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Reproductive Ecology of *Podocnemis erythrocephala* (Testudines: Podocnemididae) in the Lower Inírida River, Colombia

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Abstract. – The reproductive ecology of a population of *Podocnemis erythrocephala* was studied between December 1996 and April 1997 in the lower Inírida River, Orinoco basin (Guianan shield), Colombia. Peak nesting occurred between the last two weeks of December and the first two weeks of January. The nesting sites utilized by turtles in the region were flooded plains, sand beaches, or clearings in the flooded forests. The substrate varied from coarse and fine sand to clay soils with or without organic matter. Eggs are ellipsoid with hard coriaceous shells, and measured on average 41 x 26 mm. Clutch size varied from 5 to 10 eggs, with a mean of 7.2 (n = 23). Incubation averaged 90 days and 41% of nests (n = 37) produced at least one hatchling, with hatching success approximately 9.7% (n = 176 eggs). Hatchlings averaged 39.7 mm in carapace length. The temperature range in the upper part of the nest varied from 24.6 to 33.1°C (maximum reached at midday) and in the lower part of the nest from 25.9 to 31.2°C (maximum reached in mid afternoon). During the dry season this species is an important resource for indigenous people who exploit eggs, juveniles, and adults for food and sale. Other causes of losses of eggs and hatchlings were flooding and red ant (*Solenopsis* sp.) predation. Our documentation of the presence of *P. erythrocephala* in the mid-range of the Inírida River drainage expands the known distribution for the species.

Key Words. – Reptilia; Testudines; Podocnemididae; *Podocnemis erythrocephala*; turtle; ecology; reproduction; conservation; nests; nest predation; Guianan shield; Colombia

Podocnemis eryhtrocephala, known in the Orinoco region as *chipiro*, *chimpiro*, *chipire*, or *chimpire* (Fig. 1), is the smallest and least known turtle from the family Podocnemididae in the Americas; it is currently classified by the IUCN as Vulnerable (Hilton-Taylor, 2000). Its distribution is restricted to eastern Colombia, southern Venezuela, and northern Brazil (Iverson, 1992), on the western part of the Guianan shield. It has been reported to inhabit lakes and small to medium rivers of black or partially black waters (Hoogmoed and Avila-Pires, 1990).

For many years the only published information available for *P. erythrocephala* was Mittermeier and Wilson (1974), who redescribed the species and summarized available information. Later, Lamar (1986) reported collecting a juvenile from the mouth of the Inírida River in the Colombian Orinoco basin. Castaño-Mora (1997) extended the range of distribution for Colombia to the region of the lower Inírida and Atabapo rivers, reporting that during the dry season, the second-most important source of animal protein for the indigenous communities in the region (after fishing), were the eggs and meat of *P. erythrocephala*. Castaño-Mora (1997) also published the first morphometric and reproductive data for a Colombian population, and raised concern about the overexploitation of this species. This problem had already been mentioned for the Venezuelan region of the Orinoco by Paolillo (in Groombridge, 1982).

METHODS

Study Area. — The region of the lower Inírida River where the study was conducted (Fig.2) is part of the Guianan shield and has been classified as "Bosque de Campina" on sandy soil (Prance, 1978), Guyanan Biogeographic Province, Complejo Vaupés District (Hernández et al., 1992), or sandy savannas of the high Orinoco basin (Huber, 1995). The sclerophytic forest with low trees and open canopy alternates with small savannas of different types in areas of quartzitic sand pits of extreme sterility and rocky outcrops. The rivers and streams of the region correspond mainly to black waters rich in tannins coming from the sclerophytic vegetation which produces a dark amber coloration; they are extremely nutrient-poor waters. The black waters are slightly acid and generally have bottoms of white sand covered in many parts by decomposing leaves or trunks (Mago-Leccia, 1971).

Data from the HIMAT meteorological station of Puerto Inírida, Guianía (HIMAT, 1980–96) show that the climatic regimen of the area is unimodal; generally the dry season lasts from late November to March and the rainy season from late March to mid-November, with most of the region flooded during this period. The annual mean precipitation is 3175 mm with monthly peaks reached in May (650 mm), June (710 mm), and July (778 mm). The yearly mean

Figure 1. *Podocnemis erythrocephala* from Colombia. Photo: W.W. Lamar.

temperature is 26.2°C; with peaks between February and March, when it reaches more than 29°C.

