

Influence of Geological Factors on Reproductive Aspects of *Podocnemis unifilis* (Testudines, Pelomedusidae) on the Javaés River, Araguaia National Park, Brazil

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ABSTRACT. – *Podocnemis unifilis* nests in extensive sandbanks on the margins of the Javaés River in Araguaia National Park, Tocantins State, Brazil. These sandbanks are made up of sedimentary deposits of diverse constituents which combine in a complex textural and granulometric arrangement. In morphological terms, the sandbanks, which are referred to as beaches, can be divided into two categories of nesting sites: shoals and flat areas near the river channel, and areas in front of sand dunes. The turtles nest in shallow pits 12–25 cm deep, and their eggs are subject to intense predation by birds and reptiles. In the 1999 season, all turtle nests deposited in the shoals and flat areas adjacent to the river were depredated. The only nests not depredated were those located at the foot of sand dunes, where, due to wind action, the beach sediments are continuously re-worked and deposited along the front portion of the dunes on top of the nests. The piling up of sediments on these nests was, on average, over 10 cm, with additional depths of up to 36 cm being recorded, providing extra protection for the eggs and allowing successful incubation.

KEY WORDS. – Reptilia; Testudines; Pelomedusidae, *Podocnemis unifilis*; turtle; nesting; dune; reproduction; sandbanks; geology; Brazil

The *tracajá* turtle (*Podocnemis unifilis*), along with the giant Amazonian river turtle (*Podocnemis expansa*), is one of the most important and well-known pelomedusids in the Amazon and Tocantins-Araguaia river basins. The intense hunting pressure on these animals during the first centuries of the occupation of the northern and central-western regions of Brazil caused population declines that were aggravated by slow recruitment (IBAMA, 1989). These turtles were widely used as food sources by people dwelling on the river margins; indeed, prior to the 20th century, they were their main source of animal protein.

The result of these long years of exploitation was that the animals were threatened with extinction and this led government authorities to establish the Centro de Conservação e Manejo de Répteis e Anfíbios (RAN), an agency which is currently subordinate to the Instituto Brasileiro de Recursos Naturais Renováveis (IBAMA). The work undertaken by RAN is related to the management of the turtles, both in the wild and in captivity, the study of biological aspects of their reproduction and ecology, and the inspection and control of protected areas.

In Tocantins State, a RAN base was established at the northern part of Araguaia National Park, along its western border, defined by the Javaés River. In this area, human interference is small, and the characteristics of the physical environment provide favorable conditions for turtle populations.

Studies undertaken on the Javaés River during *P. unifilis* nesting and hatching seasons show that the choice of nesting site by *P. unifilis* could influence the incubation stages, and

for the eggs to hatch, some geological conditions could influence the process. These two areas of knowledge, geology and the reproductive biology of turtles, may seem quite distinct, but their interplay can soon be resolved by a practical example of the direct relationship which exists among the following factors: sex determination, incubation temperature, and sediment type. A large number of chelonians exhibit temperature-dependent sex determination, including marine turtles (Yntema and Mrosovsky, 1980; Spotila et al., 1987; Mrosovsky and Provancha, 1989), freshwater turtles (Alho et al., 1985; Bull, 1985; Souza and Vogt, 1994; Valenzuela et al., 1997) and tortoises (Eendebak, 1995). Milton et al. (1997) pointed to the importance of the mineralogical composition of the substrate, since quartz sand can be up to 3.4°C warmer than carbonate sand under identical insolation regimes. The depth of the nest can also affect temperature (Burger, 1976; Wilhoft et al., 1983; Thompson, 1988; Milton et al., 1997), as can the location of a nest in relation to vegetation (Vogt and Bull, 1984; Janzen, 1994), or the coastline (Spotila et al., 1987). It is crucial to understand how the various elements involved in temperature control may vary if one is to come to any conclusions about incubation conditions and their influences on sex determination in turtles.

This study focuses on the relationship between the choice of nesting site by *P. unifilis* and the influence of the geological environment on the incubation and hatching period. The nests of *P. unifilis* on the Javaés River are subject to heavy predation by birds (the caracara, *Polyborus plancus*, and vultures, *Coragyps atratus* and *Cathartes aura*) and

reptiles (the tegu lizard, *Tupinambis teguixin*), since the egg clutches are laid in very shallow pits which facilitates predation. Nonetheless, some nesting sites, such as at the foot of sand dunes, offer extra protection to the nests and facilitate successful embryonic development and hatching of the young.

METHODS

Study Site and Physiography. — The research was conducted on the Canguçu, Jaburu, and Marreca beaches on the Javaés River in Araguaia National Park (Fig. 1). The Jaburu and Marreca beaches have similar geomorphological characteristics in terms of their dimension, positioning, and height in relation to the river level. These two beaches are located on the left bank of the Javaés River where there is a

concentration of smaller sandbanks as compared to those which occur on the right bank. In the dry season (May to November), when the rivers are low, the length of the beaches is around 800 m each and the width varies between 250 and 350 m (Fig. 2). The upstream portion of the beaches is low-lying in relation to the river level, but their height increases continuously in the downstream direction, reaching elevations of up to 3 m in the final sections. The Canguçu beach, situated on the right bank of the Javaés River, has a distinct morphology, and larger in size than the Jaburu and Marreca beaches; its length exceeds 3200 m and its width is over 400 m.

Sedimentology. — Because this paper deals with procedures and terms which are beyond the scope of conventional biology, this section will begin with a brief overview of the geological processes associated with river dynamics.

