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Reproductive Ecology of the Magdalena River Turtle (*Podocnemis lewyana*) in the Mompos Depression, Colombia

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ABSTRACT. – We studied various aspects of the reproductive biology of the Magdalena River turtle (*Podocnemis lewyana*) during 2 nesting seasons in 2 locations in the Mompos Depression in northern Colombia. We monitored 53 nests; 22 that completed incubation in situ, 24 that were transferred to protected areas (transferred nests), and 7 that were constructed using eggs removed from females that had been consumed by local people (“oviductal” nests). For each nest, we registered the oviposition date, distance to the nearest body of water, soil type, vegetative cover, exposure to sunlight, depth to the first egg, and maximum depth of the nest chamber. We also quantified egg dimensions and clutch sizes, mean incubation temperatures and duration of incubation periods, hatching success rates, and sex ratios. Most nests were located within 15 m of the shoreline, in open or grassy areas with permanent exposure to sunlight, and in sandy soils. The 3 nest types (natural, transferred, and oviductal) did not differ in hatching success rates. In both seasons, the majority of the nests produced hatchlings of both sexes, but the sex ratios differed between the nesting beaches and seasons. Incubation temperatures influenced incubation periods and hatching success rates, but not hatchling sizes or weights. The management implications of the findings are discussed.

KEY WORDS. – Reptilia; Testudines; Podocnemididae; *Podocnemis lewyana*; turtle; nesting; incubation temperature; sex ratios; Colombia

The reproductive biology of a species constitutes an important component of its overall life history strategy (Gibbons and Greene 1990; Stearns 1992); thus, obtaining information on reproductive ecology is important for turtle management and conservation (Dodd 1997; Passmore and Brooks 1997; Tucker and Moll 1997; Horne et al. 2003). Studies of turtle nesting ecology have revealed important direct and indirect effects on fitness and demography (Weisrock and Janzen 1999; Valenzuela 2001; Spencer and Thompson 2003; Moll and Moll 2004; Janzen et al. 2007; Páez et al. 2009a). The process of selecting a nesting site is important to females in an immediate sense because they are more vulnerable to terrestrial predators at this time (Spencer 2002) and because terrestrial predators also are often the major causes of nest mortality (Yerli et al. 1997; Burke et al. 1998; Escalona and Fa 1998). Nest site selection may also have indirect influences on a female’s fitness. First, in many species, incubation temperature determines the sex ratio of the clutch (Valenzuela and Lance 2004). Incubation temperature and humidity also have been shown to influence embryo metabolism, development, and survivorship, as well as incubation period and hatching success, neonate size, residual yolk mass, and hatchling performance attributes such as growth and survivorship (Congdon and Gibbons 1990; Packard et al. 1993; Tucker and Paukstis 2000). For these reasons, many studies have attempted to identify the microhabitat variables that influence thermal and hydric conditions of

nests, such as soil composition, soil grain size (Remor de Souza and Vogt 1994; Milton et al. 1997; Ferreira-J. and Castro 2003; Ferreira-J. et al. 2003), nest depth (Valenzuela 2001), and vegetative cover (Vogt and Bull 1984; Janzen and Morjan 2002). The distance of a nest from the shoreline is another important variable in nest site selection that may influence the probability that a nest will be depredated (Drummond 1983; Spencer and Thompson 2003), parasitized (McGowan et al. 2001; Hall and Parmenter 2008) or flooded (Plummer 1976; Escalona and Fa 1998), as well as influence subsequent hatchling survival (Weisrock and Janzen 1999; Kolbe and Janzen 2002).

The Magdalena River turtle (*Podocnemis lewyana*) is an endangered species endemic to the Magdalena, San Jorge, and Sinú river drainages of northern Colombia (Ernst and Barbour 1989; Páez et al. 2009b). Given the levels of intraspecific variation in reproductive ecology that have been documented in other species of *Podocnemis*, both among sites (Thorbjarnarson et al. 1993; Fachín-T. and von Mülhen 2003) and within or among nesting seasons (Foote 1978; Gibbons et al. 1982), detailed studies of the nesting ecology of *P. lewyana* at more than one site and for more than one nesting season are warranted but have yet to be undertaken. For this reason, we conducted a study of the nesting ecology of *P. lewyana* over 2 years at 2 contrasting sites within the Mompos Depression of the Magdalena River drainage in Colombia. This is the first detailed report on the nesting ecology of

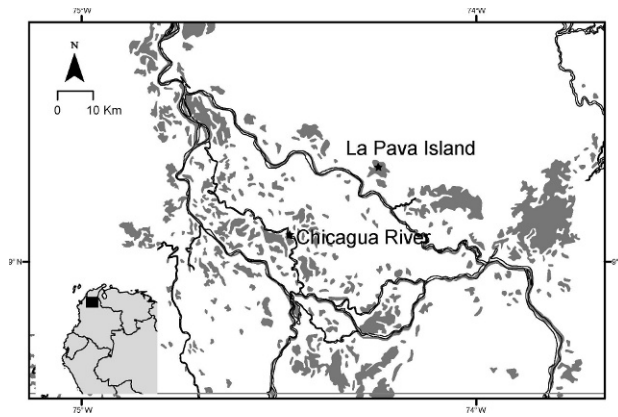


Figure 1. Location of the 2 study sites in the Mompos Depression of northern Colombia.

this endangered species (Restrepo et al. 2008; Páez et al. 2009b) that provides data necessary to develop management plans in this area.

METHODS

In 2005, we conducted field work on La Pava Island, a small island within the La Rinconada wetland (lat $9^{\circ}13'50''\text{N}$, long $74^{\circ}14'35''\text{W}$) in the northeastern region of the Mompos Depression of the Magdalena River drainage in northern Colombia (Restrepo et al. 2008). In 2006, we worked at 2 sites in the Chicagua River, which flows north through Isla Margarita, an island formed by the split of the Magdalena River into the Mompos and Loba branches (Fig. 1). The Chicagua River data obtained in 2006 were collected specifically in the Jorobado Channel (lat $9^{\circ}09'59''\text{N}$, long $74^{\circ}40'43''\text{W}$) and the nearby La Bella Island (lat $9^{\circ}10'10''\text{N}$, long $74^{\circ}70'42''\text{W}$).

In both years, we conducted field work from February to May, the peak months of nesting activity in this region. Study beaches were searched daily in the company of a local inhabitant who located nests visually or with the aid of dogs. We also obtained oviductal eggs from females that had been harvested by local people. These oviductal clutches were incubated in artificial nests constructed high on a beach on La Pava Island to minimize the risk of nest flooding. The artificial nests were constructed to resemble natural nests in terms of their size, shape, and substrate type. Hereafter we refer to these as “oviductal” nests (Table 1).

