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Nesting, Nest Predation and Hatchling Emergence of the Carolina Diamondback Terrapin, Malaclemys terrapin centrata, in Northeastern Florida

JOSEPH A. BUTLER,[1] CHRISTIAN BROADHURST, MARIE GREEN AND ZACH MULLIN

Biology Department, University of North Florida, Jacksonville 32224

ABSTRACT.—In 1997 and 2000 we monitored nesting by diamondback terrapins daily from 1 May through 31 October at a beach on an island in northeastern Florida. During our visits we recorded and marked newly oviposited intact nests, monitored previously marked nests for depredation, hatching or washout and identified nest predators. We recorded nest deposition from late April through late July, but most nests were found in June (2000) or July (1997). Most nests were depredated within 48 h of oviposition. Most depredated nests were found in June or July, and those from July included both newly deposited and recently hatched nests. Depredated nests in August and September were all recently hatched. The major nest predators were raccoons, but we also noted crows, boat-tailed grackles, armadillos, ghost crabs and two species of plant roots. Hatching and emergence began in early July and continued into October. The mean emergence period for 54 nests was 68.9 d. In 1997, 21.9% of marked nests were washed out by high tides or storms and 8.9% suffered that fate in 2000.

INTRODUCTION

Diamondback terrapins (*Malaclemys terrapin*) exist as seven subspecies inhabiting brackish water habitats from Massachusetts to Texas (Ernst *et al.*, 1994). The Florida coastline with its saltmarshes, lagoons, bays, mangroves, islands and keys represents roughly one third of their range. Five subspecies live in Florida, but the only published studies of terrapins in the state concern *M. t. tequesta* of the central Atlantic coast (Seigel, 1980a, b, c, 1983, 1984, 1993) and *M. t. rhizophorarum* in the Keys (Wood, 1992).

The northern subspecies, *Malaclemys terrapin terrapin*, exhibits 6 wk nesting seasons in June and July (Burger and Montevecchi, 1975; Lazell and Auger, 1981; Goodwin, 1994). Average incubation/emergence period is 10–11 wk, and hatching occurs from mid-August to mid-October. Raccoons are the major nest predators, and most nest depredations occur within 24 to 48 h of oviposition in the northern populations (Burger, 1977; Roosenburg, 1991; Goodwin, 1994). Seigel (1980c) found gravid Florida east coast terrapins on Merritt Island from late April through 1 July. However, nothing is known concerning natural incubation/emergence times, nest predation or nest predators in the southern range.

Our research focused on *Malaclemys terrapin centrata*, the Carolina diamondback in northeastern Florida, which is intermediate in its geographic range and physical characteristics between *M. t. terrapin* and *M. t. tequesta*. The objectives of our study were to characterize nesting biology by measuring the following variables: (1) the length of and peaks in nesting activity, (2) the total number of nests present and how many survived to hatching, (3) the identity of nest and hatchling predators and peaks in predator activity and (4) the mean emergence period.

[1] Corresponding author: Telephone: (904)620-2831; FAX: (904)620-3885; e-mail: jbutler@unf.edu

METHODS

Study area.—The terrapin nesting beach is on an island adjacent to the Intracoastal Waterway in Duval County, Florida. The island is roughly triangular with an area of approximately 100 ha. The 750 m long beach occupies the northeastern side of the triangle and ranges in width from about 10–25 m at high tide. Open sandy sections grade to higher areas with vegetation including saltgrass (*Distichilis spicata*) and saltwort (*Batis maritima*). The area south of this narrow beach, representing over 90% of the the island, is typical saltmarsh, flooding often with spring tides, and with continuous stands of cordgrass (*Spartina alterniflora* and *S. patens*).

Nests and season.—Once daily from 1 May through 31 October in both 1997 and 2000 two or three researchers walked up and back a 10 m wide corridor, roughly bisected by the high tide line, along the terrapin nesting beach and counted all intact and depredated nests. In most cases, terrapins left distinctive tracks to and from nests (crawls), and following crawls was the most reliable method we found for locating intact nests. When disturbed sand suggested a nest, we excavated by hand to confirm the presence of eggs. We wore vinyl examination gloves when digging in an effort to mask human scent which could be a signal to nest predators. Not every crawl or pair of crawls yielded a nest because many nests were deposited in vegetated areas beyond where we could no longer follow crawls. With these methods we missed many nests, and the ones we found may have been more or less vulnerable to predation than others.