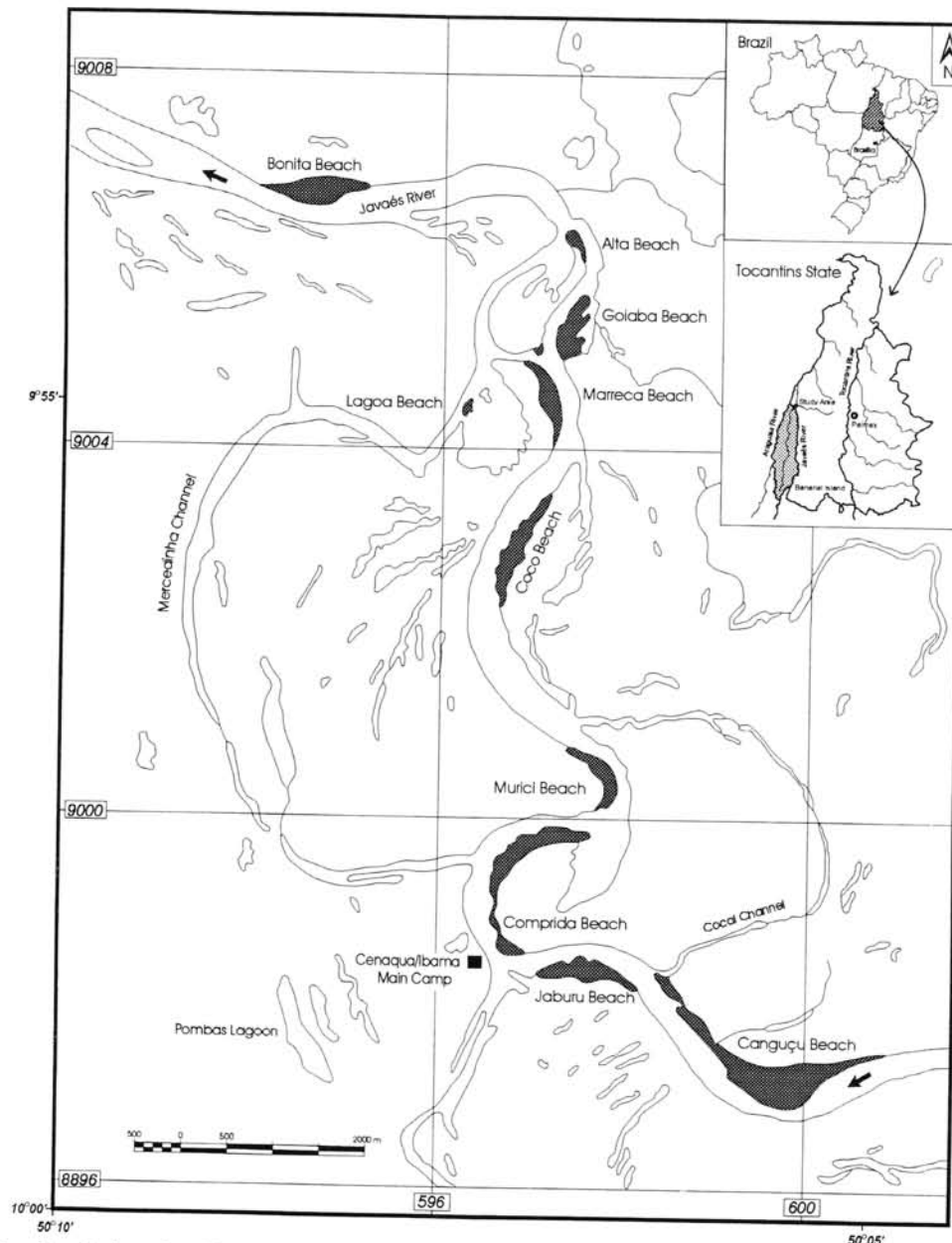


Figure 1. Map showing the location of beaches and the study sites (Jaburu, Marreca, and Canguçu) on the Javaés River, Araguaia National Park, Tocantins, Brazil.

