

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 1835

JUNE 28, 1957

59.81.3

The Ecology and Migrations of Sea Turtles, 2⁸ Results of Field Work in Costa Rica, 1955

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The present paper is a summary of results of a season's field work at the green turtle (*Chelonia mydas mydas*) rookery at Tortuguero on the Caribbean coast of Costa Rica. Most of the information was obtained through work at the beach during July and August, 1955. This is supplemented by observations made in previous seasons at Tortuguero and elsewhere. The work was supported by a grant from the National Science Foundation (G-1684) and will be continued during two more nesting seasons. Results of a study of green turtle populations of the Gulf coast of Florida, a part of the same general program of research, are given elsewhere (Carr and Caldwell, 1956).

Tortuguero, or Turtle Bogue as it is known in Caribbean English, is a 24-mile extent of unbroken sand beach on the Costa Rican coast between Puerto Limon and the Nicaraguan frontier, extending from the mouth of the Tortuguero River to that of the Parismina (Reventazón) River (fig. 1). It is widely known through the Caribbean as a nesting ground of the green turtle and is thought by many to be the only remaining breeding site of any importance to the maintenance of the species in the Caribbean. While this may not be wholly true, Tortuguero is almost certainly the only rookery of significance anywhere on the mainland Atlantic shores of Central or South America, and it was for this reason that

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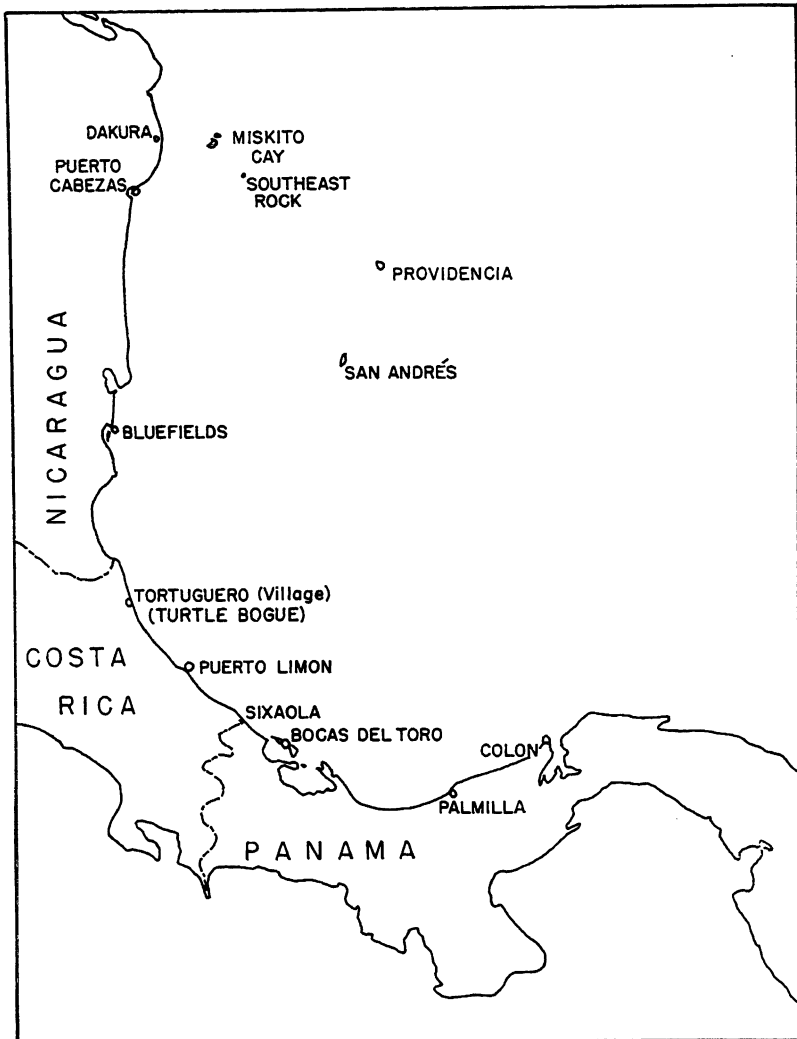


FIG. 1. Map showing western Caribbean localities involved in the tagging program.

it was chosen as the locale for a tagging program (figs. 2, 3; see also Carr, 1954a, 1954b, 1956).

After reconnaissance during three preceding summers, we set up a tagging camp on July 1, 1955, in the little settlement of Tortuguero, in a *manaca* shack furnished by Señor Teodoro Quirós C., of the Atlantic Trading Company, which takes out timber and bananas from the hinter-



FIG. 2. A section of Tortuguero Beach, Costa Rica, showing evidence of heavy use by nesting green turtles.



FIG. 3. A hatchling green turtle, newly emerged at Tortuguero, Costa Rica, and heading for the surf.

land by way of the Tortuguero River. We were allotted a 2-mile section of the beach adjacent to the camp, on which commercial interference was excluded, and we retained local good will by hiring for our own work the men who usually turned turtles on these 2 miles for export interests in Limon.

Turtles turned at night by these *veladores*, as the beach-watchers call themselves, were tagged and released, where caught, the next morning, all the catch of a night usually having gone back into the water by mid-day if not much earlier (fig. 4). In the case of each turtle tagged, straight-line measurements of the length and width of the shell were made, the point of capture was recorded as exactly as possible, and the postocular scales of each side were counted.

Two kinds of tags were used during the summer. One of these was a monel metal elliptical disk with perforations at the ends for wiring to the after edge of the shell (fig. 5). This was used for all turtles except 40 marked during the last two days of the field work (August 25 and 26). These latter were tagged with standard "cow-ear tags" of monel metal, clamped through punched holes in the thin, tough after-edge of the upper part of the front flipper, as suggested by J. R. Hendrickson¹ in

¹ Not by Tom Harrison, as stated by Carr and Caldwell (1956).

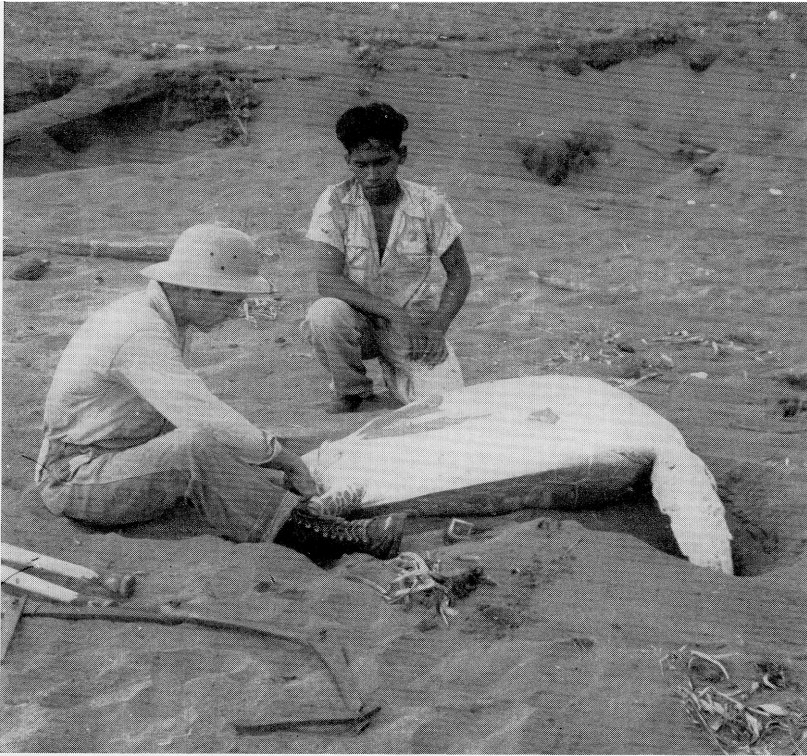


FIG. 4. Giovannoli and an assistant tagging a green turtle by the shell-tag method later discarded in favor of a flipper tag.

a paper read at the 1955 meetings of the American Society of Ichthyologists and Herpetologists. This type of tag is now being used exclusively.

