TRAVELOGUE

The Backdoor Turtles of Tortuguero

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Photographs by the author.

Casa Verde, the weathered, palm-sheltered former field headquarters of the Caribbean Conservation Corporation's venerable Green Turtle research program, and now its modernized successor, the John H. Phipps Biological Field Station, stand squarely between two great biological worlds. To the fore stretches the Caribbean Sea with all its teeming marine life. Its edge here is the black sand beach of Tortuguero, named for the small coastal village adjacent to the station, and the most important sea turtle nesting site in the entire western Caribbean. To the rear lie the rich Costa Rican lowland rainforest and a complex network of freshwater canals, rivers, and swamps threaded through its verdure.

For the biologist, few if any other places on earth offer so many opportunities, the nature of which depends simply upon the door from which one emerges. Archie Carr and the legion of biologists upon whom the reputation of Tortuguero has been built went out the front door to the dark beaches and their droves of nesting Greens and Leatherbacks. Instead, I go out the back to study an equally fascinating but poorly known assemblage of smaller turtles resident in Tortuguero's freshwater and forest habitats. Long ignored and overshadowed by the huge, spectacularly abundant sea turtles, these non-marine species have unobtrusively gone about the business of living without much attention from biologists. However, recent investigations that I have conducted on their ecology have revealed much of interest in these small packages. Their natural history, unique and worthy of record for its own sake, also provides insight into the origin of the Neotropical non-marine turtle fauna and the evolutionary strategies that allow its survival. One of the freshwater species has led me through a proverbial revolving door. In spite of my original intentions to stay in the jungle, it took me back to the beach to observe a critical phase of its life history in the Tortuguero ecosystem.

Studying the turtles of Tortuguero is a singular experience in itself. Cruising the green-walled streams while four-foot iguanas launch themselves from overhanging branches, and parrots, toucans, and howler monkeys scold, gurgle, and roar overhead adds a dimension to turtle trapping that can't be matched in the Temperate Zone. The presence of caimans, Bull Sharks, and stingrays in the rivers, and Jaguars, fer-de-lances, and rov-

Adult male Meso-American Slider (*Trachemys venusta*), with a carapace length of about 40 cm, on the beach at Tortuguero.

A hatchling slider at a nesting site in cocoplum scrub along the beach at Tortuguero.

ing herds of White-lipped Peccaries in the forest also contribute spice to the ambience.

Our efforts to date have yielded data concerning five of the six species inhabiting the Tortuguero area. The rare Narrow-bridged Mud Turtle (*Kinosternon angustipons*) occasionally turns up at Tortuguero, but we have not yet located its apparently rather specialized habitat. The observed species range across the niche spectrum from the almost totally aquatic South American Snapping Turtles (*Chelydra acutirostris*) and Meso-American Sliders (*Trachemys venusta*), which emerge from water only for egg-laying, occasional movement into other aquatic habitats and, in the latter, for sunbathing on emergent logs, to the semiaquatic White-lipped Mud Turtle (*Kinosternon leucostomum*) and Black River Turtle (*Rhinoclemmys funerea*), which spend significant amounts of time both in water and wandering on the forest floor, to the fully terrestrial Brown Wood Turtle (*Rhinoclemmys annulata*), which enters water only to drink or soak in forest puddles.

Besides these more traditional taxonomic and habitat approaches to classifying Tortuguero's turtles, ecological information may help to categorize them according to their respective biogeographic histories. While all of Tortuguero's turtles are certainly tropical in terms of their current geography, their survival here depends upon strikingly different adaptive approaches to coping with the tropical environment. These varying strategies provide clues to their past. From this perspective, two of Tortuguero's turtles seem out of place indeed.

Reproductive patterns are especially diagnostic in this regard. The two mud turtles and the Black River and Brown Wood turtles lay one or only a small clutch of small (mud turtles) to relatively very large eggs (Black River and Brown Wood turtles) on the forest floor, either asynchronously throughout the year or over extended periods during the rainy season. They characteristically make little or no effort to bury the eggs other than scraping a little leaf litter over them before they permanently leave the scene. This reproductive pattern has been observed in small to medium-sized rainforest-dwelling turtles in both the New and Old World tropics and is considered to be indicative of long-term tropical residency — perhaps an adaptive response to the myriad egg and hatchling predators that roam the rainforest floor. Unpredictability in laying time and location discourages predators from ganging up on the turtles' reproductive effort as they can, for example, on the nearby Green Sea Turtle nesting beach.

