Reproductive Biology of a Flood-Season Nesting Freshwater Turtle of the Northern Neotropics: *Dermatemys mawii* in Belize

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ABSTRACT. – The findings of two years of field research on the reproductive biology of *Dermatemys mawii* in northern Belize are presented. *Dermatemys* breeds between March and September. It exhibits a solitary nesting pattern, in which multiple ($x = 2.05$, range 1-4) clutches of 2 to 20 ($x = 10.98$) large ($x = 61.6 \times 35.8$ mm, 50.2 g) brittle-shelled eggs are laid during the latter part of the rainy season (late September through December) when the probabilities of flooding are high. The existence of post-ovipositional diapause is suggested by the ability of the eggs to withstand over 30 days of flooding with no reduction in viability. Hatchling emergence is timed to coincide with the resumption of summer rains. The slope of the regression of total annual reproductive output against body size is steep for smaller females, but decreases for larger females, primarily due to variation in clutch frequency. Body size at maturity varies among stream types in both sexes.

KEY WORDS. – Reptilia; Testudines; Dermatemydidae; *Dermatemys mawii*; turtle; ecology; reproduction; nesting; egg immersion; Belize

The Central American river turtle *Dermatemys mawii* (Fig. 1) is a large herbivorous freshwater turtle of the Atlantic lowlands of southern Mexico, Belize, and northern Guatemala (Alvarez del Toro et al., 1979; Iverson and Mittermeier, 1980; Iverson, 1992). *Dermatemys* is the sole living representative of the formerly widespread and diverse family, Dermatemydidae, known from the Jurassic of Europe and the Cretaceous of North America, Europe, and East Asia (Romer, 1956; Hutchison and Bramble, 1981). Throughout its restricted range, *Dermatemys* is under heavy pressure for its meat (Holman, 1964; Lee, 1969; Mittermeier, 1970, 1971; Alvarez del Toro et al., 1979; Moll, 1986a, 1988; Vogt and Flores-Villela, 1992b). International concern that *Dermatemys* could be hunted to extinction has resulted in its being listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 1984), as endangered under the provisions of the U.S. Endangered Species Act (Code of Federal Regulations, 1987), and as a high priority species in the IUCN Species Survival Commission Action Plan for the Conservation of Tortoises and Freshwater Turtles (IUCN/SSC, 1991). Despite the socioeconomic importance and vulnerability of *Dermatemys*, few accounts of its biology and life history have entered the scientific literature.

Prior to this investigation, descriptions of the basic reproductive biology of *Dermatemys* were scarce, and mostly based on anecdotal observations. Holman (1964) and Lee (1969) described the hard-shelled oval eggs. Moll (1988) found clutches of 8 to 14 eggs in slaughtered females in Belize. Alvarez del Toro et al. (1979) reported clutch sizes of 6 to 16 eggs, with estimates from fishermen as high as 20. Since *Dermatemys* is barely capable of movement on land, the nests were presumably always laid very near water (Alvarez del Toro et al., 1979). The timing of courtship, oviposition, and ovarian quiescence were unclear. Turtle

vendors in Veracruz considered December to be part of the "breeding season" (Alvarez del Toro et al., 1979). Pritchard (1979) speculated that laying was coincidental with the flooding of rivers in September, October, and November. Another account speculated that *Dermatemys* nested twice a year, in April and December (Alvarez del Toro et al., 1979). Lee (1969) observed mature eggs in the oviducts of females slaughtered for meat in Guatemala during February and March. There were reports from Mexico of a laying season between April and September (Smith and Smith, 1979; Alvarez del Toro, 1982). Moll reported one (1986b) or two (1988) clutches during March and April in Belize. He thought this description might be incomplete and encouraged further study (D. Moll, *pers. comm.*).

This confusing array of contradictory reports suggested errors, intraspecific variation, or a prolonged multiclutching reproductive pattern. Between September 1989 and September 1991, I conducted field research on the reproductive biology of *Dermatemys mawii* in northern Belize, which complements the simultaneous research of Vogt and Flores-Villela (1992a, 1992b) in Mexico. This paper discusses reproductive cycles, minimum sizes at maturity, reproductive potential, nesting ecology and incubation periods, capability of *Dermatemys* eggs to withstand prolonged immersion, and the environmental correlates of reproductive chronology.

MATERIALS AND METHODS

Study Area. — The research was conducted in the northern half of Belize, a small country on the Caribbean coast of Central America (Fig. 2). Northern Belize has a broad coastal plain dissected by numerous rivers and freshwater and brackish lagoons. The research was initiated in response to an invitation from a series of seven rural villages

Figure 1. Adult male *Dermatemys mawii* from Belize.

on the Belize River that maintained 32 km of the riparian forest as a sanctuary for black howler monkeys (*Alouatta pigra*) (Horwich, 1986, 1990; Horwich and Lyon, 1988, 1990). Villagers provided turtle reproductive tracts for analysis. As the project evolved, five additional villages volunteered reproductive material, and the study area expanded to include an additional 54 km of the Belize River and 39 km of its tributary systems, including sections of Spanish Creek, Mussel Creek, Cox Lagoon, and White Water Lagoon (Fig. 2). Although precise elevations are not available, probably no part of this area exceeds 50 m above sea level.

Winter mean monthly air temperature minimums in the study area were 16–17°C. Summer mean monthly air temperature maximums were 32–33°C. Total annual precipitation for the two years was 2404 mm and 1911 mm. The dry season in northern Belize typically extends from February through May, although it started later in 1990 and lasted longer in 1991.

Dermatemys inhabits three types of streams in the study area. Mussel Creek and Spanish Creek are sluggish darkwater streams, contrasting with classic oligotrophic blackwater streams (Goulding, 1980; Sioli, 1984; Payne, 1986) in that they support a productive fishery. The deepest sections are 4.6–6.0 m. White Water Lagoon is a clearwater system, but differs from the nutrient-poor clearwater streams of the Amazon (Goulding, 1980) by possessing a luxurious community of aquatic macrophytes. Vegetation is absent in the deepest pools (9 m).

The aforementioned systems are tributaries of the Belize River. Often turbid, with very limited transparency, the Belize River is similar to the whitewater rivers of the Amazon (Goulding, 1980; Sioli, 1984; Payne, 1986). During periods of low water the sediments are reduced and underwater visibility improved. Velocities range from 0.04 to 0.15 m/sec (Gonzalez, 1980), and mean annual discharge is between 99.8 m³/sec (upstream) and 155.4 m³/sec (downstream) (Hartshorn et al., 1984). Channel widths are 35–60 m and in many places the river exceeds 9 m in depth. During high water the larger eddies probably exceed 18 m in depth.

Due to its extensive watershed, the Belize River is subject to frequent oscillations in water levels during the rainy season (Fig. 2). These are sometimes a result of distant upstream precipitation, and can occur without significant local rainfall. The highest water levels occur between June and November (Fig. 3). Water level oscillations in the tributaries follow a similar pattern, but are less extreme. The river is bordered by semi-evergreen seasonal broadleaf forest (Wright et al., 1959; Horwich and Lyon, 1991). During floods the surface area of the river and its tributaries expand severalfold and vast sections of riparian forest and savannahs become inundated.