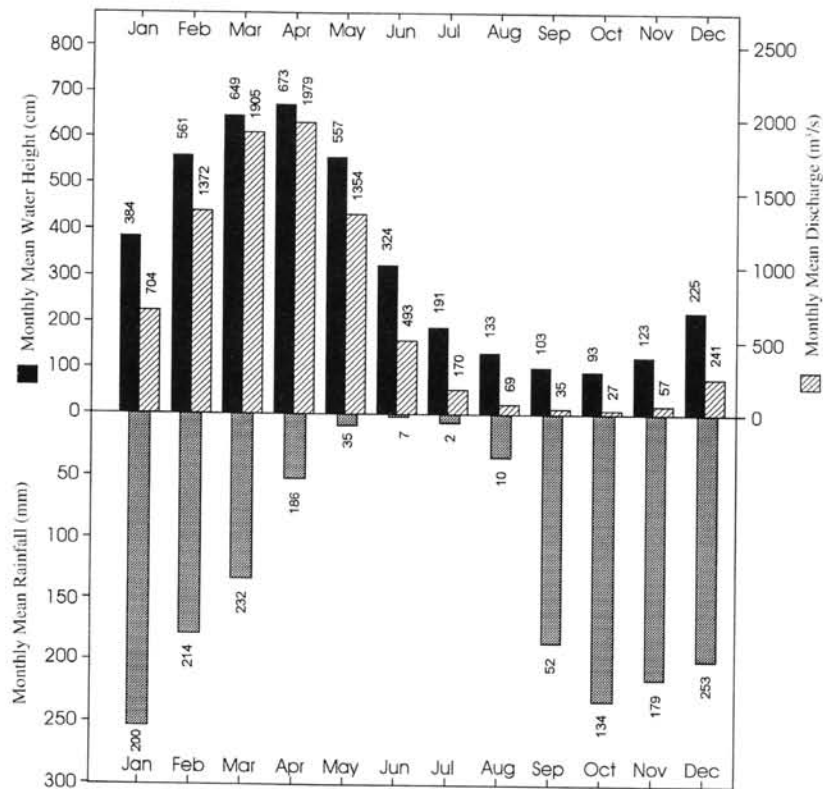


Figure 2. Data relating to the flow and the variation in water level of the Javaés River, collected at the Fluvimetric Station in Barreira da Cruz, located 45 km southeast and upstream of the research area. The measurements cover the period 1969–99 and although there are a few gaps, they are a reliable record for the area. The rainfall data were collected at the Canguçu Station near the research area and comprise a complete data series for the period 1984–94.

Rivers transport sediments which accumulate slowly at irregular intervals ranging from minutes to centuries. Water flow acts on these sediments, dispersing and transporting them individually. Grains transported close to the river bed in the sand fraction (i.e., grains with diameters between 0.062 and 2.0 mm), or in larger classes, generate repetitive structures known as bed forms. These sandy deposits are not fixed, and they move (or migrate), impelled by the force of the canalized water flow, forming an asymmetric structure known as a dune. Dunes are characterized by a short and

abrupt frontal section with a sharp incline (known as the front or lee side) and a long reverse slope (or back) which has a gentle incline and which is known as the stoss side (Fig. 3). The highest point of the dune, at the division between the stoss side and the front side, is known as the crest. The migration of bed forms occurs when detritic grains, transported along the long stoss side of the dune, fall in small avalanches down the short front lee side of the dune. Continued and successive avalanches of this type cause the dune to migrate, and its external geometry is con-

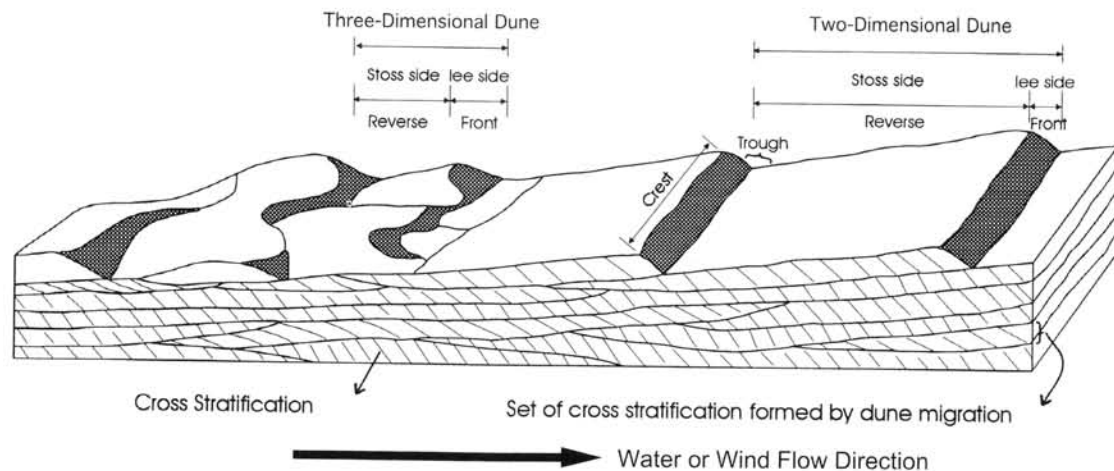


Figure 3. Block diagram showing the migration of bi-dimensional and tri-dimensional dunes. Cross-stratification is produced by the migration of bed forms following successive avalanches at the fronts of the dunes (lee side).

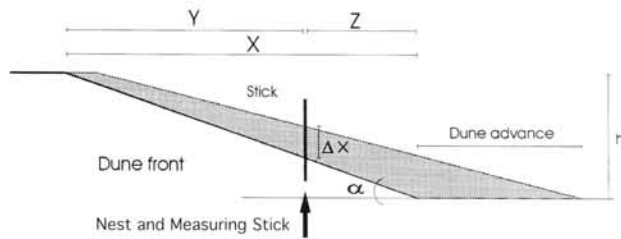


Figure 4. Schematic profile of the front of a dune showing the advance of the dune over a nest of *P. unifilis*. The measuring stick was inserted close to the nest, and the shaded portion shows the sediment increase over the nest area (ΔX). Y is the distance from the original crest of the dune to the measuring stick, Z is the distance from the stake to the original base of the dune, and X is the sum of these two measurements, α is the angle of the slope of the front of the dune.

stantly modified by this process. Dunes can be classified as bi-dimensional (2D) when their frontal sections are perpendicular to the direction of flow, and tri-dimensional (3D) when they have a frontal section which is sinuous in relation to the flow direction (Fig. 3).