We marked each unharmed nest with a numbered stake so we could monitor its subsequent status. So that predators were not attracted to nests by our stakes, we placed them 5 m away at an angle of 240° from the nest. Early in the 2000 season we placed survey markers at 25 m intervals along the beach, and that year we also measured the distance and angle of each nest to its nearest survey marker in order to locate nests more accurately later. To avoid following old crawls on subsequent days, we swept them away daily with brooms. Each day we checked previously marked nests and recorded if they had been depredated, inundated, washed out by tides, were unchanged, or if hatchlings had emerged.

Nest predation.—We recorded depredated nests in three categories: marked nests that were subsequently raided; unmarked nests that had been oviposited and depredated overnight, as indicated by a fresh crawl to a raided nest; and unmarked depredated nests without crawls. For the last category we counted only holes with terrapin eggs or eggshells, or live or dead hatchlings associated with them as depredated nests, but other diggings that may have been nests were evident. We collected all eggshells, carcasses and hatchlings and filled in nest holes daily. We also recorded all predators we detected from tracks or by actually seeing them and we swept away all predator tracks daily.

Hatching and emergence.—To evaluate hatching and emergence we recorded the presence of hatchling crawls, the number of hatched nests and the presence of live or depredated hatchlings. We found solitary hatchling crawls, but often clusters of crawls were left by a single nest cohort. Because the presence of hatchling crawls was indicative that emergence had occurred, we considered each cluster to represent a single event of equal importance to a solitary crawl. We also recorded crawl direction toward or away from the surf when possible.

We located hatched nests three ways: in some cases we could follow hatchling crawls back to their origin; some intact hatched nests were recognized by the emergence hole that measures about 5 cm in diameter with margins tending to cave in; some raided nests (both marked and unmarked) had obviously hatched, as evidenced by the presence of live hatchlings or carcasses left behind by the predator.

We found most live and dead hatchlings on the surface near hatched or raided nests or by excavating raided nests or emergence holes. A few were found by following hatchling crawls.

TABLE 1.—Total number of terrapin nests found intact and depredated in 1997 and 2000. Data scored as depredated includes nests that were depredated when found and nests found intact that were subsequently depredated in each month

	1997		2000	
Month	Total nests	Depredated (%)	Total nests	Depredated (%)
April	1	0 (00.0)	1	0 (00.0)
May	109	65 (59.6)	170	129 (75.9)
June	123	105 (85.4)	181	167 (92.3)
July	169	150 (88.8)	98	91 (92.9)
August	34	34 (100.0)	25	24 (96.0)
Sept	18	18 (100.0)	0	0 (00.0)
Total	454	372 (81.9)	475	411 (86.5)

Fates of marked nests.—Daily monitoring allowed us to evaluate the fates of most marked nests. However, at the end of October of each year there were several nests which had neither hatched nor been preyed upon, so we excavated them to determine their status. Using compass readings and measurements from our nest stakes, and in 2000 from our survey markers, we dug holes at the nest sites up to 1 m in diameter and 0.5 m deep in search of them.

RESULTS

Nests and season.—Most nests were near the high tide line or beyond it in several sandy, sparsely vegetated areas. Including depredated and intact nests we recorded 454 in 1997 and 474 in 2000 (Table 1). Total nests for the 2 y were similar, but the monthly distribution differed with most nests occurring in July of 1997 and June of 2000. All but one nest recorded in August and September of both years were depredated when found. The intact nests represent a subset which we monitored daily, and there were 114 of these in 1997 and 112 in 2000. In both years we found most intact nests in May (Fig. 1). The earliest and latest nests recorded were 27 April and 13 August, respectively, both in 2000. Discovery of intact nests declined by the last week in July in both years, and we consider the nest found in August, the only one discovered in that month in either year, to be an aberration.

