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Movement and habitat use of female subadults of *Podocnemis expansa* (Testudines: Podocnemididae) in northern Brazil

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Abstract

Movement and habitat use of female subadults of *Podocnemis expansa* (Testudines: Podocnemididae) in northern Brazil. The Giant South American River Turtle, *Podocnemis expansa,* is recognized for its social interactions across all sexes and age/size groups. Its movement patterns, especially those of subadults, are poorly understood. Movement is a crucial factor for the effective conservation and management of wildlife. From October 2010 to September 2011, using VHF radio-tracking methods, we studied the movements of eight subadult females in the Trombetas River Biological Reserve (REBIO do Rio Trombetas) in Pará State, Brazil. We observed subadult females utilizing lake-channel systems near the Trombetas River with their movement rates positively influenced by their size and negatively by the water level of the river. Individuals remained in the flooded forest (igapó) during flooding, likely feeding on fruits and seeds. During the nesting season, we observed interactions between adult and subadult females near the nesting sandbanks. The proximity of subadult and adult Giant South American River Turtles suggests that social interactions, such as learning reproductive and nesting behaviors, could be vital for the movement of subadult females, going beyond simple resource availability.

Keywords: Amazonian turtles, Home range size, Radio-tracking, Social behavior, Water level.

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Resumo

Movimentação e uso do habitat de fêmeas subadultas de *Podocnemis expansa* (Testudines: Podocnemididae) no norte do Brasil. A tartaruga da Amazônia, *Podocnemis expansa*, é reconhecida pelas suas interações sociais em todos os sexos e grupos de idade/tamanho. No entanto, seus padrões de movimento, especialmente os dos subadultos, são pouco conhecidos. O movimento é um fator crucial para a conservação e gestão eficaz da vida selvagem. De outubro de 2010 a setembro de 2011, usando métodos de monitoramento de rádio VHF, estudamos os movimentos de oito fêmeas subadultas na Reserva Biológica do Rio Trombetas (REBIO do Rio Trombetas), no Estado do Pará, Brasil. Observamos fêmeas subadultas utilizando sistemas de lagos e canais próximos ao rio Trombetas, com suas taxas de movimentação influenciadas positivamente pelo seu tamanho e negativamente pelo nível da água do rio. Os indivíduos permaneceram na floresta inundada (igapó) durante a cheia, provavelmente se alimentando de frutos e sementes. Durante a época de nidificação, observamos interações entre fêmeas adultas e subadultas próximas aos bancos de areia de nidificação. A proximidade entre subadultos e adultos sugere que interações sociais, como o aprendizado de comportamentos reprodutivos e de nidificação, podem ser vitais para o deslocamento de fêmeas subadultas, indo além da simples disponibilidade de recursos.

Palavras-chave: Comportamento Social, Nível da água, Radiotelemetria, Tamanho da área de vida, Tartaruga-da-amazônia.

Introduction

Turtles in the Family Podocnemididae Cope, 1868 exhibit movement patterns and habitat use that are closely linked to changes in water levels that result from the annual flooding of Amazonian rivers (Fachín-Téran *et al.* 2006, Leite 2010, De la Ossa and Vogt 2011, Perrone *et al.* 2014, Leão *et al*. 2019). Research on chelonian movement in Amazonia remains limited. Understanding animal movements and interactions, as well as how environmental processes shape species distributions, helps develop targeted conservation strategies, manage natural resources sustainably, and predict how species might respond to environmental changes such as habitat loss, climate change, and human disturbances (Famelli 2013, Hussey *et al.* 2015, Cueva *et al.* 2018). Radio-tracking studies are essential for understanding life history and determining ecological patterns in wildlife populations (Magnusson *et al.* 1997, Hussey *et al.* 2015, Famelli *et al.* 2016, Leão *et al.* 2019). Over the past decade, radio-tracking studies on freshwater turtles have increased substantially, generating valuable insights into movement patterns, habitat use, seasonal migrations, linear displacements, and comparisons between methods for measuring home range sizes (Ribeiro *et al.* 2024). Despite this progress, significant gaps persist in our knowledge of most species in the Neotropical region, which is especially concerning given the region's high endemism and exceptional diversity of freshwater turtles (Ribeiro *et al.* 2024). The Giant Amazonian River Turtle, *Podocnemis expansa* (Schweigger, 1812), is the largest South American freshwater chelonian found in the basins of the Orinoco and Essequibo rivers and the drainages of the Amazon River, spanning Colombia, Venezuela, Guyana, northwestern Peru, eastern Ecuador, northern Bolivia, and northern and central-western Brazil (Rueda-Almonacid *et al.* 2007, Ferrara *et al.* 2017, Forero-Medina *et al.* 2019). The species also migrates over hundreds of kilometers (Pezzuti *et al.* 2004, Carneiro and Pezzuti 2015), and, as the largest member of Podocnemididae, it is expected to show the largest home ranges among the species within the taxonomic group. Therefore, studies on the movements of *P. expansa* will provide valuable insights into the biology of Amazonian chelonians.

Although individuals of *P. expansa* with carapace lengths exceeding 1 meter were once commonly observed in Amazonian rivers (Ernst and Barbour 1989), sightings of such large specimens have become rare. This decline is primarily attributed to the historical loss of adult females during nesting activities, as evidenced by the reduction in the number of hatchlings released annually in certain areas inhabited by *P. expansa,* despite decades of nesting site protection (Cantarelli 2006, Vogt 2008, Forero-Medina *et al.* 2019, Lacava *et al*. 2024). Females of the species reach sexual maturity around 50 cm (Alho and Pádua 1982a, von Hildebrand *et al.* 1997), whereas males mature around a carapace length of 30 cm (Portelinha *et al.* 2013, 2014). The species is fully aquatic, with large groups of females observed aggregating in the water during the dry season, when sandy nesting beaches emerge, and leaving the water as a group in what is known as arribada nesting (Alho and Pádua 1982a, b, von Hildebrand *et al.* 1997, Hernandez *et al.* 1998, Rueda-Almonacid *et al.* 2007, Simoncini *et al.* 2022). Among freshwater chelonians, *P. expansa* is undoubtedly one of the most social turtle species worldwide (Ferrara *et al.* 2013, 2014). This species exhibits a complex vocal repertoire and audible communication across all age categories, coordinating mass nesting, nights without nesting, synchronized emergence of hatchlings from nests, and post-hatchling parental care (Ferrara *et al.* 2013, 2014, Jorgewich-Cohen *et al.* 2024).

Extensive exploitation of *P. expansa* since the late 18th century has driven significant population declines. This species has been severely targeted by humans for its high nutritional-value protein and subjected to illegal trade in clandestine markets (Bates 1863, Smith 1979, Rebelo 2002, Pezzuti *et al*. 2004, Cantarelli 2006, Rueda-Almonacid *et al*. 2007, Forero-Medina *et al*. 2019). As a result of ongoing threats, *P. expansa* has recently been reassessed and is presently in the process of being categorized as Endangered by the International Union for Conservation of Nature Red List of Threatened Species (IUCN; C. R. Ferrara *et al.* pers. obs.). In the Trombetas River Biological Reserve, Pará, Brazil, human impact has caused the number of nesting females to drop from over 8000 in 1976 to just 850 in 1989 and further declining to fewer than 350 females since 2008 (Ferrara *et al*. 2010, Forero-Medina *et al*. 2019). In this context, understanding the movement patterns and home range needs of *P. expansa* in the Trombetas River is essential, especially as this region once harbored one of Brazil's largest populations of *P. expansa,* with significant decreases over the years (Forero-Medina *et al*. 2019). Examination of movement patterns across various size classes and life stages is critical to informing effective, targeted management strategies.

Concerns about significant declines in *P. expansa* populations have driven numerous research and conservation approaches in Amazonia, compelling scientists, NGOs, and community programs to implement protective strategies aimed at understanding and preventing the underlying causes, ecological impacts, and potential conservation measures to protect and restore this endangered species (Forero-Medina *et al*. 2019, Andrade *et al*. 2022). Despite being extensively studied, conservation efforts for Amazonian chelonians primarily focus on safeguarding nesting sites to protect females and the early life stages (eggs and hatchlings) (Cantarelli 2006, Miorando *et al*. 2013, Cantarelli *et al*. 2014). A significant research gap exists concerning other life stages of *P. expansa,* particularly subadults, which are crucial in the population's transition to adulthood (Pritchard and Trebbau 1984, Cantarelli 2006). There is evidence, however, that prioritizing the survival of juveniles and adults over fecundity is the most effective conservation strategy for reversing population decline (Mogollones *et al*. 2010). Given the scarcity of data on ontogenetic shifts of the movement, activity, home range sizes, and habitat of *P. expansa,* this study aimed to elucidate these aspects by radio-tracking subadult females throughout the hydrological cycle in the Biological Reserve of Trombetas River, Pará. This study (a) evaluates the effect of the Trombetas River level on the average monthly distance traveled by individuals; (b) estimates their areas of use or home range sizes; (c) assesses the degree of overlap and social interactions in areas of use; (d) and characterizes habitat use across dry-flood periods.

Materials and Methods

Study Area

The Trombetas River Biological Reserve (REBIO Trombetas: 00°39'–01°29' S, 56°17' –57°03' W) covers approximately 385,000 ha, and is situated in the municipality of Oriximiná, Pará state, Brazil. This area encompasses a significant portion of the northeastern region of Pará and is nestled within the Amazon Basin in the interfluve of the Trombetas and Acapu rivers (Figure 1). The Trombetas River is a clear-water river that extends 800 km toward the Venezuelan border and is the second largest tributary on the left margin of the Amazon River (IBAMA and STCP 2004). Many species of *Podocnemis* utilize the large sandbanks in the region for nesting during the dry season. These large nesting sites provided critical habitat for the reproduction of turtles; thus, their presence was instrumental in the creation of the reserve in 1979 (IBAMA 1989). The biologically diverse area within the REBIO do Rio Trombetas encompasses a rich array of aquatic habitats, including numerous lakes and channels that flow into the rivers (IBAMA and STCP 2004).

