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NOTES ON THE NESTING BEHAVIOUR OF *PODOCNEMIS EXPANSA* IN THE AMAZON VALLEY (TESTUDINES, PELOMEDUSIDAE)

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INTRODUCTION

In October, 1965, while on a general collecting trip in the State of Pará, Brasil, I had the opportunity to observe the nesting activities of the Amazonian turtle, *Podocnemis expansa*. Field work was done for only three nights, and the photographic documentation was rather unsatisfactory, but it was possible to obtain a consistent and fairly detailed description of the behaviour, which opens the way to the consideration of some problems.

MATERIALS AND METHODS

SITE

The site where the present observations were made is a sand beach in the Rio Trombetas, a tributary of the Amazonas on the left side. The approximate position is 1°15'S, 56°50'W, ca. 140 km above the city of Oriximiná, 5-6 km below the mouth of Lake Jacaré and 50 km below the first falls of the river, called Porteira. The region is satisfactorily represented in sheet SA-21 (Santarém) of the "Map of Hispanic America ou the scale of 1:1,000,000" of the American Geographical Society, New York.

The distance between banks is some 600 m, but the actual channel, which runs close to the right bank, is only some 80 m wide, the remainder being shallow. As the dry season progresses, a narrow and long bar ("taboleiro") begins to appear and spread until, at lowest water, the beach measures about 2 km by 400-500 m, broadly contacting the bank on its upper two thirds, but separated from it by a narrow (20 m wide) arm of very calm water on the downriver third. It is to this pool ("poço") of still water that the local people ascribe the preference of the turtles for this beach. In the pool they congregate in large numbres for a long time prior to nesting and from it they leave the water to nest.

In fact, about 1 and 5 km respectively above the traditional taboleiro there are two others, similar in every respect but the presence of the pool; these beaches are extensively used by

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another species, *P. sextuberculata,* but not by the herds of *expansa,* although isolated specimens are said to lay there in years of exceptional population density or of intensive persecution.

The surface of the taboleiro is not regular; it is higher (some 2 m above water level) on the median third, sloping gradually up and downriver. More than one animal species breeds there. The highest ground is used by *P. expansa,* the latest comer. The area immediately adjacent upstream, a little lower, was, at the time of observation, being used by a breeding colony of the Large-billed Tern, *Phaëtusa simplex* (Gmelin). The upper end of the beach showed a regular number of tracks of *Podocnemis sextuberculata,* whose breeding season was nearing its end. There was no overlap between the three nesting areas.

NUMBERS

I found it very difficult to estimate the number of turtles present on the beach at any time. The following calculations are therefore offered with a word of caution.

In the morning of October 7, I measured the area pitted by the turtles (Fig. 6): it was roughly 200 x 200 m. In the fore center the holes touched each other, sometimes even overlapping; towards the edges of the area distance between pits increased to about 2-4 m. Assuming the densely pitted area (1 hole per square meter) to be one tenth of the total, we would have some 4,000 holes there. Taking the average density of the remainder to be ten times less, we would have another 3,600 holes. Allowing 3 holes per turtle (a gratuitous but conservative figure), we would have in the neighborhood of 2,500 diggers.

This, the morning after the first night of activity on the beach, was the only time this method of estimation could be used, as from then on the same area was worked daily by the turtles, and it was impossible, even after heavy rain, to discern the results of each day's activity.

On the night of October 10 an attempt at counting was made. In 5 minutes of steady flux of turtles, under exceptionally bright moonshine, 130 specimens were counted. That group kept coming ashore for 2 hours. Again we would have a total number in the low thousands.

SIZE

Thirty eight turtles were measured when leaving the nest. To avoid turning them, the measurement taken was length of carapace, along the convexity.

The original data are shown in the following table. From these are calculated: average, 70.05 ± 0.531 cm; standard deviation, 3.27 cm; coefficient of variation, 4.67. The distribution is skew towards the right.

Distribution of shell length (cm), laying females of *P. expansa*

Length	Frequency	Length	Frequency
65	3	73	2
66	2	74	1
67	3	75	1
68	3	76	1
69	7	77	1
70	7	78	—
71	2	79	1
72	4		
			38

PERIODS OF OBSERVATION

It was possible to dedicate three complete nights to observation. The habits of the turtle being well known in the region, I knew that breeding females had been massing for some time in the pool, and that nesting was imminent. My camp being 6 km from the taboleiro, I had people watching for the first signs of activity on the beach. On October 6, a lookout reported "sand flying" early in the morning. The beach was examined during the day; a few tracks were discovered, as well as some shallow pits, but no actual nests.

That night was spent in observation, from 2030 to 0300 hours. A large platoon of turtles came ashore at 2235 and many individuals dug nests, but no eggs were laid. About 0230 the last individuals left, and at 0300 there was heavy rain (it had been from the beginning a squally night) and observation became impossible. In the morning the site was inspected, no signs of further activity being found.

Field work on the beach was very strenuous, demanding crawling on one's belly for hours on end, even when the turtles seemed not to mind company; for this reason it was deemed best to work only on alternate nights. Thus on the evening of October 8, I returned, accompanied by my technician Dionisio Seraglia. Unfortunately, our arrival was delayed until 2150, and at this time a good sized platoon was already actively digging. It was possible to observe oviposition, covering of the nest and return to the water. Around 2330 this platoon left, and at 0030 another one landed; all phases of behaviour were observed in good detail until daylight and it was possible to time all stages of the process. The last individuals left at about 0430; we remained on the spot until 0800, but no further activity was noticed.

These field data were submitted to preliminary analysis, and plans laid for the next observation period, starting at 1850 hours of October 10. Two platoons came ashore, one at 2230 and the other at 0130, the second arriving while the first was still at work. Activity on the beach continued till 0800. During this period all previous observations were verified.

METHODS

As very properly stated by Carr & Giovannoli (1957: 23), practically all families of turtles adhere to the same general pattern of nesting. Thus, the breaking down of the process into phases or steps is of little importance in itself, while the detailed description and analysis of the motor patterns and social components is of the highest interest.

When planning the present trip I was unaware of the Trombetas taboleiro; upon getting acquainted with its existence I changed plans, but it was too late to read on the subject. For this reason I planned to spend one first night observing the over all pattern of activity on the beach, in order to identify phases of the process and to decide on how to obtain accurate records. This was done, and it was from the beginning quite obvious that the routine method of describing step by step the activity of single specimens should afford the best results. In the subsequent 2 nights available for observation, each phase of the process was completely followed and timed at least once. Unfortunately, as it is bound to be the case quite frequently with *expansa*, it was impossible to follow any single specimen from beginning to end. However, at least three spot checks, qualitative and quantitative, were run for each phase, and I am fairly sure that the pattern described, although composite, is close to reality.

With regard to the actual technique of observation, I had the benefit of two nights (October 8 and 10) of full moon on a clear sky, which made every detail on the beach sharply visible. The first, rainy night (October 6), demanded the use of a flashlight: a two-battery torch was used, with purposely weak cells.

The initial phases were observed from a distance of 30-50 m, from hollows previously scooped in the sand. Approach was effected by slowly crawling on the belly, with lowered head. The observers were naked or wearing only neutral-colored pants and hats. Twice it was possible to reach the predicted path of the platoon and stay there, flat and motionless; the turtles, upon arriving, seemed unconcerned, some even butting us out of an eventual spot which caught their fancy.

As it was impossible for one single person to clock and take notes at the same time, I took the notes and my assistant kept time. It was decided that the time unit should be 5 seconds; smaller intervals turned out to be unreliable, due to numerous causes, especially false or sudden starts of the turtle under observation, and lags in whispering information back and forth.

It was not feasible to time individual bursts of activity; they were computed by subtracting from a certain length of time the sum of the included rest periods.

