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FROM GLOBAL FRESHWATER TURTLE TELEMETRY TO LOCAL CONSERVATION: THE SPATIAL ECOLOGY OF *PODOCNEMIS UNIFILIS* IN THE MIDDLE XINGU RIVER

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Tese apresentada ao Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade da Universidade Estadual de Santa Cruz requisito para obtenção do grau de Doutor em Ecologia e Conservação da Biodiversidade. Área de concentração: Ecologia e Conservação de Populações.

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“Fazer conservação sem dados de movimentação é como navegar sem um mapa”

Walter Jetz

SUMÁRIO

FROM GLOBAL FRESHWATER TURTLE TELEMETRY TO LOCAL CONSERVATION: THE SPATIAL ECOLOGY OF *PODOCNEMIS UNIFILIS* IN THE MIDDLE XINGU RIVER

ABSTRACT

Freshwater turtles are among the most threatened vertebrates globally, and understanding their spatial ecology is essential for conservation, especially in river systems affected by hydrological alteration. In this context, the objectives of this Thesis were to: (i) identify global trends, gaps, and methodological approaches in telemetry-based studies of freshwater turtles; (ii) investigate seasonal movement patterns, directional orientation, and space use of *Podocnemis unifilis* in a dam-regulated Amazonian river; and (iii) estimate home range areas using multiple methods to evaluate spatial responses to altered hydrology in the Xingu River basin. In Chapter I, we have conducted a systematic review of telemetry studies on freshwater turtles worldwide, analyzing 104 articles published from 1980 to 2022 using the PRISMA protocol. Our findings showed an increase in studies in recent decades, with radiotelemetry being the most widely used method and home range estimation the most common objective. Despite progress, most studies were conducted in anthropogenic landscapes and only a small proportion focused on threatened species, highlighting critical research gaps in tropical regions and conservation priorities. In Chapter II, we have used satellite telemetry to monitor 32 adult *P. unifilis* in three longitudinal sectors of the middle Xingu River between 2017 and 2022. We have assessed movement metrics, azimuthal orientation, and habitat use across hydrological seasons. Results revealed that females traveled longer distances than males, although no significant sex or seasonal differences were detected. Directional analyses did not show alignment toward nesting beaches. However, spatial behavior varied seasonally, with localized movements and site fidelity during low-water periods and broader space use during floods, especially in upstream and midstream areas. These findings suggest that hydrological connectivity drives spatial dispersal. In Chapter III, we have estimated home range sizes using five spatial methods (MCP, KDE, AKDE, LoCoH, dBBMM). Home range size varied greatly among individuals but showed no consistent effect of sex or season. However, turtles in the upstream reservoir had larger home ranges, while those in the midstream sector (Volta Grande) showed restricted movements. These results highlight the species spatial plasticity but also its vulnerability to habitat fragmentation caused by flow regulation.

Keywords: freshwater turtles, *Podocnemis unifilis*, movement ecology, satellite telemetry, home range, Amazon, dam impacts.

RESUMO

Os quelônios de água doce estão entre os vertebrados mais ameaçados globalmente, e compreender sua ecologia espacial é essencial para a conservação, especialmente em sistemas fluviais impactados por alterações hidrológicas. Neste contexto, os objetivos desta Tese foram: (i) identificar tendências globais, lacunas e abordagens metodológicas em estudos com telemetria aplicados a quelônios de água doce; (ii) investigar os padrões sazonais de movimentação, orientação direcional e uso do espaço de *Podocnemis unifilis* em um rio amazônico regulado por barragem; e (iii) estimar áreas de vida utilizando múltiplos métodos para avaliar as respostas espaciais da espécie frente às alterações hidrológicas na bacia do rio Xingu. No Capítulo I, realizamos uma revisão sistemática de estudos com telemetria em quelônios de água doce publicados entre 1980 e 2022, seguindo o protocolo PRISMA. Os resultados revelaram um aumento no número de estudos nas últimas décadas, com predominância da radiotelemetria e foco na estimativa de área de vida. Apesar dos avanços, a maioria dos estudos foi conduzida em paisagens antropizadas e apenas uma pequena proporção focou em espécies ameaçadas, evidenciando lacunas críticas em regiões tropicais e prioridades conservacionistas. No Capítulo II, utilizamos telemetria via satélite para monitorar 32 indivíduos adultos de *P. unifilis* em três setores longitudinais do médio rio Xingu entre 2017 e 2022. Analisamos métricas de deslocamento, orientação azimutal e uso do habitat ao longo das estações hidrológicas. As fêmeas percorreram distâncias maiores que os machos, embora sem diferenças estatísticas significativas. As análises direcionais não revelaram orientação em direção às praias de desova. No entanto, o comportamento espacial variou sazonalmente, com movimentos localizados e fidelidade espacial na seca, e expansão do uso do espaço nas cheias, ainda que de maneira não significativa, especialmente nos setores montante e intermediário, sugerindo que a conectividade hidrológica é um fator determinante para a dispersão espacial. No Capítulo III, estimamos as áreas de vida por cinco métodos espaciais (MCP, KDE, AKDE, LoCoH, dBBMM). As áreas variaram amplamente entre os indivíduos, sem efeito significativo de sexo ou estação. Contudo, os indivíduos no reservatório montante apresentaram maiores áreas de vida, enquanto aqueles na Volta Grande mostraram movimentação restrita. Esses resultados evidenciam a plasticidade espacial da espécie, mas também sua vulnerabilidade à fragmentação do habitat imposta pela regulação do fluxo.

Palavras-chave: quelônios de água doce, *Podocnemis unifilis*, ecologia de movimento, telemetria via satélite, área de vida, Amazônia, impactos de barragens

INTRODUÇÃO GERAL

A conservação de quelônios de água doce enfrenta desafios globais, dado que muitas espécies sofrem declínios populacionais acentuados e estão ameaçadas pela caça, perda de habitat e outras pressões antrópicas (Tortoise, & Freshwater Turtle Specialist Group, 1989, Buhlmann *et al*., 2008; Stanford *et al*., 2020; Barcenas-Garcia *et al*., 2022). Compreender a ecologia espacial desses animais, isto é, como se movimentam, utilizam habitats e distribuem suas atividades, é fundamental para embasar estratégias de manejo eficazes e direcionados (Allen *et al*., 2016; Ogbun *et al*., 2017; Fletcher & Fortin, 2018). Nesse contexto, a telemetria se apresenta como uma ferramenta valiosa, permitindo o acompanhamento remoto dos deslocamentos de animais em tempo real ou quase real (Mayo-Wells, 1963; Pride & Schift, 1992; Kimley, 2013; Cooke *et al*., 2013; Hussey *et al*., 2015; Lennox *et al*., 2017). Em relação a aplicação da telemetria para estudos com quelônios de água doce, observa-se uma tendência de crescimento significativo, como evidenciado em Ribeiro *et al*., 2024. No entanto, evidencia-se também a necessidade de expandir os estudos de movimentação, especialmente para espécies sob maior risco.

Na Amazônia, um dos grupos de quelônios de água doce de destaque é a família Podocnemididae, que inclui grandes espécies fluviais (Gaffney *et al*., 2011). *Podocnemis unifilis*, conhecida como tracajá, é uma espécie de médio porte amplamente distribuída na América do Sul ocorrendo no Brasil e países vizinhos (Vogt, 2008; Ferrara *et al*., 2017). Embora amplamente distribuído, o tracajá tem sofrido declínios populacionais severos em diversas regiões. Entre as principais ameaças estão a sobre-exploração para consumo (carne e ovos) e comércio ilegal (Alho, 1985; Rebello and Pezzutti, 2000; Fachín-Terán *et al*., 2004; Pezzutti *et al*., 2010), a perda e degradação de habitats (Conway-Gómez, 2007), inclusive pela construção de hidrelétricas (Barcenas-Garcia *et al*., 2022a, 2022b), poluição (como contaminação por mercúrio; Souza-Araujo *et al*., 2015; Pignati *et al*., 2018) e mudanças climáticas (Da Silva *et al*., 2025). Devido à sua longevidade e maturação tardia, *P. unifilis* é particularmente vulnerável a essas pressões, sendo classificada como espécie Vulnerável nas listas de conservação nacionais e internacionais (MMA, 2022; IUCN, 2024).

Apesar de sua importância, o conhecimento científico sobre a ecologia espacial do tracajá ainda é incipiente. Historicamente, poucos estudos buscaram avaliar os padrões de movimento de espécies de Podocnemididae, e a maioria concentrou-se na tartaruga-da-amazônia (*Podocnemis expansa*) usando radiotransmissores VHF somente mais recentemente, quando tecnologias como rastreamento por satélite começaram a ser aplicadas a quelônios amazônicos (Guilhon *et al*., 2011). No caso específico de *P. unifilis*, o conhecimento sobre seus padrões de movimentação permanece limitado a poucos estudos (e.g. Naveda-Rodrigues *et al*., 2018; Ponce de Leão *et al*., 2019; Hilderaker, 2021). Sabe-se que no regime natural de rios amazônicos, as variações sazonais do nível da água exercem forte influência no comportamento espacial desses quelônios (Naveda-Rodrigues *et al*., 2018; Ponce de Leão *et al*., 2019). Entretanto, não existiam estudos específicos sobre os movimentos de *P. unifilis* no rio Xingu até recentemente. Essa lacuna é preocupante, pois o rio Xingu representa um habitat com alta biodiversidade e vem passando por rápidas transformações ambientais nos últimos anos (Fearnside, 2015).

A presente pesquisa buscou integrar o conhecimento global sobre telemetria em quelônios de água doce com uma aplicação local voltada à conservação do tracajá no médio Xingu. Para isso, esta Tese foi estruturada em três capítulos que se complementam. No **Capítulo 1**, realizamos uma revisão sistemática global sobre o uso de telemetria em quelônios de água doce, mapeando as tendências, principais abordagens e lacunas nesse campo. Esse capítulo preenche a necessidade de uma síntese abrangente da literatura, revelando, por exemplo, quais regiões e espécies foram mais estudadas e quais permanecem negligenciadas. No **Capítulo 2**, nos concentramos na ecologia de movimento do tracajá no médio rio Xingu, por meio de um estudo de telemetria de campo. Neste capítulo investigamos as distâncias percorridas, a direcionalidade dos deslocamentos e diferenças sazonais e entre sexos no padrão de movimentação da espécie. Essa investigação local atende à lacuna de informação sobre como *P. unifilis* se comporta espacialmente em um trecho específico da Amazônia (até então inédito na literatura). No **Capítulo 3**, por fim, realizamos uma análise detalhada da área de vida (*home *range*) de *P. unifilis* no médio Xingu, utilizando dados de telemetria por satélite em um contexto ambiental fragmentado.

Em conjunto, os três capítulos fornecem uma visão escalonada do global ao local. A revisão global identificou lacunas e reforçou a importância da telemetria para a conservação de quelônios, justificando a realização de estudos locais em espécies e áreas pouco exploradas. O estudo no Xingu gerou dados ecológicos inéditos sobre os movimentos sazonais do tracajá, enquanto a análise de área de vida ofereceu insights aplicados para o manejo da espécie em rios sob impacto de barragens. Ao integrar esses resultados, esta Tese contribui para preencher as lacunas de conhecimento sobre a ecologia espacial do *P. unifilis*, fornecendo bases científicas para ações de conservação mais eficazes, tanto no âmbito regional (bacia do Xingu) quanto em um contexto amazônico mais amplo.

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CAPÍTULO 1

TELEMETRY IN MOVEMENT ECOLOGY OF AQUATIC AND SEMI-AQUATIC TURTLES IN WORLD FRESHWATER ECOREGIONS: A SYSTEMATIC REVIEW

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Telemetry in movement ecology of aquatic and semi-aquatic turtles in world freshwater ecoregions: a systematic review

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The study focused on advancing techniques for understanding freshwater turtle movement, aiding decision-making and management strategies against various threats. The systematic review, using the PRISMA protocol, identified 104 articles from 1980 to 2022, with a notable recent increase. Radiotelemetry was the predominant technique in tracking turtle movement, and the evaluation of species' home range was the most recurrent study type. The research covered 33 freshwater ecoregions, with a concentration in anthropized areas. Notably, only 16.2% of all endangered freshwater turtle species and 11.4% threatened by international trade were studied. Despite this, there's a growing trend toward conservation efforts. The study underscores the importance of telemetry as a vital tool for understanding and conserving freshwater turtle ecology, revealing trends and gaps in research.

ABSTRACT

The improvement of techniques and analyses to understand the movement of freshwater turtles has helped managers in decision-making and the establishment of management strategies for these animals, which suffer numerous threats. We analyzed the available scientific literature on the use of telemetry in the study of the movement ecology of freshwater turtles, seeking to assess the most commonly used approaches. To this end, we carried out a systematic review of articles published until December 2022 using the PRISMA protocol. We found 104 articles published between 1980 and 2022, with a clear increase in the number of publications in later years. We found publications in 40 journals with 295 authors, 150 institutions and 261 keywords. Three countries had major contributions, and we found studies with 50 species, the most recurrent being *Emydoidea blandingii* and *Glyptemys insculpta*. The most commonly used technique to study turtle movement was radiotelemetry. The use of Minimium Convex Polygon - MCP and Kernel Density Estimation - KDE was present in 56% of the studies in the last 10 years, and the evaluation of the home range of the species was the most recurrent type of study. The studies covered 33 freshwater ecoregions, and although most studies were carried out in anthropized areas, covering only 16.2% of all endangered freshwater turtle species and 11.4% of all threatened by international trade, the conservation approach has been increasingly recurrent. Our results highlight trends and gaps in the study of the ecology of freshwater turtle movements and highlight the importance of telemetry as an essential tool for species conservation.

KEY WORDS: scienciometry, chelonians, movements, home range, tracking.

INTRODUCTION

Animals exhibit movement patterns in search of places with greater availability of resources (Pough *et al*. 2001), and these resources can be diverse: shelter, food, sexual partners, thermoregulation and reproduction sites, as in the case of turtles (Fachín-Téran *et al*. 1995). Typically, for freshwater turtles, movement patterns are mainly influenced by annual variation in water availability (Prance 1979; Junk *et al*. 1989; Ossa-Velasquez and Vogt, 2011) but can also be associated with habitat changes, such as precipitation, water temperature, water level, or chemical pollution (Iverson, 1992; Fachín-Terán *et al*. 2006).

Several approaches have been used to study the spatial distribution and habitat use of freshwater turtles, the most common being those involving capture-recapture (Plummer 1977; Obbard and Brooks, 1981; Liuzzo *et al*. 2021), thread-bobbins (Carter *et al*. 2000; Kaye *et al*. 2005; Famelli *et al*. 2016) and, more recently, acoustic tracking (Micheli-Campbell *et al*. 2017) and radiotelemetry (Roe and Georges 2008), although each has some limitations.

The study of the movement, habitat use and home range of freshwater turtles is still incipient, and most of these studies were carried out in a certain period of the year (Magnusson *et al*. 1997; Fachín-Terán *et al*. 2006; Ponce de Leão 2019). Radiotelemetry is one of the main tools used to study the movement patterns of animals (White and Garrott 1990; Chow-Fraser 2014), but generally, this method is quite labor intensive, as it requires the presence of the researcher for all tracking efforts (Chow-Fraser 2014), which can make it impossible to collect data during all periods of the year

(Rowe and Moll 1991; Dowling *et al*. 2010; Luschi and Casale 2014; Chow-Fraser 2014; Cochrane *et al*. 2019). Although this tracking frequency is necessary to generate enough data to accurately map an animal's home range (Swihart and Slade 1985; Kie *et al*. 2010), the presence of the researcher can affect the animal's natural movements; therefore, radio tracking is not ideal for determining habitats that are rarely used or only used for short periods (e.g., travel corridors).

In the last 20 years, satellite telemetry has led to progress in the knowledge of movement ecology (Tomkiewicz *et al*. 2010; Chow-Fraser 2014; Cochrane *et al*. 2019), as this technique allows the reconstruction of the real routes followed by marked individuals (Godley *et al*. 2008; Guilhon *et al*. 2011), allowing their follow-up throughout the year, with no need to go to the field (except to initially apply transmitters, change devices or batteries). Combined with traditional radio tracking, researchers were able to increase the frequency and spatial resolution of the collected data (Schwartz and Arthur 1999; Cagnacci 2010). While on the one hand, the technique is considered to be more expensive than others (Cochrane *et al*. 2019), on the other hand, it enables obtaining very detailed information about the spatial behavior of individuals belonging to different life stages and about the main characteristics of the movements performed by individuals in their natural environment (Luschi *et al*, 2014). Along with technological advances, the last decade has also seen conceptual and analytical advances to study species movement with the use of different techniques and methods (Nathan *et al*. 2008).

Freshwater turtles are widely distributed in rivers and lakes around the world (Campbell *et al*. 2013) and represent one of the most threatened groups of vertebrates on the planet, with over 300 known species (Bour 2008; Uetz 2022). Approximately 60% of them fall under some degree of threat, and global efforts are needed to prevent the extinction of these charismatic animals (Turtle Conservation Fund 2007; IUCN 2022). Freshwater turtles have suffered a serious decline in recent years, and some species may no longer exist in the next century (Buhlmann *et al*. 2009; Hoffmann *et al*. 2010) due to numerous threats, such as habitat loss, the introduction of invasive predators (Rhodin *et al*. 2018), exploitation for food, traditional medicine and unregulated trade (Smith, 1979; Gibbons *et al*. 2000; Hernandez and Spin 2003; Turtle Conservation Fund 2007; CITES 2022; IUCN 2022), although there is a historical and social relationship with the consumption of some species (Rêbello and Pezzutti 2000; Carvalho *et al*. 2021; Da Silva *et al*. 2022).

Movement patterns and range of use are not yet known for many species of freshwater turtles. It is essential to know the life history of the species and investigate how individuals move (Gibbons 1990; Roe *et al*. 2008, 2009; Godley *et al*. 2003) and to align technological advances in the study of movement with the objective of defining appropriate conservation measures for species of conservation interest, especially those listed on the Red List of Threatened Species of the International Union for the Conservation of Nature (IUCN) (Luschi and Casale,2014; Allen and Singh 2016; IUCN 2022). In this work, we synthesized studies that evaluated the use of telemetry in freshwater turtles around the world. Our objective was to identify research trends and gaps in current knowledge and discuss the importance of using telemetry in the conservation of freshwater turtles. We hope to observe an evolution in the use of techniques, equipment, and analyses employed to comprehend the movement patterns of freshwater turtles. Additionally, we aim to understand how the application of telemetry can significantly contribute to global conservation efforts for turtles, particularly in freshwater ecoregions.

METHODS

Literature Review

We used the step-by-step approach proposed by Khan *et al*. (2003) and Pullin *et al*. (2006) for a systematic review. Additionally, we used the Preferred Reporting Items for Systematic Reviews and Meta-Analyses Standard Method (PRISMA; Moher *et al*. 2015). This method has been commonly used in systematic review studies on various subjects (Velamazan *et al*. 2020; Calzetta *et al*. 2020; Tidman *et al*. 2021; O'Dea *et al*. 2021; Mathwin *et al*. 2021) and consists of a robust protocol with 27 items that must be verified so that the risk of bias is minimized (Moher *et al*. 2015). Literature sources were accessed through the SCOPUS (www.scopus.com), Web of Science (WoS) and Google Scholar databases. These three databases were selected to allow greater coverage of the results (Fingerman 2006; Mongeon and Paul-Hus 2016), since results may vary depending on the database used (Gavel and Iselid 2008; Vieira and Gomes 2009).

We limited the search to articles published in peer-reviewed journals until July 2022, using a series of keywords combined to search for work done on the ecology of movement in freshwater turtles. For this, the following keywords were searched for in the databases: ((turtle OR chelonian) AND (freshwater* OR river*) AND (telemetry OR radiotelemetry OR satellite)) (Table 1). All Scopus and Web of Science results were considered, and in the case of Google Scholar, only the results of the first 30 pages were considered (Haddaway *et al*. 2015; Crane *et al*. 2021).

For inclusion, they had to meet the following eligibility criteria: 1) related to the movement of freshwater turtles; 2) aquatic and semiaquatic species only; 3) studies using an attached telemetry device (e.g., VHF transmitters, GPS transmitters); 4) peer-reviewed articles; and 5) studies available in full. We also added articles from personal libraries that fell within the scope of our study. Duplicates, false positives, and non-peer-reviewed "gray" literature based on title and abstract or main text if relevance was not clear in the abstract were removed (Jeffers *et al*. 2016).

Considering that many times, the same study makes comparisons between methods and analyzes and seeks to respond to more than one pattern of movement, we decided to use all this information. In this way, these were also considered in the descriptive analyses as different studies, but we did not consider them in the statistical analyses. Behavioral studies were considered as long as they addressed the movement of individuals using telemetry. Studies that were not directly related to the movement of individuals, such as essays, theoretical discussions and studies with genetic, physiological and morphological approaches, were excluded.

Literature analysis

Current species and habitat nomenclature followed Uetz *et al*. (2022). For each article, the following information was extracted: I) general characteristics: year of publication, name of the journal, impact factor, first author and institution, keywords used, species and study topic; II) location: country, geographic coordinates and place of study; III) movement variables: movement analysis (how the movement was measured), the method used and IV) conservation: threat degree, inclusion/discussion/recommendations on conservation issues and whether the study was carried out in a protected or anthropized area. Among the methodological options related to movement, there are variations dealt with in the literature, such as the kernel method: fixed kernel method (Rowe *et al*. 2009), fixed kernel estimates (Forero-Medina *et al*. 2011), fixed kernels (Refsnider *et al*. 2012a, b); and the minimum convex polygon method (MCP) 100% (Ponce De Leão *et al*. 2019) and MCP 90% (Wallace *et al*. 2020).

We standardized these methods as the kernel method (KM), minimum convex polygon (MCP), linear home range (LHR), and statistical analysis for those who used only statistical analysis to determine movement and “others”.

Studies that only sought to describe the movement of species as maximum distance traveled and average distance were grouped in descriptive analyses. Regarding the types of study, we also have a diversity, such as terrestrial movements, migration, Hibernacula, and habitat selection, among others. The studies were standardized and grouped into seasonal movements, home range, movement patterns and habitat use. Studies that involved motion ecology using telemetry but did not have specific analyses to determine motion were grouped under technical analysis and descriptive analysis. When the same article studied several species and used several techniques and analyses, the same article was included several times in the presented study counts.

To query the impact factor, we used the latest JCR Impact Factor 2022 provided by the Journal Citation Report (JCR). The coordinates taken from the studies were superimposed on shapefiles, and a map was created using ArcGis® software. When coordinates were not available in the article, we extracted an approximate coordinate for the indicated region through *Google Earth*®.

Data analysis

In addition to the descriptive analyses represented in graphs and tables, we sought to verify whether the number of publications on the ecology of freshwater turtles' movement has increased over the years through Spearman correlation analysis (Zar 1999). The same analysis was used to verify whether older studies are more cited and whether the representativeness of studies and species studied in each family is correlated to existing species (Bárcenas-Garcia *et al*. 2022). Specifically, for the analysis of keyword patterns, a “*word cloud*” was built using the Wordcloud package (Fellows *et al*. 2018). To understand the collaborative relationships between researchers and institutions, coauthorship networks were built (Barabási *et al*. 2002; Tomassini and Lutti 2007) using VOSviewer→ software. To see if there was a relationship between publication and if conservation was discussed in the articles, a Spearman correlation was performed. The conservation status of the species was taken from the IUCN (IUCN 2022) and the Convention on International Trade in Endangered Species of Wild Fauna and Flora – CITES (https://cites.org/eng; CITES 2022). We also sought to identify whether studies had been carried out in the world's freshwater ecoregions (Abell *et al*. 2000a, 2000b, 2002, 2008; FEOW 2023). All analyses were performed using R software (R Core Team 2021), and results with a probability lower than 0.05 ($P<0.05$) were considered significant (Zar 1999).

RESULTS

When and what studies have been carried out thus far?.

From 575 unique articles returned from the literature searches (Fig.1), our exclusion criteria produced a final sample of 104 studies using freshwater turtle monitoring devices (see Supplementary material). There was a slight increase in the number of publications from 2006 onwards, with the first study registered in 1980 (Fig. 2A). Significant differences were also found in the number of publications over the years (Spearman’s $R_s = 0.67$, $p < 0.001$). Despite this, between 1980 and 1990, no studies were found based on the chosen criteria. Publications from the last ten years (2013 to July 2022) correspond to 53% of the total publications. The year with the highest number of publications was 2019, with 11 published works, followed by 2018, with seven works.

The 104 articles found were published in a total of 40 journals. Of these journals, “*Chelonian Conservation and Biology*” was the most relevant in terms of the number of publications corresponding to 18.26% of the works, followed by the *“Journal of Herpetology”* corresponding to 11.53% and *“Copeia”* with 10.57% of publications. The journal with the highest impact factor is *“Copeia”,* followed by *“Journal of Herpetology”* and *“Chelonian Conservation and Biology”*. Only the Herpetological review had no impact factor (Table 2).

The average number of citations per document was 35.25, ranging from 0 to 372. The study with the highest number of citations was the one published by Compton *et al*. (2002) in the journal “*Ecology*” (372 citations). In this work, the authors used radio transmitters as a tool to model habitat selection within the range of *Glyptemys insculpta*. The second study with the highest number of citations was carried out by Burke and Gibbons (1995) and published in the journal “*Conservation Biology*” (319 citations), where telemetry was used to assess the habitat requirements of three species of freshwater turtles (*Kinosternon subrubrum*, *Pseudemys floridana* and *Trachemys scripta*). We observed that older studies were more cited (Spearman's $R_s = -0.60$, $p < 0.001$; Fig. 2.). The total number of keywords used by the authors was 270. The two most frequent keywords were *Home range* (n = 26) and *Turtle* (n = 18), followed by *Conservation* and *Radiotelemetry* (n = 11) and Movement (n = 10) (Fig. 3).

Who's tracking what and where?.

Of the 295 different authors that appeared in all 104 articles surveyed, the author with the highest number of collaborations was Sterrett, S. (total link strength = 11) from

Monmouth University, based in New Jersey, USA; Smith L. L. (total link strength = 11) from the Joseph W. Jones Ecological Research Center, based in Georgia, USA and Georges A. (total link strength = 10) from the University of Canberra, based in Canberra, Australia. Tornabene, Bramblett and Brown presented a total link strength of nine, while the other authors presented fewer than eight collaborations. Of the total, eight authors worked individually, and 35 authors worked with at least one coauthor (Fig. 4A).

Regarding the institutions, 150 participated in the 104 articles surveyed. The institutions with the highest number of collaborations were the University of Louisville (total link strength = 26), the University of Maine (total link strength = 25), the University of Illinois (total link strength = 18), and the National Research Institute of the Amazon and Maine Department of Inland Fisheries and Wildlife (total link strength = 12). The other institutions presented a total of fewer than 10 collaborations. Of the total, 10 institutions produced the articles individually, and 15 institutions worked in partnership with only one other institution (Fig. 4B). Regarding the countries with the greatest relevance in scientific production related to the subject, the United States represented more than half of the studies (57%), followed by Canada (14%) and Brazil (6.7%) (Fig. 5).

In total, 50 species have studies related to the use of telemetry to measure aspects of turtle movement ecology. Of these, the most studied were *Emydoidea blandingii*, present in 16 works, and *Glyptemys insculpta*, present in 15 articles. The most representative family was Emydidae, with 36% of the species studied, followed by the family Kinosternidae (16%). The Carettochelydae and Platysternidae family (2%, n = 1) was the least studied family and the most underrepresented Geoemydidae (Table 3) in relation to the diversity of existing aquatic turtles (Rhodin *et al*. 2018; Uetz *et al*.

2022) (Table 3). Although there was a weak positive relationship, the number of studies was not significantly correlated with the number of existing species in each family (Spearman's $R_s = 0.32$, $p = 0.32$; Fig. 6A). The number of species studied in each family was also not significantly correlated with the number of species in each family (Spearman's $R_s = 0.56$, $p = 0.08$; Fig. 6B) and followed a similar pattern to the number of studies, with most species of Emydidae most frequently studies.

How were the studies done and how were they evaluated?.

Telemetry devices (VHF) were cited in 98 of the analyzed studies of freshwater turtles, and only nine satellite devices (GPS) were used (Fig. 7A). The first study using satellite radio (GPS) is quite recent (2011), when this method was used to monitor the nesting of 10 female *Podocnemis expansa* in the Trombetas Biological Reserve, Rio Trombetas, Brazil (Guilhon *et al*. 2011). The use of statistical analysis, without pairing it with estimates via MCPs and KDEs, dominated the studies (n = 20). Next, the use of minimum convex polygons (MCPs) and kernel density estimates analysis (KDE) were present in more than 56% of the studies in the last 10 years. Studies often include estimates from both methods and rarely use KDEs without including MCPs. Several studies (n = 20) used descriptive analyses and did not include KDE and MCP analyses or statistical analyses (Fig. 7B). Eight studies used the linear home range (LHR) method, and a minority of studies (n = 2) used 'other' methods without pairing with estimates via MCPs and KDEs. These methods included the minimum polygon area method (MAP) to assess the home range of *Graptemys flavimaculata* and *Polly buff* to assess the home range of *Chelydra serpentina* (Fig. 7B). This method consists of combining the areas within minimal convex polygons calculated around the aquatic locations of each individual and was developed for studies with aquatic turtles by accurately matching aquatic areas of activity with terrestrial movement paths and therefore is more biologically and behaviorally effective (Harmenick, 2001; Harmenick *et al*. 2020).

The home range of the species was evaluated in 51 studies, followed by movement patterns evaluated in 28 studies, habitat use in 20 studies, seasonal movements in 17 studies and linear home range in eight studies. Finally, two studies sought to compare Techniques Analysis (Sattelite radio and VHF Transmitters) (Fig. 7C).

What are the contributions of studies to the conservation of species?.

Almost half of the species surveyed in articles related to the use of telemetry in the ecology of freshwater turtle movement are classified as threatened (44%), but they represent only 16.2% of all endangered freshwater turtle species, while 26% are categorized as least concern (LC) and near threatened (NT). Only one species (*Podocnemis expansa*) is considered Conservation Dependent (CD); that is, the species is characterized as facing lower risk but needs conservation efforts to avoid becoming a threatened species (Fig. 8A). Regarding CITES, 42% of the species are part of one of the annexes (I, II or III) and represent only 11.4% of all freshwater turtle species threatened by international trade. Regarding the status of the areas where the studies were carried out, slightly more than half (55%) were carried out in anthropized places, while the rest (45%) were carried out in protected areas (Fig. 8B).

