

## Temperature Effect on Incubation Period in the Yellow-Spotted River Turtle, *Podocnemis unifilis*, in the Colombian Amazon

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**ABSTRACT.** – The nesting ecology of *Podocnemis unifilis* was studied over two years at a western Amazonian location which essentially lacks a dry season. Nest loss due to flooding over these two years would have been 64% had nests not been transferred to safer areas. Frequent rains during both nesting seasons contributed to low incubation temperatures and long nest incubation periods (from 67 to 82 days). Incubation of eggs in the laboratory confirmed the significant relationship between incubation temperature and incubation period observed in the field. Eggs incubated at temperatures varying from 27 to 32°C exhibited high hatching success rates, but with incubation periods which ranged from 104 to 48 days. Calculations based upon the regression of incubation temperature to incubation period suggest that most of the nests in this study would have hatched prior to the flooding of the beach in these two years had they experienced mean incubation temperatures of 31°C or more (temperature values typical of beaches from more seasonal parts of the range of this species). It is suggested that artificially elevating incubation temperatures of *in situ* nests might represent an alternative to transferring nests in areas where incubation temperatures are low and the risk of nest loss due to flooding also is high.

**KEY WORDS.** – Reptilia; Testudines; Pelomedusidae; Podocneminae; *Podocnemis unifilis*; turtle; reproduction; nesting; incubation temperatures; incubation periods; nest survivorships; Colombia

The yellow-spotted river turtle, *Podocnemis unifilis*, occurs in lowland freshwater habitats of tropical South America east of the Andes (Iverson, 1992). Across most of its range, nesting is confined to an annual dry season (Pritchard and Trebbau, 1984; Fachin, 1993; Soini, 1995), but populations also occur in inland equatorial regions which do not have a distinct dry season. We studied the nesting ecology of *P. unifilis* in such an area in the Colombian Amazon to document nest temperatures and determine how they influenced incubation periods. It has been shown for many reptile species that, within the thermal tolerance range of their eggs, higher incubation temperatures result in shorter incubation periods. However, this generalization is based almost entirely upon studies of eggs incubated in the laboratory at relatively constant temperatures (Packard et al., 1977, 1989; Ewert, 1979; Hubert, 1985; Packard and Packard, 1988). Here we report data from both the field and laboratory on how incubation temperatures affect incubation periods in *P. unifilis*.

### METHODS

**Study Site.** — Field work was conducted in Cahuinari National Park, Amazonas Department, Colombia (1°24'S, 70°43'W; 150 m elevation). The northern border of the park is the Caquetá River, which harbors populations of both *P. unifilis* and its larger congener *P. expansa*. The Caquetá River is a whitewater river with its headwaters to the west in

the Andes Mountains. The river floods its banks each year from approximately May to September, but river levels drop as much as 10 m during the subsequent months (Duivenvoorden and Lips, 1993), primarily due to decreased rainfall in the Andes region. Although sand beaches suitable for turtle nesting form during this period, local rains continue and contribute to erratic variations in river levels throughout the incubation period (Medem, 1960, 1969; Hildebrand et al., 1988; Duivenvoorden and Lips, 1993).

The majority of the beaches which form in the Caquetá River are flat and low (ca. 2–3 m in elevation), although along the 200 km of its course which passes through the park, two or three much higher, rounded beaches (ca. 5–10 m in elevation) also emerge each year. These high beaches are the preferred nesting sites of female *P. expansa*, which are known to migrate long distances to reach them (Hildebrand et al., 1988). Female *P. unifilis* nest on these high beaches when available, but the majority of females in this population nest on the more typical and widely available low beaches.

**Natural Incubation Studies.** — We conducted our field studies on a beach which formed in 1993 and 1994 off the northwest point of an island located in the Caquetá River immediately downstream from its confluence with the Cahuinari River (Páez, 1995; Páez and Bock, 1997). The beach was approximately 100 m wide by 500 m in length at its maximum, but never attained more than 3 m in elevation at the time of lowest river levels. Nests were located by

searching the beach every morning during the nesting season and following tracks left by nesting females.