Both kinds of tags were numbered and inscribed in English and Spanish with an offer of a reward for their return and with the address of the Department of Biology of the University of Florida.

During the period of the work Giovannoli was in residence at the camp from July 2 to August 29, and Carr was present for two four-day periods (when the camp was opened and closed). Six hundred and forty-four turtles were caught—or, rather, turtles were caught 644 times, 149 of the captures having been recaptures of tagged individuals that returned to the beach, 44 of which returned for two recaptures, seven for three, and two for four. Since the camp was closed, we have had 10 returns, all from outside Costa Rica. Details and implications of the data thus secured are discussed in the following pages. All turtles involved in the study were



FIG. 5. Ventral view of after-edge of shell of green turtle, showing tag wired in place. This rig will apparently not often withstand the scrapings and clawings that attend pairing and has been abandoned in favor of a cow-ear tag on the fore flipper.

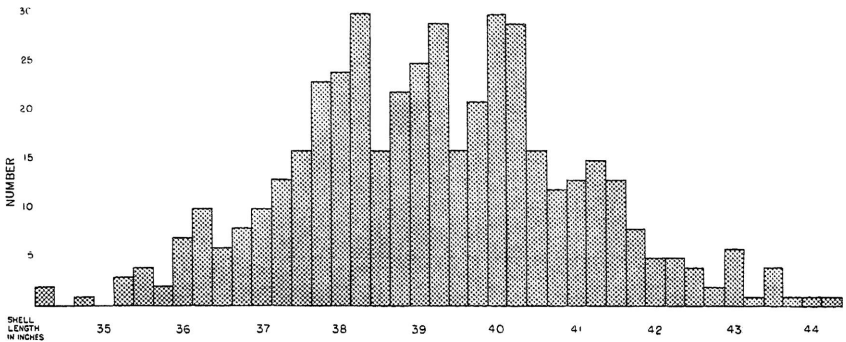


FIG. 6. Shell lengths of 362 mature female green turtles measured on the nesting beach at Tortuguero, Costa Rica, between July 2 and August 25, 1955.

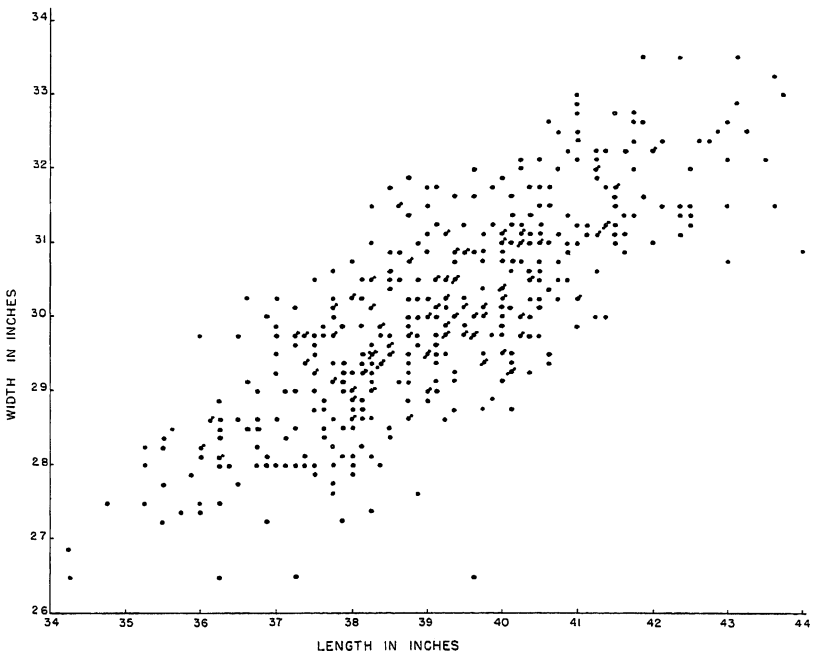


FIG. 7. Length-width relationship in sexually mature green turtles. The diagram includes all turtles measured at Tortuguero, Costa Rica, during July and August, 1955. Each dot represents a turtle. The small dots actually lie on the points covered by the large dots that they touch.

mature females, the range in size and proportions of which is shown in figures 6 and 7.

TAGGING RESULTS

The chief aim of the Costa Rican tagging program was to get information bearing on the question of mass, long-distance migrations. Pending accumulation of direct observation of schools traveling the high seas, the most direct and valuable data would seem to be those from released and recovered marked turtles. In the present project we have had a total of 149 recoveries of tagged individuals. These recoveries are of two very divergent kinds: recaptures of females that returned to Tortuguero beach within one to 35 days after being tagged, for the purpose of carrying out interrupted nesting or of nesting again; and recaptures by net or iron at points distant from the nesting beach, and clearly after the season's nesting activity of the individual involved had been finished or abandoned. Tagging results are summarized in tables 1 to 5.

TABLE 1

RETURN RECORDS INVOLVING SINGLE RECAPTURES OF GREEN TURTLES AFTER INTERVALS OF FROM 11 TO 16 DAYS, IN A 10-MILE SECTION OF TORTUGUERO BEACH, COSTA RICA, SOUTHEAST FROM THE MOUTH OF THE TORTUGUERO RIVER

Tag No.	Place Tagged ^a	Date Tagged	Date Retaken	Place Retaken ^a	Distance (in Miles) Between Sites of Emergence
313	NW. 3	8/4	8/14	NW. 3	Same place
102	NW. 4	7/3	7/15	SE. 3	$\frac{1}{4}$ - $\frac{3}{4}$
124	SE. 3	7/7	7/19	Mid 2	$1\frac{1}{2}$
105	SE. 1	7/26	8/7	NW. 2	$\frac{1}{2}$
324	SE. 2	8/5	8/17	NW. 2	$\frac{1}{2}$
381	SE. 1	8/11	8/24	SE. 1	$\frac{1}{4}$ ^b
382	SE. 1	8/11	8/24	SE. 1	$\frac{1}{4}$ ^b
466	SE. 2	8/14	8/24	Mid 1	$\frac{3}{4}$
126	NW. 1	7/7	7/21	NW. 3	$1\frac{3}{4}$ -2
277	SE. 3	7/18	8/3	SE. 2	1
295	NW. 3	7/19	8/3	Mid 3	$\frac{1}{8}$

^a Numbers in these columns represent miles from northwest to southeast; letters indicate approximate portions of individual miles.

^b Note similarity of records.

