Reproductive parameters and nesting behavior of the Amazon turtle *Podocnemis expansa* (Testudinata: Pelomedusidae) in Brazil

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The Amazon River turtle *Podocnemis expansa* was studied during the nesting and hatching seasons (October and December of 1978, 1979, and 1980) at a protected site in a Biological Reserve on the Trombetas River, a tributary of the Amazon. Mean carapace length of nesting females was 66 cm and mean carapace width 59 cm. Mean clutch size was 91.5 eggs (with 95% hatching success) and was positively correlated to carapace length, carapace width, plastron length, and plastron width. Carapace width was positively correlated to egg chamber height, and egg chamber diameter was positively correlated with nest depth, clutch size, and plastron width. There is a synchronization between low water and nesting.

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Une tortue de l'Amazone, *Podocnemis expansa*, a été étudiée durant plusieurs saisons de nidification et d'éclosion (octobre et décembre, en 1978, 1979 et 1980) dans un endroit protégé de la Réserve Biologique de la rivière Trombetas, un tributaire de l'Amazone. La longueur moyenne de la carapace chez les femelles pondeuses est de 66 cm et la largeur moyenne de 59 cm. Le nombre moyen d'œufs par portée est de 91,5 œufs (95% éclosent) et est en corrélation directe avec la longueur et la largeur de la carapace, la longueur et la largeur du plastron. La largeur de la carapace est associée à la hauteur de la chambre d'incubation et le diamètre de cette chambre est associé à la profondeur du nid, au nombre d'œufs et à la largeur du plastron. La nidification est synchronisée avec le moment où le niveau de l'eau est bas.

[Traduit par le journal]

Introduction

The biology of *Podocnemis expansa* has been poorly studied in South America particularly in Brazil. There exist some data on reproductive biology (Ramirez 1956; Neill 1965; Ojasti 1967, 1971; Vanzolini 1967; Foote 1978; Alho et al. 1979), conservation (Bates 1863; Valle et al. 1972; Smith 1974), and general natural history (Mosqueira-Manso 1945; Medem 1958, 1960, 1964, 1969, 1971; Roze 1964). However, few extensive field studies on the reproductive biology of this species have been conducted.

This paper reports on the behavior and reproduction of females during the nesting and hatching seasons.

Study site and methods

Data were obtained during three entire nesting seasons (October 1978, 1979, and 1980) and three hatching periods (December 1978, 1979, and 1980) at a sand beach, Tabuleiro Leonardo, on the Rio Trombetas (1°20′ S, 56°45′ W) close to the town of Oriximiná, State of Pará, Brazil. We selected this site because a program of protection of *P. expansa* sponsored by IBDF (Instituto Brasileiro de Desenvolvimento Florestal) has been in progress there since 1964. There are four apparently similar beaches in the area but turtles nest only on Tabuleiro Leonardo.

We began our observations each day at the beach late in the afternoon and observed the turtles throughout the night monitoring all activities of beach exploration, excavation, oviposition, nest filling, and compacting. We wore dark clothes, remained silent, and avoided carrying any material that might reflect moonlight. When the last wave of turtles reached the beach at dawn we filmed their behavior. During the day the turtles were observed from a distance to avoid disturbing those that were gathering to nest on the beach at night.

Any disturbance was avoided when turtles were choosing a nesting site and beginning to dig. At this time they were extremely timid and suspicious of any disturbance. However, after they began digging or laying eggs they became oblivious to our presence and finished nesting.

As soon as each individual had finished refilling the nest cavity and started to return to the water, we captured, measured, and tagged it. The length and width of the carapace across its curves and of the plastron at their widest points were measured with a tape measure. The greatest shell height was determined with calipers. A small, numbered aluminium tag was fixed with rivets to the bone underlying the posterior marginal scute. We also marked the nest to examine the egg chamber and count the number of eggs laid. The measurements of the nest cavity taken were (1) depth of the whole nest, (2) height of the egg chamber which is located at the bottom of the cavity, and (3) the diameter of the egg chamber. Since the conservation program at the Trombetas site, including the marking of females, has been in effect for 14 years, we could

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easily identify mature females marked in previous years. Turtle size also helped separate age classes.

