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The Ecology and Migrations of Sea Turtles, 5 Comparative Features of Isolated Green Turtle Colonies

BY ARCHIE CARR[1] AND HAROLD HIRTH[2]

As more is learned of the migrations of the green turtle, *Chelonia mydas mydas* (Linnaeus), it becomes increasingly clear that world populations of the genus, though spread broadly by post-breeding travel, are genetically isolated from one another by the habit of mating only at the few sites of aggregated nesting. These places are varyingly distant from the year-around feeding territory and are often widely separated from one another. While some mingling of individuals may occur on the pasture ground, this, of course, would be of no genetic importance. If any interchange of genes occurs at the sites of group nesting, it would be only through the straying in of the occasional individual, lost or immune to the usual drives for group travel and reproduction. Such genetic fragmentation invited study on a comparative basis. The present paper is one of a series of investigations that involve the behavior and world-wide movements and ecology of the five genera of sea turtles.

For several years Carr has hoped to augment the scant information available on the famous Ascension Island turtle ground, one of the original sources of green turtles for London soup chefs and for victualing ships of the British Navy. Eventually, with the authorization of Patrick Air Force

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[1] Research Associate, Department of Herpetology, the American Museum of Natural History; Department of Biology, University of Florida; Research Associate, Florida State Museum.

[2] Department of Biology, University of Florida.

Base and with the cooperation of officials of the British Cable and Wireless Company, work at Ascension was made possible. Hirth spent some nine weeks there during the main nesting time, arriving at the island February 19 and leaving May 2, 1960.

Meanwhile the tagging program has continued at Tortuguero, on the Caribbean coast of Costa Rica. This, and reconnaissances elsewhere, have continued to add to our understanding of the life cycle and migratory routes and schedules. It thus now seems appropriate to present comparative aspects of the biology of these two best-known stocks of the Atlantic green turtle. To extend the comparative basis, frequent references are made to populations nesting on the Sarawak Islands in the China Sea, as described by Banks, Harrisson, and Hendrickson, and the Florida population is referred to in several contexts.

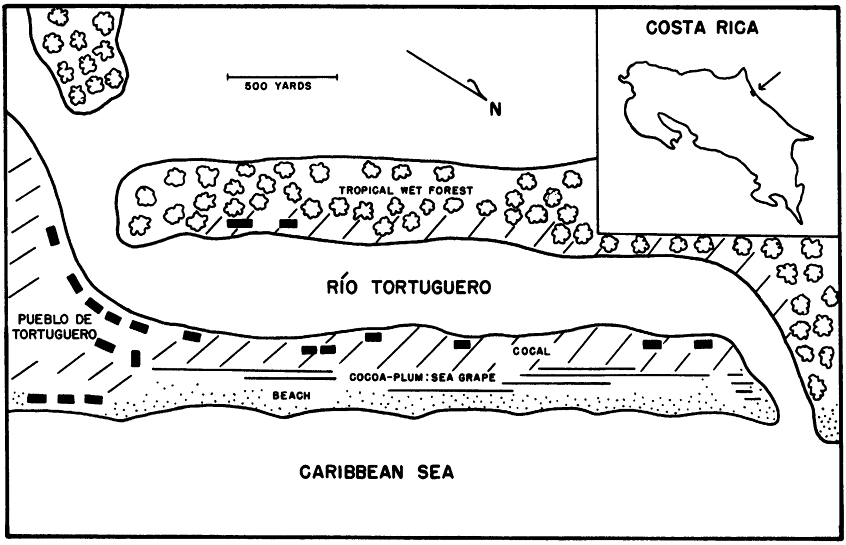

FIG. 1. Sketch map of Tortuguero and vicinity. Black rectangles are ranchos of the settlement.

THE TORTUGUERO NESTING GROUND

The work at Tortuguero, 50 miles north of Puerto Limon on the Caribbean coast of Costa Rica (see fig. 1), began with reconnaissance visits by Carr in 1954 and 1955. In 1956 the first of three grants from the National Science Foundation allowed the establishment of a seasonal camp for carrying out a tagging program. Since 1958 the hatchery operations of the Caribbean Conservation Corporation have provided additional facilities and personnel and means for accumulating data on large numbers of nests and hatchlings.

The general features of the locality and nesting assemblage have been described by Carr (1956), Carr and Giovannoli (1957), and Carr and Ogren (1959, 1960). The rookery there is by far the most important nesting site in the western Caribbean (see table 9). While others once existed (notably, the Cayman Islands: see Garman, 1888; Lewis, 1940; Carr, 1952) there is evidence (such as the aboriginal name *suerre*, meaning turtle, for the region adjacent to the nesting beach, and the Spanish *Tortuguero* and English "Turtle Bogue," since early times applied to the same shore) that the Costa Rican nesting beach has been in use since pre-Columbian times.

ASCENSION ISLAND

Ascension Island, a true oceanic island, is an exposed peak of the Atlantic Ridge, located in the middle South Atlantic (latitude 7° 56′ S.,

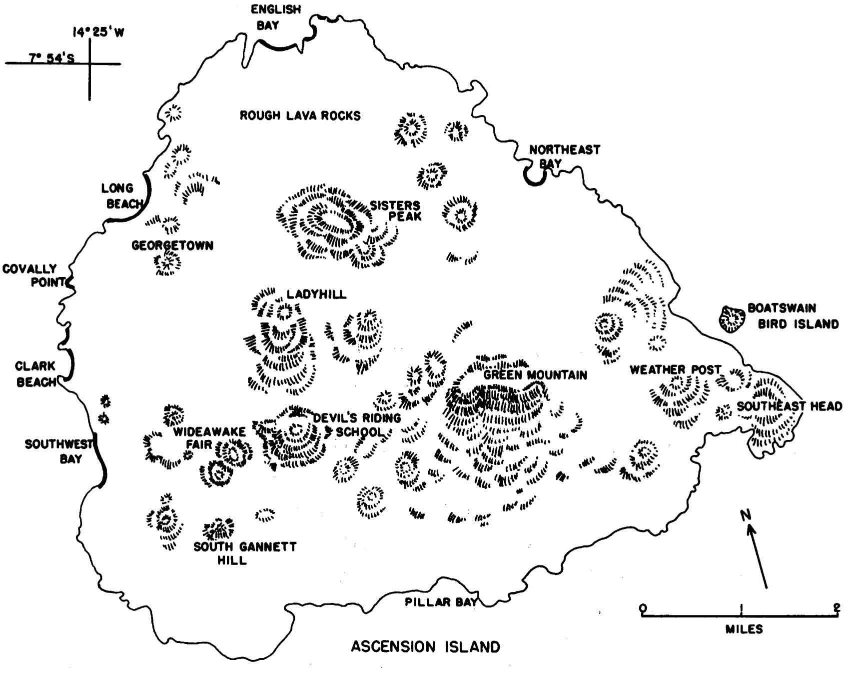

Fig. 2. Sketch map of Ascension Island, showing location and approximate extent of the six main nesting beaches (heavy lines).

longitude 14° 22′ W.). It is 7.15 miles long and 6.25 miles wide, with an area of 38 square miles and with 22 miles of shore line (see fig. 2). It is of volcanic origin, and the bottom drops abruptly away on all sides to great depths. There is no harbor. The highest point on the island is Green Mountain, which rises to 2817 feet.

Ascension lies in the zone of steady southeasterly trade winds. Wave action is exceptionally heavy. During some periods huge swells, commonly ranging between 20 and 30 feet in height, pound the rocky shore, coming in predominantly from the northwest, and less regularly from the southwest. Annual precipitation averages 6 inches at Georgetown (elevation 50 feet) on the coast and 30 inches at the top of Green Mountain. Climatological conditions at Georgetown, measured with standard instruments and under standard conditions, are shown in table 1.

TABLE 1

CLIMATOLOGICAL DATA FOR THE THREE PRINCIPAL MONTHS OF THE NESTING SEASON OF THE GREEN TURTLE, ASCENSION ISLAND, 1960

	February	March	April
Day maximum temperature (6.00 A.M. to 6.00 P.M.), degrees Fahrenheit	85.9	88.2	87.3
Day minimum temperature (6.00 A.M. to 6.00 P.M.), degrees Fahrenheit	75.3	76.4	77.0
Night maximum temperature (6.00 P.M. to 6.00 A.M.), degrees Fahrenheit	79.0	83.4	82.4
Night minimum temperature (6.00 P.M. to 6.00 A.M.), degrees Fahrenheit	74.1	76.3	76.7
Relative humidity			
6.00 A.M.	80.2	83.9	84.2
Noon	63.8	63.9	69.9
6.00 P.M.	67.9	68.7	74.3
Sunshine, hours per day	8.5	9.7	7.5
Total rainfall, in mm.	3.7	52.0	56.9

Although Ascension is well known as a nesting center for sea birds (sooty tern, *Sterna fuscata;* red-billed boatswainbird, *Phaethon aethereus;* brown booby, *Sula leucogaster;* frigate bird, *Fregata aquila*) the resident vertebrate fauna is depauperate. The only land birds are introduced. The herpetological fauna, likewise brought in by man, comprises only the two lizards *Liolaemus wiegmanni* and *Hemidactylus frenatus*, and the clawed frog, *Xenopus laevis*. Of marine turtles, both the hawksbill and the green turtle are known, but the former is a rare visitant, not known to nest on the island.

The Ascension vegetation is scrubby, without true forest. Much of the landscape is bare volcanic rock—basaltic tuff, pumice, scoria, and obsidian. The beach sand is white and mainly of calcareous origin, comprising smoothly rounded pieces of shell. Unlike the Tortuguero sand, it never gets too hot to walk on, barefoot, and imposes little of the hardship on hatchlings encountered by Tortuguero turtles emerging in the daytime on the hot dark sand there. Thermal conditions in the sand are shown in figures 5 and 6.

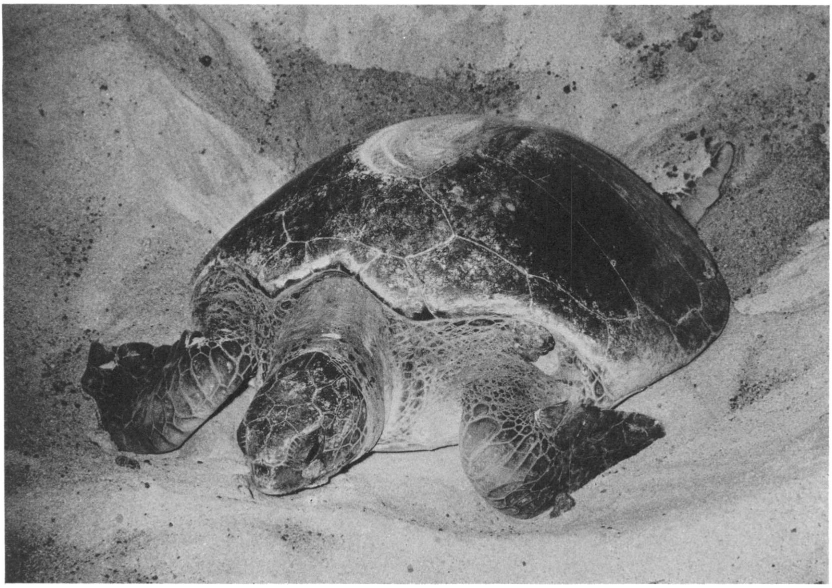

FIG. 3. Green turtle nesting at Ascension. Digging has been completed and laying begun (cf. Carr and Ogren, 1960, pl. 5, fig. 2. The more pronounced and more angular emargination of the shell over the neck of the Ascension turtle is typical of the population).