The REBIO do Rio Trombetas represents a unique and ecologically significant area within the Amazon region, offering valuable insights into the intricate relationships between hydrology, biodiversity, and human communities (IBAMA and STCP 2004, Eisemberg *et al*. 2016). Traditional communities, including riverine and quilombola communities, occur in the reserve and use chelonians for their subsistence. The area faces threats from illegal harvesting and egg collection, posing challenges to the conservation of turtles, especially related to enforcement (Eisemberg *et al*. 2016).

Data were collected along a stretch of approximately 20 km of the Trombetas River, covering an area of 70 km^2 in the central region of the river. This area includes the Jacaré and Leonardo lakes, as well as nearby systems such as the Farias and Abelardo system lakes (Figure 1). Additionally, the study site also comprises seasonally flooded forest areas during the high-water period.

Trombetas River Cycle

The Amazon Basin can be divided into four hydrological seasons related to the rising and falling of the level of the rivers. In the REBIO do Rio Trombetas, the water level is at its lowest in October and November. Rain begins in late November, and the rivers begin to rise, flooding the forests and reaching its peak in March and April. As the rain diminishes in intensity, the water gradually recedes until the forest is no longer flooded by late August, when the turtles begin congregating to migrate to the nesting beaches (Alho and Pádua 1982a, Leão *et al*. 2019). The seasons in the Trombetas River include four stages: (a) Receding (falling water level), which generally happens from July to October; (b) Dry (lowest water level), October to December; (c) Flooding (water level rising gradually), December to April; and (d) Full (highest water level), April to June.

The water level of the Trombetas River was expressed in meters, representing the difference in water column level relative to the average level of the Atlantic Ocean (*cota*) in Brazil. Elevation values were obtained from the “Base Tabuleiro” river gauge station provided by the National Water Agency (ANA). Based on daily elevation data from October 2010 to September 2011, four phases of the hydrological cycle were

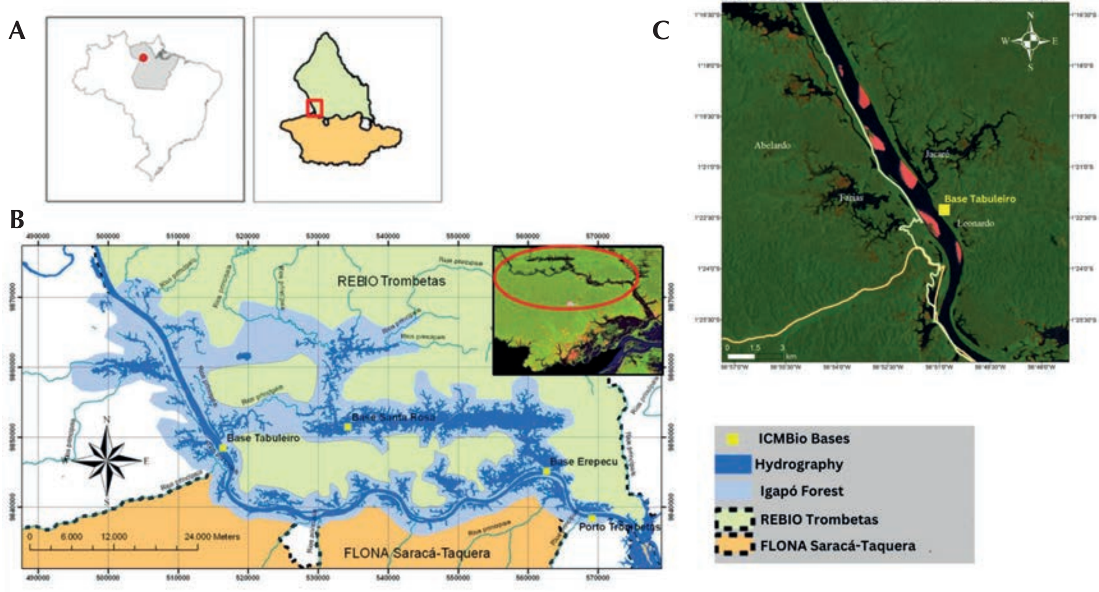

Figure 1. (**A**) Geographical boundaries of the Trombetas River Biological Reserve (REBIO do Rio Trombetas), highlighting the border with the Saracá-Taquera National Forest (FLONA Saracá-Taquera), Pará state, northern Brazil. The satellite image in the upper right corner (**B**) shows a section of the Trombetas River within the limits of the REBIO and FLONA, marked by the red circle, extending to the mouth of the Trombetas River on the left bank of the Amazon River. (**C**) Sampling area, highlighting Jacaré, Leonardo, Abelardo, and Farias lakes. Along the main course of the river are sandbanks (marked in pink) that emerge during the dry season.

established for the entire sampling period (Figure 2; Bittencourt and Amadio 2007).

Capture, Marking, and Morphometry

Between October and December 2010, and from April to June 2011, we captured a total of 14 turtles using trammel nets and active search (Enríquez-Mercado *et al*. 2024). Individuals were marked by notching marginal scutes of the carapace, following established mark-recapture protocols (Cagle 1939). We obtained the straight-line carapace length (SLC) and the body mass (BM) of each individual using caliper and spring scale dynamometers, respectively (Enríquez-Mercado *et al*. 2024). Sex was determined by observing the opening angle of the anal plate and the size of the tail (larger in males) (Vogt 2008).

Radio-tracking: Fitting and Operation

We selected 12 subadult females to be equipped with the VHF radio-transmitters (AVM Instrument Co. Model MP2, California, USA). This selection was based on criteria including CL measurements lower than the minimum maturation size established in the literature (50 cm for females; Alho and Pádua 1982a, von Hildebrand *et al*. 1997) and compatibility of individual mass with that of the radio-transmitter, ensuring it did not exceed 10% of the individual's BM (Jacob and Rudran 2006). The radio-transmitter device operates on a single frequency of radio waves between 164 and 165 MHz. We affixed the devices to a turtle's carapace using Tubolit® underwater glue, positioned on the 2nd and 3rd vertebral shields. After installation,

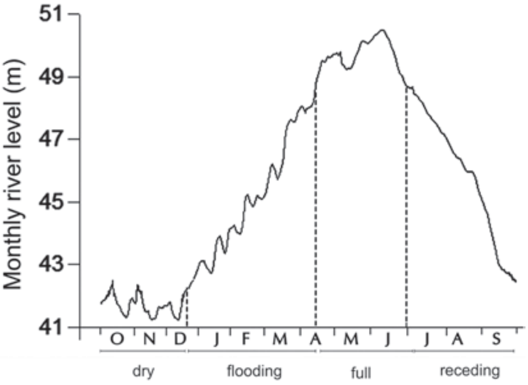

Figure 2. Monthly level of the Trombetas River (m) between October 2010 and September 2011 at Trombetas River Biological Reserve, Pará state, northern Brazil.

turtles were kept in empty fiberglass tanks for 24 hours to allow the glue to completely adhere to the carapace before being released at the capture sites. The carapace length (CL) of turtles monitored ranged from 20 to 40.2 cm (28.3 ± 2.4) and body mass (BM) from 0.9 to 6.6 kg (2.9 ± 0.7). To capture the radio-transmitter's signal we used a three-element Yagi model unidirectional antenna connected to a powered radio receiver (ATS Model R2000 Scientific Receiver) via a two-meter-long coaxial cable. An external 12V battery powered the receiver. To minimize external noise interference, we utilized a headset during tracking. Additionally, a wooden stick approximately 1.7 meters in length was employed to raise the antenna, thereby increasing the signal reception range in open areas (Jacob and Rudran 2006). We lost the signal from four subadult females the day after their release and were unable to locate them for the entire study period. Therefore, only eight subadult females were monitored.

The digital memory of the radio receiver facilitated the storage of transmitter frequencies. We used the receiver's scanner function to perform periodic scans of these stored frequencies at eight-second intervals, ensuring each radio-tagged turtle had an equal chance of being detected. After we recorded the location, we removed the corresponding frequency from the receiver's memory. Given the limited visibility caused by the dark water color in lakes and flooded forests, we directed the antenna toward the area with the strongest signal, disconnected the coaxial cable and headphones, and confirmed the location only upon hearing the distinct signal emitted by the receiver (Jacob and Rudran 2006).

The radio-tracking data were collected four to six times per week from October 2010 to September 2011, encompassing a complete hydrological cycle. Each turtle was tracked once daily to minimize the risk of losing its location, with a minimum 24-hour interval between consecutive readings to mitigate temporal autocorrelation effects and ensure statistical independence (Swihart and Slade 1985). Each location record included the date, time, geographic coordinates obtained using a Garmin GPS device (maximum satellite error of eight meters), and details regarding the environmental characteristics of the turtle's habitat.

Tracking operations were carried out from an aluminum boat equipped with a 15-hp engine, with one person navigating and another handling the tracking tasks. The boat's speed during searches was kept below 15 km/h, aligning with the natural flow of the water bodies. In flooded forest areas (igapó) during the flood season, we used a wooden boat and oars.

Habitat Use

To assess environmental variation in habitat use we conducted sampling across two distinct periods: the first in October 2010 (during the dry season) and then in the flood season (June 2011). Characterization of the environment was primarily based on observations made during the dry season, which facilitated the identification of submerged features such as surrounding vegetation types, substrate composition (e.g., silt, sand, clay, litter), and water flow speed categorized as either lentic or lotic (Table 1). Additional details observed throughout the

Table 1. Characterization of the aquatic environments identified between October 2010 and September 2011 in the sampling area at Trombetas River Biological Reserve, Pará state, northern Brazil.