Field work was conducted from 29 December 1996 to 30 April 1997 in the Orinoco River basin in two areas. The principal site was in the lower part of the Inírida River, between 3°26´49.41´´N, 67°59´29.76´´W and 3°52´30.77´´N, 67°56´06.37´´W in Caño Caimán, a blackwater affluent, and in Laguna Clara, a whitewater lake (1.66 km^2) connected with the Caño Caimán and nearby beaches and savannas (Fig. 2). The secondary site was in the lower part of the Atabapo River between 3°37´47.1´´N, 67°33´00.8´´W and 3°30´44.6´´N, 67°41´58.9´´W, in Caño Chaquita, a blackwater affluent (Fig. 2).

Data Collection. — Nests were located by walking a total of 100 km across beaches and savannas, guided by indigenous Puinaves from the community of Puerto Príncipe (Caño Caimán). For each nest we registered the following information as per Medem (1976):

a. Nest chamber: greatest and smallest diameter of the entrance, maximum depth, number of eggs, proximity to water and characteristics of the area.

b. Eggs: greatest axis (length), smallest axis (width), and weight. Egg volume was calculated by the following formulas:

1. Vanzolini (1977): $V = \pi x y^2/16$, where y was the smallest axis (least width) and x is the greatest axis (length).

2. Maritz and Douglas (1994): $V = \pi L W^2(3c^2 + 14c + 35)/210$, where L was the greatest axis (length), W the smallest axis (least width); and $c = \lambda(\sqrt{E} - 1)$, where $\lambda = 0.25$ and $E = 1.6$.

c. Temperatures: we randomly selected 18 nests for monitoring incubation temperatures, and in each we inserted three T-type thermocouples: the first over the substrate covering the nest, the second over the eggs (upper part of the nest) and the third at the bottom of the nest (lower part of the nest). The temperatures were registered with Omega digital thermometers, generally every three hours from 0600 to 2400 hrs, throughout the incubation period.

d. Incubation period: we considered the period of incubation as the time from the date we encountered the nest until