ON MISSING INFORMATION

Some important data could have been easily obtained from autopsies of selected specimens and from the examination of clutches, as well as from planned disturbances of the sequence of acts. However, we kept handling of the turtles to a spartan minimum, by request of the federal conservation authorities in charge of the site.

Turtle protection is at best a ticklish business in a region where people are used to consider natural resources as inexhaustible, and where *expansa* is a beloved and costly delicacy, at least 40 times more expensive than any other turtle. Curbing poaching, contraband, and even domestic consumption, does not endear authorities to back-country people. Furthermore, there had been recently much laxness, and even gross dishonesty, on the part of conservation officials; thus the whole region distrusted the civil service and was on the lookout for anything which could be interpreted, however maliciously, as malpractice. Actually, the present program is honest, sensible and well carried out, and deserving of all support. Thus I found quite reasonable their request that no specimens be dissected or even collected, no nests dug up and no turtles interfered with. The only exception was to measure the above mentioned 38 individuals which were returning to water after laying.

OBSERVATIONS

Prior to emergence, activity and noise in the pool were noticed, as well as basking, but only incidentally. Neither did I follow the turtles after they reentered the water. Present observations refer only to the actual process of nesting.

PHASES

The whole process can be divided into 7 phases, which are usual (Carr & Giovannoli, 1957) and certainly well set out and easy to recognize: (i) aggregation in a shallows, prior to landing; (ii) landing and reaching the nesting grounds; (iii) deambulation; (iv) excavation of the nest; (v) laying; (vi) filling and covering the nest; (vii) returning to the water. Of these only the first is qualitatively characteristic of *P. expansa*.

AGGREGATION PRIOR TO LANDING

Twice I saw this happen from the very beginning and in favourable light conditions. On a shallow embayment of the beach, some 20-30 m across, always the same in all cases observed (Plate 1, fig. 1), heads started to pop up silently, all looking inshore, and stayed, very quiet, quite distinct against the silvery background of still water under full moon. Once, after about 30 minutes, the turtles started coming out steadily and kept doing so for 2 hours, with varying intensity but no major interruption. Another time only two turtles came out, returned immediately to water and the whole group vanished.

LANDING

The landing port lies some 30-40 m from the nesting grounds, the intervening terrain being a steady ramp.

In the case completely watched, some turtles, six ou more, suddenly came out of the water, marched inshore for 2-4 m and stopped. Others followed and the whole platoon halted on the shore for 10-20 seconds.

Emergence is impressively quiet, as is the ensuing phase. Under the full moon the beasts look like nothing but a procession of ghosts of huge phosphorous beetles, the carapace presenting a distinct bluish luminescence.

At this stage some individuals effected a few scooping movements with the front feet, throwing sand over their backs.

Next some leaders detached themselves from the platoon and started climbing the slope to the nesting grounds. Others immediately followed and the invasion front stretched into a caravan.

I did some little experimenting with this phase of the behaviour, another time, when we first saw the turtles in full emergence. By distributing two other people besides myself in chosen spots, it became apparent that the turtles scanned their horizon, in the case the top of the ramp leading from the water to the laying grounds. A sitting, motionless man, aroused caution but not necessarily fear: they would approach stealthily, circle around and proceed. Any movements resulted into a stampede back to the water.

Variable number of specimens, hard to estimate but in one case reaching perhaps 10 per cent, at this point returned spontaneously to the pool, to stay again in wait or to swim away; both things were definitely seen. Some returned sedately, some blindly running, bumping and caroming off others, which would catch the fright or not. At times a disorderly if silent scene.

DEAMBULATION

Once on the general laying grounds, the turtles get to walking in all directions, colliding, veering away or climbing over each other, and from time to time scooping some sand with the front feet and throwing it over the back. This phase is still strangely silent. Some individuals very shortly start digging a nest; others take longer to begin; others still never start, returning to the water after a longer or shorter period of wandering.

Deambulation never extended beyong the limits of the highest surface of the beach, which I have called here "nesting grounds". In fact, most of the nesting took place in the area closest to the landing place.

EXCAVATION OF THE NEST

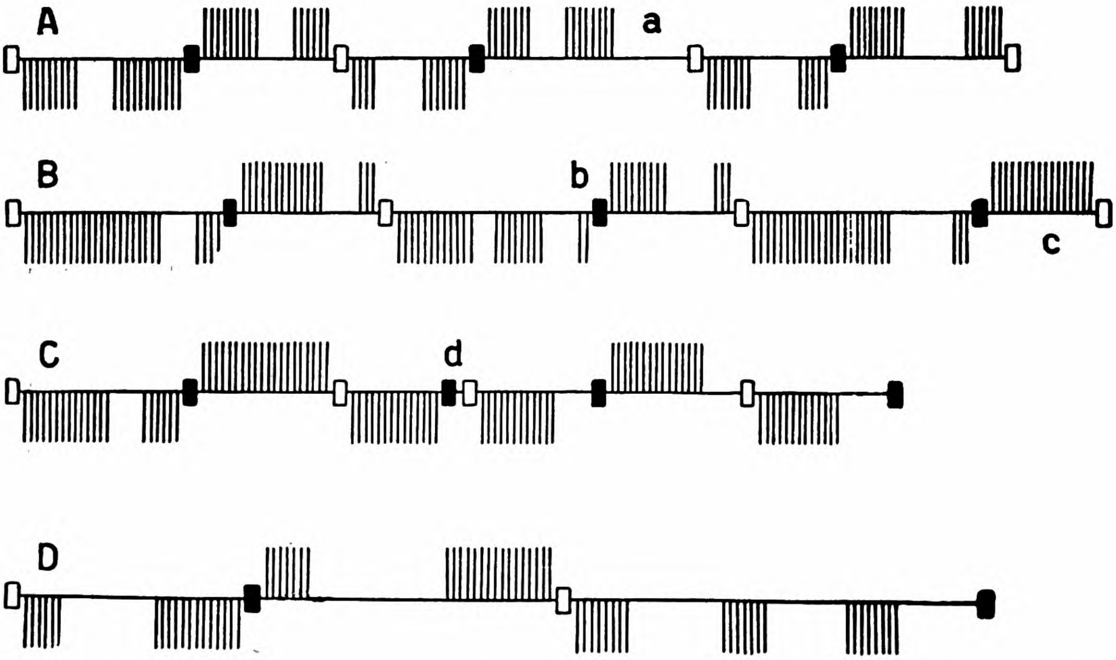
I could not discern any clues to what made a place especially attractive to a turtle. Some made quite a fuss about a chosen site, pushing others around very testily. One particular and very large female liked my own hollow in the sand, and patiently butted me out of it.

The following notes are based on the complete observation of one specimen (100 minutes from first scratching the sand to completing the hole), on the partial timing of two other specimens and on spot checks on some 15 to 20 individuals in several phases of the process. The specimen whose digging was thoroughly clocked unfortunately did not lay; after finishing the nest it stayed there for a while and then marched away. But the checks left no doubt that the procedure was typical enough.

Excavation is an interesting process, seemingly very uniform. Four phases could be discerned: (i) shaping of the pit; (ii) excavation, shallow, (iii) excavation, deep; (iv) final shaping of the egg chamber.

In the first phase the hands do a lot of spasmodic, violent scooping; the feet also help, irregularly; the body is repeatedly swung around with force. This lasts for a few minutes and results into an irregular shallow pan.

The second, and longest phase, consists of a series of rather regular bouts of activity. The specimen which was clocked stayed initially adpressed to one side of the pan, looking North. She would start scooping vigorously with the (left) hind foot which was in the middle of the excavation, throwing the sand towards the opposite side of the body. After 4 to 10 scoops she would stop for 15-30 seconds, then start another, usually shorter, series of movements with the same foot. After this, without pause, she would swing her body 90° (now looking East) and start at once digging with the right foot; then a pause, more digging with the right foot, and a swing of the body to position 1 (looking North); and so forth. Diagram 1A, a sample from the field record, shows clearly this type of cyclical behaviour.



