

The Ecology of Sea Beach Nesting in Slider Turtles (*Trachemys scripta venusta*) from Caribbean Costa Rica

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ABSTRACT.—Freshwater slider turtles, *Trachemys scripta venusta* (Cryptodira: Emydidae), enter the sea and nest nocturnally on Caribbean Sea beaches from January to March near Tortuguero, Costa Rica. Nesting behavior and reproductive biology is similar to that of other slider populations except for larger egg size, clutch size, and nest dimensions, which in turn are probably influenced by the greater size of Tortuguero females. Nesting females reach the sea from adjacent lotic habitat by crossing an intervening peninsula, swimming into the sea via the Tortuguero Estuary, or walking onto the beach from an adjoining brackish lagoon. Males reside permanently in freshwater habitats where aquatic vegetation and basking sites are present. Females at sea drift-swim southward with the longshore current before hauling up on the sea beach to nest. Nests are constructed on the upper beach berm usually under cocoplum vegetation. Berm nests have a sufficient vertical temperature gradient to produce male and female offspring. Open beach and forested areas are not used for nesting. Spent females move back across the peninsula to freshwater either directly after nesting or after re-entering the sea for a limited time. Tortuguero sliders typically display a clockwise pattern of nesting cycle movement which conserves energy during nesting activity by utilizing prevailing freshwater and sea currents to reach nesting sites. The marine phase of the cycle may minimize predation opportunities of slider adults and eggs by Tortuguero's terrestrial predators but exposes females to marine predators and physiological stresses. The extraordinary size attained by Tortuguero slider females may be an evolutionary response to minimize these nesting-associated risks. Hatchlings emerge by May and June. They probably do not enter the sea but gradually move overland into peninsular swamps and to the Tortuguero waterways in which adults reside.

While sea beaches and associated banks and dunes are the normal nesting sites for marine turtles (Ernst and Barbour, 1989) and the diamondback terrapin, *Malaclemys terrapin*, a dweller of coastal halohygic habitats, regularly uses barrier beaches and dunes, and occasionally more disturbed coastal habitats as nest sites (Reid, 1955; Burger and Montevecchi, 1975; Seigel, 1980), only a few examples of regular use of similar habitats for oviposition by other turtle species are known. Two large Asian riverine-estuarine species, the river terrapin, *Batagur baska*, and the painted terrapin, *Callagur borneoensis*, nest on islands and coastal beaches. Maxwell (1911) recorded river terrapin nesting on beaches in Burma's Irawaddy River delta and Moll (1990) reported that some nesting may still occur on island beaches within the Sunderbans of India and Bangladesh. The painted terrapin is mainly a sea beach nester in West Malaysia (Moll, 1980). Its nesting behavior and hatchling and reproductive ecology on South China Sea beaches have been described in a series of reports and papers by Moll and colleagues (Moll, undated, 1980; Dunson and Moll, 1980; Tow and Moll, 1981). *Pelochelys bibroni*, the giant Asian softshell is another freshwater species which may spend considerable time at sea and which apparently uses sea beaches as nesting sites (Rhodin et al., 1993). Similarly, another giant trionychid, *Trionyx triunguis*, is known from the eastern Mediterranean Sea and is common enough off the Turkish coast to be considered a pest by local fishermen (Pritchard, 1979). These softshells are known to nest on the margins of lakes near the mouth of a river that opens to the sea near Dalaman (Atatür, 1979). The pig-nosed turtle, *Carettochelys insculpta*,

will also use coastal beaches in New Guinea as nest sites (Georges and Rose, 1993). Other large riverine and estuarine species may also nest on island and sea beaches in deltas and near river mouths.

Evidence had begun to accumulate by 1984 that the slider, *Trachemys scripta venusta*, a large, relatively uncommon lotic species in Caribbean Costa Rica, was nesting on Caribbean sea beaches in the Tortuguero vicinity. Pritchard and Trebbau (1984) noted non-marine turtle tracks on beaches and discarded carcasses of individuals which had been collected on beaches for food by residents were always adult female sliders. On 25 June 1989 at 1730 hours, J. Spotila, T. Yocky and I encountered a hatchling *T. scripta* walking parallel to the surfline on the lower beach at milepost 2 2/8 on Tortuguero Beach. The hatchling's tracks led diagonally back to the cocoplum scrub on the upper beach. On 4 June 1990, M. Piedl (*pers. comm.*) extracted a slider hatchling from the grasp of a crab in its hole on the edge of the upper beach vegetation zone in front of the Green Turtle Research Station (milepost 6/8) on Tortuguero Beach. Pritchard and Trebbau (1984) and Moll and Moll (1990) discussed the adaptive significance of beach nesting by this species in this single area of its vast range in which sea beach nesting was thought to occur, and the probable selective forces behind its development here.

