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ABSTRACT

The biology and ecology of South American turtles is still poorly known, particularly, for the Brazilian species. Laboratory studies are essential to understand the life cycles of aquatic turtles species and to help in formulating management plans for their conservation. As a contribution to the knowledge of *Podocnemis erythrocephala* species, we give a description of its species-typical behaviors, categorized as: maintenance, locomotion, feeding, agonistic and reproduction, based on captives observations of four pairs of turtles in an aquarium in Manaus, Brazil. Similarities and differences with the repertoires of other turtle species are discussed, concluding that turtles have much more complex adaptative strategies and social life than was believed.

KEYWORDS: Ethogram, captivity, behavior, turtle, Amazon.

Descrição de padrões comportamentais de *Podocnemis erythrocephala* (Spix, 1824) (Testudines: Podocnemididae) (Irapuca) em cativeiro, Manaus, Amazonas, Brasil

RESUMO

A biologia e ecologia dos quelônios da América do Sul é pouco conhecida, particularmente para as espécies brasileiras. Estudos em laboratório são essenciais para entender o ciclo de vida das espécies de tartarugas aquáticas e ajudar na formulação de planos de manejo para sua conservação. Como uma contribuição ao conhecimento da espécie *Podocnemis erythrocephala*, nós descrevemos os comportamentos típicos nas categorias manutenção, locomoção, alimentação, agonístico e reprodutivo, baseado em observações de quatro pares de tartarugas em um aquário na cidade de Manaus, Brasil. São discutidas similaridades e diferenças com repertórios de outras espécies de quelônios, concluindo que esses animais possuem estratégias adaptativas e vida social muito mais complexas do que tem sido ponderado.

PALAVRAS-CHAVES: Etograma, cativeiro, comportamento, tartaruga, Amazonia.

763

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INTRODUCTION

The biology and ecology of South American turtles, is still poorly known (Vogt 2008), particularly, for the Brazilian species. The study of turtles in nature is difficult, partly because most of them live in aquatic or semiaquatic environments that obscure detailed observation (Carpenter and Fergusson 1977), especially in the Amazon where the water in some of the rivers is dark with low visibility. Studies in captivity are therefore critical, because it is possible to observe the behavior of turtles in greater detail (Molina 1995). The few behavioral studies that exist for the region are short and related to nesting behavior of Podocnemis vogli Müller, 1935 (Ramo 1982), Podocnemis expansa (Schweigger, 1812) (Vanzolini 1967; Alho e Pádua 1982a,b) and Podocnemis unifilis Troschel, 1848 (Foote 1978), and feeding behavior of Podocnemis expansa, P. unifilis, and P. sextuberculata Cornalia, 1849 (Malvasio et al. 2003). Nothing has been published about other aspects of behavior for these species. Laboratory studies are essential to understand the life cycles of these species and to help in formulating management plans for their conservation.

Our objective in this study is to describe the principle aspects of behavior of *Podocnemis erythrocephala* (Testudine: Podocnemididae) and organize them in categories of behavioral patterns.

MATERIAL AND METHODS

Since 2005 we began observations regarding turtle behavioral patterns and then we realized a need for a standardize list of behavioral patterns. We attempted to identify all specific behavioral patterns from our observations. We observed four pairs of Podocnemis erythrocephala from April 2005 until February 2006, from the Cumicuri River in the municipality of Barcelos (00°41'S, 63°12'W). Latter, the turtles were directly transported to Manaus where they were maintained in a 180 cm length, 60 width and 40 cm high aquarium at the Instituto Nacional de Pesquisas da Amazônia in Manaus, Brazil. We changed the water twice a week using well water, at least one hour prior to the observations. We fed the turtles every two days, also starting the observations at least one hour prior to the end of the food. In order to identify, describe and organize the recorded behavioral patterns into categories, we used the ad libitum method with qualitative character recorded by hand as they occurred. Sex of the turtles was noted by the bright red head coloration of males, in contrast to the brown coloration of the heads of adult females and by the small size of males body as well as the longer and thicker tail of males. We could identify turtles individually by their marks in the carapace probably due to agonistic events in nature.