Observations made during inventory work in the rivers, wetlands, and lagoons of the Rio Bravo Conservation and Management Area in northwest Belize (Polisar, 1991) supplemented the more detailed reproductive data collected in the primary study area.

Reproductive Biology. — The majority of the study of reproductive chronology was accomplished by opportunistically salvaging the reproductive organs of turtles that were being slaughtered locally for human consumption. More slaughters occurred in the dry season because low water facilitated capture. During periods of high water levels, captures were sparse and intermittent.

Although a number of measurements were obtained from the 567 turtles that were handled, only straightline carapace length (CL), measured with calipers, is discussed here. Ovaries, oviducts, oviductal eggs, and male urogenital systems were collected from slaughtered turtles. Tissue specimens were immediately immersed in 10–15% neutral buffered formalin. Most of the oviductal eggs obtained were incubated (Ewert, 1979; Iverson, 1979). Several eggs were preserved to provide a reference for pre-ovulatory size class ovarian follicles.

After 6–26 months of immersion in formalin, ovaries were rinsed in water for 16–20 hours, blotted dry, and measured to the nearest 0.01 g. Ovarian follicles over 5 mm diameter and all corpora lutea were measured to the nearest mm. The longest and shortest axis of each testis was measured. Testicular volume was determined using the formula for the volume of an ellipsoid:

$$V = 4/3 \, \pi \, a^2 b$$

where **a** is half of the shortest diameter and **b** is half of the longest diameter (Guillette and Bearce, 1986). Epididymal status was visually classified as follows: 1) small — virtually undetectable to the naked eye; 2) medium — quite small, but easily visible; 3) full — easy to cut a cross section; 4) swollen — obviously very full. Complete organs from 27 adult females, 6 juvenile females, and 51 adult males were examined.

Numbers of enlarged follicles, oviductal eggs, or recent corpora lutea were used as estimates of clutch size (Christiansen and Dunham, 1972). Estimates based on recent corpora lutea and oviductal eggs were considered more accurate due to the possibility that a portion of the enlarged
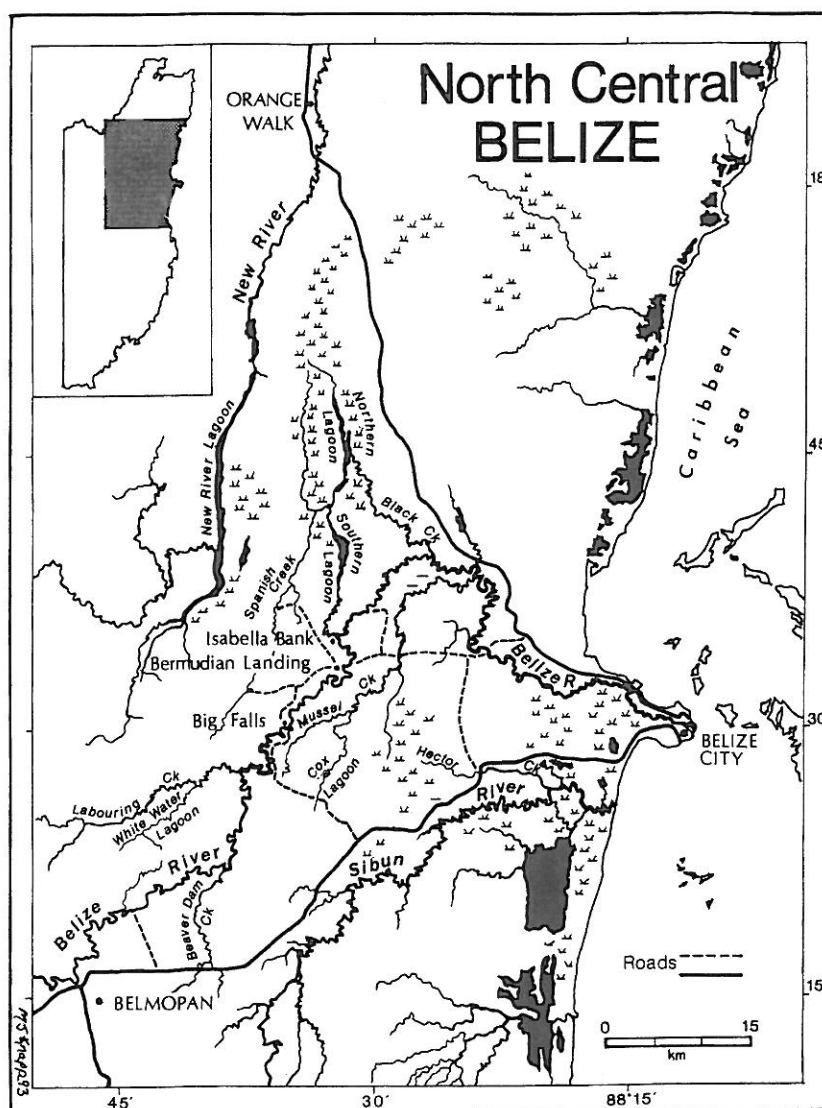
Figure 2. Villages and waterways of the primary study area in north central Belize. The work center was in the village of Isabella Bank.

follicles would not ovulate (White and Murphy, 1973) and either persist until the next laying season or become atretic. The presence of fresh corpora lutea or oviductal eggs was considered an indication of an approximate nesting date (Cagle, 1953; Jackson, 1988).

The number of clutches laid per year was estimated in several ways. The most reliable indication was the presence of two or more distinct sets of corpora lutea or corpora albicans (Christiansen and Dunham, 1972; White and Murphy, 1973). When size classes of corpora albicans were basically indistinguishable, annual reproductive output could be determined, but multiple clutches could only be inferred by dividing the total number of scars by mean clutch size. Multiple clutches were suggested when enlarged pre-ovulatory follicles were found in specimens containing oviductal eggs (Graham, 1979; Iverson, 1979; Etchberger and Ehrhart, 1987). That interpretation was made with caution as the enlarged follicles may not have been due to ovulate until the next season, or may have eventually become atretic (Christiansen and Dunham, 1972). Total annual reproduc-

tive output was assessed primarily by counts of corpora lutea and corpora albicans. Mean annual reproductive potential was calculated as the product of mean clutch size and the mean annual number of clutches (Jackson, 1988). The relationship between annual reproductive output and body size (carapace length) was examined through simple linear regression.

Testicular enlargement was considered an indication of peak periods of spermatogenic activity (Gibbons, 1968; Moll and Legler, 1971; Christiansen and Dunham, 1972). Time of breeding was interpreted through classification of epididymal volumes. Inferred capability of epididymal discharge was assumed to provide an indication of the mating season. The highly aquatic nature of the species, coupled with wide dispersal of individuals, reduced the probabilities of visual observations of mating.