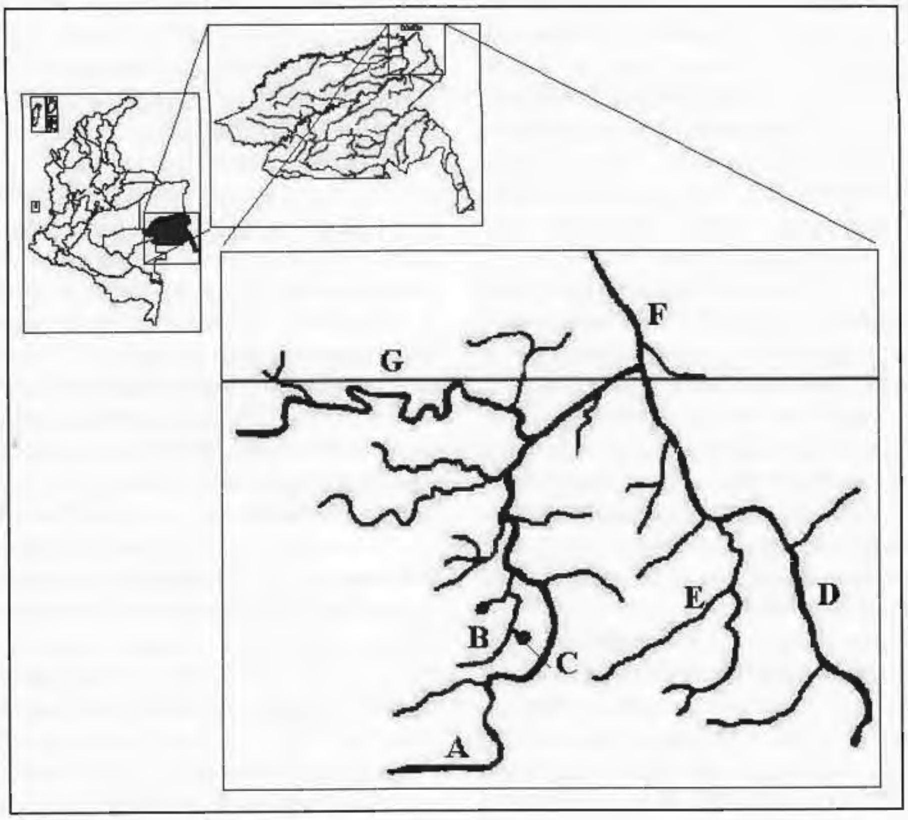

Figure 2. Study area in Colombia. A: Inírida River, B: Caño Caimán, C: Laguna Clara, D: Atabapo River, E: Caño Chaquita, F: Orinoco River, G: Guaviare River.

hatchlings emerged. We also maintained 40 eggs at ambient temperature in their original substrate inside a polyurethane box with holes in the bottom for drainage. To facilitate capture of hatchlings from natural nests, we surrounded the nests with plastic mesh (20 cm in height), sufficient to stop the hatchlings from dispersing but not enough to protect the nests from all possible predators.

e. Hatchlings: we measured each individual for straight carapace length, total plastron length, maximum breadth, maximum height, and weight.

f. Predation: nest predation was observed directly or deduced from footprints and information provided by indigeous people.

RESULTS AND DISCUSSION

It was previously believed that this species was restricted to blackwater habitats, but Vogt et al. (1991) and Rebelo (1991) registered its occasional presence in clear waters and Hoogmoed and Avila-Pires (1990) found a reproductively active population in a lake that they defined as "clear with a slight brown tint but without being completely black."

There is confusion on the classification of the types of waters present in the region of the Orinoco and the Amazon: what some authors call black water (Rebelo, 1991) is considered as clear water in other sources (Steyemark et al., 1995). In the model of classification of Sioli (1975, 1984), "white" waters originate in the Andes, are rich in nutrients, and have high conductivity; "clear" waters, generally Amazonian, have a low pH and conductivity (acidic and poor in nutrients); "black" waters are of reddish or black color (reflecting the volume observed) which have pH values usually bellow 5 and conductivities similar to distilled water. The latter drain huge sterile sand savannas covered by sclerophytic vegetation and Amazonian *caatingas* and are generally extremely poor in nutrients, and thus of an extraordinary purity.

Following this simplified model, we found populations occurring in streams and lakes with different gradations of "black" water and we registered the first population residing and reproducing in absolutely transparent and colorless "clear" water in Laguna Clara. We did not find nests or individuals of *P. erytrocephala* directly in the Inírida River or nearby areas; apparently because this turtle prefers the smaller affluents and associated lakes. Aditionally, we registered the presence of this species in streams in the mid-range of the Inírida River drainage extending its reported distributional range for Colombia.

In the area of Caño Chaquita we only found one nest, and we believe that the Curripaco Indians from this region benefit principally from adults for sale and consumption and secondarily from illegally selling hatchlings as pets, because they are not efficient in finding nests. The results refer exclusively to the area of Caño Caimán (Inírida River); the information obtained in Caño Chaquita (Atabapo River) will be used for another analysis on their population ecology (in prep.).

Nesting Sites. — The nesting sites used by *P. erythrocephala* were seasonally floodable savannas, clearings in the floodable forests, and beaches. The use of these habitats depended on the order in which they were exposed when water receded. In general, the nesting sites were similar to those from *caatingas* described by Mittermeier and Wilson (1974) and sandy beaches mentioned by Vanzolini (1977), Groombridge (1982), and Vogt (2001).

Nest substrates varied from thick and fine sand on beaches and some savannas to plain sandy to plain clay soils or with considerable organic material in other savannas and clearings of the forest. The substrates were either clear or covered with fallen leaves, or with low vegetation (principally Ciperaceae and Gramineae). Thus, the nesting sites could be grouped into two main categories: savannas and sandy beaches.

