

Vol 53 NO.3

Late Spring 1972

Ecology

QH540 E3

SITE FIXITY IN THE CARIBBEAN GREEN TURTLE¹

ARCHIE CARR AND MARJORIE H. CARR

Department of Zoology, University of Florida, Gainesville 32601

LIBRARY OF
GEORGE H. BALAZS

Abstract. Although tagged green turtles that return to Tortuguero Beach to nest show definite site fixity, their site discrimination is not absolute. The modal distance between successive returns, whether after the 2-week internesting period of a given season or after the 2- or 3-year remigration interval between nesting seasons, is 2 km; average separation of return points is 1.2 km. In view of the steady reworking of the Tortuguero foreshore by wind, waves, and longshore currents, it seems unlikely that olfaction could be an important cue in landfall and nest-site discrimination, and this new delimitation of the homing goal reinforces that belief. The straying of nesting females as far as 7 km from previous nesting sites suggests how colony proliferation may occur. No Tortuguero turtle has ever been found nesting on any other shore.

One difficulty hindering explanation of the long-distance navigation of animals is to conceive an operational relation between the long-range guidance process and the final exact destination of the successful journey. To think of a migrating animal as striving toward a distant home locality, set like a beacon in the distance, hinders interpretation of the orienting process.

Nevertheless, as a separate discriminatory process, goal recognition exists, and in some cases remains as poorly understood as the long-range navigation mechanism itself. In the case of the green turtle, *Chelonia mydas*, although tag returns have confirmed the existence of a strong homing drive and site discrimination (already implicit in the tendency to converge from different distant feeding grounds at nesting time) the character and boundaries of the individual goals of the migrants have remained vague. Where the nesting ground is a cluster of small islands, the females tend to return to the same island for consecutive meetings (Hendrickson 1958). At Ascension Island in the South Atlantic, the nesting ground is a series of crescentic beaches in little coves separated from one another by rocky promontories. There, both the turtles on migration from Brazil, and those renesting during a single season, go back to the same cove to nest (Carr and Hirth 1962, Carr, in press). When a nesting aggregation occurs on a more or less homogeneous mainland beach, as at Tortuguero on the Caribbean Coast of Costa Rica, the emergences might be expected to scatter at random. This is not the case. The nesting beach there is about 22 miles (about 35 km) of shore between the mouths of two rivers, Río Tortuguero on the north and R. Reventazón at the southern end. When our tagging program began there in 1955 it was the belief of the local professional turtle-turners that the homing

goal of a nesting turtle was some particular "spot" on the beach, and that if a person returned about 12 nights after he had seen a turtle nesting, he would see the same turtle come ashore again at exactly the same place. This belief is likewise inaccurate. The goal of the individual Tortuguero turtle has proved to be at once more generalized than a "spot" on the beach, and much more restricted than simply the whole 22-mile rookery shore. Carr and Ogren (1960) found the usual spatial interval between successive nestings to be $\frac{1}{4}$ – $\frac{3}{4}$ mile (.4 km–1.2 km), and saw no tendency for successive return-intervals to widen as time passed. Now, 11 years later, we have accumulated enough records of consecutive returns by remigrants (females returning on their successive seasonal migrations) and by reneesters (turtles that repeatedly return during a given season) to justify a reassessment of site tenacity in this population and at least to suggest what the boundaries of the homing goal are.

The sample is somewhat biased by the cut-off at mile 5 (km 8), south of which tagging has been only sporadic. Nevertheless, most of the females that nest on the northernmost 8 km of beach have clearly carried out all their consecutive nestings there, and the figures thus have considerable quantitative value. As Table 1 shows, the mean separation for all consecutive returns by individual females to our 8-km research beach, for the period 1956–69, is 1.4 km, and the mode is .2 km. There is close agreement between nest-site intervals for the 12-day renesting returns and those for remigrant turtles returning after the 2-year or 3-year cycle-period characteristic of the Tortuguero breeding colony (Carr and Carr 1970). The remigration interval is measured as the distance between the average positions of the series of renesting intervals for the two successive seasons at the beach. In Table 2 all recorded nesting emergences of three individual turtles are shown.