As a nesting habitat for *Chelonia*, Ascension is markedly different from Tortuguero. The island is a pinpoint of land hundreds of miles from other shores. The nesting ground is not a single beach but a series of sandy crescents at the heads of narrow, rock-guarded coves. The Ascension sand is, as is said above, light colored (see figs. 3 and 4), and, because it is mainly composed of shell fragments, it is loose and easy to dig in. Diel temperature fluctuations are much less than in the dark sand at Tortuguero. Also, unlike the Costa Rican beach, the shores are without clutter of logs or other debris, and there is no littoral vegetation.

The Ascension turtle colony is not molested by either commercial exploitation or natural predation. The last concession for the export of turtles expired in 1935. A few people collect baby turtles for sale to visitors, but this desultory traffic is an unimportant factor. There are no natural mammal or reptile enemies. Cats have gone wild on the island, and one of these was seen eating a baby turtle on the beach, but the damage they do is probably not great. Even ghost crabs, which at Tortuguero constantly harass emerging turtles (and which Hendrickson, 1958, found to be the most serious menace to both eggs and hatchlings in the Sarawak Islands), are lacking at Ascension. Besides its remote location, the only obvious disadvantage it presents is the combination of heavy seas and precipitous, rocky shore line (see fig. 7), which makes entrance to the beaches a hazardous maneuver. Nineteen of the 206 turtles marked had the shell more or less seriously smashed, evidently by contact with the rocks. On the morning of March 20, Hirth was called to see a female green turtle helplessly wedged in a rock crevice at the approach to Southwest Bay Beach.

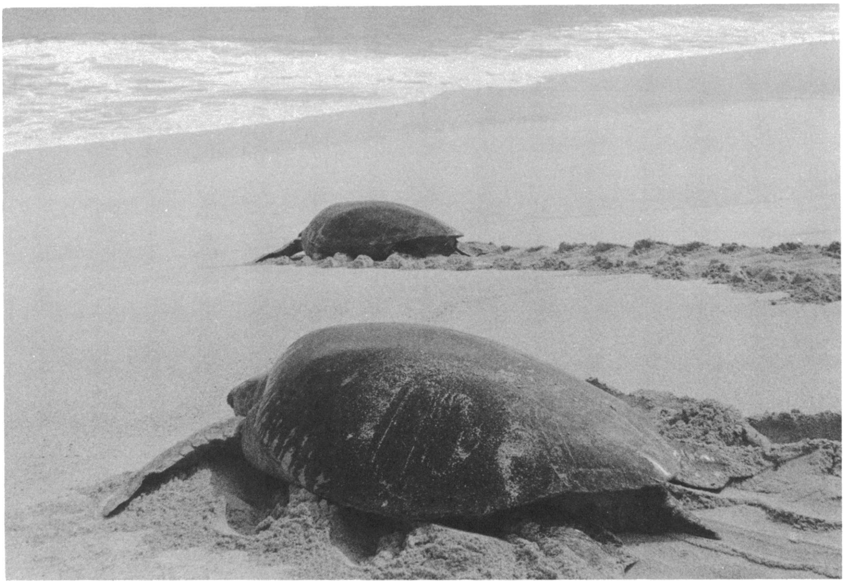

FIG. 4. Ascension turtles returning to the sea after being tagged where they had nested the night before.

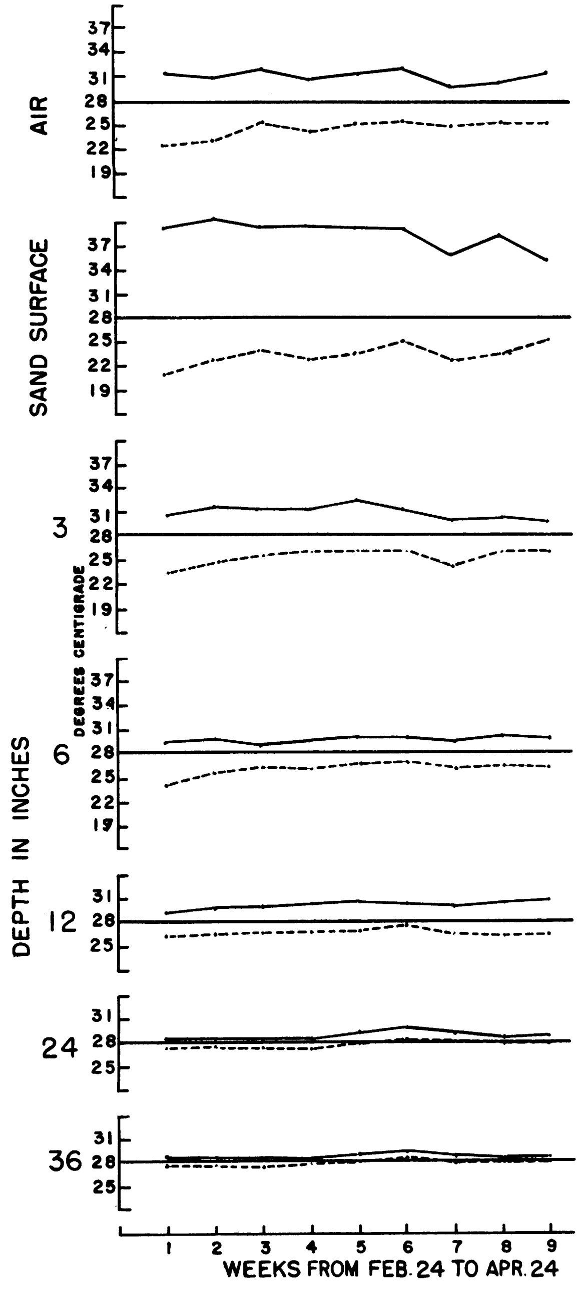

FIG. 5. Graph comparing sand and air temperatures at Ascension Island through a period of 61 days (February 24 to April 24, 1960). Upper solid lines show average weekly maxima; broken lines trace average weekly minima.

Five of the turtles tagged had barnacles, and six showed signs of attack by sharks. Fishermen occasionally find hatchlings in the stomachs of sharks and rock cod. Although predation by these and other fish (especially the common jack, which is abundant) is probably heavy, no relevant data are available.

Most of the nesting at Ascension takes place on the six beaches described below. Regular tagging was carried out at all the beaches. It was not possible to keep constant watch at each, however, and all turtles visiting each beach were thus not marked.

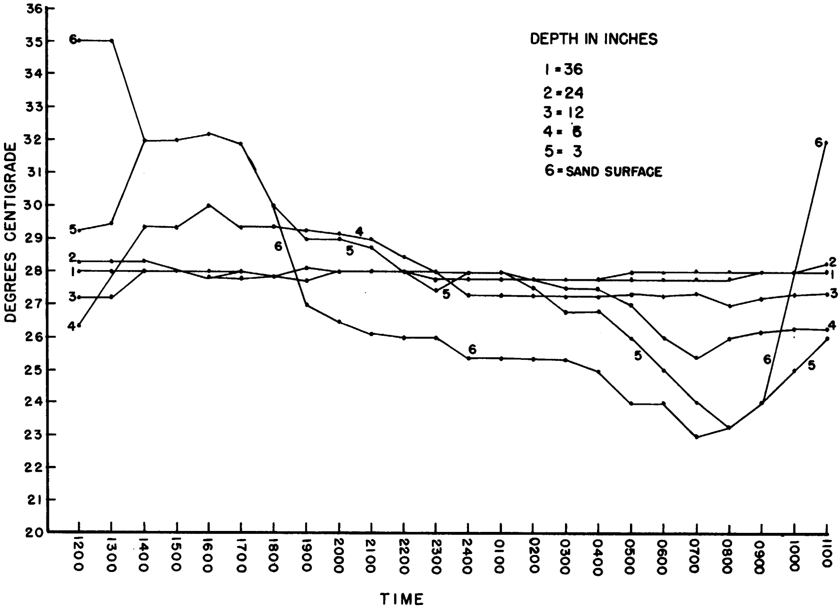

FIG. 6. Diel temperature cycle in the Ascension Island beach sand. The data are three-day averages (February 23–25, 1960).

LONG BEACH

The shore line here is 1100 yards in extent, with a maximum width of 200 yards. High waves at times inundate this entire section, as they did on two days in March, 1960. There is some debris in the form of old iron and oil drums from World War II activity. A cinder road runs along the middle of the beach. Beyond this road the shore is cluttered with debris and is unsuitable for nesting. The beach is crescentic, bounded by lava rocks and backed by Cross Hill, which rises to an elevation of 868 feet.

Most of the nesting was about midway between the points of the crescents, where the beach was widest. Thirty-nine turtles were tagged here.

ENGLISH BAY

The shore here comprises four separate nesting beaches: English Bay Beach and three others, here designated EB1, EB2, and EB3. English Bay Beach has a 310-yard shoreline and is 100 yards wide at the broadest point. It is separated by a 250-yard stretch of rocky shore from EB1, which is 50 yards long and 70 yards wide. EB1 is separated by 150 yards of rocks from EB2, which is 30 yards long and 40 yards in maximum width and strewn with lava fragments a foot or two in diameter. Three hundred yards to the eastward, beyond more rocks, lies EB3, 60 yards long and 50 yards wide, with a craggy bottleneck entrance only 30 yards across. The distribution of tagging in English Bay was as follows: English Bay Beach, 27 turtles; EB1, 10 turtles; EB2, 4 turtles; and EB3, 25 turtles.

FIG. 7. The rocky entrance to the nesting beach at English Bay, Ascension Island.

NORTHEAST BAY BEACH

The shore line is 400 yards long and 300 yards wide. It is backed by lava plains and a 100-foot hill and is without vegetation or debris. This is perhaps the best of the beaches, being almost inaccessible and rarely visited by people. Twelve turtles were tagged here.

SOUTHWEST BAY BEACH

Here the shore line is 500 yards long and 130 yards wide. About half of this section is bordered seaward by wave-smooth lava that slopes gently into the water. In coming in to nest, turtles crawl and swim over the rock to get to the sand beyond. As is said above, in March, a turtle was found wedged in a crack in this rock and would have died if it had not been freed by the work of four men. This beach is a picnic area for the American colony. The only debris was flash bulbs and beer cans. There was a small patch of beach morning-glory (*Ipomea pes-caprae*) at the northern end. Fifty turtles were tagged here.