The discussion on conservation varied greatly in the literature evaluated. In total, 42% of the articles make no reference to conservation issues. Almost half (48%) of the 50 articles published in the last ten years did not mention conservation, and only 10% (out of 104) dedicated a specific topic to discussing species conservation (e.g., conservation implications, management implications or conservation considerations). In total, 61 papers (58%) contain mentions related to conservation that included recommendations from increasing the protected area (Downling *et al*. 2010), protecting populations and peripheral areas (Forero-Medina *et al*. 2011), protecting and recovering the environment of riverine populations (Chen and Lue 2008; McCoard *et al*. 2016), controlling exotic species (Kobayashi *et al*. 2006), decreasing tourism in occurrence areas (Galois *et al*. 2002), protecting nesting and occurrence areas (Tucker *et al*. 2001; Compton *et al*. 2002; Dowling *et al*. 2010; Freeman *et al*. 2018) and encouraging studies in partnership with managers in river systems, particularly in floodplains both spatially and temporally, since the reproductive success and survival of freshwater turtles is based on the availability of aquatic and terrestrial habitats throughout the year (Bodie and Semlitsch 2000). The level of detail of the mentions varies from the need to protect the environment to more specific and denunciatory statements, as in the case of the study by Zagorski *et al*. (2019), who, when advocating a data-driven evidence-based approach in studies carried out for the construction of a quarry in a place of occurrence of the species *Emydoidea blandingii*, were victims of a defamatory attack in their careers, where the entrepreneur and hired consultants widely disseminated, in writing, allegations of academic misconduct, conflict of interest and data fabrication. Concern about conservation in the literature is increasing, and although there is a weak positive relationship, we did not find a significant relationship between the proportion of articles that discuss these concerns and the year of publication (Spearman's $R_s = 0.29$, $p = 0.167$; Fig 9).

The telemetry studies follow the richest regions and with the highest endemism of freshwater turtles (Fig. 10). The vast majority of studies were carried out in the Nearctic region (73%), followed by the Neotropical (14%), Palaeartic (6.7%), Australasian (2.8%), Afrotropic (1.92%) and Indomalayan (0.96%) regions. In total, the studies covered 33 freshwater ecoregions worldwide (Table 4). The ecoregions with the most studies were Upper Mississippi (13.46%) and Southern Hudson Bay (12.5%), both in the United States, both corresponding to the most studied habitat type (*temperate coastal rivers*; 44.23%; Table 4).

DISCUSSION

Temporal tendencies and characteristics of studies.

Following the world trend, which has been increasing in the number of publications on wildlife related to various subjects, such as ecology (Ribeiro *et al*. 2007; Collins *et al*. 2021) and conservation (Grelle *et al*. 2009), often complement each other (e.g., Oliveira *et al*. 2020), the ecology of the movement of freshwater turtles also increased over the 42 years evaluated here. Possibly, this is due to the reflection of the multiplication of journals specialized in herpetology over the years (Grelle *et al*. 2009), greater investments in research in universities, and an increase in the number of undergraduate and postgraduate courses in more remote places (e.g., Amazon; Martins *et al*. 2007; Scarano, 2008; Medeiros and Leta 2020), covering a more diverse audience and consequently increasing the number of people interested in herpetology (Campos *et al*. 2014; Rebouças, 2022), although these last two have not been the priority of some governments in recent years, such as in Brazil (Hipólito *et al*. 2022; Galvão-Castro *et al*. 2022).

Improvements in data collection and analysis techniques (Ribeiro *et al*. 2007; Doody *et al*. 2009; Christensen and Chow-Fraser 2014; Kingsbury and Robinson 2016; Cochrane *et al*. 2019) and the increase in knowledge about taxonomy, distribution and attributes of life history, basic biology and ecological characteristics of various species (e.g., Deeth and Coleman 2022; Geller *et al*. 2022) in addition to the concern with biological conservation, which has increased greatly in recent years and in all segments of society to the detriment of anthropogenic actions (Ribeiro *et al*. 2007), have also contributed to the increase in publications, not only of freshwater turtles but also of several taxa.

The predominant journals in issues of publications related to the theme are specialized in the herpetological field (e.g., Copeia, Journal of Herpetology, Herpetology review). The journal Copeia was established in 1913 and was considered one of the first devoted to studies of fish, amphibians and reptiles. Years later, its name was changed to Ichthyology & Herpetology, and it is currently internationally recognized as one of the most prestigious scientific journals of its kind (ASIH, 2022). It is noteworthy that the journal where there were more publications is specialized in turtles (= Chelonians): *Chelonian Conservation and Biology*, responsible for 18.26% of the publications, being also the journal with the greatest impact factor and the most cited journal in scienciometry studies with turtles in general (Kopperundevi 2019; Vences-Pérez *et al*. 2022). The journal Chelonian Conservation and Biology emerged in 1994 (Karen and Scott 1994) and has been the preferred journal by researchers for publications related to tortoise and freshwater on various subjects, such as diversity, geographical distribution, natural history, ecology, reproduction, morphology and natural variation, population status and issues of human exploitation or conservation management (Karen and Scott, 1994; Stearns, 1995). Keyword analysis showed a trend in works involving the ecology of movement in freshwater turtles, where the four most cited can be considered highly effective in identifying relevant articles.

Studies using telemetry were predominant in the United States (57%), followed by Canada (14%), countries with high investment in science and technology in the world (Cruz 2007; Schneeganz *et al*. 2021). Telemetry equipment has a high cost and comes mainly from the United States, which exports it to other countries. The import of research equipment and materials is considered one of the biggest obstacles to the progress of science in several countries, which comes up against bureaucracy (Rumjanek, 2006) and the variation of the dollar, which makes telemetry equipment often unfeasible, being preferable to the techniques considered more popular (e.g., spool-and-line; Boonstra *et al*. 1986), and they do not need large investments.

Another aspect that should be considered is the high diversity of freshwater turtles in these three countries (Neoarctic region and Neotropical region; Bour 2008), with a high rate of endemism, and many of them are considered threatened with extinction, which consequently raises interest in understanding aspects about the ecology of species seeking to subsidize strategic planning for conservation in a global effort (Turtle Conservation Fund 2007).

Studies with unique species were responsible for 83% of our study, and *Emydoidea blandingii* was the most studied species, present in sixteen articles. In fact, movement studies usually evaluate a species (Holyoak *et al*. 2008). This high number of studies, very close to the second most studied species (*Glyptemys insculpta*; $n = 15$), is related to the geographical location of species distribution and related to work carried out by authors who have deepened their research efforts on the conservation of the two species, both considered internationally threatened (van Dijk and Rohdin, 2011; van Dijk and Harding 2011).

Have the studies prioritized any method or analysis?.

In the 42 years of studies evaluated here, there has been an explicit increase in studies that used telemetry techniques to understand aspects related to the domestic reach and use of the space of freshwater turtles and the continuous dependence on traditional but outdated methods. Although the technique of VHF transmitters did not deviate from the standard found by Crane *et al*. (2021), in recent years, researchers have increasingly adopted the technique of GPS transmitters in the study of animal behavior and ecology (Tomkiewicz *et al*. 2010; Crane *et al*. 2021), including with freshwater turtles, sometimes individually or in conjunction with other techniques (Rowe *et al*. 1991; Christensen and Chow-Fraser 2014; Famelli *et al*. 2016). Despite this, the effectiveness of GPS trackers for aquatic and semiaquatic species has not yet been fully examined (Quaglietta *et al*. 2012; Jeffers *et al*. 2016; Cochrane *et al*. 2019), unlike other groups, such as sea turtles (Schofield *et al*. 2007; Godley *et al*. 2008; Hays and Hawkes 2018; Pheasey *et al*. 2020).

Our results showed that 56% of the studies conducted in the last 10 years have used kernel density estimates (KDEs) and minimum convex polygons (MCPs) to provide greater robustness to the results. Scientists justify the use of these two estimators due to the possibility of comparison with the broader literature on the spatial ecology of species, in this case, of reptiles (Crane *et al*. 2021). In contrast, some authors ask that these two analyses require considerable control of the methods because they are sensitive to differences in the sampling effort (for example, the number of locations, duration and frequency of tracking) and therefore should not be stimulated because they hinder comparisons (Kraunstaber *et al*. 2012; Mitchell *et al*. 2019; Silva *et al*. 2020; Crane *et al*. 2021). However, more appropriate and updated methods have not been observed in any studies (e.g., *Brownian bridge movement model* - BBMM; Horne *et al*. 2007; Kie *et al*. 2010; Silva *et al*. 2018, 2020; Signer and Balkenhol 2015).

There are several studies demonstrating the effectiveness of more recent analytical methods (e.g., Silva *et al*. 2020, 2021) and how they can be applied to radio telemetry data. Unlike traditional estimation methods (KDEs and MCPs), motion-based area estimation models (e.g., AKDEs) do not require the same prepositions as traditional methods, such as point independence, and can better protect against underestimation and overestimation (Fleming & Calabrese 2017; Silva *et al*. 2020; Crane *et al*. 2021). Low sample sizes do not exclude the use of newer methods such as AKDE and BBMMs since these methods can be effective for estimating motion pathways with a small set of VHF data (Silva *et al*. 2020, 2021; Crane *et al*. 2021).

Although researchers worldwide are still developing analytical methods within movement and spatial ecology (Laver & Kelly 2008), the proportion of studies using movement-specific methods has not increased (Joo *et al*. 2020), demonstrating a high dependence on traditional methods. The home range of the species was studied in 49% of the works involving telemetry. In the last 20 years, following the increasingly improved analytical methods (Silva *et al*. 2020, 2021), there has been an increase in studies involving the domestic reach of reptiles (Crane *et al*. 2021) since for many years, the estimate of domestic reach has been useful to investigate animal-habitat relationships and to test the effects of sex, age, physiological requirements, social status or ecological restrictions in 2002. Freshwater keloids have different ranges of domestic range, and in some cases, they can be different between males and females (Jones 1996; Tucker *et al*. 2001; Doody *et al*. 2002; Fachín-Terán *et al*. 2006; Ponce de Leão *et al*. 2019) and weight (Muller *et al*. 2019) and can be influenced by external factors such as water pollution (Luiselli *et al*. 2006) and seasonality (Remsberg *et al*. 2006; Forero-Medina *et al*. 2011; Ponce de Leão *et al*. 2019).

The review covered several species, but we identified gaps to be filled in relation to some species that need studies with telemetry. For example, in the Neotropical region, there is a great diversity of freshwater turtles, including newly described species (*Chelus orinocensis, Mesoclemmys juritiensis*) and endangered species (e.g., *Mesoclemmys vanderhagei*) that have very little information regarding their movement. In addition, better methodological comparisons are still necessary, considering that only one study in Brazil was concerned with comparing the different equipment in relation to its effectiveness (Guilhon *et al*. 2011).

Have studies been concerned with the conservation of species?.

In our study, we observed that almost half of the studies that addressed aspects of species movement are related to species that are under some degree of threat (e.g., *Carettochelys insculpta, Hydromedusa maximiliani, Mesoclemmys dahli, Rheodytes leukops, Macrochelys temminckii* and *Actinemys marmorata*), although the diversity was not as representative. Turtles represent one of the most endangered vertebrate groups on the planet, with approximately 10% of the currently recognized species considered critically endangered on the IUCN Red List of Threatened Species (Turtle Conservation Fund 2007; IUCN 2022) and approximately 63% of the assessed species and approximately 42% of all known species considered threatened (IUCN 2022).

Biological characteristics of turtles, such as delayed sexual maturity, high juvenile mortality and a long adult life with low natural mortality, have left turtle populations vulnerable to various threats potentiated by humans (Turtle Conservation Fund, 2007). Historically, many species of chelonians in various parts of the world have great food, economic and cultural importance, and their eggs, meat, viscera, fat and hull have been used intensely by humans, mainly in food and traditional medicine (Van Dijk *et al*. 2000; Gibbons *et al*. 2000; Turtle Conservation Fund 2007; Van Dijk *et al*. 2014).

More than half of the studies were carried out in anthropized areas. Despite this, a large number of studies have been carried out in protected areas from large parks (e.g., Algonquin Provincial Park and Ndumo Game Reserve; Obbard *et al*. 1980, 1981; Paterson *et al*. 2012, 2014; Price *et al*. 2022) to smaller areas (e.g., Mamirauá Sustainable Development Reserve, Adolpho Ducke Forest Reserve, The Trombetas Biological Reserve and Carlos Botelho State Park; Fachín-Terán *et al*. 2006; Guilhon *et al*. 2011; Famelli *et al*. 2016). Evidently, some species were studied only in protected areas (e.g., *Podocnemis sextuberculata, Podocnemis unifilis, Macrochelys temmninckii* and *Platysternon megacephalum*), possibly due to the greater ease in obtaining help with logistics and public–private partnership, which may promote an increase in the effectiveness of protection, handling and research with these animals (Marcovaldi *et al*. 2005).

In the present study, we evidenced geographic gaps in studies using telemetry worldwide. Although we have observed that telemetry studies follow the most diverse regions and with greater endemism of freshwater turtles, there is still much to know, especially in the less studied ecoregions. Freshwater ecoregions consist of a large area that encompasses one or more freshwater systems with a distinct set of natural freshwater communities and species and are considered priorities for biodiversity conservation (FEOW 2023) and sea turtle studies. Freshwater should be stimulated in these places, seeking to understand how the different anthropic impacts may affect the movement of species in these places, especially those that are outside the currently recognized global biodiversity conservation strategies.

Although telemetry has been used by a relatively small number of studies of freshwater turtles concentrated in a few places in the world, the studies still provide a wealth of information on the ecology of movement of some of them, particularly on the spatial distribution and movement within the study sites. Considering that few species have been studied in comparison with the global richness of these animals, it is evident that much remains to be known about the movement of dozens of species of freshwater turtles, especially in regions where the greatest diversity of these animals is found, such as the Neoarctic region, the Neotropical region and the Oriental region, in *turtle hotspots* and priority areas for the conservation of freshwater turtles.

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No potential conflict of interest was reported by the authors.

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ETHICAL STANDARD

Not applicable

AUTHOR CONTRIBUTION

Maurivan V. Ribeiro played a multifaceted role, contributing significantly to experimental design, data collection, data analysis, and writing the manuscript. Roberto L. da Silva participated in the contributions on ecology and Erik Allan P. dos Santos participated with his knowledge in analyzes using telemetry and both contributed to the writing process. Amanda dos S. Cruz helped with the data search and Adriana Malvasio focused on discussions about chelonians and were fundamental in preparing the manuscript. Mirco Solé dedicated his efforts to analyzing the data, enriching the manuscript with careful interpretations. Alexandre Schiavetti took on a leadership role, supervising the project, contributing to the experimental design, and providing substantial contributions in writing and editing the manuscript.

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SUPPLEMENTAL DATA

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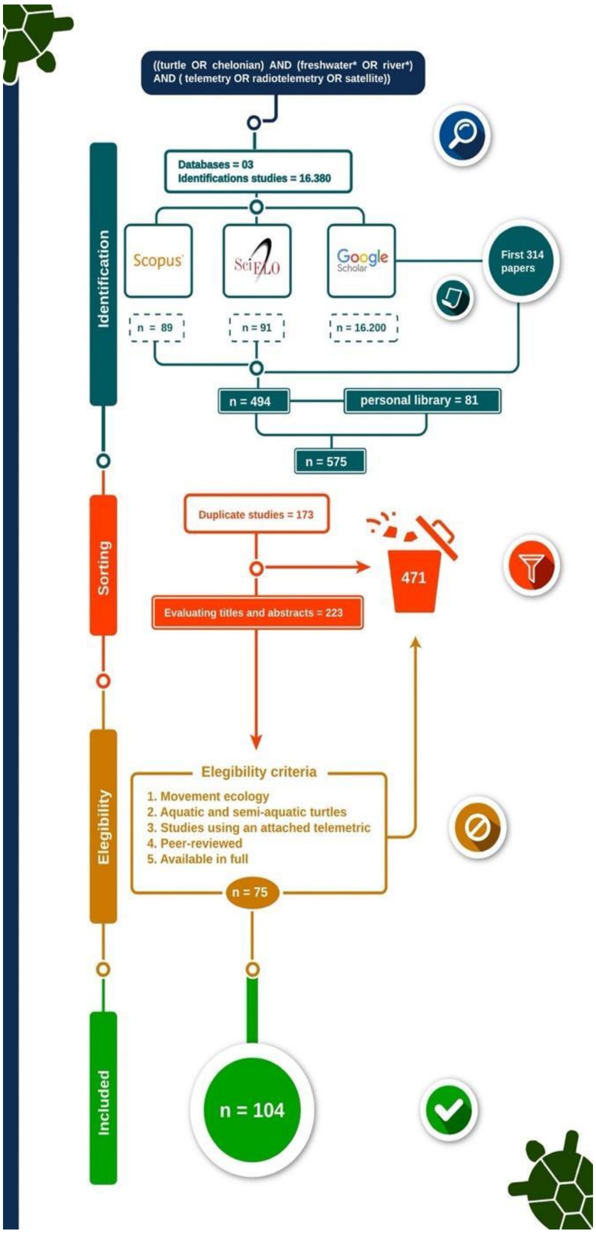

Fig. 1. — Flowchart with article selection processes and number of studies for each step of the review based on PRISMA criteria (Moher *et al*., 2020).

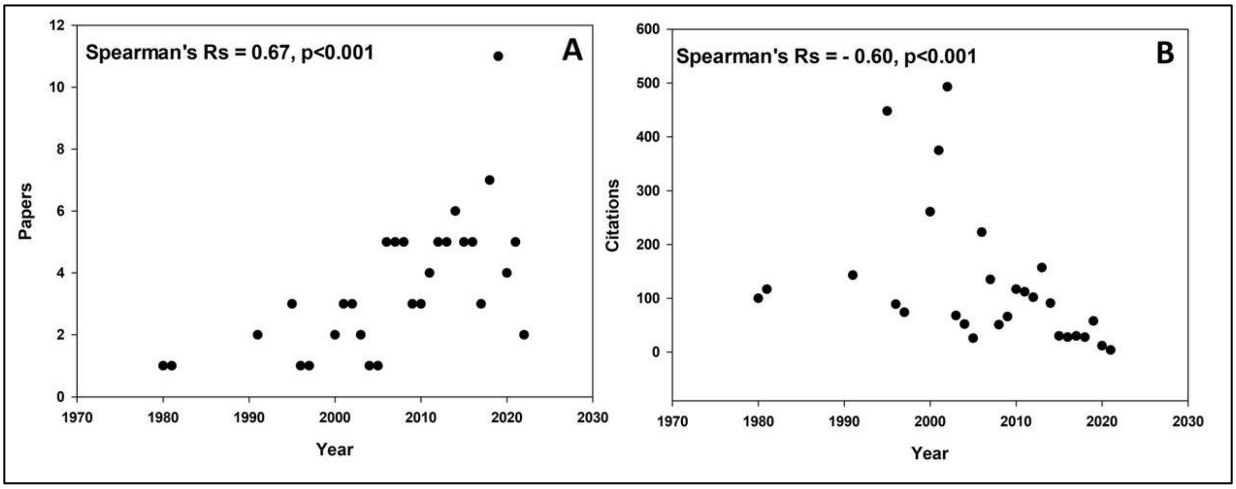

Fig. 2. — (A) Total number of movement ecology articles published per year. (B) Total number of movement ecology citations per year.

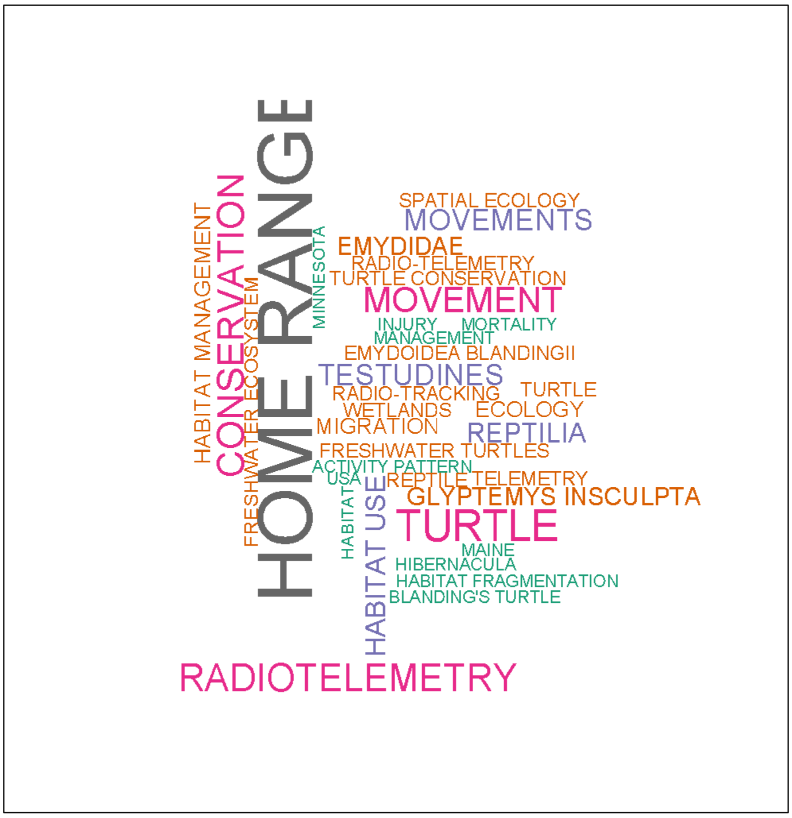

Fig. 3. — Cloud of keywords most used by authors in scientific articles, involving ecology of the movement of freshwater turtles.

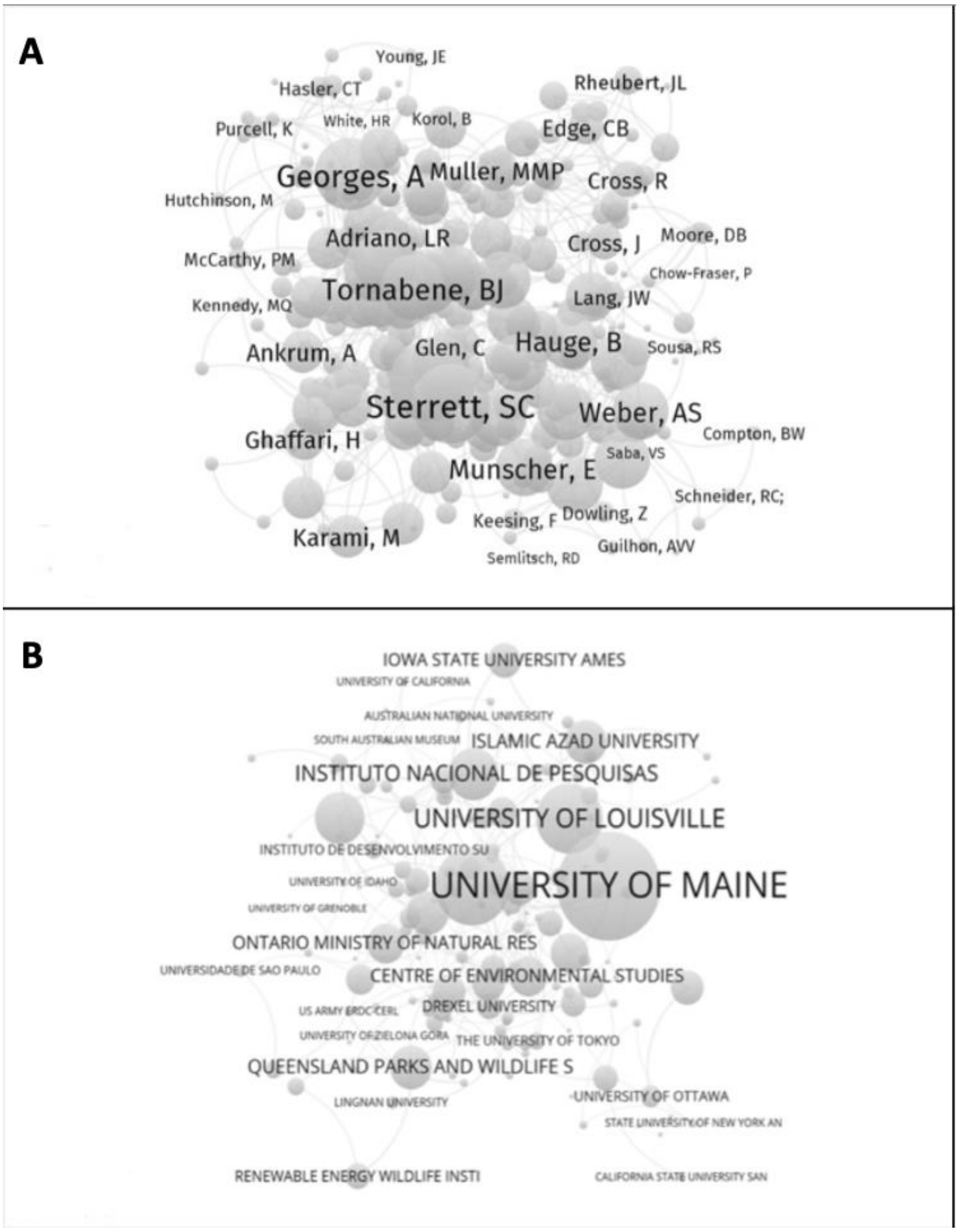

Fig 4. — Co–authorship network where the importance of each collaborator in the network is graphically presented (A) and co–authorship network presented the importance of each institution in the network (B). The font size of the network corresponding to the aut with the highest number of collaborations.

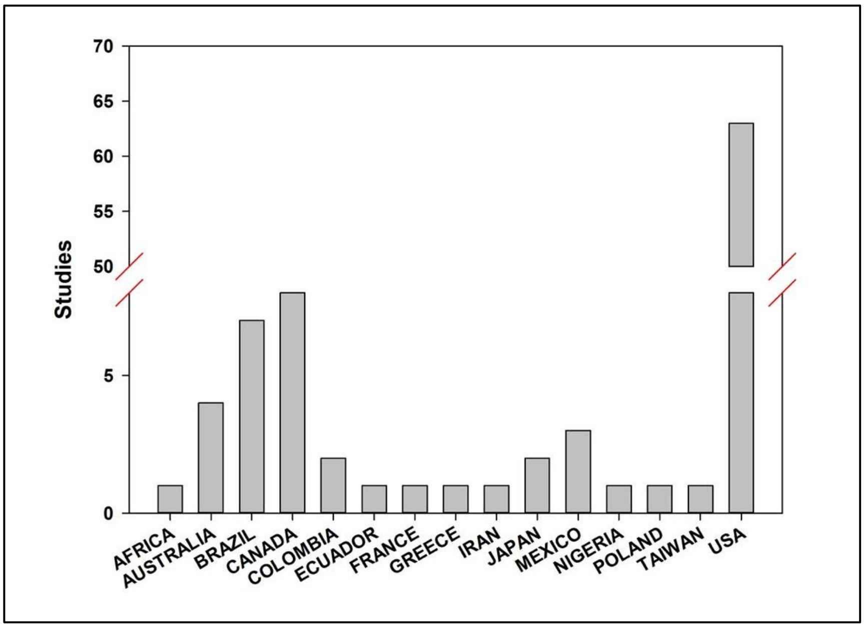

Fig. 5. — Number of studies that addressed telemetry in freshwater turtle movement ecology studies by country.

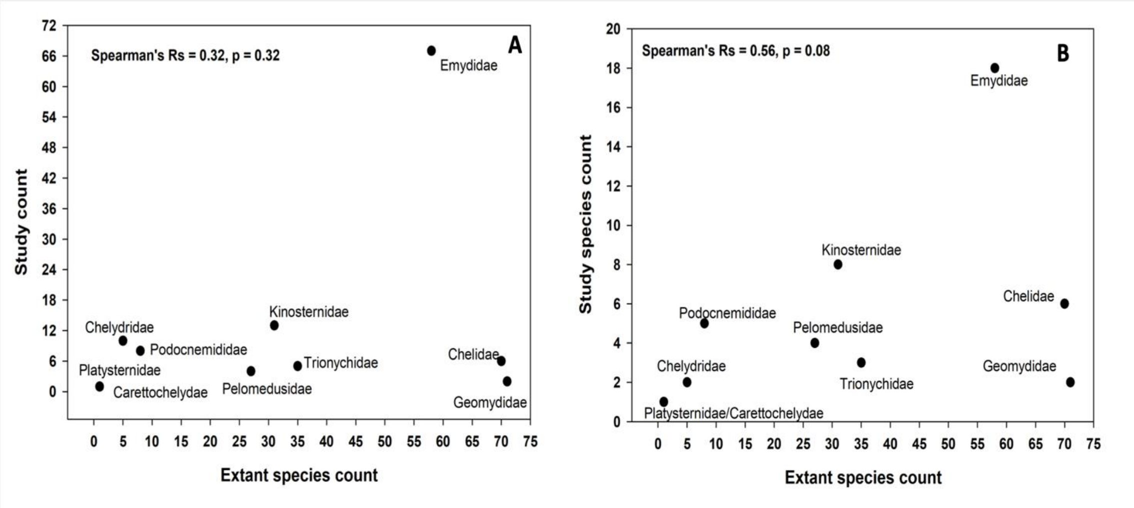

Fig. 6. — Taxonomic representativeness of articles. Comparison of extant turtle species number and (A) the number of studies and (B) studied species.

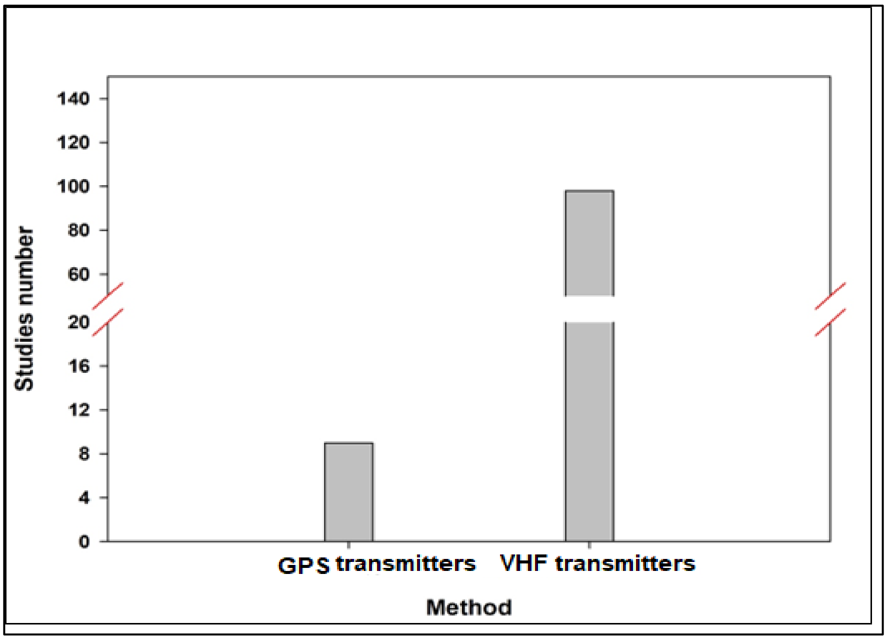

Fig. 7. — Methods used in studies that used telemetry to answer questions about the ecology of movement in freshwater turtles.