In the effort to visualize the goal to which a nesting green turtle returns, a possible clue would be

¹ Research supported by the National Science Foundation, the Office of Naval Research, and the Caribbean Conservation Corporation. (Manuscript received July 22, 1971; accepted October 16, 1971.)

TABLE 1. Distances in .2-km ($\frac{1}{5}$ -mile) units between successive nesting emergences of green turtles at Tortuguero, Costa Rica. As the term is used here, a *remigrant* is a female that returns to nest after an absence of 2 or 3 years. A *renewer* is a turtle that returns for one or more successive nestings during a single season. The remigration interval is measured as the distance between average re-nesting positions

	Number of individuals	Mean	Mode	Range	Standard deviation	Standard error
Renesters, 1967-70	286	7.57	1	0-30	7.075	0.418
Remigrants, 1967-70	181	6.60	1	0-35	6.77	0.503
Combined renesters and remigrants, 1967-70	467	7.19	1	0-35	6.99	0.34

TABLE 2. Renesting and remigration sites of three Tortuguero green turtles, to show representative individual site-tenacity records. Turtle no. 5168 remigrated after one 2-year interval; no. 3071 after a 6-year interval; and no. 3188 after two successive 3-year intervals. The nesting beach is marked off in $\frac{1}{5}$ -mile (.2-km.) sections, beginning at the northern end. The number in the "Mile marker" column represents the marker located just to the north of the nest involved. No turtle tagged at Tortuguero has ever been found nesting on any other beach, and none has ever nested there in consecutive seasons

Turtle no.	Year	Date	Mile marker
5168	1968	8 August	1 5/8
		22 August	2 5/8
	1970	2 September	1 5/8
		31 July	1 5/8
		13 August	1 3/8
3071	1964	24 August	1 4/8
		4 September	1 4/8
		24 July	2 4/8
		5 August	1 2/8
		15 August	1 2/8
	1970	3 September	1 4/8
		13 September	1 4/8
		13 August	1 7/8
		2 September	1 4/8
		12 September	1 6/8
3188	1964	10 August	1 4/8
		22 August	1 2/8
	1967	27 August	1 2/8
		20 September	5/8
	1970	4 September	2 1/8
		15 September	1 4/8

clumping of the nests along the nesting shore, and any consonance of this general clumping with discernible physical features of the shore. Nest-track tallies along the Caribbean Coast of Central America reveal an abrupt concentration of nesting on Tortuguero beach. The whole rookery is therefore a clump—and one for which no satisfactory explanation has been proposed, because there are hundreds of miles of similar-looking coast both to the north and to the south of Tortuguero. When track counts are plotted within this stretch of shore, internal clumping is clearly revealed. One peak occurs in most seasons at a point about .6 km south of Tor-

tuguero Bar, another 6.4 km–8.0 km to the south, and another, by far the strongest, at about km 18 down the shore. So far, we see no clear explanation for either the massing at the rookery beach as a whole or for these three peaks of nesting frequency. Clumping on the northernmost 5 km section of Tortuguero, where continuous site records have been kept for years, is shown in Fig. 1 and 2.

A more fine-scaled clumping of nest sites appears to occur on shorter sections of beach, which, though they vary topographically from season to season, are, on the whole, known to the tagging crews as the best places to find turtles quickly on any given night. It is probable that if the exact position of every nest on any given 1-km section of the shore were kept, consistent clumping, which might or might not shift in position through short periods of time, would be revealed.

