Brazilian Journal of Biology®

ISSN 1519-6984 (Print)
ISSN 1678-4375 (Online)

Original Article

# Reproductive biology and habitat characterization of the Scorpion Mud Turtle *Kinosternon scorpioides* (Linnaeus, 1766) in the Amazon-Cerrado ecotone region, northeastern Brazil

## Biologia reprodutiva e caracterização do habitat da tartaruga-escorpião *Kinosternon scorpioides* (Linnaeus, 1766) na região do ecótono Amazônia-Cerrado, nordeste do Brasil

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**Abstract**

In this study, we sampled populations of Scorpion Mud Turtles, *Kinosternon scorpioides,* in rivers and flooded plains of the eastern Brazilian Amazon in order to obtain information on its reproductive biology as well as the geospatial description of its habitat. The research was conducted in the basins of the Pericumã and Aurá Rivers, located in the environmental protection area of the Baixada Maranhense. Seven collections were made over a period of 24 months; 206 animals were captured (101 males and 105 females), with 18 recaptures (8.6%) and a displacement record of 7.41 km. In the Aurá River basin, we recorded six nests of *K. scorpioides* buried in association with a plant of the genus *Andropogon* sp. Turtles were observed in a variety of environments in a distribution completely dependent on seasonal changes in its habitat, fluctuating between aquatic and terrestrial microhabitats along with seasonal rains and dry periods and food availability. This study adds data on the ecology and knowledge of the dynamics and habitats of *K. scorpioides* in relation to conservation strategies of these and other turtles that use these flooded plains as habitat and survive despite many anthropogenic disturbances in the region.

**Keywords:** turtles, flooded plains, reproductive ecology, land use and cover.

**Resumo**

No presente estudo, amostramos populações de *Kinosternon scorpioides* em rios e campos alagados do limite oriental da Amazônia brasileira com o objetivo de obter informações sobre biologia reprodutiva e descrição geoespacial do habitat da espécie. O estudo foi realizado nas bacias dos rios Pericumã e Aurá, localizados na área de proteção ambiental (APA) da Baixada Maranhense. Foram realizadas sete coletas em um período de 24 meses, e foram capturados 205 indivíduos adultos e um sub-adulto, (101 machos e 105 fêmeas), e 18 recapturas (8,6%) com registro de descolamento de 7,41 km. Na bacia do Rio Aurá, registramos seis ninhos de *K. scorpioides* enterrados sempre em associação uma planta arbustiva do gênero *Andropogon sp.* Os animais foram encontrados em uma variedade de ambientes e seguem uma distribuição totalmente condicionada às mudanças sazonais do habitat. Eles transitam entre micro-habitats aquáticos e terrestres de acordo com a sazonalidade e a disponibilidade de alimentos. Este estudo fornece informações relevantes sobre a ecologia, dinâmica e hábitat da espécie, servindo como subsídio para estratégias de conservação dos quelônios que utilizam as planícies inundadas como hábitat apesar das numerosas e prejudiciais intervenções antrópicas na região.

**Palavras-chave:** tartaruga, campos alagados, ecologia reprodutiva, uso e cobertura do solo.

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Received: May 04, 2024 – Accepted: November 21, 2024

## 1. Introduction

The Amazon biome has the largest continuous tropical forest in the world, with 59% of it situated within Brazil's borders. This spatial dimension, associated with extensive availability of freshwater ecosystems, permits a rich biodiversity, especially of freshwater turtles. Added to the species richness of this group in the Amazon River basin and in other Amazonian rivers, Brazil ranks third in global species richness of turtles, with a high degree of endemism, and this biome is considered a priority region for conservation of the group – Global Turtle Hotspot (Mittermeier et al., 2015; Ribeiro-Junior and Amaral, 2016; Rhodin et al., 2021; Cunha et al., 2022; Guedes et al., 2023).

*Kinosternon scorpioides* (Linnaeus, 1766), the Scorpion Mud Turtle, is a species of freshwater turtle that is widely distributed in the Neotropical region. It occurs from Panama, along the Caribbean range to Brazil, covering the entire Amazon rainforest, the eastern Cordilleras of Colombia, Ecuador and Peru, also reaching the limit of its occurrence in south-central Bolivia, northern Paraguay and northern Argentina in the Chaco Cordillera (Cáceres-Martínez et al., 2017; Rhodin et al., 2021; Cassano and Alcalde, 2022; Hurtado-Gómez et al., 2024).

Despite its extensive distribution, it is a species that seeks specific places as its habitat and is found mainly in wetlands at the bottom of permanent or temporary bodies of water (Berry et al., 2012). In Brazil, there are records of the species in flooded plains, though it is rarely observed along the large basins in the western Amazon. To date, the greatest abundance for the species is in the region of the extreme north of Brazil (Marajó island, in the state of Pará) and in the eastern Amazon, in the Baixada Maranhense region (located north of the state of Maranhão) (Rodrigues et al., 2017).

Among the Amazonian freshwater turtle species, the Scorpion Mud Turtle is potentially the species that suffers the greatest pressure from changes in the landscape, especially due to habitat loss caused, for example, by deforestation and climate change (Fagundes, 2015; Berriozabal-Islas et al., 2020). The species suffers different types of threats in different regions of the country. In the north and northeastern regions, more specifically in the states of Pará and Maranhão, wild populations of the species are under pressure from hunting and illegal trafficking. It is a regional delicacy and is consumed both for subsistence and in traditional regional cuisines (Barreto et al., 2020; Medeiros et al., 2023).

To date, the conservation status of *K. scorpioides* is one of Least Concern, according to the Red List of the International Union for Conservation of Nature and Natural Resources (IUCN) (Rhodin et al., 2018); however, there are still gaps concerning the ecology of the species in many areas of its distribution. Few data are available on its reproductive aspects, ecological niche and the population structure for Brazilian populations (Bedoya-Cañón, et al., 2018; Barreto et al., 2020; Cassano and Alcalde, 2022). The collection of other information, such as sex ratio and morphological variation between size and sex, is also important for conservation actions for the species (Reyes-Grajales et al., 2021).

Knowledge of the population dynamics and reproductive ecology of turtles is essential for understanding their life history (Stearns, 1992) and for their management and conservation (Hamann et al., 2010). Comparative analyses of these ecological aspects and natural history data allows for improved risk assessment for conservation purposes in areas where animals occur in proximity to human populations (Bernardes et al., 2014).