Category	Habitat characteristics
Freshwater lake (FL)	Permanent lentic environment and marginal vegetation; occurrence of "pools" (places with high depths, greater than 8.0 meters, even during the dry season). During floods (December to January), banks of wild rice (*Oryza glumaepatula*) form on the surface of the water, close to the banks. Muddy substrate covered with decomposing plant material (tree trunks, branches, leaves).
River Chanel (RC)	Lotic environment, in the main course of the river, with depths that varied between 6.0 and 19 m in the sampled locations, with the presence of pools and absence of vegetation.
Open *cuiarana* flooded forest (OCFF)	Lentic environments with flooded vegetation, where the plant species *Eschweilera* sp. predominates (*cuiarana*). The trees are restricted to the low topographic levels of the land, subject to periods of six to eight months of flooding, and are spaced apart, allowing intense light to enter. During floods, banks of wild rice (*O. glumaepatula*) can form next to "*cuiarana*" trees. Substrate formed by silt and sand.
Open flooded forest mixed (OFFM)	Lentic environment of flooded forest, with a predominance of *Symmeria paniculata* (*carauaçu*) shrubs and trees measuring between 7.0 and 15 meters, spaced apart, which include *Macrolobium* sp. (*arapari*); *Eschweilera* sp. (*cuiarana*). The topographic elevation of the land is the lowest, subjecting plant species to long periods of flooding (up to eight months). The occurrence of aquatic macrophytes is common. The substrate is made up of silt, litter, and sand.
Flooded forest (FF)	Lentic environment of flooded forest. Formed by medium to large trees (more than 15 m) and with little light passing between them. Trees such as *Acosmium nitens* (*itaubarana*), *Ormosia* sp. (*tento*), *Campsiandra* sp. (*acapurana*), *Astrocaryum jauari* (jauari), *Euterpe precatoria* (*açaí*) were common, among others.
Cano (C)	Lotic watercourse that connects a lake to the main channel of the river at flooding and beginning of ebb; at the height of the drought, the lake becomes accessible only by land. Water flows in the river–lake direction during the flood and the reverse occurs during the ebb. Presence of bushy tangles of various plant species. Silty substrate–clayey.
Vegetated ravine (VR)	The marginal area of the river with a predominance of clay soil and vertical gradient with the presence of shrub to tree vegetation, which can be seasonally flooded in places with lower topography.
Bay Beach (BB)	Lentic, shallow (up to 5 m), bay-shaped environment on the banks of sandy beaches (large sandy soil outcrops in the main course of the river). This environment is locally known as a "*ressaca*."

tracking period were incorporated into the environmental descriptions. Analysis of the collected data enabled the identification of eight primary environmental categories in this study, drawing upon the classification systems outlined by Leite (2010) and Martin *et al*. (2004), with some modifications.

Distances Traveled

We estimated the individual monthly distance (IMD) by calculating the sum of each individual's consecutive journeys per month, excluding monthly journeys of fewer than five tracking days. The average monthly distance

(AMD) traveled was estimated by summing the IMD of each individual and dividing it by the number of individuals monitored during the period. The total distance traveled (DT) by the turtles was the cumulative sum of the respective distances covered monthly during monitoring.

Home Range

We estimated the linear home range (LHR), represented by the straight-line or the maximum distance between the two most distant fixes, considering these movements as unidirectional (Morales-Verdeja and Vogt 1997, Fachín-Terán *et al.* 2006, Bernhard 2010, Freeman *et al*. 2018). We used the conventional 95% Minimum Convex Polygon ($MCP^{95\%}$) and the 95% Kernel Density Estimator ($KDE^{95\%}$) methods to estimate the size of the home range of the tracked turtles. The KDEs smoothing parameter (h) was determined using the least squares cross-validation method. Given the high autocorrelation in tracking data, we also employed the Autocorrelated KDE (AKDE; Fleming *et al*. 2015) to reduce the uncertainty associated with such data (Horne *et al*. 2007, 2019, Crane *et al*. 2021). For AKDE, we used UD2 (OUF) in the "ctmm" in R which considers the correlated positions and correlated velocities in the fixes. We also estimated the $MCP^{95\%}$ and $KDE^{95\%}$ of four adult females observed sharing the same area. These large females were equipped with VHF radio-transmitters (model MP2, AVM Instrument Company Ltd.) with a frequency of 165 MHz, during simultaneous research in the same area. Three of them were monitored during a study on underwater communication and parental care between adult females and hatchlings (Ferrara *et al*. 2013), and another one was part of a pilot project of the Richard Vogt lab (V. Bernardes, pers. comm., September 2011). Due to the limited number of relocations and the small sample size of adult individuals, these data are presented solely as exploratory and serve to provide insights into the overlap between adults and subadults.

Overlapping

We assessed spatial overlap among the monitored individuals by calculating the percentage of home range intersection. This analysis was accomplished using the $KDE^{95\%}$ method implemented in the 'adehabitatHR' package in R (Calenge 2006), which identifies centers of activity that are potentially associated with ecologically significant areas for chelonians, such as mating or nesting sites (Leão *et al.* 2019). This approach provides a comprehensive assessment of home range overlap and the potential frequency of spatial interactions among individuals (Famelli *et al*. 2025).

Data Analysis

We performed all analyses in the program R 4.3.0 (R Development Core Team 2023). The home range areas were saved either as raster or shapefiles and transferred to the ArcGIS program, version 10.5 (ESRI 2016). The comparison between home range estimators was assessed using ANOVA. We conducted a linear regression analysis to evaluate possible relationships between river monthly elevation (predictor variable) and distance traveled (response variables). We also performed linear regressions to examine the relationship among the home range sizes (response variable) to the body size (CL and BM; predictor variables), followed by ANOVA. The home range sizes of adults and subadults was compared using a Mann-Witnney *U* test. A significance level of ≤ 0.05 was adopted for all analyses.

Results

Habitat Use

We located the turtles equipped with radio-transmitters 535 times (an average of 66.9 locations per individual) between October 2010 and September 2011. Throughout the 11-month data collection, the chelonians were observed utilizing three lakes (Farias, Jacaré, Abelardo) and the Trombetas River, encompassing two micro basins situated on opposite banks of the river. The monitored turtles showed distinct variation in habitat use across different stages of the hydrological cycle. During the rising water phase, they relocated to the igapós. In contrast, during the low water phase, they predominantly utilized lakes and river habitats, favoring backwaters over the main river channel. As the igapó flooded due to lateral overflow from the Trombetas River, the turtles migrated from the river and lakes. During the low-level phase, when most igapó habitats became dry, the chelonians relocated to perennial lakes and rivers (Figures 2 and 3; Table 1). During the receding season, most turtles used River Channel (RC), Bay Beach (BB) and Open Flooded Forest Mixed (OFFM) habitats; however, during the dry season their most frequent use was nearby BB areas. During the flooding season, we noticed most of the monitored animals using OFFM and Flooded Forest (FF), the same habitats that were used during the full season (Table 1; Figure 3). Three monitored turtles were observed outside the boundaries of REBIO do Rio Trombetas near quilombola communities.

Distances Traveled

The average monthly distance traveled (AMD) was 5 ± 4.27 km, varying from 1 to 30 km a month. The mean total distance traveled (DT) by the eight subadult females was 34.51 ± 24.2 km (7.61–73.82 km). Notably, the period of reduced movement coincided with the

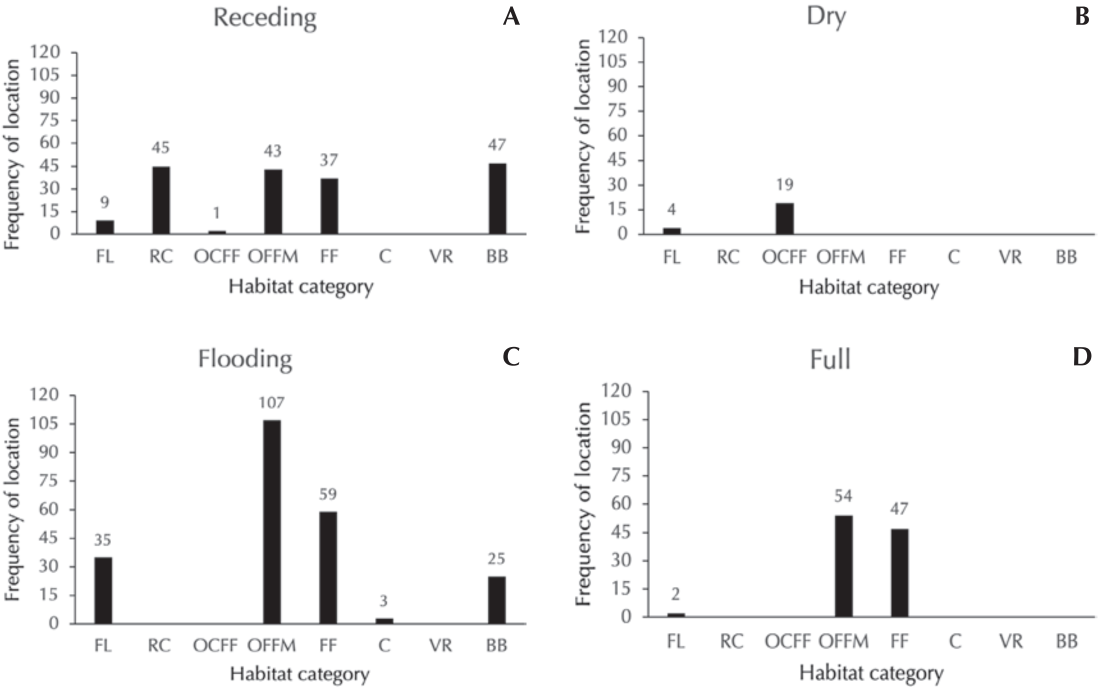

Figure 3. Frequency of habitat categories used by the young females of *P. expansa* per season in the Trombetas River Biological Reserve (REBIO do Rio Trombetas), Pará state, northern Brazil. BB: Bay beach; C: Cano; FF: Flooded forest; FL: Freshwater lake; OCFF: Open cuiarana flooded forest; OFFM: Open flooded forest mixed; RC: River channel; VR: Vegetated ravine.

high-water levels in the Trombetas river (Figures 2 and 4) with a negative correlation between river water level and DT ($F = 4.8715$, $df = 9$, $p < 0.05$).