Nest predation.—In 1997, 81.9% of all nests were destroyed by predators and in 2000, 86.5% met the same fate (Table 1). Of 372 depredated nests in 1997: 61 were marked; 107 were raided overnight; and for 204 we had no other knowledge. In 2000 we recorded 411 nest depredations: 82 were marked; 90 were taken overnight; and we had no information for 239. In both years nest depredations increased through June, and through July in 1997, then declined through September (Table 1). If predation of only marked nests is considered, then 53.5% were taken in 1997 and 73.2% in 2000 (Table 3).

We recorded survivorship times for 144 depredated nests from 1997 and 166 from 2000 for which oviposition dates were known (Fig. 2). Most of these were raided within 24 h of oviposition, and we recorded 107 (74.3%) such instances in 1997 and 90 (53.9%) in 2000. Generally, as nests aged they were less likely to be preyed upon. However, some nests were depredated after hatching (Fig. 2).

Numerous raccoons (*Procyon lotor*) live on the island, and we saw their tracks nearly every day. On the island, raccoons usually sleep in arboreal refugia during the day at all times of the year and are most active nocturnally (J. Butler, pers. obs.). Their tracks and diggings at raided nests indicated that they were the most frequent terrapin nest predators. Fish crows (*Corvus ossifragus*), American crows (*C. branchyrhynchos*) and boat-tailed grackles (*Quiscalus*

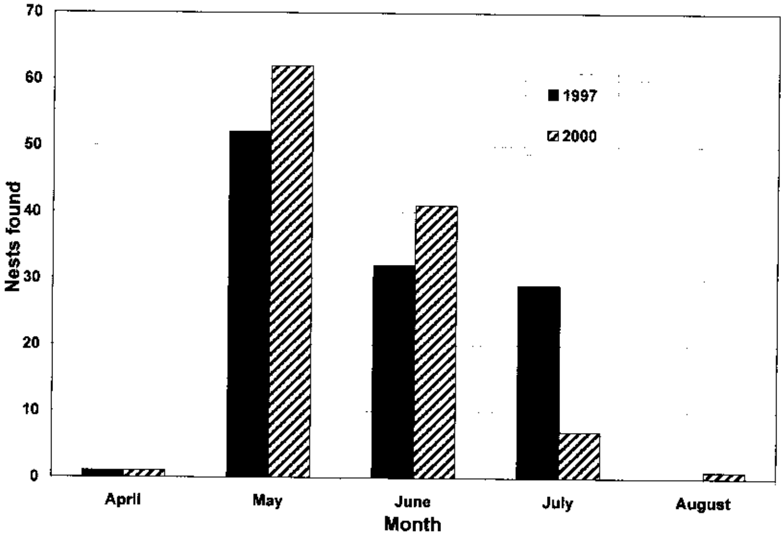

FIG. 1.—The number of terrapin nests found each month of the two-year study. Totals include both intact and depredated nests

major) were conspicuous on the island in May, but less so the rest of the season, and we saw all three bird species digging in the sand at terrapin nest sites. Raided nests often had both raccoon and bird tracks associated with them. We recorded armadillo (*Dasypus novemcinctus*) tracks on the beach for periods of several weeks in both years, and in 2000 at least seven terrapin nests were depredated by armadillos. We discovered ghost crab (*Ocypode quadrata*) tracks leading to and from several hatched nests and found injured or dead hatchlings associated with crab holes. Occasionally, we found ants (*Solenopsis invicta* and *Conomyrma* sp., probably *bureni*) inside raided nests.

Hatching and emergence.—No hatching or emergence evidence was found before July. The earliest hatchling crawls were recorded on 3 July 1997, but few were found in that month in either year (Table 2). We recorded most hatchling crawl events in August 2000 and September 1997, and the latest one was 11 October 2000. In 1997 the crawl events represented 75 individual crawls, and they all led up the beach into the vegetation rather than into the surf. In 2000 the crawl events represented 137 individual crawls, and, of 97 for which we were able to note direction, 85 (87.6%) led up the beach into the vegetation rather than into the surf.