In this study, we sampled populations of *K. scorpioides* in rivers and flooded plains of the eastern Brazilian Amazon in order to obtain information on reproductive biology (sex ratio and nesting), population structure, geospatial description of its habitat and its relation to the life cycle of this species.

## 2. Methods

### *2.1. Study area*

The study was conducted in the basins of the Pericumã (2°31'38.4"S 45°04'08.7"W) and Aurá Rivers (2°38'52.4"S 44°46'52.7"W) of the western coastal hydrographic system in the Amazon basin. These rivers are in the environmental protection area of the Baixada Maranhense (flooded area), in northeastern Brazil, which is the eastern limit of the Amazon, and they have an area equivalent to 3,851 km$^2$ and 1,185 km$^2$ respectively (Catunda and Dias, 2019). Although defined as part of the Brazilian Amazon, this protected area corresponds to an ecotone, since it lies between the Amazon Forest and the Cerrado (Araújo et al., 2011) and represents a wetland of international importance. It has been designated as a Ramsar site by the National Wetlands Committee (CNZU) for being a region that provides fundamental ecological services, meeting water and food needs for fauna and flora species and human populations. The study area aggregates part of the hydrographic basin of the Pericumã and Aurá Rivers, which are completely within the Brazilian Amazon. These rivers form extensive floodplains that characterize the environment of the Baixada Maranhense and are responsible for draining a large part of the municipalities around their basins. The environment is formed by a set of streams interconnected to these main rivers (lotic environment) and flooded plains with great contrasts in seasonal temperature, humidity and rainfall. In the rainy season (January to July), the low-lying plains are flooded when the rivers overflow, forming numerous lakes (lentic environment). During the dry season (August to December) the flooded plains give way to numerous islands of dry land and large areas with highly parched soil forming mounds – locally called *tesos* (Costa-Neto et al., 2002; Pinheiro, 2013).

### *2.2. Data collection*

Seven field collections were carried out over a period of two years, in the months of August and October 2021, April, June, October, December 2022 and April 2023. Each collection had a sampling effort of seven days, totaling 49 days and covered both the seasonal periods and microhabitats of the region. Covo-type traps (funnel traps and fyke nets) and local artisanal traps were used,

both with the same operating principle: installed only in an aquatic environment, for two days at each point and monitored every 24 hrs (De La Ossa and Vogt, 2011; Secco et al., 2013). A total of 22 points were selected (Figure 1), which were categorically divided as follows: the main channel of the Pericumã and Aurá Rivers and their streams (lotic environment); the flooded plains around these rivers (lentic environment) and the areas of dry land (*tesos*), covering their entire area of influence. An active search was carried out, only in the areas of *tesos* and in the surrounding rivers and lakes, mainly in the period of falling waters (dry season); also, when possible, presumed nesting sites were searched for active nesting (Pereira et al., 2007; Balestra et al., 2016). The active search was carried out with the help of handmade instruments such as "chuchus", which is a locally produced tool that is formed by an iron tip and a wooden base and is used to locate turtles by tapping on the ground until they feel the animals' buried shell. The animals were identified using taxonomic keys (Rueda-Almonacid et al., 2007; Páez et al., 2012). Sex was identified by body size, carapace width, plastron shape, precloacal distance, tail length and thickness (Ponce, 1979; Pritchard and Trebbau, 1984; Lima et al., 2024). Individual identification included the information of morphometric measurements, sex, georeferencing of the capture site (with a Garmin® Etrex10), as well as a marking on the marginal plates (adapted from Cagle, 1939; Gibbons, 1990). The following parameters were considered for morphometry: maximum straight-line carapace length (SCL), carapace width (SCW); plastron length (SPL) and plastron width (SPW), as well as height (H) and weight (W). We used SCL as the measure of body size, considering as adults any animals >100.0 mm, while individuals of <100 mm were classified as juveniles (Barreto et al., 2020). Following measurements, the animals were returned to the place of capture. The research was carried out under the authorization of the Chico Mendes Institute of Biodiversity Conservation (ICMBio), through the System of Authorization and Information on Biodiversity (SISBIO), permit number 74521-1.