The successive accumulation of various dunes over the passage of time generates sedimentary deposits which are in turn responsible for the formation of large sandbanks in and

at the sides of the river channel. According to Leopold et al. (1963) and Miall (1990), in meandering rivers sandy deposits concentrate and develop on the inside curve of a river bend and the results of this can be clearly seen in the curved geometry of the sandbanks which advance into the river channel (Fig. 1). Deposits which build up along the sides of the river channel and extend out into it are known as point bars. In the Javaés River, the sand bars, which frequently exceed 1000 m in length and 200 m in width, are formed by several 2D and 3D dunes which have migrated laterally, to join together into extensive sedimentary deposits. A sand bar is composed of a submerged section under water and an emerged section which lies above the water line. The abrupt change in relief noted at the front of dry (non-submerged) dunes is prolonged out into the river channel. The frontal part of a submerged dune functions as a small channel, lying perpendicular or oblique to the main channel of the river. This enables the interconnection of the deepest parts of the river (pools known locally as *boiadouros*) with the beaches. During the dry season when navigation, even in small boats, is made difficult by the drastic reduction in water volume and/or the emergence of innumerable sandbanks within the river channel, access to the beaches is made possible by these

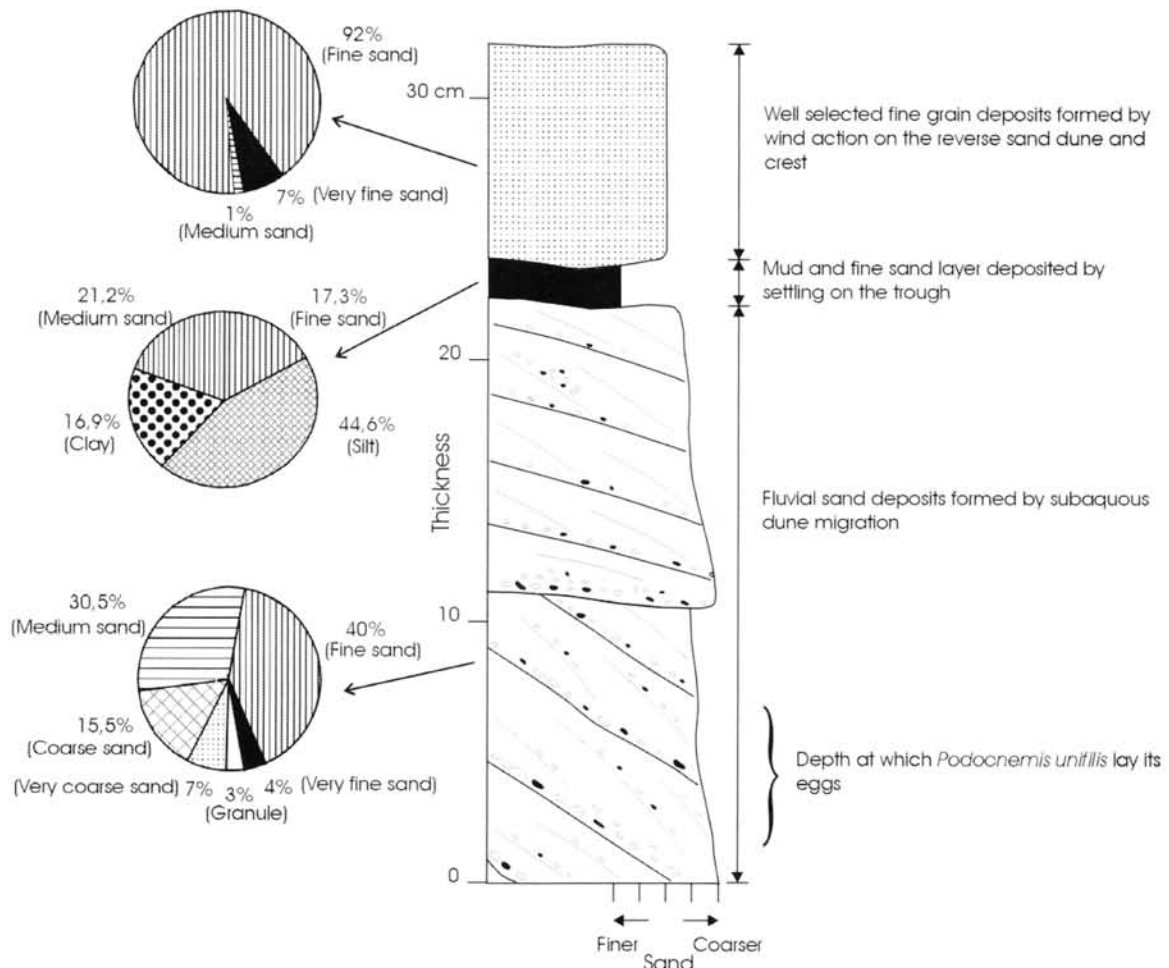


Figure 5. Typical sediment profile at nesting sites of *P. unifilis* on Canguçu beach. The upper portion (subject to wind action) is separated from the lower portion (of fluvial origin) by a thin layer of fine sediments deposited by settling. Nests were laid in sandy fluvial sediments of fine to large granulometry.

small channels located at the front of submerged sand dunes. These channels are found in the trough, this being the name given to the place where the front of one dune begins its migration onto and over the stoss side of another dune whose deposition occurred earlier (Fig. 3).

The variety of bed formations reflects the effects of channeling of the water flow and fluctuations in water level. Flow variations in the Javaés River are controlled by climatic seasonality, which is marked by a dry season (May–November) and a rainy season (December–April), resulting in significant alterations in water level (Fig. 2). The external outline of the sand bars, shaped by the migration of submerged dunes during the high water period, is preserved in the dry season when the river level drops dramatically, exposing the sandy deposits. The external surface of sand bars is irregular and distinguished mainly by the steep frontal section of the dunes where the angle of the slope can commonly exceed 30°.