These observations and interest in the factors which may influence the development of this unique phenomenon led me to initiate an investigation of the ecology of Caribbean Sea beach nesting by Costa Rican *T. scripta*. My objectives were: 1) to verify and describe the nesting phe-



Figure 1. Location of the Tortuguero study area in Costa Rica.

nomenon from direct observation; 2) to obtain basic information concerning the reproductive biology of slider females and egg characteristics for comparison with data from other slider populations; 3) to obtain information concerning the timing, related movements and location of nesting activity; and 4) to gather data concerning the ecology of hatchlings which emerge from sea beach nests.

STUDY AREA

The research was conducted from the Caribbean Conservation Corporation's Green Turtle Research Station near the village of Tortuguero on Costa Rica's northeastern Caribbean coast ($10^{\circ}34'N$; $83^{\circ}32'W$) (Fig. 1). The region is characterized by very wet tropical forest and a mean annual temperature of at least $24^{\circ}C$ (Holdridge 1947, 1959). Hirth (1963a) provided a detailed account of the climate and physical environment at Tortuguero. Two wet and two dry periods occur each year (Carr et al., 1978). Hirth recorded 59.1% of total annual precipitation in December, January, July, and August and found the driest months to be September, October, March, and April. No month received less than 50 mm of rain.

The study area generally referred to as "Tortuguero" in this paper describes the region bordered on the north by the Tortuguero Estuary or Boca, which opens to the sea about 5 km north of Tortuguero Village (Fig. 1). The interior waterway producing the estuary is formed by the confluence of the Tortuguero, Suerte, and Sierpe Rivers and drains a watershed of swamp and rain forest extending inland for about 40 km (Carr et al., 1978). The southern border of the study area

is the Parismina (Reventazon) Estuary, produced by one of the major streams of the coastal plain and located about 35 km south of the Tortuguero Boca. Most of this area is encompassed by Tortuguero National Park. The configuration of the area is such that the fresh to somewhat brackish inland waterways are separated from the Caribbean Sea by a narrow (usually 1 km or less in width) forested peninsula (Fig. 2). A sea beach extends unbroken along the seaward reach of the peninsula, except occasionally at Laguna Jalova, an evanescent boca about 6.4 km north of Parismina Village (Fig. 2) (Hirth and Ogren, 1987). Fowler (1979) described four beach zones. Zone 1 is the seaward, surf-washed section. Zone 2 is the unvegetated beach section from the high tide mark to the sparsely vegetated middle beach. Zone 3 is the middle beach up to the forest edge. Zone 4 begins at the beach vegetation border and extends into forest.

Typical beach vegetation within the study area has been described by Hirth (1963a), Hirth and Ogren (1987), and List and Robles (1991). Much of the beach has been marked in 1/8 mile sections, beginning at the Tortuguero Boca, by sea turtle workers for nest-site fixity studies and are referred to here to fix locations in this study as well. Mile 0 is currently about 1/8 mile south of the current Boca position due to the northward extension of the Tortuguero Bar subsequent to milepost placement.

On the sea side is a breaker zone with low to moderate tidal influence. Close inshore a southeast trending longshore current is present which often can be seen bearing rafts of water hyacinth and other vegetation along the coastline (Carr et al., 1978).

METHODS AND MATERIALS

Fieldwork was conducted in Costa Rica from 1989 to 1992. Most information concerning slider nesting behavior and nest characteristics was obtained from January through March, 1991, but shorter field periods in May and June of other years provided additional data.

Sliders were collected in freshwater habitats by trammel netting, snorkeling, hand-collecting, and by baited hoop traps. The sex of all sliders was determined and they were measured, weighed, and individually marked by shell notching (Cagle, 1939). One nest survey of the entire 35 km beach between the Tortuguero Estuary and the Río Parismina Estuary was conducted on 18 February and two beach surveys in the Laguna Jalova area were conducted on 14 and 20 February. Nest data and nesting females were obtained from these sea beach surveys and from regular surveys conducted from the estuary of the Tortuguero Canal to milepost 7 within Tortuguero National Park. Surveys were typically conducted once per day, commencing just after dawn or after dark on alternate days. Surveys continued until the transect could be completely covered. Females encountered, usually discovered by presence of tracks on the beach, were allowed to complete the nesting process. The direction of their movement away from the nest site was recorded before additional data were collected. Environmental condi-

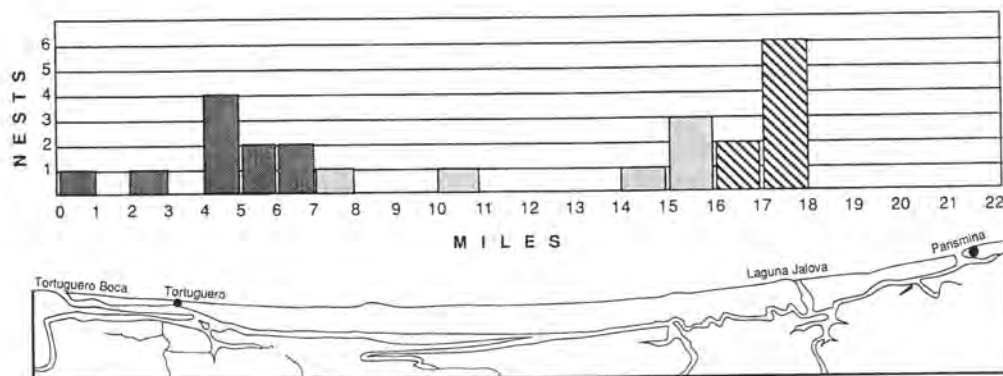


Figure 2. Number and location of slider nests encountered during January-March 1991 beach surveys in the Tortuguero study area. Darker stippled bars represent nests in main northern study area. Lighter stippled bars represent nests encountered on 18 February 1991 survey of entire beach. Diagonally striped bars represent nests in southern Laguna Jalova study area.

