

A MODEL OF THE EVOLUTION OF GREEN TURTLE  
(*CHELONIA MYDAS*) REMIGRATIONS

HAROLD F. HIRTH

**ABSTRACT:** Although it is most probable that the ultimate factors leading to long-range remigrations of green turtles are not the same for all populations, it is hypothesized in this paper that some of the better-known green turtle remigrations had their origins in short distance movements between feeding pastures and nearby nesting beaches. The feeding pasture was the center of activity, and movements to the nesting beach were based upon a familiarity with the local environment. Semipermanent residents were selected for because of changing conditions on the feeding pasture or on the nesting beach. Passive drift in dominant surface currents probably gave rise to some of the first distant remigrations. A refinement of passive drift includes an adult's identification of a previous nesting site, and this short-range discriminatory ability may have been a precursor to long-range, unidirectional homing, and this in turn to true navigation. Some of the long-distance remigrations seen today, although highly developed, may only be remnants of more widespread patterns that are now selected for because of their survival value.

Most ecological research on the green turtle (*Chelonia mydas*) has centered around the nesting beaches, and as a result much biologic information is available on such things as the nesting behavior and fecundity parameters of adult females as well as the behavior of hatchlings on the beach. Because investigators customarily tag and measure the nesting female, there now exist thousands of tagging records along with hundreds of long-distance recaptures. Discussion of tagging recoveries usually focuses on dispersion from the nesting beach along with speculation as to the sensory mechanisms which bring the adult female back to the nesting beach in subsequent years. Such conceptualizing has merit because marine turtles must lay eggs on land and as only certain beaches are appropriate, a bias for specific beaches must have appeared early in green turtle phylogeny.

In this paper, I discuss both ends of the remigration—the nesting beach and the feeding pasture. I consider the feeding pasture of the adults the center of activity (because by all accounts the typical adult turtle spends most of its life there), and I speculate on the evolution of remigrations

from the feeding pasture to the nesting beach and back to the feeding pasture. Further, drawing upon different contemporary models, I try to place what is known about the remigrations of green turtles into an evolutionary framework. I hypothesize that the first green turtles were permanent residents and that some of the remarkable long-distance remigrations observed today have evolved through ordinary mechanisms of natural selection. In this paper, I discuss only a few of the many possible steps in the evolutionary development of the remigrations, namely: permanent residents, semipermanent residents, passive drifters, drifters with short-range discriminatory powers, fixed direction remigrants, and true navigators. However, I am not proposing that every population of navigators extant today has passed through all of these stages. Each remigrating population is of course molded by specific selection pressures. Also I do not discuss proximate factors that might be involved in the remigrations. This paper is basically an attempt to discuss how such an incredible feat as navigation could have evolved over geologic time along a continuum from simple to complex movements.



#### SOME REPRODUCTIVE PARAMETERS AND DEFINITION OF TERMS

I use the word migration when referring to a one-way movement, say from the feeding pasture to the nesting beach. A remigrant is a reproductively mature female or male who makes periodic movements from the feeding pasture to the nesting beach and back to the feeding pasture. Based on the available remigration records, it is generally accepted that most green turtles nest every 2, 3 or 4 years. Tagging records also indicate that adult females tend to return to the same nesting beach for oviposition (recent data reviewed by Carr and Carr, 1972).

A renester is a female who nests several times during a single season and whose sites of oviposition throughout the season are relatively near each other or at least in the same general area of the beach. Carr and Carr (1972) have described the site fixity in the Caribbean green turtle on the most intensively studied green turtle beach in the world—that at Tortuguero, Costa Rica.

Most green turtles nest from 4 to 6 times each season at 10- to 15-day intervals. However, evidence is accumulating that fewer renestings are not uncommon. The number of eggs laid in each clutch varies from 1 population to another but in most populations averages somewhat in excess of 100. Females usually remain in the vicinity of the nesting beach during intervals between nesting.

As far as I know, copulation takes place only in shallow water off the nesting beach. Whether this insemination serves to fertilize the current season's eggs or whether spermatozoa are stored to fertilize subsequent clutches (2, 3 or 4 years later) remains unresolved (Carr, 1965; Booth and Peters, 1972; Simon et al., 1975).

