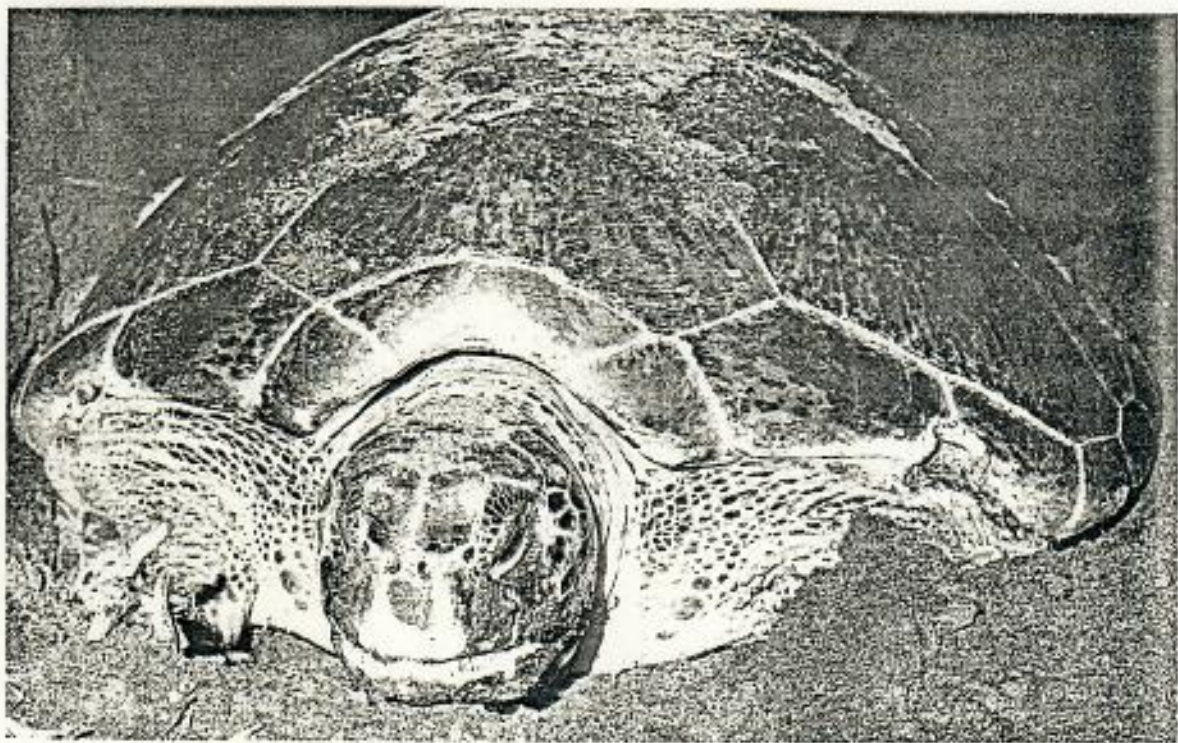


2

1. The right hind foot has broken an obstructing root, has resumed the scooping of sand from the hole, and is swinging a palmful out to the side to be dropped. Note difference in dry surface sand and sand just uncovered
2. A nearly completed nest cavity, shaped like a lopsided flask, with the bottom enlarged anteriorly and the sides somewhat squared (cf. Carr, 1948)



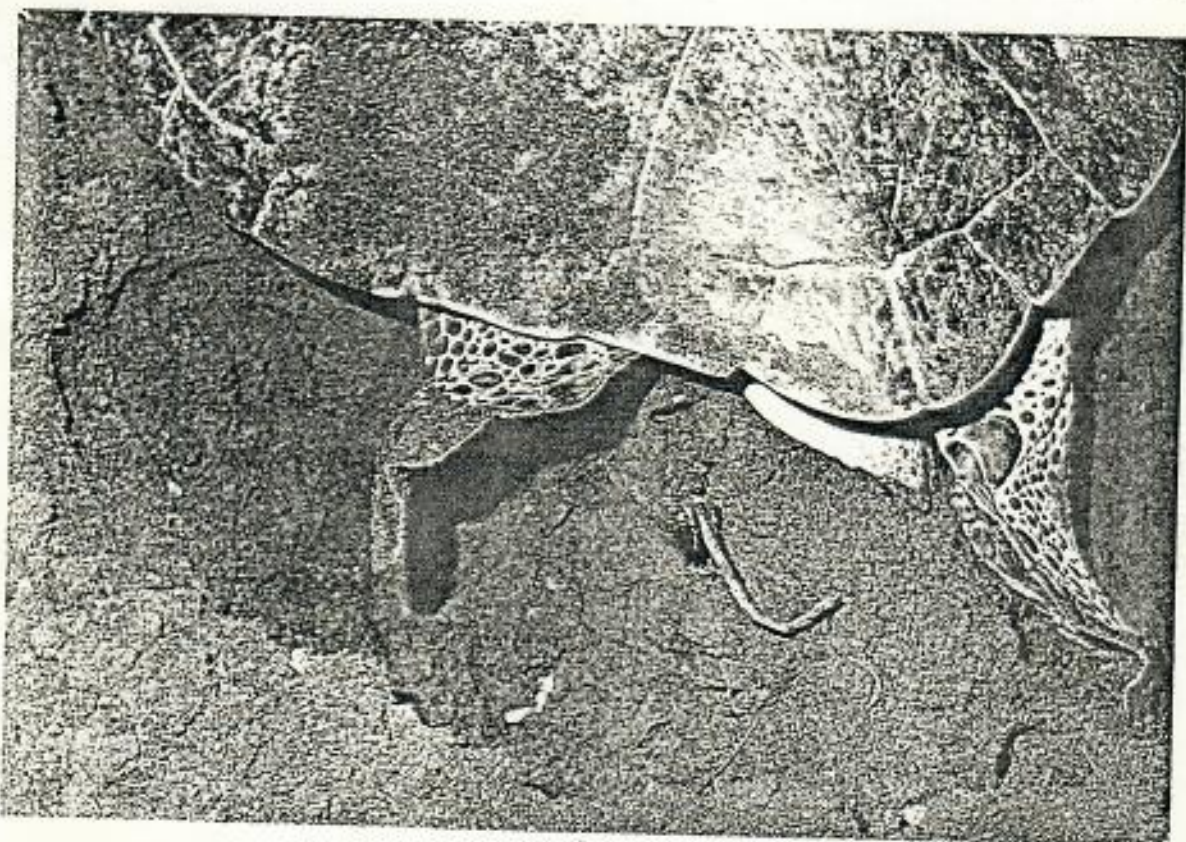
1



2

1. The end of the laying process, showing the hind fins in the position they usually hold throughout oviposition. We pulled the right foot slightly towards the right to expose the eggs for the picture (cf. Carr and Giovannoli, 1957, fig. 12)

2. Anterior view of a Tortuguero green turtle laying her eggs. The deep notch on each side of the anterior shell margin was made by the grappling nail of the male during copulation

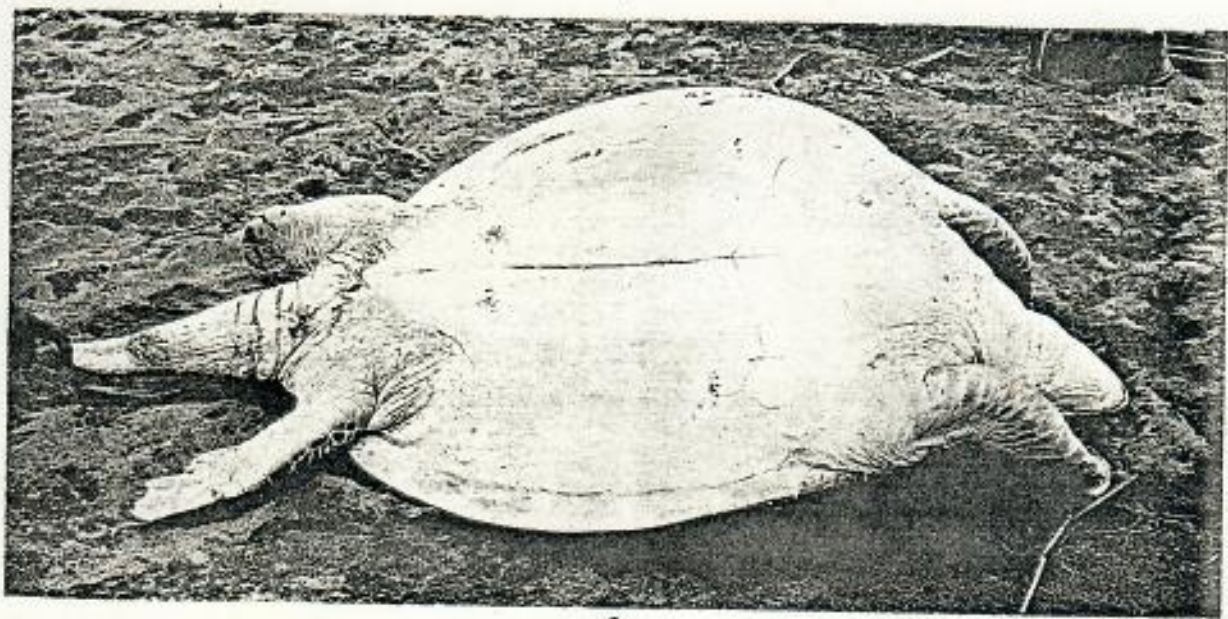
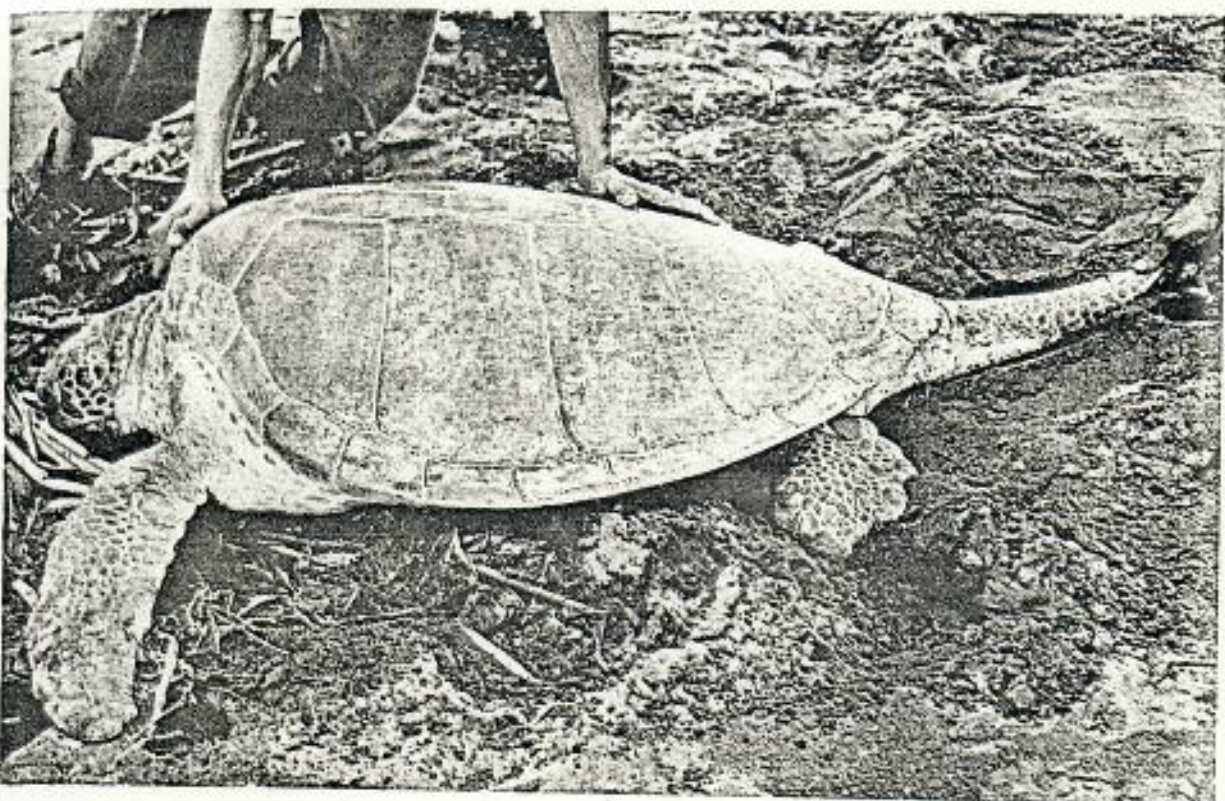