Diagrams of digging activity, excavation of nest. A: Bouts 11 to 16; *a,* extra pause; B: Same individual, bouts 38 to 43; *b,* extra burst; *c,* absence of pause; C: Same individual, bouts 46 to 52; *d,* change of position without digging; D: Another individual, stage comparable to B.

Key: *Empty rectangles.* turtle looking North. *Black rectangles,* turtle looking East. *Lines below base line,* scooping motions with left hind foot. *Lines above base line,* scooping motions with right hind foot. *Pauses between bursts* drawn to scale, the first pause of diagram A corresponding to 15 seconds. *Pauses between motions* not drawn to scale.

When the body of the turtle swung from right to left, the head described a much smaller arch in the opposite direction: the vertical axis of the movement passed through the neck.

While the main digging is done with the hind feet, the front feet and shoulders, as well as the head, shape their side of the hole. Thus the pit, though roughly conical, has two sides a little steeper, with low irregular parapets of sand (shaped by the head and shoulders) and one broad semicircular side, shaped by the digging motions of the hind feet and with margins smooth, covered with fine thrown sand.

The rhythm above described was noticeable from the beginning of the excavation; in the case of this individual it lasted for 75 minutes out of a total of 100. Small variations occurred, such as extra pauses and spurts of digging (as shown in Diagram 1A), but in general the process was remarkably regular, both in number of scoops (10 to 26, average 13) and length of rest periods (15 to 25 seconds).

As the hole got deeper, the initial rhythm began to deteriorate (Diagram 1B). The number of scooping motions per foot tended to increase (to average 18), and the pauses to become irregular. This was a transitional phase, lasting some 10 minutes; a new rhythm was soon adopted for the finishing phase of the excavation. This consisted (Diagram 1C) of series of 12 to 15 digging motions with each foot, followed by some 15 seconds of rest and by the swing of the body to a new position. This swinging of the body was also less regular, both in extent and in smoothness of movement, than in the previous phase.

Another specimen, clocked for 30 minutes (Diagram 1D) exhibited longer pauses and a tendency towards a higher frequence of bouts with 3 bursts of digging motions.

I have the impression that the speed of the movements varied from individual to individual, but the data are not adequate for analysis.

The turtle, at the time of finishing the pit, looks tired. In the beginning the sand is made to fly to a height of 1 m or more, forming a semicircular fan with a radius of up to 3 m. At the end, rhythm is poor, and frequent ineffective movements are made.

In many specimens the hind margin of the shell, and sometimes the limbs, are worn raw, staining the sand with blood.

As for the duration of the process, I am certain of 3 specimens, which took respectively 100, 95 and 100 minutes.

The finished pits were about 70 to 100 cm deep. The diameter of the mouth varied from 100 to 150 cm.

When the hole is so deep that the turtle's head is on a level with the surface of the beach, the beast slides back, and pushes the hind margin of the carapace into the opposite side of the excavation, thus forming the egg chamber or nest hole. For some minutes one hears the noise of some further scooping going on; this is what I call the fourth phase of the process, the final shaping of the egg chamber.

OVIPOSITION

The laying position is highly characteristic. The body is kept at an angle of more than 45°, sometimes almost vertical. The neck is very tense and arched, and the head held obliquely in the same place where it had been from the beginning of the second phase of digging. One foot rests at the bottom of the nest, the other on a side wall. Three cases were timed with certainty: 15,30 and 35 minutes.

The end of the laying is signalized by a deep sighing noise and by a wave of tremors. The animal disengages itself and climbs a bit over the wall of the nest, causing sand to slide and to cover the eggs. Then it starts at once to fill the pit.

FILLING AND COVERING THE NEST

This consists fundamentally in destroying the front walls of the nest and in spreading the sand backward over a broad area (Plate 1, fig. 2). The body pivots again as in the beginning of the digging phase; the hands scoop sand and throw it backward; the feet, one at a time, feel around for sand and shovel it away with force (Plate 1, fig. 2; plate 2, fig. 1).

Initially the foot movements are similar to those made in the second phase of digging and the sand flies high. Soon, however, the sand is thrown horizontally and with such a curve that at times it reaches the turtle's contralateral shoulder. As the foot kicks, the body is raised some 3-5 cm and heavily lowered with a definite thud. After an irregular beginning, the animal settles down to a rhythm: each period of activity lasts from 60 to 90 seconds, and is followed by a pause 20 to 30 seconds long. The head and shoulders keep pushing at the sandy parapets, at times violently, and the animal looks hurried and fretful.

The end result (Plate 2, fig. 2) is a perfectly smooth oblong surface some 2 m x 50 cm, surrounded by fine spread sand. Trampling by wandering individuals soon masks almost completely the covered nest.

Three specimens carefuly timed took respectively 43, 47 and 50 minutes to complete the process. Individuals were seen to abandon the nest at any stage of the work.

RETURN TO THE WATER

Now the turtles return to the river. A majority uses the same port of entry (Plate 3, fig. 1), but a sizeable number take other routes — some even cross the beach and enter directly the channel.

The march is not continuous; the animal advances 5-20 m, stops for 5-20 seconds, proceeds, stops again, and so on. Some walk with tail high, others drag it. Some urinate as they walk, some leave a dry track.

The entrance in the water is noisy, with a lot of splashing, in contrast with the silent exit. Local people say it is because the carapace is now dry.

DESCRIPTIVE LITERATURE AND COMMENTS

The collective nesting of *Podocnemis expansa* is one of the most spectacular phenomena which can be witnessed in tropical America, and one of considerable sociological importance. No wonder it has been reported upon by travelers since the sixteenth century (e.g., Carvajal, Acuña, and Rojas, *in* Mello-Leitão, 1941). In these days the species was much more abundant than today and nested in many areas now deserted. However, the nesting season is short and it took some luck for one to happen to be at the right place and time. It was more frequent to observe the huge "corrals" full of adult females taken at oviposition, or the "harvest" of eggs and young, or to have one's native helpers dig up eggs for food, which, at least in Amazonia, borders on mania. Thus, most of the old accounts deal with gathering of eggs, extraction of oil, danger of extinction, etc, and include only hearsay or vague evidence on the actual behavior at nesting. Good eyewitness accounts are rare.

A surprisingly good report was written by Vieira in 1654, of a taboleiro he saw in the Tocantins in December 1653 (Cartas, 1925: 368). Vieira had very little feeling for natural history; he must have been much impressed by the spectacle in order to dedicate several pages to it.

Alexander von Humboldt (1814, *in* Humboldt & Bompland) witnessed the harvest of eggs in the middle Orinoco (a note on his localities, with correct spellings, is given by Blohm & Fernandez-Yépez, 1948). His data on nesting include: (i) performed at time of lowest water level the rivers; (ii) activity nocturnal with some individuals ("crazy turtles") remaing until broad daylight; (iii) digging done with the hind feet; (iv) moistening of the nest with urine; (v) pits measuring 3 x 2 feet; (vi) unearthing of previous clutches.

Spix & Martius (1839) twice mention the process. Once (p. 1138) they had at the beach of Goajaratuva (Guajarátuba) an experience similar to Humboldt's, similarly reported. In a footnote to the same page, however, they explicitly state having seen the laying process in the Japurá (tributary of the Solimões). They improve on the previous description by noting that: (i) the hind feet are used alterniately; (ii) the body is held almost vertical at the time of actual laying; (iii) in covering the nest, the sand is packed with help of the plastron; (iv) sometimes one digging turtle partly buries a neighbor; (v) the process lasts for 3-4 hours. They also refer to the accidental unearthing of clutches.

Wallace's (1853: 465) description is too general.