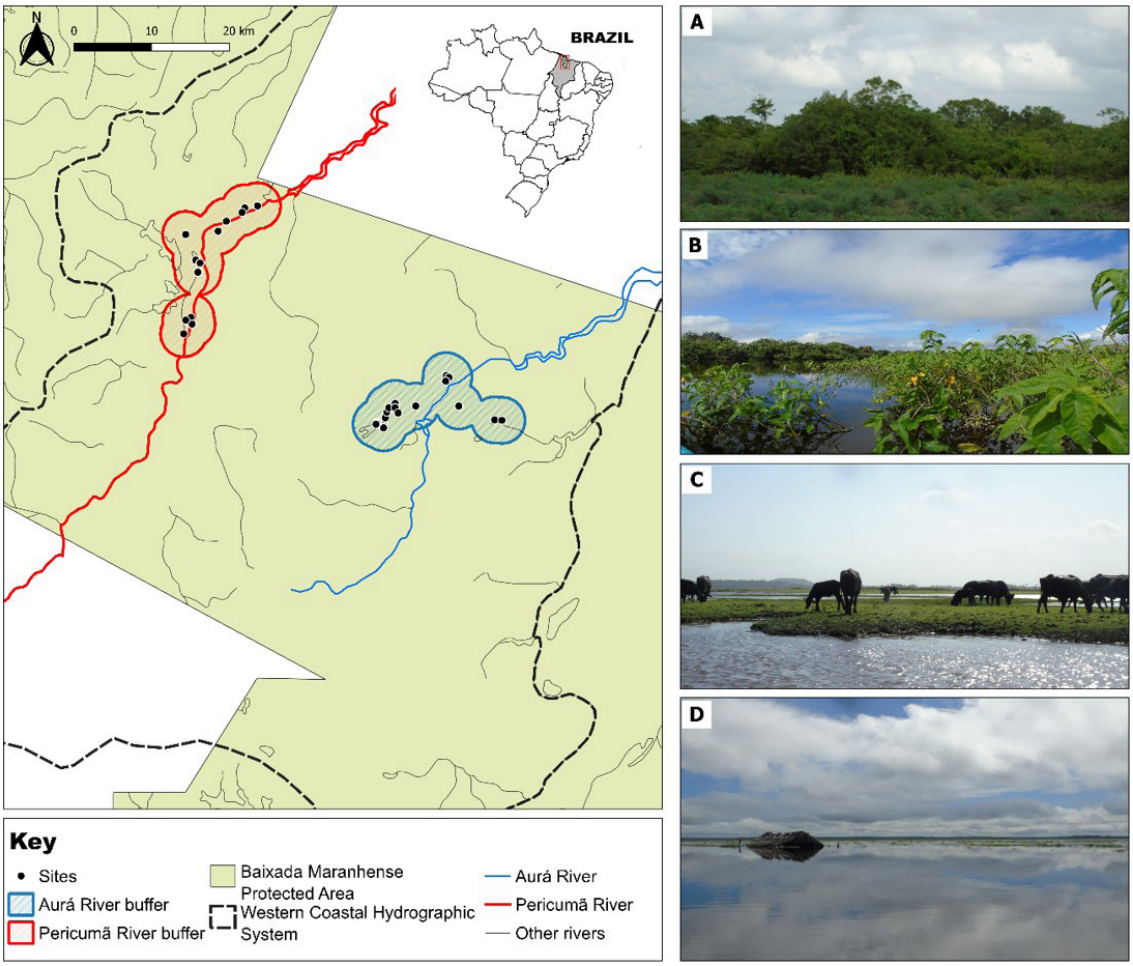


**Figure 1.** Study area. Identification of collection points distributed along the Pericumã (red) and Aurá (blue) Rivers. Selected area for habitat description around collection points (light blue and red buffers). A-Forest areas (areas of *terra firme*); B- Non-forest natural formation (lentic environment); C- Cultivation and livestock areas and D- Water areas (lotic environment). Source: Catunda and Dias (2019); MapBiomas Brasil (2023).

*2.3. Habitat description – each collection point was characterized as follows:*

1 –structural aspects: perimeter and the average depth of the water body.

2 –physicochemical variables: measured with a multiparameter probe (Akso AK88) pH, conductivity, dissolved oxygen and water temperature.

3 –vegetation cover: presence of shrubs, trees and aquatic vegetation (Cassano and Alcalde, 2022).

The QGis 3.32 software was used to characterize the habitat on a large scale, identifying the type and proportions of land cover and uses within the collection areas with the help of MapBiomas Brasil v. 07.1. For this analysis, we considered a radius of three km around the capture sites (Bedoya-Cañón et al., 2018; Cassano and Alcalde, 2022) and the buffers were dissolved on the map, taking into account two large collection areas around the Aurá and Pericumã Rivers. Zonal histograms were used to identify the type, proportions of land cover and uses, and pasture quality within the analyzed buffers. When identified, they were defined in five categories: I – forest areas (map codes 3, 4 and 5); II – Non-forest natural formation (codes 11, 12 and 32); III – Non-vegetated area (codes 22, 24, 25 and 30); IV– Farming (cultivation and livestock areas - codes 15, 39, 41 and 21) and 5); V – water areas (codes 26 and 33). The description of the map keys is available for download on the MapBiomas website (MapBiomas Brasil, 2023). To obtain the coverage percentages within the study area, the categories were reclassified according to Cassano and Alcalde (2022), with values from one to five for each coverage type and zero for the remaining unused ones. Zonal analysis functions were applied to extract the statistics for each area.

*2.4. Data analysis*

*A priori* analysis was performed to test the data for their parametric relationship (linearity and homoscedasticity). After this, descriptive analysis of the data and GLM tests were performed to test the relationship between total weight (W) and straight-line carapace length (SCL), using as a categorical variable the sex of the animals and the climatic variable (dry and rainy season). Size comparison between morphological measurements between males and females was performed using one-way analysis of variance (ANOVA). All the tests were performed in Statistica® 7.0 Software and followed the premises of Zar (2014).

## 3. Results

*3.1. Captures and recaptures*

The species was found in 17 of the 22 study locations (Pericumã and Aurá Rivers). In total, 205 adults were captured and one sub-adult (101 males and 105 females), with 18 recaptures (8.6%, Figure 2). Both captures and recaptures occurred in greater quantity in the rainy season. Recapture intervals ranged from 3 to 12 months. Two females and one male were recaptured at a distance of 7.41 km, at intervals of 6 and 9 months, respectively, maintaining the recapture location (Figure 3). However, most of the recaptured animals were in the same location, a female was recaptured twice – the first time in October 2021, in the same place and again in July 2022, at a point 2.5 km away in the vicinity of the Aurá River. A male was also recaptured in the Pericumã River at a point 2 km away from the site of the first capture.

We found six nests of *K. scorpioides* in the Aurá River basin and two nests near the Pericumã River. In both places, they were buried next to a plant of the genus *Andropogon sp*. (Hack.). Two of the nests had been predated and the other four were intact, one with four eggs and the others with three eggs and were about 10 cm deep. The area near the Aurá River is also used for nesting the species *Phrynops geoffroanus* (Schweigger, 1812) and has extensive breeding of animals such as pigs (*Sus domesticus* (Erxleben, 1777) and water buffalo (*Bubalus bubalis* (Linnaeus, 1758). The nests were found about three meters from the nearest water source (a lake formed by the floods of the Aurá River and a tributary of the Pericumã River).

*3.2. Characterization of the capture sites*

The species was consistently found in four types of environments: rivers or streams (lotic environments), flooded plains (lentic environments), and *dry land* or *tesos* (shrubby vegetation environment). The flooded plains in

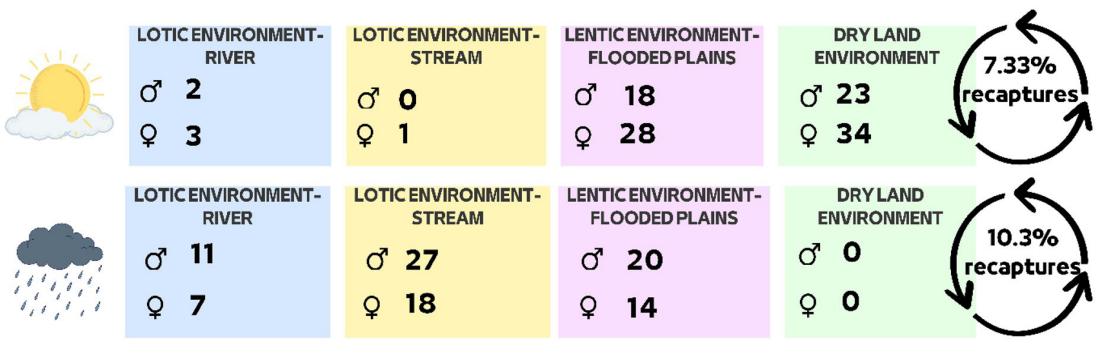


**Figure 2.** Frequencies of captures and recaptures for males (♂) and females (♀) in the rainy and dry seasons and between the collection environments.