1



2

1. Turtle covering the nest
2. Turtle covering and concealing the body pit and nest site



1. Male green turtle caught in the surf at Tortuguero on July 12, 1959, when he chased a female too close in shore and was thrown up by a breaker

2. Ventral view of the male green turtle shown in 1. Note the heavy nail curving back beneath the edge of the near front fin and the long tail, with the vent placed well back towards its end

THE STRANDING DECISION: Varied evidence (Carr and Giovannoli, 1957; Hendrickson, 1958; Caldwell, Carr, and others, 1959; see also figs. 5 and 6 and tables 3-7 of the present paper) emphasizes the tendency of this and other kinds of sea turtles to return to restricted sites for repeated nesting emergences. It seems likely that the selecting or recognizing of the place to go ashore, which may come after a long journey guided by celestial information, involves a shift to such topical cues as currents, landmarks, bottom contours, or the taste, smell, or feel of the water.

FROM SEA TO NEST SITE: A succession of local cues, as well as whatever information may furnish the bearing for the goal itself, is clearly involved here. Possibly the loom of dark areas and objects may be the beacon for the general course of the trip up the beach. One might argue that this is negative phototaxis, but the fact that a turtle never can be seen turning her head back towards the seaward horizon would seem to preclude the comparative judgment involved in simple phototaxis, negative or positive. In any event, when all the various distracting local features, and the reorientations carried out in avoiding them, are reckoned in, the problem of deciding what guides the female to the

place that becomes her nesting site seems imposing. Whatever she is pondering or perceiving, a turtle on her way up the beach does a great deal of stopping to peer ahead and to one side and the other, or merely to wait, as if for some sensation or stimulus to sink in. When the decision to stop is finally made, the observer is usually unable to discern the attractions of the place selected, or the criteria used in her deciding on it. (See Carr and Giovannoli, 1957.)

NEST SITE BACK TO SEA: The problem here is that faced by the hatchlings on emerging from the nest. Whether or not it is solved in the same way is not known. The fact that the female has, on her way up, laid a trail that could be followed in returning to the sea would seem to give her an advantage not available to the hatchling. The fact is that the back track is in every case ignored. In the hundreds of females that we have seen leave nests, we have noted no serious case of confusion. When the nest is covered and concealed the turtle usually turns abruptly and assuredly towards the sea, even though it may be hidden by dunes or bushes, and maintains a proper heading with little digression. She may stop and blink now and then or show signs of fatigue before reaching the water again; on the other hand if prompted

TABLE 7

POINTS OF EMERGENCE AT TORTUGUERO, COSTA RICA, OF FEMALE GREEN TURTLES
RETURNING AFTER ABSENCES OF TWO OR THREE YEARS

(Because of loss of tags, and of changes in our system of designating beach sections, it was possible to determine concordance of emergence points for only the 13 cases of long-time return shown here.)

Tag No.	Date Tagged	Place Tagged	Place Retaken	Date Retaken
281	Aug. 9, 1956	Mile $\frac{1}{2}$	Mile $\frac{2}{4}$	July 30, 1958
308	Aug. 15, 1956	Mile $\frac{1}{2}$	Mile $\frac{1}{2}$	Aug. 28, 1958
320	Aug. 16, 1956	Mile $1\frac{1}{4}$	Mile $\frac{1}{2}$	Aug. 24, 1958
338	Aug. 19, 1956	Mile $\frac{2}{4}$	Mile 1	July 13, 1959
381	Aug. 28, 1956	Mile $\frac{1}{2}$	Mile $\frac{2}{4}$	Aug. 25, 1958
382	Aug. 30, 1956	Mile $\frac{1}{2}$	Mile $\frac{1}{2}$	Aug. 17, 1958
347	Aug. 20, 1956	Mile 0	Mile $1\frac{1}{4}$	July 26, 1958
520	July 22, 1957	Mile $\frac{1}{2}$	Mile 1	July 10, 1959
566	July 30, 1957	Mile $\frac{2}{4}$	Mile $\frac{2}{4}$	July 28, 1959
378	Aug. 25, 1956	Mile $\frac{1}{2}$	Mile $\frac{2}{4}$	Aug. 4, 1959
586	Aug. 4, 1957	Mile $1\frac{1}{4}$	Mile $\frac{1}{2}$	Aug. 10, 1959
377	Aug. 25, 1956	Mile $\frac{1}{2}$	Mile 1	Aug. 11, 1959
379	Aug. 25, 1956	Mile $\frac{2}{4}$	Mile $\frac{1}{2}$	Aug. 12, 1959

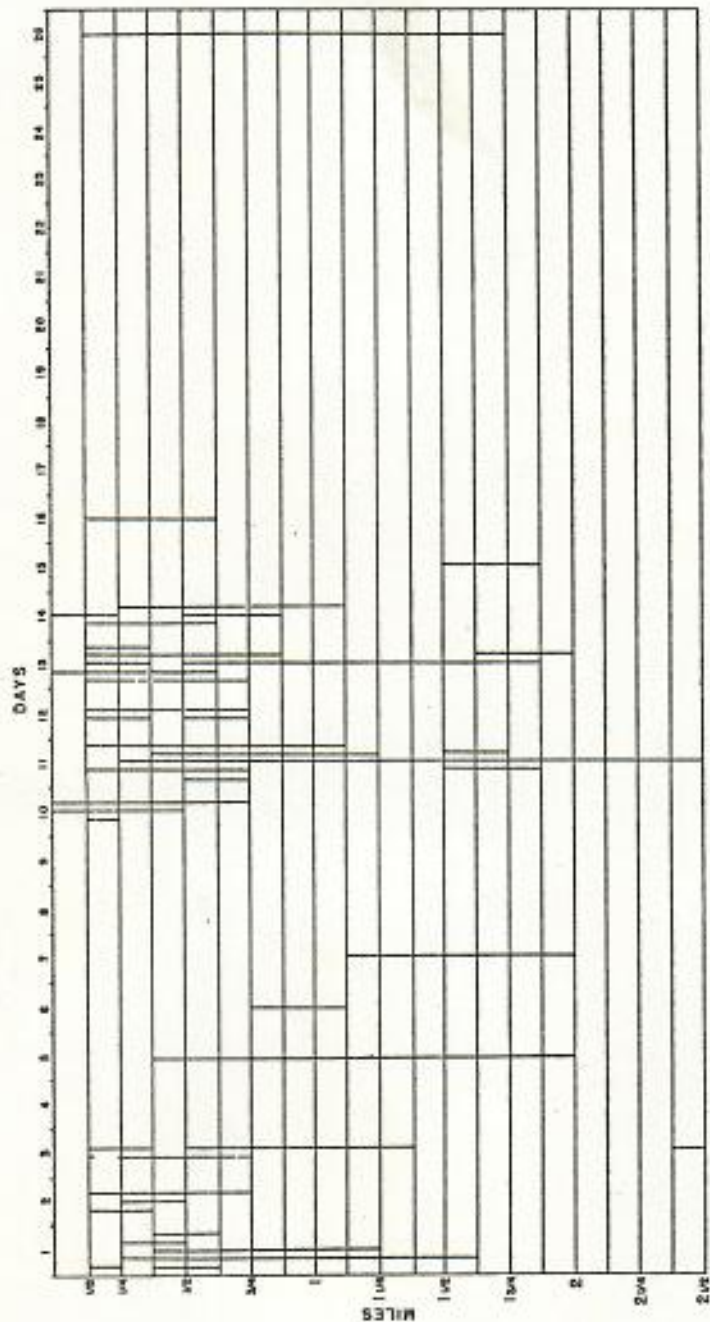


FIG. 5. Movements of turtles reneesting at Tortuguero, Costa Rica, July-September, 1956. Distance in miles along the beach (vertical scale) is plotted against time intervals between captures. Because the vertical scale shows distance southward from the mouth of the river (the northern boundary of the study strip), each of the vertical lines shows, besides time and distance, the place where each capture occurred. The lack of correlation between time and spread presumably means that the returns are not random but oriented.

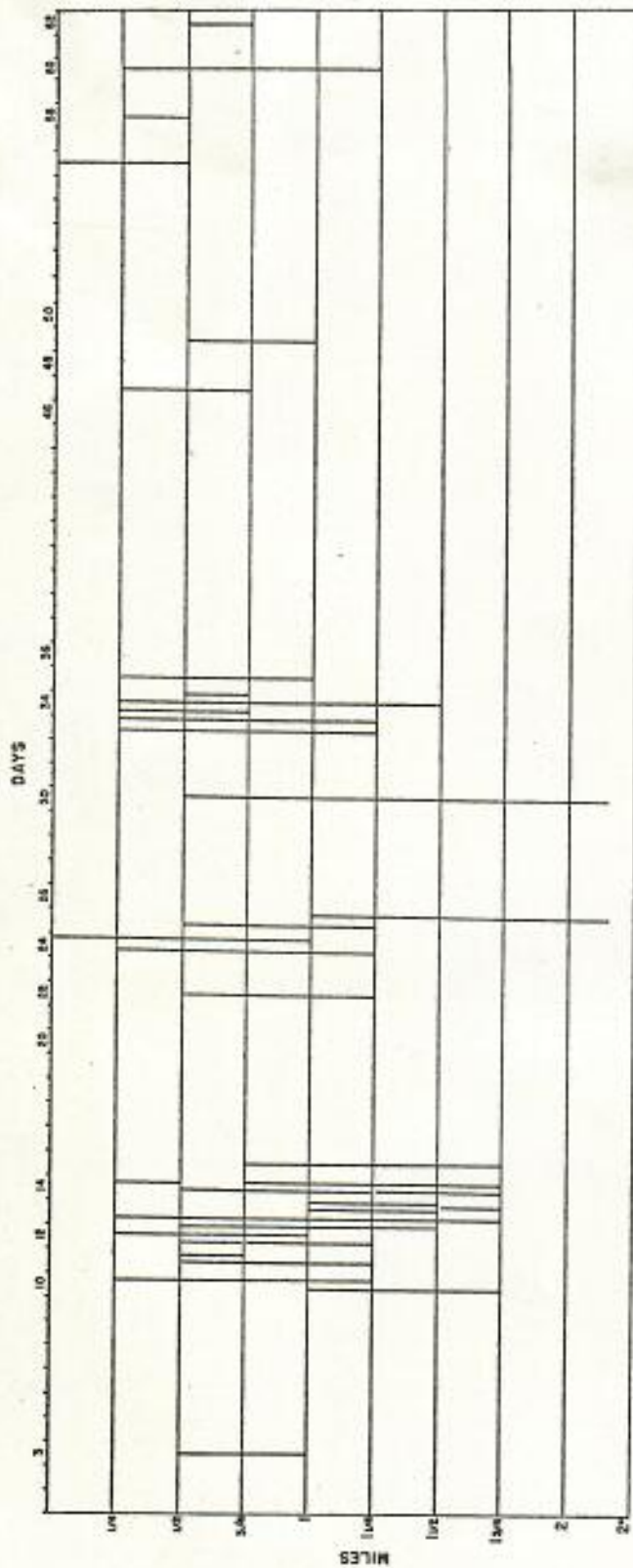


FIG. 6. Movements of green turtles reneesting at Tortuguero, Costa Rica, July-September, 1957. Distance in miles along the beach (vertical scale) is plotted against time intervals between captures. Because the vertical scale shows distance southward from the mouth of the river (the northern boundary of our study strip), each of the vertical lines shows, besides time and distance, the place where each capture occurred. The lack of correlation between time and spread presumably means that the returns are not random but oriented.