Green turtles of both sexes are chiefly herbivorous as adults, with some populations preferring algae and others preferring sea grasses. However, animal food may be an important supplement to their diet.

Little is known about the life history of the male green turtle. As far as their remigrations are concerned, I assume that males leave the feeding pasture along with the females. Whether they go back to the feeding grounds with the females at the end of the nesting season or whether they leave the breeding beaches before the females is unknown.

*The Original Pattern.*—I hypothesize that the first green turtles (or their sea turtle ancestors) nested and fed in areas that were in close proximity to each other; i.e., the turtles were permanent residents. A familiarity with sensory cues provided by both the resident area and the immediate surrounding area could serve as the basis for piloting between feeding ground and nesting site. The original condition may still be observed today near remote islands and near remote sections of mainland beach. For example, I speculate that some turtles nesting on some atolls in the South Pacific Ocean, some islands in the Red Sea, and on some beaches in Somalia, remain in the vicinity of the nesting site year round. Cornelius (1976) suggests that the green turtles nesting at Naranjo, Costa Rica, may be a resident population.

*Limitations of Nearby Nesting Sites.*—In primal times, the nesting population on beaches with limited nesting space, for example islands, was probably regulated by the mechanism of density-dependent nest destruction as described by Bustard and Tognetti (1969). Such regulation of population size can probably still be seen today on some of the Barrier Reef cays of Australia (Bustard and Tognetti, 1969), at Ithmun Beach on the Arabian peninsula during the northeast monsoon (Hirth and Carr, 1970) and on Europa Island in the Mozambique Channel (Hughes, 1971). Where several species of sea turtles use the same nesting beach at the same time, interspecific nest destruction can sometimes be very significant (Bustard, 1972).

If nesting space is not limiting, a density-intolerant female's response to a crowded nesting beach could be to move out laterally



along the island or mainland beach, thus increasing the linear size of the rookery. Another response to crowded nesting conditions could be the shifting of the time of oviposition. This response could have led eventually to year-round nesting by the population as a whole (providing availability of males for insemination). Such behavioral shifts may be operating today on crowded, isolated beaches.

Topographic changes in the size or composition of the nesting beach could also provide the impetus for oviposition on different, neighboring beaches. For example, Schulz (1975) has described how some Surinam green turtles search for new, adjacent nesting sites when their former nesting sites are no longer appropriate due to beach erosion.

On a geologic time scale, the glacial and interglacial periods could have alternately exposed and then inundated certain island and coastal nesting beaches, causing behavioral shifts in nest site selection.

High concentrations of turtles on the beach and in offshore waters no doubt attract predators. Thus, the ultimate size of a breeding population, especially those utilizing mainland nesting beaches, may be limited by beach predators (preying upon eggs, hatchlings and even adult females) and by predatory fishes in the littoral. Lists of avian, terrestrial and marine predators have been compiled by Hirth (1971).

*Movements Away from the Resident Area.*—Semipermanent residents may have evolved from permanent residents via several routes. Two such routes, already alluded to, are those of the gravid individual who is deterred from nesting on the nearest beach because of overcrowded conditions or because of beach erosion. Another route might be exemplified by a female nesting on the nearest beach to her feeding area one year and then expanding her feeding area in succeeding years with nesting in the subsequent years on the nearest suitable beach to the new feeding locality. Such a beach is found by searching. In her search the female seeks out a

nesting site similar to that selected in previous nestings. Expansion of the feeding range could be in response to changes in climate or topography, or change in quality or quantity of the food. For example, changes in climate could change such things as water salinity which affects growth of marine spermatophytes and algae and hence affects choice of feeding sites by green turtles. A semipermanent resident could also be an individual who nests on the nearest suitable beach to the resident area one year and who passively drifts with a current to a more distant beach another year.

*Passive Drift.*—Passive drift with dominant surface currents, as in a gyre, both away from and back to the feeding pasture was probably the simplest way that new, more distant nesting beaches were established in the past. The first drifters, floating randomly in a variety of currents probably suffered high mortality but selection would favor the trait if resident rookeries were overcrowded or were subject to heavy predation, and if hatching success was better on the newer breeding beaches. It seems reasonable that even today, drifting or wandering individuals could serve as important substrates for natural selection. Swimming with currents could be energetically advantageous even if sometimes such a route were indirect and involved an increase in travel distance. The use of oceanic currents by green turtles might be analogous to the use of wind currents by migrating birds.