The nesting sites of *P. unifilis* on the beaches of the Javaés River can be divided into two areas: a) shoals and flat areas near the river channel, and b) the fronts of dunes. In geological terms, the shoals and flat areas near the river channel are the reverse slopes or stoss sides of dunes and do not show any significant irregularities. These locations account for 50–70% of all *P. unifilis* nests on the beaches at the RAN/IBAMA Base on the Javaés River. All the nests deposited in the shoals and flat areas were depredated in the 1999 season. The second area at the fronts of dunes offers extra protection to the nests since the effects of wind action on the dunes cause sediments to fall down their frontal sections thereby providing a more effective cover over the eggs.

Methodology. — Marking of turtle nests was carried out by agents of RAN/IBAMA using numbered sticks recording the location and the date. Nests were identified by the tracks left by nesting turtles the previous night. Those nests situated at the fronts of dunes were chosen for the purposes of monitoring the incubation period. These nests were covered with small sections of wire netting to protect them. This procedure was necessary because, in addition to the normal levels of pressure from predators, there are indications that the practice of excavating, re-covering, and marking the nests of *P. unifilis* attracts the attention of vultures which then end up discovering and depredating the egg clutches.

Monitoring of sediment accumulation caused by wind action on the dunes was carried out by means of measuring sticks inserted into the base of the dunes close to identified nests. Three sand depth measurements were taken: one each month during September, October, and November, which enabled the quantification of sediment advance over the nests. The monitoring process involved the analysis of 8 nests, situated in 6 dunes distributed along the 3 beaches, using a total of 17 measuring sticks. Fig. 4 shows the relationship between the various measurements.

Sediment profiles of the areas of the 8 identified nests and 15 samples were taken in order to analyze alterations between the grain size of the sub-aqueous deposits and the upper parts of the sand bars exposed and subject to wind

action (Fig. 5). The classification of these samples was undertaken using the Wentworth scale (Blatt et al., 1980).

RESULTS

Just before nesting emergence, the turtles remain in the deeper parts of the rivers, awaiting the ideal time to leave the water (Vanzolini, 1967). To reach their nesting sites, they take advantage of the small channels which extend along the troughs located just beyond the base of the dune fronts (Fig. 6). These channels have depths ranging from 60 to 150 cm; channels with lesser depths than these hamper the turtles' movements and leave them vulnerable to predators. The dry season exposes innumerable sandbanks which are situated between the thalweg (the central part of the river bed where the slopes of the two margins meet) and the beaches. In the 1999 nesting season, very few nests of *P. unifilis* (and practically no nests of *P. expansa*) were recorded on those areas of beach where there were sandbanks blocking the route between the deeper parts of the river and the beach itself. The difficulty in gaining access to these areas of beach in the absence of the small channels that extend along the fronts of dunes are suggested to be the factor responsible for the very low nesting densities in these places (Fig. 6). This observation was made on the basis of an analysis of the emergence points used by the turtles, which can be detected by the tracks left by the females as they climb out of the water onto the beach to lay their eggs. In Fig. 6 arrows indicate the paths followed by turtles from the deep stretches of the river to the nesting sites.

As a consequence of analogous sedimentary processes, the external conformation of the Jaburu and Marreca beaches on the Javaés River which are exposed during the dry season exhibit very similar geometrical characteristics. The spacing between the dunes varies from 10 to 40 m, between crests, with most being around 20 m apart. The height of the dunes on both beaches lies in the 50–150 cm range (average around 100 cm).

On Marreca beach, five measuring sticks were inserted, two of which were uprooted by birds, and two dunes were monitored. On Jaburu beach, four measuring sticks were used to monitor one dune. The increase in sediments, caused by the advance of the dunes during the monitoring period varied from 6 to 14 cm (Table 1) and averaged 11 cm.

The dimensions and morphology of the Canguçu beach are distinct from those of the Jaburu and Marreca beaches (Fig. 1). In the upstream section of the Canguçu beach, the dune fronts develop in a direction parallel to the river channel, which makes it difficult for *Podocnemis* to access the extensive, flat table-land that comprises the upper portion of the beach. A large dune about 2.5 m high divides the Canguçu beach into two distinct sections (Fig. 6). The upper section of the beach is generally flat with a gentle slope declining in the upstream direction. This part comprises the stoss side of a large dune advancing in a direction parallel to the river channel. The height of the dune is greatest nearest the river, and diminishes gradually as the crest of the dune curves to assume an orientation oblique to the river channel.