by a foot or a poke from a stick she may scuttle across the whole space without stopping. At such times the sight of the sea itself cannot be ruled out as an orienting cue. Especially if the water is flaring rhythmically with phosphorescence, as tropical surf is likely to do, and not hidden by objects in the foreground, simple inspection of the prospect should (as it would for a man) furnish all the necessary information. We do not suggest, however, that this alone would be a reasonable explanation of sea-finding capacity of the returning female, any more than it would be for what a sea-seeking hatchling does.

GROUP MOVEMENTS AND SITE TENACITY

Because of the character of the nesting localities in which his studies of the Pacific green turtle were made—a series of small islands, separated by varying distances and each thoroughly patrolled throughout the season—Hendrickson (1958) was able to show a clear tendency for females returning for re-nesting to go back to the same island (and by inference, to the island where they themselves had hatched). Although Hendrickson said, unaccountably (p. 503), "It is not known yet whether the individual female turtle consistently returns to the same island previously used for nesting . . .," he had, as we have said, earlier shown strong evidence to the contrary, and we suppose the quoted statement to be a slip of some sort. In another section he points out that, of several thousand observations of females returning to re-nest during a given season, only 3.7 per cent changed islands and suggested that these might have been frightened away from their preferred island by patrol activity.

From our data and observations there seems, as we have said earlier, little doubt that both group travel and a strong site tenacity and "homing" capacity are characteristic of the green turtle and, perhaps, of sea turtles generally. Here again, however, as in the case of attempts to judge population sizes and distribution from long-range tag recoveries, evaluation of the data is made difficult by the uneven character of the sampling method. Moreover, it will readily be seen that data seeming at first glance to prove concerted or concurrent group activity may

actually be evidence of homing, although there can be no real doubt that both phenomena (site tenacity and mass travel) occur.

Carr and Giovannoli (1957) and Caldwell, Carr, and others (1959), in seeking examples of group movements in sea turtles as evidence of mass migration, pointed out cases of grouped re-nesting by turtles that had been tagged at the same place and time as proof that the turtles had traveled together during the interval between their simultaneous appearances on the beach. We now see more clearly that these data may reflect only site fixity and hormonal periodicity in separately acting animals and may have no bearing on gregariousness or group travel at all. Consider, for example, Nos. 294 and 295 in table 3, tagged at the same time and the same place on the beach, and 12 nights later found together at a spot so close to the site of tagging that our record plot of the beach fails to separate the two localities. Such a coincidence could of course be taken to mean that the turtles were acting as a pair, perhaps as a section of a larger breeding aggregation. It also could mean, however, that each of them merely had the same "homing" drive, and, as the Tortuguero turtles adhere closely to a 12.5-day re-nesting schedule, there would be nothing remarkable about their turning up together for the second nesting, even though they might have passed the interim in widely separated places. Yet another shading of explanation of the simultaneity in returning is possible. There is a broad, shallow, rocky bank just to the north of the mouth of the Tortuguero River. While not densely covered with vegetation, this flat seems to offer enough forage and denning cover to hold a fair number of turtles there for at least part of the interval between their nesting emergences (although it does not seem to offer an answer to the troublesome question of where the bulk of the nesting colony goes between the nesting emergences of a given season). If the two turtles referred to above went to this bank after being tagged, stayed there for the interval between nestings (even perhaps without coming in contact with each other during the whole time), their returning to re-nest at the same time and the same place could still be attributed to individual site sense plus endogenous periodicity.

Still other factors should be considered in evaluating the cases of grouped return. One is the oddly uneven character of the Tortuguero shoreline. This is not a straight beach but an even series of shallow scallops forming a sequence of spits and coves. This topography almost certainly would influence the stranding reacting of the coasting turtles, tending to bunch emergences independently of the finer homing response of each individual involved. Another fact that must be considered is that breeding activity is not evenly distributed from one end of the 22-mile rookery beach to the other. There is, for instance, an above-average concentration of nesting on our study section (the 3-mile strip from Tortuguero village to the mouth of the Tortuguero River), possibly due, in part, to the proximity of this end of the beach to the above-mentioned bank. This seems unlikely, however, when one considers that the other site of especially heavy nesting (the heaviest for the whole 22 miles) lies between Mile 7 and Mile 11 from the mouth of Rio Tortuguero, where there is no adjacent flat to serve as a temporary feeding or loafing center.

With increasing government interest in green turtles, more rigid protective restrictions have come into force, and there are parts of each season when there is no turning of turtles at all on the miles south of our beach. During such times, of course, we have no way of knowing what is happening there. When commercial turtling was going on, we regularly paid rewards for all tags taken, even if they had been attached only the night before. At those times a fairly adequate sampling of return distribution was possible, especially for the 1955 season (see Carr and Giovannoli, 1957), when we were not waiting out the egg-laying operation of each turtle encountered and were able to make more than 600 captures.

The returns to Tortuguero beach after the two- or three-year interval of the reproductive cycle furnish the most dramatic evidence of "homing," or site tenacity (in fact, the occurrence of even a single case such as that of No. 566 in table 7 appears unlikely to be the result of chance alone). The re-nesting returns, however, during a single season seem also to show non-random spread. Tables 3-6 give dates and places of all re-nesting recoveries

for the years 1956-1959 (see also figs. 5 and 6). Such cases as those of Nos. 657, 664, and 679 (table 5), frightened at the time of an attempted stranding and later found nesting elsewhere, show that the homing falls short of a real "spot tenacity," although returns to the exact same spot sometimes do occur (see No. 669). The usual spatial interval would be of the order of $\frac{1}{2}$ to $\frac{3}{4}$ mile. The greatest spread in successive emergences recorded by us is to be seen in the case of No. 674, which moved from Mile $\frac{3}{4}$ to Mile 10.

In spite of such aberrant cases and of the lack of statistical support for the belief, we are convinced, as we have said, that the re-nesting returns alone indicate a marked homing urge and ability in the female Caribbean green turtle.

FIELD TESTS OF ORIENTATION CAPACITY

Although ontogenetic changes in feeding requirements (and thus in habitat) must confront green turtles with corresponding shifts in orientation problems, it seemed possible that the navigational sense of the adult might to some extent be represented in the capacity of the young to go from the nest to the sea. This possibility suggested a feebly promising approach to the difficult navigation problem: tests in the field with goal-driven hatchlings. The difficulty of clearing up even this most testable phase of the orientation life of a sea turtle may be seen in the diversity and inconclusive character of the observations and experimental results of others. While nothing of the sort has been published on *Chelonia*, the general similarity of all turtles with respect to nesting behavior suggests that factors guiding the young from the nest, through a drastically varying beach landscape, to the water that they only genetically know exists might be similar in all aquatic species. The principal conclusions that have resulted from previous tests with emerging hatchlings are summarized in table 8.

During July and August, 1957 and 1958, we conducted a variety of informal tests of the ability of green turtles on shore to find the sea. These were arranged after preliminary trials had shown that even this short orientational feat is probably a complex chain of events, with cues and responses changing

with each change of outlook or of the local substrate, or of time and weather.

For each test a group of 10 reactors was used. The group was built up to standard size by our submitting hatchlings to the conditions of the test release, until 10 had shown signs of active response, the unresponsive individuals being discarded. The criterion for responsiveness was merely whether or not the turtle crawled away when released.

Before the tests were begun, we had established the fact that hatchlings retain their sea-finding urge and ability long after emergence from the nest, even after having been kept in a dry box or, more surprisingly, after having been allowed to develop swimming and feeding reflexes in a tank of water. This flexibility made it possible to hold specimens for times convenient for testing.

While the size of the test groups used was not great enough to give them much statistical stature, to the observer on the ground, seeing the lay of the land and taking note of the degree of energy and "assurance" with

which each individual met the problems of the test, there were few cases in which some useful information was not forthcoming.

It was not possible in the field to achieve rigid control of conditions or to use hatchlings with standard background. Our tests thus must be regarded as exploratory efforts to identify cues, and to assess flexibility in goal sense and guidance receptivity in the green turtle when on land. We set out to learn whether and, so far as possible, how they find the sea by day and at night, in fair weather or in rain, from nests in the open and from release points behind bushes or logs, or amid miscellaneous clutter, or where the seaward slope led upward to a crest hiding the water from view. Because no one situation clearly involved one single variable, we recount the trials here in series, grouped arbitrarily according to the character of the water goal or to the location of, and the lay of the land at, the release point. The places and conditions of release in these manipulations were: (1) on open beach with normal gradi-

TABLE 8
SUMMARY OF PREVIOUS WORK ON ORIENTATION IN TURTLE HATCHLINGS

Observers	Kind of Turtle	Experimental Results
Hooker (1908)	<i>Caretta</i>	Preference demonstrated for blue over red, orange, or green (intensities of colors not known). Attracted by large areas of light rather than intense point sources. After entering water attracted by darker blue of deep water
Parker (1922)	<i>Caretta</i>	Positively geotropic, i.e., guided by downward slope of beach to sea. Repelled by broken horizon and attracted by low, unbroken horizon
Noble and Breslau (1938)	<i>Chelydra</i> , <i>Sternotherus</i> , and <i>Chrysemys</i>	Attracted towards maximum area of open, illuminated sky
Daniel and Smith (1947)	<i>Caretta</i>	Guided by phototaxy and photokinesis. Attracted by bright surf. Orientation capacity diminished on dark nights. Repelled by dark patterns
Anderson (1958)	<i>Trionyx muticus</i> , <i>Graptemys pulchra</i> , <i>Graptemys oculifera</i>	Suggestion that primary orientation is by negative response to dark objects, with telotaxis and "direct visual response" to water perhaps reinforcing factors. "It is apparent that many variations in orientation mechanism exist in turtles"
Carr and Ogren (1959)	<i>Dermochelys</i>	Positive reaction to openness of outlook and large areas of illumination. Basic kinesis clearly supplemented by capacity to use information of various sorts for repeated topical reorientation in complex landscape

ent, i.e., sloping evenly downward to the surf: (2) on open beach with an upward gradient leading to a crest making a sand horizon and requiring an initial upward climb; (3) behind obstructions (debris, vegetation, or buildings), with extreme cases combining compound gradient and heavy clutter; (4) on the shore of an alien body of water (bank of a lagoon; Pacific beach across isthmus); (5) where a choice between home water and alien water was presented (a peninsula between lagoon and sea; a point surrounded by sea, pass, and cove). The results of these tests, and of a few inconclusive trials with mature female turtles, are recounted below.