Given the complex nature of environmental influences on sex ratio and hatchling condition, thermal effects on incubation have been studied considerably in turtles; however, the relation of nest temperature to nest hydric environment and thus site selection, is also important (Vogt and Bull, 1982; Packard et al., 1987; Cagle et al., 1993). In this study, we found fresh nests in substrates varying from dry to completely saturated with water, in sandy beaches as well as in floodable savannas; this situation differs from that observed by Hildebrand et al. (1997) for *P. expansa* on the lower Caquetá River in Colombia and by Soini and Soini (1995) for the same species and for *P. sextuberculata* in the Pacaya River region, Perú, where females of these species wait for up to 8 days for beaches to dry before laying their eggs. In contrast, *P. erythrocephala*, like *P. unifilis*, may nest immediately after the river subsides, as reported by Soini and Soini (1995), and both use different types of substrates in savannas and beaches.

During the dry season, vertical fluctuations in river levels may reach up to 7 m where the river bed is most narrow. Where river banks have slight slopes, distances to the water of nesting sites on beaches and in nearby savannas may increase very quickly, so that if a nest is not detected soon after it has been constructed, it is difficult to calculate its initial distance from the water. In our study, the average distance from the water for newly constructed nests was 3.14 m ($n = 11$). Vogt (2001) mentioned that females of this species in the Rio Negro, Brazil, may nest more than 200 m inside the forests.

Nesting Season. — Even though the study began when the nesting season was already underway, in general terms the nesting dates extend from mid-December until the first two weeks of January, comparable to the Venezuelan Atabapo (Groombridge, 1982). It is not known how many times a female may nest each season in this population; Vogt (2001) found in the Rio Negro that females nested from September to November and could lay up to four clutches during the season.

Nests and Eggs. — We found 39 nests with eggs, 2 partially depredated and 37 intact. We opened 23 in order to measure nest chambers and eggs dimensions, and/or for monitoring incubation temperatures, but the remainder were

Table 1. Dimensions of the nests of *P. erythrocephala.*

	Mean	S.D.	Range	*n*
Greatest diameter of entrance (cm)	8.8	1.82	6.5-11.5	9
Least diameter of entrance (cm)	7.2	1.08	5.8-8.8	9
Depth (cm)	10.1	1.21	8.7-12.3	8

Table 2. Dimensions of the eggs of *P. erythrocephala.*

	Mean	S.D.	Range	*n*
Greatest axis (length) (mm)	41.0	2.5	31.9-47.6	116
Smallest axis (width) (mm)	27.6	1.6	20.7-31.5	116
Weight (g)	19.2	2.3	16.0-25.5	66

only opened enough to permit the introduction of thermocouples. Nests consisted of simple chambers with the anterior walls (in relation to the turtle´s position when digging) more concave than the others. The maximum breadth was in the middle of the chamber, not in the base, so in general they were very similar to those described by Ramo (1982) for *P. vogli*. Due to their fragility, we only measured dimensions of nine nests (Table 1).

Average nest depth for *P. erythrocephala* is the least of the three smallest species of *Podocnemis*: 10.1 cm (n = 8), versus 17.0 cm (n = 22) for *P. sextuberculata* (Soini and Soini, 1995), and 10.6 cm (n = 9) for *P. vogli* (Alarcón-Pardo, 1969). Inside the nest the eggs are organized in one or several layers with the uppermost between two and six cm deep. The eggs are ellipsoid, with a hard coriaceous shell, which is slightly flexible immediately after oviposition. In time or with contact with air, the shell crystallizes and becomes fragile; if eggs are extracted from the nest it becomes impossible to reaccomodate them into the nest in the same fashion.

We examined 23 nests containing a total of 176 eggs (mean 7.2 eggs per nest, range 5–10). This was less than the 5 to 14 eggs registered by Ernst and Barbour (1989) and the 4 to 18 eggs (mean 8, n = 65) recorded by Vogt (2001) for *P. erythrocephala* in the region of Barcelos, Rio Negro, Brazil. Assuming that there is a positive correlation between the size of females in a populatin and their mean clutch size, as occurs in *P.vogli* (Ramo, 1982), *P. unifilis*, and *P. expansa* (Soini and Soini, 1995), it is possible the females from Caño Caimán may not reach the maximum size registered for the species, perhaps due to the intensive predation and exploitation to which they are subjected.