Each year, we monitored incubation temperatures of ten nests. In 1993, all ten of the monitored clutches were laid on 11 January. In 1994, nests which had been made on two successive nights were monitored (five clutches each on 4 January and 5 January). The nests were opened to the level of the first egg (mean depth = 10 cm) and a copper-constantan thermocouple was inserted another 10 cm into the egg mass. Incubation temperatures were recorded to the nearest 0.1°C using an Omega HH-25-TC digital thermometer.

During the 1993 incubation period, we recorded temperatures in the 10 nests 119 times on 60 separate days (usually twice daily; once during the morning and a second reading during the afternoon, but at different times each day). In 1994, 86 temperature readings were recorded from the 10 nests in a similar fashion on 40 separate days. It was not normally possible to record nest temperatures at night, so the analyses reported here are limited to data collected during daylight hours (mean diurnal nest temperatures). Our data therefore overestimate actual nest temperatures and underestimate temperature variances. The magnitude of this bias was lessened, however, due to the frequent rains which fell throughout both incubation periods (Fig. 1), which effectively dampened diel cycles in nest temperatures.

We conducted an experiment to determine whether nesting females had laid preferentially in areas of the beach with specific thermal characteristics. Five locations on the beach were selected at random and a thermocouple was installed in the sand at each location to a depth of 20 cm (10 cm is the average depth to the first egg in *P. unifilis* nests; Foote, 1978; Páez and Bock, 1997). Temperatures were

recorded from these "false nests," as well as from the natural nests, twice daily over an 8 day period.

*Podocnemis unifilis* hatchlings may remain in the egg for 2–7 days after pipping the shell and may wait two weeks or more after emerging from the egg shell before making their way to the surface and emerging (Soini, 1995). However, most eggs in a clutch hatch synchronously over the period of a few days. Once most individuals in a clutch have hatched, a depression typically forms in the sand over the nest chamber. When we noticed depressions over the nests, we opened them to verify that the majority of eggs had hatched. We defined the incubation period for clutches on this beach as the number of days from oviposition to the day the majority of individuals had hatched.

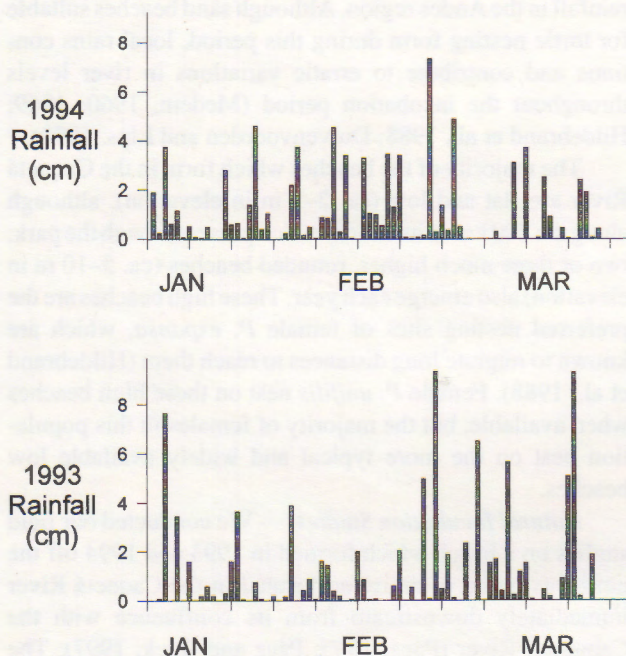
In both years, the river level rose while some clutches were still incubating. When the river threatened to inundate a clutch, the eggs were transferred (without rotation) to the highest point on the beach, where they were reburied in chambers constructed to resemble natural nests. Temperature-monitored clutches were reburied with their thermocouples, as before. In 1993, the river eventually completely flooded even the highest portion of the beach before all of the clutches had hatched, so some clutches were transferred a second time to an artificial incubation area we had prepared off the beach.