TESTS ON OPEN BEACH, WITH GRADIENT LEADING DOWNWARD TO SEA

TEST 1

DATE, TIME, AND SAMPLE: August 26, 1958; 2230 hours; 10 young, hatched same night.

CONDITIONS OF TEST: (See fig. 7). Sky clear, moon high, in last quarter. The turtles were covered with 2 inches of sand in a shallow pit on open beach 75 yards from the surf, with an even downgrade leading seaward and without major obstructions. These conditions were as nearly average for emergence of *Chelonia* at Tortuguero as could be arranged. The reburial in a second artificial nest constituted the only obviously irregular factor.

RESULTS: The turtles scratched their way out of the covering sand and without hesitation headed for the water. Three, which came out on a course parallel with the shore, made a semicircular path that ended in a correct heading. All others took and held correct courses, with no stopping or evident perusal of surroundings, except when the beam of a

flashlight was played upon them. In such cases all but one turtle, which crawled steadily seaward in spite of the light, stopped, turned, and headed up the light beam for as long as it was there. The spread of the seaward trails of the 10 hatchlings was 6 yards at the point of release and 20 yards at the water.

TEST 2

DATE, TIME, AND SAMPLE: August 27, 1958; 0810 hours; 10 young, hatched night of August 26.

CONDITIONS OF TEST: (See fig. 7). Clear morning. The turtles were placed in a shallow pit and covered with a few inches of sand. The site was a level terrace on open, unobstructed beach 36 paces from the surf. The terrace extended seaward for 18 paces, after which the ground sloped evenly for the rest of the way to the water.

RESULTS: Three turtles came out directly; the rest had to be prompted with a stick. Those coming out on the land side made short semicircular crawls, then stopped, peered, and reoriented correctly towards the water. Those that came out on the sea side crawled towards the surf without preliminary reconnaissance or hesitation. The spread of the trails of the orientating turtles was 2 yards at the point of release and 22 yards at the surf.

TEST 3

DATE, TIME, AND SAMPLE: August 20, 1958; 2000 hours; 10 young, emerged night of August 17 and kept in a dry box prior to trial.

CONDITIONS OF TEST: (See fig. 8). Clear night. Moon in first quarter, 35 degrees up in west. Group released on open, evenly sloping beach in front of camp, 32 yards from the sea.

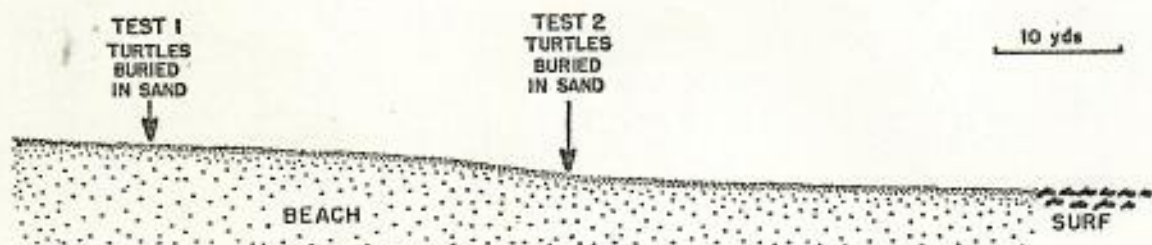


FIG. 7. Beach profile, showing conditions of tests 1 and 2.



FIG. 8. Beach profile, showing conditions of tests 3 and 4.

RESULTS: All oriented correctly. Spread of tracks at release point 2 yards; at water, 15 yards.

TEST 4

DATE, TIME, AND SAMPLE: September 3, 1958; 0948 hours; 10 young, emerged during night of August 29, kept thereafter in shallow water, in which swimming reflexes were developed.

CONDITIONS OF TEST: (See fig. 8). Cloudy day, squall over sea. Point of release 20 yards from surf, on open beach free of obstacles and sloping towards sea. As trial progressed, squall moved in; the last turtles entered the sea in a heavy rain.

RESULTS: At the site of release, the spread of the orientation trails of nine turtles was 3 yards. One individual wandered over 9 yards before finding and keeping a correct heading. The combined trails spread for 12 yards along the surf line.

TEST 5

DATE, TIME, AND SAMPLE: September 4, 1958; 0906 hours; 10 young, emerged during night of August 24, kept in water, in which swimming and feeding behavior had developed.

CONDITIONS OF TEST: Site of release 28

yards from surf on almost level beach unobstructed towards the sea.

RESULTS: Three turtles quickly moved off on correct headings. Five others circled indecisively and gradually headed off on correctly oriented headings towards the surf line. One turtle showed no reaction at all. When poked with a twig, it burst into a frenzy of swimming movements, then quieted down and started crawling off seaward. After five minutes the first turtle had entered the water; after nine minutes the last entered. The track spread was 5 yards at the point of release and 18 yards at the surf line.

TESTS ON OPEN BEACH, WITH RISING SEAWARD GRADIENT

TEST 6

DATE, TIME, AND SAMPLE: August 18, 1958; 1630 hours; 10 young, emerged during night of August 17-18, kept in pen before trial.

CONDITIONS OF TEST: (See fig. 9). Sky partly cloudy. Turtles released on uncluttered beach 20 yards out from coccal, with a slight upgrade making a sand horizon between the site of release and the sea, which was 29 yards away.

RESULTS: After 15 seconds all but one turtle had taken seaward headings. At the end of

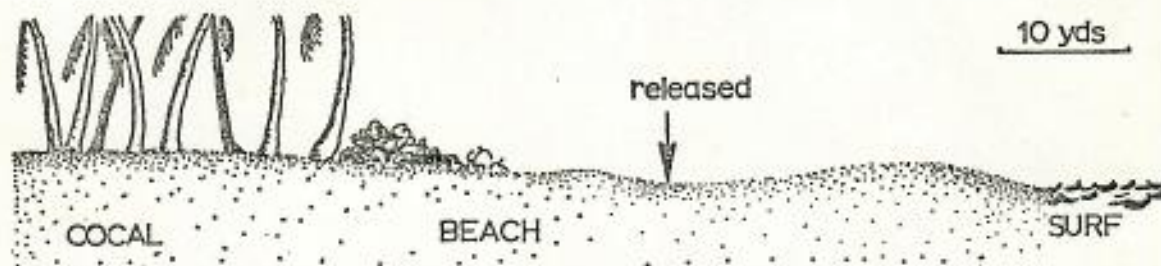


FIG. 9. Beach profile, showing conditions of test 6.



FIG. 10. Beach profile, showing conditions of tests 7 and 8.

a minute all were heading towards the water. A fast, "confident" pace was maintained by all of these. One, chased briefly by a black vulture, sped up and got away safely. There was no circling or hesitation among the hatchlings. The first reached the water within three minutes, the last within eight minutes. The spread of trails was 8 yards at the site of release and 38 yards at the surf line.

TEST 7

DATE, TIME, AND SAMPLE: August 28, 1958; 1225 hours; 10 young, just emerged (morning of August 28).

CONDITIONS OF TEST: (See fig. 10). Sky completely clouded over. Turtles released 40 yards out from the cocal, on clear beach, 40 yards from the sea which was hidden from turtle-eye view by the crest of a rise.

RESULTS: When the group was placed on the sand, one turtle made off at once towards the sea; 45 seconds later all had taken correct courses. The pace of all these was exceptionally fast. The first turtle reached the surf after four minutes; the last, after six minutes. Extreme separation of trails was 3 yards at the point of release and 24 yards at the surf line.

TEST 8

DATE, TIME, AND SAMPLE: August 28, 1958; 1237 hours; 10 young, emerged August 26, 2100 hours, kept in dry pen after emergence.

CONDITIONS OF TEST: (See fig. 10). All factors as in the preceding trial, except that the sample had been held for two days before release.

RESULTS: One turtle took a proper heading immediately; all had oriented within one minute. The first reached the water after three and a half minutes, the last after five minutes. The response of this group was like that of the younger turtles in trial 7, except for more frequent pausing by the slower members of the present sample.

TEST 9

DATE, TIME, AND SAMPLE: August 16, 1958; 0830 hours; 10 young, emerged during night of August 10, kept in tank of water prior to test.

CONDITIONS OF TEST: (See fig. 11). Slight overcast; sun 60 degrees over sea. Release point on open beach with sand horizon (a 10-degree grade leading up to it) confronting



FIG. 11. Beach profile, showing conditions of test 9.



FIG. 12. Beach profile, showing conditions of test 10.

turtles to seaward, and with coco fringe behind them.

RESULTS: The first turtle had oriented within one minute; the last, within three minutes. The spread of the combined trails was 3 yards at the site of release and 17 yards at the surf.

TEST 10

DATE, TIME, AND SAMPLE: August 15, 1958; 1700 hours; 23 young, emerged during night of August 11. The sample was carried by airplane across the isthmus to Quepos, on the Pacific, and back—a three-day trip in a sack.

CONDITIONS OF TEST: (See fig. 12). Site of release was a clean beach separated from the sea by a slight upgrade and a crest 10 feet away. Beyond this crest there was an even downward slope to the water. The glow of the sunset made a broad area of intense illumination in the west.

RESULTS: Turtles very active, showing no sign of weakness or loss of capacity as a result of their abnormal background (the round trip, involving climbs to 11,000 feet in altitude, to the Pacific side and back). Within one minute all had taken seaward headings that needed no further correction, and all

held these in spite of repeated attacks by ghost crabs. The spread of trails they left was 6 feet across the point of release and 33 feet at the water line.

TEST 11

DATE, TIME, AND SAMPLE: August 24, 1958; 1840 hours; 10 young, emerged August 23 at 2000 hours, kept in dry pen until time of trial.

CONDITIONS OF TEST: (See fig. 13). Clear night with three-quarter moon high in sky to southward. Site of release in front of coco fringe, with a low slope rising to a crest about halfway to the surf, which was 32 yards away. The crest of the slope made a sand horizon from turtle-eye level; otherwise there was no important obstruction of the seaward path.

RESULTS: All oriented properly within 30 seconds, crawled rapidly, and entered the water on almost perpendicular courses three minutes after release. Spread of trails 1 yard at point of release, 8 yards at water.