Figure 4. Movement (mean monthly distance traveled) by the young females of *Podocnemis expansa* (orange bars) and monthly river level (blue line) at the REBIO Trombetas, Pará state, northern Brazil.

Home Range

The mean values of the home range for female subadults varied depending on the estimator applied (Table 2; Figures 5 and 6). The linear home range (LHR) varied from 2.13–12.93 km (6.92 ± 3.70 km). However, using the estimators, we observed that the home range size of the young turtles monitored varied from 0.59 (MCP) to 293.43 km^2 (AKDE) with no significative difference among the home range estimations ($F = 0.922$, $df = 8$, $p = 0.5046$). The larger areas were estimated with AKDE, followed by KDE and MCP (Table 2). In August, we noticed young females near the aggregation of adult females by the nesting sites. On more than 20 occasions, subadult females were observed in proximity (≤ 30 m) to groups of adult females of *P. expansa* nesting on beaches (Figure 6). Notably, one of these large females equipped with radio-transmitters and monitored during a simultaneous study (Ferrara *et al*. 2013) was observed floating with a subadult female near the nesting site. The MCP for these four adult females with transmitters varied from 0.63 to 33.16 km^2 (10.97 ± 7.58 km^2). The KDE for these females ranged from 7.9 to 172.7 km^2 (98.1 ± 34.9 km^2). There was no significant difference between the MCP ($U = 14$, $Z = 0.25476$, $p = 0.7989$) nor the KDE ($U = 7$, $Z = 1.4437$, $p = 0.14884$) of adult females in comparison to the young females (Figures 5 and 6).

Home Range Overlap

The overlap analysis using KDE$^{95\%}$ revealed distinct patterns of spatial use among female turtles. Adult females exhibited higher mutual overlap (0.52 ± 0.09), with several pairwise values above 0.25 (ranging from 0.26–0.89), indicating shared or adjacent core activity areas. In contrast, subadult females showed none to lower overlap among themselves (ranging from 0.00–0.37), with median value of 0.14 ± 0.02.

Table 2. The home range of the subadult radio-tracked females of the Giant South American River Turtle (*Podocnemis expansa*) monitored from October 2010 to September 2011 in the Trombetas River Biological Reserve, Pará state, northern Brazil. LHR: linear home range; MCP: Minimum Convex Polygon; KDE: Kernel Density Estimator; AKDE: Autocorrelated Kernel Density Estimator. The measurements are shown in km^2, except for LHR in km.

	LHR	MCP 95%	KDE 95%	AKDE 95%
Mean ± SD	6.92 ± 3.7	13.63 ± 13.86	36.84 ± 33.25	64.51 ± 95.91
Range	2.13–12.93	0.59–42.60	3.09–99.71	2.40–293.43

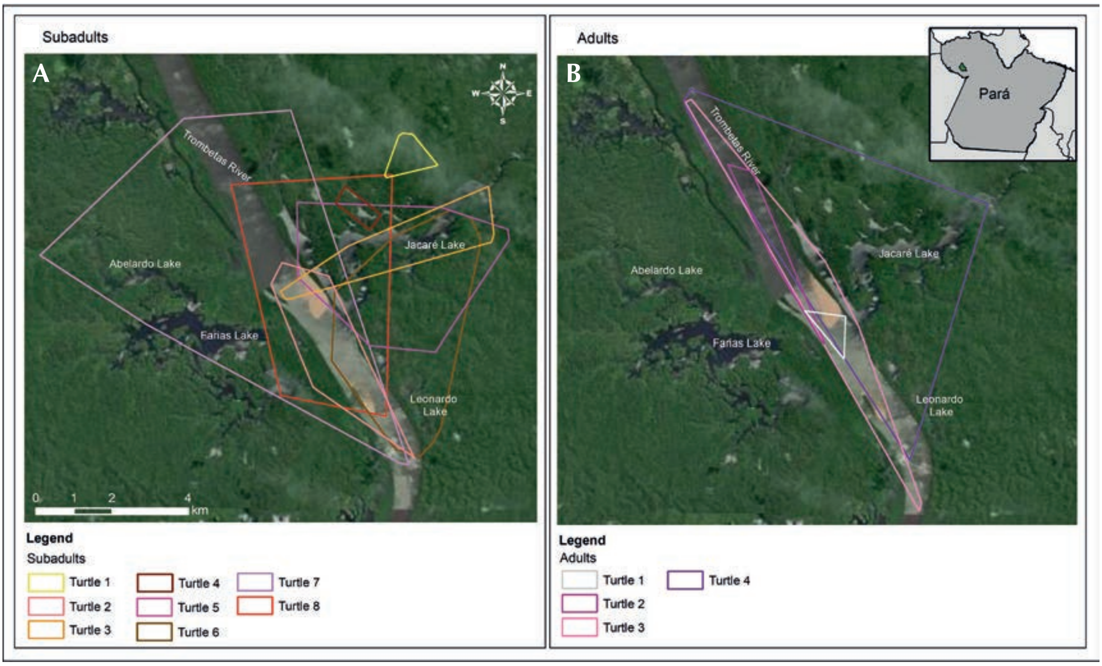

Figure 5. Minimum Convex Polygon (MCP$^{95\%}$) of subadult females of *Podocnemis expansa* (**A**) and exploratory MCP$^{95\%}$ for some adult females (**B**) radio-tracked at REBIO Trombetas, Pará state, northern Brazil.

Interactions between age groups were also observed with 75% of adult females overlapping with at least one subadult, while approximately 44% of subadults shared moderate to high spatial overlap with an adult (0.23 ± 0.03; 0.00–0.68). Interestingly, one of the smallest subadult individuals (CL = 22 cm and BM = 1.72 kg) exhibited relatively high home range overlap with two adult females, with values of 0.68 and 0.36, respectively (Figure 6).

Discussion

Female subadults of *Podocnemis expansa* exhibited distinct patterns of habitat use throughout the hydrological cycle of the Trombetas River. In our study, females make larger movements during the nesting season (August, September, and November to December), which is linked to low water levels. This pattern was observed for adult females in other areas of Amazonia (Carneiro and Pezzuti 2015). Subadult female *P. expansa* turtles monitored over the 11 months in our study moved between the Trombetas River and three perennial lakes (Jacaré, Abelardo, and Farias) located near nesting beaches and flooded forest areas. During the rising water phase, they migrated to the igapós, where the dense tree trunks and shrubs provided both shelter and abundant food resources (Almeida *et al.* 1986, Balensiefer and Vogt 2006, Vogt 2008). Turtles frequently use flooded forests, which serve as a vital habitat for feeding and refuge (Fachín-Téran *et al.* 1995). *Podocnemis expansa* primarily feeds on vegetation (Fachín-Téran *et al.* 1995, Malvasio *et al.* 2003, Cunha *et al.* 2020), with the igapó forest serving as a vital source of fruits and seeds in its diet due to the relatively low abundance of aquatic macrophytes