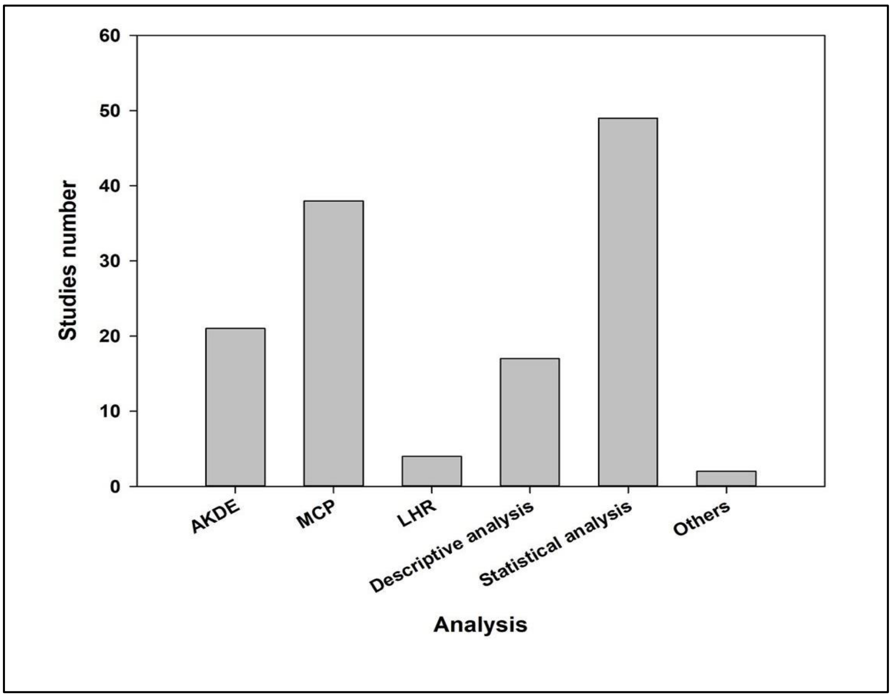

Fig. 8. — Methods of analysis used in the studies surveyed. Legend: AKDE = Adaptative Kernel Density; MCP = Minimum Convex Polygon; LHR = Linear Home Range.

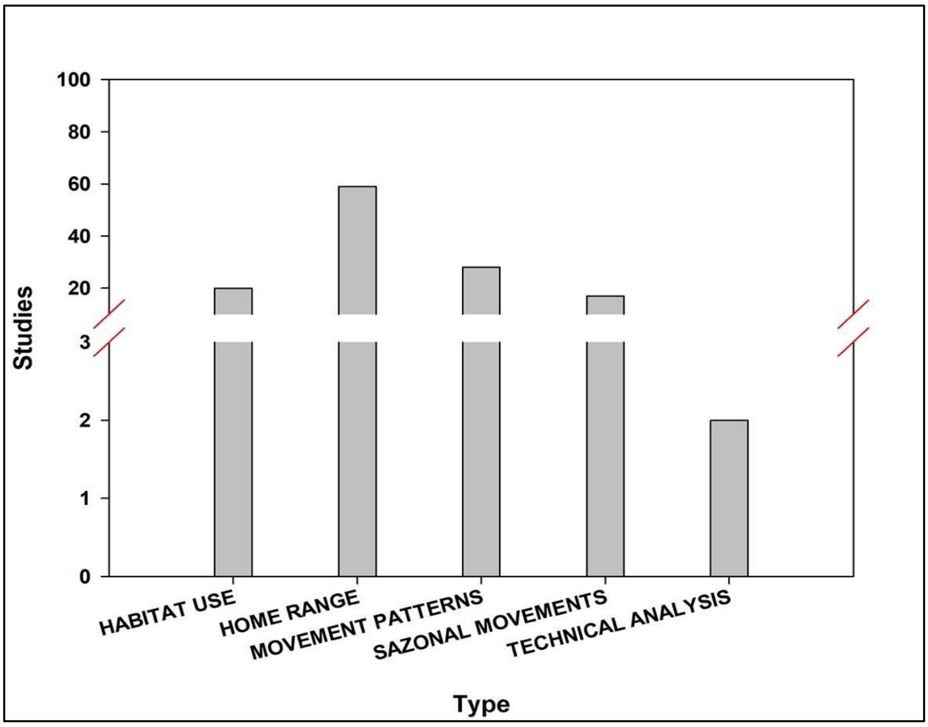

Fig. 9. — Types of studies conducted using telemetry in the ecology of the movement of freshwater turtles.

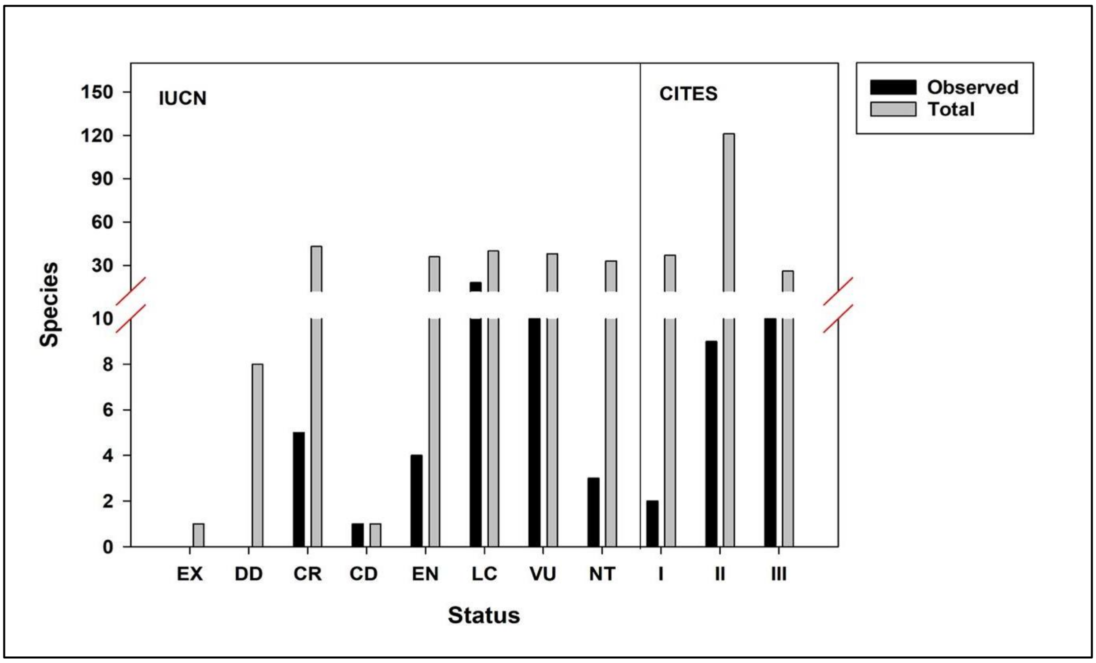

Fig. 10. — Species threat status with telemetry studies conducted worldwide considering IUCN and CITES.

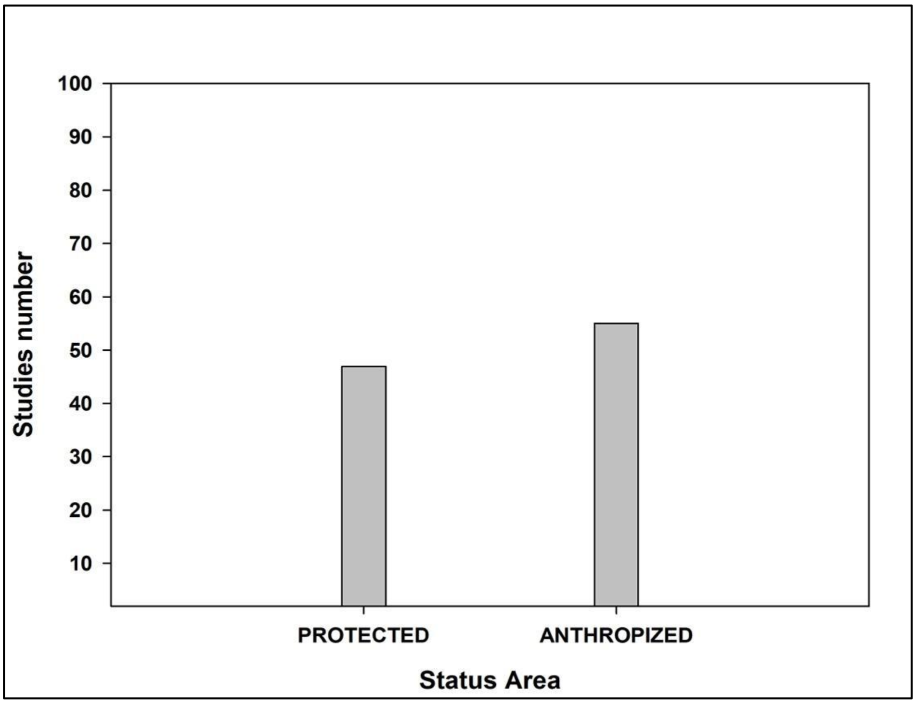

Fig. 11. — Status of areas where studies using telemetry were performed.

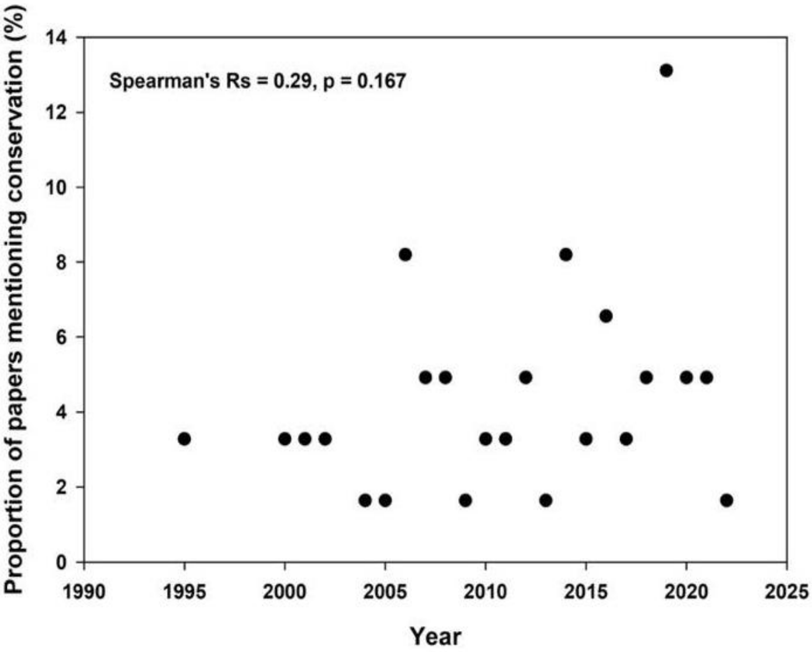

Fig. 12. — Proportion of works that mention conservation. There was no significant relationship between the year of publication and whether conservation was discussed in articles.

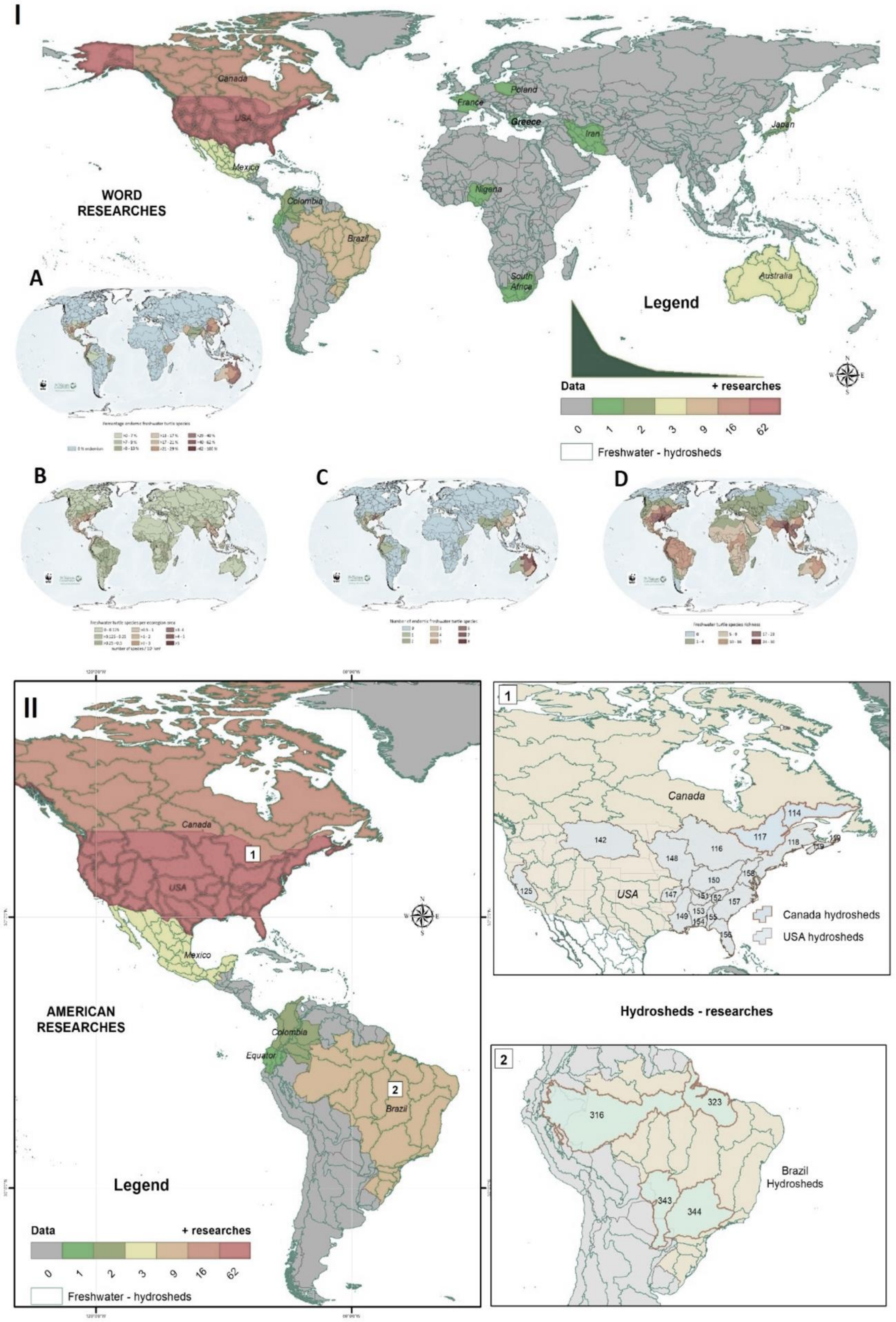

Fig. 12. — Geographical distribution of articles following the world's freshwater ecoregions (Abell *et al*. 2008; FEOW, 2022). **(I)** General map of the distribution of articles published in all freshwater ecoregions. The smaller maps, available at <https://www.feow.org/global–maps/biodiversity>, indicate (A) the percentage of

endemic freshwater turtle species; (B) freshwater turtle species per ecoregion area; (C) the number of endemic freshwater turtle species; and (D) freshwater turtle species richness. (II) Highlight for the two continents with the highest number of publications and their respective.

Table 1.Bibliographic base construction criteria.

Criterion	**Definition**
Database	Scopus, Web of Science and Google Scholar and private collection
Document type	Scientific articles
Keywords	((turtle OR chelonian) AND (freshwater* OR river*) AND (telemetry OR radiotelemetry OR satellite))
Study areas	No restrictions
Publication period	July 2022
Research institution	No restrictions
Language of publication	English

Table 2. List of the most relevant journals in terms of the number of scientific articles published.

Ranking	**Journals**	**Nº Publications**	**%**	**Impact factor**
1°	Chelonian Conservation and Biology	19	18.26	1.209
2°	Journal of Herpetology	12	11.53	1.43
3°	Copeia	11	10.57	1.857
4°	Herpetological Review	8	7.69	–
5°	Herpetological Conservation and Biology	6	5.76	0.959

Table 3. Species cited in the 104 articles surveyed in the present work.

Taxon	**Common name**	**Species citations**[a]	**Author**
Testudines			
Carettochelyidae			
Carettochelys insculpta	Pig–nosed Turtle	1	Doody *et al* (2002)
Chelidae			
Chelodina expansa	Giant Snake–necked Turtle	1	Bower *et al*. (2012)
Elseya irwini	Irwin's Turtle	1	Freeman *et al*., (2018)
Hydromedusa maximiliani	Maximilian’s Snake–headed Turtle	1	Forero–Medina *et al*. (2011); Famelli *et al*. (2016)
Mesoclemmys dahli	Dahl’s Toadhead Turtle	1	Forero–Medina *et al*. (2011)
Phrynops geoffroanus	Geoffroy’s Toadhead Turtle	1	Muller *et al*., (2019)
Rheodytes leukops	Fitzroy River Turtle	1	Tucker *et al* (2001)
Chelydridae			
Chelydra serpentina	Common Snapping Turtle	8	Obbard *et al* (1980); Obbard and Brooks (1981); Saba and Spotila (2003); Kobayashi *et al* (2006); Paisley *et al*. (2008); Steen *et al*. (2010); Strain *et al*. (2012); Anthonysamy *et al*. (2014); Hughes *et al*., (2019)
Macrochelys temminckii	Alligator Snapping Turtle	2	Howey and Dinkelacker (2008); Moore *et al*. (2014)
Emydidae			
Actinemys marmorata	Western Pond Turtle	2	Bondi and Marks (2013); Zaragoza *et al*. (2015)
Chrysemys picta	Eastern Painted Turtle	6	Saba and Spotila (2003); Bowne and White (2004); Bowne *et al* (2006); Tran *et al*. (2007); Bowne (2008); Anthonysamy *et al*. (2014)
Clemmys guttata	Spotted Turtle	7	Joyal *et al* (2001); Compton *et al* (2002); Kaye *et al* (2005); Anthonysamy *et al*. (2014); Buchanan *et al*.,

Taxon	Common name	Species citations[a]	Author
			(2017); Oxenrider *et al*. (2018); Odell *et al*., (2021); Hjort Toms *et al*. (2022)
Emydoidea blandingii	Blanding's Turtle	16	Rowe and Moli (1991); Piepgras and Lang (2000); Joyal *et al* (2001); Innes *et al*. (2008); Beaudry *et al*. (2010); Dowling *et al*. (2010); Millar and Blouin–Demers (2011); Fortin and Dubois (2012); Paterson *et al*. (2012); Anthonysamy *et al*. (201); Anthonysamy *et al*. (2014); Christensen and Chow–Fraser (2014); Paterson *et al*. (2014); Hasler *et al*. (2015); Zagorski *et al*. (2019); Hamernick *et al*. (2019)
Deirochelys reticularia	Eastern Chicken Turtle	1	Buhlmann (1995)
Emys orbicularis	European Pond Turtle	2	Cadi *et al* (2004); Najbar *et al*. (2015)
Glyptemys insculpta	Wood Turtle	15	Brewster and Brewster (1991); Remsberg *et al*. (2006); Greaves and Litzgus (2007); Paterson *et al*. (2012); Parren (2013); Paterson *et al*. (2014); McCoard *et al*. (2016); McCoard *et al*., (2018); Thompson *et al*., (2018); Cochrane *et al*., (2019); Lapin *et al*. (2019); Hagani *et al*. (2021); Otten *et al*. (2021)
Glyptemys muhlenbergii	Bog Turtle	2	Morrow *et al*. (2001); Somers *et al*. (2007)
Graptemys barbouri	Barbour's Map Turtle	1	Sterrett *et al*. (2015)
Graptemys flavimaculata	Yellow–blotched Map Turtle	1	Jones (1996)
Graptemys geographica	Common Map Turtle	4	Tran *et al*. (2007); Ouellette and Cardille (2011); Freedberg (2020); Nagle and Russell (2020)
Graptemys pseudogeographica	False Map Turtle	1	Bodie and Semlistch (1999)
Malaclemys terrapin	Northern Diamondback Terrapin	1	Lamont *et al* (2021)

Taxon	Common name	Species citations[a]	Author
Pseudemys rubiventris	Northern Red–bellied Turtle	1	Saba and Spotila (2003)
Pseudemys nelsoni	Florida Redbelly Turtle	1	Kramer (1995)
Pseudemys floridana	Florida Cooter	1	Burke and Gibbons (1995)
Trachemys scripta	Yellowbelly Slider	6	Burke and Gibbons (1995); Bodie and Semlistch (1999); Saba and Spotila (2003); Tran *et al*. (2007); Mali *et al*., (2016)
Geoemydidae			
Mauremys rivulata	Western Caspian Turtle	1	Chelazzi *et al*. (2007)
Mauremys sinensis	Chinese Striped–necked Turtle	1	Chen and Lue (2008)
Kinosternidae			
Kinosternon baurii	Striped Mud Turtle	1	Stemle *et al*., (2019)
Kinosternon integrum	Mexican Mud Turtle	2	Pérez–Pérez *et al*., (2017); Aparicio *et al*., (2018)
Kinosternon leucostomum	White–lipped Mud Turtle	1	Morales–Verdeja and Vogt (1997)
Kinosternon sonoriense	Sonoran Mud Turtle	1	Ligon and Stone (2003)
Kinosternon subrubrum	Eastern Mud Turtle	3	Burke and Gibbons (1995); Steen *et al*. (2007); Cordero *et al*. (2012)
Sternotherus carinatus	Razorback Musk Turtle	1	Kavanagh and Kwiatkowski (2016)
Sternotherus odoratus	Stinkpot Turtle	3	Rowe *et al*. (2009); Anthonysamy *et al*. (2014); Laverty *et al*., (2016)
Sternotherus peltifer	Stripeneck Musk Turtle	1	Ennen and Scott (2008)
Sternotherus minor	Loggerhead Musk Turtle	3	Ennen and Scott (2008); Ennen and Scott (2013); Munscher *et al*., (2021)
Pelomedusidae			
Pelomedusa galeata	South African Helmeted Terrapin	1	Price *et al*. (2022)

Taxon	Common name	Species citations[a]	Author
Pelusios castaneus	African Mud Turtle	1	Luiselli *et al* (2006)
Pelusios niger	West African Black Forest Turtle	1	Luiselli *et al* (2006)
Pelusios sinuatus	Serrated Turtle	1	Price *et al*. (2022)
Platysternidae			
Platysternon megacephalum	Big–headed Turtle	1	Sun *et al*. (2014)
Podocnemididae			
Peltocephalus dumerilianus	Big–headed Amazon River Turtle	1	Guilhon *et al*. (2011)
Podocnemis expansa	South American River Turtle	4	Guilhon *et al*. (2011); Ferrara *et al*. (2013); Carneiro and Pezzuti (2015); Bernardes *et al*. (2017)
Podocnemis lewyana	Rio Magdalena River Turtle	1	Alzate–Estrada *et al*., (2019)
Podocnemis sextuberculata	Six–tubercled Amazon River Turtle	2	Fachín–Terán *et al* (2006); Guilhon *et al*. (2011)
Podocnemis unifilis	Yellow–spotted Amazon River Turtle	3	Guilhon *et al*. (2011); Naveda–Rodríguez *et al*. (2018); De Leão *et al*., (2019)
Trionychidae			
Apalone mutica	Smooth Softshelled Turtle	1	Ross *et al*. (2019)
Apalone spinifera	Eastern Spiny Softshel	4	Galois *et al* (2002); Tornabene *et al*., (2017); Schneider *et al*., (2019); Tornabene *et al*., (2019)
Rafetus euphraticus	Euphrates Soft–shelled Turtle	1	Ghaffari *et al*. (2014)

[a] When the same article studied multiple species, the same article is included multiple times in the species study counts presented.

Table 4. Number of articles published in each of the world's freshwater ecoregions (FEOW, 2022).

State	ID	Studies number	Realm	Major Habitat Type	Ecorregion
USA	116	9	Nearctic	Large lakes	Laurentian Great Lakes
	117	1	Neartic	Temperate coastal rivers	St.Lawrence
	118	1	Neartic	Temperate coastal rivers	Northeast US & Southeast Canada Atlantic Drainages
	125	3	Neartic	Temperate coastal rivers	Sacramento – San Joaquin
	132	1	Neartic	Temperate upland rivers	Upper Rio Grande – Bravo
	140	2	Neartic	Temperate coastal rivers	East Texas Gulf
	144	1	Neartic	Temperate upland rivers	US Southern Plains
	145	2	Neartic	Temperate upland rivers	Ouachita Highlands
	148	14	Neartic	Temperate floodplain rivers and wetlands	Upper Mississippi
	149	2	Neartic	Temperate floodplain rivers and wetlands	Lower Mississippi
	150	7	Neartic	Temperate upland rivers	Teays – Old Ohio
	156	3	Neartic	Tropical and subtropical coastal rivers	Florida Peninsula
	157	8	Neartic	Temperate coastal rivers	Appalachian Piedmont
	158	6	Neartic	Temperate coastal rivers	Chesapeake Bay
Canada	110	13	Neartic	Temperate coastal rivers	Southern Hudson Bay
	114	3	Neartic	Temperate coastal rivers	Gulf of St.Lawrence Coastal Drainages
Australia	807	4	Australasia	Temperate coastal rivers	Eastern Coastal Australia
Brazil	316	3	Neotropic	Tropical and subtropical floodplain rivers and wetland complexes	Amazonas Lowlands
	343	1	Neotropic	Tropical and subtropical floodplain rivers and wetland complexes	Paraguay
	344	1	Neotropic	Tropical and subtropical upland rivers	Upper Parana
	323	4	Neotropic	large river deltas	Amazonas Estuary & Coastal

State	ID	Studies number	Realm	Major Habitat Type	Ecorregion
					Drainages
Mexico	169	2	Neotropic	Tropical and subtropical coastal rivers	Rio Balsas
	171	1	Neotropic	Tropical and subtropical coastal rivers	Papaloapan
Japan	642	2	Paleartic	Temperate coastal rivers	Honshu – Shikoku – Kyushu
Taiwan	757	1	Indo–Malay	Tropical and subtropical coastal rivers	Western Taiwan
Iran	701	1	Paleartic	Xeric freshwaters and endorheic (closed) basins	Baluchistan
Poland	404	1	Paleartic	Temperate floodplain rivers and wetlands	Central & Western Europe
Spain	403	1	Paleartic	Temperate coastal rivers	Cantabric Coast – Languedoc
Nigeria	506	1	Afrotropic	large river deltas	Niger Delta
South Africa	578	1	Afrotropic	Temperate coastal rivers	Cape Fold
Colombia	302	2	Neotropic	Tropical and subtropical upland rivers	Magdalena – Sinu
Equador	301	1	Neotropic	Tropical and subtropical coastal rivers	North Andean Pacific Slopes – Rio Atrato
France	403	1	Palearctic	Temperate coastal rivers	Cantabric Coast – Languedoc
Greece	421	1	Palearctic	Temperate coastal rivers	Ionian Drainages

Suplementary material

List of articles used in this article

1. Alzate–Estrada, D.A., Páez, V.P., Cartagena–Otálvaro, V.M. and Bock, B.C. 2020. "Linear Home Range and Seasonal Movements of *Podocnemis lewyana* in the Magdalena River, Colombia." Copeia 108(1).
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3. Anthonysamy, W.J.B., Dreslik, M.J., Mauger, D. and Phillips, C.A. 2014. "A Preliminary Assessment of Habitat Partitioning in a Freshwater Turtle Community at an Isolated Preserve." Copeia 2014(2): 269–278.
4. Aparicio, Á., Mercado, I.E., Ugalde, A.M., Gaona–Murillo, E., Butterfield, T. and Macip–Ríos, R. 2018. "Ecological observations of the Mexican mud turtle (*Kinosternon integrum*) in the Pátzcuaro Basin, Michoacán, México." Chelonian Conservation and Biology 17(2): 284–290.
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CAPÍTULO 2

DIRECTIONAL ANALYSIS AND SPATIAL USE OF *Podocnemis unifilis* IN THE MIDDLE XINGU RIVER, BRAZIL

Manuscrito em Preparação

DIRECTIONAL ANALYSIS AND SPATIAL USE OF *Podocnemis unifilis* IN THE MIDDLE XINGU RIVER, BRAZIL

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RESUMO

Compreender como os regimes hidrológicos influenciam o comportamento espacial de quelônios de água doce é fundamental para a conservação em sistemas fluviais cada vez mais regulados. Neste estudo, investigamos os padrões sazonais de movimentação, orientação direcional e uso do espaço da tartaruga tracajá (*Podocnemis unifilis*) no médio rio Xingu, Amazônia brasileira, sob influência do complexo hidrelétrico de Belo Monte. Utilizamos dados de telemetria via satélite de 32 indivíduos monitorados entre 2017 e 2022, para analisar métricas de deslocamento, orientação azimutal e uso sazonal de habitat ao longo de três setores longitudinais do rio (Montante, Intermediário e Jusante). Foram registradas 2.264 localizações válidas ao longo de 1.637 dias de rastreamento. Embora as fêmeas tenham percorrido distâncias totais maiores em comparação aos machos, não foram observadas diferenças estatisticamente significativas entre os sexos, setores ou estações hidrológicas nas métricas de deslocamento total ou linear. As análises direcionais também não indicaram orientação significativa entre sexos ou estações. Notavelmente, os testes de V não evidenciaram alinhamento direcional em relação às praias de desova. Apesar disso, o comportamento espacial apresentou variação sazonal: durante o período de águas baixas, os indivíduos demonstraram movimentos localizados e forte fidelidade a algumas praias. Em contrapartida, o período de águas altas foi associado à expansão do uso do espaço e à ocupação de habitats temporariamente acessíveis. Essa expansão foi mais evidente nos setores Intermediário e Montante, sugerindo que a conectividade hidrológica é um fator chave na dispersão espacial. Nossos resultados mostram que *P. unifilis* apresenta plasticidade comportamental no uso do espaço, mas ausência de movimentos direcionais consistentes. Esses padrões reforçam a importância de habitats locais heterogêneos e a necessidade de preservar a conectividade sazonal em ambientes fluviais impactados por empreendimentos hidrelétricos.

Palavras-chave: Quelônios amazônicos, Influência hidrológica, Ecologia aquática, Estatísticas circulares, Métricas de movimentação, Análise direcional.

ABSTRACT

Understanding how hydrological regimes influence the spatial behavior of freshwater turtles is essential for conservation in increasingly regulated river systems. In this study, we have investigated seasonal patterns of movement, directional orientation, and space use of the yellow-spotted river turtle (*Podocnemis unifilis*) in the middle Xingu River, Brazilian Amazon, under the influence of the Belo Monte hydroelectric complex. Using satellite telemetry data from 32 individuals monitored between 2017 and 2022, we have analyzed displacement metrics, azimuthal orientation, and seasonal habitat use across three longitudinal sectors of the river (Upstream, Midstream, and Downstream). A total of 2,264 valid locations were recorded over 1,637 tracking days. Although females traveled greater total distances compared to males, no statistically significant differences were found between sexes, river sectors, or hydrological seasons in either total or linear movement metrics. Directional analyses also revealed no significant orientation by sex or season. Notably, V-tests showed no directional alignment toward nesting beaches. Despite this, spatial behavior varied seasonally: during the low-water period, individuals exhibited localized movements and strong fidelity to specific beaches. In contrast, the high-water period was associated with an expansion in space use and the occupation of temporarily accessible habitats. This expansion was most pronounced in the Midstream and Upstream sectors, suggesting that hydrological connectivity is a key driver of spatial dispersal. Our results show that *P. unifilis* exhibits behavioral plasticity in space use but lacks consistent directional movement. These patterns underscore the importance of maintaining heterogeneous local habitats and preserving seasonal connectivity in riverine environments affected by hydropower development.