TESTS WITH CLUTTERED FOREGROUND AND COMPOUND SEAWARD GRADIENT

TEST 12

DATE, TIME, AND SAMPLE: September 3, 1958; 0932 hours; 10 young, emerged during

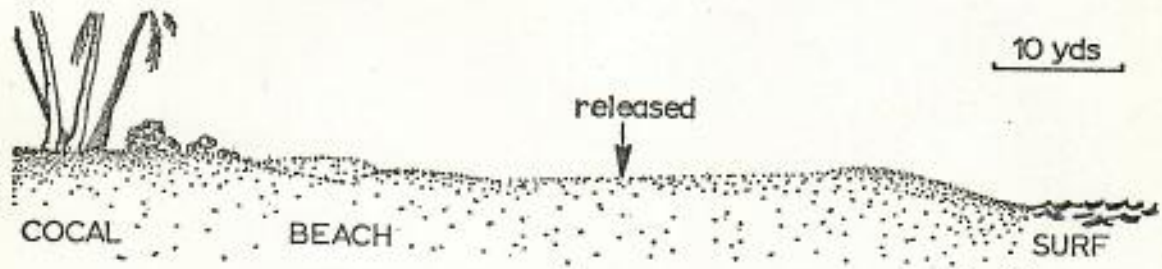


FIG. 13. Beach profile, showing conditions of test 11.



FIG. 14. Beach profile, showing conditions of test 12.

night of August 29, kept in tank with very shallow water.

CONDITIONS OF TEST: (See fig. 14). Sky cloudy, squall over ocean. The turtles were released between two low dunes, the crests of which made both the seaward and landward horizons for the sample. The coccal was 30 yards away and the sea 54 yards away. The beach was littered with heavy debris and much torn up by nesting turtles.

RESULTS: At the end of one minute one turtle had taken a correct heading. After five minutes all had oriented correctly, but the trip to the water was repeatedly interrupted by pauses, irregular circling, and temporary reversals of course. At the end of 14 minutes all the turtles were making progress towards the sea, but very slowly, two being still only 7 yards from the site of release. The test was then ended, because of the difficulty of keeping the hatchlings in sight amid the beach drift.

TEST 13

DATE, TIME, AND SAMPLE: August 24, 1958; 1928 hours; 10 young, emerged August 23 at 2000 hours, kept in dry pen.

CONDITIONS OF TEST: (See fig. 15). Three-quarter moon high in the south; sky clear. Site of release just in front of coccal (3 yards

away) and separated from sea, 72 yards away, by debris, by several low ridges, and by a mass of coco-plum bushes 30 feet long and 4 or 5 feet high.

RESULTS: Within one minute, all the turtles had found correct headings; all reached the sea the first 16 minutes after release. The spread of trails was 2 yards across the side of release and 19 yards at the water.

TEST 14

DATE, TIME, AND SAMPLE: August 28, 1958; 2200 hours; 10 young, emerged during night of August 27, kept in dry pen.

CONDITIONS OF TEST: (See fig. 16). Clear night, with full moon in south. Point of release 56 yards from the sea, the way to which was blocked by dense growth of sea grape, 4 feet high, and by the crest of a low dune beyond the bushes.

RESULTS: All immediately took seaward headings and kept them for the 9 yards to the sea grapes, where six turtles went around the bushes at the northern end and four rounded the southern end. All then reoriented on routes that would have taken them almost straight to the water. Because it was not possible to keep track of the split sample in the dark, the test was abandoned before the turtles reached the sea.



FIG. 15. Beach profile, showing conditions of test 13.



FIG. 16. Beach profile, showing conditions of test 14.

TESTS ON SHORES OF ALIEN BODIES OF WATER

TEST 15

DATE, TIME, AND SAMPLE: August 27, 1958; 0800 hours; 10 young, emerged evening of August 26.

CONDITIONS OF TEST: (See fig. 17). Clear morning. Turtles released on shore of lagoon, under overhanging roof of boat shed, 6 feet from the water on sloping sandy bank. The site of release was heavily shaded; the western shore of the lagoon, about 250 yards away, was brightly lighted by the morning sun.

RESULTS: Although the movement towards the water was less positive and rapid (less "confident") than that of hatchlings going towards the sea, the whole sample nevertheless reached the water within one minute. For a time all swam directly away from shore, bobbing up repeatedly as if to take new bearings. Just before the heads disappeared, they were seen to be angling off downstream, perhaps simply being carried by the ebbing tide.

TEST 16

DATE, TIME, AND SAMPLE: August 16, 1958; 1100 hours; 20 young, emerged during night of August 10, kept in tank of water prior to test.

CONDITIONS OF TEST: (See fig. 17). Site of release on bare, sloping sand shore under boat shed, 2 feet from edge of lagoon, which was 250 yards wide at point of release, with heavy woods on the far side. Sample released in two groups of 10 turtles each.

RESULTS: Hatchlings slow to respond, showing much hesitation, peering, and craning of necks, and little sign of rising interest as they neared the water. Once in the water, all headed straight across towards the far bank. For the whole distance across the river they swam under water and bobbed up at the surface, where they stopped and for some moments peered about as if scanning the landscape. When approached by the observer in a canoe, all quickly dived and made evasive changes of course, resuming the heading towards the far shore when the canoe dropped back. Within 10 minutes all had reached a zone of shallow water over a bed of *Potamogeton* that extended 50 feet out from shore. Here they scattered, the majority making off downstream, the direction in which, from the boat, the sky seemed to be most intensely lighted.

TEST 17

DATE, TIME, AND SAMPLE: September 21, 1957; 1630 hours; 11 young, emerged (at Tortuguero on the Caribbean shore) September

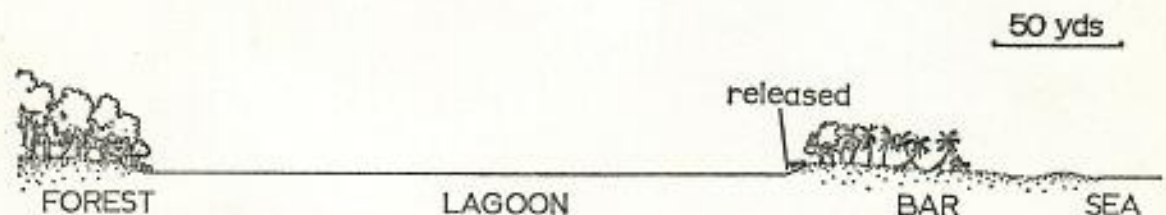


FIG. 17. Profile of Tortuguero beach and lagoon, showing conditions of tests 15 and 16.



FIG. 18. Profile of beach near Quepos, Pacific coast of Costa Rica, showing conditions of test 18.

9, kept for part of the time prior to release in a tank of water and for part in a dry box.

CONDITIONS OF TEST: Site of release the open beach at San Isidro, near Punta Arenas, Costa Rica, on the Gulf of Nicoya, exposed to full Pacific surf. Turtles placed in a shallow hole, with a log on the seaward side.

RESULTS: One turtle scrambled quickly out of the pit, stopped, craned its neck, peered about briefly, and then made off straight for the sea. The others emerged with varying degrees of dispatch. The most active of these took a heading straight inland. When picked up 30 feet from the nest and replaced, the turtle came out at once and took the same diametrically incorrect heading. This hatchling was retrieved four more times (six times in all), and in every case it emerged without hesitation and headed off in the same inland direction. At the end of half an hour six of the turtles had oriented properly. Four were slow to respond, and, as replacements were not available, they were carried down to hard, flat, wave-wet sand and released there. All immediately crawled into the water, where they were watched throughout the period of their traversal of the breakers. Although the character of the long-period, powerful Pacific surf was markedly different from that of the Caribbean, in which their ancestral responses developed, none of the turtles seemed at a loss in the long rollers, and all eventually appeared in the calm water seaward of the breakers. Although the stubborn selecting of an inland heading by one of these hatchlings seemed dramatic confirmation of what a prejudiced manipulator would expect of little turtles carried from an Atlantic to a Pacific shore, the fact that its siblings found the sea without setbacks makes the behavior of the

one individual seem to be only an accidentally appropriate aberration.

TEST 18

DATE, TIME, AND SAMPLE: August 12, 1958; 1613 hours; six young, emerged morning of August 12 (the same day) at Tortuguero, carried in bag on flight across the isthmus.

CONDITIONS OF TEST: (See fig. 18). Quepos, Pacific coast of Costa Rica. Clear sunny day, with some clouds over sea. High mountains some miles back of beach, partly in cloud. Most extensive and intense illumination down the shore to the northwest, not over the ocean. Site of release the crest of a dune, with a strong seaward slope, then a low rise to the top of another lower dune, then a steep downgrade to the sea, 140 feet away.

RESULTS: After three minutes the first turtle had oriented correctly; within eight minutes all had correct headings. There was some pausing to pivot about and scan the landscape, with necks stretched at a 45-degree angle, after which the seaward movement was resumed. On the strongest downward slopes the pace was most rapid, and the turtles moved with necks stretched far forward, parallel with the ground. Evidently positive geotaxis may enter the orientation pattern as a subsidiary stimulus, although it is easily overridden. The spread of the six trails was 6 yards across the point of release and 12 yards at the surf line.

TESTS IN WHICH HATCHLINGS WERE OFFERED A "CHOICE" BETWEEN BODIES OF WATER

TEST 19

DATE, TIME, AND SAMPLE: August 12, 1958; 1636 hours; five young, emerged morn-



FIG. 19. Profile of beach and dunes (from sea to lagoon) near Quepos, Pacific coast of Costa Rica, showing conditions of test 19.

ing of August 12 (the same day) at Tortuguero on Caribbean shore; turtles carried in bag on flight across isthmus.

CONDITIONS OF TEST: (See fig. 19). Open Pacific beach north of Quepos, Costa Rica. Weather clouding, sun hidden for most of time of test; clouds low on mountains inshore from the beach. Sample released 35 yards from the surf on the strongly inclined landward side of a high dune, the crest of which hid the sea from turtle-eye level. The landward slope led back to a sparse growth of sea oats, with the water of a lagoon visible in the background.

RESULTS: After two minutes, one turtle had reacted and was correctly headed. The others straggled into seaward courses. The spread of trails was 7 yards at the site of release and 36 yards at the water.

TEST 20

DATE, TIME, AND SAMPLE: September 3, 1958; 0907 hours; 10 young, emerged during night of August 26, kept in shallow water in tank prior to test.

CONDITIONS OF TEST: (See fig. 20). Turtles released in coconut grove, 50 feet from lagoon shore. The camp house obstructed the path towards the sea, and the most open and

strongly illuminated outlook was that down a 10-degree sector, bounded on the north by trees and on the south by the boat shed, leading to the lagoon.

RESULTS: After three minutes of vacillation, during which they several times headed temporarily towards the camp house, five turtles were heading almost directly towards the lagoon. After eight minutes, and much circling and hesitation, the sixth hatchling had found a course to the lagoon. The remaining four turtles showed no reaction at all and were replaced with four fresh ones. After four minutes all these were well down the 10-degree sector towards the lagoon, which the first turtle entered 19 minutes after the start of the test.

TEST 21

DATE, TIME, AND SAMPLE: August 29, 1958; 1445 hours; 10 young, emerged during night of August 26, kept in dry pen prior to test.

CONDITIONS OF TEST: (See fig. 21). Light rain, complete overcast. This test involved maximum confusion and obstruction of the horizon and surroundings and, in addition, offered a choice between bodies of water. The sea was 100 yards, the lagoon about 40, away.



FIG. 20. Sketch of premises of camp, showing conditions of test 20.



FIG. 21. Sketch of premises of camp, showing conditions of test 21.

