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Spatio-Temporal Ecology of Amazonian Freshwater Turtles

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"The song of the dodo, if it had one, is forever unknowable because no human from whom we have testimony ever took the trouble to sit in the Mauritian forest and listen."

- David Quammen, The Song of the Dodo: Island Biogeography in an Age of Extinctions.

Abstract

Amazonian freshwater turtles are a key component of the Amazonian waterscape and an important resource for riverine communities. However, extensive exploitation combined with habitat alteration and climate change has endangered the giant South American river turtle (*Podocnemis expansa)* and the yellow-spotted river turtle (*Podocnemis unifilis)*, two of the largest freshwater species in the region, reducing their numbers to only a fraction of pre-colonial levels. The survival of these species is therefore dependent on successful conservation efforts. For conservation to be successful, knowledge on where and when animals spend their time is necessary in order to successfully implement appropriate actions. However, little is known about the spatial ecology of Amazonian river turtles. To obtain information on spatio-temporal movement patterns and habitat use, 7 individuals of *P. expansa* and 3 *P. unifilis* were tracked in the central Juruá River region of the Brazilian Amazon using ARGOS satellite transmitters from 2011 to 2016. Space-use varied widely within and between the two species. *P. expansa* has a considerably larger home range than *P. unifilis* with a mean of 74,881 (±81,453 SD) hectares compared to 31,167 (±27,550 SD) ha, respectively. Both species show a high affinity to the main river, but *P. expansa* use the flooded forest and oxbow lakes to a larger degree than *P. unifilis*. After nesting at seasonally exposed beaches in August-September, *P. unifilis* moves into the surrounding flooded várzea forest as the water level starts to rise. *P. expansa,* nesting a month later, generally started moving at the end of November and early December. Upon leaving the nesting site, *P. expansa* leaves the river and moves into the forest until it returns when the water level drops rapidly in June. *P. unifilis* appears to move the furthest away from the river in November, towards oxbow lakes in the forest. Conservation of nesting beaches and the surrounding areas will continue to be important due to high site fidelity among the turtles. However, community-based protection along the river during seasonal movements and of flooded forests during high-water could improve survival and reproduction of *P. expansa*, within and outside protected areas, while the area around the nesting beach is a key habitat for *P. unifilis*.

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1 Introduction

The Amazon rainforest is the largest remaining tropical forest on Earth, covering approximately 5 million km^2, and almost half the remaining tropical forests (Hansen *et al.*, 2013). It is home to a diverse array of flora and fauna, and is so vast it creates its own weather (Sheil, 2014; Leite-Filho *et al.*, 2021). However, rapid human population growth and access to the global market have led to detrimental impacts on wildlife populations through extensive habitat degradation and loss, hunting for bushmeat, and trapping for the wildlife trade (Benítez-López *et al.*, 2019; Chaves, Monroe and Sieving, 2019; Morton *et al.*, 2021). This dramatic exploitation has resulted in considerable species declines, affecting the function and resilience of Amazonian ecosystems (Doughty, Wolf and Malhi, 2013; Peres *et al.*, 2016).

Most conservation effort has focussed on mammals and birds, while reptiles have received less attention (Roll *et al.*, 2017), despite many species experiencing dramatic population declines (Fitzgerald *et al.*, 2018; Saha *et al.*, 2018). For example, more than 35% of turtles and tortoises are now considered Critically Endangered (CR) or Endangered (EN) (Böhm *et al.*, 2013; Lovich *et al.*, 2018; Rhodin *et al.*, 2018). While Protected Areas (PAs) have shielded many terrestrial species from overexploitation and habitat loss, they have also failed to protect many species, particularly in aquatic systems (Brooks *et al.*, 2006; Antunes *et al.*, 2016; Oliveira *et al.*, 2017). Several fish and turtle species have therefore lacked habitat protection and consequently left them vulnerable to exploitation (Fagundes, Vogt and De Marco Júnior, 2016; Frederico, Zuanon and De Marco, 2018). As a result, freshwater turtles are now among the most threatened vertebrate taxa in the world, and many species are therefore dependent on targeted and effective conservation efforts in order to protect or recover populations (Fagundes *et al.*, 2018).