tions were recorded. All nests were temporarily marked with a stake to allow later observations concerning nest and egg characteristics. Eggs were reburied and an array of standardized 24 gauge Cu-Cn thermocouples were buried at depths of 0, 50, 100, 150, 205 (mean nest depth), and 230 mm (maximum nest depth) within five slider nests for determination of thermal profiles and fluctuation in the nests (all nests were in shaded locations of Fowler's zone 3). Two similarly positioned thermocouple arrays were buried in the unshaded middle beach zone (Fowler's zone 2) and in the forest (Fowler's zone 4) for comparison. Temperatures were recorded with a BAT 12 thermocouple meter from Bailey Instrument Co. (technique adapted from Spotila et al., 1987).

Five sliders captured in freshwater habitats and two nesting females were affixed with one stage, 1" x 1/4", 7.5-8g transmitters coated with dental acrylic and powered by 1.4V mercury batteries from L&L Electronics, Mahomet, Illinois. Their subsequent movements were monitored on an AVM Model 12 receiver using a hand-held M-Yagi directional antenna or miniature loop antenna for closer work.

RESULTS AND DISCUSSION

Reproductive Characteristics

A total of 24 slider nests were located during the January-March study period in 1991 (Fig. 2). Six of these were located during a survey of the entire 35 km beach between the Tortuguero Canal and Río Parismina estuaries on 18 February; five of these were only cursorily examined. Detailed data were collected from 18 nests and five nesting females encountered within my main northern (Tortuguero Estuary to milepost 7) and southern (Laguna Jalova vicinity, miles 16 and 17) study areas, and from one of the nests (at milepost 7) encountered during my 18 February survey. One other old nest (and two hatchlings) was found near milepost 4 1/8 on 14 June 1990.

Except for their sea beach locations, the nests and other reproductive characteristics of Caribbean Costa Rican sliders are similar to those of other populations which have been studied (Moll and Moll, 1990; Table 1). Most differing characteristics probably result from the greater size of

Tortuguero sliders. Although some temperate emydids of the *Trachemys/Pseudemys* complex such as *Pseudemys concinna suwanniensis* and *Pseudemys nelsoni* may equal or exceed the size of tropical sliders (Pritchard, 1980), the latter, with some exceptions, tend to reach larger mean and maximum sizes than temperate sliders (Pritchard and Trebbau, 1984; Moll and Moll, 1990). Tortuguero's sliders are extremely large even by tropical standards, although *T. s. grayi* may grow as large or larger (Alvarez del Toro, 1982; Obst, 1985) (Table 2; Fig. 3). Nests of Costa Rican sliders are typically flask shaped but are deeper and wider than in other populations (Moll and Moll, 1990) (Table 1). The eggs are larger and more numerous per clutch than in other populations, and the mean egg mass index of 0.41 (egg mass divided by the mass of the spent female x 100) (EMI) corresponds with a typical slider pattern indicating less energy investment per egg correlated with increasing adult female mass (Moll and Moll, 1990) (Table 1). The significance of the relative clutch mass (clutch mass divided by mass of the spent female) (RCM) value of 0.14 is as obscure as it is in other populations (Moll and Moll, 1990) (Table 1). As sliders were not killed for reproductive tract analysis, and no marked or radio-affixed females were encountered at subsequent nestings, the clutch frequency could not be determined. An indication of the capacity for multiple clutches



Figure 3. Adult female slider, *Trachemys scripta venusta*, from Tortuguero, Costa Rica (380 mm carapace length).

Table 1. Reproductive data concerning Tortuguero sliders with available data from other tropical sliders provided for comparison (adapted from Moll and Moll, 1990).