In 1993, one of the temperature-monitored nests was depredated by humans, who carefully reburied the sensor so that the act was only discovered at the end of the incubation period. Data from this nest were excluded from the analyses. In 1994, one nest also was lost to predation near the end of the incubation period. While this nest could not be included in the analysis of the effects of temperature on incubation duration, data obtained from it were used in comparisons of incubation temperatures among nests and between years.

**Laboratory Incubation Studies.** — We incubated four recently oviposited clutches in the laboratory (one clutch in 1993 and three clutches in 1994). The eggs were placed (without rotation) in semi-porous plastic bags containing a 1:1 by weight mixture of rain water and sterilized vermiculite. Three eggs per bag were half-buried in the vermiculite and the bags were sealed to conserve moisture.

We made incubators from styrofoam boxes by equipping them with thermostats and 5 Watt light bulbs as heat sources. The thermostat-light bulb units were powered by 12 Volt batteries which were kept charged with solar-voltaic panels. A thermocouple was inserted into each incubator so that its internal temperature could be recorded to the nearest 0.1°C without opening.

In 1993, eggs from the single clutch were divided randomly among two incubators adjusted to maintain temperatures of approximately 27 and 32°C. In 1994, eggs from three clutches were randomly divided among three incubators set to maintain temperatures of approximately 27, 30, and 32°C. The temperatures within each incubator were recorded three to four times daily and the thermostats adjusted when necessary.



**Figure 1.** Daily rainfall during the 1993 and 1994 incubation periods, recorded at La Pedrera, Amazonas Department, Colombia (approximately 200 km east of the study beach).

We briefly opened the incubators every other day to inspect the eggs. When the eggs began to hatch, the incubators were checked more frequently so that the exact hatching date for each egg could be determined. The incubation period for an egg was defined as the number of days from oviposition to the day the turtle completely hatched from the egg.

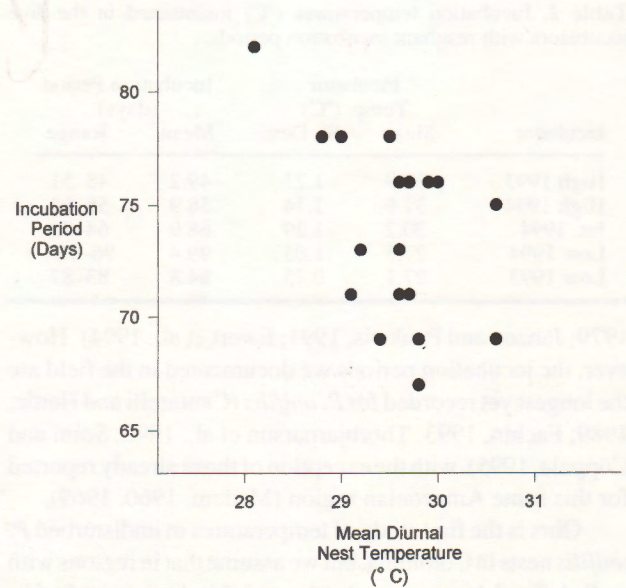
RESULTS

*Natural Incubation Studies.* — Nest loss due to flooding would have been 64% over both years if we had not transferred threatened nests (19 of 26 nests in 1993 and 18 of 32 nests in 1994). Transferring the clutches to the highest part of the beach did not significantly alter incubation temperatures, but those clutches which had to be transferred again to an artificial incubation area off the beach experienced cooler conditions (Table 1; ANOVAs, experiment-wide  $p < 0.05$ ). Mean diurnal incubation temperatures recorded from initial nest locations ranged from 28.1 to 30.6°C (mean over all nests = 29.5°C). Temperatures recorded from randomly located “false nests” did not differ significantly from temperatures recorded from actual nests (ANOVA,  $F_{(1,222)} = 0.44, p > 0.05$ ). Incubation temperatures recorded in 1993

**Table 1.** Comparison of mean diurnal incubation temperatures from natural nest locations with those recorded after transferring the clutches first to the highest part of the beach and then to an incubation area off the beach. There were no significant differences between temperatures at the highest area on the beach vs. the original nest locations, but temperatures in the third site were significantly lower. An experiment-wide significance level of  $p < 0.05$  was achieved by adjusting the acceptance criterion of individual ANOVA tests using the sequential Bonferroni technique (Holm, 1979).