According to Ernst and Barbour (1989) the eggs of *P. erythrocephala* have an average size of 43 x 27 mm, but they did not provide a range or the sample size for comparisons; Medem and Mittermeier (*pers. comm.* in Pritchard and Trebbau, 1984) provided the following ranges for comparing eggs of this species, coming from the Cuieiras River (a tributary of Rio Negro, near Manaus, Brazil): length 42–45 mm, width 27–28 mm, and weight 16.7–20 g (without providing sample sizes). Vogt (2001) reported 37–47 mm for egg length and 19–30 mm for width (n = 202). Our results (Table 2) showed similar ranges.

Comparing these means with those provided for *P. sextuberculata* (length 43.8 mm, width 26.6 mm, Soini, 1995) and for *P. vogli* (length 42.5 mm, width 25.9 mm, Alarcón-Pardo, 1969), it is clear that the eggs of *P. erythrocephala* are the least elongated and thus those with the greatest volume in relation to their length.

The calulation of volumes and surface areas of eggs has been used for evaluating hydric and gas interchange rates during incubation and changes during embryonic development, and also is useful for determining the density of eggs, and for predicting their viability. In addition to the weight and dimensions of the eggs, other variables may be used (see methods) which give more precise results. We present volumes and densities estimated via two different methods. The difference between the means of volume calculated according to Maritz and Douglas (1994) and Vanzolini (1977) exceeds 10% of the total volume (Table 3).

Table 3. Volume and density of the eggs of *P. erythrocephala.* 1 = method of Maritz and Douglas (1994), 2 = method of Vanzolini (1977).

	Mean	S.D.	Range	*n*
Volume 1 (cm^3)	16.98	2.03	12.50-23.79	116
Density 1 (g/cm^3)	1.16	0.12	0.89-1.60	66
Volume 2 (cm^3)	16.54	1.98	12.18-23.17	116
Density 2 (g/cm^3)	1.19	0.13	0.91-1.64	66

Nesting Behavior. — According to local indigenous people, in the peak of the nesting season it is possible to find many females nesting simultaneously in a small area, but as the nesting season progresses, the tendency is towards solitary nesting, contrary to the aggregated arrivals of *P. expansa* (Ernst and Barbour, 1989). During our investigation, nesting occurred from late afternoon until dawn.

The greatest densities of nests verified in this study were at Laguna Clara at a nesting beach with a density of 0.78 nests/m^2 (n = 63) and a flooded savanna in Caño Caimán with a density of 0.31 nests/m^2 (n = 57). It must be emphasized that these high densities are typical of only a very few sites among those apparently available along the channels or margins of the lake.

Monitoring of Nest Temperatures. — Of the 18 nests randomly chosen for monitoring of incubation temperatures, we could only follow 6 until the end of the hatching period. Three of them produced live hatchlings and these were the ones we included for the analysis of incubation temperatures (Fig. 3, Table 4). No apparent differences were found among average temperatures at all three depths between nests that produced hatchlings and those that failed.

The three nests that produced hatchlings were found in a clearing of a flooded forest in a substrate with a different proportion of clay and organic matter. We were not able to obtain temperatures from nests laid on sandy beaches because these were either raided by indigenous people or flooded.

The substrate covering the nest was effective insulation during the hottest hours of the day (0900–1500 hrs) and the coldest hours of the early morning (Fig. 3, Table 4). The