Location - Subspecies	Eggs per clutch \bar{x} =mean (range)	Clutches per year	Egg Characteristics \bar{x} =mean (sizes in mm)	Nest Characteristics	EMI/ RCM	Incub. period (days)	Nesting Season
Tortuguero, Costa Rica <i>T. s. venusta</i>	\bar{x} =20 (12-32)	unknown; prob. multiple	\bar{x} = 29.5 x 45.0	Flask shaped, sea beach location, mean size (mm): 205 deep x 112 wide at top x 142 wide at base	.41/.14	unkn.	at least Jan-Mar probably longer
Pacific coast of Isthmus of Tehuantepec, Mexico <i>T. s. grayi</i>	(16-18)	--	Oblong, oval 16 x 45	--	--	--	Mar
Atlantic drainage, Chiapas, Mexico <i>T. s. venusta</i>	(12-20)	--	Elongate 25 x 40	Communal, flask-shaped, 200 mm deep	--	--	Jan-Apr
Pacific drainage, Chiapas <i>T. s. grayi</i>	(10-20)	--	--	On beaches of rivers and lakes	--	90	Feb-Apr
Atlantic drainage, Chiapas <i>T. s. venusta</i>	(5-21)	(1-3)	--	--	--	--	Feb-May
Corozal district, Belize <i>T. s. venusta</i>	(8-20)	(2-3)	Oblong, leathery, flexible 28 x 41	Flask-shaped cavity in fields	--	--	Feb-May
Lake Nicaragua, Nicaragua <i>T. s. emolli</i>	\bar{x} =20 (15-25)	--	--	--	--	--	--
Rio Chagres, Panama Canal Zone <i>T. s. venusta</i>	\bar{x} =17 (9-25)	(1-6)	Oblong, leathery, flexible \bar{x} = 42.2 x 28.8	Communal, sealed, flask-shaped	.49/.10	(71-86)	Dec-May
Department of Choco, Colombia subspecies unclear, possibly <i>T. s. venusta</i>	(12-24)	--	--	--	--	--	--
Northwestern Venezuela and northern Colombia <i>T. s. callirostris</i>	(9-30)	(2-3)	Oblong, soft- shelled, flexible 21 x 27 to 26 x 41	Flask-shaped, max. size (mm): 180 deep x 110 wide at top x 130 wide at base	--	(69-92)	Colombia: Dec-Apr, perhaps 2nd seas. in Aug; Venezuela: Apr-June prim. seas.
Northern Venezuela <i>T. s. chichiriviche</i>	(11-28)	--	--	--	--	--	--

was provided by a dead 40 cm CL female which washed up on the beach near the Tortuguero Estuary on 1 February 1990. She contained a set of 15 oviducal eggs and 32 corpora lutea in two distinct size classes in addition to a set of 15 enlarged follicles. These data suggest that at least two and possibly three clutches of eggs could have been laid during the 1991 season by this female.

Beach Nest Location and Access

Nests were always located on gently sloping beach sections behind low dunes in vegetation-shaded areas of the upper beach berm (Fowler's zone 3). The nests were usually located under the spreading cover of cocoplum, *Chrysobalanus icaco* (Fig. 4), but occasionally were associated with other vegetation of the upper beach. Cocoplum provided ideal nesting cover as it served to camouflage nesting females, nest sites, and emerging hatchlings from predators while providing shade for nests without obstructive root entanglements. Although apparently suitable habitat for nesting occurred along nearly the entire 35 km beach between Tortuguero Boca and Parismina Boca, most nests

were concentrated near the northern and southern sections and only one nest was located in the central section of Tortuguero National Park (Fig. 2).

Nest Temperature Characteristics

Temperature profiles at various depths in five slider nests in cocoplum shaded sites were monitored and compared with a temperature profile of similar depths in a section of dark colored open beach near one of the nests, and within the forest (Table 3). Mean and extreme high temperatures recorded were higher at similar depths from the open beach site than in the five nests, and lower within the forest site. Daytime surface and near-surface temperatures in unshaded beach sites can rise rapidly in a short time and reach surface temperatures as much as 30°C higher than those recorded at nest sites.

Slider nests were never found in unshaded open beach locations. It is doubtful whether slider eggs could survive nest temperatures which change so drastically and may approach 73°C near the surface (Hirth, 1963a). Temperatures at all depths in the unshaded beach site never dropped



Figure 4. Beach profile of Tortuguero Beach. Sliders nest in the cocoplum scrub of the upper beach shown on the right of the photograph.

below the threshold temperature of 29°C Vogt (1990) established for production of males in tropical Mexican sliders and never rose above it in the forest site. Spotila et al. (1987) also found that mid-beach green turtles' nest temperatures (50–70 cm depth) seldom dropped below 29°C but unlike the shallower slider nests in shaded areas the deeper green turtle nests in these areas remained well below 29°C at all times. If Vogt's (1990) Mexican temperature-dependent sex determination (TSD) standards hold for Costa Rican sliders, as seems likely (Bull et al., 1982), then only the temperature gradient observed in cocoplum shaded nest sites of Fowler's zone 3 would be adequate for production of both sexes (Table 3).