All the sea turtles, and the world's Temperate Zone freshwater and terrestrial species, practice a very different nesting strategy. These turtles typically lay one or more large clutches of relatively small eggs in carefully constructed subterranean nests that are sealed after egg deposition. Nesting takes place within a distinct season and nests often are concentrated in suitable areas that provide both easy access for nesting females and the proper micro-environment for the developing embryos. As predators often home in on these nesting areas with great efficiency, these species are more likely to survive as a result of their ability to "swamp" predators through their high annual fecundity and the long reproductive life of adult females. The snapping turtles and sliders of Tortuguero reproduce in this typical Temperate Zone pattern.

Tortuguero's crazy-quilt amalgam of species with such divergent nesting strategies is best explained by the relatively recent invasion of the closely related ancestors of the latter two species into the Neotropics from temperate North America. With closure of the Central American isthmus during the Pliocene and the subsequent climatic turmoil of the Pleistocene, the time was ripe for faunal exchanges between the two continents. During drier periods when the forest shrank and rainforest specialists were at a disadvantage, the opportunistic snapping turtles and sliders probably colonized Central and South America. Today, the snappers range as far south as Ecuador and the sliders' range extends into temperate Argentina. During wetter periods, as in the current interglacial, however, these Johnny-come-latelies are apparently at a distinct disadvantage in the re-coalescent rainforest, as their distributions are extremely disjunct through this vast area and their present population sizes often are low compared to the temperate habitats in which they often dominate the turtle fauna. Characteristically, both species are relatively uncommon at Tortuguero. One focus of my work was to determine how these species live at Tortuguero, which, with the exception of the area around the village, is still characterized by primary rainforest as dense as that anywhere in the Neotropics.

Currently, two tropical species in the genus *Chelydra* and as many as nine mainland Latin American species in the genus *Trachemys* are recognized — all very closely related to their Temperate Zone ancestors, the Common Snapping Turtle (*Chelydra serpentina*) and the Slider (*Trachemys scripta*), respectively.

Although little comparative information was available concerning the ecology of snapping turtles in other tropical locations (i.e., limited natural history observations in Chiapas by Miguel Alvarez del Toro and in Colombia by the late Federico Medem are available), the collective data from several studies of sliders in tropical Mexico, Belize, Colombia, Venezuela, and especially Panama indicated a remarkably similar ecology to that of populations in temperate North America. Observed ecological differences in the tropics (e.g., greater size, annual egg production, longer nesting seasons, etc.) were more a matter of degree, largely related to greater opportunities for foraging, growth, and reproduction in the year-long warmth rather than substantive change in lifestyle. While I found essentially the same patterns at Tortuguero, the sliders here were unique in two characteristics that warranted further study. First, they are huge, even by tropical slider standards, with some females attaining carapace lengths of 44 cm and weights up to 10 kg. Second, circumstantial evidence had accumulated that sliders used Caribbean Sea beaches for nesting — a very unslider-like trait, and

A slider nesting track on Tortuguero Beach.

An adult South American Snapping Turtle (*Chelydra acutirostris*) at Tortuguero

known in only a handful of other non-marine turtles. Turtle biologist Peter Pritchard had previously observed that non-marine turtle tracks observed on Tortuguero beaches were always those of adult slider females (which are much larger than males) and that the discarded carcasses of sliders that had been collected on beaches for food by Tortuguero residents were also adult females. These observations suggested that beached sliders were not just waifs washed out of the Tortuguero Estuary during flood periods. In addition, in June 1989, Jim Spotila, Tom Yocky, and I were searching for Leatherback nests along Tortuguero Beach when we encountered a small strange track that we followed to a single slider hatchling on the lower beach near the surf line. We backtracked it to its probable nesting site in the cocoplum scrub of the upper beach berm. These observations intrigued me, and I resolved to study the ecology of sea-beach nesting and its adaptive significance for sliders in the Tortuguero ecosystem. I was particularly interested in why, of all the slider populations across the vast range of these species, sea-beach nesting had evolved only here, and whether the huge size characteristic of Tortuguero females was somehow linked to this phenomenon.

Peter Pritchard, who has thought about most things "turtle" at some time or another, had previously suggested that beach nesting was probably a response to the need for open nesting sites, always in short supply in virgin rainforest, and that large size provided physiological advantages during the period of sea travel required to reach appropriate nesting sites. A study of the ecology of Panamanian sliders by my brother Edward Moll and John Legler in the 1960s had established that golf courses, plantations, and other more open sites were used to the exclusion of rainforest for nesting in their

Snapper habitat near Tortuguero.