River turtles of the genus *Podocnemis* are among the many taxa exploited in the Amazon waterscape, the most threatened being the endangered giant South American river turtle (*P. expansa*) and the vulnerable (VU) yellow-spotted river turtle (*P. unifilis*; Turtle Taxonomy Working Group, 2017). The abundance of *P. expansa* was once so high that it could make traveling along the Amazon River challenging at times (Smith, 1974). However, intense exploitation ultimately led to a detrimental decline, despite voices of concern in the local population and among naturalists (Bates, 1892). With the decline of *P. expansa*, increased pressure was put on the smaller species such as *P. unifilis* (Schneider *et al.*, 2011), subsequently contributing to the current threatened status of this species as well.

Amazonian freshwater turtles, including *P. expansa* and *P. unifilis*, are an important resource among traditional lifestyles throughout the basin (Peñaloza *et al.*, 2013; Pantoja-Lima *et al.*, 2014), and have played an integral role in the livelihood of riverine people through history (Schneider *et al.*, 2011). The sheer numbers of *P. expansa* gave it the term “river cattle”, as it ensured a stable source of food in periods of high water-level when fishing was difficult (Smith, 1974). The historical utilisation of turtles was nearly unlimited. Shells were used both as bowls and as stepping stones on roads (Smith, 1974), while fat from the turtles and eggs lit cooking fires and street lights in both smaller communities and cities like Manaus (Santos and Fiori, 2020). They continue to be valued by Amazonian people today, both as a source of food and for their role in cultural traditions (Alves *et al.*, 2012; Pantoja-Lima *et al.*, 2014).

Turtles also play various important, but often unappreciated roles in their ecosystems (Stanford *et al.*, 2020). These functions include environmental regulation of factors such as sedimentation, nutrient cycling, and dispersing and enhancing germination of seeds (Lindsay *et al.*, 2013; Lovich *et al.*, 2018). The ectotherm nature of turtles makes them highly efficient secondary producers capable of maintaining higher population densities than any other taxa, effectively passing energy to the next trophic levels (Iverson, 1982; Jodice, Epperson and HenkVisser, 2006). Where they are not over-exploited, turtles can contribute to a large standing crop of biomass and act an important pathway of energy from producers to secondary consumers.

The life histories of *P. expansa* and *P. unifilis* are tightly linked to both the meandering rivers and streams of the Amazon, and the seasonally flooded várzea forest. Várzea forest is seasonally flooded by sediment-laden white-water rivers spilling over their banks onto the adjoining floodplain. These floodplains are therefore highly productive due to the seasonal deposition of new sediment (Furch, 1997), and are accessible for aquatic animals like *P. expansa* and *P. unifilis* during the inundation period (Gottsberger, 1978; Junk and Piedade, 1993; Teran, Vogt and Gomez, 1995), allowing seasonal movement between flooded and unflooded forests across the landscape (Haugaasen and Peres, 2005; Hawes and Peres, 2014). The nesting of both species is tightly linked to the seasonal flood pulse (Alho and Pádua, 1982b). As the water level in the flooded várzea forest declines, *P. expansa* and *P. unifilis* are known to return to the main rivers in order to nest on seasonally exposed fluvial beaches after the water level reaches its lowest point (Ferreira Júnior and Castro, 2003; Ferreira and Castro, 2010). In the case of *P. expansa*, the adults tend to congregate in front of the nesting beaches, waiting for the hatchlings to emerge (Alho and Pádua, 1982a). The hatchlings then move together with adults into the flooded várzea forest in groups, seemingly using vocalisations as hatchlings and females have been observed to move together (Ferrara, Vogt and Sousa-Lima, 2013; Ferrara *et al.*, 2014).

The life history of *P. expansa* and *P. unifilis* plays a major part in their vulnerability to threats like exploitation, habitat alteration and climate change (Castello *et al.*, 2013). Both species are long-lived and mature late (Gibbons, 1987; Mogollones *et al.*, 2010). This makes them vulnerable to exploitation throughout their lives and poses a risk of being exploited before they have a chance of reproducing. The reliance on suitable nesting beaches limits their reproduction to scarce and exposed habitats, rendering them susceptible to predation by both animals and humans (Santos and Fiori, 2020). In addition, exceptionally severe flooding events can cause up to 100% natal mortality (Alho and Pádua, 1982a), and are projected to increase in frequency with climate change (Eisemberg *et al.*, 2016; Butler, 2019).