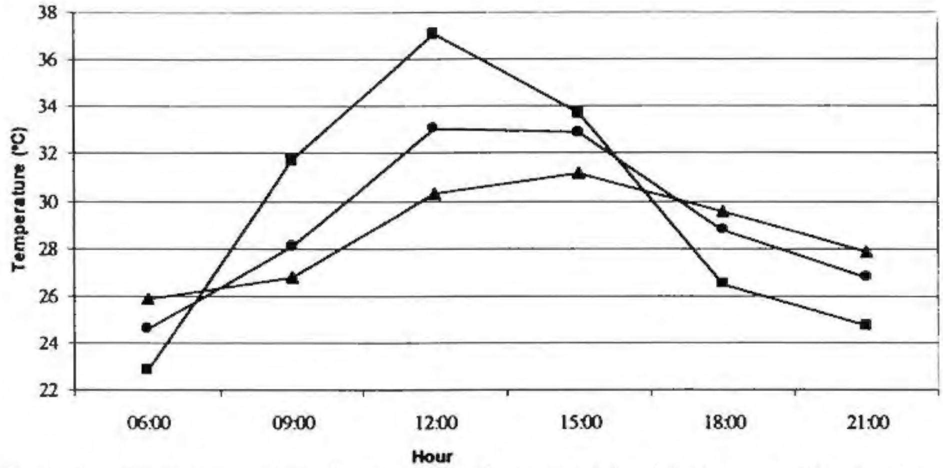

Figure 3. Average incubation temperatures in three *P. erythrocephala* nests with hatchlings. ■ = environmental temperature over the substrate; ● = temperature in the upper part of the nest; ▲ = temperature in the lower part of the nest.

fluctuation of the inner temperature of the nest depended on the variation of the environmental temperature and this influence was more direct in the upper layer of the nest. In the lower part of the nest the maximum temperature was registered aproximately three hours after the maximum environmental and upper nest temperatures were reached.

The maximum temperature in the upper part of the nesting was reached at midday (Fig. 3), for the lower part of the nests the maximum temperature was reached around 1500 hrs; the difference in the ranges of temperature between the upper and the lower part of the nest was almost 2°C (Fig. 3 and Table 4). Souza and Vogt (1994) suggested that even this difference may be enough for producing males and females in a same nest. It must be noted that the incubation temperature also depends on the characteristics of the substrate.

The only previous information about *P. erythrocephala* incubation temperatures is that of Vogt (2001) who recorded means of 30.4 and 29.5°C for two nests with ranges from 20.1 to 41.1°C. However, because he did not specify the position of the thermocouples inside the nest, it is difficult to compare his data with our resuts (Table 4).

Predation. — We believe that predation of nests located on sandy beaches is near 100%, and this agrees with Vogt´s (2001) calculations for beaches in the region of Barcelos, Rio Negro, Brazil. For other nesting sites, we estimate that less than 10% escape human predation. The second most important predator was the red ant *Solenopsis* sp. (Formicidae). The results for the 33 monitored natural nests were: 11 were flooded by a sudden rise in the water level (common during this season), 11 were invaded by *Solenopsis* sp., 6 were found with dry or decomposed eggs, 2 were depredated by *Cerdocyon thous* (Canidae), and 2 by *Leopardus* sp. (Felidae). Only one nest remained intact and all of its eggs hatched. Also, we documented predation by *Tupinambis* sp. (Teiidae) and *Panthera onca* (Felidae) and ocupation of nests by *Nasutitermes* sp. (Termitidae). It was not clear whether the latter were egg predators or secondary invadors of previously decomposed eggs. The predators and proportion of eggs damaged observed in this study differ from the reports by other authors (Fachin-Teran, 1982; Soini and Correa, 1995) for species in the Amazon with similar reproductive habits (Castaño-Mora and Galvis-Peñuela, in prep.). It is possible that some hatchlings survive with mutilations due to attacks by ants, as it is common to find mutilated turtles.

Incubation. — The mean incubation period was 90 days, ranging from 81 to 102 (n = 24, S.D. = 5.7). None of the nests where we knew the exact date of laying produced hatchlings, so the data presented are approximations that probably underestimate the actual incubation periods.

Hatchlings. — The percentage of nests that produced at least one hatchling was 41% (n = 37), while 176 monitored eggs produced 17 hatchlings, representing a hatching success of approximately 9.7%. It is not possible to make comparisons with other areas because these are the first data concerning hatching success for this species. The information about basic morphometrics of the hatchlings is summarized in Table 5.