Keywords: Amazonian Chelonians, Hydrological Influence, Aquatic Ecology, Circular Statistics, Movement Metrics, Directional Analysis.

INTRODUCTION

The Amazon Basin, encompassing an extensive area of approximately 5 million km², is recognized as the largest tropical rainforest in the world and harbors an enormous diversity of flora and fauna (Perkison, 1968; Haugaasen and Peres, 2006; Hansen *et al.*, 2013; Ter Steege *et al.*, 2013; Sheil, 2014). The Amazon is fundamental to global climate balance and the maintenance of ecological processes, acting as a prominent carbon sink and affecting regional and global precipitation dynamics (Davidson *et al.*, 2012; Malhi *et al.*, 2008; Matricardi *et al.*, 2020; Lapola *et al.*, 2023). Furthermore, this biome plays an important role in biodiversity conservation, accommodating a multitude of endemic species and providing essential ecosystem services (Goulding *et al.*, 2003; Lewinsohn *et al.*, 2005; Fearnside, 2005).

However, population growth and the intensification of economic activities have resulted in environmental degradation in the Amazon, including intensive hunting and wildlife capture for trade, leading to worrying population declines of fauna species (Smith, 1979; Fearnside, 1990; Betts *et al.*, 2008; Lapola *et al.*, 2023). Agricultural expansion, mining, and the construction of roads and hydroelectric dams have also contributed to these declines, causing ecosystem fragmentation and reducing forest cover, directly affecting biodiversity (Fearnside, 1990, 2005; Alho, 2011; Laurance *et al.*, 2014).

Among the most concerning species, *Podocnemis unifilis* (yellow-spotted river turtle) has suffered drastic population reductions (Tortoise & Freshwater Turtle Specialist Group, 1996; Santos-Arraes *et al.*, 2016; Flores-Ponce *et al.*, 2022) due to overexploitation (Bates, 1863; Smith, 1979; Pritchard and Trebbau, 1984; Pantoja-Lima *et al.*, 2014; Rebêlo and Pezzuti, 2000; Moll & Moll, 2004; Fachín-Terán, 2005; Vogt, 2008; Ataídes *et al.*, 2010; Pezzuti *et al.*, 2010; Casal *et al.*, 2013), habitat loss (Tortoise & Freshwater Turtle Specialist Group, 1996), illegal trade (Kemenes and Pezzuti, 2007), climate change (Eisemberg *et al.*, 2016; Butler, 2019; Forero-Medina *et al.*, 2021), and exposure to heavy metals (*e.g.*, mercury and pesticides; Pignati *et al.*, 2018 a,b; Borges *et al.*, 2022).

The species is classified as “Vulnerable” by the International Union for Conservation of Nature - IUCN (IUCN, 2022) and as “Near Threatened” on the national list of threatened species (MMA, 2022). It is also included in Appendix II of CITES and is considered endangered by the U.S. Fish and Wildlife Service (USFWS) (Vogt, 2008).

This species is considered threatened also due to its longevity and late sexual maturation (Pritchard, 1979), which make individuals particularly susceptible to exploitation throughout their lives (Norris and Michalski, 2013). These characteristics significantly increase the risk of capture before they reach reproductive maturity, compromising the long-term viability of populations (Smith, 1979; Moll and Moll, 2004). Moreover, their dependence on suitable beaches for nesting restricts reproduction to scarce and often exposed habitats, increasing their vulnerability to predation by both animals and humans (Júnior *et al.*, 2009; Pignati *et al.*, 2013; Arraes *et al.*, 2014; Guimarães *et al.*, 2023). The exposure of these reproductive sites also makes them susceptible to extreme climatic events, which can lead to nest destruction (Ferrara *et al.*, 2014; Fagundes *et al.*, 2018; Guimarães *et al.*, 2023). Additionally, temperature plays a crucial role in determining the sex ratio of hatchlings, a process that can be altered by environmental changes, resulting in population imbalances (Alho and Pádua, 1982; Ferreira-Júnior and Castro, 2006; Lubiana and Ferreira Júnior, 2009; Bonach *et al.*, 2011; Alves Júnior *et al.*, 2012).

P. unifilis holds significant ecological importance, being responsible for seed dispersal and maintenance of water quality (Moll and Jansen, 1995; Vogt, 2008), and also has great economic value for some regions of the Amazon (Smith, 1979; Alves and Santana, 2008; Fachín-Terán *et al.*, 2004; Pezzuti *et al.*, 2010; Santos and Fiori, 2020). Although this species has been protected in Brazil since 1979 (Cantarelli *et al.*, 2014), its protection has been less effective in certain areas (Jaffé *et al.*, 2008; Cantarelli *et al.*, 2014). The lack of adequate enforcement and the difficulty in controlling illegal activities in vast areas of the Amazon, specifically in their reproductive environments, make this species highly vulnerable (Kemenes and Pezzuti, 2007; Jaffé *et al.*, 2008; Cantarelli *et al.*, 2014; Forero-Medina *et al.*, 2021). Furthermore, changes in hydrological regimes along rivers, due to the construction of hydroelectric dams and climate change, are known to directly impact nesting sites and migration routes of river turtles (Alho and Pádua, 1982; Alcântara *et al*., 2013; Eisemberg *et al*., 2016; Simoncini *et al*., 2019; Ataídes *et al*., 2021).

Both adult individuals and eggs are widely consumed by riverside populations in the Amazon, which further aggravates the population decline of these species (Alcântara *et al*., 2013; Ataídes *et al*., 2010; Pantoja-Lima *et al*., 2012; Norris and Michalski, 2013; Cajaiba *et al*., 2015). This practice, deeply rooted in cultural traditions, represents an important source of protein for local communities, but at high and unmanaged levels, it significantly contributes to the overexploitation of populations (Miorando *et al*., 2013; Arraes *et al*., 2016). The continuous removal of reproductive females and egg collection directly decrease the reproductive success and recruitment rate of the species, impacting their recovery capacity over time (Caputo *et al*., 2005; Arraes *et al*., 2016).

The increasing demand for consumption and trade of these turtles, not only in riverside communities but also in urban markets, has increased the pressure on wild populations (Fachín-Terán *et al*., 2000; Camillo *et al*., 2012; Lopes *et al*., 2012). Therefore, intensive capture in nesting areas and the illegal trade of eggs and meat intensify the risk of local extinction in various regions, especially when coupled with habitat loss and natural predation (Vogt, 2008; Ferrara *et al*., 2014; Pantoja-Lima *et al*., 2014), and have resulted in an evolutionary trap for Amazonian chelonian populations (Hale *et al*., 2016; Quintana *et al*., 2019; Robertson & Blumstein, 2019).

P. unifilis has distribution areas that reflect its need for specific resources for feeding and reproduction (Naveda-Rodríguez *et al*., 2018; Cueva *et al*., 2018; Ponce de Leão *et al*., 2019). The home range of this species can vary significantly throughout the year, depending on factors such as food availability, hydrological conditions, and reproductive needs (Moll and Moll, 2004; Fagundes *et al*., 2018; Ponce de Leão *et al*., 2019). The nesting period of *P. unifilis* in the Xingu River generally occurs in August and September, with an incubation period of approximately 65 days, which may vary in response to environmental conditions (Vogt, 2008; Ferreira-Júnior and Castro, 2010; Lacava & Balestra, 2019).

Females of this species tend to select higher nesting sites to minimize the risk of nest flooding during the rainy season (Vanzolini, 2003; Ferreira-Júnior and Castro, 2010; Pignati *et al*., 2013; Ferrara *et al*., 2014). However, the species demonstrates considerable behavioral plasticity, apparently not having strict requirements regarding nesting site selection, with nesting already recorded in anthropogenic areas, indicating its ability to adapt to different types of environments (Santos, 2013).

Few studies have sought to evaluate the movement patterns of Podocnemididae species, relying mainly on VHF radio telemetry techniques (Book *et al*., 1998; Guilhon *et al*., 2011; Naveda-Rodríguez *et al*., 2018; Ponce de Leão *et al*., 2019) and, in some cases, on the use of GPS (Guilhon *et al*., 2011; Souza, 2012; Carneiro and Pezzuti, 2015). Most of these studies have been conducted on the giant South American river turtle (*Podocnemis expansa*). More recently, the use of technologies such as satellite tracking has been increasingly employed to understand the movement patterns and habitat use of species, particularly turtles (Godley *et al*., 2008; Schofield *et al*., 2010; Christensen and Chow-Fraser, 2014; Cochrane *et al*., 2019; Ribeiro *et al*., 2024). Despite technological advancements, little is still known about the movement patterns of *Podocnemis unifilis*.

What is known is that the movement of *P. unifilis* is intrinsically linked to the hydrological cycles of the Amazon, being shaped by different phases that directly influence the availability of areas for feeding, resting, and reproduction (Ponce de Leão *et al*., 2019; Fagundes *et al*., 2021). During the reproductive period, females generally move over greater distances in search of suitable beaches for nesting, while males tend to remain in more restricted foraging areas (Moll and Moll, 2004; Ferrara *et al*., 2014). Seasonal variation in water levels also directly impacts turtle movements, with Flooding season expanding available habitats and facilitating greater dispersion, while the Dry season restricts their movements to remaining water bodies, limiting their activities (Bodie, 2001; Fagundes *et al*., 2021).

However, to date, there are no specific studies focused on evaluating the movement patterns of *Podocnemis unifilis* in the Xingu River. In light of this gap, the present study aims to fill this need by investigating how the movement patterns of *P. unifilis* and the hydrological cycles of the Xingu river shape the displacements and behavior of this species.

The specific objectives of this study were to: i) assess the directional orientation behavior of *Podocnemis unifilis*; ii) investigate the seasonal movement patterns of the species in the middle Xingu

River by comparing spatial metrics such as total distance traveled, linear displacement, and average daily movement between low-water and high-water periods; iii) identify, map, and characterize areas of highest use intensity; and iv) compare space use among the different river sectors (Upstream, Midstream, and Downstream).

MATERIALS AND METHODS:

Target species – *Podocnemis unifilis* Troschel, 1848, commonly known as "tracajá," is a medium-sized species with a carapace length of up to 46.5 cm and a weight of 11 kg (Vogt, 2008). This species occurs in South America, where it is registered in Colombia, Venezuela, Guyana, French Guiana, Suriname, Brazil, Peru, Ecuador, and Bolivia (Pritchard & Trebbau, 1984; Dixon & Soini, 1986; Peñaloza *et al.*, 2013; Uetz *et al.*, 2024). In Brazil, it is found in the Amazon and Cerrado biomes, and its distribution covers the Amazon, Tocantins/Araguaia, Atlantic Northeast and Paraguay river basins (Vogt, 2008).

Due to the historical exploitation and threats faced by species of the Podocnemididae family in the Amazon, the Brazilian government established the Amazon Turtle Project (PQA) in 1979 (IBAMA, 1989; Cantarelli *et al.*, 2014; Fagundes *et al.*, 2021; Lacava *et al.*, 2024). This program aims to protect the nesting areas of these and other species across several states. In this context, the need to develop a comprehensive conservation plan incorporating various strategies was identified, with a particular focus on preserving nesting areas (Cantarelli *et al.*, 2014; MMA, 2019). In 2015, the Federal Government established the National Action Plan for the Conservation of Amazonian Turtles (PAN Quelônios Amazônicos), targeting the same species covered by the PQA (MMA, 2019; Fagundes *et al.*, 2021). Currently, PAN Quelônios Amazônicos serves as the main strategic instrument for the conservation of Amazonian turtles, particularly *P. unifilis* in Brazil.

Study area – The study was conducted along the Xingu River (Pará, Brazil), covering three sections defined by their position relative to the Belo Monte Hydroelectric Complex: upstream (above the Pimental dam, near Altamira), midstream (between the Pimental dam and the main powerhouse), and downstream (below the powerhouse, including Volta Grande and the REVIS reserve) (Figure 1). The region has a humid tropical climate with a distinct hydrological seasonality—rainy season from December to April and dry season from June to November (ANA, 2013; IBGE, 2020).

The Xingu River, a major clearwater Amazonian tributary, spans ~2,500 km and drains 510,000 km² across Amazon–Cerrado ecotones (Sioli, 1985; Goulding *et al.*, 2003). Its geomorphological complexity—floodplains, rapids, anastomosing channels, and várzea—supports diverse aquatic habitats, particularly in Volta Grande (Sawakuchi *et al.*, 2015; Kalacska *et al.*, 2019). Recognized for its ecological importance, the basin is targeted by conservation policies such as the National Action Plan for Endemic and Threatened Species of the Lower and Middle Xingu (ICMBio, 2012).

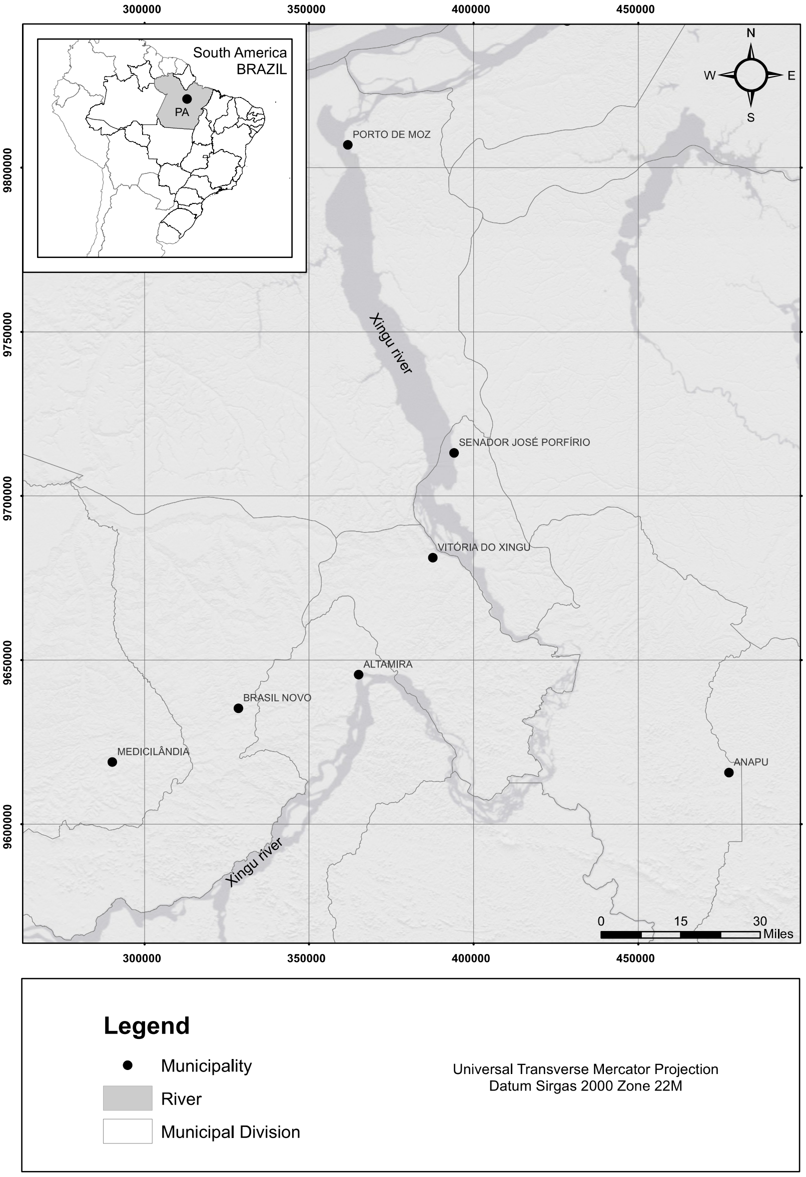

Figure 1 - Map of the Xingu River stretch in Pará, Brazil, indicating the study area of 32 individuals monitored between 2017 and 2022.

Data Collection. – Transmitters. Individuals were captured using various methods (Balestra *et al.*, 2016) during multiple field campaigns along the Xingu River, as part of the Turtle Conservation and Management Program of the Belo Monte Hydroelectric Power Plant. Each turtle was fitted with a satellite transmitter attached to the posterior portion of the carapace using non-toxic epoxy resin. The transmitters (models Kiwisat K2G 158A, K2G 273C, and K2G 173A) were programmed to record geographic positions at regular intervals of 2 to 3 hours, storing date, time, and coordinates (latitude/longitude, WGS84 datum). Locations were transmitted via satellite uplink (Argos system) whenever the animal surfaced, allowing for remote tracking without the need for frequent recapture.

Data Analysis – Data Filtering. A preliminary evaluation of the telemetry dataset was conducted to ensure data quality. This involved the manual exclusion of anomalous or biologically implausible locations (*i.e*. urban areas or roads) as well as all Class Z records, which are known for low positional accuracy (Vincent *et al*., 2002; Costa *et al*., 2010; Patterson *et al*., 2010; ARGOS, 2016; Hooten *et al*., 2017). Data segments with gaps longer than 3 to 5 days were split into independent records, following Douglas *et al*. (2012). The Douglas-Argos Filter (DAF) was applied, using spatial criteria such as distance and turning angle thresholds, combined with a conservative speed limit of 0.5 m/s based on related freshwater turtle species (Freitas *et al*., 2008; Shimada *et al*., 2012). In addition, the Local Outlier Factor (LOF) method was used to identify and exclude statistical outliers (Breunig *et al*., 2000; Aggarwal, 2015).

Sampling Effort and Bias Control - To ensure that movement patterns were not influenced by variation in tracking effort, a Spearman correlation was performed between the number of monitored days and the number of valid locations per individual (Corder & Foreman, 2014).

Directional Analysis and Orientation Structure - The direction of movements was analyzed through the calculation of azimuths between successive locations, representing the direction of each movement performed by an individual. For each set of azimuths, the Rayleigh test was applied to assess whether the angular distribution was random or concentrated in a predominant direction (Batschelet, 1981; Pewsey *et al*., 2013; Landler *et al*., 2021). Directional patterns were graphically visualized using rose diagrams (Fisher, 1995; Afonso *et al*., 2020; Ferreira *et al*., 2022).

Additionally, descriptive circular statistics such as mean direction, circular standard deviation, and the concentration parameter κ were calculated to describe the consistency of orientation within each group of individuals (Otieno & Anderson-Cook, 2006; Pewsey *et al*., 2013).

Statistical Modeling of Movement Metrics - The movement metrics evaluated included total distance traveled (Total_km), linear range (Linear_km), and mean daily distance (Daily_km). These variables were analyzed using generalized linear models (GLMs) with a Gamma distribution and a log link function, appropriate for the asymmetric and positive distribution of the data (McCrimmon, 2018).

Hotspots and spatial fidelity – In order to identify areas with greater intensity of space use, Kernel Density Estimation (KDE) was applied based on the telemetry-derived location data (Silverman, 1986; Borger *et al*., 2006; Kie *et al*., 2010). The resulting density maps allowed the identification of regions with higher clustering of locations, interpreted as core areas associated with critical behaviors such as thermoregulation, foraging, or nesting (Cagnacci *et al*., 2010)

RESULTS

Locations and Temporal Distribution. - After applying the filtering criteria described in the methodology, a total of 2,264 valid locations for *Podocnemis unifilis* were obtained over 1,637 days of monitoring. These locations were distributed among 32 individuals tracked throughout the study. The number of locations per individual ranged from 11 to 510, with an average of 71.31 ± 94.77 locations per individual (Table 1).

The individuals with the highest number of records and monitoring duration were PTT 183643, with 510 locations over 497 days, and PTT 163009, with 254 locations over 284 days. In contrast, individuals PTT 183664, PTT 183655, and PTT 183660 presented the lowest tracking intensities: the first had 11 locations over 60 days, the second 13 locations over 39 days, and the third 13 locations over 333 days. The mean tracking duration across individuals was 160.59 ± 129.99 days, indicating substantial variation in monitoring effort and temporal coverage. These differences in effort and record distribution should be considered in the interpretation of spatial metrics and comparative analyses. There is a moderate and statistically significant positive correlation (ρ = 0.58; *p* = 0.0005; Figure 2) between the two metrics, indicating that individuals monitored for a longer period of time tend to have a greater number of valid locations recorded throughout the study.

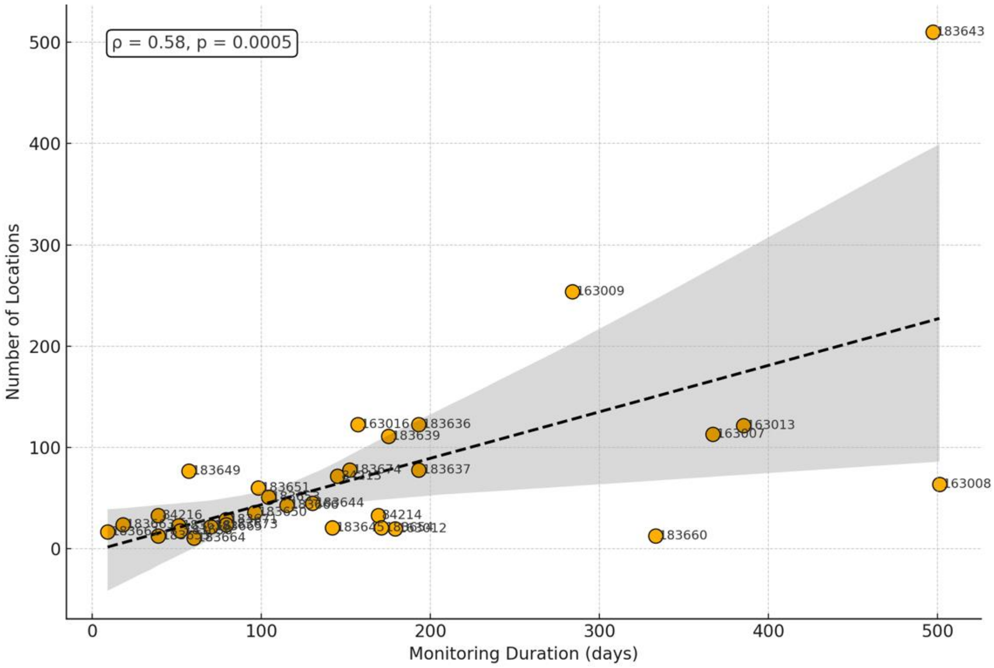

Figure 2 - Relationship between monitoring duration and number of locations for each tracked *Podocnemis unifilis* individual.

Table 1 - List of *Podocnemis unifilis* individuals monitored by satellite telemetry. The table presents the species, the sex of the individual (M for male and F for female), and the ID (PTT number) code used for satellite monitoring.

ID	Sex	Model Tag	Installation Date	First Record	Last Record	Total Days Monitored	Total Locations	Coordenates (Capture)		Records by Year
								lat	long	
84213	M	K2G 158A	13/07/2019	2019-07-13	2019-12-05	145	72	-3,4556	-51,9632	{2019: 72}
84214	M	K2G 158A	13/07/2019	2019-07-13	2019-12-29	169	33	-3,4535	-51,9655	{2019: 33}
84216	F	K2G 158A	16/10/2019	2020-02-15	2020-03-25	39	33	-3,4235	-51,7271	{2020: 33}
163007	F	K2G 273C	24/11/2014	2017-07-16	2018-07-18	367	113	-3,3889	-52,0186	{2017: 84, 2018: 29}
163008	F	K2G 273C	16/07/2017	2017-07-24	2018-12-07	501	64	-3,4724	-51,9221	{2017: 6, 2018: 58}
163009	F	K2G 273C	17/07/2017	2017-07-17	2018-04-26	283	254	-3,3906	-52,0318	{2017: 156, 2018: 98}
163012	F	K2G 273C	17/07/2017	2017-08-09	2018-02-03	178	20	-3,3364	-51,9997	{2017: 17, 2018: 3}
163013	F	K2G 273C	17/07/2017	2017-07-21	2018-08-09	384	122	-3,4863	-51,9572	{2017: 34, 2018: 88}
163016	F	K2G 273C	26/10/2017	2017-10-29	2018-04-04	157	123	-3,3420	-51,9854	{2017: 33, 2018: 90}
183636	F	K2G 173A	23/09/2019	2019-10-28	2020-05-08	193	123	-3,5140	-51,7027	{2019: 2, 2020: 121}
183637	M	K2G 173A	17/10/2019	2019-11-01	2020-05-12	193	78	-3,5110	-51,7053	{2019: 17, 2020: 61}
183638	F	K2G 173A	17/10/2019	2020-01-12	2020-03-02	50	23	-3,5147	-51,7210	{2020: 23}
183639	M	K2G 173A	17/10/2019	2019-12-07	2020-05-29	174	111	-3,4413	-51,7270	{2019: 5, 2020: 106}
183643	F	K2G 173A	17/10/2019	2019-10-22	2021-03-02	497	510	-3,4457	-51,9400	{2019: 38, 2020: 400, 2021: 72}
183644	M	K2G 173A	19/10/2019	2019-11-27	2020-04-04	129	45	-3,2684	-52,1979	{2019: 6, 2020: 39}
183645	M	K2G 173A	19/10/2019	2019-10-29	2020-03-19	142	21	-3,3357	-52,2081	{2019: 2, 2020: 19}
183649	F	K2G 173A	18/10/2019	2019-10-20	2019-12-16	57	77	-2,7363	-52,0675	{2019: 77}
183650	F	K2G 173A	20/11/2019	2020-01-17	2020-04-21	95	36	-3,4879	-52,2573	{2020: 36}
183651	F	K2G 173A	18/11/2019	2019-12-10	2020-03-17	98	60	-3,6205	-52,3539	{2019: 5, 2020: 55}
183653	M	K2G 173A	18/11/2019	2019-11-27	2020-03-09	103	51	-3,5532	-52,3886	{2019: 38, 2020: 13}

ID	Sex	Model Tag	Installation Date	First Record	Last Record	Total Days Monitored	Total Locations	Coordenates (Capture)		Records by Year
								lat	long	
183654	M	K2G 173A	29/01/2020	2020-01-30	2020-07-19	171	21	-2,7321	-52,0682	{2020: 21}
183655	M	K2G 173A	13/02/2020	2020-02-14	2020-03-24	39	13	-3,3613	-51,7303	{2020: 13}
183658	F	K2G 173A	13/02/2020	2020-02-14	2020-04-06	52	18	-3,4029	-51,7474	{2020: 18}
183660	M	K2G 173A	13/02/2020	2020-04-17	2021-03-16	333	13	-2,7311	-52,0645	{2020: 4, 2021: 9}
183661	M	K2G 173A	23/09/2019	2020-04-20	2020-04-29	9	17	-2,7308	-52,0473	{2020: 17}
183663	F	K2G 173A	27/04/2020	2020-04-28	2020-05-15	17	24	-3,4557	-51,9640	{2020: 24}
183664	F	K2G 173A	27/04/2020	2021-04-23	2021-06-22	60	11	-3,2363	-52,0903	{2021: 11}
183665	F	K2G 173A	17/04/2021	2020-11-17	2021-01-26	70	22	-3,2121	-52,1670	{2020: 7, 2021: 15}
183666	F	K2G 173A	17/11/2020	2020-12-19	2021-04-12	114	43	-3,2862	-52,0727	{2020: 5, 2021: 38}
183671	F	K2G 173A	28/06/2021	2021-10-21	2022-01-07	78	29	-3,2219	-52,1845	{2021: 18, 2022: 11}
183673	F	K2G 173A	13/07/2019	2021-10-21	2022-01-07	78	24	-3,2841	-52,0871	{2021: 18, 2022: 6}
183674	F	K2G 173A	19/07/2019	2019-11-11	2020-04-11	152	78	-3,4321	-51,9430	{2019: 5, 2020: 73}

Directional Structure and Spatial Variability in Movement – For males, the mean azimuth was 103.13°, with a circular standard deviation of 136.12°. The Rayleigh test did not indicate statistical significance (R = 0.0595; p = 0.1936), suggesting the absence of a predominant direction (Figure 3). During the low-water period, the males presented a mean orientation of 119.34° (SD = 137.15°), also without significance (R = 0.0570; p = 0.2693) (Figure 3).

In high water, the mean was 53.64° (SD = 113.43°), equally not significant (R = 0.1409; p = 0.3050), reinforcing the pattern of high seasonal directional dispersion among males (Figure 3). For females, the overall mean azimuth was 80.22°, with a circular standard deviation of 149.67°. The Rayleigh test was also not significant (R = 0.0330; p = 0.1434), indicating widely distributed movement and no predominant orientation trend (Figure 3). In low water, the mean was 79.25° (SD = 155.00°; R = 0.0257 and *p* = 0.3356). Comparisons between males and females in both low water (W = 3.4771, df = 2, p = 0.1758) and high water (W = 0.27084, df = 2, p = 0.8733) were non-significant, indicating similar movement patterns between the sexes. Similarly, within each sex, no seasonal differences were observed: for females (W = 1.3836, df = 2, p-value = 0.5007) and for males (W = 1.9026, df = 2, p = 0.3862) (Figure 4; Table 2).

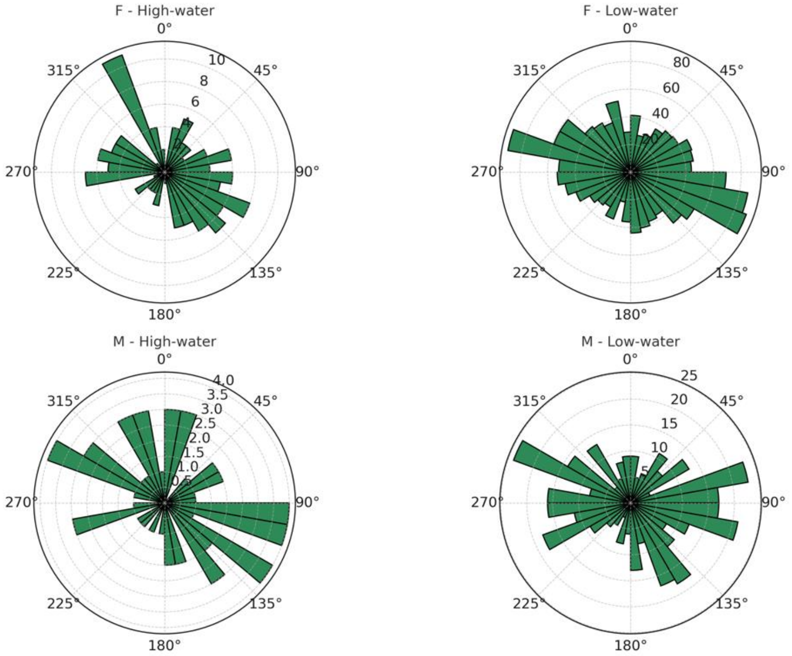

Figure 3 - Directional distribution (azimuth) of successive displacements of *Podocnemis unifilis* in the Xingu River, Brazil, according to sex and hydrological season.

Table 2 - Descriptive statistics of the orientation of *Podocnemis unifilis displacements* in the Xingu River, Brazil, based on azimuths between successive locations.