In 1997 we found 65 hatched nests, most of which were in September (Table 2). In 2000 we realized we could discern between depredated eggshells that had been newly deposited and those that had already hatched. New eggshells were very white inside and out, and comparatively thick. Hatched shells were somewhat of a dirty white outside, sometimes with faint dark speckles, and the inside was shiny gray. They were thinner and more parchment-like with the outer white layer flaking off. Telling the difference was important, because in July nests laid earlier in the season were beginning to hatch while new nests were still being deposited, and both were being raided. In 2000 we recorded 94 hatched nests, most of which were in July, with very few in September (Table 2).

From July through October in both years we found live or dead hatchlings. The earliest date we found hatchlings was 19 July 2000, and we recorded most in September 1997 and August 2000 (Table 2).

TABLE 2.—Number of hatchling crawl events, number of hatched nests and the number of hatchling events recorded during the 1997 and 2000 terrapin nesting seasons. Groups of hatchling crawls and hatchlings from single nest cohorts are listed as single events with the same weight as solitary hatchling crawls and hatchlings. Total numbers of crawls and hatchlings are discussed in the text

	Hatchling crawl events		Hatched nests		Hatchling events	
Month	1997	2000	1997	2000	1997	2000
May	0	0	0	0	0	0
June	0	0	0	0	0	0
July	4	12	4	49	4	12
August	4	55	13	41	1	13
September	14	1	47	3	5	2
October	1	1	1	1	1	1

We recorded emergence periods for 19 intact marked nests that hatched in 1997 and 35 in 2000. These periods ranged from 55–97 days with a mean of 68.9 (SD = 9.7).

Fates of the marked nests.—Our last known hatching event in 1997 was on 2 October, so we ceased daily beach monitoring on 31 October. At that time we knew 20 marked nests hatched, 39 were depredated and 18 were washed out (Table 3). The fates of 37 marked nests were still undetermined, so on 1 November we excavated them. We found hatching evidence in six excavations: four had eggshells but no hatchlings and two had hatchlings. Two other nests had two undeveloped eggs each, but nothing else. In the other 29 we found nothing at all. Seven of those were near enough to the spring tide line that we believe they were washed out in storms (Table 3). The remaining 22 nests were situated where they were unlikely to have been washed away. If they had successfully hatched we should have found eggshell remnants, but there were none. Thus, we assume they had been depredated, and we missed the signs. Therefore, in 1997 61 marked nests (53.5%) were depredated, 25 (21.9%) were washed out and 26 (22.8%) survived until hatching (Table 3).

In 2000 we stopped daily beach monitoring on 31 October to conform to our methods of 1997. At that time we knew that 36 nests hatched, 57 were depredated prior to hatching and 5 were washed out (Table 3). The fates of 14 marked nests were still unknown, so we excavated several that day and the rest on 2 November. We found hatching evidence in two excavations: one had eggshells only and one had hatchlings. Three other nests had eggs: one had six developed unhatched eggs and two others had eggs surrounded by roots. One of the rootbound clutches was surrounded by saltwort roots (*Batis maritima*) that did not penetrate the eggshells and had nine well-developed, but dead, embryos. The other was surrounded by roots of seashore saltgrass (*Distichilis spicata*) which had penetrated the shells, and nothing was left inside. We found no sign of the other nine nests. In five cases the nests were within the spring tide ranges and were likely washed out. The other four were far enough from the surf that washout was not likely, and we assume we missed when they were depredated. In 2000, combining nests depredated prior to hatching, at hatching, the two rootbound clutches and those "likely depredated," 82 (73.2%) marked nests experienced predation at some point, 5 (4.5%) were washed out and 38 (33.9%) hatched (Table 3).

In both years, as we excavated we discovered live hatchlings in nest cavities and we monitored one cavity each year on a weekly basis in an attempt to determine if the hatchlings overwintered in the nest cavities. Our monitoring consisted of a combination of observing emergence holes and digging to see if hatchlings were still present. In both years hatchlings exited at various times throughout our monitoring, and all were gone by January (2000) or February (1997).