CLARK'S BEACH

This beach, located about 500 yards north of Southwest Bay Beach, is made up of two sections. One is 450 yards long and 90 yards in greatest width, without vegetation and with a low hill behind it. There is a bottleneck entrance from the sea. Twenty-five turtles were tagged here. The other section, separated from the foregoing by 150 yards of lava shore, is a crescent 100 yards long and 50 yards wide, without vegetation but with scattered rock outcrops both on the beach and in the water. Twelve turtles were tagged here.

COVALLY POINT BEACH

The beach is 180 yards long and 80 yards wide in greatest dimensions. It is bordered and cut off at both ends by lava fields and is backed by a 200-foot hill. There is no litter or shore vegetation. Two turtles were tagged here.

NESTING SEASON

Old reports summarized by Carr (1952) stated or implied that the nesting season of the Ascension colony extended from November or December to midsummer. These limits were evidently dilated by preseason and post-season observations of single females emerging on one or the other of the five nesting beaches there. It now appears that the main breeding season is strongly limited to the period from February to April. As figure 8 shows, there was during April a marked decline at all the beaches, of both turtles coming ashore and of untagged turtles. After April 25 it became pointless to continue tagging at Ascension.

There is the slight possibility that at some other time during the year

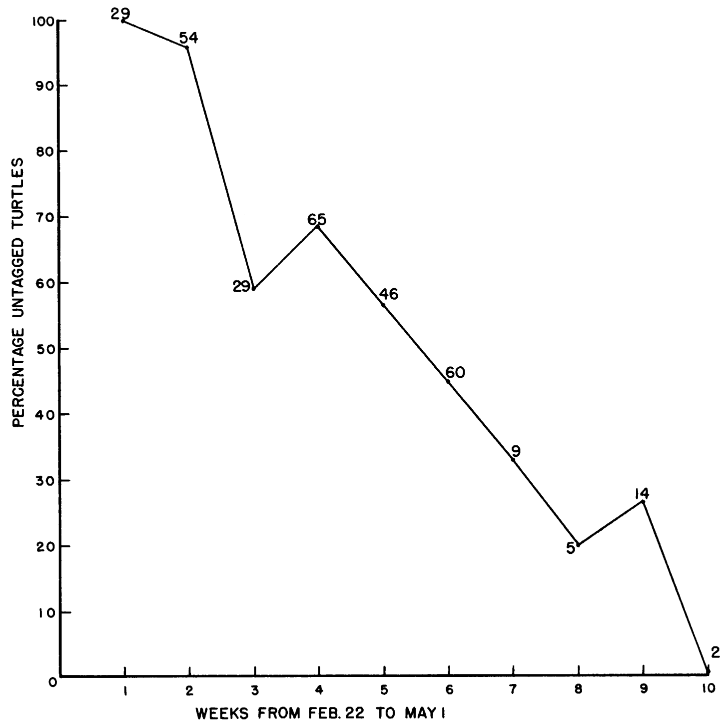

FIG. 8. Graph showing percentages of untagged turtles coming ashore at Ascension during the 10-week period from February 22 to May 1, 1960. The numbers adjacent to the curve indicate all turtles, tagged and untagged, seen on the beach during the week involved. The data suggest that the time of the study was actually, as local opinion holds, the main nesting season at the island.

another curve like that in figure 8 could be drawn, when another flotilla of green turtles arrived from some other place. Or, even if the history of the year at Ascension is well shown by the one curve for 1960, in other years the turtles might come from other points of origin, and might theoretically show different seasonality. If the visits to the island are made on two-year and three-year schedules, as at Tortuguero, this variation might also affect seasonality in some way.

A reappraisal of the surprisingly little evidence available for other years and for other seasons, however, mostly in the form of letters or word-of-mouth reports from Ascension visitors or residents, suggests that our curve may show a typical year at the island and that only desultory nesting occurs at other times.

For the two areas here being compared, then, the nesting season may be defined roughly as follows: Ascension, February to May; Tortuguero, June to November. In the Sarawak Islands breeding occurs throughout the year, with a strong peak in July and August (Hendrickson, 1958).

MATING SEASON

Mating apparently takes place at Tortuguero, at Ascension, and at the China Sea rookeries (Harrisson, 1951) after the mature males and females have moved to the nesting beach. There is no evidence that it ever occurs away from the breeding area. Carr and Ogren (1960) discussed the difficulty of determining the timing of copulation with respect to the several nesting emergences of the female. Both at Tortuguero (see fig. 9) and at Ascension, courtship and mated pairs were seen only during the first half of the nesting season: in July and early August at Tortuguero, and in February and early March at Ascension. We have no additional data on the precise timing of copulation relative to nesting. Since mating brings about fertilization of eggs that will be laid two or three years later and has nothing to do with the eggs of the season, it seems likely that copulation could take place equally well before or after nesting, and that it may occur at both times. Observations along the coast of Sinaloa, Mexico (Carr, 1961a), seem to indicate that the same is true of *Lepidochelys olivacea*, which nests there.

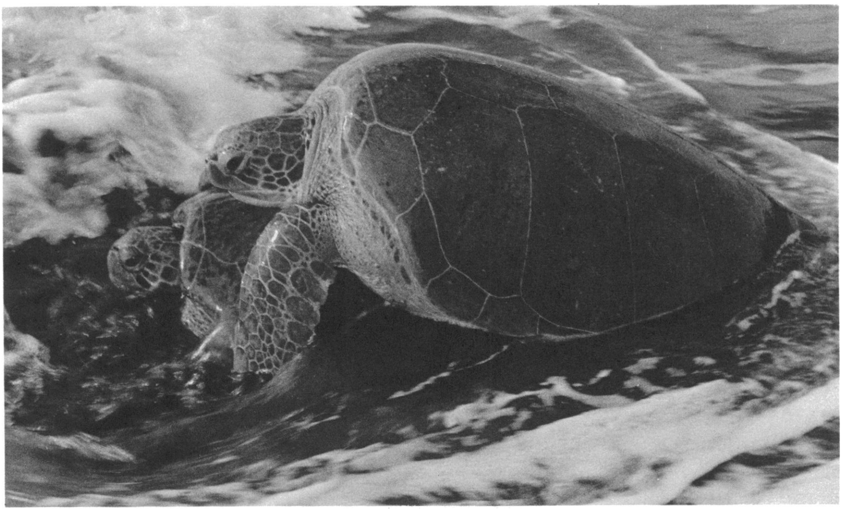

FIG. 9. A pair of mating Tortuguero green turtles, thrown ashore by the surf.

Because there has never been any report, anywhere in the world, of the mating of green turtles at any time except the nesting time, and at any place except near the breeding ground, the question arises: When are the eggs of the *virgin* females fertilized? From what we know now, we must conclude that the young females accompany the older turtles to the nesting ground, mate there, and return to the home pastures without laying. Whether they await only the next season to return to lay, or wait through a whole cycle of the two-year or three-year reproductive term characteristic of the species, is of course also unknown.

TABLE 2

Incubation Periods of Three Colonies of the Green Turtle

(The data for the China Sea are from Hendrickson, 1958, who found the period to vary from an average of 54 days to an average of 70 days, depending upon the season.)

Years of Observation	Locality	Number of Nests	Mean Period of Incubation	Range
1956–1960	Tortuguero	217	55.6	48–70
1960	Ascension	10	59.5	58–62
1952–1953	China Sea	354	54.0–70.0	—

INCUBATION AND EGG COMPLEMENTS

Incubation time is here defined as the period between oviposition and the appearance on the surface of the largest number of young of a given complement. The arrival at the surface may follow actual emergence from the egg by several days. The difficulty of seeing what is going on in the nest has precluded the gathering of quantitative data on the actual embryonic period. Comparative data for Ascension and Tortuguero appear in table 2. The lesser range for Ascension may be attributable to the more even climate that prevails there during the nesting season. There is almost no rain at that time, while at Tortuguero there may be daily showers, days of almost constant rain, or periods of drought. Incubation time as indicated by our data agrees surprisingly well with that given by local people who watch nests to get young turtles to sell to visitors. Some of these residents were confident that the incubation time is two months "to the hour."

The number of eggs in a complement varies markedly from one nesting, and from one individual, to another. At Tortuguero the range in number in 406 complements counted in 1959 and 1960 was 18–193 (average, 110.0). At Ascension the range in 140 complements was 53–181 (average,

TABLE 3

Observed Renesting Returns of Female Green Turtles, Tortuguero, Costa Rica, 1960

(The quarter-mile beach sections referred to in the columns headed "mile" are numbered from the river mouth southward.)

Tag	First Observed Emergence Date	Mile	First Return Date	Mile	Second Return Date	Mile
1101	June 30, P.M.	½	July 11, P.M.	2¾	—	—
1103	June 18, P.M.	1	June 28, P.M.	1¼	July 10, P.M.	1¼
1109	June 27, P.M.	¾	July 10, P.M.	2	—	—
1112	June 23	3¼	July 5	3¼	July 18, P.M.	1¾
1114	June 24, P.M.	2½	July 7, A.M.	1¾	—	—
1122	June 27, A.M.	3¼	July 9, A.M.	3	—	—
1126	June 27, P.M.	1¾	July 12, P.M.	2½	—	—
1129	June 28, P.M.	4	July 10, P.M.	1	—	—
1139	June 29, A.M.	½	July 13, P.M.	¾	—	—
1141	June 29, P.M.	1¾	July 11, P.M.	2	—	—
1153	June 30, P.M.	1¾	July 13, P.M.	2	—	—
738	July 1, A.M.	3¼	July 12, P.M.	¾	—	—
1173	July 3, P.M.	2	July 17, P.M.	3¼	—	—
1181	July 5, A.M.	1	July 18, P.M.	¾	Aug. 3, P.M.	3
1189	July 5, P.M.	2½	July 17, P.M.	3	—	—
1191	July 5, P.M.	2½	July 18, P.M.	3¼	—	—
1193	July 5, P.M.	2¾	July 17, P.M.	1	July 30, A.M.	2
1197	July 5, P.M.	2	July 17, P.M.	1¼	—	—
454	July 7, A.M.	2¾	July 20, P.M.	2	—	—
786	July 8, P.M.	¾	July 21, P.M.	2¼	—	—
1237	July 12, P.M.	½	July 24, P.M.	2½	—	—
1242	July 12, P.M.	3¼	July 24, P.M.	1¾	Aug. 7, P.M.	1½
1244	July 12, P.M.	3	July 24, P.M.	2¼	—	—
1260	July 13, P.M.	2¾	July 25, P.M.	3¼	—	—
1272	July 17, P.M.	1¼	July 31, P.M.	½	—	—
1273	July 18, P.M.	2½	July 31, P.M.	2¾	—	—
1294	July 18, P.M.	1½	Aug. 1, P.M.	1	—	—
1295	July 18, P.M.	¼	Aug. 1, P.M.	½	—	—
1296	July 19, A.M.	2	Aug. 2, P.M.	2	—	—
1297	July 18, P.M.	1	Aug. 1, P.M.	1½	—	—
1298	July 18, P.M.	1	Aug. 3, P.M.	½	—	—
1300	July 18, P.M.	½	Aug. 1, P.M.	¾	—	—
1301	July 25, A.M.	2	Aug. 5, P.M.	1	—	—
1302	July 25, P.M.	2	Aug. 4, A.M.	1	—	—
1310	July 27, P.M.	1½	Aug. 7, P.M.	2¼	—	—
1317	July 27, P.M.	1	Aug. 5, A.M.	2¾	—	—
1328	July 21, P.M.	1¾	Aug. 3, P.M.	1¾	—	—
1329	July 24, P.M.	2	Aug. 7, P.M.	2	—	—
1322	July 24, P.M.	2¾	Aug. 4, P.M.	3	—	—