RESULTS

We identified 37 behavioral patterns for *Podocnemis* erythrocephala grouped in five categories: Maintenance, locomotion, feeding, agonistic and reproductive. All the behavioral patterns are described below.

Maintenance

Stretching the head: turtles stretch the neck, raising or lowering the head. It is often performed while displaying dominance between individuals.

Lowering forelimbs: Turtle's forelimbs start falling slowly until reaching a 90 degree angle to the body. This behavior can be performed while resting.

Raising forelimbs: turtles raise the forelimbs usually to start swimming.

Resting: retracting or not some or all the forelimbs or lowering forelimbs, the turtle remains stationary, looking continually in a particular direction. Turtles often switch this behavior with sleeping behavior for long periods of time. They can sleep with part of the head out of water (mouth, nostrils and eyes at the water level) or even in the bottom of the aquarium, with the hind limbs touching the aquarium and forelimbs retracted into the shell or not. When turtles look at other co-specifics, it is not a resting behavior; it is part of the agonistic event.

Sleeping: the main difference between sleeping and resting behavioral patterns is that when the turtle sleeps it keeps the eyes closed. During the performance of the sleeping behavior they also can keep the limbs anywhere, elevated, down, retraction of the hind limbs touching the aquarium. Sometimes they retract the head into the shell by the side as all pleurodiran turtles. When all individuals are sleeping and one of them wakes up, all the group wakes immediately afterwards. In addition, there seems to be a hierarchy for sleeping and resting behavioral patterns since we observed that the females were positioned above the males, dominating him and preventing other females to approach him. The dominant female (the largest one) slept at a higher level than the other individuals. If a male tried to get in a position in a higher water level than her, she went towards him even biting to put him down.

Grooming: they scratch their head with the forelimbs and bite their forelimbs. The neck can reach to their forelimbs and the grooming behavior results in the removal of dead skin from the soft parts. They were not seen scratching other parts of the body or scratching conspecifics.

Vigilance: it seems that the task of vigilance was always designed for one member of the group, changing between individuals throughout the day. The turtle responsible for vigilance at the time gets in resting position sometimes



stretching the head and open eyes looking in many directions. When all the group is sleeping, the turtle responsible for vigilance is the first to wake up when some external signals such as light or movements happen and after that the other individuals wake up as well. They could be communicating by sound and the vigilance turtle alerting the group.

Breathing: swim up to emerge at the surface, sometimes only the nostrils out of the water or sometimes all the head and the turtle with open mouth.

Bubbling from nostrils: turtle makes bubbles in the water so we can see the bubbles coming from the nostrils going up in the water. It is probably a strategy to exhale CO_2 and remain under water longer before emerging to breath.

Emerging: the turtle rises in the water toward the surface, emerging the head out of the water.

Submerging: the turtle sinks to the bottom of the aquarium

Locomotion

Approaching: any locomotion of one turtle toward another one; only counted for turtles within 0.5m of each other.

Leaving: Any locomotion directly away from another turtle.

Avoiding: any movement (e.g. withdrawal of the head), or evasive locomotion, which tends to maintain or increase the distance between two turtles.

Swimming forward: the turtle moves the limbs in many directions, but when they move for long distances they intercalate the limbs (e.g. right forelimb forward and left forelimb back and vice versa). The forelimbs make more diversified movements than the hind limbs. The hind limbs make semi-circle lateral movements almost exclusively. When swimming the turtles always direct the head in the direction that they are swimming. Sometimes they swim with only one side to direct the flotation to that limb's side (e.g. swim with the right forelimb to go to the right side). When swimming short distances, they get pulse with a forceful movement and stop swimming by just floating taking advantage of velocity received by this forceful movement.

Swimming back: they swim backwards to circle around themselves (when they want to move to the opposite side). They only swim backwards very short distances and the limbs move from outside inward.

Walking: turtle walks on the bottom using two or four limbs. When walking with two limbs, the forelimbs make swimming motions.