In the Jorobado Channel we also located nests by daily searches with local inhabitants and dogs. Nests that were deemed particularly vulnerable due to their proximity to the shoreline were transferred to artificial nest chambers constructed in a beach on La Bella Island to protect them from flooding and the high levels of human and natural nest predation at the Jorobado Channel site. Natural nests also were found on the La Bella Island beach, and rising river levels prompted us to transfer some

Table 1. Numbers of different nest types by year and location.

Nest type	La Pava Island (2005)	Chicagua River (2006)	
		Jorobado Channel	La Bella Island
Naturally oviposited nests	42	39	9
Depredated nests	28	16	0
Protected in situ (= natural nest)	14	7	1
Protected after transfer (= transferred nests)	0	16	8
Protected eggs from oviducts (= oviductal nests)	7	0	0

of them to the artificial nest area located higher up on the same beach. We hereafter refer to these as “transferred” nests (Table 1). In both years, all intact natural, transferred, and oviductal nests were covered with 1×1 cm mesh galvanized chicken-wire cylinders measuring 40 cm in diameter and 50 cm in height that supported a 3×3 cm plastic mesh to afford some protection from predators and permit capture of emerging hatchlings.

We collected the following data for each nest: oviposition date; distance to the nearest body of water measured perpendicularly to the shoreline; soil type classified according to its texture and humidity (Jaramillo 2002); vegetative cover (grass, shrub, leaf litter, or open) quantified using a 1 m^2 plot divided into 10 cm^2 divisions (Escalona and Fa 1998; Restrepo et al. 2006); exposure to sunlight categorized as full shade (nests that received no more than 3 hours of direct sunlight each day), half shade (nests that received up to 6 hours direct sunlight each day), and full sun (nests completely exposed to full solar radiation all day); depth to the first egg; and maximum depth of the nest chamber.

For most nests, we quantified clutch size, measured the length (x) and width (y) of each egg to the nearest 0.1 mm with digital calipers, and weighed egg mass to the nearest 0.1 g with a digital balance. We calculated egg volume using the formula $V = \pi xy^2/6$ (Vanzolini 1977). Eggs were replaced (natural nests) or transferred to artificial nest chambers (transferred nests) by burying them in the same approximate position as they were found, without rotation, to avoid embryo mortality (Limpus et al. 1979; Soini and de Soini 1995a). Eggs were manipulated only during the first 24 hours following oviposition. For a subset of unopened natural nests, we estimated clutch size at the end of the incubation period by summing the number of live hatchlings, dead hatchlings, and eggs found in the nest chamber.

Nests were inspected daily and opened at the first signs of hatching to quantify the number of empty egg shells, unhatched eggs, dead hatchlings, and live hatchlings still present. Nests that failed to show signs of hatching after 75 days of incubation were also opened. Invertebrates encountered in the eggs or nest chambers were collected and preserved in 70% ethanol for later

identification. Samples were collected from eggs with fungal infections for microscopic identification.

For each nest, we calculated the following: incubation period (duration) as the interval between the day of oviposition or removal of the eggs from the oviducts of harvested females to the day of first evidence of hatching activity; hatching success as the percentage of the oviposited eggs that hatched; predation rate as the percentage of oviposited eggs to suffer depredation by vertebrates; and infestation rate as the percentage of the oviposited eggs to suffer invertebrate or fungal infestation.

To investigate the effect of incubation temperature on the hatchlings, we monitored nest temperatures in 21 nests (6 natural nests in 2005 and 4 natural and 11 transferred nests in 2006) by burying HOBO data loggers at nest depth, 3 cm to one side of the nest chamber (so as to not disturb the clutch by placing the relatively large data loggers directly into the nest chamber). We measured the following on each hatchling: straight-line carapace length (SCL), carapace width, plastron length, and body mass (BM) using the same calipers and balance as for the egg measurements described earlier. Hatchlings were then transported to the Universidad de Antioquia, where they were sacrificed with an injection of 2% xylocaine in the axial region. One gonad was removed from each hatchling and fixed in 10% buffered formalin for histological preparation and staining with hematoxylin and eosin. Sexual determinations were made based upon the criteria of Danni and Alho (1985) and Estrada and Uribe (2002). Voucher specimens were deposited in the Museo de Herpetología of the Universidad de Antioquia (MHUA 17239–49; 17264–5; 17289–651; 17653–702; and 17713–27).

Statistical analyses were conducted using the JMP software package (SAS 1995). Mean values are presented as ± 1 SD. When data were normally distributed and variances were homogeneous, Student *t*-tests were used; otherwise, comparisons were made using nonparametric Kruskal-Wallis or Mann-Whitney tests. Frequency data were compared using χ^2 tests. Results were considered significant at $p < 0.05$.

RESULTS

During the study we measured 16 *P. lewyana* adult females and weighed 11, yielding a mean SCL of 40.1 ± 2.2 cm (range 37.4 to 44.3 cm) and a mean BM of 5.6 ± 1.8 kg (range 4.6 to 7.8 kg). At La Pava Island, we located 42 nests, 28 of which had already been depredated, and at the Jorobado Channel we located 39 nests, 16 of which had already been depredated.

We evaluated nest site characteristics for 81 nests in the 2 nesting sites (42 in 2005 and 39 in 2006), although we were unable to quantify the distance to the nearest water body for 1 nest in 2006. Combining data for both years, nest site locations ranged from 0.6 to 39.2 m

Table 2. Descriptive statistics for *Podocnemis lewyana* eggs from the Mompos Depression.

	Mass (g)	Length (mm)	Width (mm)	Volume (cm ³)
Mean	24.0	40.3	32.0	6.23
SD	3.4	3.3	2.4	1.20
Min.	17.4	27.7	19.6	2.02
Max.	31.6	49.3	33.9	8.66
<i>n</i>	274	596	596	596

distance from the nearest water, with a mean of 10.3 ± 8.4 m. When we classified nests into 5 m interval groups, the frequency of nests in each interval was not homogeneous ($\chi^2 = 56.4$; $df = 7$, $p < 0.001$; $n = 80$), with only 11 nests (13.7%) located more than 15 m from the nearest water body.