A total of 393 adult females and their respective nests was measured during the nesting season in 1978. During the hatching season, 5482 nests were examined after hatching to check for egg shells and unhatched eggs to estimate clutch size. Nesting population size was estimated based on the number of clutches. Temperature data were collected with an automatic thermograph with the bulb placed inside an egg chamber. Data were obtained from day of egg laying through day of eclosion. Temperature was also measured by a thermometer buried just below the sand. Ambient temperatures were collected from a station at Mineração Rio do Norte, 50 km away.

There were always two trained observers during all nights of the nesting season and, in addition, four helpers to capture the 393 adult females for measurement and to do the total count of nests after hatching.

In 1978 we sampled during three successive nights, marking each animal (168 total) on the beach with a colored spot on its carapace. Each night we used a different color to determine if the same individual returned to the beach more than one night.

Results

When the turtles reached the nesting beach, they remained offshore for about 15 days with their heads out of the water and oriented toward the beach. Hundreds of heads were observed during the hottest hours of the day (1100 to 1500). During the initial phase of nesting behavior we observed turtles aggregating 10–50 m from the beach. The turtles would sit, heads out of the water at night and during the day they would bask (Fig. 1). During the day, when individuals moved into the beach to bask, a few turtles occasionally bent their heads downwards and touched their noses to the sand on the nesting beach. Others raised their heads as if apparently smelling the air. In 1978, the nesting season lasted from 13–25 October. About 10 days before nesting started the turtles were found gathering close to the beach. In 1979 the nesting period started on 5 October but the females stopped the nesting activity on 9 October, because of the sudden unusual rise of the waters (known in the Brazilian Amazon as a "repiquete"). After the water stabilized at a lower level the nesting behavior started again at the end of October. In 1980 again, unusually high water occurred at the beginning of the hatching season on 8 December. Only about 2000 turtles hatched that year.

During the nesting season, each night 200–500 turtles were observed on the beach. They moved towards the beach quietly and slowly emerged from the water in waves of approximately 20 individuals. These individuals were oriented in a line at an oblique angle to the edge of the beach. They walked around, sometimes two individuals colliding, their shells producing a cracking noise. Most of the turtles in the area of the collision returned rapidly to the water. Some individuals took 2 h to reach the nesting grounds from the water, a distance of 50 m.

From evening through early morning females moved ashore to nest. Morphological and reproductive data from females of our study site are presented in Table 1. Female weights ranged from 15 to 46 kg ($N = 160$, $\bar{x} = 25.8 \pm 8.12$ SD). In 1978, about 5000 females nested in Tabuleiro Leonardo producing about 400 000 hatchlings; in 1979, 6823 females produced about 580 000 hatchlings. The smallest nesting female had a carapace length of 50 cm. The majority of nests were constructed on the top of sand mounds on the beach. There were two large elevated areas, 50–100 m far from the water, each having an area of about 2000 m^2, where the highest nest concentrations occurred. Beyond these two areas, nests were scarce. The egg chambers in these two elevated areas were located between 162 and 167 cm above the water level, whereas the egg chambers on the other areas were located between 76 and 79 cm above the water.

In 1978, 1979, and 1980 turtles mostly nested in these elevated areas.

We applied Morisita's index to study the spatial distribution of the nests on the beach (Morisita 1962, 1964). An aggregated distribution of the nests was found (I delta = 5.33; $N = 25$; $n = 259$; $F = 46.61$, where I delta is the index of aggregation, N is the number of samples, and n is the number of nests).

We have never found multiple clutching even though in a preferred area the turtle can dig the nest close to another or even destroy an existing nest to build another. The latter was common in the concentrated nesting areas where hundreds of unearthed eggs littered the ground.

We wished to test whether the smaller females nested later in the nesting season, after the more mature females. Since clutch size was positively correlated with carapace length, carapace width, plastron length, and plastron width ($r^2 = 0.35$, $N = 393$, $P < 0.001$), then if older females laid earlier, mean clutch size should decrease as egg laying occurs later in the nesting season. Although mean clutch size varied significantly during the nesting season (Table 2), there was no significant correlation between clutch size and day of nesting ($r^2 = 0.07$, not significant). We performed a Duncan's multiple range test to determine if a relationship existed between mean clutch size and a certain period of the nesting season. Although no apparent association was detected (Table 3), days 1–9 and 21–24 had low clutch sizes, i.e., the beginning and end of the season. The reasons for higher mean clutch sizes during the middle of the season are not yet clear.