The site of release was the back yard of the camp, where buildings, trees, boxes, dogs, chickens, and miscellaneous debris broke the horizon in every direction, except for a 10-degree slot angling obliquely towards the surf line by the north end of the house. Although the sea was not visible, the narrow seaward outlook was by far the least obstructed and best illuminated one.

RESULTS: After one minute, one turtle had taken a heading towards the corridor leading towards the ocean. After three minutes, all were heading into it. As they approached the house there was much confusion and stopping and taking of what, for want of a good name, we have called the "inspection stance"—a standard attitude in which the hatchling stops, raises its body slightly off the ground anteriorly, and, with neck outstretched at a 45-degree angle, remains motionless for several or for many seconds. This could conceivably be a simple act of landscape appraisal, but more likely it involves a sensory search for some more special cue. In any case, the turtle usually moves off with evidently renewed energy ("confidence") at the end of such a stop. Perhaps this is a rudimentary, or vestigial, form of the "orientation circle" of hatchling *Dermochelys* (see Carr and Ogren, 1959), which the pivoting and irregularly circular interruptions of heading observed in other young green turtles may be also. In the present case, all the turtles entered the sea, the last being found on the lower beach an hour after the time of release. The trail of this last individual showed that it had abandoned the clear path taken by the others and had come around the south end of the house. When found, it was evidently tired and was crawling slowly and jerkily towards the water. On reaching the wave wash, it was thrown

back three times before finally getting into and past the surf.

TEST 22

DATE, TIME, AND SAMPLE: August 20, 1958; 2015 hours; 10 young, emerged during night of August 17, kept in dry pen.

CONDITIONS OF TEST: Clear night; three-quarter moon, 35 degrees up in west. Site of release, back yard of camp, as in preceding daytime test.

RESULTS: During the first few minutes all hatchlings found headings, but the grass in front of the house, when reached, interrupted progress towards the beach. After two hours two turtles were found still crawling in the yard, and the others had been lost from view in the grass. This performance seemed much less effective than that of the sample released in the same place by daylight. (Cf. Anderson, 1958, who found fresh-water hatchlings unable to orient on dark nights amid clutter characteristic of nesting sites of fresh-water turtles.)

TESTS 23-37

Tests 23 through 37 were made on the low sandy tip of the spit at the northern end of the Tortuguero peninsula. A curve of the river cuts into the peninsula just short of the tip, making a deep cove there. The river then swings inland, then directly seaward, to join the Caribbean at the bar (as the Creoles call the pass). The end of the peninsula is thus a spit shaped like a golf club, with the head almost completely surrounded by water—the cove, the river, and, to the east, the sea. This whole oblong area is low and sandy and, although strewn with flood litter from the river and sea and set with low brush or patches of grass, is without woody vegetation. The

cleanest distant horizons from any point on the spit are the horizon to seaward and that upstream across the cove. Various degrees of blocking of the outlook were achieved by varying the point of release with reference to foreground litter on the spit; to the spread of open (or hyacinth-covered) water of the cove; to the relatively narrow river (bordered on the west by high shore forest); and to the pass, with the isolated mass of Cerro Tortuguero rising to the north, and with open ocean to the east.

TEST 23

DATE, TIME, AND SAMPLE: August 20, 1958; 1025 hours; 10 young, emerged during night of August 17, kept in dry pen prior to test.

CONDITIONS OF TEST: (See fig. 22). Cloudy day, with intermittent light rain. Turtles released on bank of cove, where a clean, hard sand beach, 10 feet wide, lay between the in-shore litter and the water. The cove was free of hyacinths; the water was only a few inches deep for some 20 feet out from shore.

RESULTS: Five turtles headed directly for, and entered, the water. The other five showed some hesitation, making frequent reversals of direction, going in and out of the inch-deep water for eight minutes before the last entered. Once in the water, for a time all swam straight away from the bank (which ran in an east-west direction) and across the cove in an

upstream direction. About 20 yards out from shore each in turn seemed to become confused, abandoned its straight course, and swam about in aimless, irregular sallies separated by pauses, during which it dog-paddled about with neck upstretched. In this disoriented and seemingly helpless state the group gradually scattered. After 15 minutes the only turtle in sight was one still pursuing an erratic course in the river parallel to the west shore of the peninsula. The initial drive in this case soon broke down. Such behavioral breakdown suggests that successful orientation, after the water is reached, may depend in part on the orderly sequence of the stimuli presented during the normal approach to and traversal of sea surf. After the first 20-yard movement to the southward the movements of all these hatchlings in the calm water of the cove and river seemed wholly random.

TEST 24

DATE, TIME, AND SAMPLE: August 20, 1958; 1005 hours; 10 young, emerged during night of August 17, kept in dry pen.

CONDITIONS OF TEST: (See fig. 22). Cloudy day, with intermittent light rain. Turtles released in a litter of old hyacinth rafts on shore of cove, where the shortest route to water was 25 feet in an upstream direction (towards a bright horizon and parallel to the sea beach beyond which the sky was also brightly illuminated).

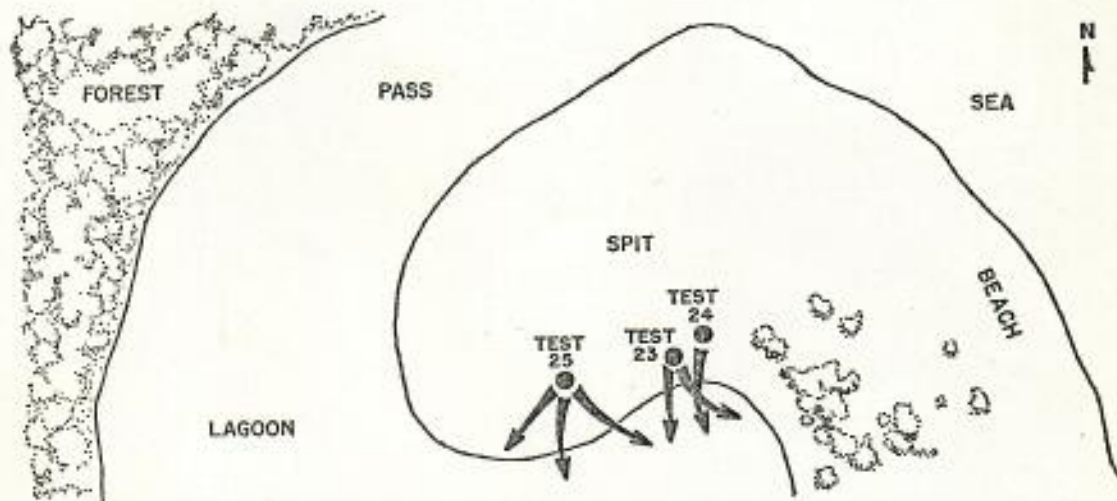


FIG. 22. Region at mouth of Tortuguero River, showing conditions of tests 23, 24, and 25. The arrows indicate general headings taken by individuals or by subgroups of the sample.

RESULTS: Five found direct paths to the cove; five others hesitated and wandered aimlessly for a while, four minutes elapsing before the last had found a proper course not later abandoned. The progress of all these was hindered by the litter of sticks and hyacinth wrack. As each entered the water it encountered hyacinths drifting about in the back-water. These were various distances from shore and in masses of various sizes, and they seemed to be a disorienting factor for all the hatchlings, causing them to veer about on aimless headings. The only consistent tendency was an eastward heading by four turtles which bore away from the rafts and towards the west shore of the peninsula (with the ocean sky behind it). Twenty-five minutes after release, the heads of some of the turtles were still bobbing up among the hyacinths, but soon afterward they were lost to view.

TEST 25

DATE, TIME, AND SAMPLE: August 23, 1958; 1313 hours; 10 young, emerged during night of August 11, kept in tank of water prior to test.

CONDITIONS OF TEST: (See fig. 22). Day bright, with some haze. Turtles released on north shore of cove, 25 feet from the water and slightly to the west of release point in preceding test. Although no major obstruction

lay to seaward, the generally clearest and brightest prospect was that across the cove and up the river to northward.

RESULTS: Reaction of sample immediate and strong. All headed at once for the water of the cove, one angling towards the river, the rest going almost directly. The spread of all the trails at the water's edge was 3 yards. Once in the water, three seemed confused, returning repeatedly to shore and swimming parallel with the bank for a long distance. The rest fanned out over the cove and were lost to view.

TEST 26

DATE, TIME, AND SAMPLE: August 23, 1958; 1328 hours; 10 young, emerged during night of August 11, kept in tank of water.

CONDITIONS OF TEST: (See fig. 23). Day hazy-bright, with thin clouds and intermittent full sun. Turtles released just south of site of release in preceding test, where 7 feet of litter and 12 feet of clean beach separated them from the water of the cove. Heavy debris in all other directions.

RESULTS: One turtle headed southwest towards the river, across the trash-strewn spit. The rest took almost direct headings, the first reaching the water within one minute, the last within three minutes. The spread of the trails of these was 30 feet at the edge of the water. The hatchling that took the west-

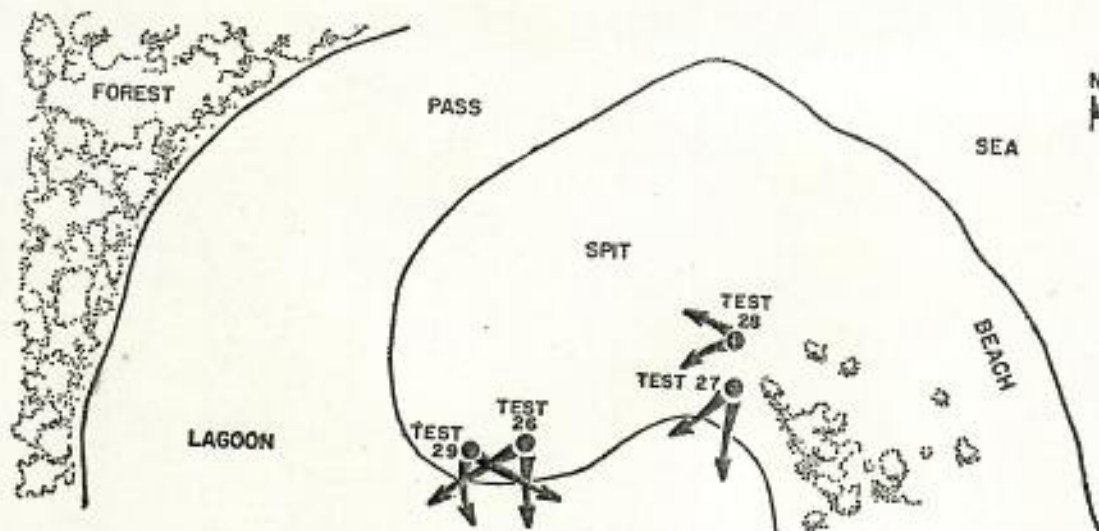


FIG. 23. Region at mouth of Tortuguero River, showing conditions of tests 26, 27, 28, and 29. The arrows indicate general headings taken by individuals or by subgroups of the sample.

erly course eventually entered the lagoon. Once in the water, all swam off upstream, their heads bobbing up at intervals of about five seconds for as long as they remained in view.

TEST 27

DATE, TIME, AND SAMPLE: August 27, 1958; 1228 hours; 10 young, emerged during night of August 25, kept in dry pen.