Nesting Macrohabitat and Microhabitat Selection

There seem to be compelling reasons responsible for the development of the unusual nesting macrohabitat (sea beach) and microhabitat (cocoplum) selection by Tortuguero sliders. As Pritchard and Trebbau (1984) and Moll and Moll (1990) have discussed, tropical sliders are normally absent from unbroken rain forest since densely forested shorelines do not offer suitable open areas for nesting. Moll and Legler (1971) discussed some possible reasons for the forest's unsuitability as slider nesting habitat and my substrate temperature data taken from the forest suggest that female production could be a problem for a TSD species. Other thriving populations which do exist in rain forest areas, such as the Panamanian population studied by Moll and Legler (1971) and another in the Río Chucunaque of Panama's Darién noted by Breder (1946), depend for nesting completely upon disturbed areas such as golf courses, plantations, and other areas denuded of dense overstory vegetation. A few cases of sliders nesting on open, human-altered habitats have also been reported at Tortuguero (A. Gutierrez, *pers. comm.*). The nesting sites of a low density population of *T. s. chichiriviche* in forested areas of Venezuela's Río Yaracuy are not currently known (Pritchard and Trebbau, 1984). Coastal Costa Rican sliders were able to survive in the region's pre-settlement unbroken rainforest by migrating to

proximate Caribbean Sea beaches for nesting. Here, optimal circumstances for the development of this phenomenon are present with freshwater non-nesting habitats separated from sea beaches by relatively narrow intervals of terrestrial rain forest of one km or less. Morreale et al. (1984), Parker (1984), and Morreale and Gibbons (1986) have shown sliders to be capable of overland movement of this and considerably greater extent.

The cocoplum's protective cover for both nesting adults and emerging hatchlings, its spreading nature well beyond its root clumps, its ubiquity along the upper beach berm away from influence of the highest tides, its proximity to the protective coral and forest behind, and its relatively moderate thermal regime all contribute to its importance as nesting habitat. In most turtle TSD studies conducted to date, nest placement in microhabitats which vary from shaded areas to open beach has been shown to produce only a few mixed sex nests along with a majority of unisexual nests (e.g., Vogt and Bull, 1984; Bull, 1985; Mrosovsky et al., 1984; Schwarzkopf and Brooks, 1987; Maxwell et al., 1988; Mrosovsky and Provancha, 1989; Janzen, *In press*). At Tortuguero, where both forest and open beach are apparently totally unsuitable for nesting by sliders, the development of both sexes in cocoplum shaded beach nests (whether scattered unisexual



Figure 5. Movement patterns of two radio-tracked slider females. Dotted line-arrows and numbered circles A-E represent direction of movement and important stages in the nesting sequence of a gravid female. "A" indicates position of slider nonreproductive habitat in which female was collected and affixed with transmitter; "B" is point of entry into the Caribbean Sea; "C" is nesting location on Tortuguero Beach; "D" is point of return of female into the Tortuguero waterway; and "E" is the position from which the last radio-signals were received. Dashed line-arrows and numbered circles F-G represent direction of movement of a spent female radio-tagged immediately after nesting at "F"; "G" is location at which the female left the sea and began moving across the peninsula; and "H" is the location in the Tortuguero waterway from which the last signals were received (see text for more detail).

Table 2. Comparative carapace lengths (CL) in males (M), females (F), and hatchlings (H) in selected tropical *Trachemys scripta* populations. Tortuguero sample size N = 68. Data from present study, P.C.H. Pritchard, *pers. comm.*, and Moll and Moll, 1990.

Subspecies	Location	Record CL (mm)	Normal CL (mm)
<i>T. s. venusta</i>	Tortuguero, Costa Rica	350.1 M, 440.2 F	279.1 M, 377.9 F, 41.8 H (means)
<i>T. s. venusta</i>	Belize	332 M, 345 F	180.6 M, 292.2 F, 36.0 H (means)
<i>T. s. venusta</i>	Panama	342 M, 352 F	est. 175 M, est. 260 F, 37 H
<i>T. s. callirostris</i>	Colombia	252 M, 300 F	150-200 M, 190-240 F, ---
<i>T. s. chichiriviche</i>	Venezuela	---	195-325 (M,F), ---

or mixed sex or both) is necessary. My nest temperature data suggest the possibility that these nest environments could produce mixed sex nests, a pattern which has also been found to be prevalent in green turtles (*Chelonia mydas*) at Tortuguero (Spotila et al., 1987) and in Surinam (Mrosovsky et al., 1984). Janzen (In press) suggested that assessment of vegetational cover at potential nest sites may allow Illinois *Chrysemys picta* to choose the thermal environment of nests, hence the sex ratio of the offspring. A similar capability could be present in Tortuguero's beach nesting sliders.

Slider Track Patterns

Based upon observations of tracks and data from two transmitter-affixed females, nesting sliders may reach their nest sites and leave them in various ways. Most nest sites (54.2%) were reached by females which emerged from the sea, moved more or less directly to the cocoplum scrub to oviposit, then returned to the sea after nesting. This nesting pattern produced a two-way track typical of nesting marine turtles. At Laguna Jalova sites where the inland brackish lagoon and marsh were adjacent to the beach (Fig. 2), six females (25%) moved onto the beach from the rear lagoon side and returned directly to the lagoon after nesting. Other two-way track patterns were occasionally observed in which tracks led to and from nests which had been abandoned before oviposition occurred and those which formed "half moons" in which emergence onto the beach and return to the sea occurred without sign of nesting activity. One-way track patterns to and from nests were also encountered. Three females (12.5%) moved from the sea to the nest site without returning to the sea (at least directly) and two other females (8.3%) apparently moved into the sea directly after nesting but left no ingress track to indicate their route to the nest site. Other one-way track patterns not associated with nesting activity (both from the sea to the scrub and vice-versa) were frequently encountered along the 35 km beach. Within the northern study area 12 one-way track sets from the scrub into the sea were observed with 75% located between the Tortuguero Canal Estuary and milepost 4. In addition, two female sliders were observed moving from the cocoplum scrub onto the beach and into the sea on February 12 and 17 respectively. There was no sign of nesting activity by either and one examined closely was determined to be gravid, indicating nesting had not occurred. The first individual was observed through binoculars from about 0.2 km distance as it emerged near milepost 7/8 at 0545 hrs. The second