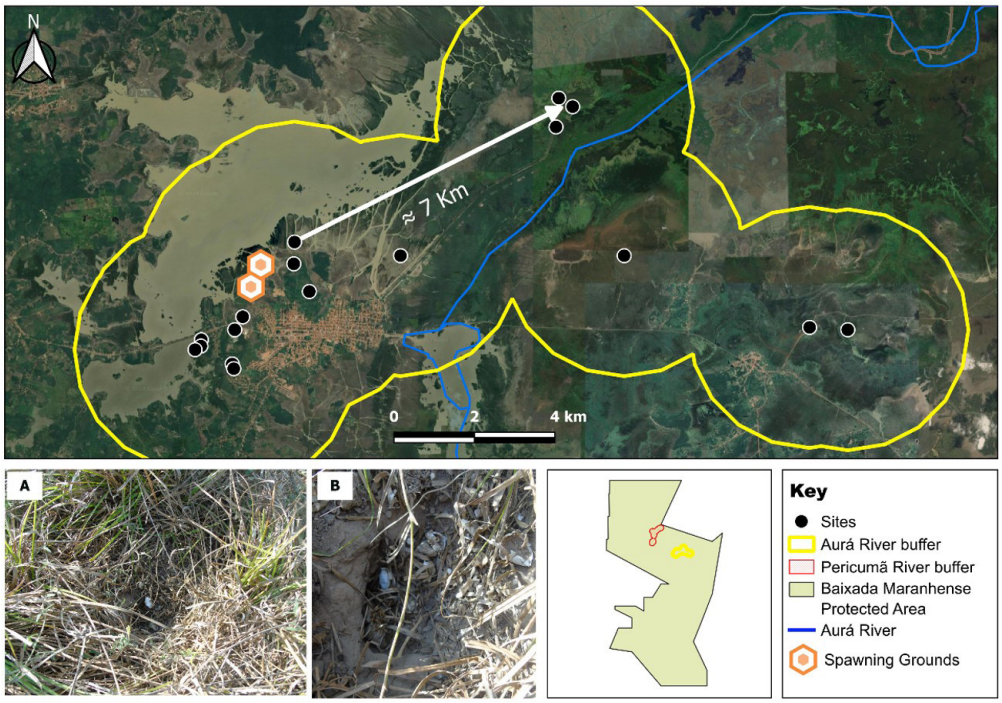


**Figure 3.** Displacement area (arrow) between captures and recaptures in the Aurá River. Location of spawning grounds (eggs). A, B-Nests. Source: Catunda and Dias (2019); MapBiomas Brasil (2023).

which the specimens were captured have a size ranging from medium (perimeter of 68 to 140 m and depth of 35 to 50 cm) to large (more than 1.5 km and depth greater than two m), with an irregular shape and always surrounded by the typical matrix of areas of non-forest natural formation, close (about less than 500 m) or distant from houses (distance of more than three km). The areas of the mounds are basically formed by shrubby vegetation and areas of cultivation and livestock and become more common in the dry season.

The sites with successful collections in all the environments were always associated with vegetation, this being shrubby, aquatic or semi-aquatic, with a great frequency of *Ipomoea fistulosa* (Martius ex Choisy) (wild cotton) both in the dry and rainy season; *Neptunia oleracea* (Lour.), *Nymphoides indica* ((L.) Kuntze) and *Eichhornia crassipes* ((Mart.) Solms) (mururu) in the rainy season and *Andropogon* sp. or *Paspalum plicatulum* (Michx) (both known locally as *capim-açu*), in the dry season. The traps installed in the course of the rivers, in areas of flow of the current or at depths greater than 1.5 m did not collect any specimens of this species.

The analysis of land use and land cover carried out in the areas surrounding the Aurá and Pericumã Rivers (Figure 4) showed similarities between them and in the habitats where the species was found. The areas of non-forest formation (shrubby vegetation or flooded plains) and areas of water represent the highest percentages within the buffers (Figure 5) – 48.87% and 22.75% for the Aurá River and 41.36% and 27.4% for the Pericumã River respectively, followed by forest and agricultural areas.

The environmental matrix of pasture quality (Figure 4) showed that up to 17.8% of the collection sites are being used as pasture for extensive livestock rearing, with about 9.8% for severe degradation of these sites. Regarding the abiotic parameters of the environment, high water temperatures were observed for all the locations (between 27.3ºC and 30.4ºC), relatively acidic Ph values (5.1-6.8) and neutral pH mainly in the rainy season (7.1-7.7), and variable values of dissolved oxygen: 1.8-4.4 mg $L^{-1}$ (Pericumã River), 2.6-6.9 mg$L^{-1}$ (Aurá River).

### *3.3. Population structure*

The smallest individual captured was a sub-adult female with an SCL of 9.8 cm, and the largest a male had an SCL of 17.8 cm. Most individuals were in the medium size class (from 12 to 16 cm) and only a few were in the smaller or larger size classes (Figure 6). Of the 206 turtles captured, 45% belonged to the 14-16 cm class, with a majority of males, and 40% to the 12-14 cm class with a greater number of females. The other size classes had abundances that represented less than 9% of the sample. The number of females captured was slightly higher than that of males, representing a sex ratio of 1.03 females per male (Figure 2).

Of all the morphometric measurements (SCL, SCW, SPL, SPW, H and W), SCL was higher for males, while females were bigger in all the other measurements (Table 1). Weight and SCL showed correlation in linear regression tests with a moderate to high dependence relationship between these measurements. Males, although larger in carapace length than females, are smaller in carapace width, plastron and height, which mostly makes them less heavy.