Bates (1863: 246) slept one night camped on an island near Teffé, on the Solimões, while the turtles were nesting. He saw a large herd retreating in the morning. His data, admittedly from hearsay, do not improve on or deviate from previous accounts, except for a note on the fact that several individuals lay successively in the same pit, until it is full, and is then covered. This idea must be based on the observation of turtles which, having dug up some other's nest, lay their eggs on top of the previous, partly destroyed clutch.

Coutinho (1868, 1886 and *in* Goeldi, 1906) also conforms to previous reports, adding that one "master" turtle is said to emerge one day before the others and to mark, with her tracks, the laying grounds to-be.

This "fact" is widely believed throughout the Amazons; Vieira quotes it; I've heard it many times, with the master turtle called "captain". In fact, before the onset of the massive nesting behaviour, one or a few turtles emerge at night or at dawn, to do some shallow digging and wandering around. On October 6 I saw tracks left by such individuals: they actually encompassed what turned out to be the entire nesting grounds. This seems to me to mean that there is some clue or clues that differentiate the favorable area from adjoining ones. Such clues may be topographical (only the highest ground being used) or related to some property of the sand, possibly the complex moisture-looseness. The role, if any, of the first tracks in determining the movements of the herd remains to be ascertained.

Orton (1870) recounts the harvest (p. 215) and the nesting (p. 297), repeating Bates' data, including successive layings in the same pit.

H.H. Smith's (1879) description is too succint and, to us, irrelevant. Verissimo (1895), Goeldi (1897, 1906), and Hagmann (1909) add nothing of interest to the present context.

The Orinoco taboleiros have been the object of several modern studies, of which I have seen Mosqueira-Manso (1945), Blohm & Fernandez-Yépez (1948), Ramirez (1956) and Roze (1964).

Mosqueira-Manso (1945) saw and photographed the nesting of *P. expansa* in Pararuma, one of Humboldt's sites. His description, barring minor descrepancies, agrees in general with what I have seen, but there is one major difference. He presents a diagram (his fig. 1) of a section of a nest. This has one vertical and one very gently sloping wall, and a sharply differentiated egg chamber.

Blohm & Fernandez-Yépez (1948) add little to the subject. Their paper is a blend of long straight citations from Humboldt and Mosqueira-Manso with personal observations. On nesting proper they repeat the latter's description and drawing.

Ramirez (1956) fully agrees with his forerunners and presents a very good photograph of the egg chamber.

Roze has also worked in the middle Orinoco. He has reported twice on his work, unfortunately neither time a technical paper. In 1962 he presented orally a moving picture to the II Latin American Zoological Congress (S. Paulo), and in 1964 he published a vulgarization paper in "Natural History". I quote only from this paper. He also describes the digging of a well differentiated egg-chamber.

The shape of the nest depicted by Mosqueira-Manso and Ramirez differs sharply from what I saw in the Trombetas. Here the pits, as described, were almost perfectly conical, and the position of the turtle very steep. In fact, both Mosqueira-Manso and Roze present photographs which perfectly resemble the pits I saw.

As to the matter of the egg-chamber, it undoubtedly exists in the Orinoco: Ramirez' photograph is unmistakable. I frankly did not see the digging of such a chamber. I found, at the time of observation, no reason to guess that the limited time spent scooping after the jamming of the hind margin of the shell against the wall of the pit were sufficient to shape a well differentiated cylindrical hole. However, I was not aware, at the time, of the relevance of the point, and intend to check it more carefully in the future.

I find my notes in disagreement with Roze's in another respect: that of tears. Carr & Ogren (1960) note and comment upon the "crying" of sea turtles. Roze says (p. 38): "By this time, the stupendous effort has filled the female's eyes with tears that roll down her sand-covered face". I frankly saw no tears, but, as I worked one night with a dim flashlight and two with natural moonshine, I cannot be sure.

Finally, both Ramirez and Roze say, on the covering of the hole, that a small area is left partly unsmoothed ("a small depression in the ground"). I have seen (Plate 2, fig. 2) nests so covered, but the completely smoothed surface was the rule.

GENERAL COMMENTS ON BEHAVIOUR

It is no doubt arbitrary to consider the nesting behaviour of *P. expansa* separately from the remaining events of its complex reproductive cycle, and even from the birth and first migration of the young, which certainly influence adult behaviour patterns.

On the other hand, the materials here included constitute, from the viewpoint of time and space, a natural unit of field work. The remainder of the cycle is much harder to observe and demands different methods; some analysis of the present incomplete and crude data is both desirable and unavoidable.

The sequence of acts comprised between emergence from and return to water is strictly linear. I shall briefly consider: (i) the stimuli which may determine the beginning and end of each phase of the sequence, (ii) the variability of the process, (iii) synchronization and interaction, and (iv) organization of space.

STIMULI.

It is obviously not possible yet to enter into a conceptual consideration of the phases of nesting behaviour and related releasing mechanisms. At most a series of reasonable guesses can be made about the type of stimuli involved.

Aggregation in front of the landing beach. This may be broadly ascribed to hormonal causes. Basking, so prominent in the preceding phase, must have an important role here. It is also safe to assume some degree of "contagion" (social releasers). I'll return to this point.

Landing and climbing to the nesting grounds. Sight of the sky line may orient and release this phase of behaviour. The pause on the beach, broken by some leaders, may be ascribed to caution or to a taxis component of the upward movement, or to both. Social components are again highly probable.

Arrest at the nesting grounds. Disappearance of the high sky line, or change of slope of the beach may be involved here. This would be in keeping with the coincidence between the area marked by the tracks of the "captain" and the actual nesting grounds: all turtles would react alike to the same stimulus. This regularity in behaviour would be very important, as clutches laid in lower portions of the beach are usually drowned by the December rise of the river.

Initiation of digging. A few individuals make scooping movements soon after landing, but do not insist. Possibly contact with dry sand induces continued digging. Presence of a social component is also possible, but variability in deambulation (to be discussed below) speaks against it.

Changes in motor pattern during digging, filling and covering behaviour. I believe that these changes are associated with the shape of the pit (the stance of the turtle becoming more and more vertical) or with changes in stimulation of the feet by loose sand.

Cessation of digging and oviposition. These may also be associated with stance, or with the height of the turtle's head above ground level, which seems to be very uniform among individuals engaged in laying.

Filling and covering. Obviously released by the end of oviposition.

Return to water. The flat surface of the covered nest may be the stimulus, and the slope of the beach the orientation clue. This would explain why a majority of individuals return to water at the landing port: as they have begun to dig shortly after reaching the nesting grounds, they are closer to the entrance slope than to any other, and consequently orient towards it.

It is apparent that a great variety of stimuli are involved: hormonal, visual, tactile and proprioceptive. Social releasers are also present, but only in the initial phases of the process, i.e. landing and climbing, and, possibly, aggregation prior to landing.

VARIABILITY

I shall present here data on variability of time spent and of achievement within a given phase; abandonment of the sequence will be treated separately.

Landing. I saw the process twice. Once it was a very orderly procedure: after a large number of individuals had assembled, landing proceeded rather smoothly for about 2 hours. The other time there were about as many turtles assembled; two individuals came ashore, prowled around briefly and returned to water, after which the whole group disappeared. This would seem to indicate that, at this time, motivation is not very strong.

Deambulation and initiation of digging. Once on the nesting grounds, orderliness vanishes abruptly. Digging motions had been briefly displayed next to the water by a few individuals; now a great many make the sand fly. Some get to serious digging immediately, but others stop, wander around and wait for up to two hours or perhaps more before beginning. I am sure that some individuals do "trial" scoopings two or three times (meanwhile walking all over the place) and then settle down to a firm pattern, while others, after the same sampling around, return to water or simply keep wandering.