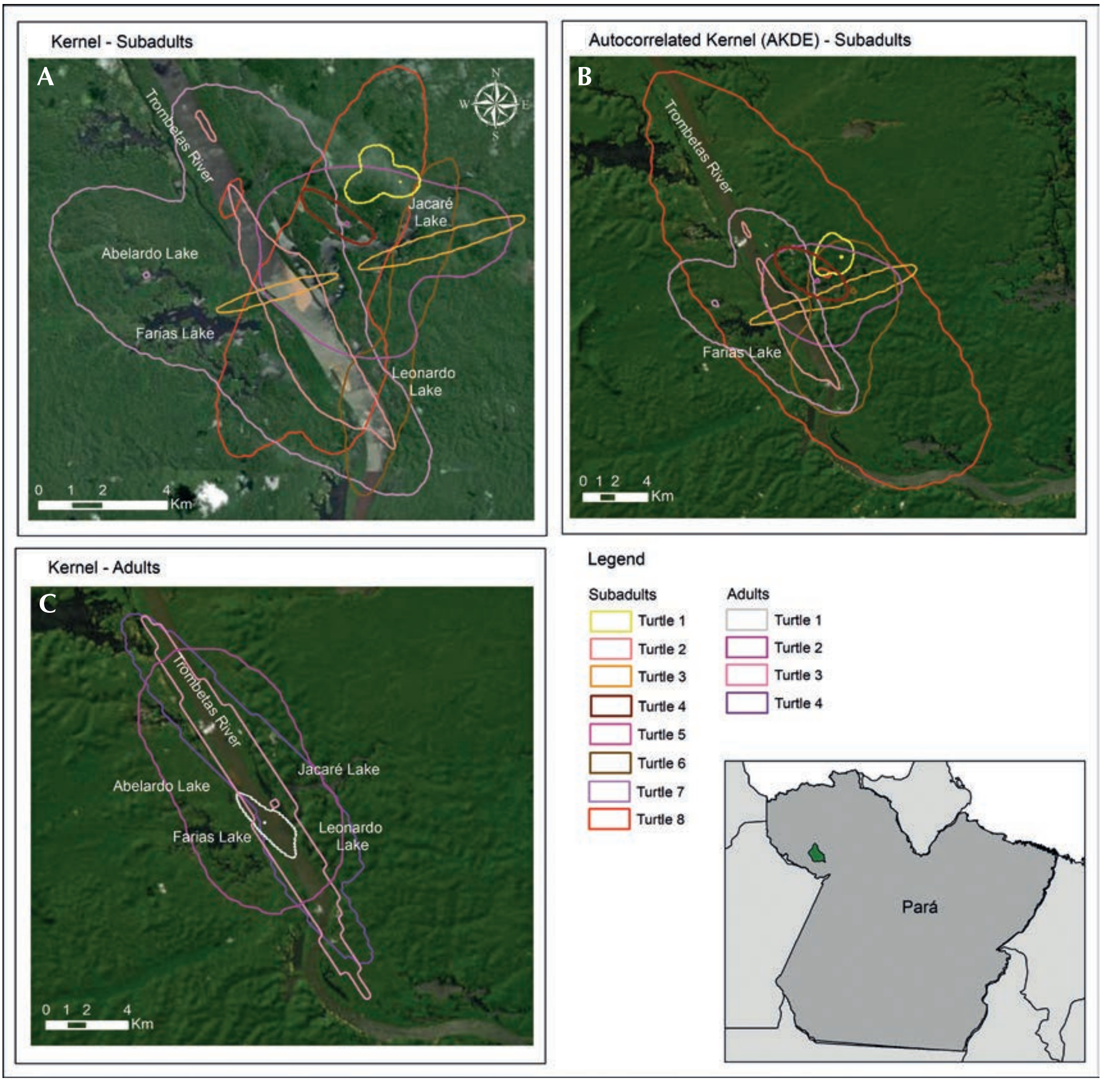

Figure 6. Kernels of the *Podocnemis expansa* turtles radio-tracked at the REBIO Trombetas, Pará state, northern Brazil. (**A**) Kernel Density Estimator (KDE95%) of subadult females; (**B**) Autocorrelated Kernel Density Estimator (AKDE) of subadult females; (**C**) Exploratory Kernel Density Estimator (KDE95%) of adult females.

in the Trombetas region (Vogt 2008, Cunha *et al.* 2020). In contrast, during the low water phase, they primarily inhabited lake and river environments, remaining in available water bodies such as lake pools and the river's main course with a preference for backwaters over the main river channel. This preference is likely influenced by the resistance provided by the sandbanks at nesting sites along the Trombetas River, making these areas more accessible and stable for small and young individuals. Consequently, the reduction in movement rate with increasing elevation and the subsequent flooding of the igapós, coupled with the abundant fruiting of vegetation (Armond 2008), suggests that the chelonians are finding food sources nearby and easily accessible. Similar behavior has been described in adult females of this species approximately two months after nesting in the same study area (Moreira and Vogt 1990, Castelblanco-Martinez *et al*. 2006), as well as in the Xingu River (Carneiro and Pezzuti 2015) and the Juruá River (Hinderaker 2021). For other species of Podocnemididae, such as *Podocnemis unifilis* Troschel, 1848, studies by Leão *et al*. (2019) and Hinderaker (2021) revealed similar habitat use, with individuals favoring the main river courses and lakes but using flooded forests less frequently than *P. expansa* during peak flooding.

The flood pulse remarkably influences the movement of aquatic vertebrates (Junk 1984, Junk *et al*. 1989). The effect of flood pulse on the movement of various species in the Amazonian rivers has been documented, including Peacock Bass (*Cichla* spp.; Hoeinghaus *et al*. 2003), Amazonian manatee [*Trichechus inunguis* (Natterer, 1883); Arraut *et al*. 2009)], the caimans, *Caiman crocodilus* (Linnaeus, 1758) (Silveira *et al.* 2010) and *Melanosuchus niger* (Spix, 1825) (Silveira *et al.* 2011), and turtles such as *Podocnemis sextuberculata* Cornalia, 1849 (Fachín-Terán *et al.* 2006) and *Podocnemis unifilis* (Leão *et al.* 2019). In the Trombetas region, the flood pulse results in an average annual elevation variation of up to six meters, which has a marked negative correlation with chelonian movement. Yet, subadults of *P. expansa* displayed movement patterns comparable to adult females of *Podocnemis erythrocephala* (Spix, 1824), *P. sextuberculata,* and *P. unifilis*, despite these species being smaller podocnemidid turtles within the Amazon biome (Fachín-Terán *et al.* 2006, Bernhard 2010, Cueva *et al.* 2018, Naveda-Rodríguez *et al.* 2018). Adult female *P. unifilis* exhibited an average displacement of 2.53 km (Leão *et al.* 2019) to approximately 16 km in the Napo River, Ecuador (Naveda-Rodrigues *et al.* 2018). *Podocnemis sextuberculata* displayed linear movements averaging 29.8 km in the Mamirauá Sustainable Development Reserve, Amazonas (AM; Fachín-Terán *et al.* 2006), and up to 60 km for one adult female in the Trombetas River, Pará (PA; Perrone *et al.* 2014).

Despite the growing availability of tracking technologies capable of addressing specific ecological questions (Guilhon *et al*. 2011), studies on *P. expansa* hatchlings and juveniles are scarce. Silva *et al*. (2017) recaptured a juvenile nine months after release, 38.47 km upstream in the Jaú River (AM), showing the displacement capacity of the species in early stages. Nevertheless, adults of *P. expansa* are known to display migration distances greater than 500 km, as documented in Xingu River (Carneiro and Pezzuti 2015, Carneiro 2017). On the Meta River, Colombia, Nieto-Vera (2024) reported a LHR average of 35.1 km (range 1.6–107.9 km) for adult females, while in the Trombetas River, adult females have been documented traveling over 45 km (Moreira and Vogt 1990) and 65 km downstream toward the Amazon River (Castelblanco-Martinez *et al.* 2006). In our study, adult females were frequently observed in nearby lakes several months after the nesting period. For instance, the radio signal of one adult female was recorded in Lake Jacaré during the flooding season of the Trombetas River. This finding suggests that long-distance migratory movements may not be a consistent behavior for all adult females of the species and that variations may exist among populations across the geographic range of the species and within a population.

As anticipated, the home range sizes estimated for subadult *P. expansa* in this study (average of 7 to 64.5 km^2) were smaller than those reported for adult females. Although, we did not observe significant differences in home range sizes between adults and subadults, the adult home range estimates were based on a limited sample size. These estimates may not fully capture the critical areas used by adults and for that reason they are not presented here for comparison with the literature.

Studies on the home range of *P. expansa* reveal variability across different regions and estimator methods applied. Castelblanco-Martínez *et al*. (2006) reported a mean home range of 22.7 km² (MCP$^{95\%}$) for adult females in the Trombetas River. In the Juruá River, Hinderaker (2021) calculated the FK$^{95\%}$ area to be 748.81 km² for the species. Nieto-Vera (2024) reported an average of 8.22 km² with a FK$^{95\%}$ for adult females in the Meta River, Colombia. These differences underscore the impact of the size and age of an individual, ecological conditions, habitat availability, and methodological approaches on estimating home ranges for this species, highlighting the importance of developing conservation strategies tailored to specific contexts. Our results of home range for subadult *P. expansa* are more comparable to those observed for adults of *P. unifilis* than *P. expansa*. In the Juruá River, Hinderaker (2021) reported an average home range for *P. unifilis* of 311.67 km² using the FK$^{95\%}$ method, while the core area (FK$^{50\%}$) was estimated at 0.06 km². Naveda-Rodriguez *et al*. (2018) estimated home ranges for adult males and females in the Napo River, Ecuador, with AKDE$^{95\%}$ values averaging 5.2 km² (range 3.8–7.0 km²) and core areas (AKDE$^{50\%}$) averaging 1 km² (range 0.5–1.5 km²). In the Trombetas River the estimated MCP$^{100\%}$ of *P. unifilis* was 1.83 km², while the KDE$^{95\%}$ was 0.87 km² and core areas were 0.20 km² for females (Leão *et al*. 2019). These findings suggest that *P. unifilis* utilizes relatively smaller and more localized areas compared to *P. expansa*, with patterns resembling those of subadult females. In Brazil, *P. expansa* and *P. unifilis* are among the most extensively studied chelonian species, enabling comparisons. A recent study on *Podocnemis lewyana* Duméril, 1852 in Colombia reported a MCP of 7.5 km² and a KDE$^{95\%}$ of 3.71 km² for the species (Alzate-Estrada *et al.* 2020). Factors such as species-specific traits, population dynamics, and environmental conditions must be considered when drawing comparisons, as variations in home range size are influenced by habitat characteristics, resource distribution, and individual behavior. These results underscore the need to understand species-specific and regional differences to establish effective conservation and management strategies.

The presence of both subadult and adult females of *P. expansa* congregating near nesting beaches prior and during the nesting season is known across its geographical distribution (Ferrara 2012, Portelinha *et al*. 2014, Fonseca 2022). The simultaneous use of space by subadults and adults highlights the social behavior of the species, as previously observed among adult females and hatchlings during movement to the igapós after hatching (Ferrara *et al.* 2013). The arrival of the monitored subadults in the Trombetas River in August 2010–2011 coincided with the aggregation of adult female *P. expansa* pre-nesting (a couple of months before the beginning of nesting season in October). This finding indicates that social interactions are present and potentially meaningful across different age groups in *P. expansa.* Overall, spatial overlap appears to align with age or maturity, potentially reflecting differences in nesting behavior, habitat preferences, or social interactions. The overlap analysis revealed that adult females exhibited greater spatial overlap compared to subadult females, indicating shared or adjacent space use, likely associated with the utilization of sandbanks for nesting. The moderate to low overlap observed among subadult females may reflect more individualized or peripheral movement patterns. Our findings indicated that variations in movement patterns and habitat use were influenced by the size and maturity of individuals, resulting in different levels of home range overlap (Harestad and Bunnel 1979).