Feeding

Cutting: they first cut the food in smaller parts with the tomilla. Turtles use the foreclaws to help them to manipulate food items, making movement as if they were swimming but

in fact they were moving the food towards their mouths. The bite precedes an extension movement of the neck and head, followed by a retracting movement.

Swallowing: After cutting in small pieces, they swallow the small pieces. It is a very simple movement and they do not chew the food.

Foraging: The turtles bend the neck down exhibiting olfaction behavior, while walking or swimming on the bottom of the aquarium.

Agonistic

Raising the head: after stretching they raise the head to possibly show dominance.

Throat pulsating: turtles pulsate the gular region of the neck when a conspecific approaches.

Biting: movements of nipping or snapping with mandibles or jaws. Usually they bite the back part of the plastron (Figure 1) as well as limbs, head and the neck while trying to copulate.

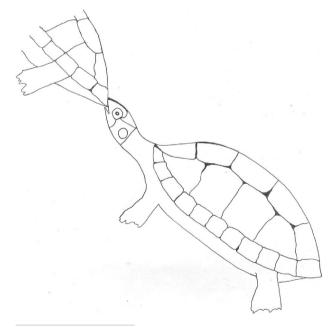


Figure 1 - Biting onto the carapace of another turtle. Usually females bite the male.

Gapping: the turtle opens the mouth briefly and then closes it directing the gesture toward another turtle. This behavior usually repels the other turtle.

Pursuing: one turtle follows another individual constantly in semicircles. Usually pursuing behavior is followed by attempted bites or actual bites.

Following – one turtle follows another individual straight, but never passing by laterally, during the following behavior, turtles try to bite each other or to smell the cloaca. This



behavior happens when the turtles are walking on the bottom or when swimming. Usually this behavior is followed by copulation.

Approaching: One turtle approaching another individual to repel the conspecific, gapping or not. If the conspecific does not move away, the turtle may bite this conspecific.

Retracting head: the turtle when feeling at risk retracts the head followed or not by swimming away behavior.

Staring: The turtle, usually the dominant female, looks at the conspecific fixed for a long time. The conspecific swims away or the turtle starts to approach, to chase or even to bite the conspecific.

Reproduction

Searching: the turtle swims searching for a turtle of the opposite sex and may or may not copulate.

Olfaction: male extends neck and lowers the head to smell the cloaca region of another turtle (Figure 2). This behavior is used to identify a female and test if she is receptive. They can smell the conspecific, if it is the same sex they swim away. Sometimes they smell the other parts of the body, like limbs and carapace. When the individual smells the other individual, the individual smelling sometimes keeps the neck outstretched.

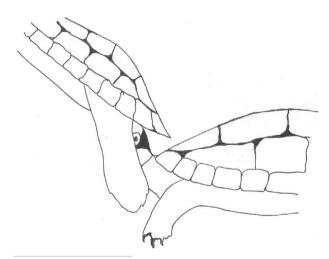


Figure 2 - Sex recognition by olfaction.

Nudging: when the turtle is touching any part of the other turtle with the head. Usually turtles display this behavior during mounting.

Mounting: male positions his plastron on the posterior part of the female's carapace and also places his forelimbs on her carapace while attempting to copulate. The male stretches his neck and keeps it bent downward sometimes touching female's carapace and head. The male caresses the female's neck probably to stimulate her.

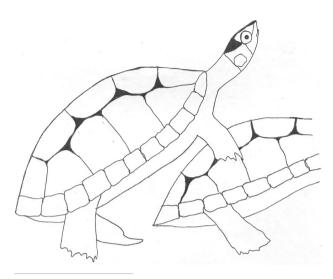


Figure 3 - Male stretching the tail to find the female cloaca to insert the penis.

Bending tail: when male approaches the female, if he is stimulated, he starts to stretch the tail to find the female cloaca and to insert the penis (Figure 3). The male moves the tail up or down or laterally. If the female is stimulated, she stretches her tail to help the male to find her cloacal region.