Nests were not distributed homogeneously among the 3 available soil types, with no nests located in clay substrates and significantly more nests located in sandy soils (80.2%) than in loam substrates ($\chi^2 = 29.6$; $df = 1$, $p < 0.001$). No nests were located under shrubs, but there was a significant difference in the proportion of nests in the remaining 3 categories, with 56.2% of the nests in open areas, 36.2% in grassy areas, and only 7.5% covered by leaf litter ($\chi^2 = 29.85$; $df = 2$, $p < 0.001$). Open and grassy areas did not differ in their frequency of use but were used significantly more than areas with leaf litter ($\chi^2_{\text{grass}} = 15.11$; $\chi^2_{\text{open}} = 30.77$; $df = 1$; $p < 0.001$). A significantly greater proportion of the nests were constructed in areas that received direct sunlight (87.6%) than in areas of half-shade (6.1%) or full shade (6.1%; $\chi^2 = 107.55$; $df = 3$, $p < 0.001$).

Nest chambers were asymmetrically bottle-shaped, with oval entrances leading to chambers that sloped to one side. The mean depth to first egg was 9.4 ± 3.9 cm ($n = 35$; range 3 to 18 cm), while mean depth of the nest chamber was 19.4 ± 4.6 cm ($n = 37$; range 12 to 35 cm).

Mean clutch size was 20.5 ± 4.6 eggs ($n = 64$ clutches, range 10 to 31 eggs). We measured 596 eggs and weighed 274 (Table 2). Eggs varied from roundish to ellipsoid with a slightly flexible parchment texture and pallid rosy gray color that turned to chalk white a few days after oviposition. Hatching success rates were quantified for 41 nests over the 2 years (Table 3). The 3 nest types (natural, transferred, and oviductal) did not differ in hatching success rates (Kruskal-Wallis test, $H = 5.48$; $p = 0.065$). There were no differences among years/sites in hatching success rates (Mann-Whitney test, $U = 1.13$; $p > 0.10$), with a mean hatching success rate of 36% at La Pava Island in 2005 ($n = 21$, range 0% to 100%) and 50.5% at the Chicagua River in 2006 ($n = 20$, range 0% to 90.91%). Of the 44 nests lost to predators during the 2 seasons (28 in 2005 and 16 in 2006), we observed or inferred (based on tracks) that 72.7% were consumed by the teiid lizard, *Tupinambis teguixin* (Teiidae), 25% were lost to humans, and one nest (2.2%) apparently was trampled by cattle.

Table 3. Hatching success rates (%) in natural, transferred, and oviductal *Podocnemis lewyana* nests in the Mompos Depression.

	Natural nests	Transferred nests	Oviductal nests	Total nests
Mean	40.5	57.6	21.2	43.0
SD	39	27	24	35
Range	0–100	4.5–90	0–50	1–100
<i>n</i>	20	14	7	41

In 2005, we documented that *P. lewyana* eggs were infested by invertebrates, particularly ants (Hymenoptera). The most common genera found in nests were *Solenopsis* and *Crematogaster*, although we also documented infestations by species of *Dorymyrmex*, *Campenotus*, and *Paratrechina*. Nests also were infested by hemipterans of the family Cydnidae, and larval and adult coleopterans of the families Tenebrionidae and Carabidae, as well as larvae of the dipteran family Sarcophagidae. Many nests were infested with fungi, although we do not know whether the fungi were responsible for the eggs dying or whether they opportunistically infested eggs that were unviable for other reasons. We were able to identify 5 fungi to genus or species: *Trichocladium* sp., *Scedosporium apiospermum*, *Fusarium* sp., *Penicillium* sp., and *Chrysosilia sitophila*. Mean nest infestation rate (invertebrates and fungi pooled) in natural nests was 35.3%, with a comparable rate for artificial nests (34.2%; Mann-Whitney test, $U = 0.05$; $p > 0.10$; $n = 21$). Logistic regression showed that the probability of nest infestation was not related to the distance of the nest from the nearest water body ($\chi^2 = 0.08$; $p > 0.10$; $n = 19$). Nest infestation incidence was not related to the type of vegetative cover (Kruskal-Wallis test, $H = 2.06$; $p = 0.356$; $n = 21$), substrate type (Kruskal-Wallis test, $H = 6.21$; $p > 0.10$; $n = 21$), or exposure to sunlight (Mann-Whitney test, $U = 0.39$; $p > 0.10$; $n = 21$).

Mean incubation period for all nests that hatched was 59.1 ± 8.4 days (range 50 to 89 days; $n = 32$). In 2005, mean incubation period was significantly longer than in 2006 (Table 4; Mann-Whitney test, $U = 9.70$; $p = 0.002$; $n = 32$). In 2005, mean incubation period of the natural nests was not different from that of the oviductal nests (Table 4; Mann-Whitney test; $U = 1.05$; $p > 0.10$; $n = 12$), but in 2006, mean incubation period for the natural nests was significantly longer than for the transferred nests (Table 4; Mann-Whitney test; $U = 4.5$; $p < 0.001$; $n = 20$).

Table 4. Mean incubation period (days) for *Podocnemis lewyana* nests in the Mompos Depression.

	La Pava Island (2005)	Chicagua River (2006)
All nests	64.7 ± 11	55.9 ± 3.8
Natural nests	63.0 ± 9.1	60.2 ± 3.7
Oviductal nests	69.7 ± 16.7	—
Transferred nests	—	54.4 ± 2.7

Table 5. Descriptive statistics for incubation temperatures measured in *Podocnemis lewyana* nests in the Mompos Depression.

	2005	2006		
	All nests	All nests	Natural nests	Transferred nests
Entire incubation period				
Mean (°C)	30.8	33.8	33.1	34.1
SD	1.4	0.7	0.9	0.2
Range	28.7–32.8	31.8–34.6	31.8–34.0	33.7–34.6
Middle third of incubation period				
Mean (°C)	31.4	34.0	34.0	34.1
SD	1.5	1.0	1.6	0.7
<i>n</i>	6	15	4	11

We measured 350 neonates, finding all 4 of the measured variables positively correlated (Spearman correlations, $p < 0.001$), so we here only report results in terms of SCL and BM. The neonates in 2005 were significantly larger and heavier (mean SCL: 43.2 ± 2.9 mm; mean BM: 17.4 ± 3.3 g; $n = 110$) than those obtained in 2006 (mean SCL: 42.2 ± 2.9 mm; mean BM: 15.7 ± 2.4 g; $n = 240$; Mann-Whitney test, SCL: $U = 2.60$, $p = 0.009$; BM: $U = 3.71$, $p < 0.001$). However, in neither year did neonates from the different nest types differ in BM (2005, natural vs. oviductal, $n = 110$, Mann-Whitney test, $U = 0.745$, $p > 0.10$; 2006, natural vs. transferred nests, $n = 240$, $U = -1.26$, $p > 0.10$), but they differed in size in 2006 (2005, natural vs. oviductal, $n = 110$, SCL: Student *t*-test, $t = 1.045$, $p > 0.10$; 2006, natural vs. transferred, Mann-Whitney test, SCL: $U = 7.01$, $p < 0.001$).