When nestings converge in both space and time, the arrival of schools of turtles that have either traveled together from the feeding ground or gathered in bands during intervals between nesting emergences might be suspected. When the clumping is nonsynchronous, however, its cause should be looked for in either shore topography or hydrologic features. In either case, there is the likelihood that the factors responsible for the clumping are likewise the site-discrimination cues used by the individual female, and that she went ashore there on her first visit because of imprinted responses from her hatching days. It is hard to see what features of a short stretch of ocean beach might repeatedly bring a turtle back to it—after her 12-day internesting intervals, after her 2- or 3-year remigration absences, and presumably also after the 6 years it takes her to reach sexual maturity and return for a first nesting at the place where she hatched and first entered the sea. When the accumulated records define the modal home site as a 200-m section of sandy beach that is constantly being resurfaced by winds and waves, which changes in profile as shore vegetation grows or dies down, and which is sporadically remodeled by storm seas, the goal in the mind of the turtle becomes as

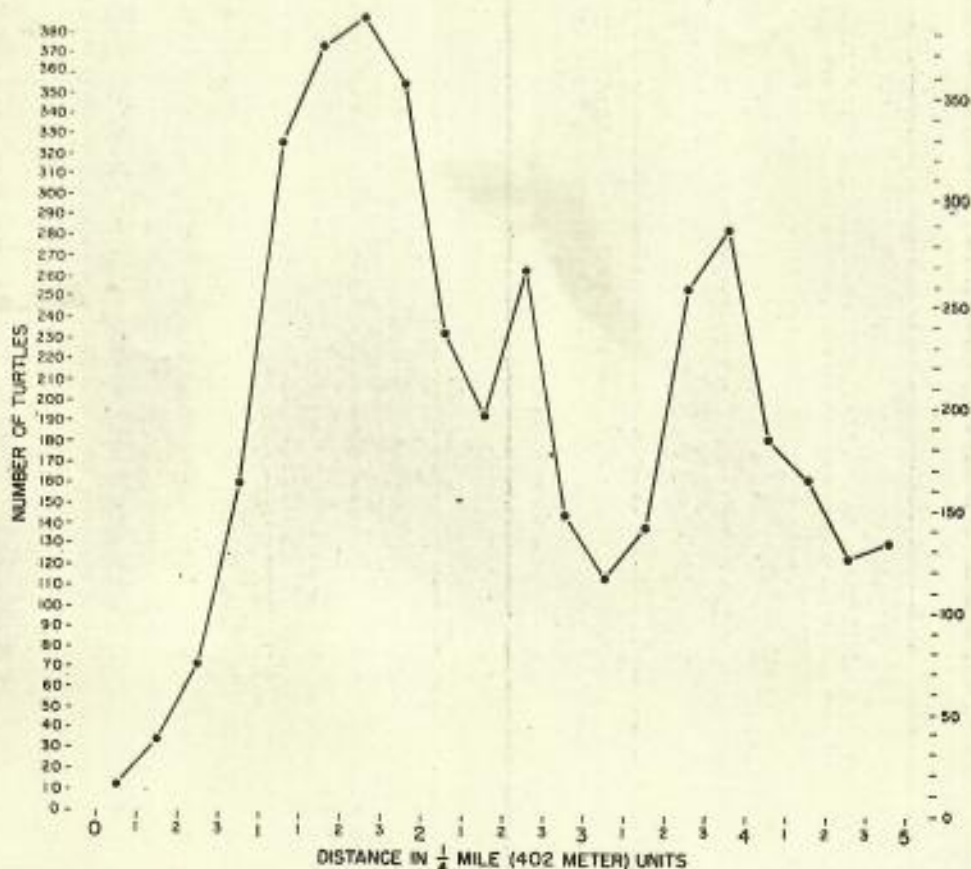


FIG. 1. Location to the nearest $\frac{1}{4}$ mile (.4 km) of the nesting sites of 4,002 green turtles recorded on Tortuguero Beach, from 1960 through 1970. The zero point on the distance scale represents the mouth of Tortuguero River at the northern end of the nesting beach. The total span is about 5 miles (8 km).

elusive a concept as her high-seas navigation mechanism has proved to be.

The advantages of site fixity are obvious. Going back to a natal site to breed enables a turtle both to retain a favorable nesting place and to join a reproductive aggregation that will bring the sexes together after the long trip from the distant pasture grounds. At the same time, some mechanism for colony proliferation must be built into the system. Even the limited sort of nest-site tenacity that our data show makes one wonder how new breeding colonies could form. In the behavioral ecology of nesting, as in any biological process, a balance between conservative and diversifying factors seems essential. The range of returns in Table 1 appears to show such interplay. The 35-unit intervals in the record suggest the kind of variation that might result in the occasional establishing of new nesting colonies. Even though both are advantageous, it is not clear how site fixity and a pioneering tendency based on a breakdown of site fixity could be built into a species by natural selection, but perhaps the wandering tendency can be

thought of as merely a fortunate defect in the hereditary homing drive or mechanism.