DATA FROM LOCAL RETURNS

CLUMPED RETURNS: While the local returns, of which, as noted above, we had 149 in 1955, are of interest mainly for their bearing on individual orientation and on the natural history of nesting, they should also be examined for any possible clues bearing on schooling or group movement. The most direct evidence of this sort would be clumped retakes of turtles that had been tagged together. Although the word "together" as thus used is clearly relative, there are nevertheless to be seen in tables 1 to 3 and in the case histories numerous examples, which range from the suggestive to the virtually conclusively demonstrative, of associative movements. That is to say, if turtles tagged at the same place and time are after long intervals retaken together (especially if they are retaken together at another place) and if the coincidence is not attributable to chance alone, then the turtles clearly moved together in the interim, and by extension perhaps in the migration that brought them to the beach to start with. Admittedly our cases do not add up to imposing statistical stature, and the numerous factors involved make both the application and the interpretation of probability tests pointless. But when viewed against the agreement of our case-history results with widespread lore of professional turtle hunters, the implications seem noteworthy.

As an example, the following case of clumping may be pointed out (the

TABLE 2
RETURN RECORDS INVOLVING SINGLE RECAPTURES OF GREEN TURTLES AFTER
INTERVALS OF 20 DAYS OR MORE, IN A 10-MILE SECTION OF
TORTUGUERO BEACH, COSTA RICA, SOUTHEAST FROM THE
MOUTH OF THE TORTUGUERO RIVER

Tag No.	Place Tagged ^a	Date Tagged	Date Retaken	Place Retaken ^a	Distance (in Miles) Between Sites of Emergence
259	NW. 3	7/14	8/16	NW. 2	1
273	Mid 1	7/16	8/16	NW. 2	$\frac{1}{2}$ - $\frac{5}{8}$
254	SE. 10	7/12	8/10	Mid 1	9
204	Mid 2	7/12	8/7	NW. 2	$\frac{1}{4}$ or less
153	Mid 2	7/22	8/14	SE. 1	$\frac{5}{8}$ - $\frac{3}{4}$
314	Mid 2	8/4	8/24	Mid 1	1
			8/25	NW. 3	$1\frac{3}{4}$
307	SE. 2	8/3	8/24	NW. 3	$\frac{1}{4}$ - $\frac{3}{8}$

^a Numbers in these columns represent miles from northwest to southeast; letters indicate approximate portions of individual miles.

TABLE 3

RETURN RECORDS INVOLVING TWO OR MORE RECAPTURES OF GREEN TURTLES
IN A 10-MILE SECTION OF TORTUGUERO BEACH, COSTA RICA,
SOUTHEAST OF THE MOUTH OF THE TORTUGUERO RIVER

Tag No.	Place Tagged ^a	Date Tagged	Date Retaken	Place Retaken ^a	Distance (in Miles) Between Sites of Emergence
170	SE. 1	7/9	7/11	Mid 2	$\frac{3}{4}$
			7/21	NW. 3	$\frac{3}{4}$
420	Mid 1	8/12	8/12	SE. 2	$1\frac{1}{4}$
			8/24	NW. 3	$\frac{1}{4}$ or less
405	NW. 3	8/12	8/12	SE. 1	$1\frac{1}{4}$ - $1\frac{1}{2}$
			8/24	SE. 2	$\frac{3}{4}$
265	SE. 2	7/19	8/3	Mid 2	$\frac{3}{8}$
			8/8	Mid 2	Same place
255	Mid 2	7/14	8/3	Mid 1	1
			8/5	SE. 1	$\frac{1}{4}$
167	SE. 2	7/10	7/12	Mid 3	$\frac{3}{4}$
			8/3	Mid 2	1
137	SE. 2	7/8	8/11	NW. 1	$1\frac{1}{2}$
			8/12	NW. 1	Same place
205	NW. 4	7/19	8/14	SE. 1	$2\frac{1}{2}$
			8/16	NW. 3	$1\frac{1}{2}$
206	SE. 1	7/12	8/8	SE. 1	$\frac{1}{4}$ or less
			8/9	Mid 1	$\frac{1}{4}$
263	NW. 3	7/16	8/10	Mid 3	$\frac{1}{4}$ or less
			8/11	NW. 2	$\frac{3}{4}$
390	Mid 1	8/11	8/12	Mid 2	1
			8/23	NW. 1	$1\frac{1}{4}$
413	NW. 1	8/12	8/23	NW. 1	Same place
			8/24	SE. 1	$\frac{1}{2}$
314	Mid 2	8/4	8/24	Mid 1	1
			8/25	NW. 3	$1\frac{1}{2}$
190	SE. 1	7/11	7/15	Mid 1	$\frac{1}{4}$ or less
			7/18	Mid 1	Same place
			8/11	SE. 1	$\frac{1}{4}$ or less
394	NW. 1	8/11	8/11	SE. 2	$1\frac{1}{2}$
			8/12	SE. 2	Same place
			8/16	NW. 2	$\frac{1}{4}$
			8/18	SE. 1	$\frac{1}{4}$
383	SE. 1	8/11	8/11	SE. 1	Same place
			8/12	NW. 1	$\frac{1}{4}$
			8/13	Mid 3	$2\frac{1}{4}$
			8/24	SE. 1	2^b
448	SE. 1	8/13	8/23	SE. 1	Same place
			8/24	Mid 1	$\frac{1}{4}$

^a Numbers in these columns represent miles from northeast to southeast; letters indicate approximate portions of individual miles.

^b Same place as first emergence.

numbers used are tag numbers of turtles marked ; further details of their history may be seen in the tables) :

Numbers 381, 382, 383, and 393 were tagged on August 11, all within an extent of a quarter of a mile or less. All were retaken 13 days later, on August 24, as follows: No. 381 about 2 miles from the tagging site; No. 393 about 1 mile from the tagging site and 1 mile from the point of emergence of No. 381; Nos. 382 and 383 at the place where all were tagged, or no farther than one-quarter of a mile from it.

Numbers 405 and 420 were tagged on August 12 (one day after the above-named group), and all were retaken with them on August 24 on the same 2-mile extent of beach.

The explanation for the return of a turtle to the beach is discussed in the section on multiple laying. The above-mentioned turtles probably nested successfully on or shortly after the date they were tagged and released, then came back to lay again on August 24. Such reappearances at the original point of emergence as the above, and as those shown in the tables, seem obviously indicative of some sort of orientation accomplishment. It is not clear, however, how imposing the feat of orientation has been. It is conceivable that the days, or weeks, between emergences were waited out loafing or courting in the open sea off shore, adjacent to the nesting site. This, however, seems unlikely. The shore is completely exposed, with strong long-shore currents and heavy surf and with few feeding flats or sleeping rocks available. Reconnaissance by small airplane shows no great accumulation of females such as would occur if every female there for a two- or three-stage nesting venture waited around during the periods between her trips ashore.

It seems more reasonable to suppose that between times the turtles depart for areas about the mouths of rivers up and down the coast, where bars and shallows afford both protection and vegetation for food. If this is the case, the returns to precisely located points on the nesting beach become feats of greater stature.

While the many variables that must have been coordinated in the accomplishment of these localized reappearances seem to rule out chance, it should nevertheless be noted that extremely divergent cases were recorded, in which returns to the beach occurred as far as 10 miles away.