To determine whether or not *P. expansa* females lay all their eggs on one night or whether they lay more than once, 168 females were marked with paint on the nesting

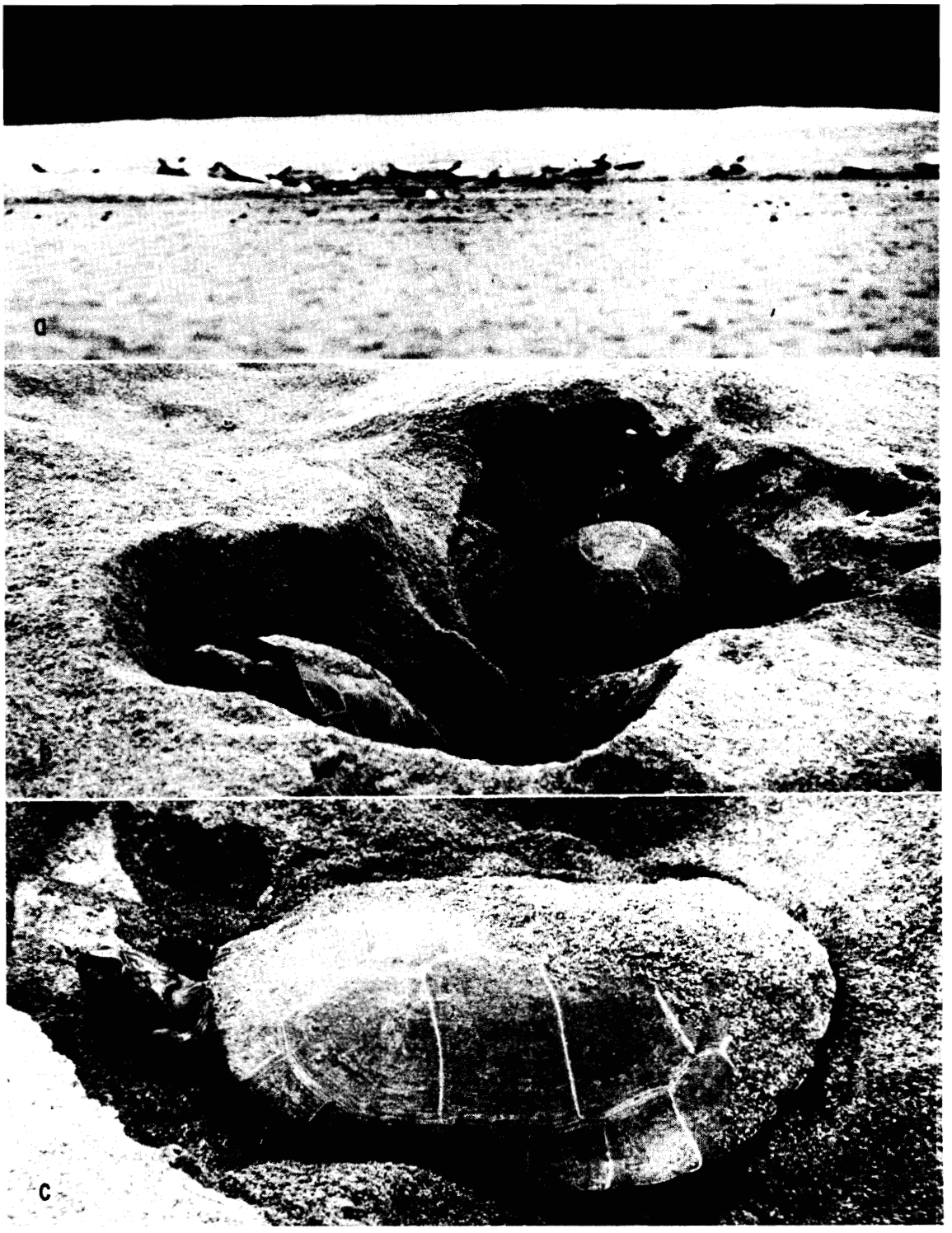

FIG. 1. Photographs of the three most important phases of the nesting behavior. (*a*) Turtles (25–30 females) 10–50 m offshore and basking on the beach. Heads can be seen out of the water. (*b*) Two females laying. (*c*) Filling the nest and compacting the sand.