CONDITIONS OF TEST: (See fig. 23). Clear day. Site of release opposite head of cove, 12 feet from water, on clean, flat beach just in front of a 4-foot stand of panic grass.

RESULTS: All headed for the shore of the cove, and within two minutes all were in the water. One later crawled back onto the bank but quickly reentered the water.

TEST 28

DATE, TIME, AND SAMPLE: August 27, 1958; 1240 hours; 10 young, emerged during night of August 25, kept in dry pen.

CONDITIONS OF TEST: (See fig. 23). Clear day. Turtles released 30 feet from north shore of cove, in an uncluttered area of sand, with scattered shrubs and tall grasses to seaward.

RESULTS: Reaction of sample weak and erratic, although there was a general tendency to head overland towards the river, more than 100 yards away. The extreme heat of the sand appeared to be the cause of the feeble response. When one turtle died, evidently from the heat, the rest were picked up, and the test was ended.

TEST 29

DATE, TIME, AND SAMPLE: August 20, 1958; 1045 hours; 10 young; emerged during night of August 17, kept in dry pen.

CONDITIONS OF TEST: (See fig. 23). Sky overcast. Site of release 15 feet from water at the northern side of the cove where it joined the river.

RESULTS: One turtle headed for lagoon by the most direct route, reaching it after five minutes' travel. The others all took headings towards the sea (thus "inland" with respect to the tip of the peninsula) and parallel to the shore of the cove. At first much hindered by debris (stranded hyacinth rafts) these, one by one, worked into the incurving, clear, shore zone of the cove and entered the water. Here each continued its "seaward" course, swim-

ming across the cove towards its inner shore. In the middle of the cove all were lost to view when caught by current and eddies or hidden by drifting hyacinths. There seemed a clear tendency here for the sample hatchlings, after entering the water, to swim towards the bright sea-sky rather than to the locally less obstructed up-river outlook.

TEST 30

DATE, TIME, AND SAMPLE: August 20, 1958; 1100 hours; 10 young, emerged during night of August 17, kept in dry pen.

CONDITIONS OF TEST: (See fig. 24). Sky overcast. Turtles released 15 feet from water on clean, hard sand at north side of cove, where it joins the river. The most unobstructed outlook lay to the south, across the cove, and upriver. The brightest sky seemed to be that over the sea in the direction of the pass. The path in this direction lay across low, relatively flat ground. There was only low clutter to obstruct the way in this direction, and from turtle-eye level it must have offered the most open outlook.

RESULTS: After 15 minutes three turtles were heading "inland," that is, were crossing the broadest expanse of dry land that presented itself—that leading to the sea and the pass. The others had gone directly to the lagoon, where all swam eastward until they, too, were heading in a seaward direction. This sample was clearly faced by two competing initial attractions: the bright seaward sky, with relatively open foreground, and the more immediately accessible water of the lagoon. Although separated at the start, all the hatchlings eventually headed eastward (seaward), part on land and part in the water.

TEST 31

DATE, TIME, AND SAMPLE: August 20, 1958; 1120 hours; 10 young, emerged during night of August 17, kept in dry pen.

CONDITIONS OF TEST: (See fig. 24). Overcast sky. Sample released on west tip of spit, 5 feet from water of river.

RESULTS: All crawled directly into the river, and there swam away upstream against the current.

TEST 32

DATE, TIME, AND SAMPLE: August 23, 1958; 1340 hours; 10 young, emerged during

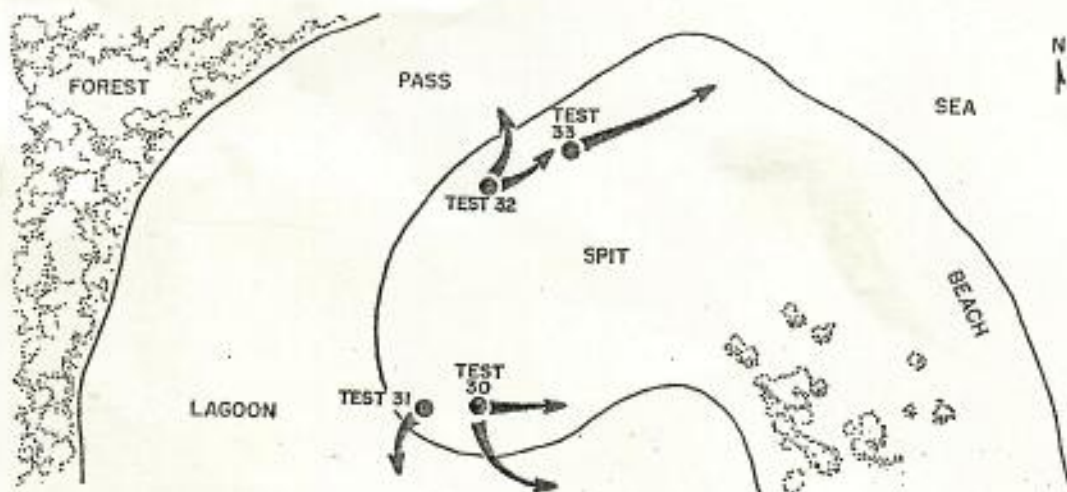


FIG. 24. Region at mouth of Tortuguero River, showing conditions of tests 30, 31, 32, and 33. The arrows indicate general headings taken by individuals or by subgroups of the sample.

night of August 11, kept in tank of water prior to test.

CONDITIONS OF TEST: (See fig. 24). Hazy-bright day, with intermittent full sun. Turtles released in trash on shore of pass 10 feet from nearest water. All took initial headings parallel to edge of water, and towards the sea off the mouth of the pass. Three soon turned towards pass, entered it, and swam upstream. The rest were slowed by heavy debris. The test ended when the observer's dugout drifted away and had to be retrieved.

TEST 33

DATE, TIME, AND SAMPLE: August 20, 1958; 1130 hours; 10 young, emerged during night of August 17, kept in dry pen.

CONDITIONS OF TEST: (See fig. 24). Sky overcast. Turtles released 25 feet from pass on clear, level sand, surrounded by water for about 300 degrees. The sea was 100 yards away and made the horizon from turtle-eye level.

RESULTS: After four minutes all were heading seaward parallel to shore of inlet, crawling steadily and actively. The spread of trails was 6 yards at the site of release and 42 yards where the turtles entered the sea.

TEST 34

DATE, TIME, AND SAMPLE: August 23, 1958; 1435 hours; 10 young, emerged during night of August 11, kept in tank of water.

CONDITIONS OF TEST: (See fig. 25). Hazy and partly cloudy, with occasional full sunshine. Site of release 50 feet back from the water of the pass, near the mid point in the long, east-west axis of the spit, where the sea horizon and surf were visible off the mouth of the pass, 100 yards away. In the opposite direction the upstream horizon was open and bright.

RESULTS: At the outset the sample broke up into three groups, one going towards the sea parallel to the shore of the inlet, one heading directly for the inlet, and the third going directly away from the sea and towards the eastern shore of the river. The four individuals heading towards the ocean moved with markedly more "confidence" and energy than the others. Those that went west hesitated and made several reversals of course before finally reaching the water.

TEST 35

DATE, TIME, AND SAMPLE: August 23, 1958; 1428 hours; 10 young, emerged during night of August 11, kept in water in tank.

CONDITIONS OF TEST: (See fig. 25). Day hazy-bright, with thin clouds and intermittent full sunlight. Point of release midway between sea and river (100 yards from each), 40 feet back from the pass. Surrounding terrain with considerable low clutter.

RESULTS: This was an unusually active group. All reacted immediately and quickly

took courses not later abandoned. Five went towards the ocean off the pass and five headed in the opposite direction, towards the cove. As in some of the preceding tests, the nearest water (the river) was not sought, perhaps because the forest on the far shore blocked the prospect. Each of the two groups went towards what, to a man, seemed the bright and unobstructed horizons.

MISCELLANEOUS TESTS WITH
HATCHLINGS AND WITH MATURE
FEMALES ASHORE TO NEST

TEST 36

DATE, TIME, AND SAMPLE: September 9, 1957; 1400 hours; 17 young, just emerged.

CONDITIONS OF TEST: Clear day. Hatchlings blindfolded with hoods of adhesive tape. Released on almost flat expanse of beach very slightly inclined upward towards the sea.

RESULTS: One of the group not blindfolded made off directly towards the sea and entered the surf. The others scuttled aimlessly about, evidently completely lost. After seven minutes, three had reached the water by circuitous courses, quite clearly by accident. The rest scattered for about 20 yards up and down the beach, making only incidental progress towards the sea. Eventually two managed to scrape off their blindfolds, and these immediately oriented properly and entered the water.

The test was repeated with 11 hatchlings,

not the same ones used above, but from the same egg clutch. One of these reached the water on a long, angling heading. The rest scattered up and down the beach.

TEST 37

DATE, TIME, AND SAMPLE: August 15, 1957; noon; four mature females, turned when they emerged to lay the night before.

CONDITIONS OF TEST: Clear day. Eyes of turtles heavily covered with gauze bandage and adhesive tape. Released on open shore, 15 to 65 feet from wave-washed sea beach.

RESULTS OF TEST: All four moved about at random, with frequent stops during which they craned their necks or twisted their heads sideways. Reversals of heading and circular interruptions of course were frequent. These blinded individuals showed more marked tendency to make an "orientation circle" than any turtles we had tested except the trunk-back (see Carr and Ogren, 1959). While making one such circle, one of the turtles reached the sea when she tumbled down an undercut bank some distance down the shore from the point of release. The others kept moving at random, until finally the blindfolds were removed. Each then quickly took direct seaward headings and entered the surf.

TEST 38

DATE, TIME, AND SAMPLE: August 16, 1958; 0900 hours; one adult female, taken

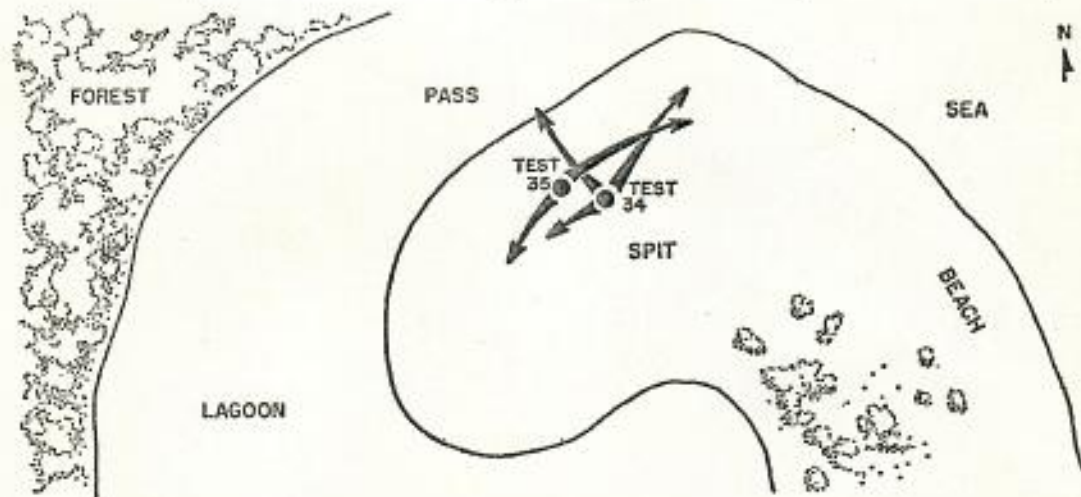


FIG. 25. Region at mouth of Tortuguero River, showing conditions of tests 34 and 35. The arrows indicate general headings taken by individuals or by subgroups of the sample.