Mean incubation temperature for all monitored nests was $32.8^\circ\text{C} \pm 1.7^\circ\text{C}$ (range 28.7°C to 34.6°C ; $n = 21$). Mean incubation temperature for the 6 nests monitored in La Pava Island was 30.8°C , while in La Bella Island at the Chicagua River site, the mean incubation temperature recorded in the 15 nests was 33.8°C (Table 5). Considering only natural nests, mean incubation temperatures differed significantly among years/sites (Table 5; Student *t*-test, $t = 11.052$; $p = 0.006$). In 2006, the incubation temperatures of natural nests were significantly lower than temperatures of transferred nests (Table 5; Mann-Whitney test, $U = -2.663$; $p = 0.008$).

We calculated mean incubation temperatures during the thermosensitive portion of the incubation period (second third of the incubation period; Valenzuela et al. 2003), obtaining a mean for all monitored nests of $33.6^\circ\text{C} \pm 1.3^\circ\text{C}$ ($n = 21$). Based upon inspection of only data from the second third of incubation, mean incubation temperatures of natural nests were significantly lower in 2005 than in 2006 (Table 5; Student *t*-test, $t = 23.44$; $p < 0.001$; $n = 21$). In 2006, mean incubation temperatures during the second third did not differ significantly among natural nests and transferred nests (Table 5; Mann-Whitney test, $U = -0.196$; $p > 0.10$; $n = 15$). Logistic

regression showed that the probability of a nest hatching successfully was related to its incubation temperature, with lower hatching rates in cooler nests ($\chi^2 = 4.67$; $p = 0.03$; $n = 21$), although incubation temperature did not influence hatchling size (SCL: $R^2 = 0.023$, $p > 0.10$; BM: $R^2 = 0.071$, $p > 0.10$, $n = 21$). Incubation period (duration) was positively correlated with mean incubation temperature ($R^2 = 0.63$; $p < 0.001$; $n = 21$).

Sex was successfully determined for 244 neonates both by examination of the external morphology of the gonads and with histology. External determination of sex was corroborated as correct in 94% of these cases, so we assigned sex to the remaining 38 neonates for which adequate histological sections were not obtain based only on their gonadal morphology. In 2005, the sex ratio documented was 1♀:1♂, while in 2006 the sex ratio was significantly skewed in favor of females (8.4♀:1♂; $\chi^2 = 51.77$; $df = 1$; $p < 0.001$). In 2006, sex ratios also differed among natural nests (2.6♀:1♂) and transferred nests (6♀:1♂; $\chi^2 = 30.14$; $df = 1$; $p < 0.001$).

DISCUSSION

The body sizes recorded for reproductive females of *P. lewyana* at La Pava Island were within the range reported for the species elsewhere (Dahl and Medem 1964; Rueda-A. et al. 2007; Gallego-G. and Castaño-M. 2008; Páez et al. 2009a, 2009b). The range in clutch size that we documented was also similar to previous reports for females from the Sinú River (Dahl and Medem 1964; Gallego-G. and Castaño-M. 2008) and the Ayapel wetland (Castaño-M. 1986).

The fact that most nests in the Mompos Depression were located within 15 m of the shoreline suggests that females reduce their exposure to terrestrial predators (including humans) by not venturing far inland to nest. In other species of turtles an inverse relationship has been documented between the distance of nests from the shoreline and local human population density; the latter being an indirect measure of predation pressures (Moll and Legler 1971; Temple 1987; Spencer 2002; Spencer and Thompson 2003).

Both our study and that of Gallego-G. and Castaño-M. (2008) found that a majority of the nests were constructed in sand substrates, similar to reports for other species of *Podocnemis* (Vanzolini 1977; Thorbjarnarson et al. 1993; Soini and de Soini 1995b). Sand substrates warm faster (decreasing the incubation period), are more porous (offering better drainage), and do not harden upon drying (facilitating neonate emergence; Moll and Moll 2004). In contrast, excessively humid soils could lead to fungal or bacterial infestations (Garduño-A. and Cervantes-H. 1996) and restrict gas exchange between the soil and nest chamber (affecting embryo development; Congdon and Gibbons 1990; Etchberger et al. 1991).

Our data showed *P. lewyana* to nest principally in areas without vegetative cover, although females occa-

sionally used soils covered with leaf litter or low grass. The vast majority of nests were exposed to direct sunlight (87.6%), consistent with other reports of freshwater turtles that seem to prefer to place nests in open areas without vegetative cover (Moll and Legler 1971; Congdon and Gibbons 1990; Thorbjarnarson et al. 1993; Wilson 1998). These conditions presumably are optimal, as nests incubating at high temperatures have reduced incubation periods, minimizing their risks of being depredated or flooded by unpredictable, precipitous rises in water levels.

Our descriptions of the form, color, and texture of the egg shells, as well as our data on the length, width, and weight of the eggs of *P. lewyana*, agree with previous reports (Ramo 1982; Castaño-M. 1997; von Hildebrand et al. 1997; Pezzuti and Vogt 1999; Fachín-T. and von Mühlen 2003). Upon comparing our results to data published on other *Podocnemis* turtles, egg length is comparable in all species, while egg width and weight are more variable, with larger species having wider and heavier eggs (Ramo 1982; Castaño-M. 1997; von Hildebrand et al. 1997; Pezzuti and Vogt 1999; Fachín-T. and von Mühlen 2003).

The positive relationship we documented between incubation temperature and hatching success rate may have been an artifact, because nests that failed to develop for whatever reason would subsequently exhibit lower incubation temperatures than viable nests that were producing metabolic heat. Metabolic heat production has been shown to be important in other species that, like *P. lewyana*, lay relatively large clutches in deep nests (Remor de Souza and Vogt 1994; Páez and Bock 1998; Godley et al. 2001; Broderick et al. 2001; Restrepo et al. 2005). However, *P. lewyana* eggs incubated under constant but low temperatures (28°C) in the laboratory experienced higher mortality, even early in the incubation period, compared to eggs incubated at higher temperatures (Páez et al. 2009a), implying that the cool nests in the field we studied actually suffered higher mortality rates.