In order to improve the efficiency of protective measures and guiding policymakers, it is vital to know how species behave and interact with their environment. Home ranges are often used as key measures in studies of spatial ecology. A home range is defined as the area an individual utilises in search of food and mating opportunities, and provides insight in the mobility and extent of habitat a species utilises (Burt, 1943). The home range size may vary depending on habitat, resource distribution, seasonality, and sex, and provides some information on how a species utilise a landscape and its resources (Burt, 1943; Powell and Mitchell, 2012). However, a home range cannot fully explain the behaviour of an animal. Utilising data on habitat and other spatial attributes is therefore necessary to understand the basic behaviour of animals

(Powell and Mitchell, 2012). With a stronger understanding of where and when animals move in relation to spatial attributes, conservation planning and policy can target vulnerable life stages, movement routes, and key habitat (Böhm *et al.*, 2013).

Given the vulnerability and importance of *P. expansa* and *P. unifilis*, there is an urgent need for targeted actions in order to protect the species from extinction and restore extirpated populations. Most effort on these species has focussed on exploitation history, genetics, population structure, and reproduction (Valenzuela *et al.*, 1997; Mogollones *et al.*, 2010; Schneider *et al.*, 2011; Miorando, Giarrizzo and Pezzuti, 2015). Besides coarse descriptions of nesting behaviour and seasonal movement, little is known about the spatio-temporal ecology of these species. Most work is in the form of unpublished work, often only available in Portuguese or Spanish (Eisemberg *et al.*, 2017). Only a few robust studies have attempted to track *P. unifilis* with VHF (Very High Frequency radio; Naveda-Rodríguez, Cueva and Zapata-Ríos, 2018; Ponce De Leão, Famelli and Vogt, 2019), and apart from smaller GPS tracking studies (Souza, 2012; Carneiro and Pezzuti, 2015), only rudimentary tag-and-release attempts have so far been used to estimate linear home ranges for *P. expansa* (Carneiro and Pezzuti, 2015; Fagundes *et al.*, 2017). The spatial ecology and seasonal movements of these species therefore remains particularly poorly understood.

This study addresses this knowledge gap to investigate the spatio-temporal behaviour of *P. expansa* and *P. unifilis* by analysing multi-year GPS tracking data. More specifically, I investigated 1) home range size, 2) habitat use, and 3) seasonal movement patterns during the dry and wet season for both *P. expansa* and *P. unifilis*. The results are discussed in relation to previous knowledge, and future conservation efforts.

2 Methods

2.1 Study area

The study was conducted along the central Juruá River, largely within the Médio Juruá Extractive Reserve (253,227 ha) and the Uacari Sustainable Development Reserve (632,949 ha), both in the municipality of Carauari, State of Amazonas, Brazil (5°22'10.758"S, 67°13'17.389”W, Figure 1). The two PAs are located approximately 20-60 km southwest of the town of Carauari, which has a population of roughly 20,000 people (Endo, Peres and Haugaasen, 2016). Both PAs allow for subsistence consumption of natural resources such as fish, forest game, and freshwater turtles, and are home to about 4,000 people depending on these resources (Endo, Peres and Haugaasen, 2016).