TABLE 1. Measurements of nesting female *P. expansa* (in centimetres) and their reproductive parameters ($N = 393$), 1978–1979

Variable	Mean	Standard deviation	Minimum value	Maximum value	Coefficient of variation
Carapace length	66.00	3.06	50.0	80.0	4.62
Carapace width	59.00	2.44	36.0	70.0	4.15
Plastron length	54.50	3.27	40.0	63.0	6.01
Plastron width	50.00	3.16	37.0	60.0	6.32
Nest cavity depth	64.00	13.96	43.0	80.0	21.65
Egg chamber depth	18.16	2.13	15.0	20.0	11.76
Egg chamber diameter	15.50	0.54	15.0	16.0	3.53
Clutch size	91.50	22.10	63.0	134.0	24.16
Hatchlings per nest	85.98	21.10	53.0	128.0	32.13

TABLE 2. Analysis of variance table showing the number of eggs of *P. expansa* laid per day during the nesting season of 1978

Source of variation	Degrees of freedom	Sum of squares	Mean square	Coefficient of variation	*F* value	R^2
Model	24	176 075.94	7 336.49	22.01	17.47*	0.0697
Error	5 595	2 350 133.24	420.04			
Total	5 619	2 526 209.18				

*$P < 0.01$.

beach. Of these, 151 turtles (90%) successfully nested on the night of their marking and they were not seen again. Only 17 (10%) were found again, in all cases successfully nesting on the night of their subsequent sighting. The nests begun but abandoned by those 17 individuals were examined on the following morning. In 11 cases (65%) water was found in the bottom of the pit, and in 6 cases (35%) the nests were on hard soil.

The nest digging operation was a sequence of integrated stereotyped movements. The first movement was to thrash out the nesting pit by violent throwing of sand with all feet. A broad depression of about 1.2 m diameter was dug where the sand was soft and of smaller diameter where the soil was compact. The body meanwhile rotated slowly. The female continued digging until she had lowered herself several centimetres below the surface of the sand. When the nest became deeper, the back feet had more function in scraping the sand. With the nails downward, one hind foot was inserted into the enlarging egg chamber, pressed to the bottom, and moved around the circular edge, molding the exact shape. The foot was cupped, and the outer edge was pointed inwards. The other hind foot remained flat, relaxed near the egg cavity or supported the inclined body of the turtle. Meanwhile the two front feet helped support the animal. The turtle shifted its body so the other hind foot came into position over the hole and repeated the process with this foot. Thus the hind feet were used alternately for digging. The other foot touched the chamber wall and then moved in a circular path, catching the loose sand and throwing it out of the hole. The front feet helped by sweeping sand backwards.

The nests were flask shaped and extended to a depth of 75–80 cm. The nesting pit was bowl shaped and had a diameter of 80–100 cm. Usually the actual nest cavity was displaced to one side of the center of the nesting pit. This pit could only be located the morning following the nesting night. When the surface sand dried a few hours later, the nest could no longer be located by sight. Table 4 shows the relationship between turtle size and different measurements of the nest cavity.

As soon as the egg chamber was ready, the tail was inserted and the body of the turtle covered the cavity opening. The animal's position in relation to the surface was at an angle greater than 60°. During the laying process the neck stayed outstretched with the head up (Fig. 1). When all of the eggs were laid, nest covering and nest compacting began immediately. The sand was packed with the plastron, the animal raising its body on its legs and suddenly relaxing them, particularly the hind ones, causing the falling body to pound the sand. The loose sand was then pressed by the plastron which rotated constantly over the nest. During the filling and packing process the head was also raised and the animal produced tears. The noise of compacting or pounding could be heard a couple of meters away. When crawling off the nest, the turtle usually left a trail of a liquid expelled from the cloaca. The inclined position of the tail, pointing into the sand surface, was also a good indicator that the turtle had laid. She moved only 3–5 m

TABLE 3. Duncan's multiple range test for the variable clutch size during the 1978 nesting season of *P. expansa*