	Mean temp. at	# of days at	Mean temp. at	# of days at	Mean temp. at	# of days at
	original nest location		highest area on the beach		area off of beach	
1993						
#1	28.1	61	28.9	7	26.2	14
#2	29.0	61	29.6	8	25.9	9
#3	29.2	60	29.1	9	25.5	4
#4	30.6	61	29.7	8	—	—
#5	29.5	61	29.1	7	25.8	10
#6	29.4	61	29.4	8	—	—
#7	28.8	61	30.1	8	25.7	9
#8	29.7	61	29.4	7	25.5	8
#9	29.1	60	29.2	9	25.2	2
1994						
#1	30.0	62	30.2	14	—	—
#2	29.6	73	—	—	—	—
#3	29.1	—	—	—	—	—
#4	29.8	69	—	—	—	—
#5	29.9	62	31.0	14	—	—
#6	30.6	75	—	—	—	—
#7	29.7	71	—	—	—	—
#8	29.8	67	—	—	—	—
#9	29.7	61	30.1	15	—	—
#10	29.6	71	—	—	—	—

Mean = 29.5°C



**Figure 2.** Relationships between mean diurnal nest temperature and nest incubation period, for natural nest site data only.

were significantly cooler than those in 1994 (29.3 vs. 29.8°C; ANOVA,  $F_{(1,1501)} = 14.02, p < 0.001$ ).

Nest incubation periods ranged from 67 to 82 days (mean = 73.8 days). Incubation period was negatively correlated with mean diurnal incubation temperature (Fig. 2), regardless of whether temperature data recorded after nest transfer were considered (all temperature data, Pearson  $r = -0.58, n = 18, p < 0.05$ ) or not (natural nest site data only, Pearson  $r = -0.50, n = 18; p < 0.05$ ). Although incubation periods in the two years did not differ significantly (Mann-Whitney  $U_s = 54, p > 0.05$ ), the range in incubation periods was slightly longer in 1993 (69 to 82 days) than in 1994 (67 to 76 days).

*Laboratory Incubation Studies.* — The two incubators in 1993 maintained mean temperatures that exceeded the highest and lowest mean nest temperatures recorded from the monitored natural nests, while in 1994 the three artificial incubators maintained mean temperatures at different points intermediate to these extremes (Table 2). All but one of the 88 eggs incubated in the laboratory hatched, with incubation periods ranging from 48 to 104 days (Fig. 3). Incubation periods differed significantly among the five incubators (Table 2; ANOVA,  $F_{(4,80)} = 278.56, p < 0.001$ ) and mean incubation period was negatively correlated with mean incubation temperature (Pearson  $r = -0.95, n = 5, p < 0.05$ ).

DISCUSSION

Reviews of the literature on nesting ecology in turtles have shown that those species which nest in ephemeral habitats like river beaches are also those which tend to exhibit the shortest incubation periods (Packard et al., 1977; Ewert, 1979; Packard and Packard, 1988). Our laboratory results demonstrated that when *P. unifilis* eggs are incubated at high temperatures, they complete incubation rapidly, comparable to those of most other turtle species (Ewert,

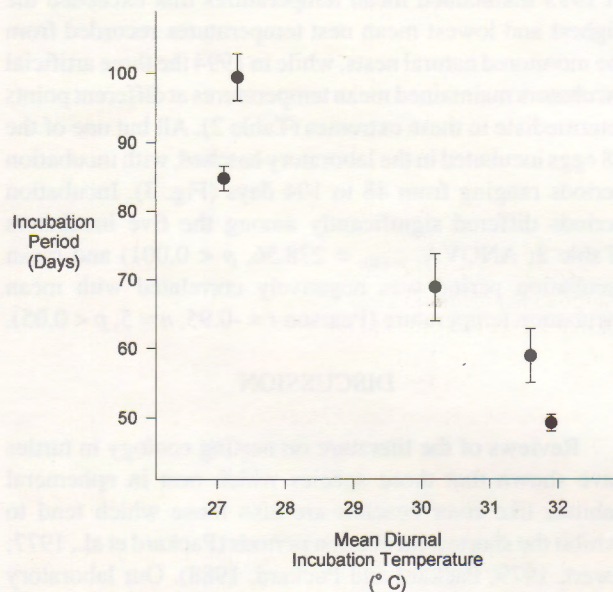
**Table 2.** Incubation temperatures (°C) maintained in the five incubators with resultant incubation periods.