Copulating: occurs when the tail begins to contact the cloaca and the male inserts the penis into the cloaca of the female. During this moment the tails of both sexes are kept outstretched and their necks are extended. When they are copulating on the bottom of the aquarium, the forelimbs of the male are rested on the carapace of the female, while the hindlimbs are touching the bottom of the aquarium. Sometimes the females do not stop moving during copulation, and the males move along with the female without dismounting. During copulation the male usually rubs the ventral aspect of his neck on the carapace of the female. This movement is repeated continually.

Rejecting: during copulation females can reject the male. She moves until dismounting the male. If the male tries to copulate again, the female swims in the direction of the male with the mouth open in a threatening posture. The male reacts by swimming backwards, with the neck outstretched towards the female. This threatening behavior of the female towards the male occurs until he desists, at this moment the female desists as well.

Dismounting: when copulation is finished, the male retracts his forelimbs and lets them float freely, dismounting from female and his penis is retracted while leaving her cloaca. Both male and female move to different areas and the interaction is finished.

The sequences of reproductive behavioral patterns are displayed in a fluxogram (Figure 4).



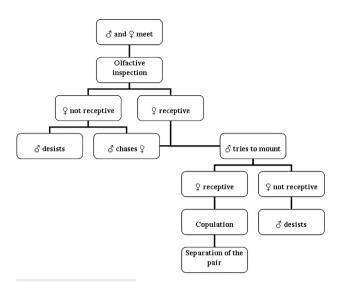


Figure 4 - Fluxogram displaying the sequence of reproductive behavioral patterns.

DISCUSSION

Literature regarding the description of behavioral patterns of South American freshwater turtles are lacking. The most complete paper concerning turtle behavioral pattern categories is Carpenter and Ferguson (1977) in which they made a literature survey of stereotyped reptilian behavioral patterns listing 86 behavioral patterns that they thought to be potential stereotyped actions, acts and act systems that have been observed for turtles.

Maintenance

The gapping behavior was followed by some type of avoidance, like leaving, biting, pursuing, retracting head or staring. The gapping behavior is also referred to in the literature as gaping, gasping, panting or yawning (Lovich 1988; 1990). Moll e Legler (1971) described gaping behavior as a thermoregulatory behavior to lower body temperature. However Lovich (1988) and Bury and Wolfheim (1973) described gaping as a behavior that has no effect in lowering body temperature but has a social function since it was stimulated by one turtle to avoid a conspecific approach or during courtship. From a broader prospective, Bury and Wolfheim (1973), Bury et al. (1979) and Lovich (1988) say that gapping behavior differs from the others since it is always directed at another turtle in an aggressive manner and as Lovich (1990), the confusion is due to the fact that in nature the difference between gaping and open mouth gesture is hard to establish since turtles respond to gaping signals from conspecifics while they are basking. We did not detect gaping behavior related to thermoregulation since we observed the turtles in an aquarium inside a lab. But we clearly observed

Podocnemis erythrocephala gaping which appears to function as a threat and is frequently followed by agonistic behavioral patterns in conspecifics.

Grooming behavior was described for *Chelodina expansa* Gray, 1857, with them often biting at their own bodies. *Podocnemis erythrocephala* also can reach its forelimbs with the mouth to display this behavior. According to Legler (1978), it is clear that this biting results in the removal of dead skin from the soft parts by grooming.

The feeding behavior displayed by *P. erythrocephala* is not complex, with two basic movements of extending and retracting the head while swallowing the food. Feeding behavior was described by Malvasio *et al.* (2003) as having five distinct phases to complete the ingestion of food in *Podocnemis*. This more complex feeding category described might be due to the larger variety of food ingested in their study.

Malvasio *et al.* (2003) and Molina (1991) suggest that the anatomy of these animals facilitates the use of the forelimbs to obtain food. Molina (1991) remarks that this behavior is common in the sub-ordem Pleurodira. However, Molina *et al.*(1998) did not observe the movements of theforclaws of *Phrynops hilarii* Duméril and Bibron, 1835 to help them to ingest food. In addition, Molina (1991), Molina *et al.* (1998) and Malvasio *et al.* (2003) described cleptoparasitism as the active behavior of one turtle taking food from the mouth of another turtle. We do not agree with this terminology, suggesting instead robbing behavior for this activity.