TIME, DISTANCE, AND DIRECTION IN RECAPTURES: An effort was made to augment the direct evidence for associative movement obtainable from case records by a tabulation of the time and distance between recaptures and the direction of the site of recapture from that of release. It not only seemed of interest to know whether turtles, on visiting the beach a second time, showed a tendency to come out near the point of their

first emergence, but also whether emergences *not* near points of release showed any associative trends in distance, time, and direction that might quantitatively bolster the more striking individual cases. If second and later emergences generally proved to show no relation to the original site, we wanted to see whether they tended to group elsewhere, or at least to occur northward or southward of release points. Such trends might be interpreted, cautiously, as indications of group long-shore movement which might be part of, or of the quality of, seasonal migratory movement.

Table 4 shows the sort of analysis that might be expected to reveal such movements. The fact that it fails to show any arresting trends may merely be due to the small sample that remained for such treatment after the weeding out of ineligible cases. Most of our work was done on the first 3 miles (northernmost miles) of the beach, and the eccentric position of this site made it necessary to throw out all returns for individuals tagged there (except for some of those included in the zero column) in this analysis. The restriction of the sample to turtles tagged towards the middle miles of the beach left only the 60 returns tabulated north and south of the zero column.

Data in the zero column itself have little bearing on movement but are most striking evidence of orientation capacity and perhaps of a special kind of "homing" ability, as the 36 individuals listed there all came back to a section of beach less than a mile long—many of them to within a few hundred yards of the site of their first emergence.

COUNTS AND MEASUREMENTS

In addition to the clues and evidence available in the tag returns, indications of school movement might be expected to appear in seasonal changes in counts and measurements made on emerging turtles, providing characters involved in school-specificity could be found. Our efforts in this line were exploratory and unproductive, but we do not believe that the fact that our data on the postocular scales show no definite secular trends rules out the desirability for continuing a search for characters suitable to this sort of inquiry.

There seems to be no reason why traits could not be found that announce the arrival of separate schools because each school is slightly more of a stamp with respect to that trait than it is like any other school. There is strong circumstantial evidence that (1) turtles arrive at Tortuguero in schools, (2) schools arrive at different times, and (3) some, at least, of the schools come from different and separate home (feeding-sleeping) ground north and south of the Tortuguero nesting ground. The sugges-

tions of concurrent emergence behavior shown elsewhere in this paper may be attributable to school cohesion by such variously derived groups. There also seems to be the possibility that, because of the completely herbivorous, herd-grazing habits of the green turtle its populations are broken genetically into demes, which, because partly isolated from other similar populations, may acquire measurable differences from them.

It might be objected that the isolation on the separate feeding ground can be of no evolutionary importance, because, theoretically at least, the schools all repair to a common breeding center, where not only egg laying occurs but also the pairing off and copulating that might be expected to mix the gene pools of whatever groups were concurrently present and not only overcome any drift effect but also dilute any selective effects produced in the populations by differences in conditions in their home areas.

Opposing this objection, however, is the likelihood of separate, synchronous periodic action by the different schools, the members of each of which, reacting to the same set of periodic factors, depart for the nesting ground simultaneously and thus on the whole tend to mate with one another more often than they mate with members of any other school. This effect would be reënforced by the fact that copulation in green turtles occurs just before or just after oviposition (see section on Natural History of Reproduction), with the males closely attending the nesting females, following them into the surf on the way ashore or catching them the moment they are afloat on their return. (Harrisson, 1954, and our own observation.)

It seems unreasonable to suppose that these rutting males would be any more inclined to mount a female of their own population than one from a concurrently present population from a different source. But the schooling tendency would nevertheless tend to increase the relative frequency of intrapopulation matings, and with time this would inevitably result in differences in gene frequencies. The only question is whether these differences are morphometrically detectable.

POSTOCULAR COUNTS: One of the most promising variables with which to test for differential school "makeup" seemed to be the number of postocular scales (the big scales that form the hind rim of the orbit and in the species range in number from two to five). The modal and greatly predominating number counted was four on both sides. As table 5 shows, the range in our data was from three to five, with asymmetry more frequent than symmetry in the non-modal counts. It was hoped that any incipient population divergence that might exist would appear as seasonal clumping on an average basis. But, as table 5 shows, the 4-4 count is so

TABLE 4

TAG RETURNS FOR TORTUGUERO, JULY-AUGUST, 1955, SHOWING RELATION BETWEEN TIME, DISTANCE TRAVELED, AND DIRECTION OF SITE OF RECAPTURE FROM SITE OF RELEASE

Days	Miles South of Point of Release				Miles North of Point of Release		
	3-10	2-3	1-2	0 ^a	1-2	2-3	3-10
1-5	7	4	18	18	11	4	4
5-15	1	1	2	11	4	1	0
15-25	0	0	0	4	2	0	0
25-35	0	0	0	3	2	1	1

^a This does not represent a fixed point on the beach but rather any point within the 10 northwesternmost miles where turtles were released and from which recovery distances were measured. Only cases in which the sites of release and recovery were precisely known are included.

TABLE 5

POSTOCULAR SCALE NUMBER, TOTAL AND MONTHLY FREQUENCIES, IN 493 GREEN TURTLES, TORTUGUERO, COSTA RICA, 1955

	3-2 ^a	3-3	3-4	4-4	4-5	5-5	3-5
Total	5	25	30	362	48	22	1
July	1	10	18	166	26	9	0
August	3	15	12	198	21	13	1

^a Counts for the left and right sides, respectively.

much the most frequent that our samples of all the aberrant counts were small, and no significant seasonality could be detected.

SEASONAL LENGTH-FREQUENCY: Another variable, in which we met with more success in finding significant seasonal trends, was shell length. School differences in this character may, of course, not be genetic at all but merely indicative of differential richness of pasturage in feeding grounds or of differential periodicity in movements of ontogenetic groups within a single population. Admittedly, a significant seasonality in clumps in shell length lacks the sure evolutionary relevance that clumps in scale frequency would carry, but it nevertheless implies schooling of some sort, and that is the central interest of this study.

What we interpret as probably valid evidence of periodicity of size groups may be seen in figure 8.

SEX RATIO

Because of the heavy and widespread killing of female turtles during their vulnerable period on shore, a growing preponderance of males in mature sea turtle populations might be expected. Our results at Tortuguero furnish no evidence on this subject, because the observations there involve only the mature female turtles that use the rookery, with occasional sight records of males chasing females in the surf or, from an airplane, seen courting or copulating.

At the Miskito Cay fishery, however, some 300 miles to the northwest, the turtling operation is not selective with respect to sex, and the sex ratio in the net-taken catch there can probably be taken as representative.

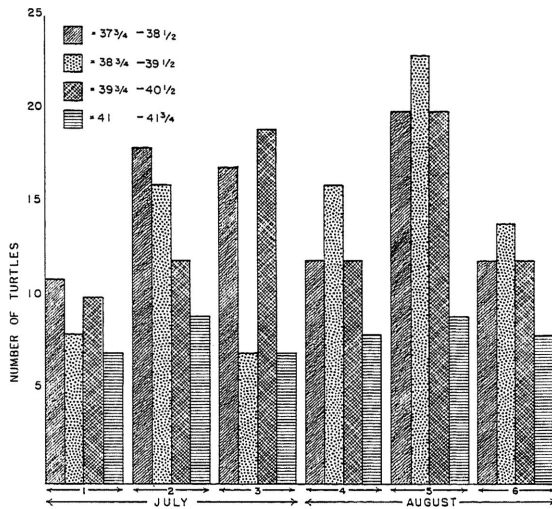


FIG. 8. Fluctuation in four somewhat arbitrarily chosen (see fig. 6) measurements (in inches) of length classes of nesting green turtles during six periods, of five collecting days each; July and August, 1955; Tortuguero, Costa Rica; miles 1-10.