We found no differences in hatching success rates among natural, transferred, and oviductal nests, despite the fact that in other species like *P. unifilis* and *Chelonoidis carbonaria*, there is evidence that manipulating clutches affects hatching rates (Marcellini and Davis 1982; Soini and Cóppula 1995; Fachín-T. and von Mühlen 2003; but see Ortega et al. 2000). Our observations indicate that the teiid lizard is the principal predator of *P. lewyana* nests in the Mompos Depression, as has been shown elsewhere for other species of *Podocnemis* (Soini and Cóppula 1995; Soini and de Soini 1995b). We also detected nest infestation by a number of species of ants that voraciously attacked both eggs and recently emerged hatchlings, similar to reports in other turtles (Fowler 1979; Ramo 1982; Fachín-T. 1994; Moulis 1997; Buhlmann and Coffman 2001; Parris et al. 2002). We do not know whether the other invertebrates we found

infesting nests (cydnid hemipterans, sarcophagid and phorid flies, and coleopterans) actually killed the embryos or were merely opportunistic scavengers (Fowler 1979; Iverson and Perry 1994; Broderick and Hancock 1997; McGowan et al. 2001; Rosano-H. and Deloya 2002). More likely to cause embryo mortality were the fungi we found with hyphae growing on the external and internal surfaces of intact egg shells, which presumably affect embryo development by impeding gas exchange and calcium uptake.

We found comparable fungal infection rates in natural and oviductal nests, reaffirming that interring eggs obtained from the oviducts of sacrificed females is a viable management method to obtain hatchlings. We found no relationship between the incidence of nest infestation and environmental variables, despite our a priori expectation that nests located under vegetative cover, in the shade, and/or in moister soil substrates would be more vulnerable to ants and fungal attack than nests located in dry, sandy substrates (Fachín-T. 1994; Soini and de Soini 1995b; Garduño-A. and Cervantes-H. 1996).

Mean nest incubation temperatures documented for *P. lewyana* in the Mompos Depression were comparable to those reported for 2 transferred nests in the Sinú drainage (Gallego-G. and Castaño-M. 2008). Incubation temperatures are influenced by the interaction of climatic conditions and characteristics of the nest micro-environment (Vogt and Bull 1982; Schwarzkopf and Brooks 1987). For example, in our study nest temperatures at La Pava Island in 2005 were lower than those in the Chicagua River site in 2006, presumably because at the latter site, all nests were located in sand substrates with no vegetative cover, and most were in the full sunlight.

These differences in incubation temperature among the sites were also reflected in differences in mean incubation periods (durations), with La Pava Island nests incubating significantly longer. At La Pava Island in 2005, eggs obtained from recently sacrificed females and buried in artificial nest chambers had incubation periods comparable to those of natural nests. In contrast, at the Río Chicagua site, natural and transferred nests differed in incubation periods in 2006, presumably due to differences in environmental conditions at the site where the artificial nests were constructed.

The sex ratio differences we found between the 2 sites and years are consistent with differences in mean incubation temperatures, with more females being produced at higher incubation temperatures. While mean incubation temperature or duration of the incubation period have been shown to not be the best predictors of nest sex ratios (Georges 1989; Georges et al. 1994), this result is still consistent with laboratory studies that documented temperature-dependent sex determination in this species (Páez et al. 2009a).

The mean SCL we documented in hatchling *P. lewyana* from the Mompos Depression was lower than

previously reported for the species (Dahl and Medem 1964), and hatchlings from the Río Chicagua site were smaller than those from La Pava Island. Given that we did not monitor water potentials or humidities of the nesting substrates at either site, it is impossible to make inferences concerning differences in body size since these variables have been shown to influence hatchling size in other species (Valenzuela and Lance 2004). In 2006 the natural nests had both longer incubation periods and produced larger hatchlings, suggesting temperature also may affect hatchling size in this species (Tucker and Paukstis 2000; Páez et al. 2009a).

Studies with other freshwater turtle species (*Trachemys scripta* and *T. callirostris*) have shown that adult female size, and hence egg size and hatchling size, are influenced by the level of human exploitation a population experiences (Close and Seigel 1997; Bernal et al. 2004; Daza and Páez 2007). It is possible that sustained exploitation of *P. lewyana* has led to comparable changes in mean female, egg, and hatchling size in the Mompos Depression over historical times (Dahl and Medem 1964; this study) or currently is maintaining differences among more heavily (Río Chicagua) vs. less intensely (La Pava Island) hunted sites.

Our results indicate that nest transfer or careful interment of eggs obtained from sacrificed female *P. lewyana* did not negatively affect embryo viability, suggesting that these represent viable management methods for this threatened species (see Tucker 1995). However, such management efforts should be careful to insure that nests do not incubate at cool temperatures (less than 29°C) because such nests may show reduced hatching success rates (Páez et al. 2009a).

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RESUMEN

Durante dos temporadas de anidación estudiamos varios aspectos de la biología reproductiva de la Tortuga de Río del Magdalena (*Podocnemis lewyana*), en dos localidades de la Depresión Momposina, Norte de Colombia. En total, monitoreamos 53 nidos, de los cuales

22 fueron incubados in situ, 24 fueron transferidos a áreas protegidas (nidos transferidos), y siete fueron construidos usando huevos removidos de los oviductos de hembras sacrificadas para consumo por pobladores locales (nidos “oviductales”). Para cada nido, registramos la fecha de ovoposición, la distancia al cuerpo de agua más cercano, el tipo de suelo, la cobertura vegetal, la exposición a la luz solar, la profundidad al primer huevo y la profundidad máxima de la cámara del nido. Igualmente, cuantificamos las dimensiones de los huevos y el tamaño de la nidada, la temperatura promedio de incubación, la duración del período de incubación, el éxito de eclosión y las proporciones sexuales de los neonatos. La mayoría de los nidos fueron localizados dentro de los primeros 15 m al cuerpo de agua, en áreas abiertas o pastos, en suelos arenosos, con una exposición permanente a la luz del sol. Los tres tipos de nidos (naturales, transferidos y oviductales) no presentaron diferencias en los éxitos de eclosión. En ambas estaciones, la mayoría de los nidos produjeron neonatos de ambos sexos, pero las proporciones sexuales fueron diferentes entre playas y estaciones. La temperatura de incubación influyó tanto la duración del periodo de incubación como el éxito de eclosión, pero no el tamaño o peso de los neonatos. Se discuten las implicaciones para el manejo de la especie de nuestros resultados.