Group	**Mean Azimuth (°)**	**Circular SD (°)**	**R**	**p-value**
Males (overall)	103.13°	136.12°	0.0595	0.1936
Males (low-water)	119.34°	137.15°	0.0570	0.2693
Males (high-water)	53.64°	113.43°	0.1409	0.3050
Females (overall)	80.22°	149.67°	0.0330	0.1434
Females (low-water)	79.25°	155.00°	0.0257	0.3356
Comparison	**Season**	**Factor tested**	**W-statistic**	**df**
Male vs Female (Low-water)	Low-water	Sex	3.4771	2
Male vs Female (High-water)	High-water	Sex	0.27084	2
Females (seasonal)	All sectors	Season (Females)	1,3836	2

When considering the river sectors, the results indicated subtle variations in average displacement patterns. In the Intermediate sector, the mean azimuth was 101.41°, with an SD of 142.92° and a non-significant Rayleigh test (R = 0.0446; p = 0.0775). The Upstream sector had a similar mean of 102.15°, with greater dispersion (SD = 168.98°), and no significance (R = 0.0129; p = 0.8696).

In the downstream sector, a distinct pattern was observed: the mean azimuth was 46.14°, with a standard deviation of 102.45°, and the Rayleigh test indicated significant directional orientation (R = 0.2022; p = 0.0061), suggesting that the displacements in this sector were more directionally concentrated (Figure 4).

Despite the visual differences observed in the average directions and amplitudes of dispersion between the sectors of the Xingu River, differences were observed only between the Upstream and Intermediate sectors (*W* = 1.3612; *df* = 2; *p* = 0.5063). On the other hand, the comparisons between Amount and Downstream (*W* = 8.8815; *df* = 2; *p* = 0.0118) and between Intermediate and Downstream (*W* = 7.1168; *df* = 2; *p* = 0.0285) were not significant (Table 3).

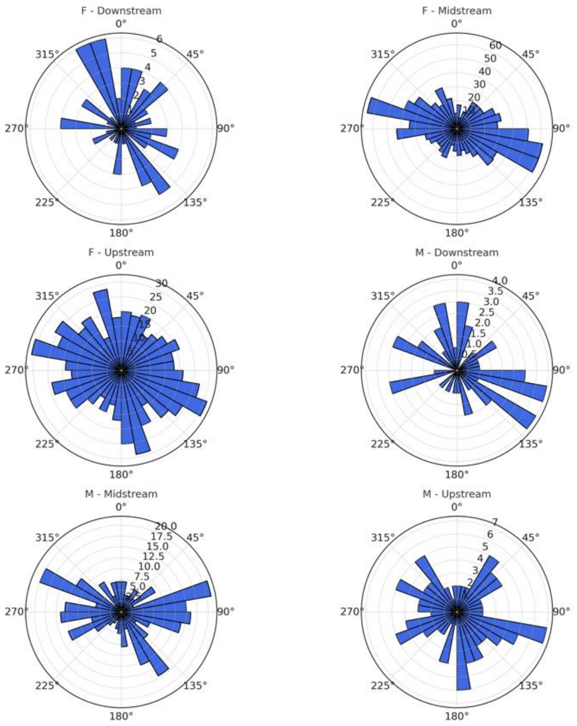

Figure 4 - Directional distribution (azimuth) of successive displacements of *Podocnemis unifilis* in the Xingu River, Brazil, according to the longitudinal sector of the river and the sex of the individuals.

Table 3 - Descriptive statistics of the orientation of the displacements of *Podocnemis unifilis* by sector of the Xingu River (Upstream, Midstream and Downstream) And paired comparisons between the sectors based on the Mardia–Watson–Wheeler test, with the respective values of the W statistic, degrees of freedom (*df*) and *p-values.*

River Sector	Mean azimuth (°)	Circular SD (°)	Rayleigh R
Midstream	101.41	142.92	0.0446
Upstream	102.15	168.98	**0.0129**
Downstream	46.14	102.45	0.2022
Comparison	**W-statistic**	**df**	**p-value**
Upstream vs. Midstream	1.3612	2.0	0.5063
Upstream vs. Downstream	8.8815		**0.0118**
Midstream vs. Downstream	7.1168		**0.0285**

In all the groups analyzed, movements were not significantly oriented toward the nearest river beaches. No combination of sex, river sector, and hydrological season showed *p*-values below the significance threshold ($p < 0.05$), indicating no preferential orientation toward the expected azimuth (Figure 5; Table 4).

In the Upstream sector, females during the low-water season had a mean movement direction of 114.46°, while the expected direction toward the nearest beach was 156.22°. The V-test statistic was V = 8.37, with *p* = 0.259. During the high-water season, the observed mean direction was 335.87° (Expected = 135.29°; V = –8.53; *p* = 0.730; Figure 5; Table 4).

In the Midstream sector, females showed a mean direction of 106.74° during high water (Expected = 191.62°; V = 4.34; *p* = 0.394), and 326.27° during low water (Expected = 172.21°; V = –7.57; *p* = 0.690). Among males, results were likewise not significant, with *p*-values > 0.25 (Figure 5; Table 4).

In the Downstream sector, where beaches are spatially closer, females during the low-water season had a mean movement direction of 37.28°, compared to the expected direction of 136.30° (V = –2.63; *p* = 0.665). Males, monitored only during the high-water season, had a mean direction of 63.08° (Expected = 136.81°; V = 3.46; *p* = 0.238). None of these values reached statistical significance (Figure 5; Table 4).

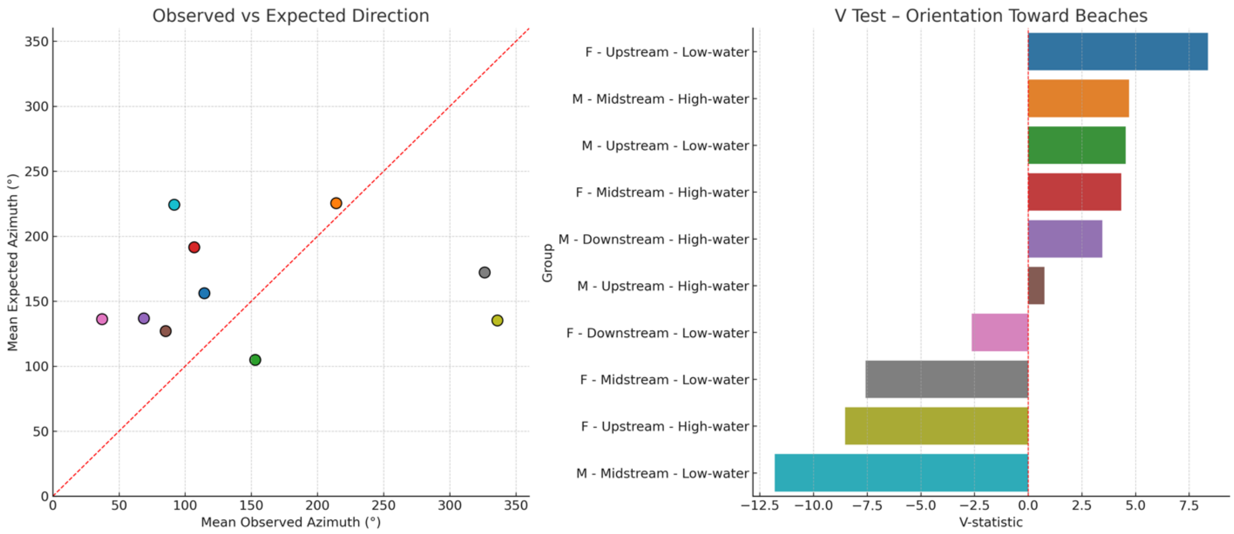

Figure 5 - Directional alignment of *Podocnemis unifilis* movements in relation to the nearest river beach, based on group-level V-tests.

Table 4 - V-test results evaluating movement orientation of *Podocnemis unifilis* individuals toward the nearest river beach, grouped by sex, river sector, and hydrological season.

Group	Mean_Observed (°)	Mean_Expected (°)	Nearest Beach	V-statistic	p-value
F - Midstream - High-water	106.7	191.6	Arapuja (Praia Do Arapuja)	4.344	0.394
F - Midstream - Low-water	326.2	172.2	Arapuja (Praia Do Arapuja)	-7.566	0.690
F - Downstream - Low-water	37.2	136.3	Pitanguinha	-2.628	0.665
F - Upstream- High-water	335.8	135.2	Altamira (Lago Da Olaria)	-8.528	0.730
F - Upstream - Low-water	114.5	156.2	Altamira (Lago Da Olaria)	8.373	0.259
M - Midstream - High-water	214.1	225.5	Furo Trindade (Ilha Do Pirulito)	4.700	0.310
M - Midstream - Low-water	91.6	224.2	Arapuja (Praia Do Arapuja)	-11.808	0.934
M - Downstream - High-water	68.7	136.8	Pitanguinha	3.461	0.238
M - Upstream- High-water	85.2	127.1	Altamira (Lago Da Olaria)	0.755	0.450
M - Upstream - Low-water	152.8	104.9	Altamira (Lago Da Olaria)	4.541	0.164

Movement Patterns and Spatial Use - Individuals of *Podocnemis unifilis* traveled an average total distance of 53.8 km (SD = 64.3), with values ranging widely from 1.8 km to 304.5 km throughout the monitoring period (Table 5). Although some individuals registered cumulative displacements exceeding 300 km, their maximum linear ranges were considerably smaller, averaging 9.8 km with a maximum of 25.0 km, suggesting movement predominantly restricted to localized river stretches. One particular female (ID 163009) traveled over 300 km in total but remained within a ~23 km stretch of the river, repeatedly moving within that area. In general, long-distance movements were rare, and most individuals exhibited relatively localized spatial use patterns.

On average, females traveled approximately 63 km over the monitoring period, while males traveled ~35 km, with mean daily movement rates of ~0.42 km/day and ~0.34 km/day, respectively. However, these differences were not statistically significant after controlling for monitoring effort, and no effect of sex was detected on total distance traveled (GLM Gamma, p = 0.798) or on linear range (GLM Gamma, p = 0.918).

Females in the Midstream sector during the dry season traveled on average 109.8 km (SD = 49.9), with daily movements of approximately 0.4 km/day over monitoring periods lasting up to 501 days. In the Upstream sector during the dry season, females also showed extensive movements (mean = 74.6 km, maximum = 304.1 km). In contrast, females in the Downstream sector during the dry season traveled on average only 18.7 km, with a daily movement rate of ~0.3 km/day. Males showed similar patterns: for example, males in the Downstream sector during the dry season traveled an average of 13.4 km, with a daily mean of ~0.2 km/day.

Nevertheless, similar to the pattern observed by sex, sector effects were not statistically significant in the GLM ($p = 0.109$ for Downstream; $p = 0.713$ for Upstream). On the other hand, hydrological season (Season) showed a marginal effect in the model for total distance, with an estimated twofold increase in expected distance during the dry season (coefficient = 0.70, $p = 0.094$, 95% CI = [–0.12, 1.52]). Although this value did not reach statistical significance, the observed variation may be partially associated with differences in monitoring duration. For the linear range (Linear_km), no predictor variable (sex, sector, or season) had a statistically significant effect (all $p > 0.35$; Table 6).

Table 5 - Descriptive statistics of movement metrics for *Podocnemis unifilis* by sex, river sector (Upstream, Midstream, Downstream), and hydrological season (Low-water and High-water).

Sex	**Sector**	**Season**	**Tracking_days_mean**	**Tracking_days_sd**	**Tracking_days_min**	**Tracking_days_max**	**Total_km_mean**	**Total_km_sd**	**Total_km_min**	**Total_km_max**	**Linear_km_mean**	**Linear_km_sd**	**Linear_km_min**	**Linear_km_max**	**Daily_km_mean**	**Daily_km_sd**
F	Midstream	High-water	40,0	15,8	18,0	52,0	16,6	14,0	1,8	32,6	11,5	12,0	0,4	25,0	0,6	0,8
	Midstream	Low-water	345,6	165,4	152,0	501,0	109,8	49,9	36,7	157,5	11,0	5,9	5,1	17,6	0,4	0,2
	Downstream	Low-water	57,0	Not calculated	57,0	57,0	18,7	Not calculated	18,7	18,7	8,7	Not calculated	8,7	8,7	0,3	Not calculated
	Upstream	High-water	78,0	25,5	60,0	96,0	11,9	0,5	11,5	12,3	4,0	1,6	2,9	5,1	0,2	0,1
	Upstream	Low-water	158,7	103,5	70,0	367,0	74,6	97,0	3,4	304,1	12,3	7,0	2,8	22,4	0,5	0,4
M	Downstream	High-water	39,0	Not calculated	39,0	39,0	44,4	Not calculated	44,4	44,4	20,6	Not calculated	20,6	20,6	1,1	Not calculated
	Midstream	Low-water	170,5	19,8	145,0	193,0	53,6	39,8	11,1	99,3	10,0	4,5	6,4	16,2	0,3	0,2
	Downstream	High-water	171,0	162,0	9,0	333,0	13,4	7,2	5,0	17,6	7,1	4,9	2,7	12,3	0,2	0,3
	Upstream	Low-water	125,3	19,4	104,0	142,0	30,1	17,6	10,6	44,7	11,6	6,9	3,8	16,9	0,2	0,1

Table 6 - Results of generalized linear models (GLMs) with Gamma distribution and log link function evaluating the effects of sex, river sector, hydrological season, and tracking effort on movement metrics of *Podocnemis unifilis.*

Predictor	Coef.	Std.Err.	z	P>|z|	[0.025	0.975]	Response
Intercept	2,85	0,38	7,41	0,00	2,09	3,60	Total_km
C(Sex)[T.M]	-0,09	0,36	-0,26	0,80	-0,79	0,61	Total_km
C(Sector)[T.Jusante]	-0,87	0,54	-1,60	0,11	-1,93	0,19	Total_km
C(Sector)[T.Montante]	-0,13	0,37	-0,37	0,71	-0,85	0,58	Total_km
C(Season)[T.Low-water]	0,70	0,42	1,67	0,09	-0,12	1,52	Total_km
Tracking_days	0,00	0,00	2,59	0,01	0,00	0,01	Total_km
Intercept	2,30	0,30	7,70	0,00	1,71	2,88	Linear_km
C(Sex)[T.M]	0,06	0,28	0,22	0,82	-0,48	0,60	Linear_km
C(Sector)[T.Jusante]	-0,45	0,42	-1,06	0,29	-1,27	0,38	Linear_km
C(Sector)[T.Montante]	-0,05	0,28	-0,17	0,87	-0,60	0,51	Linear_km
C(Season)[T.Low-water]	0,04	0,33	0,13	0,89	-0,59	0,68	Linear_km
Tracking_days	0,00	0,00	0,54	0,59	0,00	0,00	Linear_km
Intercept	-0,34	0,41	-0,82	0,41	-1,14	0,47	Daily_km
C(Sex)[T.M]	-0,32	0,38	-0,84	0,40	-1,06	0,42	Daily_km
C(Sector)[T.Jusante]	-0,66	0,58	-1,13	0,26	-1,79	0,48	Daily_km
C(Sector)[T.Montante]	-0,37	0,39	-0,94	0,35	-1,13	0,40	Daily_km
C(Season)[T.Low-water]	0,14	0,45	0,31	0,76	-0,74	1,02	Daily_km
Tracking_days	0,00	0,00	-1,60	0,11	-0,01	0,00	Daily_km

During the low-water period, spatial distribution was characterized by high-density cores concentrated in restricted areas, mostly associated with stable and predictable environments such as beaches and exposed riverbanks. These cores, observed mainly in Juncal and Petereçu (downstream; Figure 6) Pimental and Rabecas Channel (midstream; Figure 7), and the Palhau region (upstream; Figure 8), suggest spatial fidelity and relatively sedentary behavior during this period.

In contrast, the high-water season was marked by a notable expansion in the area of use, with increased spatial amplitude and dispersion of density cores, reflecting greater mobility and the exploitation of temporarily accessible habitats. This dynamic was most pronounced in the midstream (Figure 6) and upstream (Figure 7) sections, where seasonal flooding enhanced connectivity among coves, lateral bays, and inundated margins. New usage cores were recorded in Murituba, Veríssimo, Batata, and Carão (downstream; Figure 6), Boca da Bacaba (midstream; Figure 7), and in additional floodable compartments in the Palhau region (upstream; Figure 8).

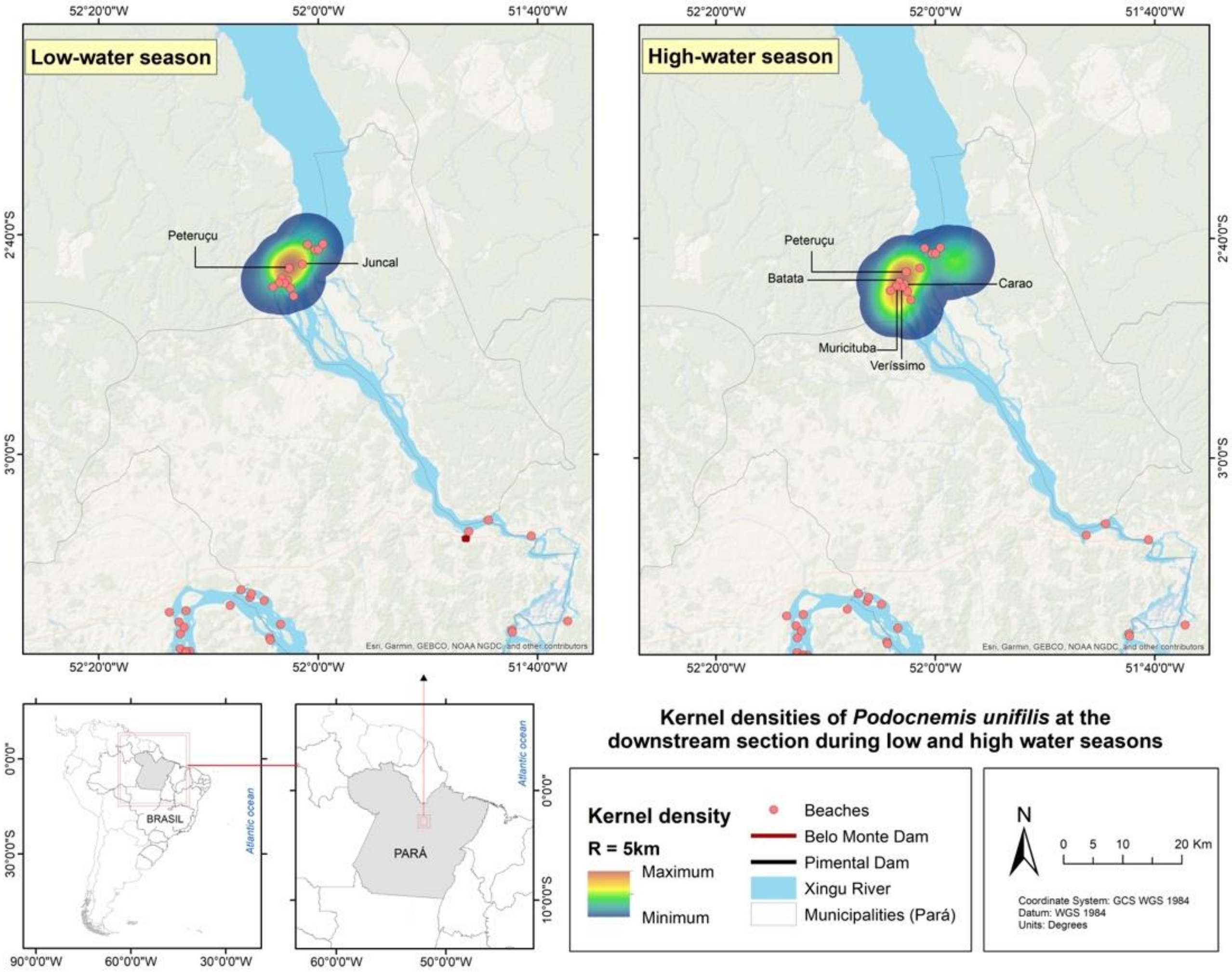

Figure 6 - Kernel Density Estimation (KDE) of *Podocnemis unifilis* spatial use in the downstream section of the Xingu River during low-water (left) and high-water (right) seasons.

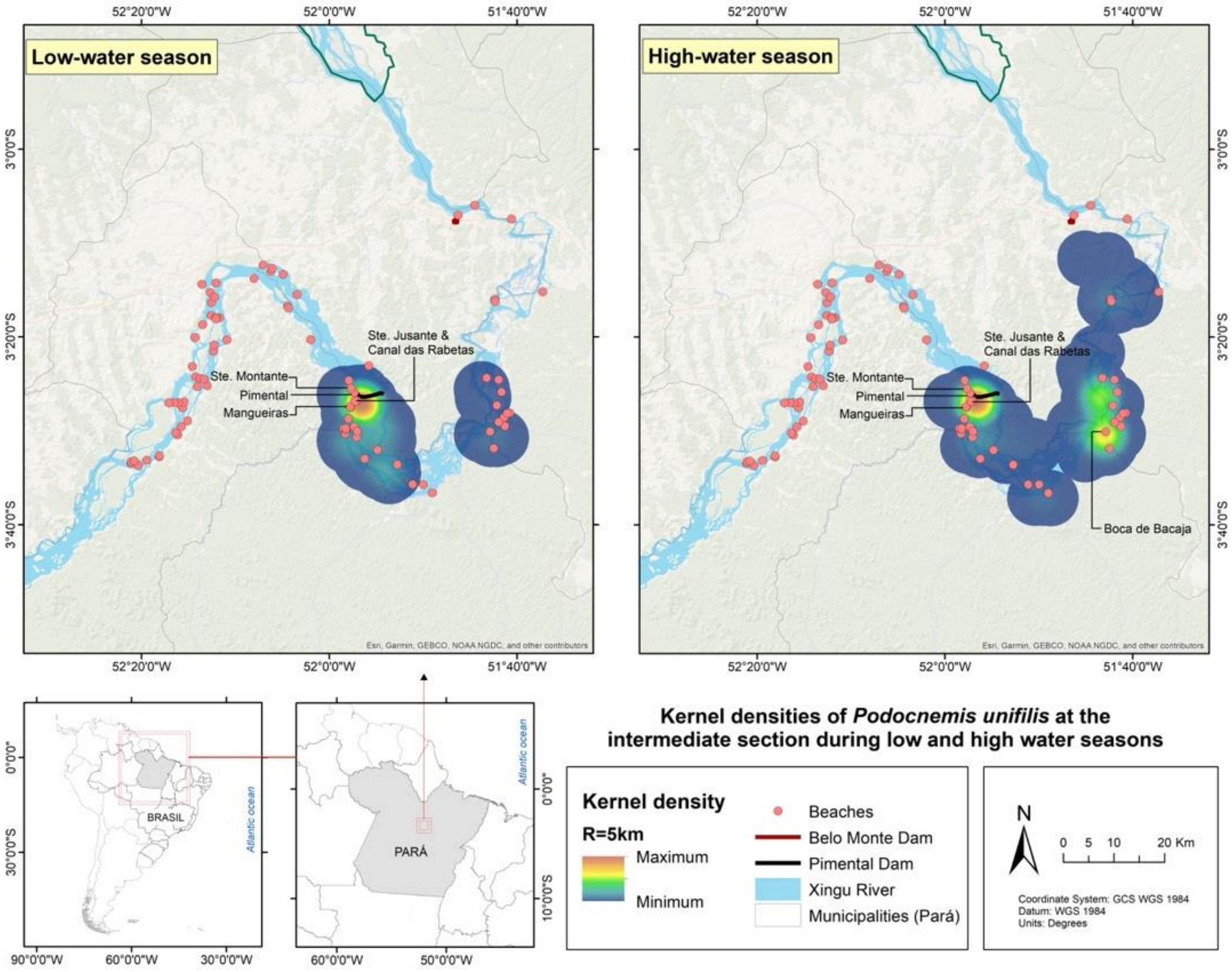

Figure 7 - Kernel Density Estimation (KDE) of *Podocnemis unifilis* in the midstream section of the Xingu River during low-water (left) and high-water (right) seasons.

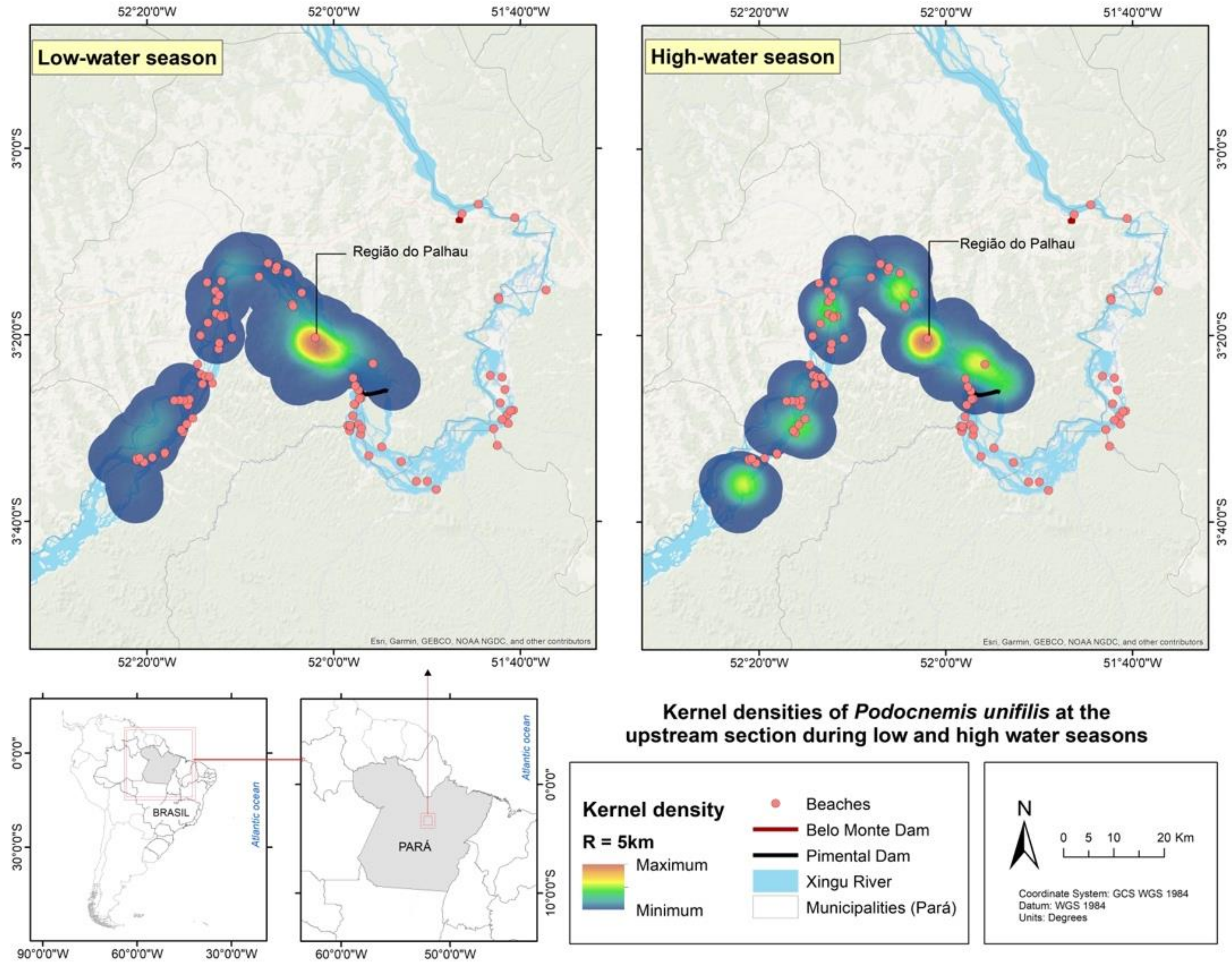

Figure 8 - Kernel Density Estimation (KDE) of *Podocnemis unifilis* in the upstream section of the Xingu River during low-water (left) and high-water (right) seasons.

DISCUSSION

The results of this study substantially broaden current knowledge on the movement patterns of *Podocnemis unifilis*, especially regarding spatial fidelity and behavioural resilience within a hydrologically fragmented context such as the Xingu River, and can be regarded as a milestone in the species' spatial-ecology research. In light of our findings, we emphasise that the seasonal movements of *P. unifilis* are tightly linked to the hydrological regime of Amazonian rivers, corroborating observations that flood-pulse dynamics in tropical floodplain ecosystems strongly influence turtle behaviour, whereby individuals adjust their displacements and habitat use in response to seasonal shifts in climate and water level (Gibbons 1986; Bodie & Semlitsch 2000; Moreira et al. 2011; Simoncini et al. 2022; Rosas et al. 2022). The annual hydrological cycle, alternating between flood and drought periods, generates a dynamic and complex habitat mosaic. During high water, flooded forests and extensive floodplains predominate, whereas permanent water bodies and exposed beaches prevail in the low-water season (Junk et al. 1989; Alcantara et al. 2013).

In our study, we found that during the low-water period the turtles remained concentrated near nesting sites and main channels, whereas in the rainy season, with rising water levels, they moved more intensely, although without venturing far and covering relatively short linear distances that rarely exceeded 25 km. They exhibited strong spatial fidelity, particularly to areas such as Juncal and Petereçu beaches (Downstream sector), the Pimental and Rabecas channels (Midstream sector) and the Palhau region (Upstream sector). This pattern aligns with studies from other Amazonian tributaries in which *P. unifilis* showed short movements and high fidelity to core areas, concentrating near nesting beaches in the dry season and accessing flooded forests and temporary waterbodies in the wet season (Naveda-Rodríguez et al. 2018; Ponce de Leão et al. 2019; Hinderaker 2021). Thus, for *P. unifilis*, the seasonal pulse acts more as a catalyst for localised displacements than as a trigger for long-distance migrations, in contrast with larger species that may travel great distances in response to seasonal changes (Moreira et al. 2011; Fachín-Terán et al. 2006).

Despite expectations of wider movements due to increased habitat availability during the flood season, as shown by Naveda-Rodríguez et al. (2018), Ponce de Leão et al. (2019) and Hinderaker (2021), our results revealed only modest spatial expansion. This sedentary strategy, previously characterised as "short-distance migrant" for the species, reflects a strong attachment to critical habitats such as nesting beaches and nearby lagoons, and has been reported for populations in Ecuador and Trombetas Biological Reserve, Brazil (Naveda-Rodríguez et al. 2018; Ponce de Leão et al. 2019) as well as for *Podocnemis lewyana* in Colombia, which maintained restricted home ranges and repeatedly reused shelters between seasons even in areas with high connectivity among floodplain lakes (Forero-Medina et al. 2021). Similarly, *Kinosternon leucostomum* and *Phrynops geoffroanus* remained faithful to specific floodplain areas and channels despite greater habitat availability in the wet season, preferring predictable sites with suitable substrate for digging or thermoregulation (Ernst & Lovich 2009).