TABLE 3—(*Continued*)

Tag	First Observed Emergence Date	Mile	First Return Date	Mile	Second Return Date	Mile
1333	July 24	3	Aug. 5	2	—	—
1334	July 24	3	Aug. 6	¾	—	—
1336	July 24, P.M.	4	Aug. 7	1¾	—	—
1340	July 25	2½	Aug. 7	2¼	—	—
1341	July 25	2¾	Aug. 7	1¾	—	—
1344	July 26	2½	Aug. 8	3¾	—	—
1351	July 27	1¾	Aug. 8	2	—	—
1358	July 27	2¾	Aug. 7	3	—	—
1493	Aug. 8	1½	Aug. 20	1¾	—	—

115.5). Hendrickson gave the range in 8147 clutches as 3–184, and the average 104.7. Such variation, of course, completely overshadows any regional differences in this trait.

In ratio of egg number to carapace length (in inches), in 80 cases at Tortuguero and the same number at Ascension, the mean was in both instances 2.76 (Ascension range, 1.17–4.72, S.D.± 0.57; Tortuguero range, 1.64–4.33, S.D.± 0.47).

Survival in nests of green turtle eggs is surprisingly low. Hendrickson (1958) recorded a hatch of 50 per cent in 354 nests (average number of eggs per nest, 104.7) on China Sea beaches. At Tortuguero, 50.7 per cent of 12,000 eggs hatched in 1959, and 50.8 per cent of 30,484 in 1960. At Ascension there was a hatch of 54.4 per cent among 1208 eggs. The removal of eggs from the nest and installation in artificial nests impose no additional mortality.

The mean diameter of 100 eggs from five nests (20 from each) at Ascension was 54.60 mm. (range, 49.0–58.7). At Tortuguero 400 eggs, comprising 20 from each of 20 nests, had a mean diameter of 45.7 mm. (range, 41.1–50.1). At Ascension the mean diameter of 100 eggs representing a first nesting for the season was 55.60 mm., and the mean diameter of another hundred representing a second laying by the same turtle was 53.75 mm.

At Ascension, in 80 per cent of the cases of renesting noted, the first egg complement was bigger than the second. Of cases involving three or more nestings, in 80 per cent a regular decrease in egg number continued throughout the third nesting (i.e., 1 > 2 > 3). In 50 per cent of the cases involving more than three nestings, the same regular decrease occurred (i.e., 1 > 2 > 3 > 4, and 1 > 2 > 3 > 4 > 5).

Adaptive aspects of complement size are discussed by Carr and Hirth (1961).

RENESTING

Of 392 turtles tagged at Tortuguero during the 1960 nesting season and recovered that same season (see table 3), 72 nested twice, and seven nested three times. The range and average internesting intervals for Tortuguero and Ascension were as follows:

TORTUGUERO

1956–1959, 92 renestings, interval 12–14 (average, 12.5) days
1960, 48 renestings, interval 9–16 (average, 12.56) days

ASCENSION

1960, 76 renestings, interval 10–17 (average, 14.5) days

Hendrickson (1958) found the average interval (4493 cases) in the China Sea to be 10.50 days, with a range of from eight to 17 days.

The greatest number of observed emergences by any turtle, during our studies, was two cases of five nestings at Ascension during 1960. That the maximum number of nestings per season is higher seems evident from the size groups of eggs found in oviducts of slaughtered females, and from maxima derived by the division of local internesting interval into the number of days that separated the earliest and latest emergences. Carr and Ogren (1960) found the maximum calculated in this way to be six nestings.

RETURNS FROM PREVIOUS YEARS

Carr and Ogren (1960), in their reports of the results of the 1959 season, when 988 turtles had been tagged during four preceding seasons, recorded the retaking of 33 turtles that had been tagged previously. Of these, 66.6 per cent were back after an absence of three years, and 33.4 per cent after one of two years. None from the 1958 season was retaken. That the two-year cyle was not represented among the turtles tagged in 1955, although these were the biggest group of all (495), was an anomalous feature of the record, still not explained.

As tables 4 and 5 show, results of the 1960 season confirm the reality of both the three-year major cycle and the two-year undercurrent. With a backlog of 1178 turtles tagged during previous years, eight returned in

TABLE 4

Points of Emergence at Tortuguero, Costa Rica, of Female Green Turtles Returning after Absences of Two, Three, or Four Years

(Figures in parentheses refer to renesting dates and location in which turtles were taken more than once during the season of their long-term return to the area.)

Tag No.	Date Tagged	Place Tagged	Place Retaken	Date Returned
353	Aug. 21, 1956	Mile ⅛	Mile 2¾	July 1, 1960
398	July 3, 1957	Mile ½	Mile 2½	July 27, 1960
417	July 6, 1957	Mile ¼	Mile 1½	July 1, 1960
425	July 8, 1957	Mile 1	Mile 1	July 27, 1960
454	July 11, 1957	Mile 1¼	Mile 2¾ (2)	July 7 (July 20), 1960
462	July 14, 1957	Mile 1¼	Mile 1	August 7, 1960
472	July 14, 1957	Mile ¾	Mile 1	August 1, 1960
623	Sept. 5, 1957	Mile 1	Mile 2¾	July 18, 1960
635	Sept. 5, 1957	Mile 1	Mile 1 (1)	July 18 (Aug. 6), 1960
654	June 26, 1958	Mile 1½	Mile 1¼	August 2, 1960
676	July 19, 1958	Mile 1½	Mile 2½	July 26, 1960
738	Aug. 6, 1958	Mile ¾	Mile 3¼ (¾)	July 1 (July 12), 1960
786	Aug. 28, 1958	Mile ¾	Mile ¾ (2¼) (2)	July 8 (July 21), (Aug. 3) 1960

1960 after three years, four after two years, and one after four years. The last, involving a multiple of two, but not of three, should evidently be added to the total for the two-year cycle.

For the five seasons of the study since the tagging of the first group in 1955, the total number of turtles is 1570, and the total retaken in later seasons on the beach at Tortuguero is 46. Of these, 65.2 per cent returned after three years and 34.8 per cent after two years. None has come back after an interlude of only a single year.

Because only one season's tagging at Ascension has been carried out, there are no data on season-to-season returns. Harrisson's results (1951, 1954, 1956) in the China Sea suggests that the two-year cycle is not represented in colonies there.

TABLE 5

Returns of Tagged Turtles to the Nesting Beach at Tortuguero, Costa Rica, After Absences of Two, Three, and Four Years

Year	No. Tagged	Returns from Previous Years	
		Year	No. of Returns
1960	392	1956	1
—	—	1957	8
—	—	1958	4

When more is known about the life history of *Chelonia*, it may be possible to see some ecologic or zoogeographic basis for the odd dichotomy of the Caribbean form in its nesting periodicity. Possibly the two-year and three-year periods represent intervals required to complete a developmental migration and an aftermath of residence at the permanent feeding ground. On the other hand, they could represent simply two degrees of physiological efficiency in recuperating from the previous nesting venture. Why two degrees should exist, and whether they show separate geographic distribution or occur within single populations, are not known. An interesting question concerning the initiation of virgin females into the cycles is raised in our section below on Mating Season.

NESTING BEHAVIOR

As a step in a projected long-term program of ethologic study of world populations of sea turtles, careful behavioral observations were made on the Ascension nesting ground. As would be expected, the nesting process there proved to follow the same general pattern as that at Tortuguero. Only a few minor differences, or degrees of emphasis, in the various mannerisms attending the landing and nesting venture were noted.

One such difference is the greater number of trial holes dug by the Ascension turtles. Like certain fresh-water species, the female turtle at Ascension often digs one or more holes of standard size and shape and leaves them empty and open, before finally carrying out the laying, covering, and concealing processes. Such indecision is not unknown among Tortuguero green turtles, but it happens only rarely. No explanation for this difference can be suggested.

Perhaps because of the looseness of the Ascension Island sand, the nesting female there digs a much deeper body pit than at Tortuguero, even taking into consideration the larger average size of the Ascension turtles. Because of the lack of predators on the island, the trait would seem to have no special protective value. It is likely that some (as yet unrecognized) difference in thermal or moisture conditions of the Ascension sand lends advantage to a gaining of nest depth by digging in the bottom of a deep body pit.

Carr and Ogren (1960) referred to the "smelling" of the sand by Costa Rican green turtles coming ashore to nest. From the time she first can be observed in the wave wash until she reaches dry sand, the emerging female may repeatedly bend her neck downward at a sharp angle, touch the end of her snout against the ground (the bottom under shallow water, or the wet sand above wave reach) and hold it there for half a minute or so before raising her head and going up on the beach. This habit appeared to be even more prevalent among the Ascension turtles, although it may simply have been that observation was facilitated there by the greater visibility on the light sand and by the lesser skittishness of the emerging turtles, itself a noteworthy point of divergence of the two populations (see below). Just what sense the sand-nuzzling may bring to bear is not clear, but the mannerism would logically appear to be an adjunct to the general process of site choice or recognition.

The high alarm threshold of the emerging Ascension turtle is the most striking behavioral difference between it and the Tortuguero population. When a Costa Rican turtle strands and starts up the beach, she can be turned back into the surf by the slightest show of artificial light—a match struck 50 feet away, for example, or by the moving of a man or dog, even some distance up the shore, across the starlit sky. With the Ascension population the unswerving train of stereotypes, which in most turtles begins with the digging process and thereafter keeps the animal oblivious to outside interference, appears to take over at the time of stranding. The turtles could thus be watched at close quarters, and there can be no doubt that the "sand smelling," whatever its function may be, is standard procedure with the Ascension turtles.

COMPARATIVE MEASUREMENTS AND COUNTS

The green turtles of the Ascension colony evidently include individuals larger than those of any known population (see tables 6 and 7). Of some 1146 mature nesting female turtles measured during the course of the work at Tortuguero, the smallest was 27.25 inches in over-all shell length, the largest 46.25 inches. The average there, however (39.40 inches), corresponds closely with that of the China Sea populations studied by Hendrickson (1958), about 38.50 inches. Whether size differences are genetic or are controlled in part by regional environment is not known. It is also impossible to say to what extent maximum size in modern green turtles has been reduced by commercial exploitation. Old reports speak of 800-pound green turtles both at Ascension and in Florida. No such weights are ever reported today. Although the animals evidently continue growing indefinitely, at diminishing rates, the heavy drain by the turtle industry has in many places clearly reduced the group life expectancy, and presumably the maximum size.