LITERATURE CITED

- BERNAL, M., DAZA-R., J.M., AND PÁEZ, V.P. 2004. Ecología reproductiva y cacería de la tortuga icotea *Trachemys scripta callirostris* (Testudinata: Emydidae) en el área de la Depresión Momposina, norte de Colombia. *Revista de Biología Tropical* 52:229–238.
- BRODERICK, A.C., GODLEY, B.J., AND HAYS, G.C. 2001. Metabolic heat and the prediction of sex ratios for green turtles (*Chelonia mydas*). *Physiological and Biochemical Zoology* 75:161–170.
- BRODERICK, A.C. AND HANCOCK, E.G. 1997. Insect infestation of Mediterranean marine turtle eggs. *Herpetological Review* 28: 190–191.
- BUHLMANN, K. AND COFFMAN, G. 2001. Fire ant predation of turtle nests and implications for the strategy of delayed emergence. *The Journal of the Elisha Mitchell Scientific Society* 117:94–100.
- BURKE, V.J., RATHBUN, S.L., BODIE, J.R., AND GIBBONS, W. 1998. Effect of density on predation rate for turtle nests in a complex landscape. *Oikos* 83:3–11.
- CASTAÑO-M., O.V. 1986. Contribución al conocimiento de la reproducción de *Podocnemis lewyana*, Dumeril 1852 (Reptilia: Quelonia: Pelomedusidae). *Caldasia* 15:71–75.
- CASTAÑO-M., O.V. 1997. La situación de *Podocnemis erythrocephala* (Spix, 1824) (Testudinata: Pelomedusidae), en Colombia. *Caldasia* 19:55–60.
- CLOSE, L.M. AND SEIGEL, R.A. 1997. Differences in body size among populations of red-eared sliders (*Trachemys scripta elegans*) subjected to different levels of harvesting. *Chelonian Conservation and Biology* 2:563–566.
- CONGDON, J.D. AND GIBBONS, J.W. 1990. Turtle eggs: their ecology and evolution. In: Gibbons, J.W. (Ed.). *Life History and Ecology of the Slider Turtle*. Washington, DC: Smithsonian Institution Press, pp. 109–123.
- DAHL, G. AND MEDEM, F. 1964. Informe sobre la Fauna Acuática del Río Sinú. Parte II. Los Reptiles Acuáticos de la Hoya del Sinú. Santa Marta, Colombia: Corporación Autónoma Regional de los Valles del Magdalena y del Sinú-CVM. 160 pp.
- DANNI, T.M. AND ALHO, C.J. 1985. Estudio histológico da diferenciação sexual em tartarugas recém-eclodidas (*Podocnemis expansa*, Pelomedusidae). *Revista Brasileira de Biologia* 45:365–368.
- DAZA, J.M. AND PÁEZ, V.P. 2007. Morphometric variation and its effect on reproductive potential in female Colombian slider turtles (*Trachemys callirostris callirostris*). *Herpetologica* 63: 125–134.
- DODD, C.K., JR. 1997. Clutch size and frequency in Florida box turtles (*Terrepenne carolina bauri*): implications for conservation. *Chelonian Conservation and Biology* 2:370–377.
- DRUMMOND, H. 1983. Adaptiveness of island nest-sites of green iguanas and slider turtles. *Copeia* 1983:529–530.
- ERNST, C.H. AND BARBOUR, R.W. 1989. *Turtles of the World*. Washington, DC: Smithsonian Institution Press, 313 pp.
- ESCALONA, T. AND FA, J. 1998. Survival of the nests of the terecay turtle (*Podocnemis unifilis*) in the Nichare-Tawadu rivers, Venezuela. *Journal of Zoology* 244:303–312.
- ESTRADA, E. AND URIBE, M.C. 2002. Atlas de Histología de Vertebrados. Primera Edición. Mexico, DF: Universidad Nacional Autónoma de México, 222 pp.
- ETCHBERGER, C.R., PHILLIPS, J.P., EWERT, M.A., NELSON, C.E., AND PRAGE, H.D. 1991. Effects of oxygen concentration and clutch on sex determination and physiology in red-eared slider turtles (*Trachemys scripta*). *Journal of Experimental Zoology* 258:394–403.
- FACHÍN-T., A. 1994. Depredación de la taricaya *Podocnemis unifilis* en la Reserva Nacional Pacaya-Samiria, Loreto. *Boletín de Lima* 16:417–423.
- FACHÍN-T., A. AND VON MÜLHEN, M. 2003. Reproducción de la taricaya *Podocnemis unifilis* Troschel 1848 (Testudines: Podocnemididae) en la várzea del Medio Solimões, Amazonas, Brasil. *Ecología Aplicada* 2:125–132.
- FERREIRA-J., P.D. AND CASTRO, P.T. 2003. Geological control of *Podocnemis expansa* and *Podocnemis unifilis* nesting areas in Rio Javaés, Bananal Island, Brazil. *Acta Amazônica* 33:445–468.
- FERREIRA-J., P.D., MALVASIO, A., AND SANTOS-G., O. 2003. Influence of geological factors on reproductive aspects of *Podocnemis unifilis* (Testudines, Pelomedusidae) on the Javaés River, Araguaia National Park, Brazil. *Chelonian Conservation and Biology* 4:626–634.
- FOOTE, R.W. 1978. Nesting of *Podocnemis unifilis* (Testudines: Pelomedusidae) in the Colombian Amazon. *Herpetologica* 34: 333–339.
- FOWLER, L.E. 1979. Hatching success and nest predation in the green sea turtle, *Chelonia mydas*, at Tortuguero, Costa Rica. *Ecology* 60:946–955.
- GALLEGO-G., N. AND CASTAÑO-M., O.V. 2008. Ecology and status of the Magdalena River turtle, *Podocnemis lewyana*, a Colombian endemic. *Chelonian Conservation and Biology* 7:37–44.
- GARDUÑO-A., M. AND CERVANTES-H., E. 1996. Influencia de la temperatura y la humedad en la sobrevivencia en nidos in situ y en corral de tortuga Carey (*Eretmochelys imbricata*) en Las Coloradas, Yucatan, Mexico. *INP. SEMARNAP. Ciencia Pesquera* 12:90–97.