Incubator	Incubator Temp. (°C)		Incubation Period (days)	
	Mean	St. Dev.	Mean	Range
High 1993	31.9	1.23	49.2	48-51
High 1994	31.6	1.74	58.9	55-64
Int. 1994	30.2	1.29	68.9	64-75
Low 1994	27.3	1.03	99.4	96-104
Low 1993	27.1	0.75	84.8	83-87

1979; Janzen and Paukstis, 1991; Ewert et al., 1994). However, the incubation periods we documented in the field are the longest yet recorded for *P. unifilis* (Cantarelli and Herde, 1989; Fachin, 1993; Thorbjarnarson et al., 1993; Soini and Cóppula, 1995), with the exception of those already reported for this same Amazonian region (Medem, 1960, 1969).

Ours is the first study of temperatures in undisturbed *P. unifilis* nests in Colombia, but we assume that in regions with well-defined dry seasons clutches exhibit shorter incubation periods because they experience warmer incubation temperatures there. A study of the nesting ecology of *P. expansa* near our site in the Caquetá River also documented mean nest incubation temperatures comparable to those reported here for *P. unifilis* (Hildebrand et al., 1988), but that were approximately 5°C lower than the incubation temperatures reported for *P. expansa* at a site with more defined seasons in Brazil (Alho et al., 1984).

Mean diurnal nest temperatures recorded in 1994 were significantly higher than those of the preceding year, which shortened the incubation periods for these nests. This difference probably was not related to differences between years in rainfall (at least there were no significant differences between 1993 and 1994 incubation period rainfall amounts recorded 200 km to the east at La Pedrera; Fig. 1; log daily rainfall, ANOVA,  $F_{(1,148)} = 0.24$ ,  $p > 0.05$ ). Rather, nest



**Figure 3.** Mean incubation periods (and ranges) for the eggs incubated in the laboratory under the five different temperature conditions.

temperature differences between years likely were the result of restructuring of beach topography from one year to the next. In 1994, suitable nesting habitat emerged off the open north side of the island, while in 1993 most nests were located directly off the island's westernmost point, where vegetation shielded them from sunlight for an hour or two on clear mornings.

Temperature variation among nests in this study was minimal, with a range in mean diurnal nest temperatures of only 2.5°C. In a study by Souza de Remor and Vogt (1994), incubation substrate grain size significantly influenced incubation temperatures in *P. unifilis* nests, but substrates on our study beach were highly homogeneous. Temperature variation among our study nests was more likely related to whether or not they were located in areas of the beach that drained surface waters after rainfalls.

Turtles of some species appear to discriminate among sites with different thermal characteristics when selecting a nest location (Carr and Carr, 1972; Stoneburner and Richardson, 1981; Schwartzkopf and Brooks, 1985). Nesting *P. unifilis* typically wandered circuitously over the beach to the actual nest site, and then returned rather directly from the nest site back to the river, which suggests that females of this species also may be assessing aspects of beach microhabitat prior to nesting. However, we found no differences between temperatures of actual nests and "false nests" we randomly positioned on this beach. Perhaps cues other than thermal characteristics are important in influencing where female *P. unifilis* oviposit, or perhaps the long pre-nesting excursions we observed simply reflect their inability to detect significant thermal differences on the relatively homogeneous beaches available in this region.