TABLE 3.—Fates of 114 marked terrapin nests in 1997 and 112 during the 2000 season. Numbers are followed in parentheses by percentages

	1997	2000
Hatched/not depredated	26 (22.8)	19 (16.9)
Hatched and depredated	0*	19 (16.9)
Depredated before hatching	39 (34.2)	57 (50.9)
Washed out	18 (15.8)	5 (4.5)
Unhatched/undeveloped	2 (1.8)	3 (2.7)
Unknown:		
Likely washed out	7 (6.1)	5 (4.5)
Likely depredated	22 (19.3)	4 (3.6)
Total	114	112

* In 1997 the only way we knew depredated nests had hatched was if hatchlings or their carcasses were left behind, and none of our marked nests had them. In 2000 we also used eggshell characteristics to determine if depredated nests had hatched. Some of the 1997 nests categorized as depredated before hatching may indeed have hatched

DISCUSSION

Nests and season.—Butler (2000) noted that this terrapin population has the longest nesting season (78 d) of any reported from late April to late July. Five to 6 wk seasons occurred in New Jersey (Burger, 1977) and Rhode Island (Goodwin, 1994), and Roosenburg (1992) found Maryland's terrapins to nest from mid-May through late July. In central Florida gravid females were captured from 28 April through 1 July (Seigel, 1980c). Florida's warm climate appears to promote commencement of courtship and mating behavior earlier than in northern climates, and this is followed by earlier onset of nesting (Seigel, 1980b). Earlier nesting would lead to earlier hatching giving those hatchlings time to forage and grow during their initial season, which may confer benefit over those hatching later.

Nest predation.—Other studies have reported predation rates on terrapin nests varying from 41.3% to 88% (Burger, 1977; Roosenburg, 1992; Goodwin, 1994), so the rates calculated for this study are near the high end of that range. Our finding that most nests for which deposition dates were known were preyed upon within 24 h of oviposition (Fig. 2) is similar to other terrapin studies (Burger, 1977; Roosenburg, 1992; Goodwin, 1994) and is consistent with findings for some other turtle species (*e.g.*, Auffenberg and Weaver, 1969; Petrokas and Alexander, 1980; Congdon *et al.*, 2000). Congdon *et al.* (1983) suggested that the mammalian predators (including raccoons) of Blanding's turtle nests used female crawls and fresh nesting odors to locate nests, and both dissipated over time. This likely explains why only 12.1% of the nests were still depredated from ages 3–53 d (Fig. 2). Finally, a group of 26 nests (8.5%) was taken at hatching, between 54–106 d. Burger (1977) suggested that mammalian predators also used olfaction to sense metabolites released at hatching. Congdon *et al.* (2000) noted that if hatchling emergence was asynchronous, the emergence hole left by the hatchlings leaving early may also be a signal to predators.

Raccoons were the most frequent nest predator in this study, and this was true of all other terrapin studies (Burger, 1977; Goodwin, 1994; Roosenburg and Place, 1994). Raccoons have been identified as major nest predators for numerous other turtle populations (*e.g.*, Landers *et al.*, 1980; Ehrhart and Witherington, 1987; Congdon *et al.*, 2000), and Jackson and Walker (1997) suggested periodic removal of overabundant raccoons (and crows) to reduce predation on Suwannee cooter nests. Such a removal program yielded higher