- GEORGES, A. 1989. Female turtles from hot nests: is it duration of incubation or proportion of development that matters? *Oecologia* 81:323–328.
- GEORGES, A., LIMPUS, C., AND STOUTJESDIJK, R. 1994. Hatchling sex in the marine turtle *Caretta caretta* is determined by proportion of development at a temperature, not daily duration of exposure. *Journal of Experimental Zoology* 270: 432–444.
- GIBBONS, J.W. AND GREENE, J.L. 1990. Reproduction in the slider and other species of turtles. In: Gibbons, J.W. (Ed.). *Life History and Ecology of the Slider Turtle*. Washington, DC: Smithsonian Institution Press, pp. 124–134.
- GIBBONS, J.W., GREENE, J.L., AND PATTERSON, K.K. 1982. Variation in reproductive characteristics of aquatic turtles. *Copeia* 1982:776–784.
- GODLEY, B.J., BRODERICK, A.C., DOWNIE, J.R., GLEN, F., HOUGHTON, J.D., KIRKWOOD, I., REECE, S., AND HAYS, G.C. 2001. Thermal conditions in nests of loggerhead turtles: further evidence suggesting female skewed sex ratios of hatchling production in the Mediterranean. *Journal of Experimental Marine Biology and Ecology* 263:45–63.
- HALL, S.C.B. AND PARMENTER, C.J. 2008. Necrotic egg and hatchling remains are key factors attracting dipterans to sea turtle (*Caretta caretta*, *Chelonia mydas*, *Natator depressus*) nests in central Queensland, Australia. *Copeia* 2008:75–81.
- HORNE, B.D., BRAUMAN, R.J., MOORE, M.J.C., AND SEIGEL, R.A. 2003. Reproductive and nesting ecology of the yellow-blotched map turtle, *Graptemys flavimaculata*: implications for conservation and management. *Copeia* 2003:729–738.
- IVERSON, J.B. AND PERRY, R.E. 1994. Sarcophagid fly parasitoidism on developing turtle eggs. *Herpetological Review* 25:50–51.
- JANZEN, F.J. AND MORJAN, C.L. 2002. Egg size, incubation temperature, and post-hatching growth in painted turtles (*Chrysemys picta*). *Journal of Herpetology* 36:308–311.
- JANZEN, F.J., TUCKER, J.K., AND PAUKSTIS, G.L. 2007. Experimental analysis of an early life-history stage: direct or indirect selection on body size of hatchling turtles? *Functional Ecology* 21:162–170.
- JARAMILLO, D.F. 2002. *Introducción a la Ciencia del Suelo*. Medellín: Facultad de Ciencias, Universidad Nacional de Colombia, Sede Medellín, 613 pp.
- KOLBE, J.J. AND JANZEN, F.J. 2002. Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. *Ecology* 83:269–281.
- LIMPUS, C.J., BAKER, V., AND MILLER, J.D. 1979. Movement induced mortality of loggerhead eggs. *Herpetologica* 35:335–338.
- MARCELLINI, D.L. AND DAVIS, S.W. 1982. Effects of handling on reptile egg hatching. *Herpetological Review* 13:43–44.
- MCGOWAN, A., ROWE, L.V., BRODERICK, A.C., AND GODLEY, B.J. 2001. Nest factors predisposing loggerhead sea turtle (*Caretta caretta*) clutches to infestation by dipteran larvae on northern Cyprus. *Copeia* 2001:808–812.
- MILTON, S.L., SCHULMAN, A.A., AND LUTZ, P.L. 1997. The effect of beach nourishment with aragonite versus silicate sand on beach temperature and loggerhead sea turtle nesting success. *Journal of Coastal Research* 13:904–915.
- MOLL, D. AND MOLL, E.O. 2004. *The Ecology, Exploitation, and Conservation of River Turtles*. Oxford, UK: Oxford University Press, 391 pp.
- MOLL, E.O. AND LEGLER, J.M. 1971. The life history of a neotropical slider turtle, *Pseudemys scripta* (Schœpff), in Panama. *Bulletin of the Los Angeles County Museum of Natural History* 11:1–102.
- MOULIS, R.A. 1997. Predation by the imported fire ant (*Solenopsis invicta*) on loggerhead sea turtle (*Caretta caretta*) nests on Wassaw National Wildlife Refuge, Georgia. *Chelonian Conservation and Biology* 2:433–436.
- ORTEGA, A.M., BOCK, B.C., AND PÁEZ, V.P. 2000. Efecto del estado de desarrollo en el momento de la transferencia de nidos sobre la tasa de eclosión de la tortuga terecay, *Podocnemis unifilis*. *Vida Silvestre Neotropical* 7:126–131.
- PACKARD, G.C., MILLER, K., AND PACKARD, M.J. 1993. Environmentally induced variation in body size of turtle hatchlings in natural nests. *Oecologia* 93:445–448.
- PÁEZ, V.P. AND BOCK, B.C. 1998. Temperature effect on incubation period in the yellow-spotted river turtle, *Podocnemis unifilis*, in the Colombian Amazon. *Chelonian Conservation and Biology* 3:31–36.
- PÁEZ, V.P., CORREA, J.C., CANO, A.M., AND BOCK, B.C. 2009a. A comparison of maternal and temperature effects on sex, size, and growth of hatchlings of the Magdalena River turtle (*Podocnemis lewyana*) incubated under field and controlled laboratory conditions. *Copeia* 2009:698–704.
- PÁEZ, V.P., RESTREPO, A., VARGAS-R., M., AND BOCK, B.C. 2009b. *Podocnemis lewyana* Duméril 1852 – Magdalena River turtle. In: Rhodin, A.G.J., Pritchard, P.C.H., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A., Iverson, J.B., and Mittermeier, R.A. (Eds.). *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN Tortoise and Freshwater Turtle Specialist Group*. Chelonian Research Monographs No. 5: Lunenburg, MA: Chelonian Research Foundation, doi: 10.3854/crm.5.024.lewyana.v1. 2009.
- PARRIS, L.B., LAMONT, M.M., AND CATHY, R.R. 2002. Increased incidence of red imported fire ant (Hymenoptera: Formicidae) presence in loggerhead sea turtle (Testudines: Cheloniidae) nests and observations of hatchling mortality. *Florida Entomologist* 85:514–517.
- PASSMORE, H.L. AND BROOKS, R.J. 1997. Effects of geographic origin and incubation temperature on hatchling snapping turtles, *Chelydra serpentina*: implications for turtle conservation practices across the species' range. In: Van Abbema, J. (Ed.). *Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles – An International Conference*. New York: New York Turtle and Tortoise Society, pp. 195–202.
- PEZZUTI, J.C. AND VOGT, R.C. 1999. Nesting ecology of *Podocnemis sextuberculata* (Testudines: Pelomedusidae) in the Japura River, Amazonas, Brazil. *Chelonian Conservation and Biology* 3:419–424.
- PLUMMER, M.V. 1976. Some aspects of nesting success in the turtle, *Trionyx muticus*. *Herpetologica* 32:353–359.
- RAMO, C. 1982. *Biología del galápagos (Podocnemis vogli, Müller 1935) en el Hato El Frio, llanos de Apure, Venezuela*. Doñana, *Acta Vertebrata* 3:1–16.
- REMOR DE SOUZA, R. AND VOGT, R.C. 1994. Incubation temperature influences sex and hatchling size in the neotropical turtle *Podocnemis unifilis*. *Journal of Herpetology* 28:453–464.
- RESTREPO, A., JARAMILLO, U., AUBAD, P., PÁEZ, V., LÓPEZ, S., SUAREZ, A.M., AND CANO, A. 2005. Efecto de la profundidad y la distancia entre nidadas trasladadas de *Dermochelys coriacea* (Linnaeus, 1766), sobre la temperatura de incubación y supervivencia de neonatos, en la Playona, Chocó (Colombia). *Actualidades Biológicas* 83:179–188.
- RESTREPO, A., PÁEZ, V.P., LÓPEZ, C., AND BOCK, B.C. 2008. Distribution and status of *Podocnemis lewyana* in the