Neustophagia was first described by Belkin and Gans (1968) for *Podocnemis unifilis*, and it seems to be part of all *Podocnemis* species. Rhodin *et al.* (1981) also observed neustophagia in *Podocnemis erythrocephala*. Vogt (1981) also discussed this behavior for *Graptemys ouachitensi*.

Monge-Nájera and Brenes (1987) believe that vision is the main sense used to recognize the food by *Kinosternon scorpioides* Linnaeus, 1766. However, Malvasio *et al.* (2003) believes that olfaction is much more important to identify food by *Podocnemis* species and we do agree while studying *P. erythrocephala*, especially because this species inhabit black waters, where there is low visibility. Mora e Rugeles (1981), mention that olfaction and vision are used to identify food by *Geochelone carbonaria* Spix, 1824 and *G. denticulata* Linnaeus, 1766 in captivity. Vogt (personal observation, July 06 2009) notes that long distance olfaction appears to be important in *G. denticulata*. He observed that a indigenous tribe traps *G. denticulata* by tying a dead agouti over a hole dug in the ground, returning after a week or two to collect the turtles that have been attracted to the odor and fallen into the pit.



Agonistic

As Bury (1979) stated, the more turtles in the basking group, the greater is the chance of aggressive behavioral patterns. The frequent number of aggressive behavior attempts that we observed might be a result of the limited space in the aquarium. Size is an important aspect which is often used to establish dominance between individuals. In this group we observed that the largest female was dominant over all the other individuals and females were more dominant than males (females are larger than males). The social hierarchy of Podocnemis erythrocephala is probably determined by the superiority of agonistic meetings and the established hierarchy can determine the access to food, courtship or resting places. This hierarchy has also been reported in the tortoises Geochelone travancorica Boulenger, 1907 and G. radiata Shaw, 1802 (Auffenberg 1977). There is essentially a two level system: the higher, composed by the largest females which controll the activities of the individuals from the lower level. Agonistic events are common in the reproductive period but can take place all year long, e.g. during the sleeping and resting behavioral patterns, when individuals from the higher hierarchy sleep fluctuating in a higher water level than the individuals from the lower hierarchy.

For the genus Geochelone, the movements of elevation of the head can have a signaling dominance function, showing a social hierarchy (Auffenberg 1977 1978) that can be related to the access of food resources or to females. The head movements are also used in agonistic encounters that reflect the social hierarchy between individuals (Auffenberg 1977 Pough *et al.* 2003).

There is no literature mentioning that females sleep above the male. It was very clear that this position was related to dominance once the female was always repelling any other conspecific that approached the subordinate male. As in tortoises the hierarchy is known in many contexts as combats, feeding, mating and resting (Auffenberg 1977), these same contexts could be occurring in freshwater turtles as well, but they were not recorded due to the lack of studies in nature since underwater observations are very difficult.

Males were always attacked by females and they only bit to protect themselves, not to attack. In addition, the dominant females seem to have observed the group while they were resting, much more than the subordinate males. They might be communicating between them and one of the group can be responsible for vigilance, as was recorded for other species which live in groups, e.g. capybara (*Hidrochaerys hydrochaeris*) (Rodentia: Hydrochaeridae) (Alho *et al.* 1987) and hyacinth macaws (*Anodorhynchus hyacinthynus*) (Psittaciformes: Psittacidae) (Schneider *et al.* 2006). The same can occur during the *arribadas*, a mass nesting behavior, when turtles might be communicating to each other to go up to the beaches to nest when there is no risk of predation.