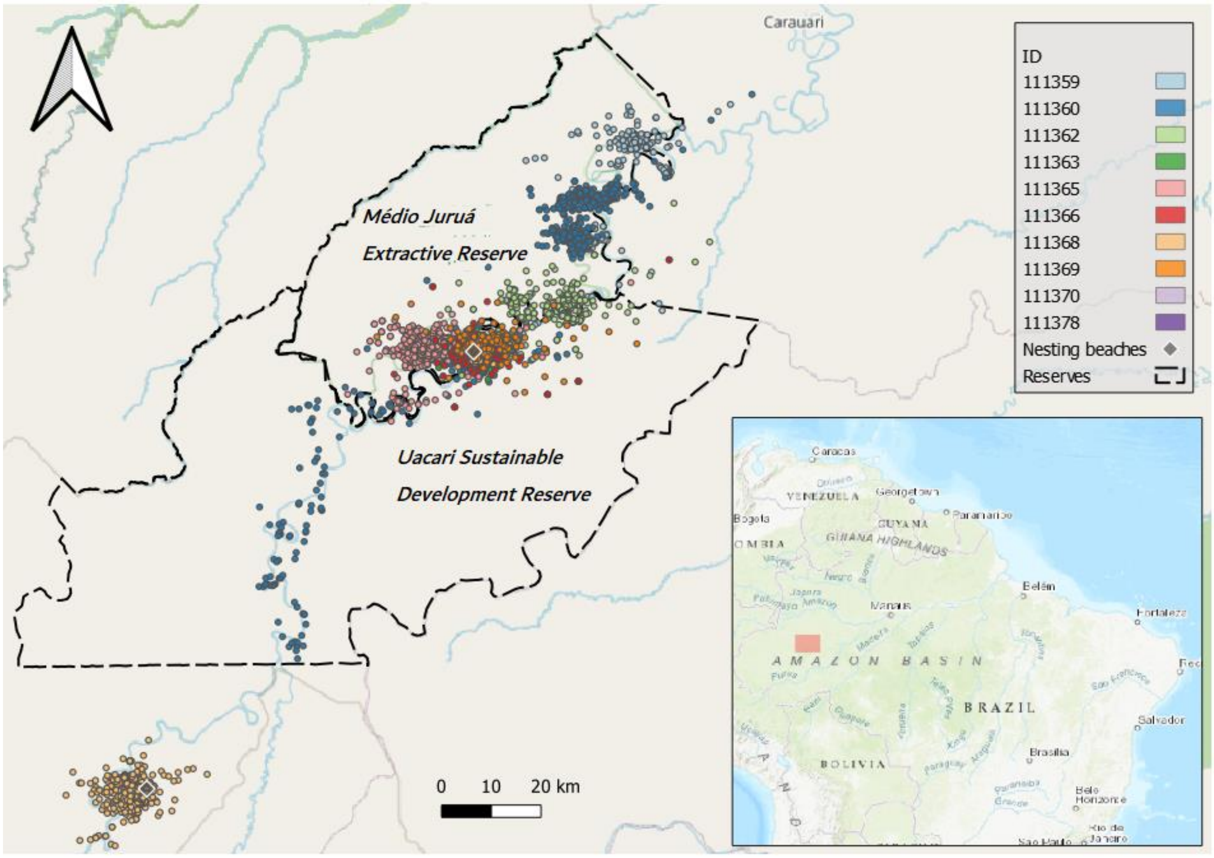

Figure 1: Map of the study area showing GPS fixes acquired for each freshwater turtle individual tracked along the Juruá River, western Amazonia, Brazil. The town of Carauari lies north-east of the Médio Juruá Extractive Reserve (253,227 ha) and the Uacari Sustainable Development Reserve (632,949 ha).

There are numerous fluvial beaches along the meandering Juruá River that provide nesting habitat for both *P. expansa* and *P. unifilis*, with many of these beaches being protected effectively through community-based management (Campos-Silva *et al.*, 2018). The seasonal rainfall pattern results in recurring flooding of the forest as the water level rises above the river banks. The surrounding forest consists of seasonally flooded várzea forest. The climate is typically wet, with a mean precipitation of 3,679 mm (Leite *et al.*, 2018). While the rainy season extends from November to April, the water level of the river is also affected by precipitation upstream and, as a result, typically starts rising in late September to October (Figure 2; Junk *et al.*, 2011; Hawes and Peres, 2016). The seasons in the mid-Juruá region are therefore commonly described as four different stages:

- Ebb (*vazante*): May to June, subsiding water level.
- Dry (*seca*): July to October/early-November, lowest water level.
- Flooding (*enchente*): mid-November to December, rising water level.
- Flooded (*cheia*): January to early-May, highest water level.