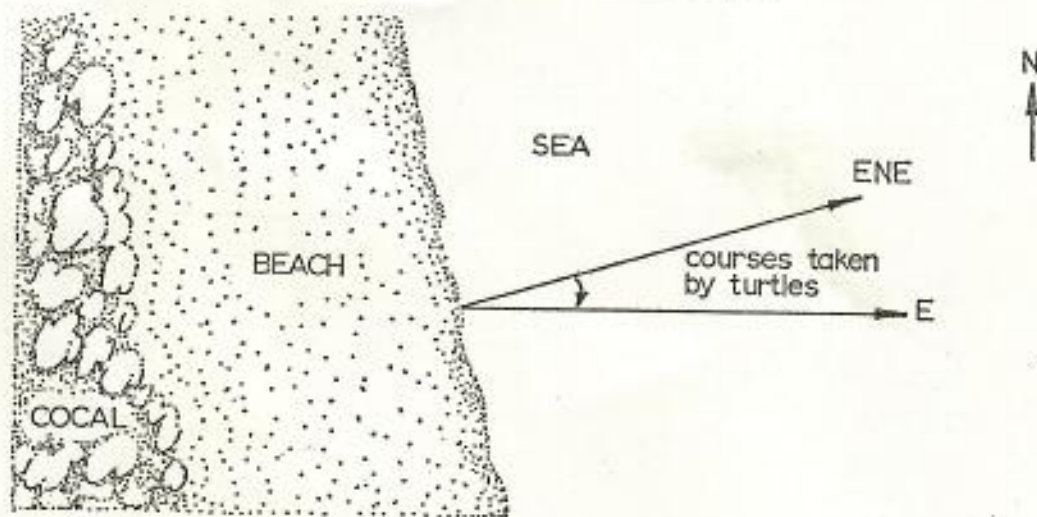


FIG. 26. Sketch showing conditions and summarizing results of trials in test 40.

the night before when reëntering the sea after a trial emergence (when she did not nest).

CONDITIONS OF TEST: The turtle was dragged on her back to a point behind the camp house 100 yards from the sea and about 30 yards from the lagoon and released amid heavy and miscellaneous clutter (including the house) which hid the sea completely.

RESULTS: The turtle turned and moved straight towards the beach on a course that took her under the camp house. After clattering about among boards and bottles there, she reversed her heading, came out from under the house, turned again, and continued seaward around its southern end. She reached the surf without further digression or hesitation.

TEST 39

DATE, TIME, AND SAMPLE: August 13, 1957; mid afternoon; three young, one year old, kept in tank at hatching site (Tortuguero camp) prior to time of trial.

CONDITIONS OF TEST: Clear day. Point of release 60 feet from sea on open beach, with slight initial grade upward towards the water.

RESULTS: All showed hesitancy at first, with short zigzag runs and reversals. Each made two or more rough circles, suggestive of the more formal orientation circles of young *Dermochelys* (Carr and Ogren, 1959). After five minutes all three had taken direct headings towards the surf. All were picked up just before they entered the water. (Of five year-

ling hawksbills with the same history, released at the same time, only one found the water.)

TEST 40

To determine initial headings and behavior on reëntering the sea, 14 mature females, taken the night before when they had come ashore to nest, were marked with balloons and released on the beach. In three cases the line fastening the balloon to the shell was too short to let it rise to the surface. Results of the 11 other tests (in which the lines used were 36 feet long) are given below. The numbers are those of the fin tags with which the turtles were marked. In each case the direction given is a bearing taken on the balloon from the point of release (see fig. 25). After the first few feet, the axial orientation of the turtle's body could of course not be seen, and the changes in position that had occurred may have been due to set as well as to actual headway.

NUMBER 641: September 7, 1957. Turned sharply southward on being lifted by surf. After about 50 yards on this course, she turned seaward. Balloon lost to view 1000 yards out, a little less than 15 minutes after release. Last bearing, east-northeast.

NUMBER 640: September 7, 1957. Angled sharply to southward immediately on entering surf and swam about 50 yards before changing course to east-northeast to east,

after about 15 minutes. Balloon lost from view about 1000 yards out when bearing was east-northeast to east.

NUMBER 652: September 8, 1957. Headed straight out through breakers, reaching calm water beyond surf after four or five minutes, blowing three times on the way. Then she turned to the right into an east-northeast heading and held this until the balloon disappeared 1000 to 1200 yards out; bearing east-northeast to east.

NUMBER 646: Conditions and results as in the preceding case.

NUMBER 644: September 8, 1957. Turned abruptly northward on being lifted by wave wash and swam about 50 yards along beach. Then she turned seaward, went through outer breakers, and after 15 minutes disappeared 1000 yards out on heading indistinguishable from that taken by preceding turtles; bearing east-northeast to east.

NUMBER 643: September 8, 1957. As observed and recorded, results exactly as in case of No. 652 above.

NUMBER 642: Conditions and results as in preceding.

NUMBER 656: July 1, 1958. Overcast sky and heavy surf. Turtle released at edge of water at 1012 hours. After three minutes she was still in the surf, heading south, but being carried northward by current. After six minutes she was 60 yards out, still in outer breakers and still heading south, but now back abreast of starting point. After 12 minutes, about 100 yards out, at seaward edge of surf zone, a little to the south of the starting point. After 23 minutes, out of sight beyond surf; bearing from release point, east-northeast to east.

NUMBER 759: August 11, 1958. Sky clear; surf moderate. Turtle released at 0750 hours. After two minutes in near breakers 200 yards out, she was directly off point of release, having blown twice up to that point. After 12 minutes, 900 yards out, bearing east-north-

east to east. After 16 minutes, about 1400 yards out. After 35 minutes, balloon barely visible, intermittently; bearing still east-northeast to east.

NUMBER 797: September 2, 1958. A turtle that had been caught during a trial emergence and had not laid was released at 0950 hours. Through the surf she took a course angling to northward. After 25 minutes she was about 1 mile offshore; bearing east-northeast to east.

UNTAGGED TURTLE: Released September 3, 1958, at 0821 hours. After four minutes, beyond outer breakers, 175 yards out. After 11 minutes 300 yards out, bearing north-northeast. After 23 minutes bearing shifted to east-northeast to east. After 39 minutes, disappeared about 1 mile out, bearing still east-northeast to east.

The fact that in all these tests the retreating turtle was almost abreast of the point of release when the balloon disappeared might be taken as indication that the initial urge was simply to get away from shore. But it is of interest to consider that, at the extreme distances involved in these scant observations, the seaward course was still evidently being found and held, in spite of strong current set and of the greatly extended open sea horizon. The brightness of the sea-sky may have been the initial cue, but to a turtle a mile off shore this horizon would have been so extended that its value as a source of guidance information to an animal that travels by light sense would seem small (unless the use of polarization patterns could be postulated). Tests of this kind with larger, helium-filled balloons and longer lines, tracked by an observer with a range finder and in an elevated station, may be expected to yield data of some relevance to the problem of high-seas navigation, or at least to the question of what turtles do between their successive nesting emergences during a season at the rookery.

SUMMARY

1. OF 1178 MATURE FEMALE green turtles tagged at Tortuguero during five seasons, there have been 35 international recoveries, some from the farthest reaches of the western Caribbean. The data strengthen the assumption that the green turtle is a migratory animal and suggest that Tortuguero may be the chief remaining nesting center for all populations of the western Caribbean.

2. The average over-all shell length for the nesting colony (1146 individuals) is 39.4 inches.

3. Returns of tagged turtles to Tortuguero reveal that a three-year nesting schedule predominates, as Harrison (1956) found to be the case in the China Sea. Of the Costa Rican turtles, however, a minority nest each two years; but two-year nesters are evidently not found in all populations. We have had no return after an absence of only one year.

4. Renesting occurs at Tortuguero at intervals of from 12 to 14 (average 12.5) days, and we find six nestings to be the calculated maximum for a season.

5. The average incubation period for 117 nests at Tortuguero was found to be 57.5 (48 to 70) days.

6. Observations on group facilitation in emerging hatchlings are discussed.

7. Nesting behavior is broken down into a series of stages that appear to be shared by all sea turtles. Ethologic divergence in this behavior involves minor mannerisms only.

8. Evidence of site tenacity, from both long-term and renesting returns, is given, and the orientation life of the green turtle is discussed in general terms.

9. Results of a series of informal field tests of orientation capacity and flexibility in hatchlings and in females on shore to nest may be summarized as follows:

A. The fundamental goal sense involves visual stimuli.

B. The fundamental response may be a modified phototaxis (or a light-compass reaction, with an angle of 0°) which superficial field tests (our own and those of others) suggest is a drive towards "openness of outlook," meaning, probably, towards the sort of illumination that comes from openness of outlook.

It conceivably could involve in part, as Anderson (1958) suggested, a negative response to the loom of dark objects.

C. Whatever the character of the guidance information, it is available to green turtle hatchlings by day or by night, when sun or moon are over the sea or over the land, when the weather is clear or overcast. We made no tests in heavy rain.

D. The fundamental goal sense in hatchlings is not specific for the ancestral body of water; any body of water of extent sufficient to provide the requisite "openness of outlook" will serve to draw them.

E. In the response of young turtles to light there is a complex relation between intensity and area. The sea-sky draws them away from the sun or from a full moon, when either is over the land. A moderate area of unobstructed foreground, however (the lagoon in our tests, at a distance of 10 feet), sometimes attracts them away from a much more extensive area in the background (such as the sea across a hundred yards of bush-strewn beach). It is of interest that this relation between intensity and area is reversed in the case of the very strong light of a gasoline lantern which overrides any other attraction when set by the water at night, as in the case of *Dermochelys* hatchlings (Carr and Ogren, 1959). Such light even draws the young turtles back on shore after they have entered the wave wash.

F. The fundamental goal drive (the telotaxis) is by no means adequate to account for the capacity to orient in normally broken beach landscape, much less in the extremes of topographic irregularity and clutter in which orientation is successfully carried out. A variety of senses and of sources of topical information clearly is involved in each trip from the nest to the sea.

G. The "orientation circle" of hatchling trunkbacks (Carr and Ogren, 1959) appears to have only rudimentary representation in the green turtle.

H. Young turtles may retain both their sea sense and their capacity for topical reorientation when held in captivity for long periods after hatching, even when kept in tanks,

where the swimming and feeding responses (which normally come after the sea finding venture) are allowed to develop. This suggests that neonate young may find the sea in the same way that a female returning from nesting finds it. If this process in turn should prove to duplicate, wholly or in part, the orientation pattern of the adult in its high-seas navigation, an approach to the study of the latter through experimentation with hatch-

lings (easily obtainable in numbers, easily manipulated, and from birth known to be provided with a strong goal drive) would seem promising. However, the fact that Caribbean hatchlings go readily to a strange ocean when allowed to emerge from an artificial nest on the Pacific shore suggests that taxes, and not compass sense, predominate in the water-finding orientation of young turtles.

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