Excavation of the nest. I timed independently 3 individuals, which took respectively 100, 95 and 100 minutes. This is suspiciously low variability. The rhythm of digging seemed, at first glance, very uniform, but later inspection of time spent in digging and in resting indicated some amount of variation, both in speed and in sequence of bouts. This would be one of the most appetitive of the phases, i.e., one in which the shape of the hole and the mechanical properties of the sand would most probably determine short-range adaptations of motor patterns.

I performed no measurements, but remained with the impression that variability in depth and shape of finished nests is rather small. This is a subject that must be studied in connection with the mechanical properties of the sand, depth of the water table, and size of the turtle.

Oviposition. The 3 specimens definitely timed took 15, 30 and 35 minutes between evincing the characteristic laying position (tense neck) and exhaling the final sigh followed by a wave of tremors.

Filling and covering the nest. It is very difficult to decide what constitutes variation in this phase and what means abandonment of the nesting sequence. Some turtles leave a barely covered clutch; a great many fill the pit but do not smooth the surface; a sizable number, but perhaps not the majority (and this must be better observed next time) perform a creditable job of filling, packing and smoothing.

Variability in rhythm is large, as it can only be expected at the end of a couple hours' hard work. However, the 3 specimens I clocked (independently) exhibit again a surprisingly low variability of time spent for the whole task: 43, 47 and 50 minutes.

Return to water. From a consideration of the tracks it is evident that there is much variability here: some tracks show a tail furrow, others not; some are wetted, some dry. But present data are insufficient, especially since turtles return to water in widely varied conditions, some having completed the nesting sequence and others having interrupted it at some particular point.

A majority of individuals return to water at the landing port (Plate 3, fig. 1), but a still considerable number at other points; this may be related to the position of the nest relative to beach topography, as discussed above.

SYNCHRONIZATION AND INTERACTION

It is obvious that the initial phases of nesting are highly synchronized, and that is, to me, one of the most importante facts in the behaviour of *P. expansa.*

A first factor contributing to such a synchronization is the stay in the pool next to the beach. There mating occurs (Roze, 1964). If the eggs then fertilized are those to be laid next, here is a cause of synchrony. The ensuing period of basking must contribute even more to equalize hormonal conditions. If, on the contrary, the eggs laid are those fertilized in the previous trip to the nesting area, then basking would be the more important factor of synchronization.

Once the turtles are sufficiently motivated, social releasers certainly interfere, as it is plainly seen in the way they congregate in the shallows, emerge, and climb to the nesting grounds.

After the phase of deambulation begins, however, synchrony gives way to highly variable behaviour, each turtle being very little influenced by the actions of its neighbours.

The end of the nesting session is a very straggling affair. Since Humboldt's days there are reports of the "crazy turtles" which are busily working a couple of hours after their fellows are back in the water; all specimens photographed by me are such variants, as I had no flash and could take photos only after sunrise.

ORGANIZATION OF SPACE

It has been repeateddy noted in the literature that frequently one *P. expansa* digs up the nest of a fellow. I saw this happen: the animal pays no attention to the eggs which are flipped around, mixed with sand (Plate 3, fig. 2). It seems that there are no clues as to the presence of a filled nest, or that there is great variability in the efficiency of the signals eventually present.

Humboldt seems appalled by the amount of egg wastage; his followers on the Orinoco (Mosqueira-Manso; Blohm & Fernandez-Yépez) attach much less importance to the fact. I saw it happen 6 times, in several thousand nestings, and am inclined to agree with the Venezuelans that the damage done must be inconsiderable, not weighing against the advantage of bunched up nesting.

The spacing of nests is very haphazard. Location of the pit seems related to the amount of deambulation done after the nesting grounds are reached. The stronger motivated individuals dig immediately over the top of the rise, in front of the landing site. Here there is an enormous disorder and all sorts of overlap of nests. In many cases (Plate 2, fig. 1) the pits coalesce; the behaviour of the involved individuals varies from paying no attention to wandering away.

INCOMPLETE SEQUENCES

As stated above several times, many individuals do not complete the nesting sequence, abandoning it at any point. The phenomenon was especially impressive on the night of October 6, when a large number of turtles engaged into digging, but none was seen laying, nor filling a pit; later on, a careful inspection of the beach revealed no nests.

This was a peculiar night in at least two respects. It was the first time that a large number of turtles came ashore (and previously only once, on the night before, a few individuals had done so) and it was a rainy, windy night. October in the Trombetas is very hot, but at 0300 hours of October 7 it was so cold that I had to have a drink and do some running up and down the beach in order to keep on working. Thus I cannot decide whether abstention of laying was due to insufficient motivation or to atmospheric causes. The latter seems probable.

But even on the perfect nights of October 8 and 10, when a large number of individuals went through the nesting behaviour sequence, there were still a great number of failures.

A few of those may have been caused by alarm. Others, in the initial stages, may be attributed to inexperience in nesting (Caldwell, 1962: 299), or to tentative acts, abandoned to be resumed and successfully concluded elsewhere.

None of these explanations seems applicable to interruption of the later stages of the sequence. Individuals which interrupted oviposition, or gave up covering the nest, obviously did not resume the task by digging a new pit elsewhere and starting everything anew. In fact, many such specimens were followed back to the water, and seen to swim away.

Several explanations may be evoked to explain this very important and prominent fact. A first would be that the nesting behaviour of *expansa* is still incompletely evolved, not well perfected, and that, at times, either a consummatory stimulus (Thorpe, 1961) interferes with the normal sequence, or an individual not ready yet for the whole performance gets carried away by the social releasers of the initial steps, to have its drive die out during the non-social stages. Finally one has to consider the possibility that tampering with hatchlings in some way interferes with the normal development of a complex behaviour pattern, involving migration, aggregation and synchronous behaviour. Turtles are born in this taboleiro (presumably in every other one in the Amazons) among people who try either to help them or to collect them, and this has been so for at least several hundred years. Nothing is known of imprinting or related phenomena in river turtles, but until such knowledge exists, remote consequences of early disturbances must be kept in mind in relation with behavioural deviations.

COMPARATIVE NOTES

The evolutionary meaning of the nesting behaviour of *P. expansa* must be assessed against the backdrop of the family Pelomedusidae and of the marine turtles, which are the only other group of chelonians to show migration and aggregation at particular nesting beaches.

NESTING BEHAVIOUR OF THE PELOMEDUSIDAE

I am personally acquainted with the general nesting behaviour of two pelomedusids, *Podocnemis unifilis* ("tracajá") and *Podocnemis sextaberculata* ("pitiú" or "cambeva") in Brasil. I have also reliable oral information on the behaviour of *Podocnemis dumeriliana* ("cabeçuda"). Mondolfi (1955) has data on *Podocnemis unifilis,* in agreement with mine, and on *P. cayennensis,* both in the Llanos of Venezuela. Hewitt (*apud* Loveridge, 1941) gives the only description I could find of an African species, *Pelomedusa subrufa*. In no case, however, are there any data on motor patterns, timing, variability and interaction. Comparisons remain so far very broad.

Podocnemis unifilis lays at night, singly. It emerges from the river at seemingly any place, even steep banks. Deambulation may be very short, the nest being dug close to the water, or very extensive, the animal wandering even into burnt areas and cultivated fields. In some parts of the Amazon valley, people have dogs and horses trained in hunting for tracajá during its deambulatory phase. The nest is shallow, quickly dug and filled. Loamy or clayey soils seem to be preferred.

Podocnemis sextuberculata lays also at night, singly or in small bands (2 to 4 individuals) in beaches of pure sand. The nest is shallow and the behaviour furtive and hurried.

Podocnemis cayennensis, according to Mondolfi (1955), seems to behave similarly to *unifilis,* even as regards preference for clayey soils.

Podocnemis dumeriliana is said by reliable informers to live and breed in the mud of the permanently flooded forest ("igapó").

The account of *Pelomedusa subrufa* refers to a small nest (2,5 inches in diameter, 4-5 inches deep, with a chamber slightly larger than a tennis ball) dug into muddy soil.