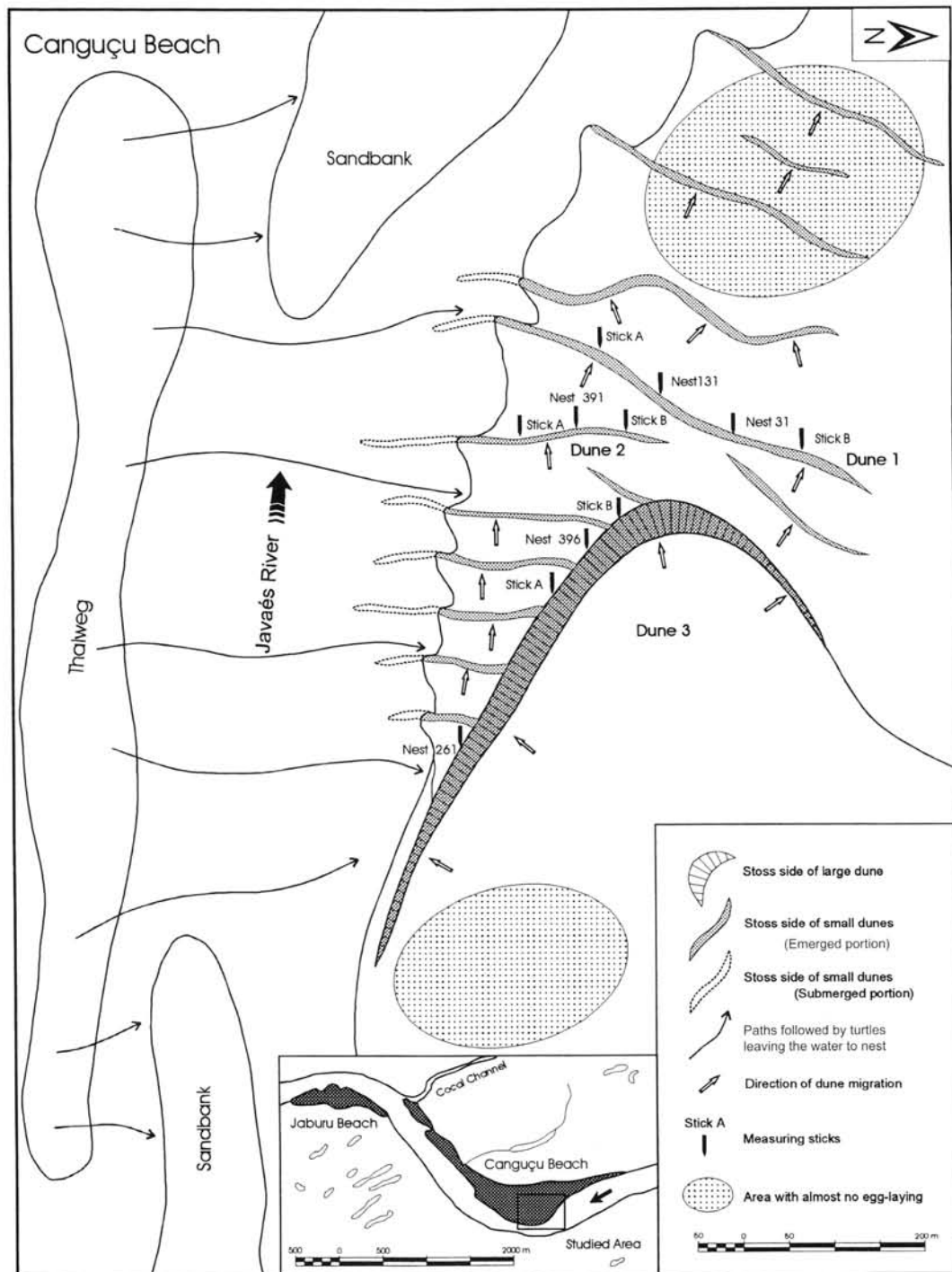


Figure 6. Schematic representation of the upstream part of Canguçu beach where, between September and November, the advance of dunes onto the nests of *P. unifilis* was monitored. Access to nesting sites is facilitated by small channels generated by the submerged parts of dune fronts linking the beach to the deeper parts of the river. Sandbanks located between these deep pools and the beach function as obstacles across the path of the turtles who are seeking nesting sites in this area.

The lower section of the beach is the downstream area at the front of the large dune where a number of smaller dunes with heights of around 1 m have been deposited in an orientation perpendicular to the river.

Where the crest of the large dune is parallel to the river, access to the flatter areas on the reverse or stoss side of the dune is difficult because the dune front is steeply sloped (up to 35°) and high (up to 2.5 m). Digging

a nesting pit in the front of the dune is also not easy because the area is very unstable and the slightest movement can provoke small sand avalanches which fall into the recently excavated cavity.

The dunes in the downstream section of Canguçu beach exhibited characteristics similar to those found on the beaches of Jaburu and Marreca. The oblique to perpendicular disposition of the dune crests in relation to the river allows access

Table 1. Advance of dunes from 10 September to 1 November 1999 on the beaches of Jaburu, Marreca, and Canguçu. The measurements given coincide with the hatching period of *P. unifilis* eggs. The relations between the measurements can be seen in Fig. 4. The depth of the nest was measured from the level of the uppermost egg on 10 September 1999.

Site	Measuring point		Height of dune (cm)	Length of dune (cm)	Distance from dune crest to measuring point (cm)	Slope of dune front	Increase in sediment over nest (cm)
Marreca	Dune 1	Nest 162	20	100	20	40°	6
		Stick A	77	164	75	26°	10
	Dune 2	Nest 36	50	120	100	18°	10
		Stick B	42	130	58	22°	12
Jaburu	Dune 1	Nest 320	95	290	220	24°	14
		Stick A	66	193	103	23°	12
		Stick B	105	255	175	20°	10
		Stick C	50	117	57	24°	14
Canguçu	Dune 1	Nest 131	100	300	230	22°	11
		Nest 31	120	400	300	21°	10
		Stick A	100	350	150	21°	13
		Stick B*	102	263	142	20°	4
	Dune 2	Nest 391	35	110	10	18°	10
		Stick C	41	125	55	21°	9
		Stick D	29	118	48	17°	13
		Nest 396	120	600	500	14°	10
	Dune 3	Nest 261	265	-	-	32°	36
		Stick E	120	320	270	21°	10
		Stake F	75	230	130	20°	10

* Measurements given are those taken on 10 October 1999; subsequent to this the measuring stick was removed.

to the beach. In this situation, turtles crawl close up to the base of the dunes until they find an appropriate nesting site. In this section of the beach, the data relating to the advance of the dunes follows the same pattern noted on the Jaburu and Marreca beaches, both in terms of the dimensions of the dunes and in terms of the sediment increases recorded over the nests (Table 1).