Females were considered reproductively mature when they contained oviductal eggs, corpora lutea, corpora albicans, and/or enlarged vitellogenic follicles (Christiansen and Dunham, 1972; Kuchling, 1988; Etchberger and Ehrhart,
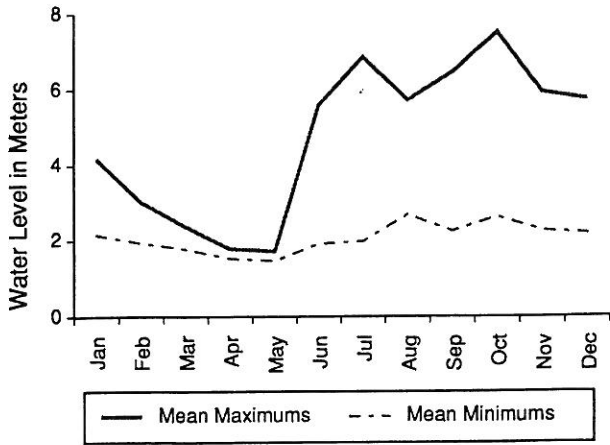
Figure 3. Seasonal and within-month variation in Belize River water levels: nine-year averages of monthly maximum and minimum water levels, based on daily means. Recorded at Big Falls station.

1988). Males were considered mature when testes and epididymides were enlarged, when dorsal head coloration was distinct, and tail length exceeded 100 mm.

Twelve live *Dermatemys* were examined laparoscopically for reproductive status. These animals were captured in Mussel Creek, retained in captivity and examined with a portable battery-powered laparoscope using sterile technique. Incisions were sutured closed and the animals observed for 2–30 days before release.

Nesting Ecology. — Nest searches were conducted between September and December. In 1989–90, eggs from 2 located nests and 1 clutch of oviductal eggs were incubated along the banks of the Belize River in predator-proof hardware cloth exclosures with a copper-constantan thermocouple inserted at the same level as the bottom of the eggs. These eggs were monitored for nine months.

By late 1989, after several months of opportunistic nest searches, it became clear that adjustments in methodology would be required to obtain adequate information about incubation period and emergence dates. Eggs were laid during a time of year when high water allowed maximum dispersal and hiding cover for nesting females. Nest encounters were extremely rare and based on chance.

In 1990, employees spent 108 hours searching for nests and eleven centrally-located posters in eight villages advertised a reward (equivalent to a full day's wage for unskilled labor) for any nests that were located and reported. The project also escalated capture efforts during the nesting season. This involved 369 net days between 15 September and 15 November in Mussel Creek, Spanish Creek, and the Belize River. Shelled oviductal eggs in *Dermatemys* are often centrally located in the body cavity and may elude detection by palpation. Radiographs on Kodak Lanex Regular screens in X-Omatic cassettes at 32 ma and 60–70 kv revealed the presence of eggs and identified clutch size.

Oviposition was induced by injecting synthetic oxytocin at about 1.0 IU per 100 g bodyweight. In some cases, oviposition was facilitated by sedation using low dosage injections of ketamine (25 mg per kg body weight). Care was taken to avoid rotating eggs (Limpus et al., 1979). Eggs obtained by induced oviposition (4 clutches) and slaughter (3 clutches) were intentionally subjected to simulated flood conditions in supersaturated "wet" vermiculite for 2–36 days before being switched to "moist" conditions (three parts vermiculite to one part water by volume, or moist soil along the banks of Spanish Creek). The eggs were placed in simulated nests inside predator-proof hardware cloth and chickenwire exclosures, with copper-constantan thermocouples inserted at the same level as the bottom of the eggs. These nests were monitored continuously for ten months.
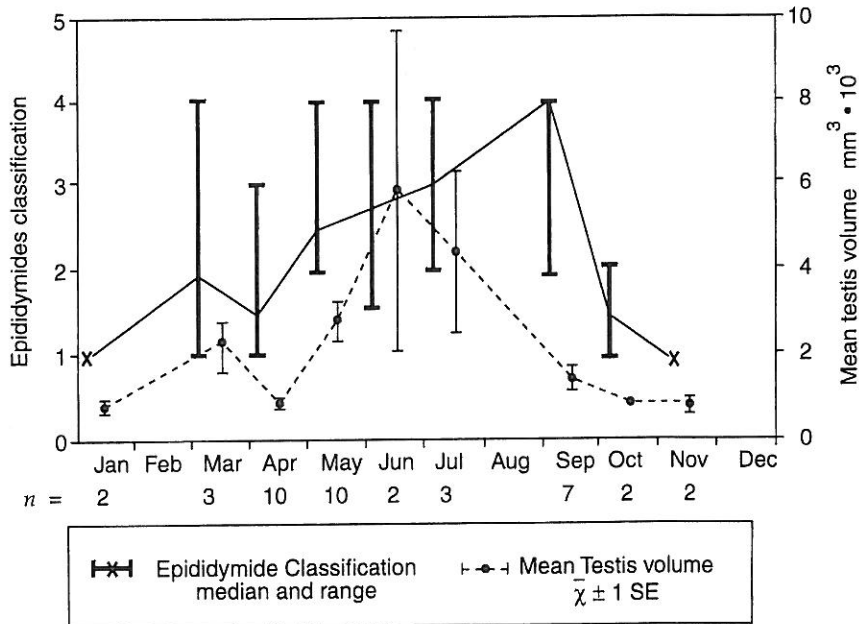

Figure 4. Correlates of the breeding season: seasonal variation in *Dermatemys* testicular and epididymal volumes. Epididymides classified on a visual scale: 1 = invisible to naked eye, 4 = very full (see text).

Nest temperatures recorded before 0900 hrs and after 1700 hrs were averaged for a daily mean.

Environmental Parameters. — Climatic and hydrology data were provided by the Belize National Meteorological Service and the Hydrology Department. Belize River temperatures (daily maximums and minimums at approximately 48 cm below surface) were recorded in the villages of Bermudian Landing and Big Falls.

RESULTS

Reproductive Cycles

Female Cycle. — Gravid females ($n = 14$) bearing hard-shelled eggs were identified via slaughters and radiographs during late September (2), October (5), and November (7). Four of the clutches recorded in late November were observed in radiographs. Those eggs were obtained through induced oviposition in early December. One slaughter in mid-September revealed 14 leathery eggs (shell formation incomplete). Another slaughter in mid-September revealed 7 pre-ovulatory follicles (31.7–35.9 mm diameter) similar in size to those found in oviductal eggs (30.2–32.8 mm diameter). One nest encountered in late September was probably laid that month. Another nest encountered in early November could have been laid during the preceding two months.

Animals slaughtered between September and December had large distinct corpora lutea (9–14 mm diameter), sometimes accompanying one or more smaller less distinct sets of corpora albicans (5–12 mm diameter). Size classes of these scars sometimes slightly overlapped. Visual appearance (color and degree of translucency, thickness, and texture) aided classification. No slaughtered females were examined during January and February. One large female examined laparoscopically in February was neither gravid, nor bearing large corpora lutea. Large corpora lutea were not present in 17 of 18 dry season (March through May) slaughters. One late April slaughter revealed luteal scars between 6.4 and 8.6 mm diameter, suggesting somewhat recent oviposition. Small corpora albicans persisted through May, allowing an assessment of total annual reproductive output and also, in many cases, an estimate of clutch frequency and sizes.