The behaviour of *P. unifilis* in the Xingu therefore exemplifies an ecological syndrome common to tropical-river turtles, characterised by localised movement, habitat selectivity and repeated use of critical environmental cores throughout the hydrological cycle (Pritchard & Trebbau 1984; Moll & Moll 2004). Studies indicate that *P. unifilis* preferentially exploits backwaters, streams, floodplain lagoons and flooded-forest areas adjacent to the river during high water rather than undertaking extended upstream or downstream migrations (Pritchard & Trebbau 1984; Peñaloza et al. 2013). We cannot discount the influence of hydrological fragmentation, which restricts longitudinal movements along the river. This behaviour contrasts with that of the larger-bodied Amazon River turtle *P. expansa*, which can move tens to hundreds of kilometres between flood-season foraging areas and dry-season nesting sites (Ferrara et al. 2013; Forero-Medina et al. 2019). *P. unifilis* exhibits more localised space use, possibly owing to its smaller body size and its ability to shelter and forage in shallow habitats available early in the flood period (Moll & Moll 2004; Fachín-Terán et al. 2006; Vogt 2008; Hinderaker 2021).

We cannot rule out alternative strategies within the basin, such as individuals remaining in isolated lagoons and nesting in situ, underscoring behavioural plasticity in relation to nesting sites (Ferreira Júnior & Castro 2010; Pignati et al. 2013). Such plasticity, documented elsewhere in Amazonia, may be an adaptive response to the high environmental unpredictability of the flood-pulse system (Fachín-Terán et al. 2006). Notably, *P. unifilis* typically initiates reproductive movements slightly earlier than *P. expansa*, with studies in the middle Amazon reporting that turtles move into flooded forests at the onset of the flood about a month before the larger species, taking advantage of small streams and newly inundated areas (Ferreira Júnior & Castro 2010; Ponce de Leão et al. 2019).

Although males showed more directional movements, statistical analyses did not confirm significant sex-based differences, supporting the idea that male movement is concentrated (Naveda-Rodríguez et al. 2018). Our findings therefore highlight that floodplain areas are as critical as nesting beaches for the life cycle of *P. unifilis* (Ponce de Leão et al. 2019; Hinderaker 2021). Orientation tests (Rayleigh and V-test) indicated an absence of significant alignment of movements towards the nearest beaches, and no group analysed by sex, sector or season exhibited preferential directionality. This suggests that *P. unifilis* adopts opportunistic space-use strategies depending on prior location and immediate habitat availability rather than undertaking systematic directional movements to nesting beaches, a behavioural pattern described as “nesting excursions” (Morreale et al. 1984; Gibbons et al. 1990) and similarly not detected by Naveda-Rodríguez et al. (2018) and Ponce de Leão et al. (2019). Nevertheless, the high spatial fidelity observed aligns with Benhamous (2011) concept of “essential use areas”, whereby individuals of territorial or highly philopatric species consistently reuse the same sites over time.

The absence of significant effects of sex, sector and season on movement metrics (total distance, linear displacement and daily displacement) identified by Gamma-GLM models underscores the stability of *P. unifilis* spatial behaviour across hydrological conditions. Although higher means were observed for females and during the dry season, these tendencies were not statistically confirmed, indicating high intra-group variability and possible influences of unmodelled individual or environmental factors (Spiegel et al. 2017).

The lack of differentiation among river sectors in terms of displacement, except for the downstream sector, which exhibited stronger directional concentration, may relate to geomorphological conditions and the accessibility of preferred environments such as beaches and backwater channels (Kalacska et al. 2019). The downstream sector was the only one to show statistically significant spatial orientation, perhaps due to well-defined natural corridors or proximity to protected areas such as the REVIS Tabuleiro do Embaubal that could act as spatial attractors (Erickson et al. 2020). Upstream and midstream, forced environmental homogenisation, such as in hydraulically regulated reaches, can constrain movement possibilities and reduce behavioural plasticity (Alho & Pádua 1982; Barcenas-Garcia et al. 2022a,b).

Local geomorphology further influences movement patterns. The midstream sector, characterised by island channels, rapids and abrupt depth variations, may restrict displacements at certain times of year, a factor not fully captured in this study (Fearnside 2015). Such features create a mosaic of micro-habitats that pose natural barriers to medium-sized turtles (Kalacska et al. 2019). In a hydrologically fragmented environment like the Xingu can become an ecological trap because remaining in degraded or intermittent habitats may threaten individuals lacking sufficient plasticity to explore new areas (Hale et al., 2016a,b; Robertson & Blumstein 2019). This is especially critical where reduced flood pulses and diminished lateral flows have drastically altered connectivity with marginal lakes and seasonal channels (Fearnside 2015).

Hydrological constraints impose a new spatial arrangement on *P. unifilis* populations, which become heavily dependent on remnant water bodies and beaches no longer renewed annually by river flow. This could intensify intra-specific competition, reduce reproductive success and compromise long-term population viability (Lapola et al. 2023). Conserving the longitudinal and lateral connectivity of the Xingu is therefore essential for maintaining biodiversity and preserving the species' ecological dynamics.

The observation that females and males share similar spatial patterns even in distinct hydrological phases suggests that the species basic ecological requirements can be met within geographically limited areas. While this promotes occupancy of high-quality sites, it also increases vulnerability to local impacts. Functional extinction of preferred habitats may trigger population collapses even without wide dispersal (Erickson et al. 2020). The desaisonalisation caused by dams can lead to disorientation, reproductive failure and life-cycle disconnection, particularly in species like *P. unifilis* that rely on environmental cues to initiate movements or select nesting areas (Pignati et al. 2013).

It is important to note that telemetry data were obtained using the Argos satellite system, which, although effective in remote areas, has recognised spatial accuracy limitations for species with prolonged submersion (Vincent et al. 2002; Costa et al. 2010). Because *P. unifilis* is predominantly aquatic, transmission frequency depends on surfacing time, leading to temporal gaps that may distort true trajectories and hinder detection of preferred orientation (Patterson et al. 2010; Hooten et al. 2017). Filters such as Douglas-Argos and Local Outlier Factor improved data quality, yet these methodological limitations were considered when interpreting orientation patterns.

There was a strong positive correlation between monitoring days and the total number of valid locations, indicating that individuals tracked longer provided more robust records. Controlling sampling effort in analytical models was therefore essential to avoid underestimation of space use for short-tracked individuals (Benhamou 2011; McCrimmon 2018). Although corrected, residual errors may still affect detection of fine-scale patterns such as orientation to beaches or micro-seasonal adjustments in activity centres. Positional uncertainty, especially in dense vegetation, rocky areas with signal reflection or prolonged cloud cover during high water, may partly explain non-significant results in directional tests.

Future studies could incorporate GPS transmitters with internal loggers that record high-accuracy locations and transmit via GSM or manual retrieval. Despite greater logistical demands, this approach has been successful for large river turtles such as *Dermatemys mawii* and

Batagur baska, offering improved resolution for orientation analysis and micro-habitat use (Plummer et al. 2008).

Hence, our results highlight the urgency of conserving continuous habitat mosaics that include not only nesting beaches but also marginal lagoons, seasonal channels, backwaters and riparian forests, all of which are essential for maintaining the spatial functionality of *P. unifilis*.

CONCLUSIONS

This study demonstrated that the movement patterns of *Podocnemis unifilis* in the middle Xingu River are strongly influenced by the seasonality of the hydrological regime. During the low-water seasons (dry and ebb periods), a high concentration of individuals was observed in permanent aquatic habitats, particularly in areas such as Juncal and Peteruçu (Downstream sector), Pimental and Rabecas Channel (Midstream sector), and the Palhau region (Upstream sector). These areas were identified as high-density cores, underscoring a behavioral strategy aimed at ensuring hydric stability and continuous access to essential resources. Males exhibited more directional and concentrated movements, prioritizing stable habitats, likely related to their need for consistent resource availability. Conversely, females displayed broader spatial dispersion, potentially driven by specific reproductive demands such as selecting elevated nesting sites to reduce risks of flooding and predation.

During the high-water seasons (flood and flooding periods), the movement patterns became notably more dispersed, with individuals accessing temporarily inundated habitats such as floodplains and flooded forests. These environments provide abundant and diverse food resources and essential refuge areas. Females showed increased spatial dispersion during these periods, likely due to heightened energetic and nutritional requirements linked to reproduction. The utilization of multiple habitat types, enabled by seasonal flooding, appears crucial for females to fulfill their biological needs and successfully reproduce.

Our analysis also indicated no significant preferential orientation toward specific nesting beaches, suggesting flexible and opportunistic reproductive strategies that could minimize predation risk and competition for nesting sites. Such spatial flexibility in nesting behavior highlights the species adaptive capability to environmental variability and resource availability fluctuations, typical of the Amazonian ecosystem. Furthermore, variability among individual turtles in spatial behavior, potentially influenced by previous experience and cognitive abilities, adds complexity to interpreting movement patterns.

The results emphasize the fundamental role of the hydrological cycle and habitat connectivity in shaping the spatial ecology and reproductive strategies of *P. unifilis*. The ecological impacts observed in different river sectors, particularly the constrained movement in the Volta Grande region, illustrate the importance of maintaining habitat connectivity to ensure species survival and ecological resilience.

This study underscores the critical importance of protecting essential habitats, including permanent aquatic refuges and elevated nesting sites, increasingly threatened by climate change, damming activities, and anthropogenic pressures. Satellite telemetry and spatial analysis techniques proved instrumental in identifying core habitat areas and refining conservation strategies. Expanding and enhancing long-term monitoring efforts using these advanced technologies will be vital to effectively manage threats and maintain viable populations of *P. unifilis* in the rapidly changing landscape of the Xingu River basin.

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DATA AVAILABILITY

Data available upon request – The data supporting the results of this study are available, upon reasonable request, from the corresponding author (a) Maurivan V. Ribeiro or (b) Norte Energia. The dataset is not publicly available because it includes sensitive information related to environmental monitoring within the scope of environmental licensing, whose unrestricted sharing could compromise confidentiality and contractual obligations with the partner company and regulatory authorities.

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Capítulo 3

HYDROLOGICAL FRAGMENTATION AND SPATIAL ECOLOGY OF THE YELLOW-SPOTTED RIVER TURTLE (*Podocnemis unifilis*) IN THE MIDDLE XINGU RIVER: HOME RANGE ESTIMATION USING MULTIPLE METHODS AND IMPLICATIONS FOR CONSERVATION

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Background: Large hydroelectric dams alter river ecosystems and can affect space use by aquatic species. The Amazonian turtle *Podocnemis unifilis*, classified as Vulnerable, exhibits site fidelity and short seasonal movements in natural environments. However, little is known about its spatial behavior under altered flow conditions. Therefore, this study aimed to estimate the home range and movement patterns of *P. unifilis* in the middle Xingu River following the implementation of the Belo Monte Hydroelectric Dam.

Methods: Thirty-two adult individuals (both males and females) were monitored via satellite telemetry (Argos system) in three segments of the Xingu River affected by the dam: upstream, intermediate (Volta Grande), and downstream. The attached satellite transmitters recorded periodic geographic positions. Home range areas (95%) and core areas (50%) for each turtle were estimated using five spatial use density methods: MCP, KDE, AKDE, LoCoH, and dBBMM. Differences in home range size between sexes, between seasons (high-water vs. low-water), and among river segments were statistically evaluated ($\alpha = 0.05$).

Results: Home range areas exhibited wide individual variation. The mean 95% home range was 14.40 ± 20.34 km^2 using MCP, 11.91 km^2 with KDE, 14.58 km^2 with AKDE, 14.78 km^2 with LoCoH, and 1.45 km^2 with dBBMM. The 50% core areas were smaller on average: 1.77 km^2 (MCP), 3.49 km^2 (KDE), 2.56 km^2 (AKDE), 2.97 km^2 (LoCoH), and 0.26 km^2 (dBBMM). There were no significant differences in home range size between males and females or between dry and rainy seasons. However, differences emerged among river segments: turtles in the upstream reservoir had the largest home ranges, those in the Volta Grande had the smallest, and individuals in the downstream stretch showed intermediate values. Most individuals remained within the same spatial domain throughout the year, making only local movements without expanding their home range.

Conclusions: *P. unifilis* demonstrated the ability to persist under these altered conditions, maintaining a restricted area of use and localized movements. However, the spatial limitation observed especially in the Volta Grande highlights the species vulnerability to habitat fragmentation. This underscores the importance of maintaining aquatic connectivity and natural hydrological variability in the Xingu River to ensure suitable habitats for the species.

Keywords: Movement ecology; Behavioral plasticity; Flow alteration; Home range estimation; Chelonian conservation

BACKGROUND

The concept of home range in spatial ecology refers to the area in which an individual performs its daily activities such as foraging, reproduction, and resting (Burt, 1943; Okubo *et al.*, 2001; Kie *et al.*, 2010; Powell & Mitchell, 2012). The size and shape of the home range vary according to a combination of biotic and abiotic factors (Lagarde *et al.*, 2003). Among the biotic factors, age, sex, reproductive stage, diet, and food availability stand out (Burt, 1943; Bodie & Semlitsch, 2000; Powell & Mitchell, 2012; Silveria *et al.*, 2022; Enríquez-Mercado *et al.*, 2024). Abiotic factors such as temperature, precipitation, water availability, habitat structure, and presence of microhabitats also affect the home range by conditioning the accessibility and quality of resources (Cagle, 1944; Ponce de Leao *et al.*, 2019; Auge *et al.*, 2023). In addition, extrinsic elements such as environmental quality, deforestation, and degradation of water bodies may restrict or alter the space used by organisms (Saunders *et al.*, 1991; Rizkalla & Swihart, 2006; Serrano *et al.*, 2020; Barcenas-Garcia *et al.*, 2022).

Therefore, understanding a species spatial ecology is essential for its conservation, and in the case of threatened species, this becomes even more relevant, as it provides scientific support for designing effective management strategies tailored to the species needs (Klemens, 2000; Collinge, 2001; Cantrell *et al.*, 2010; Fletcher *et al.*, 2018; Fletcher & Fortin, 2018; Silveria *et al.*, 2022). In other words, knowledge of movement patterns, space use, and site fidelity allows the identification of critical habitats for survival and reproduction, such as feeding, shelter, and nesting areas (Collinge, 1994; Moll & Moll, 2004; Escalona & Vogt, 2008; Norris *et al.*, 2011). Furthermore, spatial analysis enables the assessment of how environmental changes such as habitat fragmentation, dam construction, loss of connectivity between wetlands, or alteration of the hydrological pulse, can disrupt natural movement cycles, affect resource availability, and increase population vulnerability (Perry & Garland, 2002; Berry *et al*., 2005; Roe *et al*., 2009; Runge *et al*., 2014; Kays *et al*., 2015; Allen *et al*., 2016; Tucker *et al*., 2018).

Turtles of the family Podocnemididae have life cycles strongly influenced by the hydrological cycles of the Amazonian rivers (Fachín-Terán *et al*., 2006; De Souza-Alcantara *et al*., 2013; Pignati *et al*., 2013; Eisemberg *et al*., 2016; Alzate-Estrada *et al*., 2020; Erickson *et al*., 2020; Hinderaker, 2021; Ataídes *et al*., 2021; Simoncini *et al*., 2022). Species of this family use rivers and floodplains seasonally, moving into flooded forests during high-water periods (flood and rise) in search of food and shelter, and returning to the main river channels during low-water periods to concentrate in deeper pools or access nesting beaches (Alho & Padua, 1982; Vogt, 2008; Fachín-Terán *et al*., 1995; Ferrara *et al*., 2016). Several species of the genus *Podocnemis* undertake long reproductive migrations, traveling tens to hundreds of kilometers to reach suitable nesting sites (Mogollones *et al*., 2010; Carneiro & Pezzuti, 2015). *Podocnemis expansa* (Amazon River turtle), the largest species in the family, is capable of covering large distances. Individuals tracked via satellite in the Xingu River exhibited average displacements of approximately 401 km, with a maximum recorded distance of 725 km during the post-nesting period (Carneiro & Pezzuti, 2015).

Even smaller species show significant movement. Female *Podocnemis sextuberculata* (iaçá), tracked via radio telemetry, traveled between ~16 and 44 km linearly during migrations from streams to nesting beaches, while males remained mostly resident in the same river segment (Fachín-Terán *et al*., 2006). *Podocnemis lewyana*, endemic to the Magdalena River (Colombia), generally exhibits a restricted linear range (<1 km for 85% of individuals), but males were observed moving up to 5 km, and reproductive females averaged ~14 km during the dry season to reach nesting beaches (Alzate-Estrada *et al*., 2020). These examples demonstrate that some Podocnemididae species can be considered facultative seasonal migrants, ranging from short to long distances, remaining resident in a limited area for most of the year, but undertaking extensive movements when necessary (Naveda-Rodríguez *et al*., 2018; Alzate-Estrada *et al*., 2020).

The yellow-spotted river turtle, *Podocnemis unifilis* (Testudines: Podocnemididae), is a medium-sized species widely distributed throughout the Amazon basin and adjacent rivers. It plays a significant ecological role by consuming fruits, seeds, and aquatic invertebrates (Balensiefer, 2003; Vogt, 2008; Ferrara *et al*., 2016; Garcez *et al*., 2020). Culturally and economically, it is also important to riverine communities, historically subjected to high hunting pressure and egg collection (Pezzuti *et al*., 2010; Faria & Malvasio, 2018; Peñaloza *et al*., 2013; Pantoja-Lima *et al*., 2014; Felix-Silva *et al*., 2018). As a result, *P. unifilis* is classified as a Vulnerable species in conservation listings, with population declines reported in several regions (Rhodin *et al*., 2018; MMA, 2022; IUCN, 2024).

Nonetheless, until recently, little was known about its spatial ecology and movement patterns, as most studies focused on natural history, reproduction, or genetics, or were based on sparse mark-recapture data (Vogt, 2008; Escalona *et al*., 2009; Trebbau & Pritchard, 2016; Eisemberg *et al*., 2017). More robust studies using radio telemetry and GPS have only begun to address this gap in recent years. For example, Naveda-Rodríguez *et al*. (2018) tracked 63 individuals using VHF telemetry in Ecuador, providing the first home range estimates for the species—approximately 5.2 km² on average—with a mean linear range of ~16 km, indicating relatively short seasonal local movements. In Brazil, Ponce de Leão *et al*. (2019) monitored individuals in the Trombetas River Biological Reserve (Pará) and found similar home range sizes, with no marked seasonal differences, suggesting that *P. unifilis* uses distinct seasonal habitats (flooded forest versus riverbed) within the same general annual use area. These studies suggest that although *P. unifilis* does not engage in long-range migrations like *P. expansa*, it displays sufficient movement plasticity to adjust to the water pulse, thus being considered a short-distance migrator (Naveda-Rodriguez *et al*., 2018).

Anthropogenic alterations to the natural hydrological regime can, therefore, significantly impact the spatial ecology of *P. unifilis*. The construction of large hydroelectric dams in the Amazon modifies flood and drought patterns, creates upstream reservoirs, and reduces downstream flow (Castello & Macedo, 2016; Norris *et al*., 2018a; Bárcenas-Garcia *et al*., 2022).

These changes can eliminate or flood nesting beaches, alter connectivity between dry and wet season habitats, and potentially force adjustments in turtle movement patterns (Norris *et al.*, 2018a).

This study was conducted exclusively within a post-dam context, as the Belo Monte Hydroelectric Plant (UHE Belo Monte) began full operation in 2016, permanently altering the hydrology and ecological connectivity of the Xingu River. Although the immediate impacts of dam construction and reservoir filling have been widely addressed in the scientific literature (e.g., Castello & Macedo, 2016; Fearnside, 2017; Norris *et al.*, 2018a; Pezzuti *et al.*, 2024), there remains a gap regarding the medium- and long-term effects on the behavior and space use of aquatic species such as turtles. Based on this, the present research adopts a prospective approach: rather than merely documenting well-known alterations, it aims to understand how *Podocnemis unifilis* is currently using space under the new hydrosocial regime and what movement patterns are emerging following the stabilization of the plant's operational regime.

Thus, this study represents the first comprehensive assessment of the spatial ecology of *Podocnemis unifilis* in the Xingu River following the hydrological changes caused by the Belo Monte Hydroelectric Plant. Using ARGOS satellite telemetry data and multiple home range estimation methods, we aimed to understand how individuals of this species use space under altered environmental conditions. Specifically, our objectives were: (1) to evaluate the influence of biological (sex), hydrological (season), spatial (river sector), and sampling effort (monitoring days and number of locations) on home range size estimates across individuals; and (2) to compare the performance, consistency, and sensitivity of different home range estimators (MCP, KDE, LoCoH, AKDE, dBBMM), assessing their agreement and relative deviations under varying ecological conditions.

METHODS

Study area – The study was conducted along the Xingu River in the state of Pará, Brazil, encompassing three distinct sections based on their longitudinal position relative to the Belo Monte/Pimental Hydroelectric Complex: upstream, midstream, and downstream (Figure 1). The upstream region comprises the upper course of the Xingu River, located above the Pimental dam, including areas within the main reservoir and its immediate tributaries, near the city of Altamira. The midstream section is located between the Pimental dam and the main powerhouse of the Belo Monte Hydroelectric Plant. The downstream region extends below the powerhouse, covering the Volta Grande do Xingu up to the Tabuleiro do Embaubal Wildlife Reserve (REVIS) (Figure 1). The climate in the Xingu River basin is classified as humid tropical, with a rainy season coinciding with the river's rising and flooding period (approximately December to April), and a predominant dry season between June and November (ebb and dry phases), resulting in a well-defined and seasonal hydrological regime (ANA, 2013; IBGE, 2020).

The Xingu River is one of the largest tributaries of the Amazon and is classified as a clearwater river in the Amazonian typology (Sioli, 1985). It extends approximately 2,500 km and drains a basin of about 510,000 km², encompassing transitional areas between the Cerrado and Amazon biomes (Goulding *et al*., 2003). Its hydrography is characterized by a high degree of geomorphological heterogeneity, with stretches of floodplain interspersed with rapids, anastomosing channels, islands, and várzea areas, particularly prominent in the Volta Grande region (Sawakuchi *et al*., 2015). This geomorphological diversity contributes to the formation of various aquatic and riparian microhabitats, promoting high biological diversity (Kalacska *et al*., 2019). Due to its ecological complexity and high conservation value, the Xingu River basin has been recognized as one of the most important for the conservation of aquatic biodiversity in the Brazilian Amazon. It has been the focus of specific public policies for species conservation, such as the National Action Plan for the Conservation of Endemic and Threatened Species of the Lower and Middle Xingu Region (PAN Baixo e Médio Xingu) (ICMBio, 2012 – Ordinance No. 16/2012).

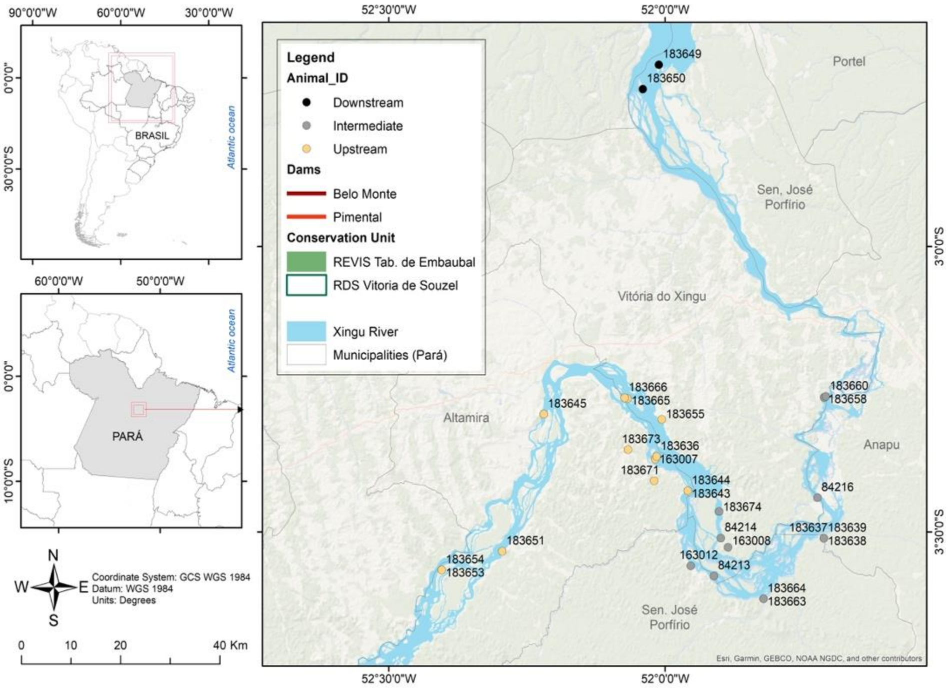

Figure 1 - Map of the Xingu River stretch in Pará, Brazil, indicating the study area of 32 individuals monitored between 2017 and 2022. The distribution of the animals is shown between the upstream portion (above the Belo Monte dam, including part of the reservoir) and the downstream portion (Volta Grande do Xingu, below the dam).

Data collection and monitoring. Individuals were captured using various methods (Balestra *et al.*, 2016) during multiple field campaigns along the Xingu River, as part of the Turtle Conservation and Management Program of the Belo Monte Hydroelectric Power Plant. Each turtle was fitted with a satellite transmitter attached to the posterior portion of the carapace using non-toxic epoxy resin (Figure 2). The transmitters (models Kiwisat K2G 158A, K2G 273C, and K2G 173A) were programmed to record geographic positions at regular intervals of 2 to 3 hours, storing each fix with date, time, and coordinates (latitude/longitude, WGS84 datum). Locations were transmitted via satellite uplink (Argos system) whenever the animal surfaced, allowing for remote tracking without the need for frequent recapture.

The temporal segmentation of the analyses was based on the hydrological dynamics of the Xingu River, which comprises four seasonal phases: Flooding (Dec–Feb), Flooded (Feb–

Apr), Ebb (May–Jul), and Dry (Aug–Oct), as described by De Souza Alcantara *et al*. (2013) and Ribeiro *et al*. (2022). For analytical purposes, these phases were grouped into two broader periods: high-water season (Jan–Jun), when the river level rises or reaches its peak, and low-water season (Jul–Dec), when the water level recedes, exposing sandbanks and beaches that serve as nesting sites (Camargo *et al*., 2015; Dos Santos Franco *et al*., 2015).

To maintain spatial independence, each individual was assigned to a single river sector (Upstream, Midstream, or Downstream) based on the sector with the highest number of location records. Summary metrics such as the total number of locations, monitoring duration (days), and point density (locations/day) were calculated for each individual and aggregated by sex, season, and river sector. All analyses were performed using R software, version 4.4.1 (R Core Team, 2024).

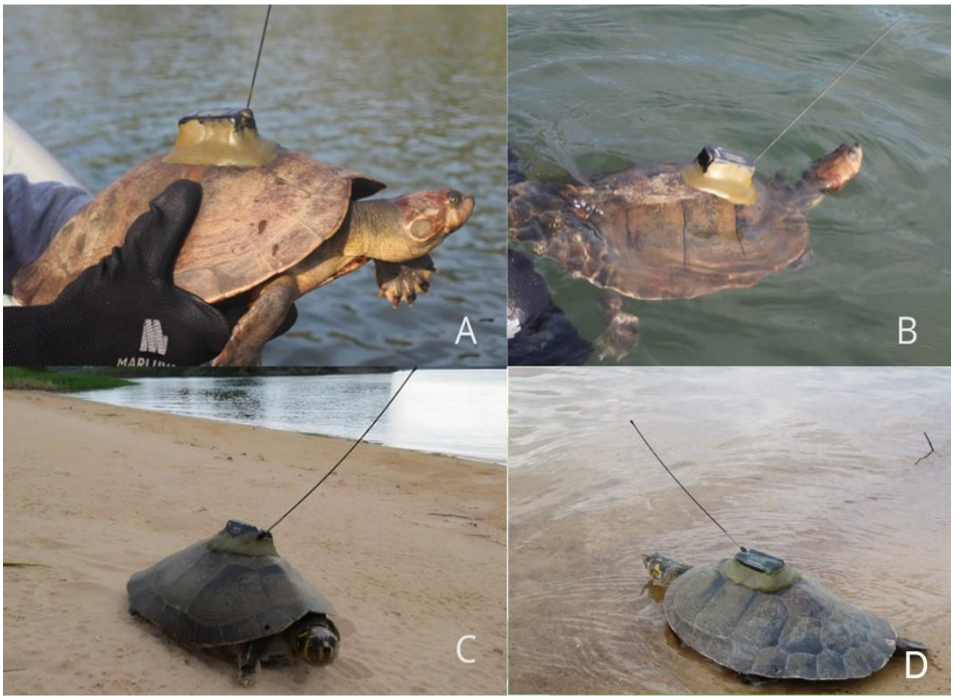

Figure 2 - Installation of satellite transmitters (Kiwisat PTT K2G 158A, K2G 273C or K2G 173A). (A) Female *Podocnemis unifilis* being handled after transmitter installation. (B) Female *Podocnemis unifilis* being released with newly installed transmitter. (C and D) Male *Podocnemis unifilis*. Image: Norte Energia S.A.

Data analysis. *Data filtering* **-** Initially, a preliminary evaluation of the collected data was performed, during which anomalous signals were excluded. As part of this initial assessment, manual filtering of locations was conducted, removing those clearly incorrect or biologically unfeasible (e.g., urban areas, roads, or locations incompatible with the ecology and typical behavior of the studied species).

Additionally, all locations classified as Class Z were excluded, as these are known to compromise the accuracy and reliability of results due to their low positional quality (Vincent *et al*., 2002; Costa *et al*., 2010; Patterson *et al*., 2010; ARGOS, 2016; Hooten *et al*., 2017).

Periods of signal discontinuity, characterized by intervals greater than 3 days without detections, were handled by separating the data segments into independent records, following the methodology propose by Douglas *et al*. (2012).

Subsequently, we employed the Douglas-Argos Filter (DAF), which considers criteria such as maximum distance between consecutive points and turning angles, aiming to eliminate trajectories incompatible with the natural movement behavior of the animals (Douglas *et al*., 2012). In the absence of data on the speed of *Podocnemis unifilis*, a conservative upper threshold of 0.5 m/s (1.8 km/h) based on studies carried out with phylogenetically close freshwater turtles (Freitas *et al*., 2008; Shimada *et al*., 2012).

Complementing the filtering process, we also applied a statistical approach using the Local Outlier Factor (LOF) method, which identifies outlier points based on the local density of data (Breunig *et al*., 2000; Aggarwal, 2015). Points identified as outliers by this method were also removed.

Home Range. The data were analyzed using multiple home range estimation methods, considering 95% isopleths (total area) and 50% isopleths (core use area). Traditional methods that assume independence among locations were applied: MCP (Minimum Convex Polygon; Mohr, 1947) and KDE (Kernel Density Estimation; Worton, 1989). In addition, a method that accounts for the temporal autocorrelation of locations was employed—AKDE (Autocorrelated Kernel Density Estimation; Calabrese *et al*., 2016).

The second approach was the Dynamic Brownian Bridge Movement Model (dBBMM; Kranstauber *et al*., 2012), a trajectory-based method that also incorporates temporal autocorrelation but does so in a non-parametric, localized manner.

Additionally, the Local Convex Hull (LoCoH) method was adapted to include these natural spatial restrictions of the Xingu, resulting in a barrier-constrained LoCoH approach (Getz & Wilmers, 2004). By automatically excluding polygons (hulls) that intersected exclusion zones (buffers) around waterfalls and high-current segments, only areas that were effectively accessible were retained during the home range construction process (Getz *et al*., 2007; Leuchtenberger *et al*., 2013).