The largest sediment increase over the nests was 36 cm at nest no. 261 on Canguçu beach, which may be explained by the fact that the nest was positioned close to the highest part of the dune where the height of the crest exceeded 2.5 m (Table 1). The smallest sediment increase was recorded at nest no. 162, located on Marreca beach, with an increase of just 6 cm; however, this was sufficient to protect the eggs from predation. This data is in accordance with the dimensions of this dune which, on 10 September 1999, measured 35 cm in height and which, as a result of wind action, had its frontal part reduced to a height of 20 cm (Table 1). In other places, the sediment increase recorded over the nests was around 10 cm. These values may appear insignificant, but the nests of *P. unifilis* are generally deposited at an average depth of 12–25 cm (measurements taken from the bottom-most egg). Comparing the values of nest depth and sediment increase, it can be seen that the latter provides extra protection against predators and may in some cases result in a doubling (or greater) of the depth of the original cover over the eggs.

DISCUSSION

The low rainfall registered during July to October, with intense sunshine, causes a reduction in the humidity of the upper layers of the sandbanks in which the eggs of *P. unifilis* are deposited. This inhibits sand aggregation and allows

winds to transport the finest particles (individual particle sizes ranging from 0.125 to 0.25 mm).

The amount of sediment transported by wind action varies along the same beach and depends on a series of sedimentological factors, such as the grain size of the sediments and geometry and position of the dunes in relation to the direction of the winds. According to McKenna et al. (2000), intermittent winds with a periodicity of 5 to 20 min duration, and moderate magnitude with speeds of between 6 and 7 m/sec are responsible for the transport of most sediments by wind action. The rate of sediment movement varies between 0.9 and 8.1 cm/min under conditions with winds between 7.2 to 13.4 m/sec (Sharp, 1963). These data show that a significant accumulation of sediments can occur over short intervals of time. The transported sediments are deposited in the front of dunes.

At the start of the monitoring of wind action on the dunes, some places at the dune fronts had already received a sediment increase of up to 7 cm. This is evident from the granulometric analysis of the sediment log (Fig. 5), since sediments transported by wind are well selected, for fine to medium sand classes, and do not exhibit cross stratifications. The deposits of fluvial origin generated by the migration of bed formations are poorly selected and concentrated in the medium to large granulometric classes of the sand fraction with the presence of pebbles and granules and are characterized by the presence of cross stratifications (Miall, 1990). At the beginning of sandbar exposure to the air, the entrapment of small pools of water along the frontal part of the dunes in the trough is common. As a result, very fine sediments (clay and silt) are deposited in these areas. Consequently a fine layer (1 to 3 cm thick) of fine sediments marks the end of deposition by water flow and the start of wind deposits. Texturally mature sediments (i.e., those with a low clay

concentration) are more easily disaggregated and transported. The clay tends to form a coating around the sand grains thereby maintaining the unity of the sediments it covers (Leeder, 1995). For this reason, the areas of beach situated near the trough of the dunes are not subject to transport by the wind because, in these areas, the fine sediments form a fine layer preventing movement of sediment by wind action.

It is important to note that the upper part of the dunes and the stoss side of the next dune are also subject to wind action. However, the accumulation of sediments in these places is very little, around 1–2 cm during the entire dry season, too little to provide protection for the eggs. Since predation of eggs tend to occur in the first days after nesting, any extra protection given by sediment movements also needs to occur over these first few days in order to be effective.

Ongoing research aims to establish the sediment increase on nests during the incubation period, since it is important to see how these data interact with the critical period of sex determination in *P. unifilis*. Sex determination in this species (Souza and Vogt, 1994), as with many other turtles, depends on the incubation temperature of the eggs during the middle third of incubation, and this temperature is influenced by factors directly associated with heat flux, such as the intensity of sunlight, shade (Vogt and Bull, 1984; Schwarzkopf and Brooks, 1987), soil humidity (Paukstis et al., 1984) and rainfall, and indirect factors such as the mineralogical composition (Milton et al., 1997) and granulometry of the sediments (Souza and Vogt, 1994), the distance of the nest from the water table (Spotila et al., 1987) and the date of nesting (Mrosovsky et al., 1984; Mrosovsky and Provancha, 1989). Since temperature declines with soil depth (Burger, 1976; Wilhoft et al., 1983; Thompson, 1988), the accumulation of sediments at the base of the dunes will cause a reduction in the incubation temperature of the eggs. Depending on its intensity, this alteration could influence sex determination in *P. unifilis*. Even a small variation in temperature can have significant consequences. Alho et al. (1985), noted that a 1°C difference in temperature is sufficient to affect sex determination in *P. expansa*. Determining the temperature variation induced by the advance of the dunes and the period in which this occurs is important for management projects which involve the transfer of eggs from one site to another.

Observations on the reproductive habits of *P. unifilis* on the Javaés River suggest that beach characteristics and nest placement are vitally important for the population's reproductive success. Nests situated on the flat areas on top of the dunes and in shoals at the margins of the river channel are subject to intense predation. Not a single nest laid in such areas during the 1999 nesting season was observed to hatch successfully. Eggs laid in the trough located along the dune fronts, although still subject to predation, proved to have a reasonable possibility of hatching. The places chosen for nesting, and the implications of a geological nature associated with this,

are conditions which are responsible for the incubation success. The reproductive cycle of *P. unifilis* on the Javaés River in Araguaia National Park depends on geological factors. Places which did not have access channels or which had sandbanks barring the way between the thalweg and the beaches exhibited very low nesting densities for both *P. unifilis* and *P. expansa*.