We have talked about the question with a number of turtle captains and have found among them the rather surprising opinion that the sex ratio varies "from year to year." What this means, if anything, it is hard to say. The most likely explanation seems to be that it is actually "from season to season" that the proportions of the sexes are seen to change. Such changes, if they occur, might be attributable to differential scheduling of migration departures and arrivals by males and females traveling in homosexual schools.

The only direct information available comes from two cargoes of unsorted green turtles caught on Miskito Bank and carried to market, respectively, in Grand Cayman and Key West. A sex tally was made of these by Giovannoli. The two schooners involved were the "Autarus" of Grand Cayman unloading at Georgetown and the "Adams" of Grand Cayman unloading at Key West. All turtles were from the vicinity of Miskito Cay, and all were caught between February and April, 1956. Sex frequency was as follows:

	MALES	FEMALES
"Autarus"	27	66
"Adams"	105	271

Elsewhere Carr (1956) has commented on the apparent predominance of male green turtles when the sea off the nesting ground is surveyed from the air. Because any female at the surface is usually attended by two or more males, and because females not immediately concerned with nesting apparently move away temporarily, an aerial survey gives an impression of a disproportionate number of males. Such observations, however, have no bearing on the actual sex ratio, as only a small, selective segment of the breeding schools is in evidence.

MULTIPLE NESTING

There is evidence of several kinds that the Atlantic green turtle may lay more than once during a season, as the form in the Pacific is known to do. For example, it has often been stated by those who habitually butcher green turtles that the egg complements of gravid females are often in two or more batches, of unequal size, and destined to be laid during separate emergences. Such persons and the *veladores* who turn turtles on the beaches generally agree that there are usually three such emergences in a summer and that these occur at intervals of from 10 days to two weeks. In various places about the Caribbean we have talked with turtle men who cite specific instances of a female turtle, recognizable because of some deformity or injury, that came ashore twice in "about two weeks."

It might be expected that a study such as the present one, yielding recaptures of turtles on the nesting beach where they were marked, would settle this question once and for all. Such is not the case. As we said above, the chief purpose of this year's project was the building up of a fleet of marked turtles that would allow the testing of the migration theories, and, as nearly any tagging program yields only scant returns, our efforts

forms, 70 mm. visible; Florida 2 conforms, not visible; New Jersey conforms, being short; New York conforms, 80 mm. visible; English Channel conforms, not visible.

The above proposition is apparently useful in the determination of species.

DISCUSSION

From the foregoing it appears that a number of diagnostic differences have in the past been proposed without due regard for the illustrated characters of the type of *gervaisi*.¹ Especially impressive is the number of propositions (1, 7, and 15) that apply quite well to all examples of *gervaisi* but the type. Because these characters distinguish all the other *gervaisi* material from all the *mirus* material, a question is raised about the relationship of the type specimen of *gervaisi* to the other specimens referred to the same species. One explanation of the differences in skull characters between the type and all other *gervaisi* may be that the differences are those between an old male and females and young males.

Parenthetically one may note the importance of explicitly stating the observed evidence as to the sex of a specimen. The genital apertures of male cetaceans are so similar to those of females that, unless mention is made at least of the mammary slits or the penis, future reviewers of the characters of the species are justified, if not compelled, to eliminate data on such specimens from any comparisons made to demonstrate sexual dimorphism or to differentiate species by the characters of the males.

There is a specimen of *gervaisi* found on the beach near Melbourne, Florida, the skull characters of which are here reported for the first time, although its occurrence has been previously noted (Moore, 1953). This skull, Florida 2, is of interest in comparison to the type of *gervaisi*, for it is like the type in having the mesirostral groove completely filled by dorsal proliferation of the presphenoid and the vomer, which is believed to be a condition of advanced age (Raven, 1937). As with the type also, its sex is unknown, but in this respect it is more enigmatic than the type, for its mandible is not available for an inference regarding its sex to be made from the size of the teeth. Because there is evidence that the type skull may be that of an old male, it should be interesting to note how this skull of an old individual from Melbourne, Florida, compares with it. This specimen agrees with the type in only a moderate number (four) of

¹ Similarly, a diagnostic character proposed while the present paper was in press (Rankin, 1956, p. 355) does not apply to the type of *mirus*.

TABLE 2—(Continued)

9	—	—	.459	.460	.500	.453	—	—	—	—	.436	—	—	—	.449	.448
10	.472	.447	.452	.453	.496	.435	.433	.426	.438	.423	.423	.431	.455	.429	.429	.431
11	.429	.425	.421	.428	.463	.409	—	.401	.414	.416	.416	.425	.442	.419	.426	.426
12	—	—	.374	.389	.407	—	—	—	—	.369	—	—	—	.370	.363	.363
13	.299	.308	.299	.286	.310	.293	—	—	—	.273	—	—	—	—	.272	.272
14	—	—	.140	.141	.146	.149	—	.154	.144	.139	.149	.149	.160	.159	.148	.148
15	.055	.050	.051	.059	.059	.057	—	—	—	.048	—	—	—	—	.053	.053
16	.220	.210	.220	.198	.214	.199	.197	.175	.203	.182	.194	.194	.184	.195	.192	.192
17	—	—	.133	.127	.139	—	—	.146	.148	.139	.142	.136	.136	.138	.136	.136
18	.146	.154	.136	.131	.144	—	—	—	—	.148	—	—	—	—	.137	.137
19	—	—	.090	.070	.083	.076	—	.084	.092	.096	.078	.091	.080	.080	.080	.080
20	.276	.270	.254	.258	.284	.252	—	.259	.246	.237	.261	.272	.249	.249	.273	.273
21	—	—	—	—	—	—	.191	—	.184	.193	—	—	—	—	.206	.206
22	.087	.089	.094	.072	.113	.083	—	.074	.082	.081	.076	.074	.084	.084	.095	.095
23	.071	.059	.068	.063	.073	.064	—	—	—	.058	—	—	—	—	.062	.062
24	.067	.062	.064	.067	.064	.067	—	.069	.072	.066	.065	.079	.067	.067	.064	.064
25	—	—	.080	.076	.077	—	—	—	—	.845	—	—	—	.093	.085	.085
26	—	—	.109	.105	.119	—	—	.114	.112	.124	.112	.114	.111	.111	.116	.116
27	—	—	.090	.104	.100	—	—	.078	.075	.080	.087	.086	.083	.083	.082	.082
28	—	.379	.384	.381	.419	.374	.358	.371	.387	.379	.380	.385	.385	.385	.372	.372
29	.858	.837	.837	.855	—	—	.800	.825	.860	.859	.878	.860	.860	.809	.834	.834
30	.177	.172	.201	.218	—	—	.199	.238	.234	.264	.231	.230	.223	.223	.242	.242
31	.158	.150	.145	.148	—	—	.150	.144	.150	.147	.139	.156	.148	.148	.142	.142
32	—	—	9	70	13	—	—	—	—	0	—	—	—	30	20	20

1. Greatest length of skull.
2. Greatest length of rostrum, from line across bases of antorbital notches.
3. Tip of rostrum to posterior margin of pterygoids, in sagittal plane.