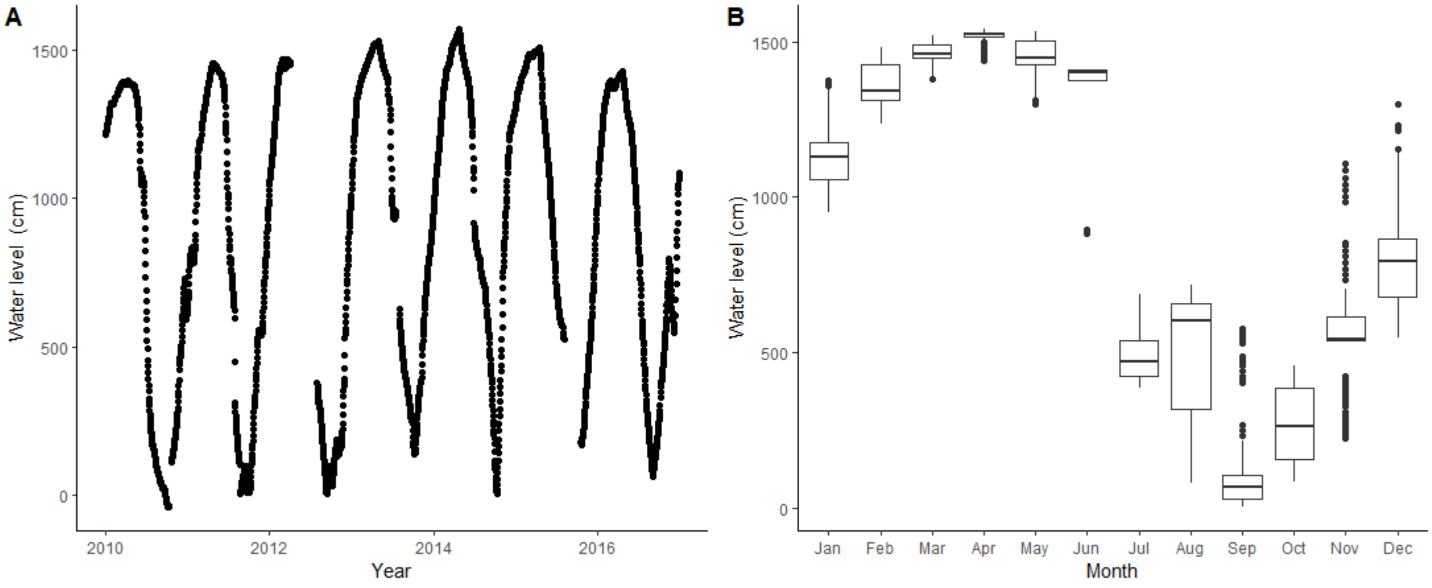

Figure 2: Water level fluctuation at Porto Gavião on the Juruá River from 2010-2016 (source: Agência Nacional de Águas, ANA). A) Daily water level throughout the study period shows the periodic cycle of water rising and falling. B) Mean monthly water level shows how the water level can vary, particularly in August, October, and December. Boxplots represent first and third quartiles, lines the median, whiskers extend up to 1.5 times the inter-quartile range, points beyond are plotted individually.

For this study, the most relevant seasonal factor is whether the forest is flooded or not, and seasons were therefore defined as high- and low-water periods for the analyses. Mid-December through June was defined as high water level, and July to mid-December as low water level. This corresponds to previous studies on *P. unifilis* (Naveda-Rodríguez, Cueva and Zapata-Ríos, 2018), and similar studies in this area (Leite *et al.*, 2018).

2.2 Study species

Both *P. expansa* and *P. unifilis* are well adapted to the rivers and flooded forests of the Amazon basin. They have a fairly similar omnivorous diet, and play an integral part in seed predation and dispersal processes in the floodplain ecosystem (Malvasio *et al.*, 2003; Cunha, Bernhard and Vogt, 2020). While they appear to utilise the same habitats, foraging might differ in micro-habitat between the two species (Cunha, Bernhard and Vogt, 2020).

2.2.1 P. expansa

The South American river turtle is a widespread species, found across the Amazon, Essequibo, and Orinoco River basins (Pearse *et al.*, 2006). While populations in sub-basins are generally genetically isolated, *P. expansa* is known to have a large range, capable of moving up to 65 km downstream from nesting beaches (Moreira and Vogt, 1990, cited in Fachín-Terán, Vogt and Thorbjarnarson, 2006). Few published studies have estimated home ranges, but one study has estimated the fixed kernel home range to be 379 ha (Souza, 2012). However, movements surpassing 100 and 400 km have been recorded for *P. expansa* individuals (von Hildebrand, Bermudez and Peñuela, 1997, cited in Fachín-Terán, Vogt and Thorbjarnarson, 2006; Carneiro and Pezzuti, 2015), suggesting that the home range is likely to be much larger.