Biting is one of the most used tactile signals used both in combat and courtship. *Podocnemis erythrocephala* bites mostly the carapace while tortoises usually bite the head and legs (MacFarland 1972; Auffemberg 1977). In the courtship of some species such as *Gopherus berlandieri* Agassiz, 1857 and *Gopherus polyphemus* Daudin, 1802, bites are concentrated in particulars part of the carapace (Auffemberg 1977). Yet, Bury *et al.* (1979) reported that threats and pushing bouts were relatively common for *Chrysemys picta bellii* Gray, 1831 whereas biting attacks were rare under natural conditions. However, in captivity biting was the most performed behavior, as we observed for *Podocnemis erythrocephala*.

Podocnemis erythrocephala interacted socially in different ways during agonistic behavioral patterns and deserves more studies concerning this category. They probably are animals which have a more social life than thought by previous researchers.

Reproductive

Chelonian courtship involves a variety of behavioral patterns including following, cloacal touching or sniffing, head bobbing, swaying, nudging or biting, titillation via long foreclaws (Carpenter and Ferguson 1977; Carpenter 1980; Mason 1992; Bells and Crama 1994;). The aquatic courtship is more complex because of the three dimensional movement patterns in the water (Miller and Dikenlacker 2007).

We observed *Podocnemis erythrocephala* in three phases of courtship: recognizing of the individuals, the foreplay and copulation. The same pattern was observed for the genera *Geochelone sp.* (Auffemberg 1977; 1978; Carpenter 1980). Some species, e.g. *Trachemys sp.* (Davis and Jackson 1973; Ernst 1990; Molina 1996), *Graptemys sp.* (Vogt 1980), *Chrysemys sp.* (Jackson and Davis 1972) can display more complex reproductive behavioral patterns, with titillation behavior as well as head bobbing behavior.

They use a sequential combination of specific visual, tactile and olfactory signals to provide a means for species and sex recognition as well as stimulation. The olfactory base is related mainly to chemical signs, which seem to clarify to the males the species of the individual approached (Carpenter 1980), the sex (Mahmoud 1967; Carpenter 1980) and the degree of receptiveness of the female (Stacey et al. 1986). Reinforcing this theory, Carpenter and Ferguson (1977) mentioned a copulation of some tortoises with a head of lettuce. If they were supposed to have a good vision, why would they copulate with a head of lettuce? Galeotti *et al.* (2007) using pheromones and peach juice in *Testudo hermanni* Gmelin, 1789 showed that this species is much more attracted by olfaction than the vision.



Tactile signs can be used in two contexts: sexual context in which females can be receptive or not, and the agonistic context, as we related above, is important to establish and keep hierarchy (Auffenberg 1977). In the sexual context, as recorded in tortoises (MacFarland 1972) we observed agonistic behavioral patterns preceding copulation in Podocnemis erythrocephala. It seems that females select the males, so the males need to court the females, allowing females to bite or nudge them. The pursuing behavior occurs in diverse chelonian species, such as the Freshwater turtles Clemmys guttata Schneider, 1792 and Trachemys gaigeae Hartweg, 1939, and Phrynops hilarii (Legler 1955; Mahmoud 1967; Ernst 1970; Stuart and Jennifer 1998; Richard 1999). It is thought to be a visual stimulus, in which the pursuing behavior might have an effect of stimulus on females or it induces the sequence of behavioral patterns which culminates in mating. This behavior can happen with copulation (Mahmoud 1967; Davis and Jackson 1970), but it is not a necessary condition.

We observed that visual stimulus might be linked with vocal communication, mostly when they display the gapping behavior in which males swim away from the females. As it was observed to *Chelodina oblonga* Gray, 1841, Galeotti *et al.* (2004) also mentioned that females select males by the sound.

From the observations in this study, we concluded that turtles have a much more complex social life than was believed. Several studies have suggested that aggressive interactions are rare in freshwater turtles except during courtship and mating (Brattstrom 1974; Waters 1974; Auth 1975). We believe that this conclusion is due to the lack of behavioral studies; in fact, the adaptive strategies and the social behavior are much more complex than was suspected. It has recently been discovered that turtles are communicating between themselves by the use of underwater emitted sound (Giles 2005). Before this study, it was thought that turtles only made a few noises during the mating and during distress situations, some researchers thought that turtles could not make sounds and were known as a silent group (Pope 1955).

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