Number of nests	Clutch size mean	Day of the nesting season	Grouping
361	98.36	10	A
374	97.85	18	B
457	97.70	15	
210	97.60	11	
385	97.29	17	
307	96.61	16	
392	96.59	20	C
365	96.04	13	D
300	95.75	19	
475	94.03	14	
185	93.00	12	E
158	91.63	9	F
15	91.00	1	
122	90.54	8	
31	88.12	2	
254	87.25	22	
306	87.13	21	
189	86.01	7	
125	85.38	5	
188	85.19	23	G
56	83.85	3	
70	83.01	4	
156	81.69	6	
97	76.48	24	

NOTE: Means with the same letter are not significantly different. $\alpha = 0.05$, df = 5595.

and stopped for about 30 s. If pursued she did not move quickly.

The mean incubation time was 48 days. The incubation period occurred during the hottest time of the year at Trombetas, when the overall mean temperature was 30°C as compared with 26–27°C during other months of the year. The sand temperature at the surface reached 60°C. The temperature in the egg chamber during the entire incubation period is shown in Fig. 2.

The eggs are spherical with a parchment-like surface, changing from pliable to brittle-shelled within 24–28 h after being laid. Egg diameter ranged from 32 to 54 mm ($N = 130$, $\bar{x} = 39.1 \pm 3.5$ SD). Egg weight ranged from 18 to 52 g ($N = 161$, $\bar{x} = 32.6 \pm 6.6$ SD). Clutch weight ranged from 3189 to 4112 g ($N = 41$, $\bar{x} = 3673 \pm 3.1$ SD). In each clutch there were one or two bigger eggs which local people call the "oil egg" (diameter ± 54 mm, egg weight ± 52 g), and these eggs never hatch.

TABLE 4. Carapace length, carapace width, shell height, and body weight of *P. expansa* at time of hatching (December 1978, 1979, and 1980) ($N = 240$)

Measurement	Minimum	Maximum	$\bar{x}$	SD
Carapace length (mm)	53	59	55.1	1.19
Carapace width (mm)	54	59	55.3	1.09
Plastron length (mm)	45	47	46.0	0.62
Plastron width (mm)	37	41	40.0	0.86
Shell height (mm)	19	22	22.0	1.05
Weight (g)	21	23	21.7	0.44

On hatching, small turtles dig to a level 20 cm from the surface. This movement creates a kind of funnel in the sand particularly easy to recognize after a rainy night. There are at least two hatching waves within one clutch. First about 60% of the eggs hatch and the first group of small turtles move to the area near the surface. The second wave is still unhatched in the base of the nest. About 3 days later, the remaining eggs hatch. This second wave moves to join the first group. The hatchlings leave the nest cavity at night, particularly on rainy ones. Hatchlings are extremely active during the night, particularly between 18 and 23 h. Table 5 shows measurements and weight of the hatchlings. Nine nests were covered with fences to trap the hatchlings and in each of the enclosures, 80% of the hatchlings were concentrated in the lower part of the cage trying to go in the direction of the water. Some of them climbed the fence and ran directly to the river. We also followed some hatchlings, maintaining a considerable distance from them, confirming their migration directly to the water.