Table 7 gives the weights of some of the larger turtles marked at Ascension Island and of a representative series from Tortuguero. Hendrickson (1958) found the average weight of 10 adult China Sea females to be 244 pounds.

TABLE 6

BODY PROPORTIONS OF 200 TURTLES TAGGED ON ASCENSION ISLAND (1960) AND OF 200 TURTLES TAGGED AT TORTUGUERO, COSTA RICA, FROM 1956 THROUGH 1960

(Forty turtles from each of the five seasons were picked at random to represent the Tortuguero colony. The sample is thus more clearly random than that from Ascension, all from one season. All measurements from mature females.)

	Ascension	Tortuguero
Carapace length in inches		
Range	33.00–55.50	32.75–46.25
Mean	42.55	39.50
S.D.	±3.38	±2.006
Width of carapace/length of carapace		
Range	0.61–1.00	0.64–0.88
Mean	0.77	0.77
S.D.	±0.063	±0.033
Length of plastron/length of carapace		
Range	0.67–0.97	0.67–0.90
Mean	0.80	0.78
S.D.	±0.05	±0.0003
Length of carapace/width of head		
Range	0.10–0.17	0.10–0.17
Mean	0.146	0.129
S.D.	±0.015	±0.0035

No mature males have been measured or weighed at Ascension, and none at Tortuguero since the one figured in Carr and Ogren (1960). The only male specimen of *Chelonia* for which both weight and reliable measurements are available was one taken on the turtle grass flats off the mouth of the Withlacoochee River, Levy County, Florida, October 31, 1960, by Captain John Gibson, the oldest turtle captain of the Gulf Coast green turtle fishery. After an exceptionally poor season, during which for weeks at a time we found it impossible to get any turtles at all for projected orientation experiments, Gibson called from Yankeetown to say that he had just brought his boat in after four days on the flats where the turtle netting is done. He said that the first day nothing was caught, but during the night turtles were heard blowing all around the boat. Beginning the next day young turtles were taken as fast as the net could be worked. They were quite clearly just arriving on the flats, according to Gibson, from a southerly direction. Both green turtles and ridleys were represented, and all but one of the green turtles were of the 20- to 90-pound weight group that usually makes up the population in that locality. One, however, was a big, very fat, mature male, the largest green turtle taken at Yankeetown in 40 years, and one of the very few mature individuals of

TABLE 7

DIMENSIONS (IN MILLIMETERS) AND WEIGHTS (IN POUNDS) OF NINE MATURE FEMALE GREEN TURTLES NESTING AT ASCENSION ISLAND IN 1960 AND OF SIX MATURE FEMALE GREEN TURTLES NESTING AT TORTUGUERO, COSTA RICA, IN 1961, RESPECTIVELY

Length of Carapace	Width of Carapace	Length of Plastron	Width of Head	Weight
39.00	32.50	35.00	6.75	310
40.50	33.00	35.00	6.00	409
42.50	35.00	35.00	6.25	340
43.25	35.50	36.50	6.25	400
43.50	36.25	36.50	7.00	380
44.00	36.00	35.00	6.75	440
44.50	33.00	38.00	6.50	460
49.50	35.00	37.50	7.50	530
52.00	35.00	39.00	6.75	500
38.50	28.00	30.00	5.00	250
40.25	30.50	32.25	5.75	335
41.00	33.00	33.50	5.75	305
41.25	31.00	33.00	5.00	295
42.00	31.50	33.75	5.50	315
42.00	32.25	32.75	5.75	310

either sex taken there during the past two or three decades (see figs. 10, 11, 18–20). Its measurements in inches were as follows: over-all shell length, 42½; least carapace length (in a straight line, middorsal, notch to notch), 42; greatest length of plastron, 34½; width of head, 5¾; depth of shell, 14½; weight, 340 pounds.

With respect to the comparative size of Atlantic and east Pacific green turtles, it seems that no measurements for series of definitely mature green turtles from the American Pacific are available. Carr (1952) gave shell lengths of what he regarded as a mature male and a female from the Gulf of Fonseca, Honduras. The size of these, however, and that of all the other Honduran specimens seen by Carr, fall within the range of size in the series recently measured about the mouth of the Gulf of California (Carr, 1961b). This was a sample from a juvenile, non-breeding population, like that of the Florida Gulf Coast derived from distant nesting grounds. Of 100 turtles and shells measured in Sonora, Sinaloa, and at La Paz, Baja California, the range in shell length (over-all) was from 17 to 34½ inches, and the average 23¼ inches. The females were not, and according to the local people never are, ovigerous. The largest of the males, in the development of its secondary sexual characters, seemed nearly mature. The only definitely known nesting ground of east

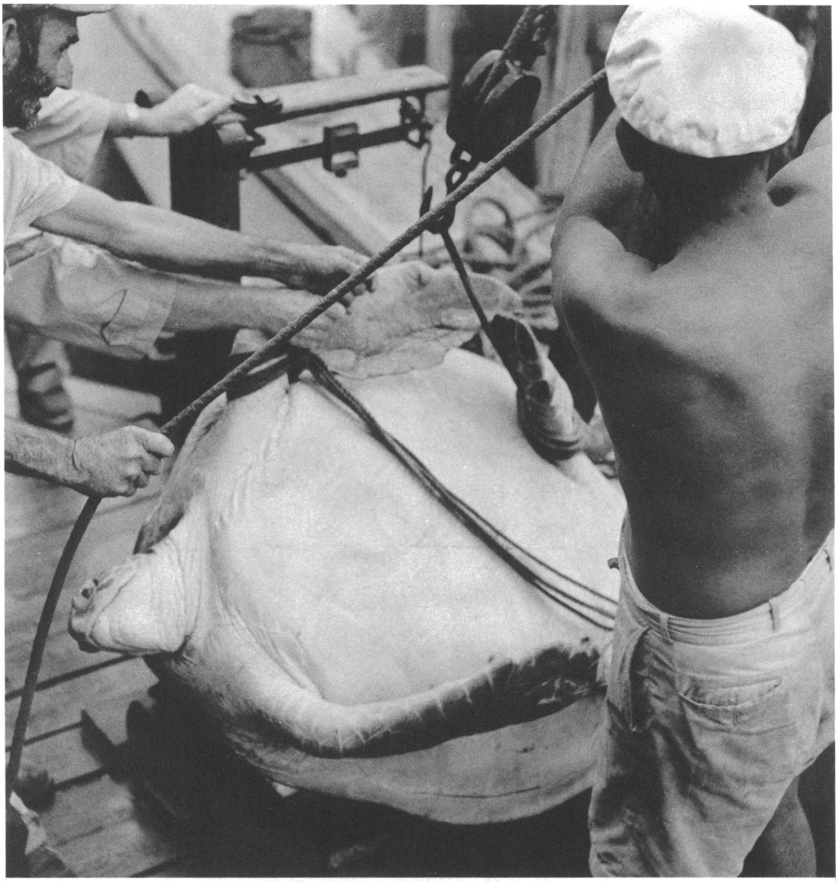

FIG. 10. Male green turtle, taken off the mouth of the Withlacoochee River, Florida, being unloaded at Yankeetown. This was the biggest green turtle caught by the West Coast industry in many years. It was used in orientation trials described in the text and is shown in later figures.

Pacific turtles in use today is that at Maruata Bay, on the coast of Michoacan. Peters (1956–1957), in describing that rookery, published no measurements of the turtles nesting there.

Tables 6 and 7 compare the Tortuguero and Ascension colonies with respect to several characters and ratios. Besides being on the average larger, the Ascension turtles have notably bigger heads. There appear to be no significant differences in other body proportions or in postorbital scale count. The comparative dimensions of hatchlings are given in table 8.

SITE TENACITY

Both Hendrickson (1958) and Carr and Ogren (1960) showed evidence that female green turtles, in returning for the successive nesting emergences of a single season, tend to go back to a place near the original nesting site. Our table 3 shows the same sort of evidence. Carr and Ogren also gave data that suggest a similar site tenacity in turtles coming back to nest after the two-year or three-year absence from the nesting ground. Table 4 shows more cases of this kind. While the sample is small, it should be kept in mind that the turtles listed are the only cases of nesting recovery, during 1960, of a female tagged by us during any previous year. That is to say, all recorded long-term nesting emergences by turtles marked at Tortuguero have been on the Tortuguero beach, and all on the same three-mile section on which they were marked. The significance of such single cases of pinpointed return as numbers 425, 635, and 786 in table 4 alone seems clear proof that other than chance landings are being made. All data on short-term (renesting) returns are given in

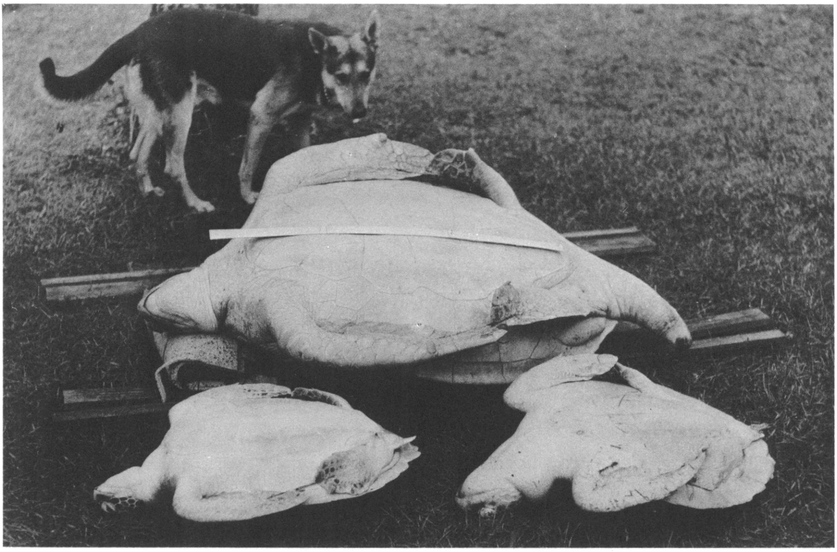

FIG. 11. Ventral view of the male green turtle shown in figure 10. At left below is an immature green turtle of a size average for the itinerant Florida colony. At lower right is a ridley, *Lepidochelys kempi* (Garman), a little larger than average for the Gulf Coast population in Florida. All three turtles were taken the same day (October 31, 1960) and in the same place.