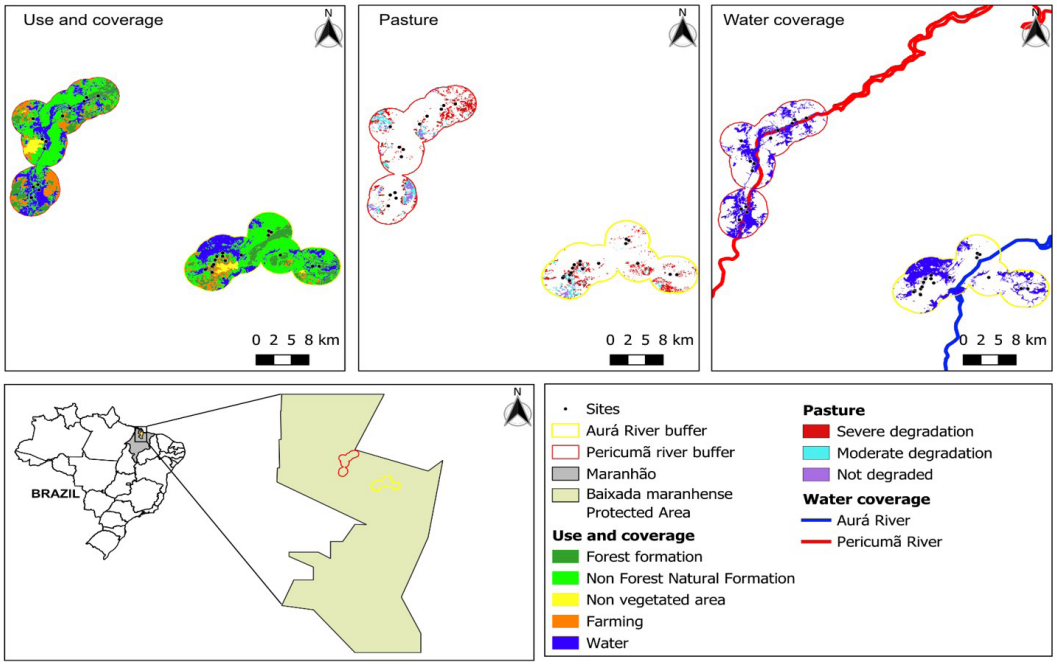


**Figure 4.** Distribution of land use and cover, and areas of water coverage and pasture along the collection points of *K. scorpioides* Source: MapBiomas Brasil (2023).

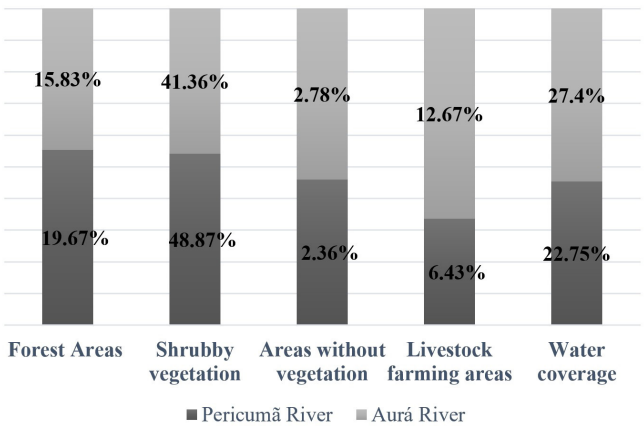


**Figure 5.** Percentages of the average (%) value of zonal statistics of vegetation cover for the surrounding areas (of 3 km) around each collection point.

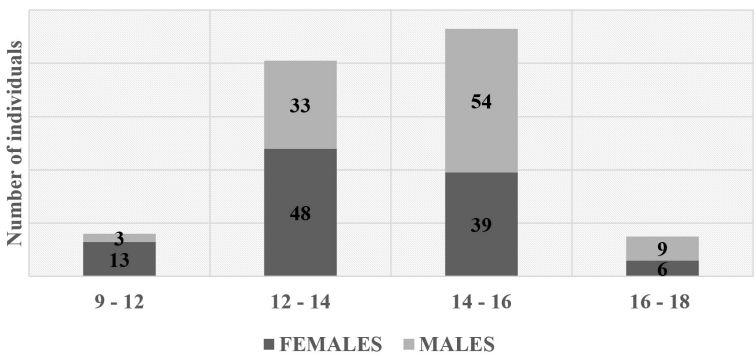


**Figure 6.** Distribution of size classes between females and males of *K. scorpioides* captured in the Baixada Maranhense, Maranhão, Brazil.

In the rainy season, the largest number of individuals were collected in almost all the environments, and it was possible to observe that males were predominant in this period (Figure 2), while the collection of females was predominant in the dry season. Tukey's post-hoc test showed a difference in SCL for males in all the collection environments analyzed and in seasonal periods ($p<0.05$). Both sexes presented differences in length and weight, and it was observed that the largest and heaviest individuals were collected in the rainy season (Figure 7), while *K. scorpioides* captured in the dry season had apparent characteristics of weight loss and dehydration.

Regarding the collection areas, there was a negative correlation between the environment, SCL and weight. It is observed that the *tesos* was the environment that presented the animals of shorter length and weight compared to other aquatic environments (Table 2). In addition, a relationship between the places of capture and the seasonal period is

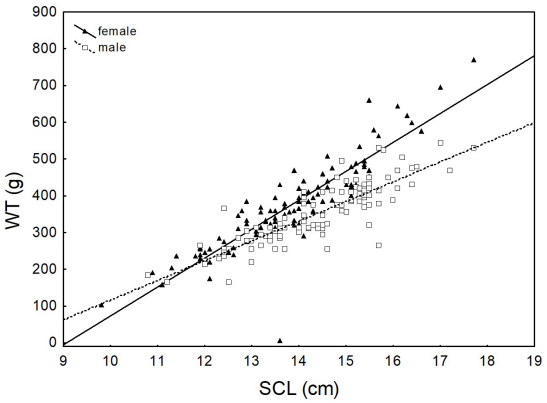


**Figure 7.** Relationship between carapace length and weight of males (squares, dotted line) and females (triangles, solid line) of *Kinosternon scorpioides* captured in the Aurá and Pericumã Rivers, in the Baixada Maranhense, Maranhão, Brazil.