TABLE 2—(Continued)

4. Tip of rostrum to most ventral point on anterior margin of pterygoid notch.
5. Greatest length of portion of vomer visible on palate.
6. Greatest length of orbit.
7. Greatest length of temporal fossa.
8. Greatest length of right nasal on the vertex.
9. Greatest width across postorbital processes of frontals.
10. Greatest width across zygomatic processes.
11. Greatest width across centers of orbits.
12. Greatest breadth of skull across occipitals.
13. Least width across the posterior margins of the temporal fossae.
14. Greatest width across occipital condyles.
15. Greatest inside width of foramen magnum.
16. Greatest width of premaxillae at their proximal expansion.
17. Least width of premaxillae opposite the anterior nares.
18. Greatest width of premaxillae anterior to the anterior nares.
19. Width of premaxillae opposite premaxillary foramina.
20. Greatest width of rostrum in antorbital notches.
21. Greatest width of rostrum in notches (if any) formed by maxillary prominences.
22. Greatest width of rostrum at midlength of rostrum.
23. Greatest depth of rostrum at midlength.
24. Greatest inside width of anterior nares (at right angles to sagittal plane).
25. Greatest width of temporal fossa without regard to orientation of skull.
26. Least distance between maxillary foramina.
27. Distance from posterior border of maxillary foramen and anterior end of maxillary prominence.
28. Height of skull, vertex to inferior border of maxillaries.
29. Greatest length of mandible.
30. Greatest length of mandibular symphysis.
31. Greatest height of mandible at coronoid process.
32. Amount added for missing portion of beak tip, to measurements involving tip of beak.

14 skull-character propositions, and in none of these four are the two different from the remaining specimens of *gervaisi*. Sharing of advanced age, therefore, does not alone appear important in the expression of these skull characters. As the Melbourne, Florida, skull does not exclusively share any of these 18 skull characters with the young male of Atlantic City, New Jersey, either, then it cannot by any means be construed to be a male. We find that on the other hand it agrees with the known female New York (as also with Florida 1) in 14 of the 18 propositions. For these reasons we are disposed to regard the skull from Melbourne, Florida, as that of an old female.

The Florida 1 specimen agrees with both the known female *gervaisi*, New York, and the old presumed female, Florida 2, in 12 of the 18 skull-character propositions, the closest agreement than any of the *gervaisi* show. It should not, therefore, test our credulity too greatly to consider these conservative three to be all females. Furthermore, these three together differ uniformly in propositions 4, 5, 12, and 14 from both the one known male, New Jersey, and the type, English Channel, which is presumed to be an old male because of its large teeth. This, therefore, logically sorts out these five specimens as three females and two males. The Trinidad specimen is less certain than these others in its associations, consorting with the New Jersey and English Channel males in only two of the four supposedly male diagnostic characters. On the other hand, it associates with the females with quite equal indifference. Our suggestion on this is that, as there is greater likelihood that males in a ziphiid species vary individually more than do females (already somewhat demonstrated by agreement of two males in only four of the skull-character propositions, when three females agree in 14), this Trinidad skull represents a male animal. It would perhaps be over-optimistic in the face of so much individual variation to hope that the two skull-character propositions in which these three males agree may correctly distinguish the maleness of future material, but they are numbers 4 and 5.

The most difficult to reconcile of the relationships shown in this re-assessment of skull characters proposed for the differentiation of *mirus* from *gervaisi* is that two perfectly good specimens, Florida 1 from Key Largo and the female from New York, agree only three times each with the type of their species in the 14 unamended propositions in which the type is treated. The type, English Channel, agrees in these 14 propositions with Trinidad eight times; with Florida 1, three times; with Florida 2, four times; with New Jersey, six times; and with New York, three times. Florida 2, by way of comparison, agrees in 18 propositions

with the other specimens in *gervaisi*, respectively, 14, 14, 8, 14, and 4 times. While some of the divergence of the type of *gervaisi* may be ascribed to sexual dimorphism as suggested, the divergence also of the Trinidad specimen and that of the Melbourne, Florida, specimen which shows in table 2 (measurements 2, 3, 4, 5, 15, 20) indicates that there is greater individual variation in the available sample of *gervaisi* than there is in that of *mirus*. Individual variation may also, therefore, be invoked to account for the peculiarities of the *gervaisi* type specimen.

MEASUREMENTS OF THE SKULL

It is customary in reporting a new specimen of a rare whale to present a series of straight-line measurements of the skull, and the tacit implication is that these data will to some extent show the taxonomic relationships of the individual being reported. To be able to compare these measurements meaningfully with those presented for other specimens by earlier authors, one must take measurements that correspond. That may seem obvious enough, but one author (Raven, 1937), in a paper dealing primarily with one new specimen each of *Mesoplodon mirus* and *Mesoplodon gervaisi*, not only neglected to present a set of measurements fully comparable to those of earlier authors reporting on these species, but did not even present the same measurements for the two skulls he was reporting so that they could be fully compared.

Although early authors had little comparative material on which to select measurements that might prove to have taxonomic value, and in the present species we still have very little material, succeeding authors have occasionally introduced additional measurements that they apparently thought might prove diagnostic. With a view to determine whether the data and material now available to us¹ has yet begun to show taxonomic value at the species level, we compare skull measurements of *mirus* and *gervaisi* in table 2. The measurements used are taken from early treatments of the species (True, 1910, 1913; Harmer, 1924), and some of the newer ones offered by later authors have been included. This comparison reveals that measurements numbered 1, 5, 8, 9, 12, 13, 16, 25, and 27 individually show a tendency to separate the two species. While it would be unwise to depend solely on any one of these measurements to identify a specimen, collectively used they should separate adult material of these two species very well.

¹ These regrettably did not include Rankin's paper (1956) which was published after the present paper had gone to press. Rankin reports skull measurements for the Jamaica adult and young and for the Cuban specimen.

ACCEPTED SKULL DIFFERENCES

It seems evident that the skull characters that have been proposed for differentiating *mirus* and *gervaisi* that have survived the tests of the present study are:

2. In *mirus* the anterior margin of the left (and sometimes the right) maxillary prominence protrudes into the lateral outline of the rostrum, intersecting it so as to form a notch with it. In *gervaisi* the lateral margin of the rostrum curves around either prominence without forming a notch.

6. The ventral outline of the rostrum in *mirus* is straight, but in *gervaisi* it is convex proximally and concave distally. This is true in five skulls examined, and in the published photographs of six more.

8. The shape of the temporal fossa as described by its outside margin is more elongate in *gervaisi* than in *mirus* as determined by the ratio of greatest length to greatest width (without reference to the orientation of the skull).

13. The dorsal surface of the maxillary in *mirus* about at midlength of the rostrum changes from being level to a downward and outward slope over an oblique bevel. In *gervaisi* it is level for the entire length or declines gradually. This is observed in the five skulls examined.

18. The vomer appears in the sagittal plane on the ventral surface of the beak in *mirus* as an elongate fusiform ridge visible for about a third of the length of the beak. In *gervaisi* it may not appear at all or is shorter and has its greatest width at the anterior end. The five skulls examined, and illustrations of five others, conformed to this proposition.

In addition to the above five characters, two others seem to be of value as supporting evidence:

3. The external free margin of the rostrum, anterior to its basal concave curve, proceeds towards the tip in a straight line in *mirus* but describes a further long, gentle, convex curve in *gervaisi*.