It seems to me that the behaviour of *Podocnemis unifilis* and *cayennensis* and of *Pelomedusa subrufa* represent the primitive pattern for the family, and one close to the general chelonian norm (Carr, 1952). It would be characterized by individual nesting, by a rapid excavation, filling and occultation of a small nest, and by use of the clayey soils most common along rivers.

Podocnemis sextuberculata differs from this pattern in preferring sandy beaches, and in emerging at times in bands of 2 to 4 individuals. Whether this group emergence represents a coincidence or incipient social behaviour it is impossible to say at present.

Thus the nesting behaviour of *expansa* is unique in the family and approached only by that of *P. sextuberculata* in what regards use of sandy beaches. Otherwise, its gregariousness and synchronization, as well as the shape and depth of the nest, set it sharply apart from everything that is known.

A COMPARISON WITH SEA TURTLES

The rationale of a comparison between the nesting behaviour of sea turtles and of *P. expansa* is gregariousness. Thus, in what follows, only the social components are compared. Motor patterns and other aspects should be studied against a broader systematic framework.

The great environmental and morphological differences between the sea turtles and the pelomedusids in some respects forbid but in others enrich comparisons of their respective nesting patterns.

My argument will follow Hendrickson's (1958) detailed and fluent account of the nesting of *Chelonia mydas* in the South China Sea, supplemented by: Carr & Ogren (1960), on the same species in the Caribbean; Carr & Ogren (1959), on *Dermochelys coriacea;* Caldwell, Carr & al. (1959) and Caldwell (1962), on *Caretta caretta;* Carr (1952), on *Eretmochelys imbricata* and *Lepidochelys olivacea.* All these forms belong to the family Cheloniidae, with the exception of *Dermochelys,* which constitutes the only genus of the family Dermochelyidae, placed in an sub-order of its own, Athecae. However, it is generally agreed (Carr & Ogren, 1960: 20) that the behaviour of *Dermochelys* closely resembles that of the thecophoran sea turtles.

Nesting site. P. expansa and the sea turtles show remarkable agreement in that their nesting sites are always sand beaches.

The taboleiros frequented by *expansa* are topographically simple and made of bare sand. Coastal beaches are many times complex (e. g. Baldwin & Lofton, 1959; Carr & Hirth, 1962) and frequently support vegetation which may complicate the digging of the nest or even cause abondonment of an initiated excavation.

This may explain why sea turtles present great intra-specific behavioural variability in the phases which precede nesting proper.

Aggregation and landing. Hendrickson (1958: 465) working in a calm beach of a shallow sea, describes a pattern which in a way approaches that of *P. expansa*: at sunset "turtles begin to enter the beach shallows and individuals may be seen moving along the beach in from two to four feet of water". Other accounts indicate emergence of single individuals or small groups. In no case, however, is there landing massive and synchronized as in *P. expansa,* which, in this respect, stands alone.

The behaviour during movement from the water to the laying grounds is correlated with the morphology of the locomotor apparatus. *P. expansa,* although a good swimmer with broad webbed feet, has good walking legs, and its mode of ascending the beach is certainly adaptive: after a inspection pause immediately after landing, a swift concerted rush upland. Sea turtles have their limbs modified into flippers, and are fated to laborious locomotion on land; their frequent stops to survey the landscape are both necessary and convenient.

Deambulation. All forms studied seem to wander to the same extent over ground favourable to nesting. A very interesting difference is apparent between *Ch. mydas* (Hendrickson, 1958: 470) and *P. expansa.* The former is stimulated to further wandering by any contact, even with other turtles. *P. expansa* shows an amazing degree of tolerance to bumping and crawling over.

Excavation. Hendrickson (1958: 470) says that his green turtles tended to use an abandoned trial pit to begin their excavation; he believes this would decrease the chances of a covered nest being dug up.

He also (p. 475) noticed that turtles were much disturbed by the vibrations produced by the digging of neighbours; in many cases they would abandon the initiated pit and move elsewhere.

This peculiarity is apparently wasteful of effort and time, but Hendrickson believes that it is adaptively advantageous, inducing a "nightly spacing of nests over all the suitable beach area". This is in keeping with the reactivity to encounters, which also tends to promote even spacing of nests. Both traits are conspicuosly absent in *expansa*.

INTERPRETATION

The nesting behaviour of *P. expansa* is characterized by some features, above discussed, which result into placing simultaneously a large number of nests into a restricted area of beach. In this it differs markedly from the behaviour of the sea turtles, which tends to an even distribution of nests in time and space.

It is possible to imagine an adaptive rationale for this pattern, and one indeed that may be important to the evolution of social breeding.

The nest of *expansa* is both relatively and absolutely deep; the depth at which the eggs are laid is not determined by the length of the digging limb, as in the majority of turtles, but by the length of the animal's whole body, with extended neck and hind limb. This restricts the beach area suitable for nesting, as the eggs must stay above the level of the rising waters. Consequently, there is a premium on mechanisms that keep the laying group within high ground on the taboleiro. In fact, we have seen that the nesting grounds proper of *expansa* are remarkably fixed during the season, and that behavioural adaptations have evolved in the direction of crowding rather than spacing, even at the cost of some accidental destruction of clutches.

This crowding and the high degree of synchrony in oviposition must be advantageous also from another, and very important, angle. Emergence of the hatchlings from a deep and tightly packed pit is not a simple matter: Carr & Hirth (1961) have proved the fundamental importance of group facilitation in the emergence of hatchling *Chelonia mydas,* and have also confirmed and extended Hendrickson's (1958) data on the heat economy of the nests. These results support a working hypothesis that the crowding of nests and the synchronous development of large numbers of clutches introduce an appreciable measure of inter-brood cooperation, complementary to the intra-brood facilitation indispensable to successful emergence.

This hypothesis is strengthened by the weakness of the alternative ones usually evoked to explain colonial breeding:

Migration in order to avoid unfavourable seasons cannot be alleged, as all movements take place inside the same climatic belt. Protection of the laying females against predators is made improbable by the consideration of other, syntopically nesting, pelomedusids. Food supply for adult or young is unimportant, as little, if any, feeding is done during the reproductive season, and there is no care of the young.

The special requirements of the nesting site — a topographically adequate taboleiro next to a stretch of calm waters — are to be considered as consequences rather than determinants of the social behaviour, as they are irrelevant to the nesting of a single animal, and essential only to large groups.

Thus we are left with the protection of the clutch by deep interment and with the consequent difficulties of emergence of the hatchlings as possible determinants of the breeding pattern of *Podocnemis expansa.*

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REFERENCES

BALDWIN, W. P., JR. & J. P. LOFTON, JR.
1959: *in* Caldwell, Carr & al., 1959, part III.

BATES, H. W.
1863: *The Naturalist on the River Amazons 2*: IV+423 pp. London: J. Murray.

BLOHM, T. & A. FERNANDEZ-YÉPEZ
1948: La Sociedad de Ciencias Naturales de la Salle en Pararuma. *Mem. Soc. Ci. Nat. La Salle Caracas 8*(21):35-69.

CALDWELL, D. K.
1962: Comments on the nesting behavior of Atlantic loggerhead sea turtles, based primarily on tagging returns. *Quart. J. Florida Acad. Sci. 25*(4):287-302.

CALDWELL, D. K., A. CARR & OTHERS
1959: The atlantic loggerhead sea turtle, *Caretta caretta caretta* (L.), in America. *Bull. Florida St. Mus. Biol. Sci. 4*(10): 293-348.

CARR, A.
1952: *Handbook of Turtles.* xv + 542 pp. Ithaca: Comstock Publishing Associates.

CARR, A. & L. GIOVANNOLI
1957: The ecology and migrations of sea turtles, 2. Results of field work in Costa Rica, 1955. *Amer. Mus. Novit. 1835*: 32 pp.