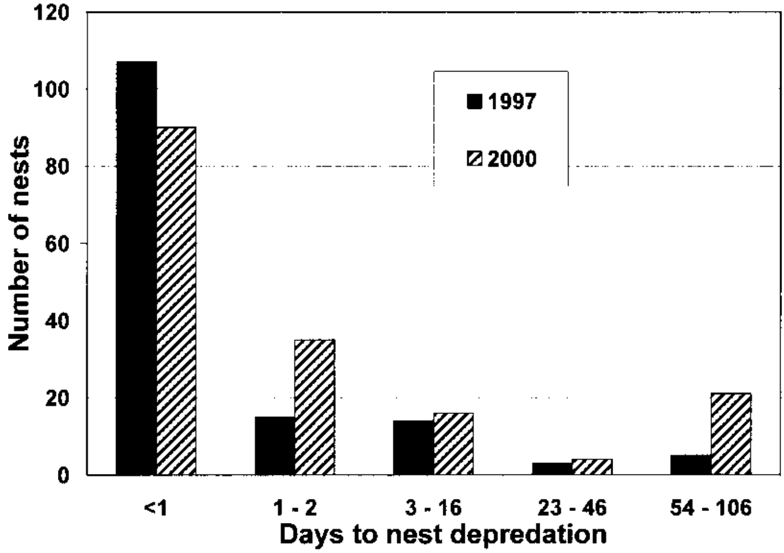

FIG. 2.—Survivorship of known age nests in 1997 and 2000. Data scored as ≤1 d were inferred from adult terrapin crawls leading to depredated nests. All other data were determined from nests marked on the day of deposition

hatchling success for yellow mud turtle nests in Iowa (Christiansen and Gallaway, 1984). Before such removal programs are implemented biologists should determine if predators are genuinely overabundant (Garrott *et al.*, 1993) and whether the level of nest depredation is detrimental to the stability of the turtle population. Answers to these questions and whether to remove predators will likely vary with each situation.

Avian predation was likely based on visual cues only present at the nesting stage. During daylight hours we saw crows and grackles perched on nearby limbs apparently searching for terrapins. When female terrapins came ashore the birds often watched them nesting, sometimes followed them up the beach, then dug up eggs with their beaks as soon as the turtles left the site (Burger, 1977; Butler, 2000). Birds usually raided nests in groups and often carried eggs away from the site to devour them.

Burger (1977) also reported that at dawn gulls took remaining eggs or hatchlings from nests partially raided by raccoons the previous night, which helped explain the presence of tracks from both species at nest sites in her study. In our study we observed birds depredating newly deposited nests which they had discovered by watching terrapins. It is possible that if the birds left some eggs in the nests during their diurnal raids, then raccoons could have discovered them during their nocturnal foraging. This scenario also would allow for tracks of both predators at the nest site the following day.

Crows were important nest predators in our study, and they were recognized in this role in New Jersey as well (Burger, 1977). Although we never saw the grackles with terrapin eggs, we saw them digging into nests, and this is the first report to implicate grackles as nest predators. Another newly recorded nest predator was the armadillo, although its importance in this role to this population is doubtful. Armadillos probably find the small marshy island to be relatively inhospitable and we recorded them in residence only for short periods of time. During their visits, however, they successfully raided several nests. We noted ghost crab predation on hatchlings which was reported also by Arndt (1991, 1994). While ghost crabs were abundant on the nesting beach, their colonies were confined to several higher sandy areas that were relatively free of oyster shell and other debris. These areas were also preferred by terrapins for nesting. The two species of ants found in raided nests may have entered nests after raids, as scavengers rather than predators. Roosenburg (1992) found an unspecified species of ant destroying eggs by mining calcium from them, and ants caused some egg loss in New Jersey (Burger, 1977).

Hatching and emergence.—When the direction of hatchling crawls could be determined, we found that most led up the beach from the nest instead of toward the open water. Just over the crest of the beach is a large marshy area that is semi-isolated and protected by the beach. This marsh likely provides refuge to hatchlings and juveniles during their early years. Arndt (1994) reported similar hatchling crawl direction, and Burger (1976) showed that hatchlings sought cover in the nearest vegetation, whichever direction that might be. In South Carolina hatchlings released offshore from their nesting beach all swam back to shore, proceeded up the beach and sought refuge beneath tidal debris (Lovich *et al.*, 1991). Roosenburg (1991) observed numerous hatchlings in salt marshes adjacent to their nesting beaches, rather than in open water. Mann (1995) noted this behavior in Mississippi and attributed it to the juvenile terrapins' need for at least some fresh water. Dunson and Mazzotti (1989) demonstrated that hatchling terrapin growth was inhibited at salinities above 21 ppt, but that growth did occur if hatchlings in the same circumstances were allowed to drink fresh water periodically. Living in the marsh may provide this and would offer vulnerable hatchlings the added benefit of avoiding aquatic predators to which larger terrapins are less susceptible.