TABLE 8

COMPARATIVE DIMENSIONS (IN MILLIMETERS) OF DAY-OLD HATCHLINGS, WITH RANGE OF MEASUREMENTS IN PARENTHESES

	Ascension	Tortuguero
Number	100	100
Length of carapace	51.7 (49.1–55.0)	49.7 (46.0–56.0)
Width of carapace	41.6 (38.0–48.0)	38.5 (35.0–48.2)
Length of plastron	42.6 (38.2–48.1)	40.0 (33.5–46.1)
Width of plastron	17.0 (15.5–20.5)	15.2 (13.0–17.2)

table 3. Of 48 turtles retaken on the beach at Tortuguero after having been tagged during the first half of the 1960 season, 24 came back south of the place where they were tagged, 20 north of it, and four at the same locality. More explicitly, sites of return were spaced, relative to tagging site, as follows: 6.2 per cent, ¼ mile north; 4.2 per cent, ½ mile north; 10.4 per cent, ¾ mile north; 8.3 per cent, 1 mile north; 12.5 per cent, between 1½ and 3 miles north; 22.9 per cent, ¼ mile south; 6.2 per cent, ½ mile south; 6.2 per cent, ¾ mile south; 14.6 per cent, between 1¼ and 2¼ miles south.

As Carr and Ogren (1960) pointed out in discussing data from previous recoveries, the returns show no precise spot tenacity. They do, however, support an assumption that female turtles seek out and recognize a relatively restricted section of the Tortuguero beach both in the repeated nesting emergences of a given season and when they come back on successive migratory visits to the breeding ground. The few cases in which a turtle returned to the exact spot on which she nested previously lend weight to the supposition that a refined site-discrimination sense of some kind must be available to her.

For studying the tendency and ability to "home" to a particular section of shore for nesting returns, Ascension offers conditions better than those at Tortuguero and almost as propitious as those at the islands where Hendrickson's work was done. The Sarawak Islands nesting ground is a series of five small islands separated by varying expanses of water. At Ascension there are six principal nesting beaches, separated not by water but by forbidding cliffs of scoria that make up most of the shore. As at Tortuguero, tagging results at Ascension showed a marked tendency for renesting turtles to go back to the same beach for successive nestings. Of 206 turtles tagged, there were 76 renesting recaptures. Of these only 13 (17%) failed to return to the beach on which they had previously emerged.

While these results are clearly of some significance, the homing achievement involved is hard to evaluate. It is still not known what female green turtles do during the 12- to 14-day interval between their renesting emergences (see Carr and Ogren, 1960). In the case of the Ascension colony it was evident that they did not stay in the sand-shored bays where nesting occurred. It was often possible for Hirth to stand on the little nesting beaches during the day and see heads of turtles moving back and forth across the rock-bound opening leading into the beach-fringed cove. On such occasions there was sure to be nesting on the beach that night. But once her nesting was done, there would be nothing to hold the turtle in the area for the fortnight that must elapse before the next nesting time. Moreover, the seas are, as is said above, extremely heavy, making it hazardous, even for a strong swimmer like a green turtle, to loaf about close inshore. Multiplying our observed number of renestings by the Ascension internesting interval would give a stay of 34.8 days for some turtles. The actual time that some remain is certainly a good deal longer. It seems unlikely that all the turtles that nest on a given beach spend all their time at Ascension simply swimming back and forth across the mouth of the cove in which their nesting beach is located. On the other hand, we can offer no suggestion as to where they go, so cannot assess the importance of their feat in finding the same beach each time they nest. Light may be shed on this point, as it has been at Tortuguero, when we return to Ascension in 1963 to watch for the return of the group tagged in 1960. As these will have presumably spent the interim in Brazil, their returning to a home beach at Ascension will be solid evidence of site fixity.

At Tortuguero a conspicuous feature of the beach landscape in early July is the marking of the sand by "half moons"—the trial emergence trails that the turtles make, perhaps as a final, fine-scale, site-finding process at the end of the high-seas journey. These half moons appear to be made only rarely by the Ascension turtles. During the 1960 season, although all six beaches were kept under surveillance, only about 10 trial trails were observed.

To account for this difference, it is tempting to attribute it to the topography of the nesting ground. When the Tortuguero flotillas come in after their open-water travel, the problem they face is to locate a short section of the beach which certain unknown senses indicate is the right one. Part of the appraisal process might be carried out some distance off shore, outside the breaker line, but the final discrimination must be made after they have bumped the bottom, or even up beyond the wave wash. The half-moon marks could thus be the trial trails of newly arrived schools searching for the "home" stretch of shore (see comments on sand "smelling" in section on behavior).

At Ascension the situation is very different. At the end of the voyage of a thousand-odd miles that takes the nesting turtles there, the problem is not to select the appropriate section of a linear, more or less homogeneous, shore, but to choose among six separate crescents of beach that are guarded, and thus marked, by craggy promontories. Once a turtle has located the narrow opening leading into the right cove, her orientation problem would be solved. The shore of the cove would funnel her directly to the nesting beach. The disinclination of the Ascension turtles to make trial half-moon trails may simply mean that no on-shore discrimination process is necessary. What bearing the relatively greater tendency of Ascension turtles to dig trial nest holes may have on these problems is not clear.

SEA-FINDING ORIENTATION

An important feature of the orientation capacity of marine turtles is the ability of newly hatched young, and of the female after nesting, to find the ocean without seeing it. Whether the same senses are involved in both cases, and whether the process to any extent duplicates the high-seas guidance achievements of the migrating adult, are questions to which we hope to find answers. Carr and Ogren (1960) gave results of field tests bearing on the problems and summarized experiments of others. Observations on two naturally emerging nests at Ascension Island, and results of a field test of yearling turtles at Daytona Beach, Florida, add to the anecdotal groundwork for such an inquiry.

A nest with emerging young was found April 16, at 4 P.M., at Long Beach, Ascension Island. The nest was in the bottom of an unfilled body pit left by the female, and the young coming out could see neither the ocean nor the mountain behind the beach. Their horizon on all sides was the rim of the pit. Numerous other such craters lay between the nest and the water, 180 feet away. After short periods of neck stretching, as if to appraise their surroundings, all the turtles (about 88) moved off towards the sea. Most were under way within a minute or so after freeing themselves from the sand. The rest (about 10) spent two or three minutes in a neck-craning perusal of the environment before moving away. All headed generally towards the sea. The first reached the water within 16 minutes; the rest, within 25 minutes. All made repeated brief neck-craning stops along the way. The spread where they entered the water was 75 feet, with no turtle outside these limits.

Another nest with emerging young was found the same day on Long Beach at 6.15 P.M. The nest was located 90 feet from water and behind a bank of sand that blocked all view of the sea. Forty-five hatchlings came out. After making a preliminary 3-foot spread of trails around the nest, all headed towards the sea, and all reached it, the greatest distance between trails at the water being 60 feet.

Brief observations were made on movements of young turtles after they passed through the surf. A hundred hatchlings from a nest at South Bay were released, and with the aid of diving apparatus were followed for a distance of 200 yards. All went generally westward. They swam at depths of from 2 to 6 feet, moving rapidly and, every 45 to 60 seconds, surfacing, gulping air, and going down again at an angle of about 45 degrees. Several times schools of the common black turbot approached hatchlings and nosed at them but were not seen to eat any, nor did either barracudas or numerous eels seen about the bottom rocks molest the swimming turtles. Observations were discontinued when all the hatchlings, still heading westward, had moved about 200 yards and had spread across a front of about 50 yards.

Newly hatched turtles were seen at night beside the hulls of ships in the bay at Long Beach. The ships had bright lights, and the hatchlings may have been attracted by these, as Carr and Ogren (1959) drew newly emerged young back out of the surf by moving a gasoline lantern to the water's edge.

Field manipulation of young green turtles to test sea-finding sense (see Carr and Ogren, 1960) has shown that the short trip from nest to ocean may involve a complex chain of events and responses. There remains much to be learned about the durability and plasticity of this capacity, however, and an orderly sorting of the senses and information involved will have to await controlled laboratory experiments. Results of some trials relevant to the problem, carried out on the broad beach at Daytona Beach, Florida, just north of Ponce de Leon Inlet, during the afternoon of October 6, 1960, are recorded below.

MATERIAL

1. Yearling green turtles (11 and 14 months old) hatched at Tortuguero, reared in the laboratory at the University of Florida. All had been reared in 2-gallon aquariums (see fig. 12) in salt water brought from the Gulf Coast, and fed on various diets. 2. Young green turtles, of about the size of the larger of the foregoing, and probably, like them, about a year old, taken in a mullet net by fishermen on Corrigan's Reef, Cedar

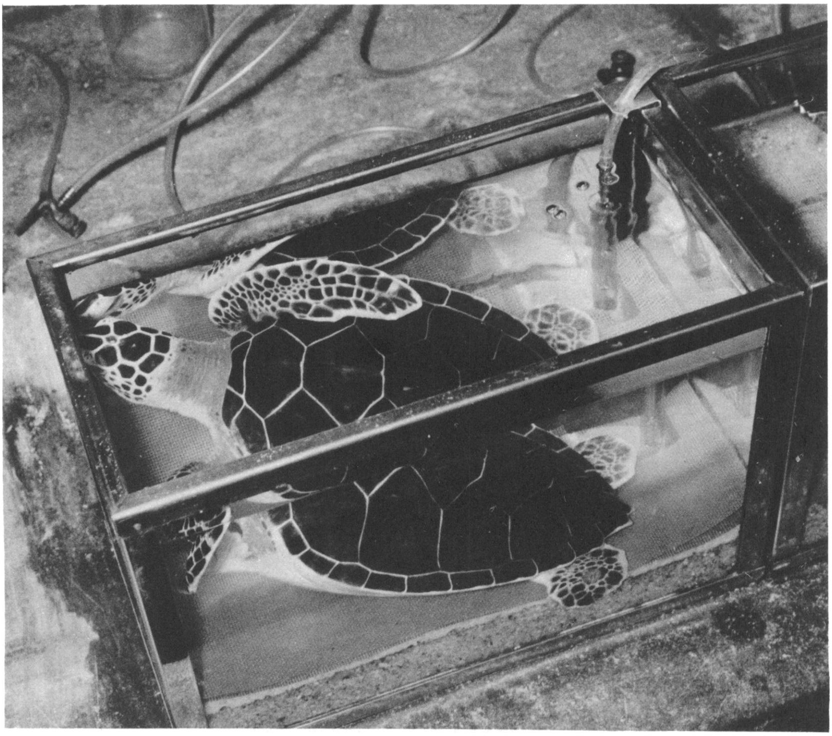

FIG. 12. Green turtle 14 months old in the tank in which it was reared, after coming from Coasta Rica as a hatchling. This was one of the group of yearlings used in orientation tests described in the text.

Key, on the Gulf Coast of peninsular Florida and held in a tank in the laboratory pending the trials.

AIMS OF THE TESTS

The trials had three purposes, as follows: (1) to test the strength of the sea-finding capacity in year-old turtles (that is, in animals of an age group in nature never called upon to find the sea, because they never go ashore between hatching time and sexual maturity); (2) to subject the sea-finding discrimination to a situation involving a shore far removed and physically very different from the ancestral shore; and (3) to observe responses when the path to the sea offers a bizarre system of obstacles, clearly requiring the test animals to make reversals in the usual chain of responses.