Statistical Analysis. – Initially, in order to verify the uniformity and quality of the sampling effort among the monitored individuals, three main metrics were calculated: (i) duration of monitoring (in days), (ii) total number of locations, and (iii) density of locations per day. The comparison of these metrics between the groups was performed using non-parametric tests: Mann–Whitney for sex (males vs. females), paired Wilcoxon for hydrological cycles (high-water; low-water), and Kruskal–Wallis for river sectors (upstream, midstream, downstream) (Zar, 2010).

Then, to identify the factors influencing the size of the home range of *Podocnemis unifilis*, Generalized Linear Models (GLMs) with Gamma distribution and log linkage function were fitted (Kie *et al*., 2010). The response variables consisted of the estimates of the life area obtained by different analytical methods (MCP, KDE, LoCoH, AKDE and dBBMM), considering separately the isochronous ones of 95% (total area) and 50% (core use) (Mohr, 1947; Worton, 1989; Getz & Wilmers, 2004; Kranstauber *et al*., 2012; Calabrese *et al*., 2016). As explanatory variables, sex, hydrological station, river sector, and sampling effort measures (number of days and number of locations per individual) were included. Each model was independently tuned for each living area metric.

In addition, in order to compare the performance between the estimation methods, the data were restructured in long format, allowing the adjustment of integrated GLM models with the fixed effects "method" and "isocline", in addition to the same environmental, biological and stress covariates. The differences between the methods were evaluated using contrasts adjusted in the emmeans package, with control for the other variables of the model (Lenth, 2020). In addition, the consistency between the metrics was examined using Spearman correlations (Zar, 2010), Bland–Altman plots (Bland & Altman, 1986; Sadler *et al*., 2018), and intra- and intergroup coefficients of variation.

All analyses were performed using Rstudio software version 4.4.1 (R Core Team, 2024).com the stats, ggplot2 (Wickham, 2016), dplyr (Wickham *et al*., 2023) and emmeans (Lenth, 2020) packages. The residuals of the models were visually evaluated, and the assumptions were verified based on the homogeneity of the variance and the fit to the specified distribution.

RESULTS

General Movement Data – Of the 32 *Podocnemis unifilis* individuals monitored between July 2017 and March 2022 (21 females and 11 males) were retained for home range analyses after the screening process (Table 1). After completing the filtering process, approximately 48,32% of the original signals were removed, reducing the initial dataset from 4,685 to 2,264 final signals (Figure 3; Figure 4; Table 1).

Monitoring effort varied widely among individuals, with tracking durations ranging from 8 to 500 days (mean = 149.47 ± 111.03 days), totaling 4,484 animal-days. The longest tracking was for female 163008 (500 days), although with low location density (0.11 loc/day). In contrast, female 183649 had the highest density (1.38 loc/day) over 57 days. Across sectors, tracking duration and location density showed high individual variability, with no significant differences between sexes (all U = 147,5, p > 0.21), hydrological seasons (W = 42.0, p > 0.06), or river sectors (U = 3.53, p > 0.17). Among the 20 individuals monitored in both seasons, no statistical differences were found in tracking duration, number of locations, or daily location density (all p > 0.06) (Table 3; Figure 5A–I).

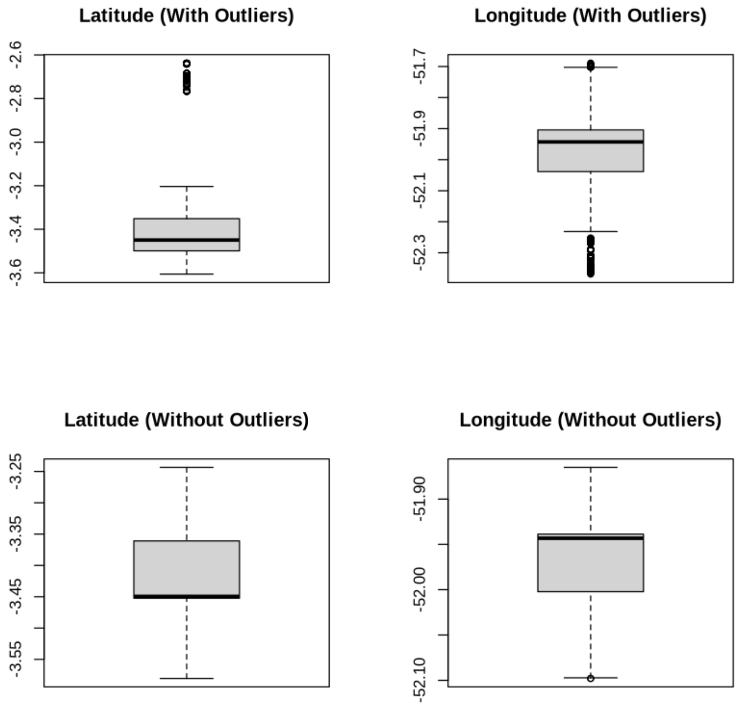

Figure 3 - Boxplots of geographic coordinates (latitude and longitude) of individuals tracked by ARGOS telemetry, with and without outliers, in the middle Xingu River, Pará, Brazil.

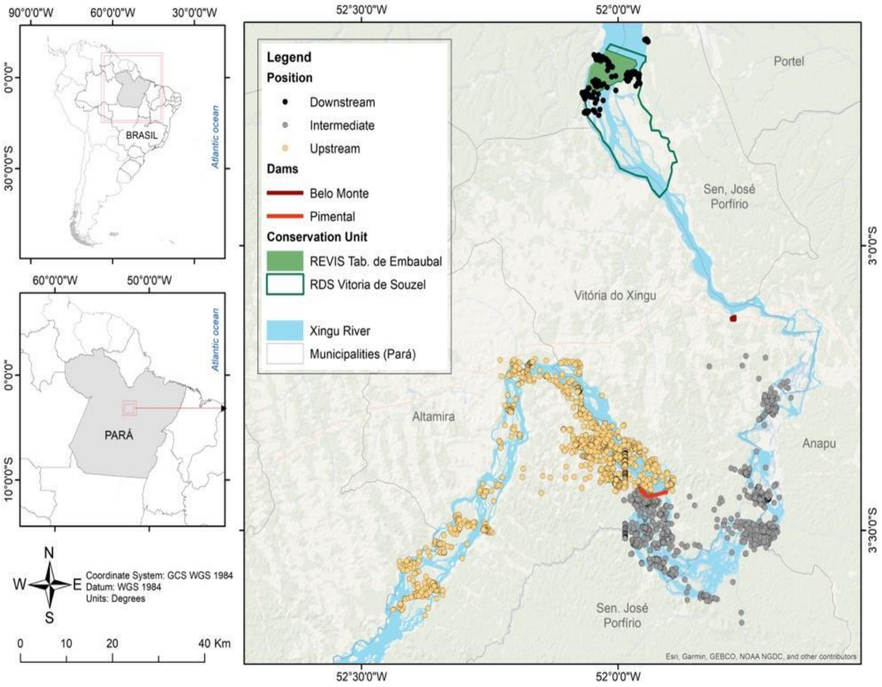

Figure 4 - Spatial distribution of turtle location records across three sectors of the Xingu River: downstream (black dots), midstream (gray dots), and upstream (orange dots).

Table 1 - List of *Podocnemis unifilis* individuals monitored by satellite telemetry. The table presents the species, the sex of the individual (M for male and F for female), and the ID (PTT number) code used for satellite monitoring.

ID	**Sex**	**Model Tag**	**Installation Date**	**First Record**	**Last Record**	**Total Days Monitored**	**Total Locations**	**Coordenates (Capture)**		**Records by Year**
								lat	**long**	
84213	M	K2G 158A	13/07/2019	2019-07-13	2019-12-05	145	72	-3,4556	-51,9632	{2019: 72}
84214	M	K2G 158A	13/07/2019	2019-07-13	2019-12-29	169	33	-3,4535	-51,9655	{2019: 33}
84216	F	K2G 158A	16/10/2019	2020-02-15	2020-03-25	39	33	-3,4235	-51,7271	{2020: 33}
163007	F	K2G 273C	24/11/2014	2017-07-16	2018-07-18	367	113	-3,3889	-52,0186	{2017: 84, 2018: 29}
163008	F	K2G 273C	16/07/2017	2017-07-24	2018-12-07	501	64	-3,4724	-51,9221	{2017: 6, 2018: 58}
163009	F	K2G 273C	17/07/2017	2017-07-17	2018-04-26	283	254	-3,3906	-52,0318	{2017: 156, 2018: 98}
163012	F	K2G 273C	17/07/2017	2017-08-09	2018-02-03	178	20	-3,3364	-51,9997	{2017: 17, 2018: 3}
163013	F	K2G 273C	17/07/2017	2017-07-21	2018-08-09	384	122	-3,4863	-51,9572	{2017: 34, 2018: 88}
163016	F	K2G 273C	26/10/2017	2017-10-29	2018-04-04	157	123	-3,3420	-51,9854	{2017: 33, 2018: 90}
183636	F	K2G 173A	23/09/2019	2019-10-28	2020-05-08	193	123	-3,5140	-51,7027	{2019: 2, 2020: 121}
183637	M	K2G 173A	17/10/2019	2019-11-01	2020-05-12	193	78	-3,5110	-51,7053	{2019: 17, 2020: 61}
183638	F	K2G 173A	17/10/2019	2020-01-12	2020-03-02	50	23	-3,5147	-51,7210	{2020: 23}
183639	M	K2G 173A	17/10/2019	2019-12-07	2020-05-29	174	111	-3,4413	-51,7270	{2019: 5, 2020: 106}
183643	F	K2G 173A	17/10/2019	2019-10-22	2021-03-02	497	510	-3,4457	-51,9400	{2019: 38, 2020: 400, 2021: 72}
183644	M	K2G 173A	19/10/2019	2019-11-27	2020-04-04	129	45	-3,2684	-52,1979	{2019: 6, 2020: 39}
183645	M	K2G 173A	19/10/2019	2019-10-29	2020-03-19	142	21	-3,3357	-52,2081	{2019: 2, 2020: 19}
183649	F	K2G 173A	18/10/2019	2019-10-20	2019-12-16	57	77	-2,7363	-52,0675	{2019: 77}
183650	F	K2G 173A	20/11/2019	2020-01-17	2020-04-21	95	36	-3,4879	-52,2573	{2020: 36}
183651	F	K2G 173A	18/11/2019	2019-12-10	2020-03-17	98	60	-3,6205	-52,3539	{2019: 5, 2020: 55}
183653	M	K2G 173A	18/11/2019	2019-11-27	2020-03-09	103	51	-3,5532	-52,3886	{2019: 38, 2020: 13}

ID	Sex	Model Tag	Installation Date	First Record	Last Record	Total Days Monitored	Total Locations	Coordenates (Capture)		Records by Year
								lat	long	
183654	M	K2G 173A	29/01/2020	2020-01-30	2020-07-19	171	21	-2,7321	-52,0682	{2020: 21}
183655	M	K2G 173A	13/02/2020	2020-02-14	2020-03-24	39	13	-3,3613	-51,7303	{2020: 13}
183658	F	K2G 173A	13/02/2020	2020-02-14	2020-04-06	52	18	-3,4029	-51,7474	{2020: 18}
183660	M	K2G 173A	13/02/2020	2020-04-17	2021-03-16	333	13	-2,7311	-52,0645	{2020: 4, 2021: 9}
183661	M	K2G 173A	23/09/2019	2020-04-20	2020-04-29	9	17	-2,7308	-52,0473	{2020: 17}
183663	F	K2G 173A	27/04/2020	2020-04-28	2020-05-15	17	24	-3,4557	-51,9640	{2020: 24}
183664	F	K2G 173A	27/04/2020	2021-04-23	2021-06-22	60	11	-3,2363	-52,0903	{2021: 11}
183665	F	K2G 173A	17/04/2021	2020-11-17	2021-01-26	70	22	-3,2121	-52,1670	{2020: 7, 2021: 15}
183666	F	K2G 173A	17/11/2020	2020-12-19	2021-04-12	114	43	-3,2862	-52,0727	{2020: 5, 2021: 38}
183671	F	K2G 173A	28/06/2021	2021-10-21	2022-01-07	78	29	-3,2219	-52,1845	{2021: 18, 2022: 11}
183673	F	K2G 173A	13/07/2019	2021-10-21	2022-01-07	78	24	-3,2841	-52,0871	{2021: 18, 2022: 6}
183674	F	K2G 173A	19/07/2019	2019-11-11	2020-04-11	152	78	-3,4321	-51,9430	{2019: 5, 2020: 73}

Table 2 - Summary of monitoring effort for *Podocnemis unifilis* individuals tracked in the middle Xingu River, organized by sex, river sector, and hydrological season. SD was not calculated for groups with only one individual.

Sector	Hydrological Season	Sex	ID	Monitoring Days	Total Locations	Density (loc/day)
Upstream	Low-water	F	163009	366	85	0.23
	High-water	F	163007	159	28	0.18
Midstream	Low-water	F	163008	500	55	0.11
	High-water	F	183643	425	183	0.43
Downstream	Low-water	F	183649	57	77	1.38
	High-water	M	183660	332	13	0.04

Sex	Sector	Season	n	Monitoring Days (Mean ± SD)	Total Locations (Mean ± SD)	Density (Mean ± SD)
F	Downstream	Low-water	1	56.0 ± nan	77.0 ± nan	1.38 ± nan
	Midstream	High-water	9	117.9 ± 123.4	58.4 ± 58.2	0.62 ± 0.41
		Low-water	5	273.6 ± 231.7	93.8 ± 134.5	0.29 ± 0.31
	Upstream	High-water	11	64.4 ± 50.6	35.5 ± 33.0	0.78 ± 0.52
		Low-water	9	89.1 ± 113.8	38.2 ± 50.7	0.5 ± 0.29
M	Downstream	High-water	3	146.0 ± 167.2	16.7 ± 3.5	0.79 ± 1.16
	Midstream	High-water	3	99.7 ± 53.4	60.0 ± 46.5	0.54 ± 0.25

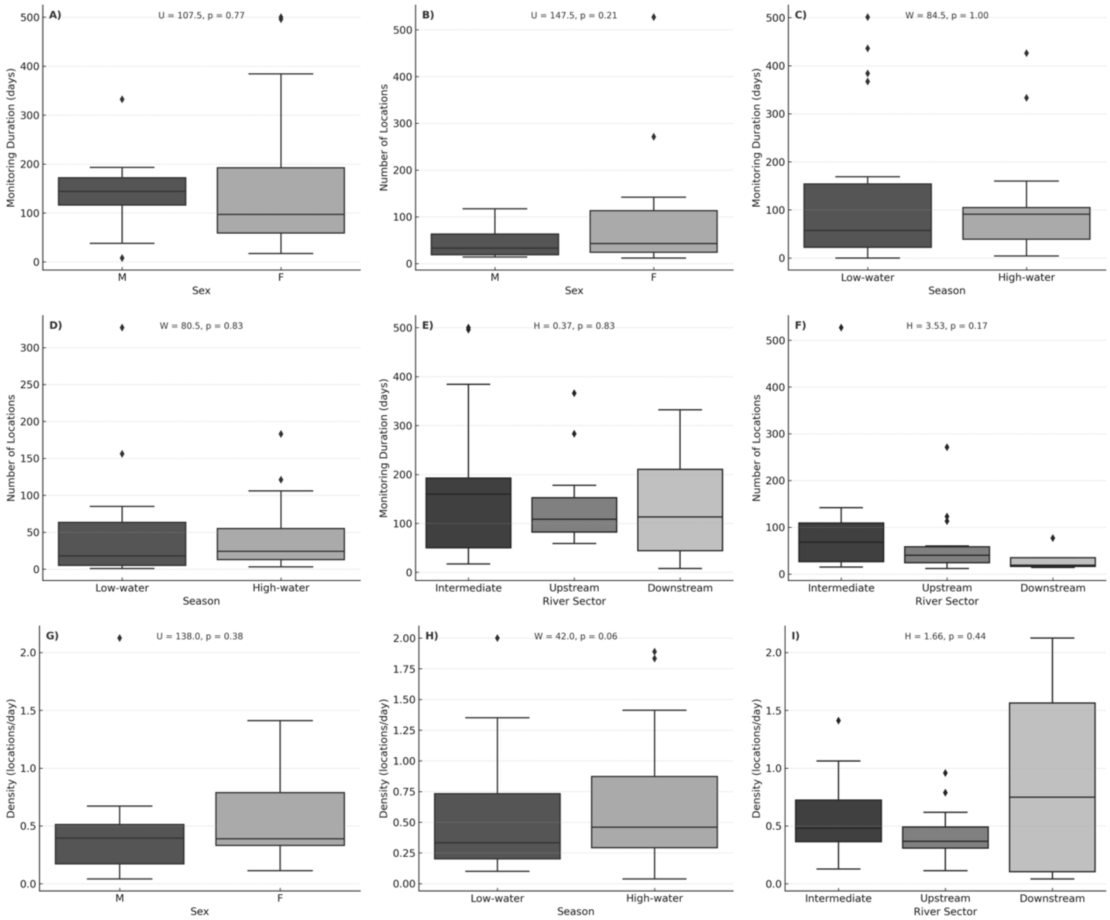

Figure 5 - Monitoring effort comparison by sex, hydrological season, and river sector for *Podocnemis unifilis* individuals monitored in the middle Xingu River. A) Monitoring duration by sex; B) Total number of location records by sex; C) Monitoring duration by hydrological season; D) Total number of location records by hydrological season; E) Monitoring duration by river sector; F) Total number of location records by river sector; G) Daily location frequency by sex; H) Daily location frequency by hydrological season; I) Daily location frequency by river sector.

Home range sizes - The mean 95% home range area was 14.40 ± 20.34 km² using MCP, 11.91 km² with KDE, 14.58 km² with AKDE, 14.78 km² with LoCoH, and 1.45 km² with dBBMM. The 50% core areas showed lower means: 1.77 km² (MCP), 3.49 km² (KDE), 2.56 km² (AKDE), 2.97 km² (LoCoH), and 0.26 km² (dBBMM). LoCoH and AKDE produced the largest 95% estimates on average, whereas dBBMM consistently returned substantially lower area values. A similar pattern was observed for the core areas, with dBBMM yielding markedly smaller 50% ranges compared to the other methods.

Females had larger average areas than males in the 95% isopleths for most methods: MCP 95% in the upstream/low-water combination: 51.62 ± 29.99 km² in females vs. 12.71 ± 4.90 km² in males. In the 50% isopleths, sex-related differences were smaller (e.g., MCP 50% in midstream/low-water: females 2.60 ± 5.19 km² vs. males 1.27 ± 0.79 km²).

For instance, in the upstream sector, females had 39.81 ± 31.64 km² during low-water vs. 24.18 ± 29.53 km² during high-water using KDE (Figure 6). Core (50%) areas varied less between seasons.

Regarding river sector, the smallest values occurred downstream (e.g., MCP 95% in males: 1.93 ± 1.65 km²), while the largest areas were observed upstream (e.g., AKDE 95% in females: 34.24 ± 14.00 km²). Core areas followed a similar trend: LoCoH 50% ranged from 0.23 ± 0.00 km² (downstream/females) to 4.63 ± 4.58 km² (upstream/females). In some cases, however, midstream males exhibited larger core areas than those upstream (e.g., KDE 50%: 4.16 ± 2.69 km² vs. 2.72 ± 2.78 km).

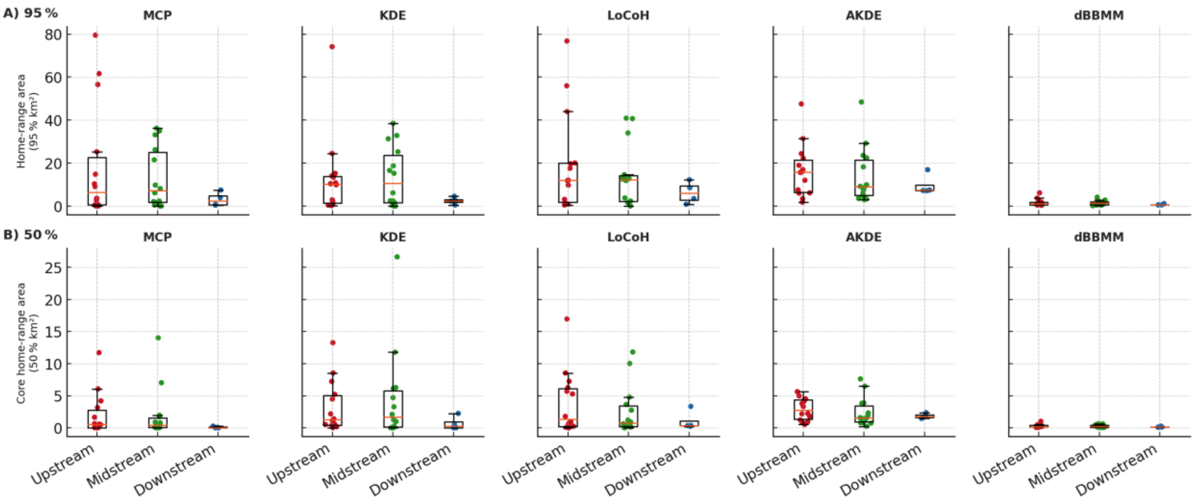

Figure 6 - 95% home range area (km²) by river section (Upstream, Midstream, Downstream) for each estimator: (A) MCP, (B) KDE, (C) LoCoH, (D) AKDE, (E) dBBMM.

Table 3 - Individual-level estimates of home range size (in km²) for *Podocnemis unifilis* in the Xingu River, calculated using multiple methods. Values correspond to isopleths of 95% (total area) and 50% (core area of use). Methods include Minimum Convex Polygon (MCP), Kernel Density Estimation (KDE), Local Convex Hull (LoCoH), Autocorrelated Kernel Density Estimation (AKDE) and Dynamic Brownian Bridge Movement Model (dBBMM).

ID	**MCP***		**KDE**		**AKDE**		**LOCOH**		**dBBMM**	
	95%	**50%**	**95%**	**50%**	**95%**	**50%**	**95%**	**50%**	**95%**	**50%**
84213	33,15	1,75	31,29	6,15	9,91	2,32	12,59	0,89	1,31	0,24
84214	0,07	0,03	1,38	0	3,35	0,77	1,58	0,06	0,43	0,09
84216	0,03	0,01	0,03	0,01	2,96	0,73	0,03	0,01	0,14	0,04
163007	25,25	4,2	10,8	0,38	31,41	5,63	12,09	5,27	2,75	0,49
163008	35,01	0,89	38,5	11,78	29,19	3,82	40,89	4,79	2,09	0,32
163009	79,54	1,65	74,14	5,22	47,54	3,31	76,77	1,78	6,16	1,02
163012	2,83	0,57	10,4	2,17	18,98	4,42	20,05	6,26	0,75	0,17
163013	36,21	14,02	15,23	3,27	48,42	7,62	34,01	11,82	4,11	0,52
163016	61,63	11,72	15,21	8,55	24,36	4,13	55,97	16,96	3,72	0,51
183636	8,13	0,77	16,56	2,1	18,23	1,95	11,87	1,2	2,8	0,63
183637	9,77	1,95	25,26	4,71	22,43	3,87	11,12	2,75	2,84	0,61
183638	0,51	0,01	0,28	0,1	5,82	1,2	1,03	0,14	0,48	0,12
183639	2,09	0,33	6,14	0,99	9,18	1,48	3,8	0,47	1,65	0,35
183643	1,66	0,14	2,46	0,26	4,83	0,82	2,03	0,15	1,42	0,17
183644	0,57	0,03	1,13	0,36	6,14	0,94	0,49	0,08	0,6	0,12
183645	9,06	0,06	14,09	4,48	7,53	1,78	19,66	0,92	0,91	0,13
183649	7,47	0,26	2,58	0,52	7,45	1,46	3,49	0,23	1,15	0,26
183650	0,52	0,09	0,67	0,52	6,03	1,22	1,37	0,24	0,71	0,16
183651	3,61	0,5	2,18	0,6	16,12	2,17	9,75	0,67	1,76	0,39
183653	14,81	6,06	13,39	7,23	22,18	4,98	11,82	7,25	1,91	0,35
183654	3,92	0,08	2,33	2,24	16,92	2,36	8,55	0,37	0,53	0,12

ID	**MCP***		**KDE**		**AKDE**		**LOCOH**		**dBBMM**	
	95%	**50%**	**95%**	**50%**	**95%**	**50%**	**95%**	**50%**	**95%**	**50%**
183655	6,17	0	32,83	26,64	23,57	6,48	36,37	3,63	0,65	0,07
183658	21,51	0,13	18,71	6,27	8,73	1,58	1,23	0,38	0,65	0,11
183660	0,42	0	4,59	0	7,17	1,89	12,26	3,34	0,55	0,1
183661	0,74	0	0,5	0,02	7,25	1,63	0,82	0,34	0,52	0,12
183663	26,22	7,02	0	0	3,56	0,24	14,6	10,03	0,65	0,08
183664	0,07	0	2,93	1,14	12,01	2,24	3,1	0,07	0,36	0,08
183665	10,33	0,64	9,92	1,41	15,66	3,78	17,61	5,68	1,01	0,19
183666	0,01	0	0,22	0,19	1,82	0,52	0,86	0,01	0,45	0,06
183671	0,65	0,01	0,43	0,02	3,39	0,79	0,71	0,17	0,51	0,11
183673	56,55	3,16	24,52	13,26	16,96	4,51	43,97	8,55	1,12	0,15
183674	2,34	0,51	2,33	1,25	7,37	1,43	2,35	0,63	1,78	0,4
Mean	**14,4**	**1,77**	**11,91**	**3,49**	**14,58**	**2,56**	**14,78**	**2,97**	**1,45**	**0,26**
SD	**20,34**	**3,41**	**15,69**	**5,50**	**11,93**	**1,86**	**18,42**	**4,15**	**1,33**	**0,22**

Table 4 - Mean home range sizes (± SD, in km²) of *Podocnemis unifilis* in the Xingu River, grouped by sex, river section (Upstream, Midstream, Downstream), and hydrological season (high-water and low-water).

Sex	**Sector**	**Season**	**MCP**		**KDE**		**AKDE**		**LoCoH**		**dBBMM**	
			95%	**50%**	**95%**	**50%**	**95%**	**50%**	**95%**	**50%**	**95%**	**50%**
F	Midstream	High-water	8.22 ± 11.07	1.76 ± 3.88	7.52 ± 8.09	1.43 ± 1.95	12.17 ± 12.3	1.77 ± 1.83	7.93 ± 10.13	1.92 ± 3.59	1.83 ± 1.03	0.32 ± 0.21
		Low-water	11.5 ± 15.43	2.6 ± 5.19	8.92 ± 11.81	2.14 ± 3.69	15.21 ± 16.95	2.35 ± 2.58	12.09 ± 15.85	2.69 ± 4.4	1.97 ± 1.0	0.25 ± 0.13
	Upstream	Low-water	7.47 ± 0.0	0.26 ± 0.0	2.58 ± 0.0	0.52 ± 0.0	7.45 ± 0.0	1.46 ± 0.0	3.49 ± 0.0	0.23 ± 0.0	1.15 ± 0.0	0.26 ± 0.0
	Downstream	High-water	37.79 ± 33.7	3.57 ± 4.59	24.18 ± 29.53	3.76 ± 3.53	24.21 ± 15.79	2.98 ± 1.42	36.18 ± 30.99	5.25 ± 6.66	3.04 ± 2.14	0.5 ± 0.34
		Low-water	51.62 ± 29.99	3.12 ± 3.1	39.81 ± 31.64	4.12 ± 3.45	34.24 ± 14.0	3.9 ± 1.29	47.01 ± 30.51	4.63 ± 4.58	4.01 ± 2.14	0.66 ± 0.35
M	Midstream	High-water	4.98 ± 3.59	0.86 ± 0.79	14.54 ± 10.26	4.1 ± 6.54	14.71 ± 6.64	2.65 ± 1.54	8.63 ± 8.48	1.47 ± 1.22	1.98 ± 0.67	0.42 ± 0.16
		Low-water	20.2 ± 15.15	1.27 ± 0.79	21.72 ± 13.12	4.16 ± 2.69	9.85 ± 5.69	2.09 ± 0.96	9.19 ± 4.84	0.91 ± 0.81	1.3 ± 0.72	0.26 ± 0.16
	Upstream	High-water	1.93 ± 1.65	0.03 ± 0.04	2.29 ± 1.59	0.9 ± 1.11	11.1 ± 4.8	1.99 ± 0.32	6.89 ± 4.64	1.13 ± 1.32	0.53 ± 0.01	0.11 ± 0.01
		Low-water	3.92 ± nan	0.08 ± nan	2.33 ± nan	2.24 ± nan	16.92 ± nan	2.36 ± nan	8.55 ± nan	0.37 ± nan	0.53 ± nan	0.12 ± nan
	Downstream	High-water	5.45 ± 5.75	1.14 ± 2.35	6.84 ± 6.36	2.72 ± 2.78	9.45 ± 6.1	1.9 ± 1.51	7.69 ± 8.43	1.62 ± 2.71	0.92 ± 0.49	0.17 ± 0.09
		Low-water	12.71 ± 4.9	5.01 ± 2.31	11.82 ± 4.19	6.21 ± 2.36	19.45 ± 6.02	4.31 ± 1.47	10.68 ± 4.3	6.04 ± 2.67	1.7 ± 0.48	0.31 ± 0.09

Despite the differences in area values estimated by the various methods, no significant differences were found between males and females in home range size across any of the estimators, nor was any consistent effect of hydrological season (high-water versus low-water) detected (Figure 7). For the 95% isopleth, the MCP, KDE, LoCoH, and AKDE methods showed a visible reduction in median home range area during the high-water season, particularly for MCP and LoCoH (Figure 7). Although dBBMM produced smaller estimates in absolute terms, it also reflected this seasonal reduction, with slightly larger median ranges observed in the low-water period compared to the high-water period.

For the 50% core areas, seasonal differences were less pronounced, but the same direction of variation was observed: in all methods, core areas tended to be larger during the low-water season and more restricted during the high-water season. Notably, AKDE and LoCoH displayed greater interindividual variability in the dry season, suggesting that some turtles expanded their space use during this period.