The proximity observed between different life stages of *P. expansa* may not solely result from the availability of resources, such as water and places for thermoregulation, but could indicate that subadult females are learning about reproductive behavior. The presence of nonmature *P. expansa* alongside adult females during the nesting season suggests that in addition to underwater communication during the aggregation period and vocalizations from young inside the nest (Ferrara *et al.* 2013), significant social interaction is taking place among females of different ages. The smallest female showed spatial affinity with adults, resembling patterns previously observed between adult females and recently emerged hatchlings (Ferrara *et al*. 2013). In a study tracking adult female *P. expansa* via satellite telemetry in the Xingu River, only one individual stayed near the nesting area (Carneiro and Pezzuti 2015). This aspect requires further investigation across the range of the species to determine whether it represents a local behavior and adaptation unique to the REBIO do Rio Trombetas.

The most suitable technique for assessing wildlife movement is an ongoing debate (Kenward 1987, Jacob and Rudran, 2006, Ouellette and Cardille 2011). For aquatic chelonians, the LHR method is commonly used to represent space utilization, particularly in Amazonia due to the linear and dendritic characteristics of water bodies (Morales-Verdeja and Vogt 1997, Fachín-Terán *et al.* 2006, Bernhard 2010, De la Ossa and Vogt 2011). In this study, there was no difference among the estimators. While the MCP method represented space use for most individuals, it failed to detect their use of river or lake environments, information revealed by the KDE and AKDE methods. Both KDE and AKDE methods better represented environmental use, particularly when individuals exhibited distinct and long-distance movement. As a movement-based method, AKDE effectively delineated core areas, useful for identifying critical shelter or feeding sites (Jacob and Rudran 2006). It was evident that employing multiple techniques to estimate space use is beneficial for understanding movement patterns. It is worth noting, however, that young individuals have not yet established their home ranges (Cagle 1944, Stickel 1950, Famelli 2013), which aligns with their learning behaviors observed in our study, especially linked to the reproductive and nesting season. This can also explain the absence of correlation between home range size and body size and the lack of difference among the estimators. We did not observe differences between adults and young females. This may happen due to the small sampling sizes of fixes of adult females and due to most of the monitoring happening during the nesting period when adult females are engaged in aggregations and nesting activities. Adult females of *P. expansa* have been documented traveling distances exceeding 45 km within a mere 48 hours (Moreira and Vogt 1990) or a maximum range of 352.9 m/day at the Xingu River (Carneiro and Pezzuti 2015), which surpasses the total distance covered by most of the monitored chelonians in this study.

According to Mogollones *et al*. (2010), protecting juveniles and adult turtles is the primary conservation action that could reverse a population decline. Understanding the needs of young female turtles is crucial for developing effective management and conservation strategies. Besides being heavily exploited for commercial purposes, *P. expansa* is at risk from the large-scale loss of natural habitats due to dam construction and climate change, which disrupts the flood pulse of rivers and lakes, with severe consequences for reproductive success and population sustainability (Castello and Macedo 2016, Eisemberg *et al.* 2016, Fagundes *et al.* 2018, Silva 2023). Caldas *et al*. (2023) indicated that key rivers for *P. expansa* have been fragmented because of dam construction, including those on the Xingu, Tocantins, and Araguaia Rivers. Another study employing distribution models for *P. expansa* revealed that it ranks as the fourth most impacted Amazonian turtle species by deforestation, primarily due to the potential loss of habitat along its distribution (Fagundes *et al.* 2018). Currently, *P. expansa* is in the process of being categorized as Endangered by the IUCN Red List of Threatened Species (C. R. Ferrara *et al.* pers. obs.). Knowledge about the social interactions between young adults and how they learn their behaviors is limited. Our study is the first to track young females of *Podocnemis expansa* and to suggest their potential social interactions with adults. We recommend the integration of long-term radio-tracking and satellite telemetry—either independently or in combination, as suggested by Guilhon *et al*. (2011)—alongside vocalization studies, to gain a deeper understanding of these interactions within their natural habitat. Satellite telemetry can also offer valuable insights into long-distance movements, spatial overlap between adults and subadults, and patterns of habitat use across different size classes and sexes. We recommend its implementation to improve our understanding of movement ecology and inform more effective conservation strategies. This information is vital for informing conservation and management strategies and to safeguard the studied species, particularly as environmental and climatic changes are expected to escalate (Oliveira *et al.* 2021, Marmontel *et al.* 2024).

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References

Alho, C. J. R. and L. F. M. Pádua. 1982a. Reproductive parameters and behavior of the Amazon turtle *Podocnemis expansa* (Testudinata, Pelomedusidae) in Brazil. *Canadian Journal of Zoology 60:* 97–103.

Alho, C. J. R. and L. F. M. Pádua. 1982b. Sincronia entre o regime de vazante do rio e o comportamento de nidificação da tartaruga da Amazônia *Podocnemis expansa* (Testudinata: Pelomedusidae). *Acta Amazonica 12:* 323–326.

Almeida, S. S., P. G. Sá, and A. Garcia. 1986. Vegetais utilizados como alimento por *Podocnemis* (Chelonia) na região do baixo rio Xíngú (Brasil-Pará). *Boletim do Museu Paraense Emílio Goeldi-Botânica 2:* 199–211.

Alzate-Estrada, D. A., V. P. Paez, V. M. Cartagena-Otálvaro, and B. C. BocK. 2020. Linear home range and seasonal movements of *Podocnemis lewyana* in the Magdalena River, Colombia. *Copeia 108:* 29–38.

Andrade, P. C. M., P. H. G. Oliveira, A. C. Lima, J. A. Mota Duarte, S. H. Silva Azevedo, A. B. Oliveira, C. D. Almeida, E. B. Silva, J. R. Garcez, J. R. Silva Pinto, L. C. N. Silva, M. S. Monteiro, W. Silva Rodrigues, T. L. Anízio, A. L. B. Pontes, R. L. Teixeira, J. M. Silva, W. L. P. Duncan, and R. C. Vogt. 2022. Community-based conservation and management of chelonians in the amazon. *Frontiers in Ecology and Evolution 10:* 1–24.

Armond, F. N. 2008. Aspectos sanitários e do parasitismo em *Podocnemis expansa* (Tartaruga-da-Amazônia) de ambiente natural e criatório comercial no Estado do Tocantins. Unplubl. Ph.D. Thesis. Fundação Universidade Federal do Tocantins, Brazil.

Arraut. E. M., M. Marmontel, J. E. Mantovani, E. M. L. M. Novo, D. W. Macdonald, and R. E. Kenward. 2009. The lesser of two evils: seasonal migrations of Amazonian manatees in the Western Amazon. *Journal of Zoology 280:* 247–256.

Balensiefer, D. C. and R. C. Vogt. 2006. Diet of *Podocnemis unifilis* (Testudines, Podocnemididae) during the dry season in Mamirauá sustainable development reserve, Amazonas, Brazil. *Chelonian Conservation and Biology 5:* 312–317.

Bates, H. W. 1863. *The Naturalist on the River Amazon*. London. John Murray. 407 pp.

Bernhard, R. 2010. Dinâmica populacional de *Podocnemis erythrocephala* no rio Ayuana, Amazonas, Brasil. Unpubl. Ph. D. Thesis. Instituto Nacional de Pesquisas da Amazônia, Brazil.

Bittencourt, M. M and S. A. Amadio. 2007. Proposta para identificação rápida dos períodos hidrológicos em áreas de várzea do rio Solimões-Amazonas nas proximidades de Manaus. *Acta Amazonica 3:* 303–308.

Cagle, F. R. 1939. A system of marking turtles for future identification. *Copeia 1939:* 170–173.

Cagle, F. R. 1944. Home range, homing behavior, and migration in turtles. *Museum of Zoology, University of Michigan, Miscellaneous Publications 1:* 1–34.

Caldas, B., M. L. Thieme, N. Shahbol, M. E. Coelho, G. Grill, P. A. Van Damme, R. Aranha, C. Cañas, C. K. Fagundes, N. Franco-León, E. E. Herrera-Collazos, C. Jézéquel, M. Montoya, F. Mosquera-Guerra, M. Oliveira-da-Costa, M. Paschoalini, P. Petry, T. Oberdorff, F. Trujillo, P. A. Tedesco, and M. C. L. Brito Ribeiro. 2023. Identifying the current and future status of freshwater connectivity corridors in the Amazon Basin. *Conservation Science and Practice 5:* 1–21.

Calenge, C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modeling 197:* 516–519.

Cantarelli, V. H. 2006. Alometria reprodutiva da tartaruga-da-amazônia (*Podocnemis expansa*): bases biológicas para o manejo. Unpubl. Ph.D. Thesis. Universidade de São Paulo, Escola Superior de Agricultura Luiz de Queiroz, Brazil.

Cantarelli, V. H., A. Malvasio, and L. M. Verdade. 2014. Brazil’s *Podocnemis expansa* conservation program: retrospective and future directions. *Chelonian Conservation and Biology 13:* 124–128.

Carneiro, C. C. 2017. Ecologia e conservação de *Podocnemis expansa* (Testudines, Podocnemididae). Unpubl. Ph.D. Thesis. Universidade Federal do Pará, Brazil.

Carneiro, C. C. and J. Pezzuti. 2015. *Podocnemis expansa* (Giant Amazon River Turtle). Post reproductive migration. *Herpetological Review 46:* 244–245.