The observations made in relation to the wind-driven sediment increases over the nests of *P. unifilis* should be considered in management projects which involve the transfer of eggs since, due to this sediment increase, the initial depth of viable nests will certainly not remain constant during the incubation period. This may cause alterations in the incubation temperature with possible repercussions for sex determination.

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LITERATURE CITED

- ALHO, C.J.R., DANNI, T.M.S., AND PÁDUA, L.F.M. 1985. Temperature-dependent sex determination in *Podocnemis expansa* (Testudinata: Pelomedusidae). *Biotropica* 17(1):75-78.
- BLATT, H. MIDDLETON, G., AND MURRAY, R. 1980. *Origin of Sedimentary Rocks*. Englewood Cliffs: Prentice-Hall Inc., 782 pp.
- BULL, J.J. 1985. Sex ratio and nest temperature in turtles: comparing field and laboratory data. *Ecology* 66(4):1115-1122.
- BURGER, J. 1976. Temperature relationships in nests of the northern diamondback terrapin, *Malaclemys terrapin terrapin*. *Herpetologica* 32:412-418.
- EENDEBAK, B.T. 1995. Incubation period and sex ratio of Hermann's tortoise, *Testudo hermanni boettgeri*. *Chelonian Conservation and Biology* 1(3):227-231.
- IBAMA—INSTITUTO BRASILEIRO DO MEIO AMBIENTE E DOS RECURSOS NATURAIS RENOVÁVEIS. 1989. *Projeto Quelônios da Amazonia - 10 Anos*. Brasília: IBAMA, 119 pp.
- JANZEN, F.J. 1994. Vegetational cover predicts the sex ratio of hatchling turtles in natural nests. *Ecology* 75:1593-1599.
- LEEDER, M.R. 1995. *Sedimentology: process and product*. London: Chapman and Hall, 344 pp.
- LEOPOLD, L.B., WOLMAN, M.G., AND MILLER, J.P. 1964. *Fluvial Process in Geomorphology*. San Francisco: Freeman, 512 pp.
- McKENNA NEUMAN, C., LANCASTER, N., AND NICKLING, W.G. 2000. The effect of unsteady winds on sediment transport on the stoss slope of a transverse dune, Silver Peak, NV, USA. *Sedimentol-*

- ogy 47:211-226.
- MIALL, A.M. 1990. Principles of Sedimentary Basin Analysis. London: Springer-Verlag, 668 pp.
- 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.
- MROSOVSKY, N. AND PROVANCH, J. 1989. Sex ratio of loggerhead sea turtles hatching on a Florida beach. *Canadian Journal of Zoology* 67:2533-2539.
- MROSOVSKY, N., HOPKINS-MURPHY, S.R., AND RICHARDSON, J.I. 1984. Sex ratio of sea turtles: seasonal changes. *Science* 225:739-741.
- PAUKSTIS, G.L., GUTZKE, W.H.N., AND PACKARD, G.C. 1984. Effects of substrate water potential and fluctuating temperatures on sex ratios of hatchling painted turtles (*Chrysemys picta*). *Canadian Journal of Zoology* 62:1491-1494.
- SCHWARZKOPF, L. AND BROOKS, R.J. 1987. Nest-site selection and offspring sex ratio in painted turtles, *Chrysemys picta*. *Copeia* 1987:53-61.
- SHARP, R.P. 1963. Wind ripples. *Journal of Sedimentology*, 71:617-636.
- SOUZA, R.R. DE AND VOGT, R.C. 1994. Incubation temperature influences sex and hatchling size in the Neotropical turtle *Podocnemis unifilis*. *Journal of Herpetology* 28(4):453-464.
- SPOTILA, J.R., STANDORA, E.A., MORREALE, S.J., AND RUIZ, G.J. 1987. Temperature dependent sex determination in the green turtle (*Chelonia mydas*): effects on the sex ratio on a natural nesting beach. *Herpetologica* 43(1):74-81.
- THOMPSON, M.B. 1988. Nest temperatures in the pleurodiran turtle, *Emydura macquarii*. *Copeia* 1988(4):996-1000.
- VANZOLINI, P.E. 1967. Notes on the nesting behavior of *Podocnemis expansa* in the Amazon valley (Testudines, Pelomedusidae). *Papéis Avulsos de Zoologia, São Paulo* 20(17):191-215.
- VALENZUELA, N., BOTERO, R., AND MARTINEZ, E. 1997. Field study of sex determination in *Podocnemis expansa* from Colombian Amazonia. *Herpetologica* 53(3):390-398.
- VOGT, R.C. AND BULL, J.J. 1984. Ecology of hatchling sex ratio in map turtles. *Ecology* 65:582-587.
- WILHOFT, D.C., HOTALING, E., AND FRANKS, P. 1983. Effects of temperature on sex determination in embryos of the snapping turtle, *Chelydra serpentina*. *Journal of Herpetology* 17(1):38-42.
- YNTENA, C.L. AND MROSOVSKY, N. 1980. Sexual differentiation in hatchling loggerheads (*Caretta caretta*) incubated at different controlled temperatures. *Herpetologica* 36(1):33-36.

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