4. In *mirus* the lacrimal extends forward of the maxilla 10 mm. or more to form the apex of the antorbital tubercle. In *gervaisi* it extends less than 10 mm. (or not at all).

SUMMARY

A stranding of a young male *Mesoplodon mirus* True is reported from Flagler Beach, Florida—the most southern record for the species. The distribution of occurrences of *Mesoplodon mirus* and *Mesoplodon gervaisi* Deslongchamps are charted, and evidence of geographic segregation

of the two species is noted and discussed. *Mesoplodon mirus* apparently occupies the temperate western North Atlantic, and *gervaisi* the tropical and near tropical western North Atlantic.

Eighteen proposed skull differences between *Mesoplodon mirus* and *M. gervaisi* are tested on the two specimens of the former and three of the latter in the American Museum of Natural History, and to some extent on published photographs of other specimens. Five of these propositions are found to be good, or modifiable so that they distinguish this material, and two others are found to be useful as supporting evidence.

In addition to the interspecific differences concurred in by this testing of the 18 skull characters, some intraspecific differences are observed in *gervaisi*. Part of this variation is shown to be sexual dimorphism, and the studied *gervaisi* material is sorted by it into three females and three males. Individual variation is evidently greater in the males.

Comparison of external body measurements suggests that the length of the flipper of *mirus* generally exceeds that of *gervaisi* in proportion to total body length. Comparison of 31 skull measurements of the two species reveals nine measurements which, used collectively, will separate skulls of these two species.

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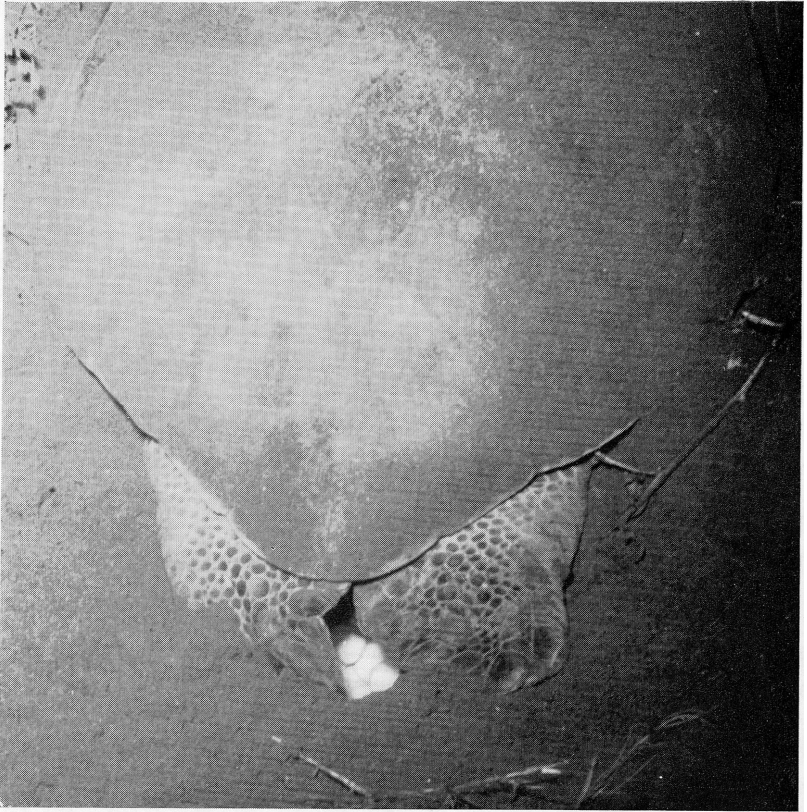


FIG. 12. Posterior view of green turtle in process of laying, showing characteristic covering position of the spread hind feet, here pulled slightly apart to show eggs.

At 11:15 P.M. work with the hind flippers stopped and the fore fins began to thrash and to sling sand. After a few strokes, the hind flippers joined in this work. As the turtle threw sand, she shifted the orientation of her body, and the indiscriminately flung sand gradually filled the nesting pit and sprinkled the surroundings through a radius of 6 to 8 feet. As the pit filled, the shifting stopped, but the scooping and throwing of sand with the fore fins continued, and eventually produced two good-sized basins (one for each flipper) at some distance from the former rim of the now indistinguishable nest excavation. Gradually the scattering of sand was discontinued, and the turtle began shuffling and scuffing about, over and near the site (but doing nothing like the pounding mentioned



FIG. 13. Green turtle filling her nest after laying. This individual (not the one involved in the accompanying description of laying) went through the whole nesting process perched on a root that was too strong for her to break out of her broad nest depression and that prevented her sinking into it in the usual way.

in the literature on other species). When all work was done the two depressions scooped out during the filling process by the fore flippers remained as the most conspicuous features of the local topography and may reasonably be regarded as diversionary in function.

At 11:32 P.M. all concern with the nest seemed to leave the turtle suddenly, and she made for the sea, moving towards it at an angle of roughly 20 degrees and disappearing in the surf at 11:43 P.M.

The features of the behavior of the above individual (shown by other observations to be characteristic) that represent departures from the nesting pattern of the loggerhead and the ridley are: (1) the peculiar striking of the shell margin by the off foot during the digging of the egg hole; (2) the very different position of the back fins during oviposition; (3) the leaving of diversionary pits; and (4) the (often) protracted period

of "smelling" of the submerged or wet sand before emerging (see below). In view of the uncertainty of evaluations of relationships among sea turtles on morphologic grounds, it will be of great interest to see how the hawk-bill, a form about which little of significance has been published, aligns itself with respect to nesting pattern.

STRANDING CUES: Interpretation of our observations in terms of possible orientation cues evoking the stranding response is not easy. It is as hard to understand how turtles know Tortuguero when they arrive there as to understand how they are guided through the long distances they travel from their feeding ranges to Costa Rica. Certainly much, if not most, of the population is transitory. Its reaching Tortuguero must involve, as well as equipment for navigation, some mechanism for "recognizing" good nesting shore (in this case Tortuguero) when it is reached.

Probably hydrologic factors are involved. It may be only a matter of the distribution and strength of long-shore currents, although these appear to vary erratically (as well as seasonally). Perhaps the distribution of fresh-water masses off the mouths of the Costa Rican rivers (either operating directly or by excluding some important stenohaline predator of baby turtles), or even such trivial things as the drifting mats of water hyacinths from the rivers, which could be a concealment opportunity for newly hatched young, are guideposts. Or possibly merely a certain degree of fatigue tells the turtles they are off the right section of the shore.

There is no doubt that a tendency towards clumped arrivals exists. Significantly more turtles come up on certain nights, or during a short period of the night, or on a certain short stretch of apparently homogeneous shore. As there seems to be little or no predictability or periodicity about these clumpings, they may be due to independent individual response to clumped favorable factors. On the other hand, the clumping may merely result from the gregariousness of the members of a migratory school, the occurrence of which is an assumption in foregoing discussions of quantitative data. But in any case, the problem of how the nesting beach is recognized remains.

The one overt sign that senses are consulted by the turtles in their coming ashore is their behavior when they go aground in shallow water shoreward of the breaker line. At this point a Caribbean green turtle habitually stops, bends her neck sharply downward, bringing her snout in contact with the bottom or with the wet sand and holding it there for as long as a minute, or sometimes even longer. It is exactly as if she were making an olfactory or gustatory evaluation of the shore as nesting ground.