Canal Zone study area, so this first idea made sense. As all sea turtles and those other freshwater species known to venture into the sea, such as the Asian river terrapins and Asiatic Giant and Nile softshells, are very large animals by turtle standards, the association of large size and seaworthiness also held merit. My sabbatical leave from teaching responsibilities during a spring semester several years ago allowed me the freedom to walk the Tortuguero beaches from January through March, the peak of the slider nesting season, to acquire more information.

Fringed by Coconut Palm and Seagrape, the black sand beach of Tortuguero extends unbroken for 35 km from the Tortuguero Canal Estuary in the north to the Parismina River Estuary in the south. Always beautiful, it nevertheless can be a difficult place to work. By day, it quickly became lethally hot, with sand surface temperatures approaching 70 °C. Upon returning from early morning surveys, I usually entered the cool gloom of the adjacent forest for a respite — often entertained by wing-snapping mating displays of White-collared Manakins and slowly foraging troops of Black Howler Monkeys in the tree tops. On moonless nights, the beach could be so black as to lose its features altogether, and I was regularly upended by beach litter and by stepping off newly wave-cut benches that changed position nightly — but, if there were hardships, they were more than offset by the lure of discovery and the beauty of the wild tropical beach. One bright moonlit night, for example, I sat watching a nesting

Eggs excavated from a snapper nest near Tortuguero.

slider in the cocoplum scrub while an early-season Leatherback, spangled with phosphorescence and moonglow, hauled out of the surf to nest just thirty meters down the beach. On another night, as I returned to Casa Verde after reaching the southern terminus of my survey route, I noticed Jaguar tracks paralleling my own footprints for more than three kilometers. It was a big animal, apparently watching me curiously (I prefer not to think hungrily) from the darkness as I trekked down the beach. Without doubt, experiences such as these were the "adventures of a naturalist on remote Caribbean shores" that Archie Carr had in mind when he wrote *The Windward Road* nearly 50 years earlier.

Gradually, through observation and radiotelemetric monitoring of sliders in the rivers, in the sea, and on the beach, a characteristically clockwise, albeit variable, nesting pattern emerged. Sliders generally moved north with river currents into the sea via the Tortuguero Estuary or by crossing a narrow strip of land that separated the river from the sea north of Tortuguero Village. They then moved south in the longshore current just beyond the surf line until they hauled up to nest in the cocoplum scrub of the upper beach a few kilometers south of the village in Tortuguero National Park. Spent females would usually return to the sea, moving down-coast for a brief period before emerging again to trek overland across

Brown Wood Turtles (*Rhinoclemmys annulata*) are fully terrestrial.

Brown Wood Turtle habitat in secondary growth near Tortuguero.

the peninsula to the Tortuguero Canal. Once in the canal, they moved north again with the current to suitable feeding and basking areas. The pattern conserved energy by utilizing the prevailing canal and sea currents, and got the turtles to the appropriate nesting sites with little time spent on land, an important point that I'll address below. The upper beach cocoplum scrub nesting sites provided a moderate thermal environment for egg development well away from the highest tides, as well as protective cover for the laying female and emerging hatchlings. Sliders, like most turtles, have temperature-dependent sex determination, in which warmer nests or nest depths produce females and cooler sites males. Substrate-temperature monitoring indicated that open beach temperatures were too hot and probably lethal to developing eggs while forest soils were root strewn, soggy, and probably too cool for adequate female production. The cocoplum, however, provided few obstructions, proper drainage, and the right thermal regime for the production of both sexes. The latter probably results from a combination of single-sex and mixed-sex nests scattered through the cocoplum scrub. Due to the relative proximity of these suitable beach nesting sites to freshwater habitats, a straight-line distance of a kilometer or less of forested peninsula in between, the sliders can survive at Tortuguero. Without it, as is often the case in more inland rainforests, they probably cannot, and are therefore usually absent from the rainforest turtle fauna.