Female *P. unifilis* in this population apparently face a dilemma, in that they usually must nest on beaches characterized by both high risks of flooding and low incubation temperatures which prolong the time their incubating eggs are at risk. Previous studies have noted the high incidence of beach flooding in the Caquetá River during the turtle nesting season (Medem, 1960, 1969; Hildebrand et al., 1988; Duivenfoorden and Lips, 1993) and we documented during two successive years that the majority of nests on one typical beach would have drowned if they had not been transferred. In our study, flooding occurred in March, when most of the clutches were almost ready to hatch. Of the 12 temperature-monitored nests that had to be transferred, 10 would have emerged safely prior to flooding if they had experienced a mean incubation temperature of 31°C or higher (estimates based upon calculations using the regression of incubation period on incubation temperature obtained in the laboratory). Such incubation temperatures are well within the tolerance range for *P. unifilis* eggs and typical of beach temperatures in more seasonal areas (Alho et al., 1984).

*Podocnemis unifilis* meat and eggs have been traditional sources of protein for local peoples in South America for centuries, but throughout most of the range of the species exploitation rates presently are non-sustainable. For this reason, *P. unifilis* has been listed as threatened (IUCN, 1991)

and management projects have been initiated in Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela. Most of these projects attempt to facilitate the recovery of protected *P. unifilis* populations through the guarding, and when necessary, transfer of incubating clutches. *Podocnemis unifilis* is known to have temperature-dependent sex determination (Souza de Remor and Vogt, 1994; Páez, 1995) and this study and others (Morreale et al., 1982; Mrosovsky, 1982; Dutton et al., 1985) have shown that transferring nests to alternate incubation areas often significantly lowers incubation temperatures. Thus, while transferring nests may save clutches, it also may masculinize the sex ratio of the neonates produced. We recommend that *P. unifilis* management projects either only transfer nests after the critical middle third of the incubation period for sex determination has ended, or at least insure that transferred clutches experience comparable incubation temperatures at their new locations. This need not imply the purchase of expensive equipment such as incubators; several projects have succeeded in elevating incubation temperatures of reptile clutches by simply placing black plastic around the nest site (Alho et al., 1984; Vogt, 1994).

Regardless of how or when it is done, nest transfer is usually a time- and labor-intensive management activity. We therefore also suggest an alternative strategy appropriate for use in areas where beaches exhibit low incubation temperatures and high risks of flooding late in the incubation period. By artificially elevating incubation temperatures of *P. unifilis* nests *in situ* (by cutting back surrounding vegetation, placing black plastic near the nests, etc.), the time the clutches are at risk of flooding and predation will be reduced. This technique also will tend to feminize the sex ratio of the hatchlings produced. While manipulating population sex ratios is still a controversial turtle conservation technique (Vogt, 1994; Mrosovsky and Godfrey, 1995; Lovich, 1996), intervention to save nests is often necessary and it would seem preferable in such cases to opt for a management strategy which errs in favor of producing female biased sex ratios.

#### RESUMEN

Durante dos años estudiamos la ecología de anidación de *Podocnemis unifilis* en la Amazonía colombiana, en donde esencialmente no existe una estación de verano. A causa de la inundación, se pudo perder el 64% de los nidos en estos dos años, de no haberlos transferido a localidades seguras. Las frecuentes lluvias en ambas estaciones de anidación propiciaron bajas temperaturas de incubación, así como largos periodos de incubación (de 67 a 82 días). La incubación de nidos en el laboratorio confirmó la relación significativa entre la temperatura de incubación y los periodos de incubación, que fueron reportados en el campo. Los huevos incubados a varias temperaturas, desde 27 hasta 32°C presentaron tasas de éxito de eclosión elevadas, con rangos en los periodos de incubación desde los 104 hasta los 48 días. Cálculos basados en la regresión de la temperatura

y el periodo de incubación, sugieren que en los dos años de este estudio, la mayoría de los nidos hubiesen podido completar su incubación natural antes de la inundación de la playa, si hubieran experimentado temperaturas de al menos 31°C (temperaturas típicas de playas en áreas más estacionales dentro del rango de distribución de la especie). Se sugiere que el incremento artificial de la temperatura *en situ* de los nidos puede representar una alternativa a la transferencia de nidos, en áreas en donde las temperaturas de incubación son bajas y el riesgo de pérdida de los mismos a causa de inundaciones es alto.

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