CARR, A. & H. HIRTH
1961: Social facilitation in Green Turtle siblings. *Animal Behaviour 9*(1-2):68-70.

CARR, A. & L. OGREN

1959: The ecology and migrations of sea turtles. 3. *Dermochelys* in Costa Rica. *Amer. Mus. Novit. 1958*: 29 pp.

1960: The ecology and migrations of sea turtles, 4. The Green Turtle in the Caribbean Sea. *Bull. Amer. Mus. Nat. Hist. 121*:1-48.

COUTINHO, J. M. S.

1886: Bedeutung, Fang und Verwertung der Schildkröten am Amazonas. *Zool. Gart. Frankfurt 27* (11): 329-335, 366-372. (A former version, published in French in *Bull. mens. Soc. Impér. Zool. d'Acclim. 5*(4)1868, pp. 147-166, was not obtained; see Goeldi, 1906: 726).

GOELDI, E. A.

1897: Die Eier von 13 brasilianischen Reptilien, nebst Bemerkungen über Lebens und Fortpflanzungsweise letzterer. *Zool. Jahrb.* (*Syst.*) *10*:640-676.

1906: Chelonios do Brazil. *Bol. Mus. Paraense 4*:699-756.

HAGMANN, G.

1909: Die Reptilien der Insel Mexiana, Amazonenstrom. *Zool. Jahrb.* (*Syst.*) *28*:473-504.

HENDRICKSON, J. R.

1958: The green sea turtle (Chelonia mydas) in Malaya and Sarawak. *Proc. Zool. Soc. London 130*:455-535.

HUMBOLDT, A. VON

1862: *Reise in die Aequinoctial-Gegenden des neuen Continents, in deutscher Bearbeitung von Hermann Hauff 4*:242 pp. Stuttgart: Gotta.

HUMBOLDT, F. H. A. VON & A. J. A. BONPLAND

1814: *Voyage aus Régions Equinoxiales du Nouveau Continent.... Pt. I. Relation historique* (not seen; cited from the German translation of 1862, *q. v. s.*).

LOVERIDGE, A.

1941: Revision of the African terrapin of the family Pelomedusidae. *Bull. Mus. Comp. Zool. 88*:465-524.

MELLO-LEITÃO, C.

1941: *Descobrimentos do rio das Amazonas, traduzidos e anotados por C. de Melo-Leitão.* 294 pp. S. Paulo: Cia Editora Nacional. (Biblioteca Pedagógica Brasileira. Ser. 5: Brasiliana, vol. 203).

MONDOLFI, E.

1955: Anotaciones sobre la biologia de tres quelonios de los Llanos de Venezuela. *Mem. Soc. Ci. Nat. La Salle Caracas 15*(42): 177-183.

MOSQUEIRA-MANSO, J. M.

1945: Las Tortugas del Orinoco. Ensayos biologicos de la Arrau (Podocnemis expansa). *Tercera Conferencia Interamericana de Agricultura (Cuadernos Verdes nº 29)*: 43 pp.

ORTON, J.

1870: *The Andes and the Amazon.* 356 pp., ills., map. New York: Harper & Brothers.

RAMIREZ E., M. V.

1956: Estudio biologico de la tortuga "arrau" del Orinoco, Venezuela. *El Agricultor Venezolano 21*(190):44-63.

ROZE, J. A.

1964: Pilgrim of the River. *Nat. Hist. New York 73*(7):35-41.

SMITH, H. H.

1879: *Brazil. The Amazonas and the Coast.* XV+644 pp. New York: Charles Scribner's Sons.

SPIX, J. B. VON & C. F. P. VON MARTIUS

1831: *Reise in Brasilien...* vol. 3: VIII+40+pp. 885-1388. München: M. Lindauer.

THORPE, W. H.

1961: *Introduction* to Part II, *Experimental studies of animal behaviour,* pp. 87-101, *in* Thorpe, W. H. & O. L. Zangwill (eds.) *Current problems in animal behaviour.* XIV+424 pp. Cambridge: at the University Press.

VERISSIMO, J.

1895: *A Pesca na Amazonia.* 207 pp. Rio de Janeiro & S. Paulo: Livraria Clássica de Alves & C.

VIEIRA, PE. A., S. J.

1925: *Cartas do Padre Antonio Vieira coordenadas e anotadas por J. Lucio d'Azevedo.* Tomo 1º XVII+605 pp. Coimbra: Imprensa da Universidade. (Biblioteca de escritores portugueses. Série C.).

WALLACE, A. R.

1853: *A narrative of travels on the Amazon and Rio Negro...* VIII+519 pp. London. Reeve and Co.

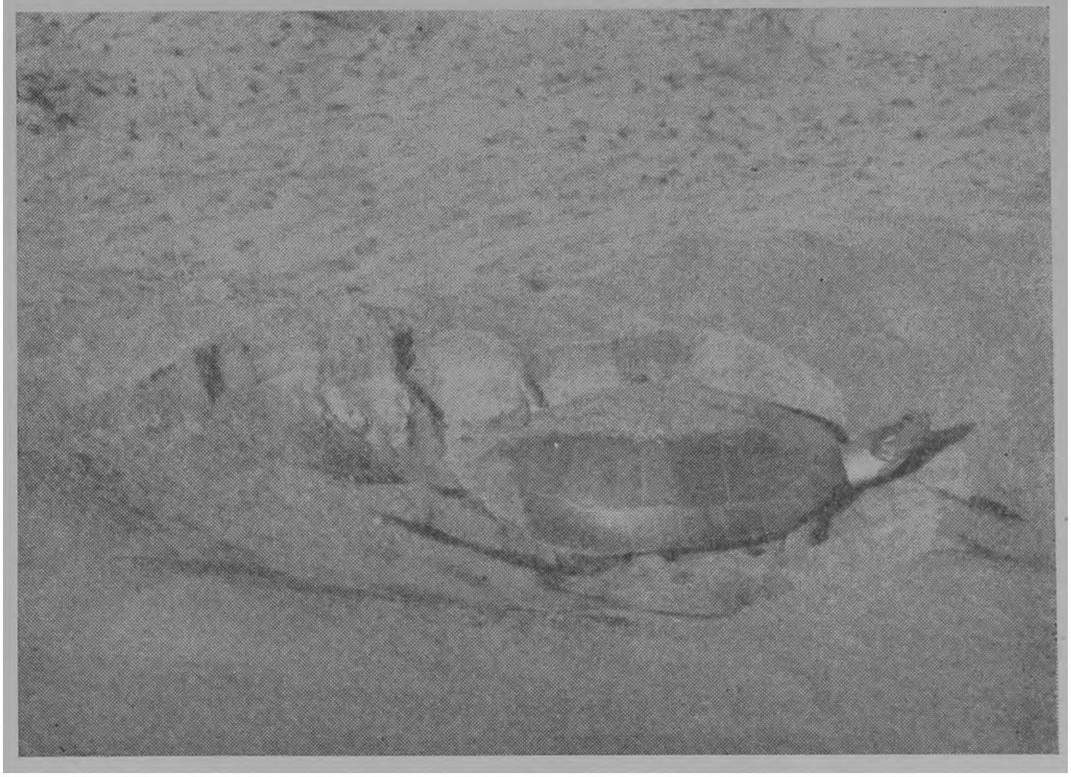

Plate 1

Fig. 1. Port of entry; one late returning turtle can be seen (0600 hours).
Fig. 2. Filling behaviour; note: right forelimb scooping sand; steep anterior and lateral edges of pit; smoothed hind edge; on foreground, immediately adjacent, covered nest.