Figure 1 outlines 2 simple remigration patterns based on passive drift with currents. In the simplest pattern, currents carry the adults directly to the nesting beach and oviposition takes place when reproductive drives peak. Adults are carried back to the feeding pasture also by currents. Richard and Hughes (1972) postulate that green turtles nesting at Tortuguero, Costa Rica, are passively carried by currents to the vicinity of that beach from feeding grounds off Nicaragua. The idea of passive drift is further discussed by



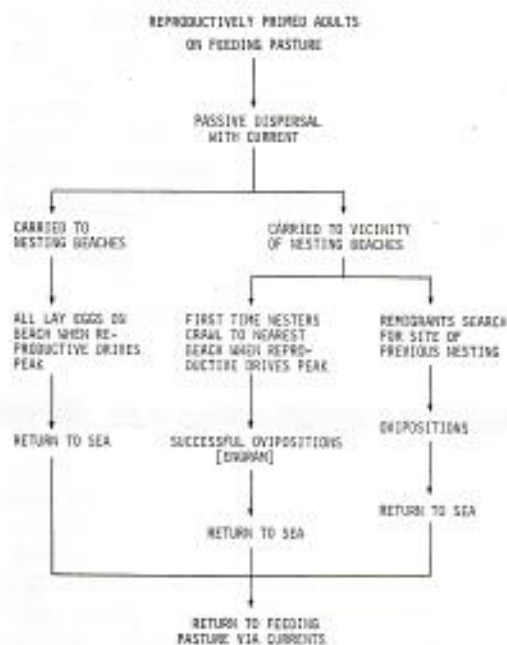


FIG. 1.—A scenario showing how passive drifters could have established some of the first distant remigrations.

Hughes and Richard (1974) with special reference to the ridley turtle (*Lepidochelys olivacea*). Conversely, Carr (1972) speculates that an olfactory and sun-compass mechanism along with current systems are utilized by green turtles nesting at Tortuguero. The available evidence seems to support Carr's position on this matter.

If currents are important means of transport to some nesting sites, it could mean that some of the beaches that were good nesting sites in the past are not now because currents have changed as a result of geomorphic processes.

A more highly developed pattern (see Fig. 1) has the currents bringing the ovigerous females and adult males to the vicinity of the nesting beaches. First time nesters simply swim out of the current and nest on the nearest appropriate beach when their reproductive drives peak. After several renestings the turtle converts its successful nesting experiences into some sort of long-term memory or engram. Experienced

females search for the conditions which were present during their previous nesting episode, i.e., they possess some kind of long-term memory and short-range discriminatory powers. These short-range cues may be both edaphic and marine, and sequentially or synergistically they may act as triggers for oviposition. Hendrickson (1958) postulates that renestings on the beaches in Sarawak are due to some sort of experience-memory fixed by a "satisfactory" nesting experience. Bustard (1976) has suggested that Australian green turtles might utilize dominant surface currents to get to the general vicinity of their nesting beaches in the Capricorn Islands; and, Balazs (1976) has pointed out that some Hawaiian turtles may be swimming with prevailing currents to get to their nesting beach on French Frigate Shoals.

Although the role of currents in the evolution of remigration is speculative there is ample ground for belief that currents play a role in the distribution of at least some green turtles today. For example, it is generally accepted that hatchlings, after an initial, brief period of swim-frenzy, drift relatively passively in offshore currents (perhaps with drifting Sargassum weed in some localities), for at least the first few weeks or months of their lives. Witham (1976) shows how currents may effect the distribution of yearling turtles. Developmental migrations involving mostly juveniles and subadults have been described (Carr and Caldwell, 1956; Mowbray and Caldwell, 1958; Carr, 1961; Burnett-Herkes, 1974) but whether ocean currents are directly involved is unknown. There is no doubt but that some of the unusual distribution records of green turtles, of all sizes, are due to strays traveling in currents. Brongersma (1972) for example, lists several green turtles found in European waters that probably crossed the Atlantic on generally eastward flowing currents.

*Fixed-Directional Movements.*—Turtles homing into their nesting beach from short ranges may have been the precursors of long-range unidirectional remigrants. For

example, Carr and Coleman (1974) describe how the present-day remigration between Brazil and Ascension Island could have evolved through a pattern of swimming roughly WNW-ESE.