The question remains, however, why the female sliders simply don't walk across the peninsula to deposit their eggs on the beach? Sliders are fully capable of walking a kilometer or more to lay eggs or moving from pond to pond in temperate habitats. Why is it better to risk travel over a substantially longer distance by sea in a physiologically difficult environment with a formidable set of predators in order to reach the beach nest site? The answer may be linked to both the size of the Tortuguero sliders and to the vulnerability of their relatively small eggs to a diverse array of terrestrial predators. I think sliders here have resorted to sea travel to avoid leading terrestrial predators to their nest sites. This could occur if predators followed a female wandering overland to the nesting site (or her scent trail) or back-trailed her to the site as she moved directly toward the canal through the forest after nesting. From this perspective, both the long sea travel phase in reaching the nest site and the return to the sea after nesting for a brief period before down-coast emergence and overland movement to the canal make sense. I also think that great size has evolved as a consequence of the sea-travel phase. While it may well confer osmoregulatory advantages by lowering the body-surface-to-mass ratio, work by Bill Dunson of Pennsylvania State University has shown that even smaller turtles have a relatively low rate of sodium influx. I think the large size here has evolved principally to provide the sea-going females with insurance against the predation risks that have been increased by their relatively long nesting migrations and en-route exposure to marine predators. The occasional mutilated carcasses of slider females I've observed washed up on the beach underscore the reality of the dangers. Whit Gibbons has advanced the general hypothesis that large size would confer an advantage in reducing predatory and environmental risks to turtles that must travel from the relative safety of their aquatic home

White-lipped Mud Turtle (*Kinosternon leucostomum*) from Tortuguero.

White-lipped Mud Turtle habitat at Tortuguero.

Black River Turtles (*Rhinoclemmys funerea*) spend time both in water and wandering on the forest floor.

range for nesting or other reasons. A side benefit of decreased travel risks would be that more time could be expended and more distance traveled in seeking the most optimal nesting sites available. If strong selection reduces terrestrial travel to minimize egg predation, then travel time in the sea must increase accordingly. The evolution of gigantism at Tortuguero is probably a response to these factors.

If the beaches provide the relatively open sites necessary for slider nesting, I wondered what sites might be used for nesting by resident snapping turtles. My studies of their ecology at Tortuguero indicated no substantive changes from the ecology of temperate populations. They were surviving at Tortuguero by living their usual generalist lifestyle characterized by habitat flexibility and omnivory. Reproductive studies by Ron Brooks in Ontario and Justin Congdon in Michigan indicated that northern snappers, like sliders, require relatively open nesting sites. I suspected that they would need such nesting sites at Tortuguero as well, but I never encountered any on the sea beaches during my slider surveys. By accident, however, I stumbled across a nesting snapper early one February morning on an abandoned milpa, an area cleared and planted for one or more years, then abandoned and allowed to return to forest. These areas remain relatively unshaded for several seasons and provide a key habitat for the survival of Tortuguero's snappers. By focusing my search in these areas adjacent to caños (small streams), I was able to discover several additional snapper nests over an extended period of the spring dry season. These were essentially identical in form and egg characteristics to temperate nests. At Tortuguero, a loose sort of mutualism existed between humans and snappers where the big Tortugas Lagartos ("Alligator Turtles") occasionally were caught for food by local residents, and, in turn, were provided with nest sites via milpa agriculture. Perhaps snapper survival in the modern Neotropics is dependent upon such human activities elsewhere in rainforested areas as well. Tree falls near waterways may provide similar nesting opportunities by letting more sunlight reach the ground, but I never encountered any nesting snappers in natural forest openings at Tortuguero.

I think of the sliders and snappers of the Neotropics as the "Beverly Hillbillies" of the turtle world — true misfits, but gamely trying to make a go of it in an alien culture. The collective ecological evidence from Tortuguero and elsewhere indicates that they have not yet blended into the rainforest community during their brief residence here. Their generalized ecology and need for non-forested nesting sites clearly evolved to cope with a different environment far from their current home. The other turtles here have become highly adapted for life in the rainforest. Reproducing and regularly foraging on the forest floor and even, as our research indicates, being involved in symbiotic seed-dispersing relationships with many local plants, these species have truly become part of the fabric of the rainforest ecosystem. In contrast, the newcomers have extended their characteristic flexibility to the extreme to survive here in spite of the all-encompassing forest. By using such tricks as beach and milpa nesting they have managed to hang on, barely, by the skin of their jaws, as the forest has reclaimed its former domain during these wetter times since the last ice age. From this perspective, the sliders and the snappers of the Neotropics may be among the few species to benefit from the continued destruction of the rainforest.

Tortuguero Beach.

The Tortuguero River provided slider and Black River Turtle habitat.