Ovaries collected between September and December usually contained groups of follicles exceeding 25 mm in diameter. The majority (12 of 18, 67%) of ovaries collected during the dry season contained groups of fairly large follicles (15–24 mm). Six out of 18 dry season specimens contained no follicles over 15 mm. Atretic enlarged follicles were not common. Four out of 18 specimens collected during the three-month-long dry season had groups of 6, 6, 6, and 2 atretic follicles which represented 8.1% of the dry season follicles over 10 mm and approximately 12.9% of the dry season follicles over 15 mm. Follicles in excess of 24 mm were rare in ovaries collected during March, April, and May. Immature females possessed no follicles greater than 5 mm. No ovaries were collected during July or August.

One specimen collected from White Water Lagoon in early March contained follicles in excess of 25 mm in diameter, seemingly destined for either oviposition or atresia. Two villagers informed me that they had observed oviductal eggs in slaughters in early May in 1990. These two clutches (15 and 13 eggs) were observed in large females from Spanish Creek. They appeared to represent an anomaly among the abundant slaughters occurring during that time of year and were communicated as such.

Clutch Size and Frequency. — Reproductively active females ($n = 21$) deposited one clutch ($n = 7$, 33%), two
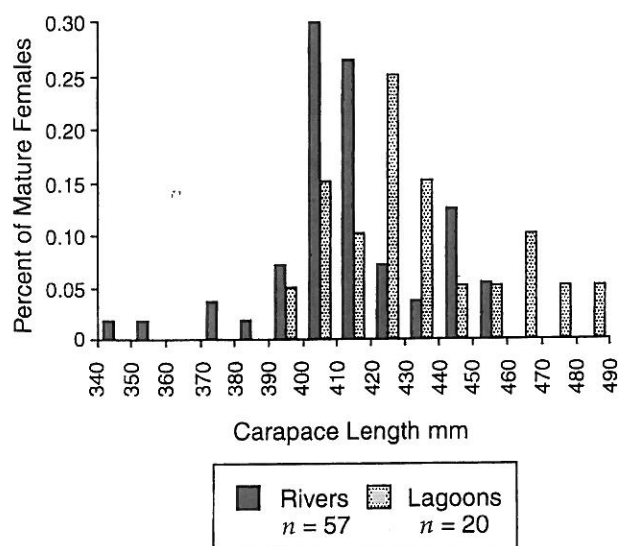

Figure 5. Significant differences (t-test, $P = 0.0009$) in minimum size at maturity: body sizes of mature females from continuous flow streams (rivers) and sluggish waterways (lagoons). Rivers include Belize River and Rio Bravo, lagoons include Spanish Creek, Mussel Creek, White Water Lagoon, and New River Lagoon.
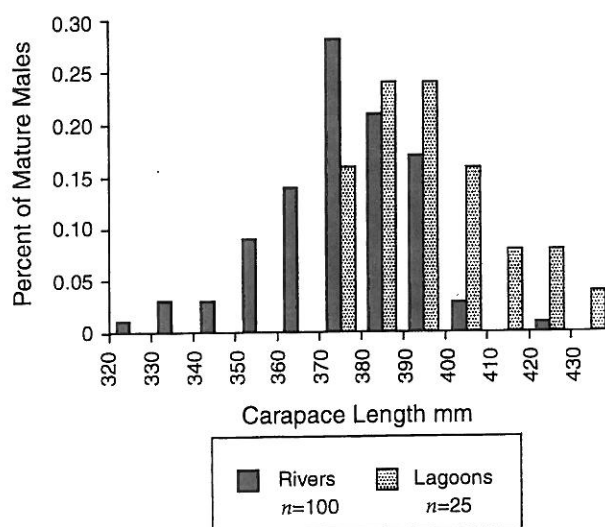

Figure 6. Significant differences (t-test, $P = 0.0001$) in minimum size at maturity: body sizes of mature males from continuous flow streams (rivers) and sluggish waterways (lagoons). Rivers include Belize River and Rio Bravo, lagoons include Spanish Creek, Mussel Creek, White Water Lagoon, and New River Lagoon.

clutches ($n = 7$, 33%), and three clutches ($n = 6$, 29%) per year. Only one out of twenty-one active females laid four clutches in a year ($n = 1$, 4%). Mean clutch frequency was 2.05. Clutch size ($n = 49$) ranged from two to twenty. Clutches of over 15 eggs were rare, and mean clutch size was 10.98 (s.d. = 3.72). Clutches of 8–14 eggs were common. Total annual reproductive output (number of eggs laid in a year) ranged from 0 to 47. Nearly equal proportions of 27 females laid between 0 and 10 (22%), 11 and 20 (26%), 21 and 30 (22%), and 31 and 40 (26%) eggs per year. Mean total reproductive output (direct estimates from 27 specimens) was 21.0 (s.d = 12.5). The product of mean clutch size (10.98), mean clutch frequency (2.05), and proportion of females annually active (0.9677) yielded an estimate of 21.8 eggs for mean annual reproductive potential.

Egg Size. — The sizes of the large brittle-shelled ellipsoidal eggs varied among clutches. In a sample of 44 oviductal and freshly laid eggs, the ranges of length, diameter, and mass were 72.0 to 54.1 mm, 49.8 to 32.4 mm, and 70.0 to 34.3 g, respectively. Mean egg length was 61.6 mm (s.d. = 3.9), mean diameter was 35.8 mm (s.d. = 3.2), and mean mass was 50.2 g (s.d. = 9.8).

Male Cycle. — Male specimens in breeding condition were observed from March through September (Fig. 4). However, only one out of three exhibited breeding condition in March. Two out of 10 slaughters in April and 5 out of 10 in May revealed full epididymides. The proportion of males in breeding condition increased until September, when 5 out of 7 specimens possessed very full, swollen epididymides (Fig. 4). Epididymal volumes dropped in October and stayed low until March. Decreasing testicular volumes preceded decreases in epididymal volumes. The highest mean testicular volumes occurred in June. From June to October, mean testicular volumes gradually decreased while median epididymal volumes increased (Fig. 4).

Minimum Sizes at Maturity

The smallest mature female was 342 mm carapace length (CL). The smallest male exhibiting the external characteristics of maturity (orange head and tail > 100 mm) was 328 mm CL. The largest immature female was 420 mm CL. The largest immature male was 386 mm CL. The largest female was over 483 mm CL. The largest male was 433 mm CL (Figs. 5 and 6).

Minimum body size at maturity of both sexes varied among water bodies. Large immature animals were found in Mussel Creek, Spanish Creek, White Water Lagoon, Hector Creek Lagoon, and New River Lagoon. These water bodies are sluggish dark or clearwater creeks and lagoons. Low stream velocity is the common denominator. Smaller animals were found in the Belize River and Rio Bravo, where the current is continuous regardless of season. In the latter two streams calm stretches are short and confined to small inlets and bends. While *Dermatemys* in lagoons and sluggish streams could rest at nearly any point on the substrate, animals on the bottom of the Belize River were almost

always found in association with submerged woody material (old root masses, flooded trees, logs imbedded in the mud), which apparently gave them some respite from the constant current. Food availability may have been more continuous in the sluggish streams due to the presence of submergent vegetation, which was absent in the Belize River. A statistical comparison of the thermal characteristics of these waterbodies was impossible due to lack of adequate simultaneously recorded water temperatures.