On many occasions we have watched a turtle come out of the surf, stop when her plastron grounded and, for as long as 15 minutes, alternately "smell" the sand (sometimes under a foot or so of water, sometimes well above wave reach), then raise her head high and move it slowly about as if in myopic study of the prospect. Often these periods of appraisal end abruptly, with the return of the turtle to the sea, as if the shore had been found unsuitable. Other times the "smelling" may continue at intervals all the way up to the zone of loose dry sand, where it is discontinued.

Carr has described elsewhere (1954a, 1956) an aerial reconnaissance of the shore south of Tortuguero where he saw on a 6-mile section of beach hundreds (perhaps thousands) of the short, V-shaped trails made by turtles that have not nested, or even gone up beyond high-tide line, but merely have come a few feet up from the waves, prospecting. In this case all the tracks had been laid down during one night. The inference is that a migratory school was passing, and one can imagine the cruising hosts, singly or by squads, turning in to the shore from time to time to test the ground with their noses, "meditate," and then move on northward towards whatever they sought in the way of a more reassuring substrate.

Whatever the nature of the responses that bring the female green turtle ashore, in the last stages of stranding, at least, some delicate discriminatory process seems to be involved. We have seen evidence that one turtle may make three or four, and possibly a good many more, painstaking appraisals at points along a section of beach, eventually either accepting the site as good for laying or moving away to try elsewhere or to await another night. The strong negative response to light was mentioned above. We have, experimentally, often sent an emerging turtle scurrying back into the water by one flick of a flashlight beam across her eyes. The *veladores* say lighting a cigarette at the coco-plum line sometimes scares away a turtle coming out of the surf. A man or dog moving between the turtle and a luminous horizon shoreward has the same effect. In this way, the green turtle seems clearly more impressionable than the loggerhead, and one is tempted to see this heightening of stranding responses and adjustments as one of the necessary adaptive concomitants of massed migratory breeding, with its complex chain of orientation reactions.

Balancing this fastidiousness in making the stranding "decision" is an incongruously dogged stubbornness in making the drive to lay, exemplified by the return (see above) to the beach of No. 227 only a few hours after the experience of spending a night on the beach on her back. Comparable cases are numerous in our records, as is shown by the first peak in the curve in figure 9. Females often come ashore dragging with them much

larger males attempting copulation. That these are not merely desperately fleeing unwelcome attentions seems indicated by the fact that a female also frequently comes up hauling a log tied to her fore flipper with a rope 6 or 8 feet long. To get turtles out to the launch that takes them to market, the *veladores* tie a wooden buoy to the fin of each turtle and make her swim to the coasting boat. Some of these escape, and they sometimes come back ashore and complete a laying venture with the log attached. We have what seems to be a reliable record of one of these escapees that was retaken at Bocas del Toro, nearly 200 miles away.

Whatever may be the nature of the senses used in coming to, and in recognizing, the beach the choice of the nest appears to be no more than the "feel" of the sand when trial scoops are made with the flippers. The turtle simply keeps going (in a direction determined by factors not well known) until she comes to an obstruction or until a few trial scrapings of the sand satisfy her. Obstructions that stop her may be dunes, vegetation, or a storm-thrown log. Any of these will probably be located above the reach of normal high tide and thus in good nesting sand, and, as a prospecting turtle usually stops and tries the sand when she meets such an obstacle, a majority of nests are found in such places.

In the case of the broad, duneless bars or spits near the river mouths, where no vegetation grows, turtles sometimes go considerable distances, sometimes as far as a quarter of a mile, in search of good ground. On the low, wide bar between the lower end of the Tortuguero River and the sea, tracks often show that turtles have pushed the futile search for deep nesting sand clear across the peninsula and, on reaching the river bank, have parted the hyacinths and entered the river.

It is of interest that the relatively small number of hawksbill trails we have seen seem to indicate a far greater tendency in that species to wander in its search for a nesting place.

COURTSHIP AND COPULATION: Mating occurs (mainly, perhaps almost exclusively) off the nesting beach, as is known to be true of the Pacific form. Whether it takes place before or after laying, or both, is not known. Certainly males often head for females as they go back into the sea, but no actual copulating has been observed to result at such times. Both of us have seen females come ashore dragging, or pursued by, males, as we mention above. Harrison (1954) said, with regard to this point, "It looks to me as if it [copulation] mainly occurs *after* the female has laid," but he gave no evidence.

Pairing is a strenuous and clumsy operation, and the female often ends an outing at the beach in bad shape—gashed, scraped, and with deep notches broken out of the fore margin of her carapace, one on either side

of her neck, where the grappling nails of the male have clawed for support. Prior to pairing there is often considerable confusion that seems to be fighting between males, but may be the striving of rival suitors to mount a female simultaneously. Carr has elsewhere (1956) mentioned the frequency with which groups of three floating turtles (a female and two attendant males) may be seen from the air off the beach in the nesting season. It is of interest that Harrison (*loc. cit.*) refers to similar observations for the Pacific green turtle.

When pursuing or trying to mount the female, a male green turtle is apparently oblivious to all other stimuli. When the *mancuernas*, as the mated pairs are called, appear close inshore, the Tortuguero boys grab irons, run out into the surf, and sometimes succeed in harpooning the male before he is aware of their presence.

During the 1955 season, courting or mated green turtles, sometimes several in an afternoon, were seen frequently during early and middle July. Towards the end of July such pairs appeared less often, and during all of August no sign of courting or copulation was observed.

ACKNOWLEDGMENTS

Aside from the sponsorship of the National Science Foundation (a *sine qua non* for its realization) this study has had support and cooperation from a number of sources.

The Limon personnel of Compañía Bananera de Costa Rica has, during four seasons, been unfailingly helpful.

Señor Teodoro Quirós C. has for the same four seasons placed at the disposal of the investigation the facilities of the timber and banana station of the Atlantic Trading Company at Tortuguero. In the Limon office of that enterprise, Mr. Stanley Lettman has been consistently cooperative.

The work on the beach was greatly facilitated by the courtesy of the Costa Rican Ministry of Agriculture, which provided aid from local conservation officials and placed at our exclusive disposal the 2-mile section of Tortuguero Beach between the settlement and the mouth of the river.

In San José Mrs. Doris Stone was of assistance in arranging for field work, and Dr. Rafael Lucas Rodríguez of the University of Costa Rica furnished valuable advice and encouragement.

At the University of Florida Dr. Arnold B. Grobman, Director, and Dr. J. C. Dickinson, Jr., Curator of Biology, the Florida State Museum, were helpful in furnishing funds and equipment in early stages of the study; and Dr. L. E. Grinter, Director of the Graduate School, was

similarly cooperative. Mr. David Caldwell of the Department of Biology collaborated in a number of ways.

The original decision to work at the Tortuguero site was reached after reconnaissance travels supported by a grant from the American Philosophical Society.

From its earliest state to the present, the work has received whole-hearted cooperation from the captains and crews of the Cayman turtle fleet and from the people of the Cayman Islands generally.

To all the above, and to the literally hundreds of fishermen all about the Caribbean, whose talk lent form to conceptions that led up to the study, we are naturally extremely grateful.

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