That imprinting of hatchlings is actually the fundamental factor in site fixity seems corroborated by the gap in nesting emergences at mile 3, in front of the village, as shown in Fig. 1 and 2. The foreshore there is in no superficial way different from adjacent sections on which heavy nesting occurs. This immediately suggests that the presence of people and their thatched cabins scattered along the coco-palm fringe are responsible for the gap. Of the two ways in which people might produce it, one would be by directly scaring turtles away. The other would be by killing off turtles with the imprinted tendency to return there to nest, which obviously would steadily reduce the numbers of hatchlings that took that trait away with them. Of the two possibilities, the second seems the more reasonable. Observations indicate that turtles are not scared away by thatched cabins placed back among trees, unless these are brightly lit. At Tortuguero there have been no bright lights along the shore until the past 2 years, and all lights there

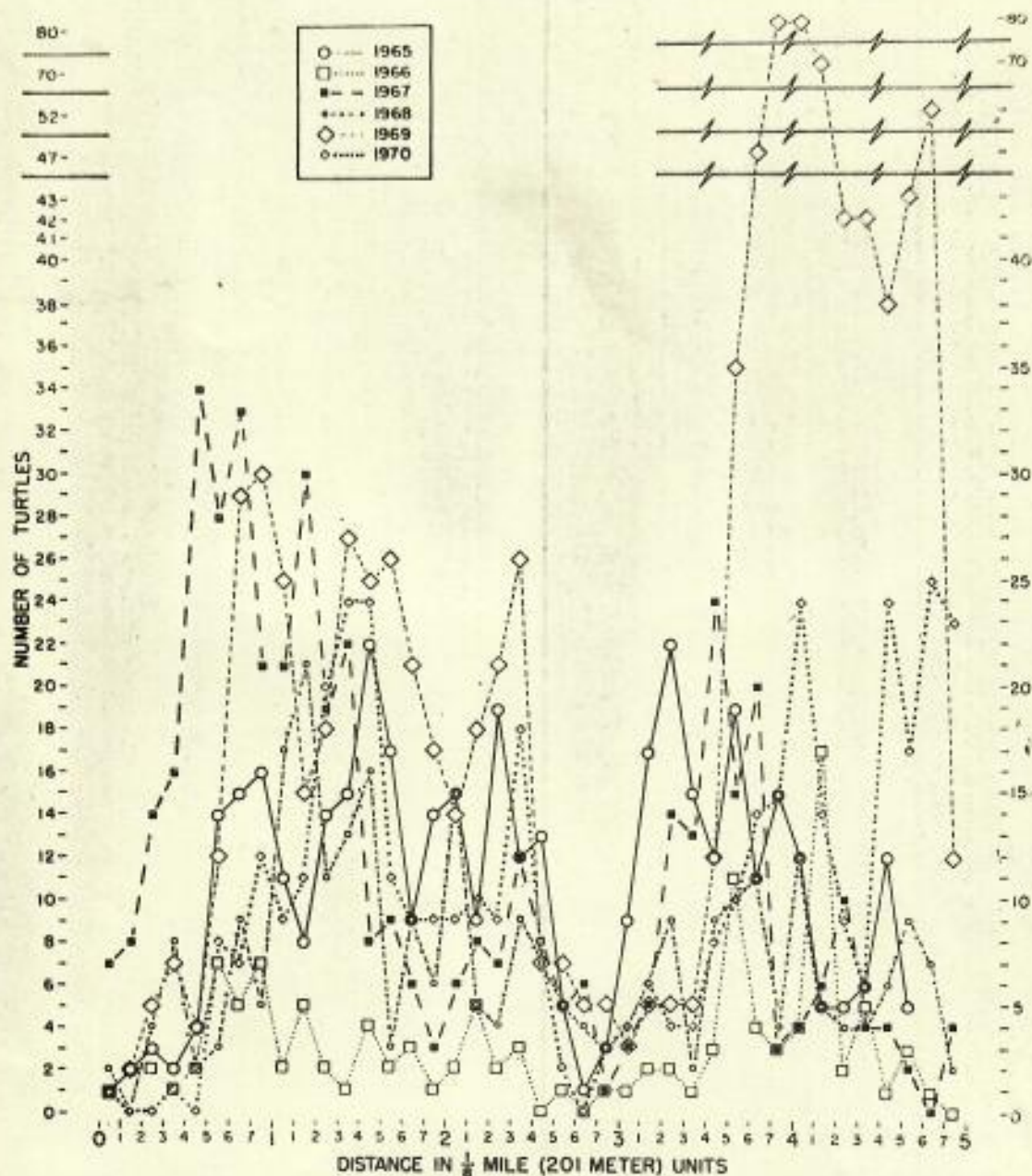


FIG. 2. Location to the nearest $\frac{1}{4}$ mile (.2 km), by year, of the nest sites of green turtles at Tortuguero, Costa Rica, from 1965 through 1970. The zero on the distance scale represents the mouth of the Tortuguero River at the northern end of the nesting beach. The total span is about 5 miles (8 km).

customarily went out early in the evening. However, during the decades in which there was unrestricted killing of turtles on Tortuguero beach, the heaviest toll naturally occurred close to the settlement. Elimination of females imprinted with the tendency to return to that part of the shore to nest, combined with the concurrent reduction of imprinted hatchlings to replace them, would inevitably delete from the colony that contingent with the imprinted tendency to nest on that section of the shore.