(gravid) 42 cm CL female was caught at 0715 hrs near milepost 2 3/8 as she entered the surf. She had been collected and marked previously in the Penitencia Canal on 8 June 1990. Another 10 one-way track sets leading from the sea into scrub were observed with 80% located between milepost 4 and 7. Telemetry data from two radio-affixed females indicated that from the sea one-way track sets (both associated with nests and without) may be explained by movement of some individuals across the intervening forested peninsula into the Tortuguero Canal.

Since nests were located by tracks left in beach sand the possibility of missing nests in cocoplum scrub or elsewhere which had been reached and left by passage through the forest cannot be excluded. I received reliable reports of female sliders moving overland on the grounds of the Green Turtle Research Station in 1990 (D. Pennick, *pers. comm.*) and of a slider nest located on a farm adjacent to the Tortuguero Canal's west side, well away from the sea beach (A. Gutierrez, *pers. comm.*).

Sliders and slider tracks are occasionally reported on Tortuguero sea beaches by sea turtle workers and residents during the summer and other times of the year. I observed adult slider tracks on Jalova Beach on 29 June 1989. Sliders also have been seen on sea beaches at Corcovado National Park on Costa Rica's Pacific Coast (by R. Kiester and D. Norman) and in El Salvador (D. Norman, *pers. comm.*). The sexes of these individuals or reasons for their presence on these beaches are not known. Some freshwater turtles undoubtedly are washed out of river mouths during flood periods. At Tortuguero, river-dwelling *Rhinoclemmys funerea* have been sighted drifting toward the estuary in mats of water hyacinth and two were found alive on the sea beach in 1992 (Jansen, 1993). Some slider sightings on beaches could be explained similarly or could be the result of a more extended nesting season and greater geographic extent for sea beach nesting than currently documented.

Telemetry Results

Three gravid females, two spent females which had recently nested, and two adult males were affixed with transmitters. The gravid females and males were captured, fitted with transmitters, and released at the capture site near basking sites and emergent and submergent vegetation beds used for feeding in the lower Penitencia Canal near its convergence with the Tortuguero Canal (see position "A" in Fig. 5). Two of the gravid females and the two males

monitored remained in the vicinity of the plant beds for as long as four weeks after tagging. Their signals were monitored at least twice each day until they were lost (whether by transmitter failure or movement out of range of the receiver is unknown). The third gravid female moved from the plant beds in the Penitencia Canal on 28 February and reached the sea beach nesting site 3 March via canal and sea travel (Fig. 5). After nesting it moved inland across the forested peninsula and into the Tortuguero Canal. The signal was received for the last time at the southern end of Isla Cuatro Esquinas on 4 March (Fig. 5).

Both spent females monitored moved into the sea perpendicular to the beach, swimming through light surf about 300 m before turning southward and moving within the longshore current on 30 January and 15 February respectively. One female's signal was lost within 30 minutes of her southward turn on 15 February. The other female was followed from her nest site approximately 2 km southward to milepost 6 where she emerged from the sea about 1130 hrs, moved across the beach into the cocoplum, and continued overland across the peninsula to the canal (Fig. 5). She remained in this area which contained emergent *Panicum aquaticum*, submergent *Hydrocotyle* sp., basking sites, and other sliders until at least 26 February when her signal was lost.

Nesting and Movement Patterns

The combined data from observations of tracks and individuals and from telemetry suggest a loose and flexible pattern of nesting activity by Tortuguero's sliders. Sliders resident in the local freshwater (or slightly brackish) canal system typically move downstream into and through Tortuguero Canal during Costa Rica's dry season. Some individuals move overland to the sea across the peninsula which separates the canal from the sea and beaches, often where it is relatively narrow north of Tortuguero village (Fig. 2). A similar pattern of nesting movement (without the sea immersion phase) is seen in green iguanas which swim across Tortuguero Canal, cross the peninsula in its narrow northern section and nest on the middle to upper beach during the dry season (Hirth, 1963b; Carr et al., 1978). Other sliders follow the canal's current all the way to the mouth, entering the sea via the estuary without overland movement. Once in the sea sliders enter the south flowing longshore

current to travel downcoast, emerging from the sea onto the beach, normally at night, to oviposit in the cocoplum scrub of the upper beach berm. After nesting is completed, most females move back into the sea, continue southward in the longshore current before re-emerging, cross the beach, and continue overland across the intervening forested peninsula to re-enter Tortuguero Canal. Mainly downstream movement brings spent females back to suitable non-nesting habitat with feeding and basking sites and represents the final phase of the cycle.