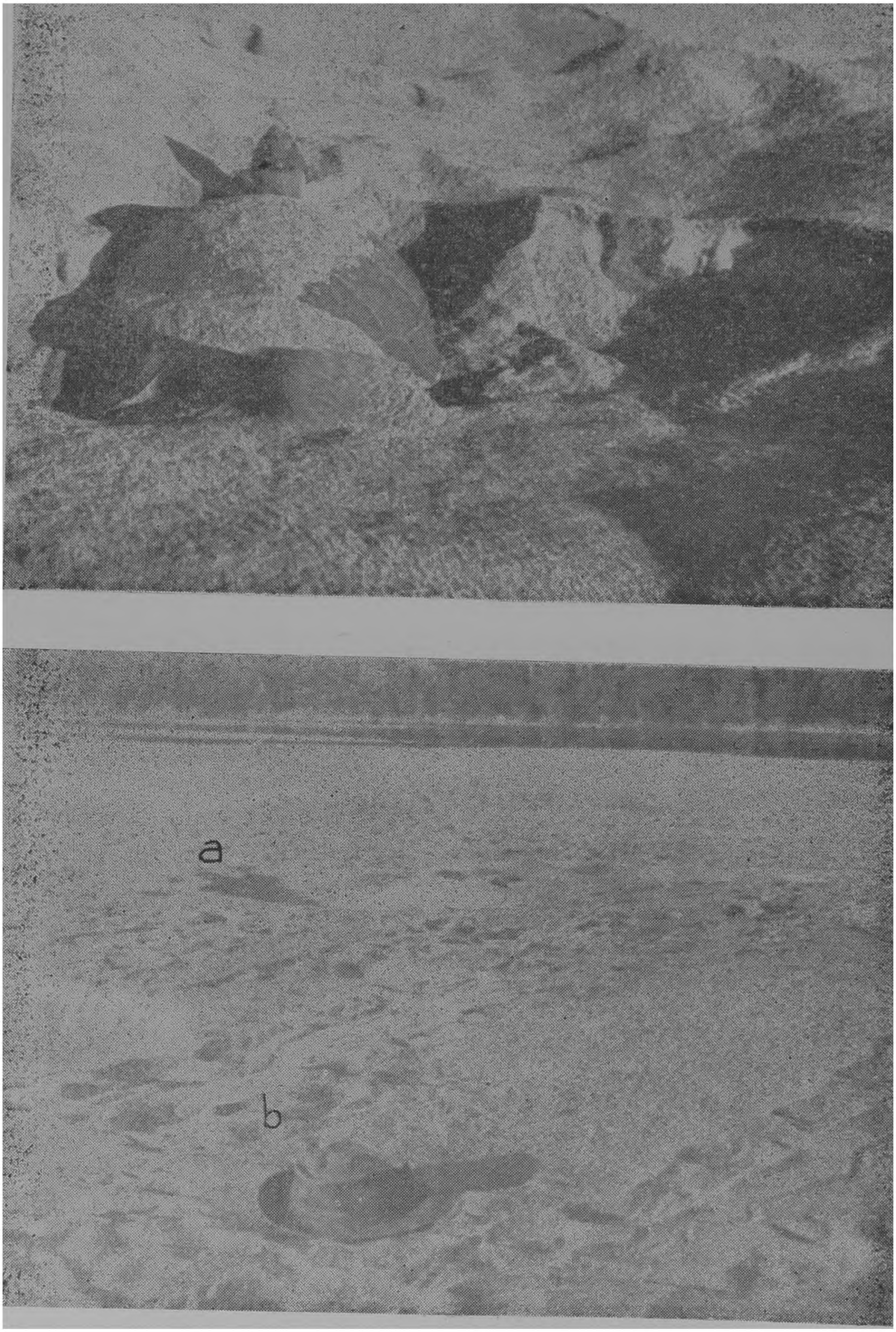

Plate 2

Fig. 1. Filling behaviour; note: hind foot flinging sand; on right side coalescod pit, abandoned. Fig. 2. Filled and smoothed nests; *a*: with a shallow remaining pit at one end; *b*: perfectly finished.

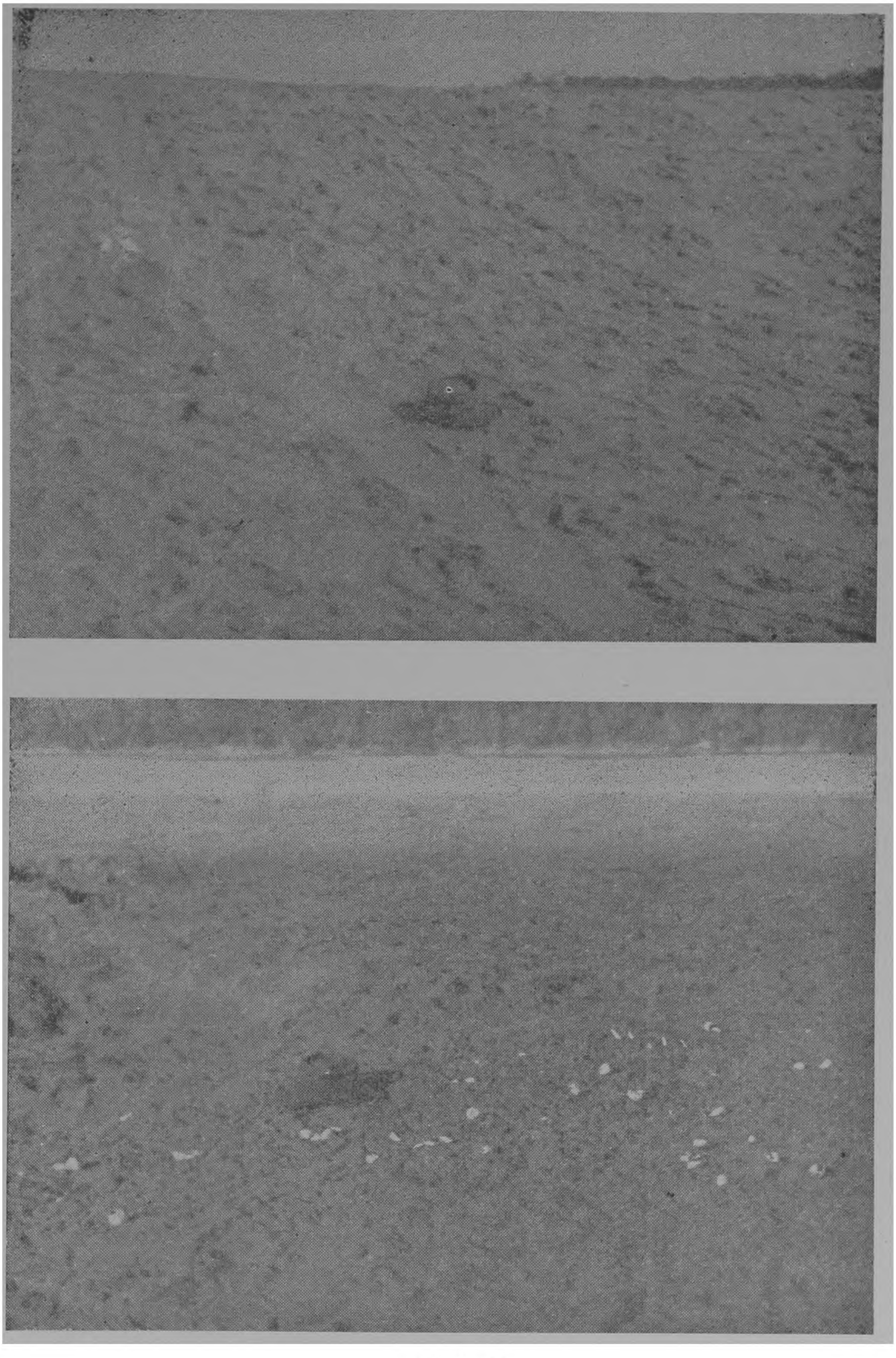

Plate 3

Fig. 1. Return tracks to port of entry. Fig. 2. Eggs excavated by turtle which laid on the same nest, on top of partly destroyed clutch.