The possible character of the imprint involved remains a complete mystery. Koch, Carr, and Ehrenfeld (1969) postulated a chemoreceptive component for the mechanism guiding the Brazilian turtles in migrating to Ascension Island, and Carr (in press) has shown how that theory might also apply in the Tortuguero migration. In both these cases olfaction was seen as the preferable theoretical alternative to the more complex adaptations requisite to any bi-coordinate navigation system. In both cases, the ol-

factory cues would serve both in long-range guidance and in recognizing the general area of the rookery—Ascension Island in the west-flowing Equatorial Current, and Tortuguero on a stretch of shore between smell-generating stream mouths. Once the area of the breeding ground is reached, however, it is hard to see how olfaction could possibly be the sense involved in nest-site choice, because the specific smell of that exact place is bound to change from season to season as the sand surface is replaced or resorted by wave-wash and storm waves. If this is indeed the case, the "sand-smelling" behavior of turtles on shore (Carr and Ogren 1960) seems less likely to be an olfactory process and more probably a tactile appraisal. In neither case, however, would the habit appear to shed any light on landfall and nest-site discrimination in *Chelonia*.

LITERATURE CITED

- Carr, A. *In press*. The case for long-range olfactory piloting in *Chelonia*. NASA Publ. S.P. 262.
- Carr, A., and M. H. Carr. 1970. Modulated reproductive periodicity in *Chelonia*. *Ecology* 51:335-337.
- Carr, A., and H. Hirth. 1962. The ecology and migrations of sea turtles, 5. Comparative features of isolated green turtle colonies. *Amer. Mus. Natur. Hist. Bull.* No. 2091. 42 p.
- Carr, A., and L. Ogren. 1960. The ecology and migrations of sea turtles, 4. The green turtle in the Caribbean Sea. *Amer. Mus. Natur. Hist. Bull.* 121, Art. 148 p.
- Hendrickson, J. R. 1958. The green sea turtle, *Chelonia mydas* (Linn.) in Malaya and Sarawak. *Zool. Soc. London, Proc.* 130:455-535, 15 fig., 10 pl.
- Koch, A. L., A. Carr, and D. Ehrenfeld. 1968. The problem of open-sea navigation: the migration of the green turtle to Ascension Island. *J. Theoret. Biol.* 22:163-179.

LIBRARY OF
GEORGE H. BALAZS