Grouping the sluggish creeks and lagoons together on the basis of stream velocity involves assumptions, but contrasts with the Belize River are consistent. The majority (ca. 70%) of river males over 370 mm CL were mature. A similar percentage of lagoon males attained maturity between 380 and 390 mm. Most (ca. 70%) females from the Belize River were mature at 400 mm CL. A similar percentage of lagoon females attained maturity between 410 and 420 mm. The differences in the relative frequencies of minimum body sizes of adult female and male lagoon and river *Dermatemys* are illustrated in Figs. 5 and 6. The same figures demonstrate contrasts in maximum size attained. While the largest river female was 452 mm CL, the largest lagoon female was 483 mm CL (Fig. 5). The largest river male was 421 mm CL (Fig. 6), the largest lagoon male was 433 mm CL. Females attained larger body sizes than males (Figs. 5, 6).

Relationship of Reproductive Potential to Body Size

Simple linear regression showed that the relationship between CL and total annual reproductive output for 26 active *Dermatemys* females was statistically significant ($P < 0.01$), but variation was high ($r^2 = 0.325$, slope = 0.219). Isolating a subset of lagoon animals removed the portion of variation due to the different body sizes of river and lagoon animals ($r^2 = 0.687$, $P < 0.01$, slope = 0.39, 7 df) between body size and reproductive output. I observed very small clutch sizes in small females apparently experiencing their first reproductive year (no visible ovarian scars). There was a strong relationship ($r^2 = 0.921$, $P < 0.01$, slope = 0.591, 3 df) between body size and reproductive output in Belize River females between 342 and 401 mm CL, which constitutes an adolescent size class. That relationship appears to deteriorate beyond 406 mm CL ($r^2 = 0.330$, $P < 0.1$, slope = 0.381, 10 df) in the Belize River sample, presumably because of inter-annual variation in clutch frequency and, correspondingly, annual reproductive output.

Nest Characteristics and Incubation Conditions

No actual nesting was observed, although three accounts were available from the accumulated experience of the hunters involved in the study. Those accounts agreed that *Dermatemys* laid its eggs at or close (within 1.5 m) to the waterline. The possibility that some of these nests are laid in shallow water, such as reported by Kennett et al. (1993b) for *Chelodina rugosa* cannot be discounted. The long-term highest water levels occurred during the latter part of the
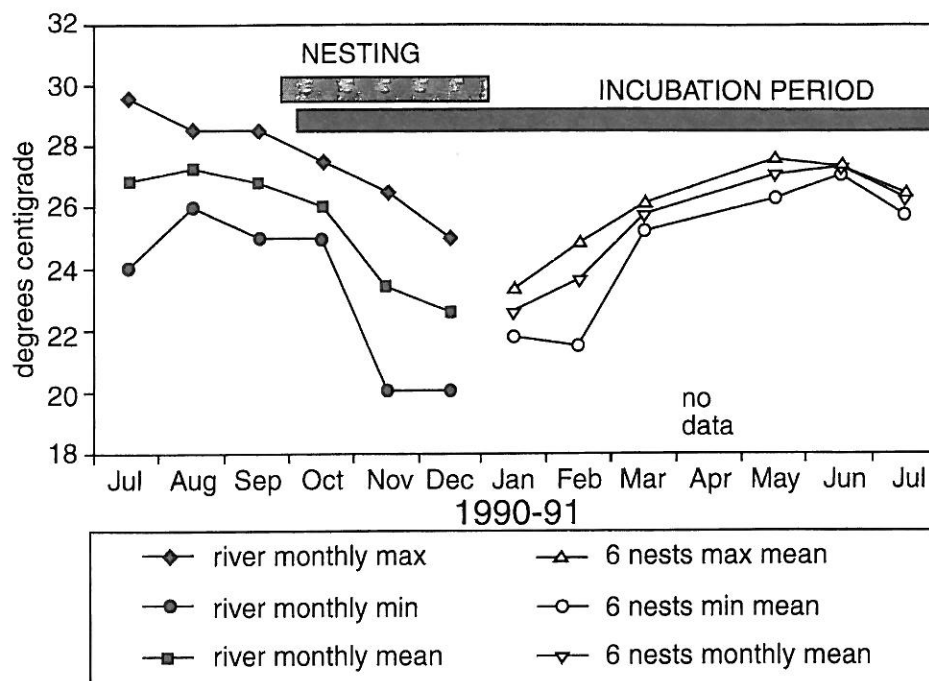
Figure 7. River temperatures, *Dermatemys* nest temperatures, and *Dermatemys* nesting season and incubation periods 1990–91.

rainy season (September through December), which was the primary nesting season in northern Belize (Figs. 3, 7).

Nests ($n = 11$) were usually located by chance after flooding or predation had opened the nest, exposing the eggs. In 1989 a nest containing 9 eggs was discovered on the Belize River. Several eggs were partially exposed in a shallow (< 13 cm) cavity situated 30 cm above the water on a steep clay bank. No other nests shared these characteristics. Four old nests located along the Rio Bravo were in low exposed clayey mounds on a flat river bank surrounded by patches of grasses. On Mussel Creek, an old nest was found amidst riparian vegetation in a moist humus soil. There was little consistency in nest site selection, but none were more than one vertical meter above the water surface when located and all were low enough to be flooded.

Prolonged Submergence of Eggs. — A single Belize River nest (9 eggs in clay along a steep bank) monitored in 1989–90 allowed observations concerning embryonic survival following submergence. Located on 4 November 1989 at 30 cm above water, the nest was under 2.75 m of water by 6 November. It remained completely submerged until 2 December (28 days) when the eggs were collected (free diving) and carefully transplanted to a higher, more convenient location. In late December, the nest was once again flooded (7 days). In January 1990 it was flooded twice, once for 9 days and once for 3 days. On 22 June I dissected two of the eggs. One was dead, interrupted at an early stage of development. The other contained a live turtle whose development was nearly complete. The 7 remaining eggs were left in the nest. An unusually violent flood occurred between 25 June and 2 July. On 25 August I dissected the remaining eggs. Although all were dead, two eggs contained small, well-defined turtles, similar in size and stage to the egg

opened on 22 June. The other five eggs were arrested at an early stage or were in decay.

During the nesting season of 1990, no natural nests were located despite increased effort. Seven nest enclosures that yielded incubation and emergence data contained eggs from induced and slaughtered females. Forty-one eggs from turtles from the Belize River, Spanish Creek, and Mussel Creek yielded 38 hatchlings (Table 1). The eggs had been intentionally subjected to 2–36 days of simulated flooding (Table 1). Sixteen out of 17 (94%) eggs collected via induction hatched. Twenty out of 23 (87%) eggs collected from slaughtered females hatched. The small clutch sizes and uneven treatment periods within some clutches (Table 1) was due to the tendency of induction to yield only portions of a clutch at a time. One egg, whose parentage was unknown, had a submersion period of unknown extent. It was recovered when emptying and cleaning the water tank in which the turtles had been held. After spending an unknown time in the bottom of the tank it was subjected to another 8 days of flood conditions. It also hatched.