In regards to the return to a feeding pasture, Pritchard (1976) hypothesizes that some green turtles, returning to Brazil after nesting in Surinam and French Guiana, swim in a rather fixed (ESE) direction until they encounter the Brazil Current which brings them to their "final destination"—i.e., the algal feeding pastures off the coast of Alagoas. Referring to the same general movement, Schulz (1975) states that because the turtles recaptured enroute to the feeding areas were taken near the coast, the green turtles nesting in Surinam perhaps do not need an open-sea navigational ability. In reference to Hawaiian turtles, Balazs (1976) also mentions the possibility of some degree of fixation to the feeding site.

*True Navigation.*—The most highly evolved remigrations are performed by what might be called the true navigators. The movement of these individuals away from the feeding pasture is goal oriented, i.e., all their movements are directed toward a specific nesting beach. A return to the same feeding pasture is also implied. One of the highest forms of navigation is portrayed by the adult female who nests on her natal beach. Whether hatchling imprinting to the natal beach could have evolved from the type of conditioning which predisposes an adult to return to the site or vicinity of her previous nesting is polemic, although it does seem reasonable that natural selection could favor the shifting of the nest site conditioning to a hatchling stage. The belief that hatchling imprinting is a viable phenomenon, was the basis for the green turtle restocking project in the Caribbean (Carr, 1967a, 1967b). Although success of this program has yet to be documented, the program does merit further experimentation. In this regard, one might consider the possibility that some turtle populations are composed

mainly of permanent residents and other populations composed chiefly of true navigators. Hence, attention should be given to matching-up donors (eggs or hatchlings) and conditions around transplanting sites. Of course, other factors, such as the number of eggs or hatchlings transplanted, could have an important bearing on their subsequent survival and behavior in the sea.

One of the most remarkable remigration patterns, encompassing a straight-line distance of ~2,000 km, involves the green turtles which feed off Brazil and nest on Ascension Island. This remigration has been discussed in terms of geotectonics (Carr and Coleman, 1974) and olfactory imprinting and a compass sense (Koch et al., 1969; Carr, 1972; Carr and Carr, 1972). In this model, the hatchlings and spent adults drift passively back to Brazil with the South Equatorial Current. The fact that turtles from different subpopulations (including Ascension turtles) may mingle on the feeding pastures off Brazil and yet sort themselves out and swim to widely distant beaches for nesting (Pritchard, 1973, 1976; Carr, 1975; Schulz, 1975) strongly suggests that turtles in at least some of these subpopulations are true navigators.

#### DISCUSSION

One example of a unique remigration but with perhaps simple beginnings is the remigration between the feeding pastures in Somalia and the nesting beaches in the People's Democratic Republic of Yemen (P.D.R.Y.) on the southern coast of the Arabian peninsula (Hirth and Carr, 1970; F.O.A., 1973). In this system, the longest direct distance between site of tagging and recapture is ~2,100 km (based on current tag returns). It is hypothesized that in the pre-Miocene when southern Arabia and northern Somalia were juxtaposed, perhaps along a 100-fathom [~183 meters] bathymetric contour leaving a water gap of 25 to 40 km (Beydoun, 1970), some of the turtles feeding off the horn of Africa nested



on the Somalia mainland and some nested on the nearby coast of the P.D.R.Y., i.e., they were permanent residents. As the Gulf of Aden was formed (commencing in the Miocene) turtles leaving Somalia pastures for Arabian beaches were forced to swim farther. In the late Tertiary, as the Arabian plate moved to the northeast (Laughton, 1966) a turtle swimming generally northward from Ras Asir (Cape Guardafui) on the horn of East Africa would make landfall near some of the best nesting beaches in the P.D.R.Y. Today, this is a straight-line distance of ~380 km. It is conjectured that a unidirectional compass sense like a northward-bearing one was gradually refined as the Arabian and African plates slowly drifted apart. A drift rate of about 2 cm/year since the Miocene has been postulated (Laughton, 1966). After arriving near the Arabian coast, experienced nesters may seek out sites of previous nesting by piloting, or they may swim directly to the nesting site with their compass sense. Spent adults might have taken a back azimuth to return to the feeding pastures when the distance across the Gulf was not too taxing, but now at least some of the spent adults might drift with or even navigate using offshore currents (F.A.O., 1973).