- Magdalena river drainage of Colombia. *Chelonian Conservation and Biology* 7:45–51.
- RESTREPO, A., PIÑEROS, V.J., AND PÁEZ, V.P. 2006. Nest site selection by female *Trachemys callirostris* (Testudinata: Emydidae) in the Mompos Depression of Colombia. *Chelonian Conservation and Biology* 7:45–51.
- ROSANO-H., M.C. AND DELOYA, C. 2002. Interacción entre trogidos (Coleoptera: Trogidae) y tortugas marinas (Reptilia: Chelonidae) en el Pacífico mexicano. *Acta Zoológica Mexicana* 87:29–46.
- RUEDA-A., J.V., CARR, J.L., MITTERMEIER, R.A., RODRÍGUEZ-M., J.V., MAST, R.B., VOGT, R.C., RHODIN, A.G.J., DE LA OSSA-V., J., RUEDA, J.N., AND MITTERMEIER, C.G. 2007. Las Tortugas y los Cocodrilianos de los Países Andinos del Trópico. Serie de Guías Tropicales de Campo No. 6. Bogota, Colombia: Conservación Internacional, 538 pp.
- SAS. 1995. JMP Statistics and Graphics Guide, Version 3. Cary, North Carolina: SAS Institute Inc., 956 pp.
- SCHWARZKOPF, L. AND BROOKS, R.J. 1987. Nest-site selection and offspring sex ratio in painted turtles, *Chrysemys picta*. *Copeia* 1987:53–61.
- SOINI, P. AND CÓPPULA, M. 1995. Informe No. 2: Estudio, reproducción, y manejo de los quelonios del género *Podocnemis* (charapa, cupiso, y taricaya) en la cuenca del Río Pacaya, Loreto-Perú. In: Soini, P., Tovar, A., and Valdez, U. (Eds.). Reporte Pacaya-Samiria: Investigaciones en la Estación Biológica Cahuana, 1979–1994. Lima, Peru: Universidad Nacional Agraria La Molina, pp. 3–30.
- SOINI, P. AND DE SOINI, M. 1995a. Informe No. 12: Ensayos de incubación de huevos de los quelonios del género *Podocnemis* (charapa, taricaya y cupiso). In: Soini, P., Tovar, A., and Valdez, U. (Eds.). Reporte Pacaya-Samiria: Investigaciones en la Estación Biológica Cahuana, 1979–1994. Lima, Peru: Universidad Nacional Agraria La Molina, pp. 169–176.
- SOINI, P. AND DE SOINI, M. 1995b. Informe No. 19: Un resumen comparativo de la ecología reproductiva de los quelonios acuáticos. In: Soini, P., Tovar, A., and Valdez, U. (Eds.). Reporte Pacaya-Samiria: Investigaciones en la Estación Biológica Cahuana, 1979–1994. Lima, Peru: Universidad Nacional Agraria La Molina, pp. 215–226.
- SPENCER, R.J. 2002. Experimentally testing nest site selection: fitness trade-offs and predation risk in turtles. *Ecology* 83: 2136–2144.
- SPENCER, R.J. AND THOMPSON, M.B. 2003. The significance of predation in site selection on turtles: an experimental consideration of macro- and microhabitat preferences. *Oikos* 102:592–600.
- STEARNS, S.C. 1992. The Evolution of Life Histories. Oxford, UK: Oxford University Press, 249 pp.
- TEMPLE, S.A. 1987. Predation on turtle nests increases near ecological edges. *Copeia* 1987:250–252.
- THORBJARNARSON, J.B., PEREZ, N., AND ESCALONA, T. 1993. Nesting of *Podocnemis unifilis* in the Capanaparo River, Venezuela. *Journal of Herpetology* 27:344–347.
- TUCKER, J.K. 1995. Salvage of eggs from road-killed red-eared sliders, *Trachemys scripta elegans*. *Chelonian Conservation and Biology* 1:317–318.
- TUCKER, J.K. AND MOLL, D. 1997. Growth, reproduction, and survivorship in the red-eared turtle, *Trachemys scripta elegans*, in Illinois, with conservation implications. *Chelonian Conservation and Biology* 2:352–357.
- TUCKER, J.K. AND PAUKSTIS, G.L. 2000. Hatching success of turtle eggs exposed to dry incubation environment. *Journal of Herpetology* 34:529–534.
- VALENZUELA, N. 2001. Maternal effects on life-history traits in the Amazonian giant river turtle *Podocnemis expansa*. *Journal of Herpetology* 35:368–378.
- VALENZUELA, N., ADAMS, D., AND JANZEN, F.J. 2003. Pattern does not equal process: exactly when is sex environmentally determined? *American Naturalist* 4:676–683.
- VALENZUELA, N. AND LANCE, V.A. (Eds.). 2004. Temperature-Dependent Sex Determination in Vertebrates. Washington, DC: Smithsonian Institution Press, 194 pp.
- VANZOLINI, P.E. 1977. A brief biometrical note on the reproductive biology of some South American *Podocnemis* (Testudines, Pelomedusidae). *Papéis Avulsos de Zoologia* 31: 79–102.
- VOGT, R.C. AND BULL, J.J. 1982. Temperature controlled sex-determination in turtles: ecological and behavioral aspects. *Herpetologica* 38:156–164.
- VOGT, R.C. AND BULL, J.J. 1984. Ecology of hatchling sex ratio in map turtles. *Ecology* 65:582–587.
- VON HILDEBRAND, P., BERMUDEZ, N., AND PEÑUELA, M.C. 1997. La Tortuga Charapa (*Podocnemis expansa*) en el bajo Río Caquetá, Amazonas, Colombia. Bogota, Colombia: Disloque Editores, 152 pp.
- WEISROCK, D.W. AND JANZEN, F.J. 1999. Thermal and fitness-related consequences of nest location in painted turtles (*Chrysemys picta*). *Functional Ecology* 13:94–101.
- WILSON, D.S. 1998. Nest-site selection: microhabitat variation and its effects on the survival of turtle embryos. *Ecology* 19: 1884–1892.
- YERLI, S., CANBOLAT, A.F., BROWN, L.J., AND McDONALD, D.W. 1997. Mesh grids protect loggerhead turtle *Caretta caretta* nests from red fox *Vulpes vulpes* predation. *Biological Conservation* 82:109–111.

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