Eggs were collected between 8 October and 16 December 1990. Emergence from nests occurred between 4 July and 12 August 1991. Time from the date of egg collection to date of emergence ranged from 217 to 300 days (Table 1). The field assistant who monitored the eggs reported that emergence events followed intermittent rainfalls punctuating a prolonged dry season. An isolated egg found exposed in the forest hatched in July (R. Young, *pers. comm.*).

Incubation Conditions. — Nesting occurred during a time of year when both temperature and day length were decreasing (Fig. 7). Eggs collected in 1990 were stored in wet vermiculite in large plastic buckets (containing thermocouples) sitting on concrete under a stilt house. In October,

Table 1. Immersion periods and emergence dates for 6 clutches of eggs obtained from gravid *Dermatemys mawii* from the Belize River (BR), Spanish Creek (SC), and Mussel Creek (MC). Simulated flood conditions in supersaturated water/vermiculite mixtures were imposed immediately after eggs were obtained. Eggs were transferred either to moist vermiculite or directly to the moist riparian soils where they were all subsequently maintained in simulated natural nests. Summer rains, which typically arrive in early June, arrived in July in 1991.

Date Eggs Obtained (1990)	Source	No. Eggs	Flood Days	Emergence Dates (1991)	Total Days	Hatch Success
8 Oct	BR	15	31	4 Jul–4 Aug	269–300	80%
11 Nov	BR	8	36	4 Jul–21 Jul	235–252	100%
21 Nov–8 Dec	BR	4	9–27	21 Jul–30 Jul	236–245	100%
8 Dec	SC	5	9	21 Jul	225	80%
10–16 Dec	MC	6	2–8	30 Jul–12 Aug	229–242	100%
16 Dec	BR	2	2	21 Jul	217	100%

the minimum temperature was 22.8°C. During December, minimum internal temperatures were as low as 20.4°C. Monthly minimum river temperatures in November and December were 20°C (Fig. 7). Monthly minimum mean temperatures for 6 nests during January and February were below 22°C (Fig. 7).

Nest and air temperatures increased from January to May (Fig. 7). Highest annual air temperatures (32–33°C) occurred in May. The six simulated nests were situated in two separate sites along Spanish Creek. Because Spanish Creek was extremely high when the eggs were deposited, it was impossible to deposit the eggs in the riparian shrub and herbaceous plant zone which lay closest to the stream channel. Both sites were in palm (*Orbignya cohune*) forest. Because I cleared vegetation in the immediate vicinity of the egg enclosures, both sites received approximately 3 hours of sunlight per day. The eggs were buried as close as possible to the existing water level and some were set partially in

water. Water levels dropped from that day on and by the end of the dry season the edge of Spanish Creek was more than 100 m from the nest sites. Monthly maximum daily means for the six nest sites did not exceed 28°C (Fig. 7).

The dry season of 1991 persisted longer than usual. Although June is typically one of the wettest months of the year, it was hot and dry in 1991. The rainy season did not resume until late July. The first emergences on 4 July coincided with a brief but significant rainfall.

Eggs that had been held for 31 days in supersaturated vermiculite (eggs collected on 8 October, Table 1) and then switched to drier (still moist) conditions, showed banding 40 days later when transferred to the ground. The banding encircling the central third of the eggs appeared similar to that described for fertile eggs of *Emydura macquarii* (Thompson, 1985) and crocodilians (Ferguson, 1985; Webb et al., 1987). Shells of eggs that were transferred directly from simulated flood conditions to the mud of Spanish Creek were translucent at the time of transfer.

Reproductive Chronology and Environmental Correlates

The timing of reproductive events and their relationship to precipitation is illustrated in Fig. 8. Increases in testicular and epididymal volume began during the spring, when water temperatures and day length were increasing. The highest air and water temperatures of the year occurred during May, coinciding with the beginning of the mating season. The cessation of the mating season coincided with decreasing temperatures in autumn. Nesting occurred during the latter part of the wet season, when air temperatures, water temperatures (Fig. 7), and day length were decreasing. This coincided with the long-term highest annual water levels
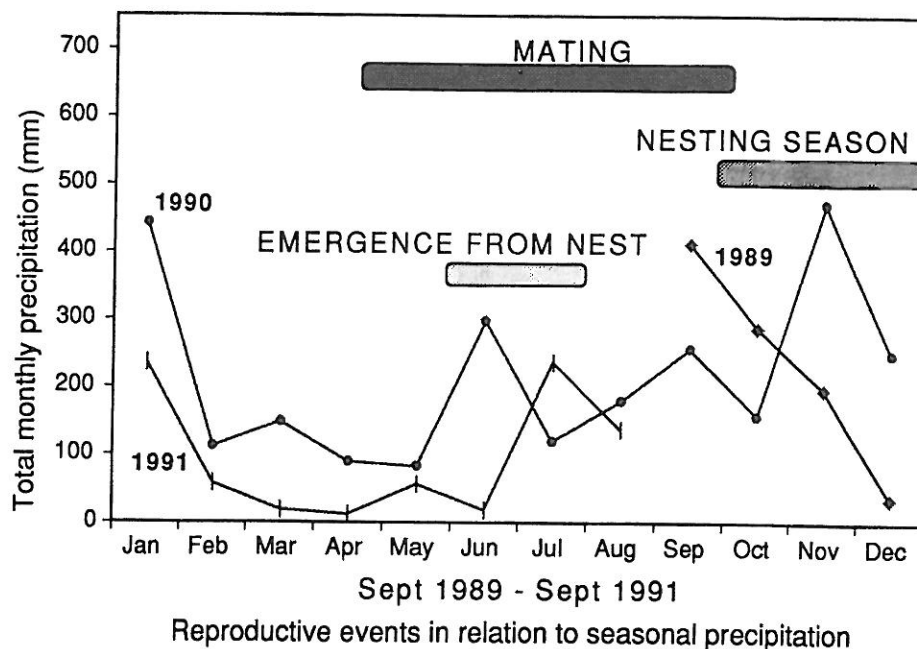

Figure 8. The relationship of *Dermatemys* reproductive chronology to seasonal precipitation patterns in the Belize River and its tributaries.

(Fig. 3) and appeared to anticipate the imminent lowering of water levels as the dry season began. The eggs were deposited during a time of year when water and nest temperatures were low (late nests) or certain to decrease (early nests) (Fig. 7). Early laid eggs (late September) were exposed to a high probability of flooding. Late eggs (December) were exposed to lower probabilities of flooding (Figs. 3, 8). Immediately after oviposition the eggs can withstand some flooding with little or no effect on survival (Table 1). Limited evidence suggests that subsequent flood intervals during early development may be destructive and that prolonged flooding during the late stages of embryonic development will be fatal. The period from oviposition to emergence from the nest is longer than that of most turtles (Table 1) but does not represent the extreme. Nest emergence appears to coincide with the onset of the rainy season in June and July (Fig. 8).