There is considerable uncertainty in the age at which *P. expansa* reaches maturity. Estimates range from 4-15 years (Mogollones *et al.*, 2010), with most suggesting an average of 7 years

(Chinsamya and Valenzuela, 2008). Adult size is assumed to be reached after 17 years (Hernández and Espín, 2006), while the lifespan is typically estimated to be 40-50 years (Chinsamya and Valenzuela, 2008), although the maximum age has also been estimated as high as 80 years (Hernández and Espín, 2006). The carapace length can surpass 80 cm (Chinsamya and Valenzuela, 2008), and weight can exceed 50 kg (Smith, 1979), with exceptional records reaching up to 90 kg (Pritchard and Trebbau, 1984, cited in Cantarelli, Malvasio and Verdade, 2014).

P. expansa has a broad diet, with fruits and seeds making up a large part, but stems, leaves, various insects, crustaceans, sponges, fish and even small reptiles have also been found in their stomach contents (Teran, Vogt and Gomez, 1995; Cunha, Bernhard and Vogt, 2020). After feeding in flooded forests, *P. expansa* returns to the main rivers (Alho and Pádua, 1982a). As the water level starts to rise, *P. expansa* initiates nesting, depositing 76-98 eggs 2.3-3.0 m above the water level, on exposed sand beaches along the river, in order to avoid flooding of the nests (Alho and Pádua, 1982b; Ferreira Júnior, Castro and State, 2005; Ferreira and Castro, 2010). *P. expansa* digs deeper nests than *P. unifilis*, which can be placed directly in the sun while achieving suitable temperatures and humidity (Ferreira Júnior and Castro, 2003). After nesting, adults rest and wait in deeper pools in the river, until the hatchlings emerge 36-75 days after nesting (Ferreira Júnior and Castro, 2003; Ferreira Júnior, Castro and Castro, 2007; Ferreira and Castro, 2010). Incubation duration depends on temperature, which is affected by factors such as nest location and height, clutch size, and sediment grain size (Ferreira and Castro, 2010). Hatching success is estimated to about 85%, but this can vary strongly according to flooding or predation (Alho and Pádua, 1982a; Vanzolini, 2003; Ferreira Júnior, Castro and Castro, 2007).

2.2.2 P. unifilis

The yellow-spotted river turtle is a widespread generalist and is typically found in the same range as *P. expansa*, utilising a wide range of habitats such as flooded forests and oxbow lakes (Teran, Vogt and Gomez, 1995; Ferreira and Castro, 2010). It is, however, considerably smaller, normally weighing less than 8 kg, with carapace length reaching 43-47 cm (Smith, 1979; Schneider and Vogt, 2018). Maturity is assumed to be reached at approximately 3-9 years, and females tend to grow larger than males (Thorbjarnarson, Perez and Escalona, 1993; Peñaloza *et al.*, 2013). The home range and movements of *P. unifilis* is also described as smaller when compared to *P. expansa*, with a linear home range of 16 km, and areas covering 77-520 ha (Naveda-Rodríguez, Cueva and Zapata-Ríos, 2018; Ponce De Leão, Famelli and Vogt, 2019).

P. unifilis is generally considered an herbivore-frugivore, consuming seeds, fruits, aquatic plants, and other plant material (Pritchard and Trebbau, 1984; Balensiefer and Vogt, 2006). However, diet appears to vary with sex and age, and older individuals are known to include animals such as fish, crustaceans and molluscs in their diet, and females eat more fruits and seeds than males (Teran, Vogt and Gomez, 1995). *P. unifilis* share a large part of its diet with *P. expansa* (Cunha, Bernhard and Vogt, 2020) but also exhibits surface skimming (neustophagia) behaviour as a way to scavenge fine particles on the water surface – a behaviour not seen in *P. expansa* (Belkin and Gans, 1968) – and appears to consume slightly more animals (Lara *et al.*, 2012).

Nesting is triggered by the water level, and occurs early in the low water season when the sandy beaches are exposed, approximately one month before *P. expansa* (Ferreira and Castro, 2010). Eggs are laid on beaches at approximately 0.8-1.1 m above water level, typically 10-20 cm into the sand (Thorbjarnarson, Perez and Escalona, 1993; Ferreira and Castro, 2010). Clutch size is smaller than for *P. expansa* and depends on female body size, with a range of 20-30 eggs (Hernández *et al.*, 2010). *P. unifilis* is less particular about its nesting requirements and, in addition to fluvial beaches, can also nest along the edges of lakes, channels, or areas covered with vegetation (R.C. Vogt, unpublished data, cited in Fachín-Terán, Vogt and Thorbjarnarson, 2006; Erickson and Baccaro, 2016). The incubation period lasts about 55-69 days (Thorbjarnarson, Perez and Escalona, 1993; Ferreira and Castro, 2010), leading to hatching at the end of October (Ferreira and Castro, 2010), with annual mortality rates from flooding typically ranging from 25-80% (Hernández and Espín, 2006).