Very little predation was observed on the nest. Only

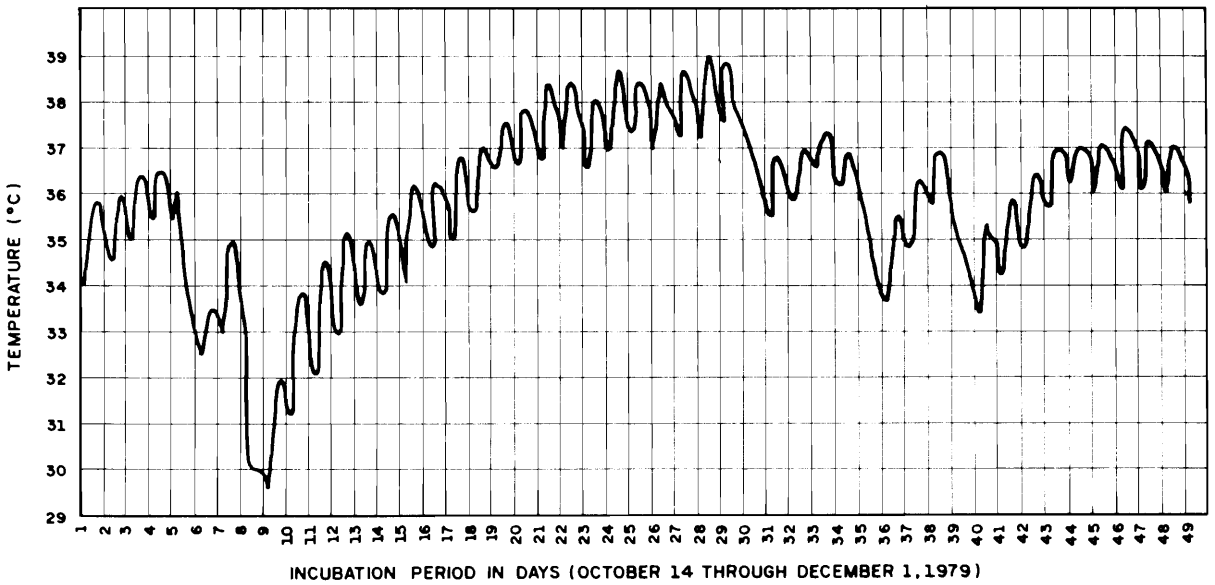

FIG. 2. Temperature in the egg chamber during an entire incubation period.

TABLE 5. Reproductive characteristics and morphological traits of *P. expansa* from regression analysis

Dependent variable (y)	Independent variable (x)	Intercept (a)	Slope (b)	r^2
Clutch size	Egg chamber diameter	42.91	2.87	0.1374
Carapace width	Egg chamber depth	50.04	0.44	0.1221
Nest depth	Egg chamber diameter	2.06	−0.04	0.1915

NOTE: Correlation coefficients are all significant. $P < 0.01$, $N = 393$.

those eggs removed by other turtles and found on the beach were eaten by black vultures and gulls early in the morning. Fishes we collected near the nesting beach contained small turtles in their stomachs.

Discussion

Carr and Giovannoli (1957), Vanzolini (1967), Alho et al. (1979), and Ehrenfeld (1979) recognized seven phases of turtle nesting behavior: (1) aggregation of the population in shallow water, prior to landing, (2) landing and reaching the nesting grounds, (3) deambulation or beach exploration, (4) excavation of the nest, (5) laying, (6) filling the nest, and (7) returning to the water. Our observations matched these phases; however, the duration of each phase may be variable.

We have not found any evidence that *P. expansa* uses its tail to arrange the eggs during laying as Foote (1978) pointed out for *P. unifilis*.

The age at which females start reproducing is not known; however, onset of sexual maturity in most chelonians correlates more with attainment of some minimum size than with age (Cagle 1950; Legler 1960; Gibbons 1968; Ernest 1971). Based on the measurements taken on the nesting beach, onset of maturity in *P. expansa* occurs at a minimum carapace length of 50 cm.

Determining the sex through sexual dimorphism (comparing the tail size with the body size) is only possible when animals are of reproductive age. Subadults with a carapace length less than 50 cm are difficult to sex.

During the nesting season, adult turtles migrate from lakes connected to the rivers to selected areas of river beach. The migration of adult males and females coincides with the ebbing regime of the river, the nesting season being more or less synchronized with lowest water. During high water males and females are in the lakes, hunters catching both sexes. As soon as the water starts lowering the animals no longer can be caught in the lakes and soon, in later September and early October, can be seen gathering close to the beach. We have caught two males in the water close to the beach but we have never seen a male on the sand beach. At lowest water, after having gathered close to the nesting beach, nesting behavior starts. If a sudden rise of the water

occurs, turtles stop nesting to resume later when the river water subsides again. Lower water appears to be the environmental factor that triggers the nesting of *P. expansa*. In the case of *P. expansa* the favored nesting beach is inundated until the dry season.

The unpredictability of the water levels in the Trombetas River is an important selective factor influencing the timing of laying of *P. expansa*. The rapid rise of the water in 1980 killed 99% of the eggs in contrast to 1978 and 1979, when 95% of the eggs successfully hatched.

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