DISCUSSION

Reproductive Cycles

The results of my examination of ovaries and gravid females were in agreement with reports of an autumn nesting season (Pritchard, 1979) and conflicted with reports of a spring nesting season (Moll, 1986b, 1988). With the exception of one laparoscopically examined female, my sample lacked adult female specimens from January and February. Two out of 18 spring specimens suggested that a spring clutch was a possibility (one set of large follicles in March, one set of large corpora lutea in April). In contrast, shelled eggs, preovulatory follicles, or large opaque corpora lutea (or all the above) were encountered in every female slaughtered or radiographed between late September and mid-December.

Although I received two reports of shelled eggs in May slaughters, they constituted a minor fraction of all the slaughters that occurred during the dry season and were communicated in part because of their novelty. Eggs laid in May would presumably forego the extended diapause seen in eggs that are flooded soon after oviposition. Embryonic development stimulated by the dry warm conditions present in May would be interrupted by rising water in June or July. A nest located along the Rio Bravo may have fit that scenario. The nest was under 0.5 m of water despite moderate water levels (late July – early August) and located because some of the dead eggs had floated up to the water surface.

Lee (1969) provided a report of "what appeared to be fully developed mature eggs" in the oviducts of slaughtered females in February and March in coastal Guatemala. The tendency of a high proportion of females to retain fairly large ovarian follicles through the dry season (spring) creates the possibility for misinterpretation and might account for his observation. Moll (1986a, 1986b, 1988) reported that the nesting season in Belize was March and April, and that there was no evidence of reproduction at other times of the year.

Misinterpretation of the nesting season of *Dermatemys* could be based on encounters with asynchronous females,

misinterpretations of the status of the large follicles present in many ovaries between March and May, or the misleading appearance of eggs encountered in nests. Eggs that have experienced suspended development in response to flooding will appear recently laid when encountered shortly after the cessation of saturated conditions. The cool water and soil temperatures that occur between November and February (minimums as low as 20°C) may also delay or slow embryo development for months. Without considering these factors, the probability of misinterpreting the time elapsed since the oviposition of *Dermatemys* eggs located in nests is extremely high.

Vogt and Flores-Villela (1992b) collected eggs from gravid females in November and December in Mexico, but reported a nesting season from September to March. A pattern in which the majority of clutches are deposited between September and December, with a progressively diminishing smaller proportion (of second and third clutches) deposited during the early dry season (January–March) would fit these conflicting accounts. Early clutches could undergo submergence induced diapause and cold inhibited development while late clutches might experience neither. All could hatch in early summer when the rains resume. Eggs subjected to submersion, cool winter temperatures, and a long dry season took 217–300 days to hatch in this study. Vogt and Flores-Villela (1992b) reported incubation periods of 115–223 days for eggs incubated at constant temperatures between 25 and 30°C. The latter regime would allow eggs laid in early March to hatch in early June.

Geographical variation in precipitation and hydrological patterns might produce variation in nesting seasons. In estuarine systems, the effects of seasonal precipitation patterns may be less distinct. Southern Belize and the Caribbean coast of Guatemala receive twice the annual precipitation of northern Belize (Hartshorn et al., 1984). Moll (1986b, 1988) conducted some of his work in the Rio Grande estuary of southern Belize and may have encountered a population adapted to climatic and hydrological patterns quite different than those of the interior of northern Belize.

My interpretation of the mating season is based on the assumption that increases in testicular volume indicate spermatogenic activity, and the assumption that increases in epididymal volume reflect sperm storage, the latter constituting evidence of breeding condition. Although I received several verbal accounts from hunters who had observed males and females near each other in late April and early May only one observation was recent, reflecting the rarity of such observations. Because *Dermatemys* spends most of its time underwater, the probability of mating observations, which is low during the dry season, becomes further diminished during the rainy season due to water turbidity. My sample of male reproductive organs was small and uneven. Our understanding of the male cycle would benefit from a more comprehensive examination of a larger year-round sample of organs.

Although the reproductive cycle of *Dermatemys* may be related to water levels and precipitation, those exogenous

factors seem unlikely stimuli for one of the most aquatic turtles in the world. Changes in water temperature are the seasonal phenomena most readily detectable to an ectotherm whose habit is to seek depths and shun sunlight. Obbard and Brooks (1987) found that accumulated water temperature heat units (the sum of the difference between the daily mean temperature and a threshold temperature), provided a reliable prediction of the date of the first annual nesting attempts of *Chelydra serpentina* in Ontario. Mendonça (1987) reported that while photoperiod had no apparent effect on the reproductive cycle of *Sternotherus odoratus*, water temperature played an important role. Prolonged exposure to elevated temperatures (28°C) accelerated and extended spermatogenesis. Cooler water temperatures (18–24°C) initiated testicular regression in the fall. High temperatures were stimulatory to partially enlarged follicles, but could inhibit follicular development when prolonged. Cool temperatures allowed follicles to continue to enlarge (Mendonça, 1987). In *Dermatemys* the inferred initiation of spermatogenesis coincided with increasing water temperatures between April and May (Figs. 4, 7, 8). The onset of the nesting season coincided with decreasing water temperatures in September (Figs. 7, 8). Isolation of water temperature as the sole stimulus for reproductive chronology may be overly simplistic. The interactive effects of temperature and day length on the reproductive cycles of many fish are well documented (Jameson, 1988), and may play a similar role in turtles as well.

Annual Reproductive Output

Vogt and Flores-Villela (1992b) reported a maximum of three clutches and 39 eggs per year (sample size not given). I report a maximum of four clutches and 47 eggs per year. However, the second most productive female was identical to Vogt and Flores-Villela's maximum. The two findings are similar.

Nesting Ecology

Because water levels oscillate during the nesting season (Figs. 4, 8) there is not one single peak water level, and the location of every shoreline is dynamic. The horizontal distance that a flooded river covers generally far exceeds the vertical rise attained. The shoreline at the same location on a stream may vary from heavy mud to intermittent stands of tall grasses and shrubs to dense riparian forest depending on water levels. For animals nesting adjacent to this dynamic shoreline, nest sites at different micro-elevations and in different vegetative surroundings could be expected.

Most of the nests that I observed were solitary. At only one site, where an old logging road met the Rio Bravo, did I observe evidence of concentrated nesting (4 nests within 6 m of each other). Another nest was located where recent logging had disturbed the bank of Mussel Creek. Whether the turtles were focusing on these disturbed areas or the nests were located due to increased visibility was not clear. According to older hunters, both turtles and nests were formerly more abundant. There were only historical verbal accounts of aggregates of nests, such as the one I encountered in the Rio Bravo Conservation and Management Area, and one that Vogt encountered in Montes Azules Biosphere Reserve in Mexico (Vogt and Flores-Villela, 1992b). Exploitation, which has reduced the numbers of laying females (Polisar, 1994), may have also selectively influenced nesting behavior.