Castelblanco-Martinez, D. N., R. C. Vogt, and G. N. Klein. 2006. Resultados preliminares do estudo de telemetria de tartaruga da Amazônia (*Podocnemis expansa*) na REBIO do Rio Trombetas, Pará. *VII Congreso Internacional sobre Manejo de Fauna Silvestre en la Amazonía y Latinamérica*, Ilhéus.

Castello, L. and M. N. Macedo. 2016. Large-scale degradation of Amazonian freshwater ecosystems. *Global Change Biology 22:* 990–1007.

Crane, M., I. Silva, B. M. Marshall, and C. T. Strine. 2021. Lots of movement, little progress: a review of reptile home range literature. *PeerJ 9:* e11742.

Cueva, R., A. Naveda-Rodríguez, and G. Zapata. 2018. *Podocnemis unifilis* (Yellow-Spotted River Turtle). Juvenile movement. *Herpetological Review 49:* 323.

Cunha, F. L. R., R. Bernhard, and R. C. Vogt. 2020. Diet of an assemblage of four species of turtles (*Podocnemis*) in the Rio Uatumã, Amazonas, Brazil. *Copeia 108:* 103–115.

De la Ossa, J. L. V. and R. C. Vogt. 2011. Ecologia populacional de *Peltocephalus dumerilianus* (Testudines, Podocnemididae) em dois tributários do Rio Negro, Amazonas, Brasil. *Interciencia 36:* 53–58.

Eisemberg, C. C., R. A. M. Balestra, S. Famelli, F. F. Pereira, V. C. D. Bernardes, and R. C. Vogt. 2016. Vulnerability of Giant South American Turtle (*Podocnemis expansa*) nesting habitat to climate-change-induced alterations to fluvial cycles. *Tropical Conservation Science Journal 9:* 1–12.

Enríquez-Mercado, I., T. G. Butterfield, R. Aguilar-Romero, and R. M. Rios. 2024. Home range of three turtle species in Central Yucatan. A comparative study. *BMC Ecology and Evolution 24:* 1–11.

Ernst, C. H. and R. W. Barbour. 1989. *Turtles of the World*. Washington. D. C. Smithsonian Institution Press. 313 pp.

ESRI. 2016. ArcGIS 10.5, Redlands, CA.

Fachín-Téran, A., R. C. Vogt., and M. F. S. Gomez. 1995. Food habitats of an assemblage of five species of turtles in the Rio Guapore, Rondônia, Brazil. *Journal of Herpetology 29:* 536–547.

Fachín-Téran, A., R. C. Vogt, and J. B. Thorbjarnarson. 2006. Seasonal movements of *Podocnemis sextuberculata* (Testudines, Podocnemididae) in the Mamiraua Sustainable Development Reserve, Amazonas, Brazil. *Chelonian Conservation and Biology 5:* 18–24.

Fagundes, C. K., R. C. Vogt, R. A. Souza, P. de Marco Jr. 2018. Vulnerability of turtles to deforestation in the Brazilian Amazon: Indicating priority areas for conservation. *Biological Conservation 226:* 300–310.

Famelli, S. 2013. Área de vida, movimentação e seleção de habitat do cágado *Hydromedusa maximiliani* (Testudine: Chelidae) no Parque Estadual Carlos Botelho, SP. Unpubl. Ph.D. Thesis. Escola Superior de Agricultura Luiz de Queiroz, Universidade de São Paulo, Brazil.

Famelli, S., F. L. Souza, A. Georges, and J. Bertoluci. 2016. Movement patterns and activity of the Brazilian snake-necked turtle *Hydromedusa maximiliani* (Testudines: Chelidae) in southeastern Brazil. *Amphibia-Reptilia 37:* 215–228.

Famelli, S., B. Gruber, A. Georges, C. Ortiz, F. L. Souza, and J. Bertoluci. 2025. Space use and home range size of the freshwater turtle *Hydromedusa maximiliani* (Testudines: Chelidae) in Southeastern Brazil. *Herpetological Conservation and Biology 20:* 67–81.

Ferrara, C. R. 2012. Comunicação acústica de tartaruga-da amazônia (*Podocnemis expansa* Schweigger, 1812), Testudines: Podocnemididade) na Reserva Biológica do Rio Trombetas, Pará, Brasil. Unpubl. Ph.D. Thesis. Instituto Nacional de Pesquisa da Amazônia, Brazil.

Ferrara, C. R., L. Schneider, and R. C. Vogt. 2010. *Podocnemis expansa* (Giant South American River Turtle). Basking before the nesting season. *Herpetological Review 41:* 72–73

Ferrara, C. R., R. C. Vogt, and R. S. Sousa-Lima. 2013. Turtle vocalizations as the first evidence of posthatching parental care in chelonians. *Journal of Comparative Psychology 127:* 24–32.

Ferrara, C. R., C. K. Fagundes, T. Morcatty, and R. C. Vogt. 2017. *Quelônios Amazônicos: Guia de identificação e distribuição*. Manaus. Wildlife Conservation Society. 180 pp.

Ferrara, C. R., R. C. Vogt, R. Sousa-Lima, B. M. R. Tardio, and V. C. D. Bernardes. 2014. Sound communication and social behavior in an Amazonian river turtle (*Podocnemis expansa*). *Herpetologica 70:* 149–156.

Fleming, C. H., W. F. Fagan, T. Mueller, K. A. Olson, P. Leimgruber, and J. M. Calabrese. 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology 96:* 1182–1188.

Fonseca, R. A. 2022. Ecologia e conservação de *Podocnemis expansa* (Testudines, Podocnemididae) no médio Rio Tapajós, Brasil. Unpubl. Ph.D. Thesis. Universidade Federal do Oeste do Pará, Brazil.

Forero-Medina, G., C. R. Ferrara, R. C. Vogt, C. K. Fagundes, R. A. Balestra, P. C. Andrade, R. Lacava, R. Benhard, A. J. Lipman, A. J. Lenz, A. Ferrer, A. Calle, A. F. Aponte, B. R. Calle-Réndon, C. S. Camilo, E. Perrone, E. Miraña, F. A. G Cunha, E. Loja, J. Del Rio, J. L. V. Fernandez, O. E. Hermández, R. Del Aguila, R. Pino, R. Cueva, S. Martinez, V. C. D. Bernardes, L. Sainz, and B. Horne. 2019. On the future of the giant South America river turtle *Podocnemis expansa*. *Oryx 55:* 73–80.

Freeman, A. B., C. Eisemberg, and H. Stoetzel. 2018. Habitat use and movements in an upland population of Johnstone River Snapping Turtles, *Elseya irwini*. *Herpetological Conservation and Biology 13:* 464–472.

Guilhon, A. V., R. Vogt, L. Schneider, C. R. Ferrara. 2011. Assessment of turtle tracking technologies in the Brazilian Amazon. *Herpetological Review 42:* 525–530.

Harestad, A. S. and F. L. Bunnel. 1979. Home range and body weight: a reevaluation. *Ecology 60:* 389-402.

Hernandez, O., I. Narvaiza, and R. Espín. 1998. Zoocriadero de tortuga del Orinoco (*Podocnemis expansa*) con fines de reforzamiento de poblaciones silvestres. Pp. 69–75 *in* J. López and I. Saavedra y M. Dubois (eds.), *El Río Orinoco: Aprovechamiento Sustentable. Memorias de las Primeras Jornadas de Investigación Sobre el Río Orinoco*. Caracas, Venezuela. Universidad Central de Venezuela, Instituto de Mecánica de Fluidos.

Hinderaker, S. E. 2021. Spatio-temporal ecology of Amazonian freshwater turtle. Unpubl. M.Sc. Dissertation. Faculty of Environmental Science and Natural Resource Management, Norges miljø-og biovitenskapelige University, Norwegian.

Hoeinghaus, D. J., C. A. Layman, D. A. Arrington, and K. O. Winemiller. 2003. Movement of *Cichla* species (Cichlidae) in a Venezuelan floodplain river. *Neotropical Ichthyology 1:* 121–126.

Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges. *Ecology 88:* 2354–2363.

Horne, J. S., J. Fieberg, L. Börger, J. L. Rachlow, J. M. Calabrese, and C. H. Fleming. 2019. Animal home ranges: concepts, uses, and estimation. Pp. 315–322 *in* D. L. Murray and B. K. Sandercock (eds.), *Population Ecology in Practice*. Hoboken. John Wiley & Sons.

Hussey, N. E., S. T. Kessel, P. D. Cowley, A. T. Fisk, R. G. Harcout, K. N. Holland, S. J. Iverson, J. F. Kocik, J. E. Flemming, and F. G. Whoriskey. 2015. Aquatic animal telemetry: a panoramic window into the underwater world. *Science 348:* 1255642.

IBAMA. 1989. Projeto Quelônios da Amazônia 10 anos. Brasília: Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis-IBAMA.

IBAMA and STCP: Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) and STCP Engenharia de Projetos Ltda (STCP). 2004. Plano de manejo da Reserva Biológica do Rio Trombetas. Available at http://www.ibama.gov.br/REBIOtrombetas/index.php?id_menu=16. Accessed on 20 July 2024.

Jacob, A. A. and R. Rudran. 2006. Radiotelemetria em estudos populacionais. Pp. 285–342 i*n* Cullen, L. Jr. and C. Valadares-Pádua (eds.), *Biologia da Conservação e Manejo da Vida Silvestre*. Curitiba. Universidade Federal do Paraná.

Jorgewich-Cohen, G., M. Wheatley, L. P. Gaspar, and P. Praschag. 2024. Prehatch calls and coordinated birth in turtles. *Ecology and Evolution 14:* 1–13.