CONDITIONS OF THE TEST

Figures 13–17

The turtles were all released together on a flat storm terrace backed by dunes and widely scattered patches of sea oats (fig. 13). Forty feet seaward, a low bluff 1 to 3 feet high (fig. 14) dropped to an inclined spread of firm tidal beach (figs. 15, 16) that led down to a lagoon-like, tidal pool several hundred yards long and 5 to 15 yards wide. The seaward bank of this pool was a rounded bar rising steeply from the water of the pool and blocking all view of the sea beyond, both from the surface of the water and from its own inshore slope. A more gradual slope led from the crest of this bank out to the surf. The shore runs north and south at this point.

FIG. 13. Yearling green turtles, all brought from Costa Rica as hatchlings and reared in small tanks in the laboratory, released in orientation test at Daytona Beach, Florida.

RESULTS

During the first six minutes, eight of the 10 Tortuguero yearlings turned towards the sea and moved off towards it, crossing the terrace with only a slight divergence of courses. Two inactive turtles were withdrawn from the test. As the trial progressed, two black squalls moved in from the southeast, and as the sky darkened the eight reacting turtles repeatedly veered (independently, not following one another) but kept a generally seaward course and diverged by no more than 10 degrees.

On reaching the bluff they slid and tumbled down it and in each case, with only brief hesitation, regained seaward courses and continued across the tidal beach, until one of the squalls brought hard rain that interrupted the tests. After the rain the eight turtles were replaced at the spots on which the rain had come upon them. All crossed the remaining expanse separating them and the tidal pool and entered the water. For a while all swam back and forth. After five minutes four turtles had emerged on the seaward side of the pool (see fig. 17), across from the place at which they had entered the water, and started climbing the steep slope on a true seaward course. At this point all the turtles were recovered.

FIG. 14. Young green turtle properly oriented on a seaward course, about to go down the declivity separating high flat terrace and the sloping tidal beach (see description of conditions of trial), Daytona Beach, Florida.

To summarize the outcome of this test, of 10 laboratory-reared green turtles a year old, eight showed sea-seeking drive when released on an alien beach; all crossed complex terrain and reoriented properly in crossing a water barrier with the sea hidden from view; and after 25 minutes four of eight had begun actively climbing a reverse grade in a seaward direction, without seeing the water.

In the late afternoon the two Cedar Key yearlings were released under

FIG. 15. Two young green turtles on seaward courses in orientation test, Daytona Beach, Florida.

conditions the same as the above, except that the tide had changed the configuration of the lower beach and had flooded the pool. One of the turtles turned immediately towards the sea and moved off towards it, crossed the terrace, went down the scarp, and moved 55 feet out over the beach, when it was picked up. The other lay quiet for 12 minutes, then almost precisely repeated the performance of the first turtle.

As far as we know, no effort has been made to determine whether the

FIG. 16. Young green turtle, halfway across the beach in test trip to sea. Such pauses to peer about, as if in appraisal of guidance cues, are typical and frequent.

FIG. 17. Two young green turtles heading straight to the sea, climbing a landward slope after swimming across a tidal pool. Both in the pool and on the slope, view of the sea was hidden by the rise of the bar.

sea-finding capacity of hatchlings and mature females is shared by old males, normally not called upon to find the water, because they never leave it. To investigate this point we took the big Florida male described above across the Florida Peninsula and, after tagging it (tag no. A409), released it among the dunes just north of Ponce de Leon Inlet, Volusia County (see fig. 18), at the site of the preceding tests. Although evidently able to orient properly for the trip to the surf, the turtle was not able to

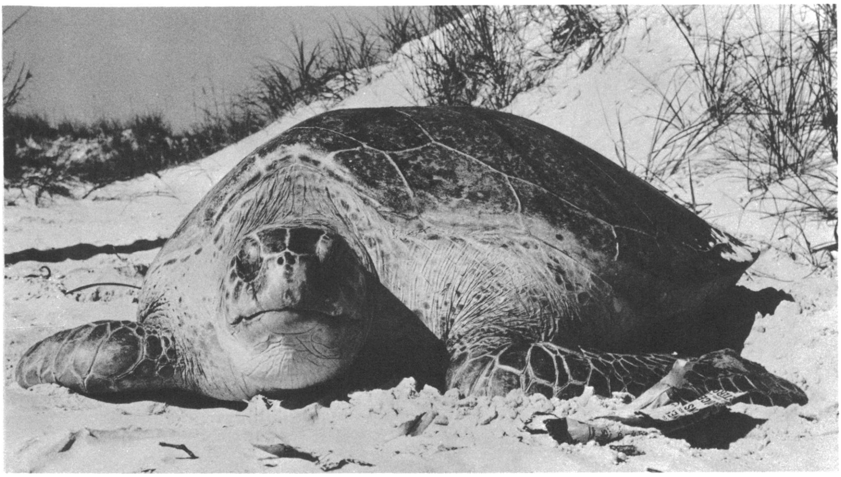

FIG. 18. Male green turtle from the Gulf of Mexico (see text and earlier figures) among dunes at Daytona Beach, Florida. Although clearly able to orient in this abnormal situation, the turtle could not crawl, either because of his obesity or because a flipper was sprained when he was unloaded from the boat.

FIG. 19. The male green turtle shown in figure 18, about to be tested for sea-sense in a natural maze of tiered long-shore bars running parallel to the beach and blocking the way to open water for about a quarter of a mile. The rectangular object held by the man at left is a styrofoam float to be towed by the turtle. The two helium balloons rise from the float on 15- and 20-foot lines.

walk, partly because of extreme obesity but perhaps also because a front flipper seemed to have been sprained during capture. Once helped into

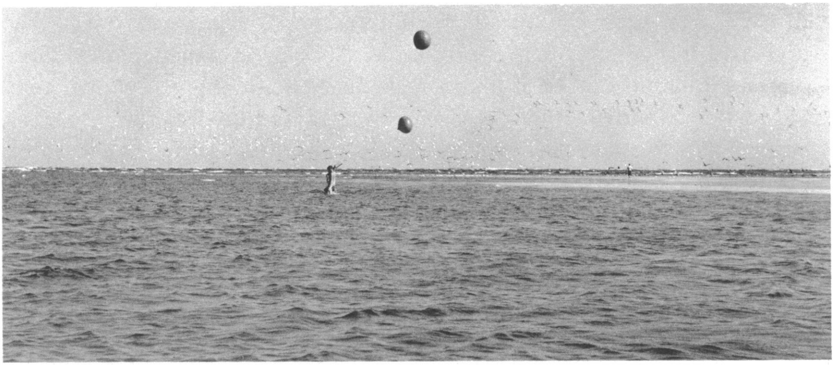

FIG. 20. Beginning of the seaward run of the male green turtle shown in figure 18. To reach the sea required a zig-zag course around the ends of the ranked short bars.

the water, the turtle, marked with a styrofoam float from which two helium-filled balloons rose on 15-foot lines (see fig. 19), showed no hesitation in running a consistently seaward course in a natural maze comprising a ranked series of short bars that extended seaward for nearly a thousand yards (see fig. 20). On reaching open water, after two hours and a half, the turtle disappeared in a northeasterly direction.

These tests involve small samples and do not lend themselves to quantitative evaluation. However, what is investigated is really not the frequency with which a given pattern of behavior is displayed but rather whether a postulated capacity exists. In evaluating the significance of a turtle guiding itself through such a complex system, one should ask not how many turtles would have performed as these few did, but what the probability is that such a course would have been chosen and held by them through such a distance by pure chance.

MIGRATION

Most of the earlier writers on the natural history of sea turtles, influenced by the opinion of fishermen throughout the tropics, regarded the green turtle as a long-distance migrant. Scientific proof, however, was slow in accumulating. Pope (1939) said: "In spite of a general belief that green turtles regularly go back and forth from feeding areas to breeding grounds, travelling hundreds of miles in doing so, there is no scientific evidence that such mass movements take place." More recent investigations of green turtle colonies shed no light on the question. In 1954, Carr began collecting and sifting circumstantial evidence bearing upon movements of green turtles in the Caribbean, with the result that the need to re-investigate the question with a systematic program of tagging was clearly indicated. Such a project was begun at Tortuguero, Costa Rica, in 1955, and has been under way since then. This has shown that green turtles do indeed move periodically back and forth between widely separated pastures and rookeries.

From the five years of work at Tortuguero there have been 54 post-season recoveries to date. All returns since Carr and Ogren summarized them are shown in table 9. The spread of the recovery sites is 1550 miles at the widest point. The data furnish grounds for generalizations bearing upon the migration problem, as follows.

1. No correlation between post-tagging interval and distance of site of recovery from Tortuguero is evident, which may be taken to mean that turtles are not wanderers but scheduled migrants between the beach and a special restricted home area.

TABLE 9

INTERNATIONAL RECOVERIES OF GREEN TURTLES TAGGED AT TORTUGUERO, COSTA RICA, AND RETAKEN DURING 1959 AND 1960[a]

Tag No.	Date Tagged	Place of Recovery	Date of Recovery	Distance Traveled (Statute Miles)
936	July 15, 1959	Gulf of Morrosquillo, Colombia	Dec. 30, 1959	540
1099	Aug. 27, 1959	Dakura, Nicaragua	Dec. 15, 1959	264
1084	Aug. 21, 1959	Riohacha, Guajira, Colombia	April 29, 1960	713
714	Aug. 1, 1959	Rio Grande Bar, Nicaragua	May 8, 1960	160
371	Aug. 24, 1956	S. of Tinkham Rock (lat. 13° 50′ N., long. 82° 29′ W.)	May 12, 1960	241
510	July 22, 1957	Doce Leguas Keys, S. coast of Cuba	April, 1960	795
451	July 12, 1957	Miskito Cays area	Jan. 18, 1960	292
1061	Aug. 15, 1959	Cortes, Pinar del Rio, Cuba	Aug. 14, 1960	800
390	July 4, 1957	Set Point, near Bluefields, Nicaragua	Aug. 29, 1960	103
1039	Aug. 10, 1959	Lat. 14° 12′ N., long. 82° 46′ W. (Cayman Reef)	July 30, 1960	255
661	July 11, 1958	Same as 1039	July 30, 1960	255
916	July 11, 1959	Flag Rock (Miskito Cays area)	May 12, 1960	264
914	July 11, 1959	Southeast Rock (Miskito Cays area)	July 13, 1960	270
1093	Aug. 23, 1959	Southeast Rock (Miskito Cays area)	July 30, 1960	270
709	July 31, 1958	Lat. 15° 00′ N., long. 82° 20′ W.	July 25, 1960	327
940	July 16, 1959	12 mi. SE. of Tasbapownie, Nicaragua	Dec., 1960	126
978	July 25, 1959	Same as 940	Dec., 1960	126
1079	Aug. 20, 1959	Lat. 14° 33′ N., long. 82° 11′ W. (just east of Miskito Cays)	Sept. 26, 1960	275
545	July 25, 1957	Lat. 14° 33′ N., long. 82° 11′ W. (just east of Miskito Cays)	Sept. 26, 1960	275
1243	July 12, 1960	10 mi. off Campeche, Campeche, Mexico	April 23, 1961	1219

[a] For earlier returns, see Carr and Ogren (1960)

2. No turtle marked at Tortuguero has ever been recovered in Costa Rica after the end of the nesting season, which suggests that the resident population in Costa Rica is small.