In 1997 September was the most important month for hatching and emergence, while in 2000 most hatching evidence occurred in July and August. Considering the mean emergence period for this population of 68.9 d, most nests hatching in September (and October) would be those deposited in July. In July 1997 we marked four times as many nests as in July 2000 (Fig. 1), and this is reflected in substantially higher hatching and emergence evidence for September 1997 (Table 2). Conversely, the few intact nests recorded in July 2000 (Fig. 1) may account for the sparse September emergence data that year (Table 2).

The large number of hatched nests (49) recorded in July 2000 (Table 2) is partly the result of our newly learned ability to use eggshell characteristics to distinguish between raided nests that had just been oviposited and those that had hatched prior to predation. In 1997 we overlooked this, and the only way we knew if a raided nest had hatched was if there were live or dead hatchlings left at the site. In many cases there were no hatchlings left behind, so we would not have considered those raided nests as hatched. Therefore, the report of four hatched nests in July 1997 is likely an underestimate.

The only other studies reporting natural developmental/emergence periods are from northern populations. Burger (1977) reported the mean incubation period for New Jersey terrapins to be 76.2 d, with another 2.5 d for mean emergence time and a range of 61–104 d. In Rhode Island the mean emergence period was 73.7 d with a range of 59–108 (Goodwin, 1994). The northeastern Florida mean emergence period of 68.9 d is slightly shorter, but standard deviations of all three studies overlap.

Fates of marked nests.—We found very low percentages of unhatched or undeveloped nests (Table 3). In New Jersey Burger (1977) found 7% of her first 100 nests with no development and that 8% and 11% of all the eggs counted failed to develop in consecutive years. Goodwin (1994) found 20 of 31 hatched clutches in Rhode Island had some undeveloped eggs.

Upon excavation in 2000 we found two clutches surrounded by plant roots. One surrounded by saltwort roots had fully developed, but dead, embryos. The roots had not penetrated the shells and the root encasement may have prevented embryos from escaping the egg. Roosenburg (1992) reported similar entrapment of hatchlings by cordgrass roots in Maryland. The eggs of the other clutch had been penetrated by roots of seashore saltgrass and were empty. Caldwell (1959) reported penetration and accompanying destruction of sea turtle eggs by sea oat roots (*Uniola paniculata*), and Lazell and Auger (1981) reported a similar fate to terrapin eggs due to dune grass (*Ammophila breviligulata*). Both of those plant species were present on the nesting beach (Butler, 2000). Further, Stegmann *et al.* (1988) demonstrated that roots of *A. breviligulata* actually absorbed several isotope labeled nutrients across the shells of terrapin eggs.

Each year, when unearthing nests of unknown fates, there were numerous sites that produced no nesting evidence at excavation. Goodwin (1994) had the same experience for four of six nests she excavated. She had not originally proofed nests for the presence of eggs, as we had, and she suggested that the turtles had simply not oviposited at those places. However, we know there were eggs at all nests we marked, and they had been monitored daily. We assumed that several of these had been washed out by storms or high tides. Sometimes washouts were evident the day after they occurred, but, when we were unsure, we either dug down to proof the nest again or simply continued monitoring daily. We concluded that some of our unknowns were in the latter group and assigned them accordingly. In 2000, 10 nests (8.9%) were washed out by high tides, while in 1997, 25 (21.9%) were lost this way (Table 3).

It is noteworthy in the 1997 group of marked nests that, even though nest loss due to washout was much greater, a higher percentage of nests successfully hatched without predation than in 2000. Additionally, overall depredation of marked nests was lower in 1997 than in 2000 (Table 3). It could be that many of the washed out nests in 1997 would have been depredated if they had survived the tides, but when they were no longer available predators might have sought other food sources.

Overwintering in nests by terrapin hatchlings has been noted by others (Lazell, 1979; Marion, 1986), and in both years we recorded data that suggested that some may overwinter in northeastern Florida. Our data are inconclusive, but most hatchlings in northeastern Florida do not overwinter.

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