**Table 1.** Morphometric data (mm) and weight (g) of the 105 females and 101 males of *K. scorpioides* captured in the Aurá and Pericumã Rivers.

| Sex | Morphometric Measurements | | | | | Weight |
|---|---|---|---|---|---|---|
| | SCL | SCW | SPL | SPW | H | |
| **Females** | | | | | | |
| *Mean* | 138 | 91 | 128 | 76 | 51 | 374 |
| *Maximum* | 177 | 135 | 169 | 98 | 68 | 770 |
| *Minimum* | 98 | 72 | 77 | 50 | 39 | 105 |
| *SD* | 1.4 | 1.11 | 1.55 | 0.87 | 0.63 | 116.0 |
| **Males** | | | | | | |
| *Mean* | 144 | 89 | 120 | 73 | 47 | 350 |
| *Maximum* | 178 | 12 | 153 | 87 | 69 | 545 |
| *Minimum* | 108 | 75 | 82 | 55 | 33 | 165 |
| *SD* | 1.35 | 0.83 | 1.34 | 0.73 | 0.56 | 84.36 |

SCL (maximum rectilinear carapace length), SCW (maximum rectilinear carapace width), SPL (maximum rectilinear plastron length), SPW (maximum rectilinear plastron width), H (maximum rectilinear carapace height), SD (standard deviation).

**Table 2.** Comparison between the average carapace length (SCL) in millimeters and the weight (W) in grams of the animals (N) collected in different environments and seasonal periods of the year.

| Seasonal period | Location/Environment | SCL | W | N |
|---|---|---|---|---|
| Dry | | | | |
| | Lotic - river | 137 | 351 | 5 |
| | Lothian - creek | 146 | 440 | 1 |
| | Lentic - flooded plains | 146 | 404.5 | 46 |
| | Teso | 132 | 306.7 | 57 |
| Rainy | | | | |
| | Lotic - river | 139 | 330 | 17 |
| | Lothian - creek | 152 | 449.2 | 45 |
| | Lentic - flooded plains | 144 | 412.3 | 34 |
| | Mounds | 0 | 0 | 0 |

also observed in the table. In the rainy season, the animals were collected in greater quantity in the flooded plains, rivers and streams, with the help of traps; while, in the dry season, they are found in greater numbers in the areas of *tesos* and flooded plains (when they are waterlogged) through active search. There was a difference in the number of animals collected by the different methods since the presence of water in the fields makes it possible to use pit traps and makes active searching difficult in the rainy season, causing the number of animals captured by traps to be much higher; the opposite happens in the dry season.

## 4. Discussion

Only adult individuals and one subadult were collected; we did not capture hatchlings or juvenile specimens. This follows the pattern of other studies carried out with the genus *Kinosternon*, since animals smaller than 9 cm are rarely caught in traditional collection nets and traps and are also rarely found in rivers and lakes. They often hide in the most varied places and escape from the nets (Forero-Medina et al., 2007; Barreto et al., 2020). A population with a large number of adults is common especially in smaller species of turtles, the low mortality in adulthood, low recruitment of offspring and high investment in maintenance and growth may explain this pattern (Rodrigues and Silva, 2015). Fagundes (2015) observed an equivalent adult population structure in *Trachemys dorbigni* (D'orbigny's slider turtle) (Duméril and Bibron, 1835) in southern Brazil, and similar patterns were found in *K. albogulare* (Duméril and Bocourt, 1870) in Colombia and *K. cruentatum* (Bibron and Duméril 1851) in Mexico (Forero-Medina et al., 2007; Iverson, 2010).

It has been suggested that the high mortality of eggs and neonates may also be the reason for the relatively low proportion of the hatchlings in such studies. In juveniles and adults, the increase in the size and hardness of the carapace makes them less vulnerable to predators, dessication and other factors that affect newborns. However, Tesche and Hodges (2015) and Rodrigues and Silva (2015) suggested that the use of a single sampling methodology, such as in the present study (covo traps), can lead to biases, such as subsampling of hatchlings and juveniles. Although the nets used have small mesh sizes (three cm on average), hatchlings and juveniles of *K. scorpioides* manage to pass through them or even escape through the entrance hole of the trap, and the active search method proved to be an ineffective approach for capturing young of this species.

The nests found represent a major advance for research with this species, as there are few data documenting its reproductive biology (Rodrigues et al., 2017) and, to date, there are no records in the literature regarding *in situ* oviposition for *K. scorpioides*. The eggs were always buried in association with a shrubby vegetation known in the region as "capim-açu" (*Andropogon* sp.), a fact often reported by riverine dwellers and fishers, who commonly find turtle nests associated with this plant, near both the Aurá and Pericumã Rivers. This demonstrates the importance of traditional knowledge for the advancement of research on the ecology of turtles (Medeiros et al., 2023), since it can be used as a tool for future conservation and management actions. This provides further evidence to support the hypothesis that the species may have a preference for depositing its eggs exclusively in this substrate.

The oviposition site near the Aurá River is an area of flooded plains, but is also used for extensive rearing of horses and pigs, in addition to fishing. Thus, it is important to evaluate the survival of eggs and hatchlings in this area, as two predated nests were found (only with eggshells). In addition to the vulnerability factors of hatchlings already mentioned, introduced or native species may be feeding substantially on these eggs, and this may cause a population decline in the future (Forero-Medina et al., 2007).

The eggs were found in the months of October and December, which correspond to periods of low river levels and arid plains. In searches conducted from January to July (the rainy season), it was not possible to find nests, nor to identify suitable places for nesting, since the soil was still submerged or very moist. The flooding of the plains defines the period for oviposition, restricting it to the dry season months. Our results were in contrast to the findings of other authors who have observed nesting periods for species of the genus *Kinosternon* in the months of May, April, and even March (in places with different climatic dynamics) and for captive animals from the month of May, thereby proving the relationship of dependence between the environment and the life cycle of these animals (Iverson, 2010; Rodrigues et al., 2017).

Studies on *K. scorpioides* indicate a prolonged oviposition period lasting approximately 6 to 8 months. In our research area, this period covers only the months of August to December, when the fields are dry and females retain their eggs and nest multiple times per reproductive season (Rodrigues et al., 2017; Barreto et al., 2020). With the onset of the rainy season, the hatchlings emerge, and adults move to the rivers and lakes in search of food and opportunities for mating.