There is year-round nesting on some of the better-known beaches in the P.D.R.Y. Although it is possible that some individuals could drift passively in surface currents all the way from the east coast of Somalia to some of the turtle beaches in the P.D.R.Y. and in Oman during the peak of the southwest monsoon (from July through September), the currents are almost reversed during the peak of the northeast monsoon (December and January) (Wooster et al., 1967), and dispersal mechanisms other than oceanic drift would have to be operating at this time, and probably also during monsoon transition periods. As is the case with other complex patterns, the use of radiotelemetry may be the only way to determine whether the turtles today are true navigators. At least it would seem that, as the Gulf of Aden continues to

widen and turtles swim increasing distances and spend more time in transit, nature would select for precise navigational skills.

If the turtle beaches in Somalia ever become overexploited (and there is some recent evidence of this) we may then eventually see only a remnant of the original pattern, i.e., a population of turtles feeding off Somalia and nesting in the P.D.R.Y.

Because of their strategic position between the feeding pastures in Somalia and the nesting beaches in southern Arabia, the islands of Abd-al-Kuri, Socotra, and The Brothers should be reconnoitered for possible nesting colonies. These islands could be easy landfalls for turtles drifting or wandering out of the pastures on the east coast of Somalia. That green turtles, along with other species, are taken by some of these islanders has been noted by Forbes (1903), Botting (1958) and F.A.O. (1968).

*Acknowledgments.*—I thank my colleagues, Marine Vaughan, Archie Carr and David Ehrenfeld, and an anonymous reviewer for helpful comments during the preparation of this paper.

#### LITERATURE CITED

- BALAZS, G. H. 1976. Green turtle migrations in the Hawaiian Archipelago. *Biol. Conserv.* 9: 125-140.
- BEYDOUN, Z. R. 1970. Southern Arabia and northern Somalia: Comparative geology. *Philos. Trans. Royal Soc. London, Ser. A*, 267:267-292.
- BOOTH, J., AND J. A. PETERS. 1972. Behavioural studies on the green turtle (*Chelonia mydas*) in the sea. *Anim. Behav.* 20:808-812.
- BOTTING, D. 1958. *Island of the Dragon's Blood*. W. Funk Co., New York.
- BRONGERSMA, L. D. 1972. European Atlantic turtles. *Zool. Vehr.* No. 121. E. J. Brill, Leiden.
- BURNETT-HERKES, J. 1974. Returns of green sea turtles (*Chelonia mydas* Linnaeus) tagged at Bermuda. *Biol. Conserv.* 6:307-308.
- BUSTARD, R. 1972. *Sea turtles*. Taplinger Publ. Co., New York.
- . 1976. Turtles of coral reefs and coral islands, p. 343-368. In O. A. Jones and R. Endean [eds.] *Biology and geology of coral reefs*. Vol. 3. Academic Press, New York.
- , AND K. P. TOGNETTI. 1969. Green sea turtles: A discrete simulation of density-dependent population regulation. *Science* 163:939-941.