The clockwise nature of the pattern affords optimal use of prevailing currents in both freshwater and marine phases of the cycle - an energy conservative strategy which allows movement over considerable distances to and from optimal nesting and non-nesting habitat while minimizing the time spent in saltwater. While the physiological tolerances of these sliders are not known, the capacity for long term saltwater immersion in most freshwater turtles is limited (Dunson 1979a, 1979b; Dunson and Moll, 1980). The concentration of nests within a few km of sea-entry points and the paucity of nests in the equally suitable nesting habitat of the central beach section of Tortuguero National Park suggest limiting factors influencing sea-time may exist.

Sea Phase of the Nesting Process

The reasons for the marine phase of the nesting cycle, which occurs before and after nesting in many females, are more obscure. Although *T. scripta* has been observed to inhabit some brackish habitats (Neill, 1958; Moll and Legler, 1971; Legler, 1990), and the rate of electrolyte influx in sliders has been demonstrated to be relatively low (Dunson, 1967), the sea must be a difficult environment for them for a variety of reasons. Even though my data suggest their time spent in the sea may be limited and mainly occurs at the end of the rainy season when inshore salinity levels are probably relatively low, it is risky, as evidenced by the slider carcasses observed. There must be strong selective forces directing and maintaining the marine phase of the slider nesting process that involve more than just the need to get to suitable beach nesting sites. These are accessible from slider non-nesting habitat at straight-line distances well within the slider's demonstrated physical capabilities for overland travel. In contrast, the more direct route to beach nesting sites, without a marine phase, seems adequate for green iguanas

Table 3. Nest temperature-depth profile of five cocoplum-shaded slider nests and at similar depths on an unshaded mid-beach location and within the forest. Temperatures at each depth were recorded daily at 6 hr. intervals (N = 712) for a mean period of 25.4 days (14-30) per site. Means are followed by one standard deviation and extremes.

Depth (mm)	Nest Temperatures °C	Beach Control °C	Forest Control °C
Surface	24.6 ± 2.39 (20.6-37.4)	32.8 ± 6.78 (23.2-65.7)	24.0 ± 2.13 (20.9-28.7)
50	27.6 ± 1.98 (25.6-32.0)	35.1 ± 2.99 (30.2-41.6)	22.6 ± 1.89 (21.4-26.3)
100	29.5 ± 1.94 (28.1-33.8)	33.6 ± 2.32 (30.0-36.7)	22.2 ± 1.63 (20.8-24.9)
150	30.2 ± 1.66 (28.3-32.4)	33.7 ± 1.89 (32.0-34.5)	21.8 ± 1.54 (19.9-24.0)
205 (mean nest depth)	30.4 ± 1.45 (30.0-33.1)	31.5 ± 1.45 (30.9-34.4)	21.4 ± 1.03 (19.9-23.4)
230	30.6 ± 0.32 (30.2-32.2)	32.8 ± 0.66 (31.9-33.5)	21.4 ± 0.54 (20.2-22.1)

(Hirth, 1963b).

Sea travel by sliders could be viewed as an adaptation in response to strong selection pressure to minimize the terrestrial phase of the nesting process. Sea immersion by sliders is less common at Laguna Jaloa where close proximity of beach nesting sites to fresh water allows direct access without long overland movement. Within my northern study area a trend seems apparent for females to cross the peninsula to the sea along its narrowest stretch or to reach the sea via Tortuguero Estuary without any terrestrial emergence before reaching the nest site. Data from the two radio-tracked individuals also suggest that direct and rapid post-nesting movement across the peninsula is normal once the return overland phase has commenced (Fig. 5). Avoidance of obstructions and terrestrial predators of adult sliders may be part of the explanation, as a diverse array of predators, both medium-sized (e.g., raccoons, coatis, tayras, grisons, smaller cats) and very large (e.g., jaguar) inhabit Tortuguero's forests. Alternatively, or perhaps in addition, marine movement to and from nesting sites may play a role in minimizing predation of nests and eggs. There are an extremely large number of potential turtle egg predators present here from avian, reptilian, mammalian, and even invertebrate (e.g., fire ants) taxa. Many of the species suspected or observed eating slider eggs in Panama by Moll and Legler (1971) are also common at Tortuguero (e.g., armadillos, *Ameiva* lizards, opossums, coatis, vultures, etc.). Movement overland directly to the oviposition site, especially over longer distances, may allow forest dwelling predators to follow females to the nest either visually or by scent trail. Similarly, egg predators in the forest might be able to back-trail females if they moved overland after nesting. The pattern of returning to the sea after nesting and moving in the longshore current for some distance before overland return movement to the canal could best be explained by the egg predation hypothesis. An alternative explanation for post-nesting sea movement could be that it serves a thermoregulatory function for the spent female.