The Scorpion Mud Turtle has a specific life cycle to make the most of the resources of the environment and its seasonal changes. The exploitation of rain events for feeding, combined with the mechanisms of late egg development and multiple ovipositions that synchronize hatching with the rainy season are behaviors that demonstrate this. This pattern also allows hatchlings to emerge only in the rainy season, under ideal conditions of growth and survival and allowing them to double their carapace length in first year (Iverson, 2010). The complex reproductive and behavioral strategy of *K. scorpioides* and its sister species *K. albogulare* and *K. cruentatum* may have been the adaptation that allowed these species to colonize most of the Atlantic slope of Central America and part of South America about 4 million years ago (Iturralde-Vinent and MacPhee, 1999).

The recapture rate of animals was relatively low, suggesting a potentially larger population than observed in this study and highlighting the need for continued research across multiple seasons. The use of classical density and mortality estimation methods is not recommended when the recapture rate is less than 20% (O'Brien et al., 2005). A higher number of recaptures can be observed in the rainy season when the traps have greater efficiency when rivers and especially plains are full, and can be better distributed

in water bodies, a fact also observed by other authors in their collections during the rainy season (Bernhard and Vogt, 2012; Barreto et al., 2020). In addition, this is the season that animals usually move more within the habitat, in search of food and opportunities for reproduction (Rodrigues and Silva, 2015). In the dry season, the method that was most successful was the active search, which is possible only at this time, since the animals are in estivation (buried) or in search of nesting sites in areas of *terra firme* (Pereira et al., 2007; Medeiros et al., 2023).

Kinosternides and other turtles often move through terrestrial habitats in search of aquatic environments. Bedoya-Cañón et al. (2018) observed a displacement of 2.5 km from the original capture site to the recapture site for *K. scorpioides*, the largest recorded so far in the literature; however, in our collections, we observed a displacement of 7.41 km in three recaptures of different animals, always moving to the same area. The animals were initially captured in October (dry season) in a region of still flooded plains (known as campo do Chagas); two females were recaptured in April (rainy season) in a stream near the Aurá River about 7.41 km away from the initial location, a third animal was recaptured in July (also in the rainy season) in the same place near the Aurá River, demonstrating that there is displacement between these regions.

Fishers and riverine dwellers report that the species usually performs this migration between these two areas as the seasonal periods change. The Chagas field is an area used for nesting and, since it is far from the main river, it usually dries up first, a fact confirmed in this research by our finding of the nests. The areas near the Aurá River are flooded for longer, presenting more availability of food resources throughout the year and are probably feeding sites for this species. According to Rocha-Barbosa et al. (2014) and Muller et al. (2019), turtles usually have reproductive and survival strategies, in which males and females move through habitats in search of food, places for nesting or partners for reproduction. It is possible that the animals captured in the first place were looking for places for estivation or nesting and, after a few months, with the onset of the rains and flooding of the plains, they moved to the Aurá River in search of food and partners for a new reproductive period, where they were again captured.

During this study, a balanced sex ratio between males and females was recorded (1:1.03 respectively), a fact also observed by Barreto et al (2020) in studies with the species on the island of Curupu, Maranhão, northeastern Brazil. However, in other gender studies, some variations between the sexes (with a female bias) were observed in field collections and museum collections (Iverson, 2010; Bedoya-Cañón et al., 2018). According to Rodrigues and Silva (2015), deviations in sex ratio are not common in Brazilian turtles, but Balestra et al. (2016) indicated that the method used for capture, the season of the year, the depth and the type of site sampled are some of the factors that can affect the sex ratio. As this research used more than one size of nets, installed in different places at different times of the year, we believe that these factors did not influence the sex ratio of our population.

Regarding the size of the animals, the sampled population followed the average of other studies conducted with this group. Some individuals were slightly larger than those observed by Barreto et al. (2020), Bedoya-Cañón et al. (2018) and Forero-Medina et al. (2007), but following the same size pattern observed by Cassano and Alcalde (2022). Larger carapace lengths (SCL) in females were recorded in *K. cruentatum* (Berry and Shine, 1988), but in our research SCL was the only measurement by which males were larger at all times of the year and in all the environments. For *K. scorpioides*, it was found that the main differences in carapace morphology are in shape and not in size, probably because of a higher and wider carapace in females allows a greater muscular and visceral volume, increasing metabolic efficiency, in addition to providing more space to hold eggs (Garces-Restrepo et al., 2013), which are characteristics that make females heavier and larger when taking into account body shape.

Studies with other kinosternides conducted in Central American countries also suggest that there is no significant difference in mean carapace length between the sexes, but there is a trend towards heavier females, presumably due to the higher and wider carapace and larger plastron (Reyes-Grajales et al., 2021). However, in other works (Ceballos et al., 2013; Agha et al., 2018), sexual dimorphisms in size were associated with habitat type, with females larger in carapace length in more aquatic turtles and with larger males in semi-terrestrial turtles, which is the case of the species evaluated in this research.

For turtles, seasonal differences can lead to ecological pressures that affect their size (Santana et al., 2022). This can be observed in the differences in length between the animals caught in the dry and the rainy season and also in the number of animals found. Changes in the weather throughout the year influence the availability of resources, the abundance and the body size of reproductive individuals (Barreto et al., 2020). This pattern was also observed in studies with *K. abaxillare* (Baur, 1925) in Mexico, where the peaks of animal activity were during the beginning of the rainy season, when individuals emerge from estivation and return to their aquatic habitat in search of food, reproduction and restoration of their pattern of water use (Reyes-Grajales et al., 2021).

The predominance of males in the collections of the rainy season may indicate that they are more active in this season (Hall and Steidl, 2007; Iverson, 2010), since the rainy months represent the beginning of a new reproductive phase, and males migrate in search of partners to mate. While females are more often captured in the dry season, which is when they are looking for nesting sites on dry land and end up becoming more susceptible to both predators and hunters, who use fires to capture large quantities of animals when the plains are dry (Medeiros et al., 2023). It was possible to observe that many of the females collected in this period were gravid; a fact also reported by fishers during our collections.