3. No turtle marked at Tortuguero has ever been taken nesting anywhere else. The implication here is that Tortuguero is the exclusive and ancestral nesting ground for the populations sampled there.

4. The tag recovery sites spread throughout the western Caribbean, enter the Gulf of Mexico (Campeche, on the western shore of the Yucatan Peninsula), and barely reach the eastern Caribbean in Colombia.

5. Each season the nesting assemblage at Tortuguero is composite,

with contingents arriving from various resident localities.

6. Although a given individual green turtle nests on a two-year or three-year cycle, the nesting schedule is not synchronous for a given resident population, because each resident area may be represented yearly at the nesting ground.

One might regard the recent extension of recovery sites into the Gulf of Mexico as evidence of the identity of the Tortuguero turtles and the juvenile summer colony of the Florida Gulf Coast. However, the problem in Florida is to account for the origin of half-grown turtles that appear in the spring (in 1961 they reached the fishery on May 6), and to learn where they go when they leave in the fall. The movements of mature females after leaving the Costa Rican nesting beach would appear to be not directly relevant to this question, which remains entirely open.

The Tortuguero results have not proved that the travel of Caribbean migrants involves navigation, that is, that it is guided by more than compass sense and land-mark piloting. Because the breeding ground is a mainland shore, it will be hard to prove that the flotillas of turtles arriving at nesting time are not reaching the place by simply moving in an initially correct compass direction, then following the coast until things smell, appear, or taste right for the ancestral breeding ground. It was to obviate this distracting possibility that work at Ascension was decided upon.

On a trip to the Atlantic coast of South America in 1957 Carr noted a complete lack of knowledge, among the people there, of green turtle nesting. Between Recife and Mar del Plata green turtles were well known to the coastal people, but no indications of nesting could be found, and no young turtles were seen anywhere. During the same trip the principal South American museums were visited, and in them no hatchling or very young specimens of *Chelonia* from the coasts of Brazil or Argentina were found. Such lack was taken as significant, because in the usual museum collection small, easily stored sea turtles by far outnumber mature specimens. The conclusion was reached that the green turtle population of the Brazilian coast is itinerant, derived from rookeries located elsewhere. The nearest known center of aggregated nesting was Ascension Island, which, as is shown elsewhere, has no resident green turtle population. Thus the implications of available information, combined with the isolated geographic position of Ascension Island, pointed to it as a logical place in which to test the migration postulate with a tagging program.

During February, March, and April, Hirth tagged 206 female turtles on the six nesting beaches at Ascension. To date, two tags have been recovered, both from Brazil. On June 19 the fisheries training vessel "Albacora," of the Escola de Pesca de Tamandare, took a green turtle marked with our tag at latitude 08° 04′ S., longitude 33° 37′ W., about 50 miles off the coast of Pernambuco. The depth at the locality was 382 meters. The turtle was taken with a harpoon while swimming at the surface. On January 2, 1962, another was recovered at Vitorio, Espirito Santo, latitude 19° 35′ S., longitude 39° 48′ W.

These two recoveries considered separately could be taken as no more than a result of random wandering. Considered against the background of relevant circumstantial evidence, however, they must be regarded as important evidence of migratory contact between the resident turtles of the Brazilian coast and the Ascension breeding assemblages.

Besides the implications of the lack of nesting by green turtles on the Brazilian coast, the case for a Brazil-Ascension migratory interchange is strengthened by the prompt disappearance of all green turtles from Ascension waters after nesting is over (see section on Nesting Season). There can be no doubt that the island assemblage is recruited from elsewhere. There are no shallow bays and lagoons there offering suitable turtle pasturage, and it would be clearly impossible for the shore waters of the island to support the nesting turtles on a year-around basis. At Tortuguero there is a similar dearth of suitable pasturage, and, as is said above, during five years none of our marked turtles has ever been taken in Costa Rica after the nesting season was over. At Tortuguero a good part of the nesting aggregation repairs to pastures in the Miskito Cays, not much more than 200 miles away. At Ascension, however, the nearest suitable year-around habitat is the coast of Africa or that of Brazil, where, as is said above, green turtles live but do not breed. Even if we had no tag returns at all, it would still be logical to postulate the Brazil-Ascension migration. The pair of recoveries thus should be regarded not as odd facts of no quantitative significance, but as pieces in a pattern of evidence.

During 1957 and 1958 Carr reconnoitered sections of the West African coast in which resident green turtle populations are not known to nest. Information also was accumulated by means of questionnaires to, and interviews with, fisheries officers from Dakar to Liberia. We are inclined to believe that, while some nesting by green turtles goes on there, Ascension may prove to be the nesting ground for some of these populations also. Results at Tortuguero have shown that one restricted shore may be visited by nesting turtles from regions more than a thousand miles apart. Meantime, with only the Brazilian colony considered, it is of interest to speculate concerning the possible routes involved in its Ascension journey.

The shortest way would be a trip up the Equatorial Current by the mature turtles going to the island, and a downstream return by the young to the bulge of Brazil. Such travel would conform to the classic pattern for marine migration: upstream movement for the strong-swimming adult stages and downstream drifting for the weak and naive young.

On the other hand, the whole round trip could be made in favorable currents if the Ascension-bound migrants swam northward and entered the part of the Equatorial Current destined to become the Gulf Stream, and then stayed with this through its whole global circuit. The time involved here seems, however, prohibitively great. Moreover, sightings of the migrant flotillas would have been recorded by ships in upstream sections of the current, and such is not the case.

The other possibility would be for the Brazilian turtles to move a few miles off shore into the Brazil Current—the south-trending extension of the Equatorial Current after it has split against the South American bulge. Once in this, a turtle could be carried across to South Africa and into the Benguela Current flowing northward along the coast of southwest Africa, joining the South Equatorial Current just south of the equator, and moving out to Ascension and then back to Brazil. Like the Gulf Stream route, this seems an unreasonably long journey. Moreover, it entails a stay of some weeks in the antarctic cold of the West Wind Drift, where the water temperatures range between 5° and 15° C. It appears, thus, the least likely route, with the long foodless ride in the Gulf Stream system only a little less probable. The direct upstream course, or some modification of it, would appear to be the most logical. Even this route presents problems that would seem insurmountable, if it were not so clear that the turtles are somehow solving them.

No matter where they come from and what path they follow, clearly the turtles going to Ascension carry out an extraordinary feat of orientation. From the island rookery back to the South American residence area, both the returning adults and, perhaps more importantly, the newly hatched young would be carried near their destination with little need for either locomotor effort or feats of navigation. The current would transport them, and the goal would be a huge target almost directly in the path. During the main part of the outbound journey to the general area of Ascension, however, it seems most reasonable to suppose that the turtles are guided by celestial information. We cannot see how to measure the improbability that the April aggregations at Ascension could arrive there by random wandering, or how long and deep the ranks of wandering turtles would have to be to provide the requisite number of accidental arrivals. If such schools of randomly wandering migrants exist, it is incredible that ships should never have sighted them.

In the search for clues as to how oriented travel to an oceanic island is made, two separate questions present themselves: (1) How is the high-seas journey to the general area of the island guided? (2) What is the character of the landfall that the migrant makes? Turtles "homing" to Ascension are not headed for a point at the land-sea interface, as at Tortuguero, but for the tip of a barely exposed spire in midocean. When they have gone as far towards the goal as celestial guidance will take them, there remains a certain distance to be traversed by piloting of some kind. No matter how delicate the nervous responses involved in navigation may be, measurements of angles from a horizon as irregular as that seen from the level of the eye of a turtle would seem bound to leave the traveler a long way from such a goal as Ascension Island. To a bird coming in high in the air, the error might be corrected by visual search. To a turtle, a low island is out of sight a few miles away. Even at Ascension, with Green Mountain and its corona of cloud, and with birds rising high above it, there would surely be a big gap between the point where sun or star navigation leaves the migrant and that at which direct view of the island or some of its features or emanations take over. To cross this gap, guidance must come from the character of the water, or from the bottom. As Hasler's review (1956) showed, such landmarks may be very elusive indeed. In the case of sea-turtle migrations, we do not know what cues islands give off or what a green turtle can taste, smell, or hear.

Nevertheless, a point in favor of the theory of upstream travel for the green turtles going to Ascension from Brazil is that it allows us to postulate an olfaction gradient in moving the migrants in for the Ascension landfall from wherever their sun or star navigation may take them. When the young hatch and leave the island, they take with them, say, the imprint of the chemical taste or smell of Ascension water. Coming back as mature adults, they may be guided by this imprint in picking up an Ascension effusion downstream from the island when it becomes perceptible in the west-bound water, and follow this in to make the visual landfall. In any case, for both the young making a first trip to the island and for the veteran migrants, there remains the problem of orientation through an open-sea journey in which the changing relations among course, current direction, and the shifting place of the migrant would make position finding and reorientation constant necessities. Wallraff (1960) has questioned the mathematical grounding of experiments important to the case for celestial navigation in animals. Whatever the outcome of the resulting discussions may be, the facts of natural history will remain. The green turtles that appear at Ascension Island each April are, during at least part of the journey, guided by cues of an unknown kind. That part of their information comes from the sun or stars or both seems at present the most logical supposition.

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SUMMARY

Data are presented on two genetically separate colonies of the Atlantic green turtle [*Chelonia mydas mydas* (Linnaeus)], one breeding at Tortuguero, Costa Rica, the other at Ascension Island in the South Atlantic. The two are compared with respect to reproductive behavior and periodicities and to various other features.

The work at Ascension was undertaken because the periodic arrival of breeding schools at that oceanic island seemed clear evidence of a refined guidance process. Circumstances suggested that the island is the

nesting center for the non-breeding green turtle populations of the coast of Brazil. Two Brazilian tag recoveries reënforce the assumption.

Of turtles tagged during five seasons at Tortuguero, there have been 54 post-season recoveries, from all parts of the western Caribbean. The one return from outside the Caribbean came from Campeche, Mexico.

Both renesting returns at Ascension and renesting and long-term returns at Tortuguero support previous evidence of strong site tenacity and discrimination in the species.

Orientation tests in Florida, involving year-old green turtles of different backgrounds, show that animals of this age retain sea-finding sense to carry them to the water under strongly manipulated conditions on a strange shore.

The migration problem is discussed in general terms, in the light of recent data, and hypothetical travel routes are proposed.

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