- CARR, A. 1961. Pacific turtle problem. *Nat. Hist.* 70:64-71.
- . 1965. The navigation of the green turtle. *Sci. Am.* 212:79-86.
- . 1967a. Caribbean green turtle: Imperiled gift of the sea. *Natl. Geogr. Mag.* 131: 876-890.
- . 1967b. So excellent a fish. *Natural History Press*, Garden City, New York.
- . 1972. The case for long-range chemoreceptive piloting in *Chelonia*, p. 469-483. In S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs and R. E. Belleville (eds.) *Animal orientation and navigation*. NASA, SP-262, U.S. Govt. Print. Off., Washington, D.C.
- . 1975. The Ascension Island green turtle colony. *Copeia* 1975:547-555.
- , AND M. H. CARR. 1972. Site fixity in the Caribbean green turtle. *Ecology* 53:425-429.
- CARR, A., AND D. K. CALDWELL. 1956. The ecology and migrations of sea turtles. I. Results of field work in Florida, 1955. *Am. Mus. Novit.* (1793):1-23.
- CARR, A., AND P. J. COLEMAN. 1974. Seafloor spreading theory and the odyssey of the green turtle. *Nature* 249:128-130.
- CORNELIUS, S. E. 1976. Marine turtle nesting activity at Playa Naranjo, Costa Rica. *Brenesia* 8:1-27.
- F.A.O. 1968. Report to the governments of the People's Republic of Southern Yemen, and the Seychelles Islands on the green turtle resource of South Arabia, and the status of the green turtle in the Seychelles Islands. Based on the work of Dr. H. Hirth FAO/TA Marine Turtle Biologist. Rep. FAO/UNDP(TA), (2467):1-59.
- . 1973. Report to the government of the People's Democratic Republic of Yemen on marine turtle management based on the work of H. F. Hirth and S. L. Hollingworth, Marine Turtle Biologists. Rep. FAO/UNDP(TA), (3178):1-51.
- FORBES, H. O. 1903. The natural history of Sokotra and Abd-el-Kuri. Liverpool, The Free Public Museums, Henry Young and Sons, London, R. H. Porter.
- HENDRICKSON, J. R. 1958. The green sea turtle *Chelonia mydas* (Linn.) in Malaya and Sarawak. *Proc. Zool. Soc. London* 130:455-535.
- HIRTH, H. F. 1971. Synopsis of biological data on the green turtle, *Chelonia mydas* (Linnaeus) 1758. FAO Fisheries Synopsis, No. 85, 1:1-8:19.
- , AND A. CARR. 1970. The green turtle in the Gulf of Aden and the Seychelles Islands. *Vehr. K. Ned. Akad. Wet. Afd., Natuurkunde, Tweede Reeks—Deel LVIII*, 5:1-44.
- HUGHES, D. A., AND J. D. RICHARD. 1974. The nesting of the Pacific ridley turtle *Lepidochelys olivacea* on Playa Nancite, Costa Rica. *Mar. Biol.* 24:97-107.
- HUGHES, G. H. 1971. Sea turtle research and conservation in South East Africa, p. 57-67. In *Marine Turtles*, I.U.C.N. Publ. New Series, Supplementary Paper No. 31, Morges, Switzerland.
- KOCH, A. L., A. CARR, AND D. W. EIBENFELD. 1969. The problem of open-sea navigation: The migration of the green turtle to Ascension Island. *J. Theor. Biol.* 22:163-179.
- LAUGHTON, A. S. 1966. The Gulf of Aden. *Philos. Trans. Royal Soc. London, Series A*, 259:150-171.
- MOWBRAY, L. S., AND D. K. CALDWELL. 1958. First record of the ridley turtle from Bermuda, with notes on other sea turtles and the turtle fishery in the islands. *Copeia* 1958:147-148.
- PUTCHARD, P. C. H. 1973. International migrations of South American sea turtles (*Cheloniidae* and *Dermochelyidae*). *Anim. Behav.* 21: 18-27.
- . 1976. Post-nesting movements of marine turtles (*Cheloniidae* and *Dermochelyidae*) tagged in the Guianas. *Copeia* 1976:749-754.
- RICHARD, J. D., AND D. A. HUGHES. 1972. Some observations on sea turtle nesting activity in Costa Rica. *Mar. Biol.* 16:297-309.
- SCHULZ, J. P. 1975. Sea turtles nesting in Surinam. *Nederlandsche Commissie Voor Internationale Natuurbescherming, Mededelingen No. 23*. Stichting Natuurbehoud Suriname (Stinasu) Verhandeling Nr. 3:1-143.
- SIMON, M. H., G. F. ULRICH, AND A. S. PARKES. 1975. The green sea turtle (*Chelonia mydas*): mating, nesting and hatching on a farm. *J. Zool. (London)* 177:411-423.
- WITRAM, P. R. 1976. Evidence for ocean-current mediated dispersal in young green turtles, *Chelonia mydas* (Linnaeus). Master's thesis, Univ. Oklahoma, Norman.
- WOOSTER, W. S., M. B. SCHAEFER, AND M. K. ROBINSON. 1967. Atlas of the Arabian Sea for fishery oceanography. Univ. California Inst. Marine Resources, La Jolla, California.

Received: 22 February 1977

Accepted: 13 May 1977

Department of Biology, University of Utah,  
Salt Lake City, Utah 84112, USA