Mortality of Adults on the Beach

Three females were found dead on the sea beach during February and March 1991, and one dead female was seen on the beach in June 1990 (Fig. 6). All of these individuals were found at or very near the surf line suggesting that they had been washed in from the sea. One individual found at dawn on 1 February 1991 was gravid and without obvious signs of the cause of mortality, but the other three were severely mutilated and missing combinations of heads, limbs, and internal organs. As these were attended by black vultures when discovered it is not clear whether the mutilation was due to scavenging or whether marine predators may have played a role in their death.

Caribbean Slider Gigantism

Large size is a characteristic of many tropical slider



Figure 6. A dead slider female washed up on Tortuguero Beach.

populations and has been variously explained as an adaptation related to avoidance of crocodilian predation, as a response to greater productivity and longer growing seasons than in temperate zones, and as a need to maximize reproductive potential in predator-rich environments (Moll and Moll, 1990). The gigantism displayed by Caribbean Costa Rican sliders is truly exceptional, even by tropical standards, and the specific selective forces responsible remain obscure. Pritchard and Trebbau (1984) suggested that large size in the Tortuguero sliders' population may result from its filling the large herbivorous river turtle niche and from the advantages it may provide during sea travel. In regard to the latter, Gibbons (1990) argued that larger size would confer an advantage in reducing predator and environmental risks to turtles which must travel from the relative safety of their aquatic home range for nesting or other reasons. While Gibbons was thinking of terrestrial travel, the hypothesis would be equally applicable to the marine phase of Tortuguero sliders' nesting migrations. Large size is a characteristic of all sea turtles and all of the previously mentioned sea-going freshwater species (i.e., *Batagur baska*, *Callagur borneoensis*, *Pelochelys bibroni*, *Trionyx triunguis*, and *Carettochelys insculpta*), and could conceivably confer such advantages as reducing predation risk, reducing rate of electrolyte influx by reducing surface area to body mass ratio, and increasing maneuverability in heavy seas. As Gibbons also pointed out, a benefit from decreased travel risk for nesting females would be that more time could be expended and distance covered in seeking the most optimal nesting habitats available. I agree with Pritchard and Trebbau (1984) and think that at Tortuguero the extraordinary sizes attained by female sliders represent an adaptation at least partially explained by Gibbons' hypothesis. Optimal sea beach nesting habitats are relatively remote from nonreproductive habitats and are separated from them by very risky expanses of sea and/or forest which must be traversed by nesting females. If there is strong selection to reduce terrestrial travel to minimize adult or egg predation, then sea travel and time to reach beach nesting sites must be increased accordingly, with concordant adaptation resulting to cope with those additional perils. The evolution of gigantism at Tortuguero, to a degree attained in few other sliders,

is probably a response to this unique juxtaposition of essential habitats, and the need for sufficient minimization of travel risks through size enhancement to successfully utilize those habitats.

Hatchling Ecology

There is limited information concerning hatchling sliders in the Tortuguero area (Fig. 7). Twelve recently hatched sliders were observed in three seasons (1989-1991), including the two individuals observed on the sea beach. Six others were located in shallow water swampy habitats in forest, cocal, and secondary growth of the Tortuguero peninsula, two were located in shallows along the margin of Tortuguero Canal, and two were excavated from the bottom of a nest which other hatchlings had apparently previously exited. Several other reliable reports of observations of small sliders in swampy and canal habitats were received from staff and sea turtle volunteers at the Green Turtle Research Station, from local residents, and from P. Pritchard (*pers. comm.*).

Hatchlings typically begin to be observed by May or June around Tortuguero. As in Panama (Moll and Legler, 1971) my data indicate that sliders in Costa Rica have extended dry season nesting activity which probably peaks in February. With an average incubation period of 80 days (Moll and Legler, 1971) hatchlings would be expected to emerge in some numbers in late spring in conjunction with the onset of the rainy season.

There is no evidence that hatchlings enter the sea after nest emergence and it seems more likely that hatchlings normally move landward upon emergence. In countless hours of beach walking by sea turtle researchers and volunteer taggers since the 1950's, mainly during the period of peak emergence by slider hatchlings, the only record of a slider hatchling observation on the lower beach that I am aware of is the one observed by Spotila, Yocky, and myself in June 1989. This individual was walking parallel to the surf line and had meandered diagonally from the cocoplum scrub along the upper beach for approximately 10 m without attempting to enter the sea. Also, while local residents and

researchers have sighted adult sliders and tracks on sea beaches none I interviewed recalled ever seeing any hatchlings there. As physiological adaptations for salt water existence are unlikely (see Dunson 1979a, 1979b; Dunson and Moll, 1980) and morphological and behavioral adaptations for movement in the sea are clearly lacking, it seems likely that newly emergent sliders normally move landward into the vegetated peninsula rather than seaward. Moll and Legler (1971) noted that Panamanian sliders spent a considerable time (up to 36 days) after emergence secreted in low terrestrial vegetation and debris before moving to water. Tortuguero sliders probably behave similarly, gradually making their way into peninsular swamps and eventually into the canal system itself via overland movement. The only apparent hatchling predation event observed in this study was the discovery of an individual in the clutches of a beach crab mentioned previously.

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Figure 7. A hatchling slider which has emerged from a nest somewhere in the surrounding cocoplum vegetation.

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