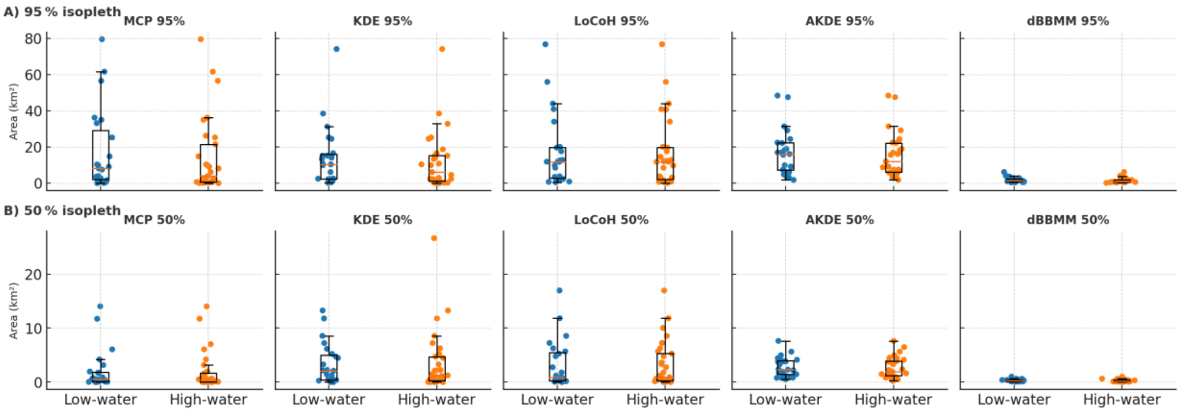

Figure 7 - Comparison of home range areas (95% isopleth and 50%) between low-water and high-water seasons for each method.

Individuals located in the upstream sector tended to have substantially larger home ranges than those in the midstream sector, while individuals in the downstream sector exhibited the smallest estimated ranges (Table 5). This pattern was most pronounced for the LoCoH and AKDE methods, where LoCoH 95% home ranges in the upstream sector were, on average, approximately four times larger ($e^{1.391} \approx 4.0$) than those in the midstream (Table 5; $p < 0.001$ for the Upstream vs. Midstream comparison), whereas LoCoH estimates for the downstream sector did not differ significantly from the midstream. A similar increase was observed with AKDE (coefficient for Upstream vs. Midstream ranging from 0.406 to 0.416; $p < 0.05$; Table 5), and also for core areas estimated by MCP, with 50% MCP in the upstream sector being significantly larger than in the midstream ($p = 0.035$; Table 5). Conversely, the downstream sector exhibited significantly smaller 95% ranges under KDE (coefficient for Downstream vs. Midstream = –1.597; $p = 0.009$; Table 5), as well as a marginal reduction in 50% areas estimated by MCP ($p = 0.063$; Table 5). In most methods, turtles in the upstream sector showed higher median 95% home range values and greater variability, while individuals from the downstream sector consistently exhibited lower estimates.

Monitoring duration had a strong positive effect on estimated home range size across nearly all methods (Table 3). Longer tracking periods resulted in significantly larger ranges ($p < 0.01$ for KDE, LoCoH, AKDE, and dBBMM; Table 5), as well as more extensive 50% core areas. For example, in the LoCoH model, an approximate 0.6% increase in estimated area was observed for each additional day of monitoring (Table 5). In contrast, the effect of the number of locations (telemetry fixes) was inconsistent after accounting for duration. In several cases, particularly in models for 50% core áreas, a greater number of fixes was associated with slightly smaller estimated ranges (e.g., KDE 50% and AKDE 50% showed small but significant negative coefficients for number of locations; Table 5).

Despite differences in absolute area estimates, the five home range estimation methods showed high concordance in the relative ranking of individuals. Spearman rank correlations between pairs of methods were high, ranging from 0.72 to 0.95 for the 95% isopleths, and although slightly lower, they were also significant for the 50% isopleths. In particular, AKDE and KDE showed $\rho \approx 0.82$, and MCP vs. LoCoH showed $\rho \approx 0.95$. Even dBBMM, despite producing more conservative absolute estimates, maintained strong correlations with the traditional methods, with ρ ranging from 0.72 to 0.81 relative to AKDE, MCP, KDE, and

LoCoH (Figure 8). For the 50% core areas, correlations remained positive but were more variable: for example, MCP vs. KDE 50% showed $\rho \approx 0.89$, while KDE vs. dBBMM 50% showed a weaker correlation ($\rho \approx 0.64$; Figure 8).

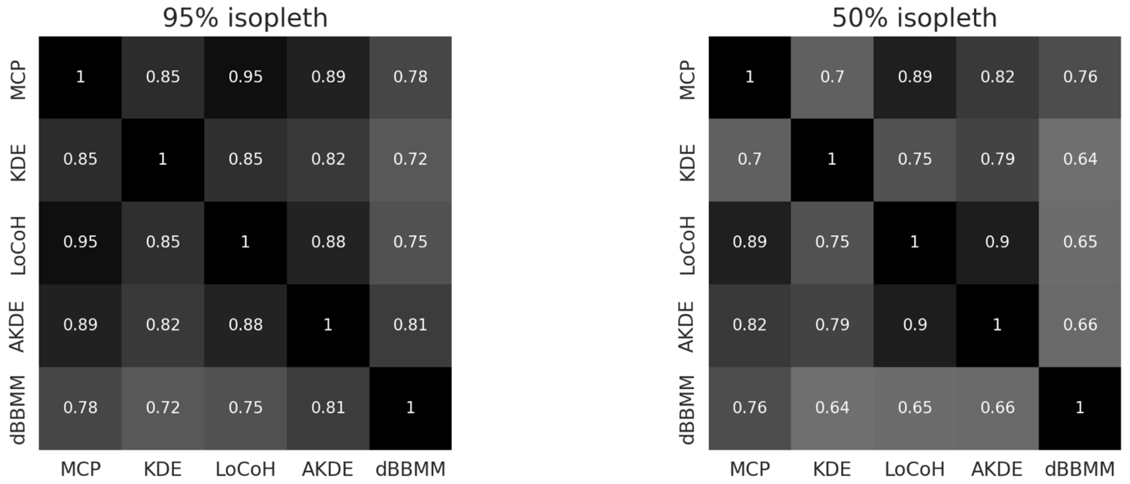

Figure 8 - Spearman correlation matrices for home range size estimates by different methods (95% isopleth and 50% isopleth).

For the 95 % isopleths, the pairs involving the trajectory-based estimator exhibited the largest discrepancies: LoCoH vs. dBBMM showed a mean bias of +13.9 km^2, with limits of agreement (±1.96 SD) ranging from –20.5 to +48.2 km^2, indicating that dBBMM systematically underestimates total home-range areas relative to LoCoH, especially for wide-ranging individuals. Among the purely polygonal estimators, differences were modest: MCP vs. KDE displayed a bias of +2.5 km^2 (–23.7 to +28.7 km^2), and MCP vs. LoCoH was virtually identical (–0.9 km^2; –20.0 to +18.2 km^2), suggesting convergence in delineating the outer contour of the home range. The comparison KDE vs. AKDE yielded a negative bias (–2.7 km^2; –24.5 to +19.1 km^2).

In the 50 % isopleths, deviations were even smaller. MCP estimated areas 1.7 km^2 smaller than KDE (–13.6 to +10.1 km^2) and 1.2 km^2 smaller than LoCoH (–5.2 to +2.8 km^2), whereas KDE exceeded AKDE by only +0.9 km^2 (–8.1 to +10.0 km^2). The largest positive bias remained in LoCoH vs. dBBMM (+2.7 km^2; –5.3 to +10.7 km^2), confirming that dBBMM remains more conservative even for core-use areas. Together, these results demonstrate that substantial method-specific differences emerge primarily when trajectory-based estimators (dBBMM) are contrasted with polygonal approaches, with the impact proportionally greater at the 95 % than at the 50 % home-range level (**Figure 9**).

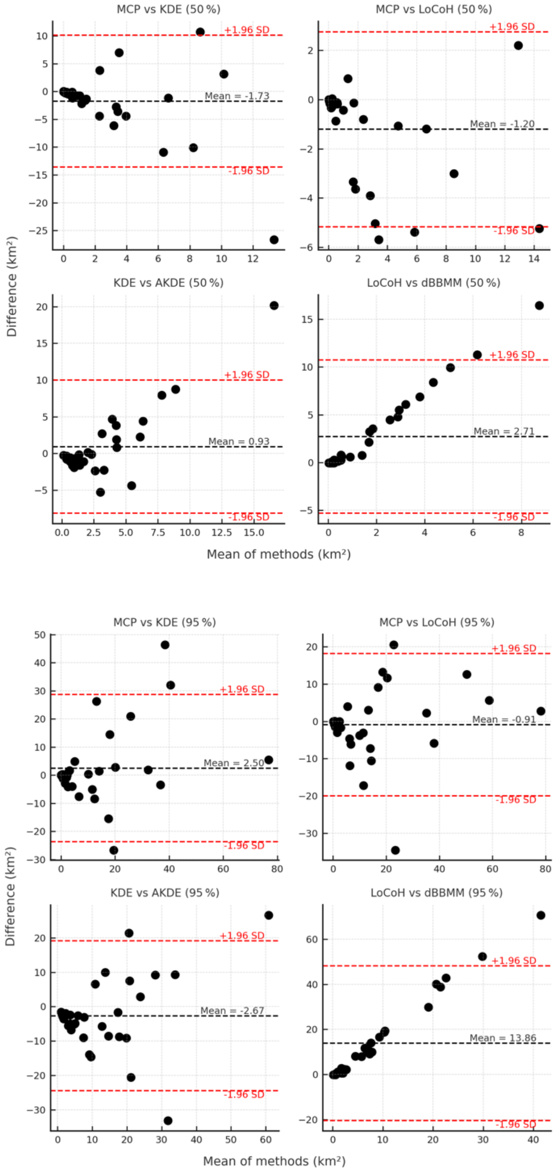

Figure 9 - Bland–Altman plots comparing four estimator pairs for home-range areas: MCP versus KDE, MCP versus LoCoH, KDE versus AKDE, and LoCoH versus dBBMM, shown separately for the 95 % and 50 % isopleths.

Table 5 - Gamma GLM results for MCP, KDE, LoCoH, AKDE and dBBMM home range area (95% and 50% isopleths). Coefficients (with standard errors) are on the log scale (Gamma regression with log-link).

	MCP				**KDE**				**LoCoH**				**AKDE**				**dBBMM**			
	95%		**50%**		**95%**		**50%**		**95%**		**50%**		**95%**		**50%**		**95%**		**50%**	
Predictor	**Coefficient (SE)**	**P-value**	**Coefficient (SE)**	**P-value**	**Coefficient (SE)**	**P-value**	**Coefficient (SE)**	**P-value**	**Coefficient (SE)**	**P-value**	**Coefficient (SE)**	**P-value**	**Coefficient (SE)**	**P-value**	**Coefficient (SE)**	**P-value**	**Coefficient (SE)**	**P-value**	**Coefficient (SE)**	**P-value**
Intercept	1.775 (0.511)	**<0.001**	-1.443 (0.661)	**0.029**	1.583 (0.434)	**<0.001**	0.574 (0.472)	0.224	0.745 (0.402)	0.064	-0.400 (0.531)	0.452	1.794 (0.251)	**<0.001**	0.313 (0.234)	0.182	-0.244 (0.238)	0.305	-1.690 (0.239)	**<0.001**
Sex (M vs F)	-0.460 (0.413)	0.266	0.086 (0.534)	0.872	0.225 (0.351)	0.521	0.243 (0.382)	0.526	-0.093 (0.325)	0.775	-0.164 (0.430)	0.703	0.028 (0.203)	0.889	0.067 (0.189)	0.724	0.027 (0.192)	0.890	0.045 (0.194)	0.815
Season (Low-water vs High-water)	0.280 (0.355)	0.430	0.355 (0.459)	0.439	0.175 (0.301)	0.560	0.123 (0.328)	0.708	0.239 (0.279)	0.392	0.113 (0.369)	0.760	0.044 (0.174)	0.802	0.062 (0.163)	0.705	0.114 (0.165)	0.488	0.107 (0.166)	0.518
Sector (Downstream vs Midstream)	-0.651 (0.718)	0.364	-1.728 (0.928)	0.063	-1.597 (0.609)	**0.009**	-0.995 (0.663)	0.133	0.079 (0.564)	0.889	-1.015 (0.746)	0.174	0.191 (0.353)	0.588	-0.000 (0.329)	0.999	-0.542 (0.334)	0.105	-0.506 (0.336)	0.132
Sector (Upstream vs Midstream)	0.663 (0.406)	0.102	1.104 (0.524)	**0.035**	0.204 (0.345)	0.553	0.516 (0.375)	0.169	1.391 (0.319)	**<0.001**	1.423 (0.422)	**<0.001**	0.406 (0.199)	**0.041**	0.416 (0.186)	0.025*	0.050 (0.189)	0.792	-0.107 (0.190)	0.574
Monitoring duration (days)	0.003 (0.002)	0.107	0.007 (0.002)	**0.007**	0.003 (0.002)	**0.048**	0.003 (0.002)	**0.048**	0.006 (0.001)	**<0.001**	0.007 (0.002)	**<0.001**	0.004 (0.001)	**<0.001**	0.004 (0.001)	**<0.001**	0.002 (0.001)	**0.027**	0.001 (0.001)	0.213
Number of locations	0.000 (0.002)	0.949	-0.000 (0.003)	0.997	0.001 (0.002)	0.481	-0.005 (0.002)	**0.016**	-0.002 (0.002)	0.385	-0.007 (0.002)	**0.004**	-0.001 (0.001)	0.277	-0.004 (0.001)	**<0.001**	0.003 (0.001)	**0.001**	0.003 (0.001)	**0.002**

DISCUSSION

The results show that yellow-spotted river turtles (*Podocnemis unifilis*) tracked in the Xingu River exhibit high site fidelity, remaining within relatively narrow river sectors despite the annual hydrological oscillations (Ribeiro et al., unpublished data). This pattern suggests that *P. unifilis* possesses a refined spatial knowledge of its immediate surroundings, routinely returning to familiar areas that provide predictable food resources, refuges, and thermal-regulation sites (Benhamou, 2011; Moll & Moll, 2004). In general, the extent of their home ranges fell within the limits reported for other Amazonian populations of the species and remained below values typical of larger congeners such as *P. expansa* (Bock et al., 1998; Fachín-Terán et al., 2006).

Although a few individuals displayed slightly broader areas of use, probably linked to body size, maturity, or reproductive demands (Ross et al., 2019) the set of estimates obtained here corroborates the restricted spatial behavior usually attributed to the species (Naveda-Rodríguez et al., 2018; Ponce de Leão et al., 2019; Hinderaker, 2021; Ribeiro et al., 2025, unpublished data).

This combination of micro-habitat fidelity and compact home ranges appears to be an energy-optimization strategy in which smaller-bodied individuals minimize long movements by concentrating in environments where food and shelter are predictably available throughout the flood–dry cycle (Gibbons, 1986; Bodie & Semlitsch, 2000). Remaining in known territories may also reduce exposure to predators and intraspecific competition, conferring an adaptive advantage in hydrodynamically complex rivers such as the Xingu (Junk et al., 1989; Alcântara et al., 2013).

Home-range estimates (95 %) varied widely across algorithms—from just 1.45 km² with dBBMM, which incorporates the temporal structure of trajectories and is therefore more conservative (Kranstauber et al., 2012), to about 15 km² with AKDE, which corrects for spatial autocorrelation (Noonan et al., 2019), and LoCoH, whose local convex hulls follow fluvial topography more precisely (Getz & Wilmers, 2004). At the 95 % isopleth, females occupied significantly larger areas than males, whereas 50% core areas were similar between sexes. This likely reflects peripheral excursions by females in search of nesting sites (Naveda-Rodríguez et al., 2018; Ponce de Leão et al., 2019) without substantially altering their central habitat, as shown here.

A longitudinal gradient was also evident: the smallest areas occurred downstream and the largest upstream across all estimators, as confirmed by GLM results. Minimal downstream values appear linked to the Tabuleiro do Embaubal Wildlife Refuge, the Amazon’s largest chelonian nesting ground, where legal protection ensures abundant nesting beaches, perennial food resources, and low human disturbance. In such settings, turtles can concentrate their activities in small spatial bands because essential resources are available within a restricted radius, obviating long movements. This mechanism has been reported for *P. unifilis* and *P. expansa* at the refuge and elsewhere in the Amazon, where dense nesting and community management limit the need for extensive travel (WWF, 2013; Oliveira, 2018). Comparable patterns occur in both marine and freshwater turtles: individuals foraging inside food-rich marine reserves show home ranges < 1 km² (Baumbach et al., 2019), while adult *Chelonia mydas* in productive bays travel only a few square kilometers (Seminoff et al., 2002). Global meta-analyses confirm that high resource availability and low disturbance are among the main predictors of reduced home-range size in turtles (Slavenko et al., 2016). Effective protection lowers hunting risk and vessel traffic, explaining the minimal values downstream compared with mid- and upstream sectors, where Belo Monte’s altered hydrodynamics and fewer beaches may necessitate larger movements.

Satellite imagery shows that the Volta Grande do Xingu (mid-sector) experienced major hydrologic reconfiguration and island loss after Belo Monte began operating, producing a more fragmented mosaic of aquatic and floodplain habitats (Kalacska et al., 2020). Hydrological studies further demonstrate that the dam altered the flood pulse, changing lateral connectivity and resource availability in this reach (Timpe & Kaplan, 2017), while cumulative-impact analyses reveal permanent flow reduction downstream and changes in sand-bar structure (Fearnside, 2006).

Rapids and waterfalls characteristic of the intermediate sector also act as partial barriers to *P. unifilis* movement, increasing longitudinal resistance (Agostini et al., 2024). Although most literature on intact Amazonian rivers reports larger home ranges during floods, our dataset shows the opposite pattern in the regulated mid-Xingu larger areas in the dry season. Likely drivers include: (i) the dampened flood pulse under Belo Monte, which limits lateral connectivity during floods (Timpe & Kaplan, 2017; Fearnside, 2016); (ii) the "dispersed-scarcity hypothesis," whereby receding waters isolate floodplain lakes and patchily distribute food and refuges, forcing longer travel (Junk et al., 1989; Fachín-Terán et al., 2006); (iii) reproductive demands leading females to make long longitudinal trips to nesting beaches at peak low water (Naveda-Rodríguez et al., 2018; Simoncini et al., 2022); (iv) individual heterogeneity typical of short-distance facultative migrants, with some turtles ranging widely in the dry season (Ponce de Leão et al., 2019); and (v) measurement geometry: during floods many moves occur within contiguous flooded forests, compressing two-dimensional outlines, whereas dry-season moves along the main channel artificially inflate MCP, KDE, and AKDE estimates—a bias shown for Amazonian turtles in the Juruá River (Hinderaker, 2021), for which Ouellette & Cardille's (2011) CLHR and Row & Blouin-Demers (2006) simulations highlight MCP/KDE overestimation in linear habitats.

Intrapopulation variation indicates strong behavioral plasticity: sex, body size, and reproductive status modulate site fidelity. Podocnemidids span a continuum from residents to long-distance migrants. For instance, 85 % of *P. lewyana* in the Magdalena River maintain < 1 km linear ranges, whereas some reproductive females travel 3–5 km (Alzate-Estrada et al., 2020).

Female *P. sextuberculata* in Mamirauá use 16–45 km linear ranges and migrate ~18 km between lakes and nesting beaches, whereas males remain almost sedentary (Fachín-Terán et al., 2006). *P. expansa* shows the extreme, with movements of hundreds of kilometers that require basin-scale corridors (Forero-Medina et al., 2019). Even *P. unifilis* in the Trombetas River display ranges from 0.6 to 215 ha, indicating a few individuals expand far beyond the population mean (Ponce de Leão et al., 2019). In this study, no permanent nomadism was observed, but occasional exploratory trips imply that, under favorable conditions (e.g., exceptional floods or localized scarcity), turtles may switch from resident to exploratory behavior, underscoring the need for management that safeguards both habitat cores and potential movement routes.

Hydrological fragmentation caused by dams drastically affects aquatic species' spatial behavior. In the Volta Grande, an ~80 % flow reduction after Belo Monte (Higgins, 2021) shrank floodable area. Tracked turtles now face much less habitat during floods, restricting movements to remnant channels and isolated pools. Our data suggest smaller home ranges and reduced seasonal movement amplitude compared with natural rivers (Ribeiro et al., unpublished; Fachín-Terán et al., 2006). In intact systems, females of *P. sextuberculata* travelled 16–45 km between feeding lakes and nesting beaches (Fachín-Terán et al., 2006), and *P. unifilis* in the Napo River ranged up to 30 km annually (Naveda-Rodríguez et al., 2018). No such distances occurred under the regulated Xingu, implying lateral-connectivity loss limits typical migrations.

Dam-imposed isolation likely keeps turtles in suboptimal habitats for long periods, increasing resource competition and hindering access to traditional foraging and nesting areas (Barcenas-García et al., 2022a, b). Similar alterations threaten Amazonian aquatic fauna broadly (Fearnside, 2016), and turtles in particular (Norris et al., 2021; Barcenas-García et al., 2022a, b). In short, Xingu turtles still display flood-pulse-modulated patterns, but fragmentation has likely dampened this dynamic, reducing natural behavioral plasticity. Such flood-regime changes already cause lateral-connectivity loss, population isolation, and turtle declines elsewhere in the Amazon (Correa et al., 2022); global reviews confirm dams disrupt migration routes, nesting-beach availability, and critical habitats, suppressing flexible responses to seasonal pulses (Barcenas-García et al., 2022). Reservoir-induced connectivity loss has also altered age structure and reduced fecundity in several *Podocnemis* species (Alho et al., 2011).

Finally, interpretation of spatial patterns must consider analytical tools. Different home-range estimators can yield distinct results from the same dataset (Börger et al., 2006; Boyle et al., 2009; Noonan et al., 2019). MCP overestimates area by enclosing unused spaces and is especially problematic in linear landscapes—its convex geometry fills meanders and side channels, creating polygons that misrepresent accessible surface. Simulations show MCP error can exceed 200 % in narrow corridors (Row & Blouin-Demers, 2006). The CLHR (Ouellette & Cardille, 2011) and Amazonian studies confirm MCP not only inflates values but can erase critical hydrological compartments (Hinderaker, 2021). KDE 95 % better delineated intensive vs. occasional-use zones (Worton, 1989) but assumes independence; autocorrelation leads to oversmoothing, and in linear rivers it projects use onto adjacent land (Swihart & Slade, 1985; Silva et al., 2022). KDE can overestimate area by 50–300 % in such settings (Row & Blouin-Demers, 2006; Ouellette & Cardille, 2011). LoCoH mitigates these issues by restricting hulls to point neighborhoods, respecting riverbanks (Getz & Wilmers, 2004), but may underestimate area if sampling is sparse (Getz et al., 2007). dBBMM incorporates time, revealing movement corridors and separating travel from residency (Horne et al., 2007; Mascarenhas-Junior et al., 2023, 2024), though it needs high fix rates (Kranstauber et al., 2012). AKDE offers statistically robust areas and confidence intervals by modeling autocorrelation (Fleming et al., 2015; Calabrese et al., 2016); ignoring autocorrelation underestimates area, and AKDE averages twice the size of traditional estimators (Noonan et al., 2019; Silva et al., 2021).

Given these trade-offs, we recommend a multimodel approach: AKDE for total area, dBBMM for functional connectivity, and LoCoH/KDE for activity centers, providing an integrated, ecologically realistic depiction of *P. unifilis* movement. Satellite-tracking effort also matters. ARGOS duty-cycle settings balance fix frequency and battery life; low-power cycles extend tracking but reduce daily fixes, while intensive schedules shorten tag life (Douglas et al., 2012; Dubinin et al., 2010). ARGOS location quality varies by class; median errors range from ~150 m (class 1) to > 1 km (classes A–Z) (McClintock et al., 2015;

Vincent et al., 2002). Filtering can remove up to 90 % of bad fixes but reduces usable effort (Douglas et al., 2012). Some tags failed before spanning a full seasonal cycle—common in humid tropics (Witt et al., 2010) so individuals with < 60 high-quality fixes may have underestimated ranges.

Overall, *P. unifilis* in the mid-Xingu relies on compact home ranges, micro-habitat fidelity, and seasonal connectivity provided by the flood pulse to reach nesting beaches, floodplain lakes, and back-water channels. Conservation priorities include (1) re-establishing partial hydrological connectivity via ecological flows maintaining ≥ 80 % natural discharge during floods (Richter et al., 2012); (2) protecting key habitat cores and corridors identified by AKDE/LoCoH and dBBMM (~15 km^2 in upstream and mid-sectors; Norris et al., 2018); and (3) fostering community co-management to protect beaches and regulate boat traffic (Campos-Silva & Peres, 2016; Pezzuti et al., 2010). Long-term telemetry, rigorous ARGOS filtering (Douglas et al., 2012), and autocorrelated estimators (Fleming et al., 2015) should guide adaptive management and dam-operation rules. Future hydropower licensing must internalize connectivity costs, provide functional passages, compensate for beach loss, and mandate post-dam monitoring. Isolated reserves are insufficient; a network protecting short migration routes, foraging hubs, and nesting beaches aligned with Brazil's national turtle action plan (ICMBio) is required. Under climate change, more severe hydrological extremes will combine with fragmentation to heighten collapse risk. Functional river corridors, genomic monitoring for bottlenecks, and public-awareness campaigns about the species' ecological and cultural value are essential parts of a robust conservation strategy for *P. unifilis* in the Xingu and other Amazonian basins under hydropower pressure.

CONCLUSION

This analysis of the spatial ecology of the yellow-spotted river turtle (*Podocnemis unifilis*) in the Xingu River, encompassing different hydrological segments, seasons, and sex classes, provides a comprehensive and integrated overview of how the species responds to a fragmented and regulated riverine ecosystem. *P. unifilis* demonstrated a remarkable capacity for behavioral adjustment, maintaining seasonal movement patterns and fidelity to key habitats even under altered conditions, albeit within the constraints imposed by water availability and resource distribution. The striking differences among the upstream reservoir, the reduced-flow Volta Grande, and the regulated downstream section eloquently illustrate the critical importance of a natural hydrological regime in sustaining the ecological processes that support these turtles life cycles.

Ecologically, we found that *P. unifilis* retains typical traits of Amazonian turtles, such as moderate reproductive movements in females, high philopatry, and a preference for lentic environments, but also experiences severe limitations when its habitat is transformed, reducing both home range size and migration opportunities. Methodologically, we emphasize the value of applying modern analytical tools and recognizing the limitations of Argos telemetry data to ensure more accurate and statistically robust interpretations. Finally, from a conservation perspective, our findings support concrete actions aimed at mitigating the impacts of the Belo Monte Hydroelectric Dam and offer recommendations applicable to other hydropower projects: the need to preserve or simulate natural flood pulses, protect critical habitats (such as nesting beaches and dry-season refuges), and manage each isolated subpopulation with targeted measures. In the face of rapid environmental change in the Amazon, studies like this, grounded in robust empirical data and informed by current ecological understanding, are essential to support effective conservation strategies.

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Ethics approval and consent to participate

This study did not require new approval from an ethics committee, as all data used were obtained from secondary sources and no new data collection or animal capture was conducted

Consent for publication

Not applicable

Availability of data and materials

The telemetry data used in this study are not publicly available due to conservation restrictions and the sensitivity of individual location information. However, the data are available from Norte Energia S.A. upon reasonable request.

Competing interests

The authors declare that they have no financial or non-financial conflicts of interest related to this study.

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Authors' contributions

M.V. Ribeiro: Conceptualization, Methodology, Data curation, Formal analysis, Investigation, Writing – original draft. **A. Malvasio:** Conceptualization (Chelonian biology and conservation), Writing – review & editing. **M. Solé:** Formal analysis, Interpretation of results, Writing – review & editing. **A. Schiavetti**: Supervision, Project administration, Conceptualization, Methodology, Writing – review & editing.

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CONSIDERAÇÕES FINAIS

Esta tese fornece uma grande contribuição para o entendimento da ecologia espacial de quelônios de água doce, com foco no tracajá (*Podocnemis unifilis)*, em um dos rios mais ambientalmente modificados da Amazônia brasileira, o rio Xingu. A abordagem escalonada, que articula uma revisão global, uma investigação empírica local e uma análise detalhada de área de vida sob diferentes métodos analíticos, permitiu explorar tanto os padrões gerais quanto as respostas contextuais da espécie frente a diferentes níveis de impacto antrópico.

No **Capítulo 1**, a revisão sistemática revelou um aumento expressivo nos estudos sobre movimentação de quelônios ao longo das últimas quatro décadas, mas também evidenciou lacunas importantes na representatividade taxonômica e geográfica, especialmente nas regiões tropicais. Embora radiotelemetria continue sendo a técnica predominante, a adoção de métodos mais sofisticados tem crescido, embora ainda limitada para espécies ameaçadas ou de interesse comercial. A análise destacou ainda a importância crescente da telemetria como ferramenta indispensável para subsidiar decisões de manejo e conservação.

O **Capítulo 2** investigou o comportamento espacial de *P. unifilis* ao longo de três setores longitudinais do médio Xingu, revelando uma expressiva variação sazonal no uso do espaço. Durante a estação seca, os indivíduos restringiram seus deslocamentos a áreas permanentes, com forte fidelidade espacial; já no período de cheias, expandiram sua área de uso, explorando habitats temporariamente acessíveis. Apesar dessa plasticidade, não se observaram orientações direcionais consistentes, nem diferenças estatísticas marcantes entre sexos ou setores. Esses padrões indicam que a espécie adota uma estratégia de movimentação oportunística, fortemente mediada pela conectividade hidrológica local e pelas condições do microhabitat, mais do que por deslocamentos orientados de longa distância.

No **Capítulo 3**, as estimativas de área de vida utilizando cinco métodos (MCP, KDE, AKDE, LoCoH e dBBMM) confirmaram ampla variabilidade individual, mas evidenciaram padrões de movimento restritos e uma notável permanência espacial ao longo do tempo. As diferenças observadas entre os setores, com maiores áreas de vida no reservatório a montante e menores na Volta Grande (intermediário) sugerem que a fragmentação afeta de maneira significativa a amplitude de movimentação da espécie. A limitação espacial observada na Volta Grande, em particular, reforça a vulnerabilidade de *P. unifilis* em ambientes fluviais altamente regulados, onde a heterogeneidade estrutural e a conectividade sazonal foram drasticamente reduzidas.

Em conjunto, os três capítulos convergem para uma conclusão crítica: embora *P. unifilis* demonstre resiliência ecológica por meio de certa plasticidade comportamental, sua persistência depende diretamente da manutenção de habitats funcionais, da integridade dos ciclos hidrológicos naturais e da conectividade longitudinal e lateral do sistema fluvial. A espécie utiliza predominantemente áreas restritas e demonstra fidelidade espacial acentuada, o que a torna sensível a alterações no regime hidrossedimentológico e à perda de habitats críticos como praias de desova.

Dessa forma, a presente tese reforça a urgência da incorporação de dados de movimentação e uso do espaço em estratégias de manejo adaptativo e licenciamento ambiental de empreendimentos hidrelétricos. Sugere-se, ainda, a implementação de um Manejo Espacial Integrado (MEI) para o rio Xingu, que contemple: (i) a proteção de núcleos de uso recorrente, (ii) a simulação de pulsos de cheia para manter a conectividade sazonal, e (iii) o reconhecimento legal e ecológico de áreas críticas para a reprodução e sobrevivência de quelônios. Ao unir síntese global, evidência local e aplicação prática, esta tese oferece fundamentos científicos sólidos para ações de conservação mais eficazes de *P. unifilis* e, por extensão, para a manutenção da integridade ecológica dos grandes rios amazônicos.