Junk, W. J. 1984. Ecology of the varzea, floodplain of Amazonian whitewater rivers. Pp. 215–243 *in* S. Harold (ed.), *The Amazon: Limnology and Landscape Ecology of a Mighty Tropical River and its Basin*. Hingham. Dr. Junk Publishers.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Pp. 110–117 *in* D. P. Dodge (ed.), *Proceedings of the International Large River Symposium*. Ottawa, Ontario, Canada. Canadian Special Publications in Fisheries and Aquatic Sciences.

Kenward, R. 1987. *Wildlife Radio Tagging: Equipment, Field Techniques and Data Analysis*. San Diego. Academic Press. 221 pp.

Lacava, R. V., D. C. Carvalho, J. C. B. Pezzuti, L. C. F. Silva, P. S. Miorando, and R. A. Fernandes. 2024. Recovery of the Giant South American River Turtle in four decades of a network-based conservation program in the Brazilian Amazon. *Biodiversity and Conservation 34:* 283–297.

Leão, S. P., S. Famelli, and R. C. Vogt. 2019. Home range of Yellow-Spotted Amazon River Turtles (*Podocnemis unifilis*) (Testudines: Podocnemididae) in the Trombetas River Biological Reserve, Pará, Brazil. *Chelonian Conservation and Biology 18:* 10–18.

Leite, R. U. 2010. Composição, distribuição, utilização de ambientes e variação sazonal na densidade de quelônios aquáticos do Lago Verde, Alter do Chão, Pará, Brasil. Unpubl. M.Sc. Dissertation. Museu Paraense Emílio Goeldi, Universidade Federal do Pará, Brazil.

Magnusson, W. E., A. C. Lima, V. L. Costa, and R. C. Vogt. 1997. Home range of the turtle *Phrynops rufipes* in an isolated reserve in Central Amazônia, Brazil. *Chelonian Conservation and Biology 2:* 494–498.

Malvasio, A., A. M. Souza, F. B. Molina, and F. A. Sampaio. 2003. Comportamento e preferência alimentar em *Podocnemis expansa* (Schweigger), *P. unifilis* (Troschel) e *P. sextuberculata* (Cornalia) em cativeiro (Testudines, *Pelomedusidae*). *Revista Brasileira de Zoologia 20:* 161–168.

Marmontel, M., A. Fleischmann, A. L. Val, and B. Forsberg. 2024. Safeguard Amazon's aquatic fauna against climate change. *Nature 625:* 450–450.

Martin, A. R., V. M. F. Silva, and D. L. Salmon. 2004. Riverine habitat preferences of botos (*Inia geoffrensis*) and tucuxis (*Sotalia fluviatilis*) in the central Amazon. *Marine Mammal Science 20:* 189–200.

Miorando, P. S., G. H. Rebêlo, M. T. Pignati, and J. C. B. Pezzuti. 2013. Effects of community-based management on Amazon river turtles: a case study of *Podocnemis sextuberculata* in the Lower Amazon Floodplain, Pará, Brazil. *Chelonian Conservation and Biology 12:* 143–150.

Mogollones, S. C., D. Rodríguez, O. Hernández, and G. R. Barreto. 2010. A demographic study of the Arrau turtle (*Podocnemis expansa*) in the Middle Orinoco River, Venezuela. *Chelonian Conservation and Biology 9:* 79–89.

Morales-Verdeja, S. A. and R. C. Vogt. 1997. Terrestrial movementes in relation to estivation and the annual reproductive cycle of *Kinosternon leucostomum. Copeia 1997:* 123–130.

Moreira, G. and R. C. Vogt. 1990. Movements of *Podocnemis expansa* before and after nesting in the Trombetas River, Brazil. *38th Annual Meeting Herpetologists League and the 33rd Annual Meeting of the Society for the Study of Amphibians and Reptiles*. New Orleans. 79 pp.

Naveda-Rodrigues, A., R. Cueva, and G. Z. Rios. 2018. Space use of yellow-spotted river turtle (*Podocnemis unifilis*) in Yasuni National Park, Ecuador. *Chelonian Conservation and Biology 17:* 37–43.

Nieto-Vera, M. T. N. 2024. Área de acción y variación estacional en los movimientos de hembras de *Podocnemis expansa* (Schweigger, 1812) en el medio río Meta Orinoquia colombiana. Unpubl. M.Sc. Dissertation. Universidad Nacional de Colombia, Colombia.

Oliveira, B. F. A., M. J. Bottino, P. Nobre, and C. A. Nobre. 2021. Deforestation and climate change are projected to increase heat stress risk in the Brazilian Amazon. *Communications Earth & Environment 2:* 207.

Ouellette, M. and J. A. Cardille. 2011. The complex linear home range estimator: representing the home range of river turtles moving in multiple channels. *Chelonian Conservation and Biology 10:* 259–265.

Perrone, E. L., M. M. Souza, F. S. Rodrigues, N. G. D. Castro, V. C. D. Bernardes, S. P. Leão, G. M. Costa, M. A. Lima, C. R. Ferrara, R. A. Souza, and R. C. Vogt. 2014. *Podocnemis sextuberculata* (Six-tubercled Amazon River Turtle). Movements. *Herpetological Review 45:* 486–487.

Pezzuti, J. C. B., G. H. Rebelo, D. F. Silva, J. P. Lima, and M. C. Ribeiro. 2004. A caça e a pesca no Parque

Nacional do Jaú. Pp. 213–230 *in* S. H. Borges, S. Iwanaga, C. C. Durigan, and M. R. Pinheiro (eds.), *Janelas para a Biodiversidade no Parque Nacional do Jaú: Uma Estratégia para o Estudo da Biodiversidade na Amazônia*. Manaus, Amazonas. Fundação Vitória Amazônica.

Portelinha, T. C. G., A. Malvasio, C. I. Piña, and J. Bertoluci. 2013. Reproductive allometry of *Podocnemis expansa* (Testudines: Podocnemididae) in southern Brazilian Amazon. *Journal of Herpetology 47:* 232–236.

Portelinha, T. C. G., A. Malvasio, C. I. Piña., and J. Bertoluci. 2014. Population structure of *Podocnemis expansa* (Testudines: Podocnemididae) in southern Brazilian Amazon. *Copeia 2014:* 707–715.

Pritchard, P. C. H. and P. Trebbau. 1984. *The Turtles of Venezuela*. Ohio. SSAR. 403 pp.

R Development Core Team. 2023. A language and environment for statistical computing. R Foundation for Statistical Computing. Version 4.3.0. Viena, Austria.

Rebelo, G. H. 2002. Quelônios, jacarés e ribeirinhos no Parque Nacional do Jaú (AM). Unpubl. Ph.D. Thesis. Instituto de Biologia, Universidade Estadual de Campinas, Brazil.

Ribeiro, M. V., R. L. Silva, A. S. Cruz, A. Malvasio, M. Solé, E. A. P. Santos, and A. Schiavetti. 2024. Telemetry in movement ecology of aquatic and semi-aquatic turtles in world freshwater ecoregions: a systematic review. *Ethology Ecology & Evolution 36:* 463–489.

Rueda-Almonacid, J. V., J. L. Carr, R. A. Mittermeier, J. V. Rodrıguez-Mahecha, R. B. Mast, R. C. Vogt, A. G. J. Rhodin, J. DelaOssa, J. N. Rueda, and C. G. Mittermeier**.** 2007. *Las Tortugas y los Cocodrilianos de los Países Andinos del Trópico*. Bogotá. Editorial Panamericana, Formas e Impresos. 274 pp.

Silva, I. B. 2023. O futuro dos quelônios amazônicos no contexto das mudanças climáticas. Unpubl. M.Sc. Dissertation. Universidade Federal do Pará e Museu Paraense Emílio Goeldi, Brazil.

Silva, L. C. N., C. R. Ferrara, C. K. Fagundes, and T. Morcatty. 2017. *Podocnemis expansa* (Giant South American River Turtle). Juvenile movement. *Herpetological Review 48:* 622–623.

Silveira, R., J. V. Amaral, W. E. Magnusson, and J. B. Thorbjarnarson. 2011. *Melanosuchus niger* (Black Caiman): Long distance movement. *Herpetological Review 42:* 424–425.

Silveira, R., E. E. Ramalho, J. B. Thorbjarnarson, and W. E. Magnusson. 2010. Depredation by jaguars on caimans and importance of reptiles in the diet of jaguar. *Journal of Herpetology 44:* 418–424.

Simoncini, M. S., H. C. Sousa, T. C. G. Portelinha, G. B. Falcon, E. Collicchio, R. A. M. Balestra, V. L. F. Luz, G. R. Colli, and A. Malvasio. 2022. Hydrological effects on the reproduction of the Giant South American River Turtle *Podocnemis expansa* (Testudines: Podocnemididae). *Ichthyology & Herpetology 110:* 547–560.

Smith, N. J. H. 1979. Aquatic turtles of Amazonia: an endangered resource. *Biological Conservation 16:* 165–179.

Stickel, L. F. 1950. Populations and home range relationships of the box turtle, *Terrapene c. carolina* (Linnaeus). *Ecological Monographs 20:* 351–378.

Swihart, R. K. and N. A. Slade. 1985. Influence of sampling interval on estimates of home-range size. *Journal of Wildlife Management 49:* 1019–1025.

Vogt, R. C. 2008. *Tartarugas da Amazônia*. Lima. Wust Ediciones. 104 pp.

von Hildebrand, P., N. Bermudez, and M.C. Penuela. 1997. *La Tortuga Charapa (*Podocnemis expansa*) en el* Rıo *Caquetá*, Amazonas *Colombia: Aspectos de la Biología Reproductiva y Técnicas para su Manejo.* Santa Fé de Bogota. Disloque Editores, 152 pp.

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