In several points, the environment described in this research resembles the other places where *K. scorpioides* was found, ranging from Panama to Brazil, through countries in South America to northern Argentina (Caceres-Martinez et al., 2017; Rhodin et al., 2021). In Brazil, despite

being present in several parts of the Amazon, the species was recorded in significant populations only on the island of Marajó (Pará) and environmental protection area of the Baixada Maranhense (Rodrigues et al., 2017). These are places that have similar phytophysiognomies and are composed of floodplains that have a large seasonal variation throughout the year.

The environments in which *K. scorpioides* was captured most frequently in our collections have in common the strong dependence on seasonal rains to maintain their characteristics throughout the year. However, this does not seem to affect the survival of the species, which has also shown itself to be adapted to periods of drought. The Scorpion Mud Turtle seems to prefer shallow aquatic habitats, without current, with the presence of vegetation and subject to daily changes in physical chemical patterns. This was also observed by Pereira et al. (2007) and Cassano and Alcalde (2022), who also demonstrated in their studies that *K. scorpioides* inhabits warm waters (28ºC to 30.8ºC) that can range from acidic to neutral (pH from 4.26 to 7.83) and with moderate dissolved oxygen values. These data are very similar to those of our research.

The presence of this turtle in lakes and plains near the city suggests some tolerance to impacted or polluted environments. This behavior leaves the species in greater contact with humans and more susceptible to capture, since it is widely used as a food source in the region and its illegal trade is very common (Medeiros et al., 2023). Tolerance to anthropogenically altered habitats has also been reported by Pritchard and Trebbau (1984) and more recently by Cassano and Alcalde (2022).

Despite being a protected area, the Baixada Maranhense region is allowed the sustainable use of resources. The economy revolves around agricultural practices such as the extensive rearing of cattle, horses, pigs and particularly water buffalo (as they are animals that are highly resistant to the environmental variety of the region); in addition to subsistence crops, aquaculture and fishing, the latter activity being highly widespread and practiced in the region (Catunda and Dias, 2019). The precariousness in the services of regulation and supervision of these resources causes practices to grow unrestrained, in addition to illegal activities such as hunting of wild animals.

According to studies by Mendes (2018), in the area of influence of the Aurá River, the increase in the population of water buffalos has brought several environmental impacts in the areas of flooded plains and contributes to the decrease in biodiversity, suppression of plant species and soil compaction, reducing the living area and viability of the species in the region. Our analysis of the pasture coverage points to the existence of these buffalo rearing areas in association with the habitat used by the Scorpion Mud Turtle and also to the increase in the percentage of severe degradation of these pastures. The introduction of species such as pigs can also contribute to the reduction of hatching, as they feed on eggs of *K. scorpioides* and other species of turtles (Aresco, 2004; Mendes, 2018).

The analysis of soil cover around the collection points revealed prevalence of non-forest natural formations (at least 40%) with emphasis on shrubby vegetation and flooded plains, in addition to areas with water cover, but the species was also found in areas with a prevalence of agricultural activities. As noted by Cassano and Alcalde (2022), the Scorpion Mud Turtle is capable of inhabiting a wide range of aquatic environments and tolerates some degree of forest fragmentation, a fact that may explain its wide distribution throughout the tropics.

The water cover matrix showed differences between the range and volume of water between the Pericumã and Aurá Rivers over a period of 35 years. It was observed that rainfall dependence can alter the scenario of floods and formation of flooded plains around these rivers over the years and, in this comparison, the Pericumã River demonstrated more stability in its water bodies. The studies by Mendes et al. (2018) and Costa (2018) reported that the loss of volumetric area of the Aurá River may be related to the growth of cities, construction of highways and leveling of fields and the construction of dams along its path. The lack of regulation of these practices threatens the survival of the river, its tributaries and the existence of the floodplains around it. The presence of dams was also observed during our collections in both rivers.

Knowledge of the habitat requirements, population dynamics and distribution of a species is crucial for evaluating its conservation status and developing optimal protection strategies (Cassano and Alcalde, 2022). In this study, it was observed that the distribution of Scorpion Mud Turtle is entirely dependent on the seasonal changes of the habitat in which it occurs. As the seasonal rains cease and the availability of food becomes scarce, *K. scorpioides* fluctuates between aquatic and terrestrial micro-habitats. The species migrates long distances to streams and flooded plains during the rainy season in search of food and mating partners and, as the plains dry up and the dry season begins, the males seek shelter for estivation and the females seek nesting sites in areas of shrubby vegetation. The hatchlings emerge synchronously with the initial precipitation and follow the adults that were estivating seek aquatic environments.

Despite its widespread distribution, *K. scorpioides* remains a relatively understudied species *in situ*. Many authors have reported great difficulty in capturing significant numbers of any defined populations, resulting in the distribution of the species being determined by a multitude of chance findings. This study contributes to the ecological and behavioral knowledge of *K. scorpioides* and provides insights into the dynamics and habitats of this species. These findings are relevant for the conservation strategies of these and other turtles that use these flooded plains as habitat and survive despite many anthropogenic disturbances in the region.

## 5. Implications for Conservation

Our findings indicate a necessity for the implementation of management and conservation strategies not only for *K. scorpioides*, but also for the other turtles found in the region. The data found on the species' nesting areas, seasonal migration and behavioral preferences allow for the development of an action plan with strategies for the protection of nests and the effective monitoring of

hunting and fishing activities during the species' breeding periods. These strategies should integrate permanent monitoring studies and effective community participation to develop an initial action plan and a comprehensive threat assessment. The results of this research will be used to inform public agencies including the Brazilian Environmental Institute (IBAMA), the State Secretariat of Environment (SEMA) and the ICMBio about the necessity to promote and guide the proposed action strategies and the importance of an effective control over the utilization of environmental resources. Inspection sites can be guided by the data provided by this research and should promote a reduction in the consumption and trade of turtles and other wild animals.

## Acknowledgements

The authors thank Dr. Anders G.J. Rhodin, Professor Danilo Lopes, Paulo Menezes and all the fishers and riverine dwellers who patiently accompanied us and contributed to our work, especially Seu João. We thank the Universidade Estadual do Maranhão, the Instituto Federal do Maranhão and the CAPES (Coordination for the Improvement of Higher Education Personnel) for their support during the trips to the Baixada Maranhense. This work was funded by the Fundação de Amparo à Pesquisa e Desenvolvimento Científico e Tecnológico do Maranhão/FAPEMA (UNIVERSAL Process No. 00880/19 and POS-GRAD Process-02434/21).

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