Hatchlings obtained from nests without any disturbance had hardened carapaces and lacked traces of an external yolk sac with only a flat umbilical scar which was soft to the touch. The hatchlings that emerged prematurely due to attack by ants had softer carapaces and a prominent yolk sac,

Table 4. Ranges of incubation temperatures (°C) at three different depths in three nests of *P. erythrocephala.*

	Daily Means	Daily Range
Above the substrate	22.83–37.10	–
Upper part of the nest	24.63–33.07	18.1–45.2
Lower part of the nest	25.90–31.19	20.1–39.7

Table 5. Morphometrics of hatchlings of *P. erythrocephala.*

	Mean	S.D.	Range	n
Carapace length (mm)	39.7	2.6	35.8-47.4	22
Plastron length (mm)	34.3	1.9	30.1-37.4	22
Carapace width (mm)	32.0	2.8	24.8-36.3	22
Shell height (mm)	18.3	1.7	13.3-20.9	22
Weight (g)	12.3	1.7	7.9-15.3	21

which made it difficult for them to walk, and in contrast to normal hatchlings, they struggled weakly or remained immobile when manipulated. All hatchlings had a transverse fold in the plastron at the level of the pectoral-abdominal sutures, with the marginals curved inward, but these two characteristics were much more pronounced in premature hatchlings.

The carapace of hatchlings was brown dorsally, with a light orange border; the plastron and the marginals were salmon-yellow ventrally; the skin and head gray-brown and the head markings a dirty orange. We found no individuals with red head coloration, which disagrees with the original description of the species, or the ones from Rio Negro, as previously mentioned by Castaño-Mora (1997).

During the dry season or summer it is common to see indigenous families searching for eggs, juvenile turtles, and nesting females. The eggs are considered delicacies and turtles are hunted regardless of size, with juveniles and hatchlings sold, eaten, or given to children as pets.

Vogt (2001) viewed this species as a viable alternative as a source of animal protein for the inhabitants of the region of Rio Negro, Brazil, in terms of quality and quantity. According to our observations, the small size of the turtle and its eggs makes its food value minimal, but considering the poverty of the indigenous people and the paucity of other food resources, the turtles are very important. In the study area, the use of this species is due to cultural traditions as well as a food alternative for the indigenous people.

The incubation period represents the most vulnerable phase of the turtle's life cycle, principally due to predation by indigenous people and other predators. The people in the region acknowledge that *P. erythrocephala* densities have diminished dramatically during the last 50 years. The response of populations of *P. erythrocephala* to overexploitation is not known. It is necessary to continue investigating aspects related to *P. erythrocephala* reproduction, ecology, and demography that could help in designing management plans. Studies also are needed to establish whether other populations of *P. erythrocephala* are present in the affluents of the Amazon River inside Colombian territory and to clarify the taxonomic status of the Colombian populations.

RESUMEN. – La ecología reproductiva de *Podocnemis erythrocephala* se estudió entre diciembre 1996 y enero 1997 en el bajo río Inírida, cuenca del Orinoco, escudo Guayanés, Colombia. La máxima actividad de postura ocurrió entre las dos últimas semanas de diciembre y las dos primeras de enero. Los sitios utilizados por las tortugas para anidar fueron sabanas inundables, playas de arena o claros en bosques inundables. El sustrato varió desde arena cuarcítica hasta suelo arcilloso con o sin materia orgánica. Los huevos son elipsoidales con cáscara coriacea y midieron en promedio 41 x 26 mm. La cantidad de huevos por nido varió entre 5 y 10 con un promedio de 7,2 (n = 23). El promedio de incubación fue de 90 días y el 41% de los nidos (n = 37) produjo al menos una cría. El 9,7% de los huevos eclosionó (n = 176). Los neonatos midieron en promedio 39,7 mm de longitud. La temperatura en la parte superior de la nidada osciló entre 24,6 y 33,1°C y el máximo se alcanzó a mediodía. En la parte inferior de la nidada la varió entre 25,9 y 31,2°C y el máximo se alcanzó a media tarde. Durante la temporada de aguas bajas *P. erythrocephala* es un importante recurso para las poblaciones indígenas quienes explotan huevos, adultos, y juveniles para alimentación y comercio. Otras causas de pérdida de huevos son la inundación y el ataque de una hormiga (Formicidae: *Solenopsis* sp.). Se amplía el rango de distribución conocido en Colombia para *P. erythrocephala*.

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