Presumably many *Dermatemys* nests escape inundation. However, it is clear that some nests are flooded and capable of surviving prolonged immersion. This is very rare for reptilian eggs, and thus far, scarcely documented (Kennett et al., 1993a, 1993b). Prolonged flooding often kills entire broods of turtle and crocodilian eggs. Plummer (1976) found that the eggs of *Trionyx muticus* could endure only brief periods of flooding. Inundation longer than 2 days during early embryonic stages significantly decreased the likelihood of normal development and no eggs survived inundation periods longer than 6 days. Magnusson (1982) reported complete mortality in 37 out of 38 *Crocodylus porosus* nests located beside rivers that flooded. He also reported complete mortality in *C. porosus* eggs after more than 13 hours of submersion in water that approximated the temperatures and dissolved oxygen content observed in natural flooded nests. Kennett et al. (1993a) reported that the eggs of the temperate-zone turtle *Chelodina longicollis* died when immersed for longer than one week. In contrast, the eggs of *Chelodina rugosa*, a tropical flood season nesting turtle have submersion survival capabilities similar to what is reported here for *Dermatemys* (Kennett et al., 1993a).

Eggs in oviducts develop to late gastrula stage and then undergo a pre-ovipositional arrest until oviposition (Ewert, 1985, 1991). In this study seven clutches were subjected to flooding immediately after departure from the oviduct. That treatment constituted a switch from one aqueous environment to another, and the mechanism allowing the eggs to survive might have been a simple 2–36 day continuation of pre-ovipositional arrest. However, *Dermatemys* eggs laid in late September and October are exposed to the possibility of two to three months of submersion-emergence cycles due to oscillating water levels before entering the dry season. *Chelodina rugosa* eggs die when submerged after development has begun (Kennett et al., 1992a). What happens to *Dermatemys* eggs laid during moderate water levels in October or early November if the highest flood does not come until early December? A natural nest that I observed was dry when encountered on 4 November, then exposed to a sequence of 28 days of flooding, then 13 days dry, 7 flooding, 27 dry, 9 flooding, 7 dry, and finally 3 days flooding before the dry season began. The three eggs that survived this hydric gauntlet suggest that something in addition to simple extension of pre-ovipositional arrest may be involved in the development of *Dermatemys* eggs. Kennett et al. (1993a, 1993b) described the underwater nesting of *Chelodina rugosa* and conducted experiments revealing the hypoxia-induced continuation of the pre-ovipositional arrest in its eggs. The mechanisms of developmental arrest in

Dermatemys eggs, particularly during water level oscillations, merit more attention.

November and December river temperatures of 20°C, December nest temperatures as low as 20.4°C, and January and February nest temperatures of 22°C (Fig. 7) make *Dermatemys* a "winter nesting" turtle, similar to *Deirochelys reticularia* in Florida (Jackson, 1988). Average internal nest temperatures of most Testudines are usually between 26 and 32°C (Packard and Packard, 1988). The simulated *Dermatemys* nests monitored in 1991 did not reach 26°C until late March to early April (Fig. 7).

Between March and May daily mean internal temperatures in the simulated nests were between 25 and 28°C (Fig. 7). Monthly maximum air temperatures during the same period were between 30 and 33°C. Because the water of Spanish Creek had advanced past the riparian fringe into the taller cohune palm (*Orbigyna cohune*) forest when the eggs were deposited, the shaded nests were probably cooler than nests laid earlier. However, the nest sites we were forced to select represent a subset of those available to *Dermatemys*. Turtles laying at that time would have been forced to do so in the forest. Many nest sites (e.g., exposed clay banks along the Rio Bravo and the Belize River) could be expected to be warmer, and might require less time for development. Webb et al. (1986) found that eggs of *Carettochelys insculpta* incubated at 32°C developed nearly twice as fast as eggs incubated at 28°C.

In this study, most hatchlings from a clutch did not emerge simultaneously (Table 1). Typically a fraction of the clutch would emerge after one of the rainfalls punctuating the long dry season. The significance of the asynchronous emergence is unclear. It appeared that, after pipping, some hatchlings would wait in the nest for appropriate conditions. Vogt and Flores-Villela (1992a) also report embryonic estivation in *Dermatemys*, which may discourage hatching and emergence until conditions are very wet, and consequently, suitable for the hatchling of this highly aquatic turtle.

Vogt and Flores-Villela (1992a) reported temperature-dependent sex determination for *Dermatemys*. Based on a sample of 36 eggs incubated at constant temperatures of 25, 28, and 29°C, they reported that males were produced below 28°C, both sexes at 28°C, and females at 29°C. It appears that most wild *Dermatemys* eggs are laid prior to the coolest months of the year. Episodic exposures to temperatures of 20–22°C occur between November and February, and mean nest temperatures may never exceed 25°C during those four months. Simulation of the complex environmental seasonality experienced by this "winter nesting" turtle of the northern neotropics may be desirable in future experiments.

There are several potential advantages to nesting during the late rainy season. The capability of the eggs of *Dermatemys* to withstand submersion allows it to take advantage of the unpredictable conditions of the late rainy season. If the nutritional status of *Dermatemys* is enhanced by increased access to terrestrial and emergent vegetation during high water, then the nesting season is timed to coincide with the period when fat stores should be at their maximum. This could be tested by collecting a year-round sample of measurements of the mass of the large yellow fat bodies found in the inguinal and axillary regions and adjusting those masses by the total mass of the female they were collected from.

The relationship between the vertical rise of a river and the horizontal expansion of its shoreline is probably exponential in some areas. Increased shoreline would facilitate dispersal of nesting females, which would reduce their vulnerability to predation. The same factor would allow maximum dispersion of nests. The increased vegetative cover available when streams overflow their banks could also impart some protection against predation. Although these advantages are hypothetical in the context of natural predators, they are clearly real when it comes to hunting by humans. The nests are so difficult to find that some natural protection is thereby conferred (Polisar, 1994).

Finally, depositing eggs in nests that are subsequently flooded could provide protection against predation. Congdon et al. (1983) reported that 84% of the predation on *Emydoidea blandingii* nests occurred within the first five days after nest completion. Seventy-three percent of the predation on *Chelydra serpentina* nests occurred within the first six days after nest completion (Congdon et al., 1987). Immersion of nests under water seems a clever defense against terrestrial egg predators.

The questions this paper raise will become increasingly difficult to address if numbers of *Dermatemys* become so low that capture logistics become prohibitive. In fact, the latter is already the case in most areas. Laguna Yaxha in the Petén of Guatemala, and the upper New River Lagoon and Cox Lagoon in Belize offer the rare combination of less impacted populations without prohibitive difficulty of access.

Low-income rural people who share riverine habitats with *Dermatemys* view it as a commodity roughly equivalent to a common catfish. Though disappointed if it disappears, their concern is solely economic. They are unaware of its endemism, its antiquity, or its ecological uniqueness. Scientific investigations of *Dermatemys* can emphasize its significance to decision-makers whether they be rural hunters or urban politicians. This investigation resulted in increased chances for the survival of *Dermatemys* in Belize (Polisar, 1994), but much work remains. A note to any that follow: return the research findings to their source. Basic research combined with persistent pragmatic interactions with decision-makers can help accomplish the long-term goal of maintenance of *Dermatemys* across its entire range.

Acknowledgments

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