2.3 Data collection/ Field Methods -

Between December 2011 through December 2016, 7 individuals of *P. expansa* and 3 individuals of *P. unifilis* were tagged with ARGOS satellite tags, tracking the location of the turtles. The turtles were captured and released at Manaria beach (05´28 ° 13 "S, 67´28°28"W). GPS devices were attached to the with durepoxy two-component epoxy glue, set to harden for 48 hours. *P. expansa* was fitted with “Sirtrack KiwiSat Argos 101PTT” GPS units weighing 475 to 485g, and an additional VHF transmitter (“AVM Instrument Company LTD carapace mount MP2”, frequency 164-165 MHz) weighing 125 g. *P. unifilis* was fitted with similar but smaller units weighing 323 to 330g, limiting the weight of the units to 3% or less for the animals in this study. While the GPS units were projected to last for 720 days, some of them lasted much longer, providing movement data up to 1860 days (not including breaks, for the longest one; Figure 3, Appendix Table 3). Funding shortages resulted in a gap in location data for early 2012 and mid-2013.

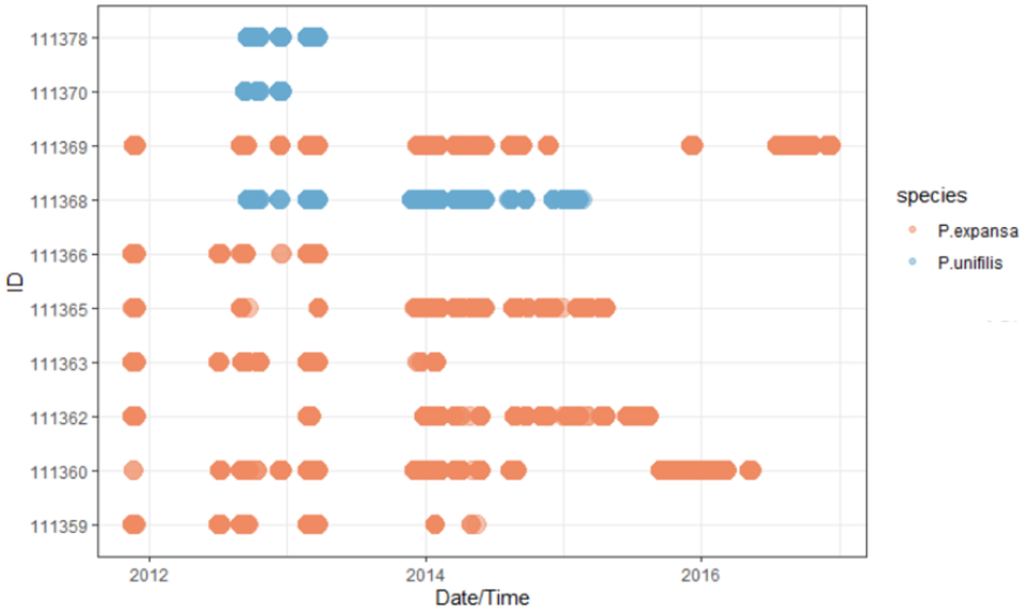

Figure 3: Tracking duration and intensity of each freshwater turtle individual tracked for P. expansa (red) and P. unifilis (blue).

2.4 Data analysis

Data management and analysis was primarily conducted in R version 4.0.3 (2020-10-10), with some basic edits made in Excel (Microsoft Office Enterprise 365). Modification and preparation of spatial shapefiles and maps was performed using QGIS version 3.8 (2019-07-23).

Duplicate rows and outliers were filtered, first by excluding all latitudes and longitudes outside the study area, and then manually according to local knowledge of ground conditions.

Home range estimates and habitat use were estimated using the R-packages: "adehabitatHR" (Calenge, 2006), and distances between spatial points and objects were calculated using the "sf", "sp", and "move" packages (Bivand, Pebesma and Gomez-Rubio, 2005; Pebesma, 2018; Kranstauber, Smolla and Scharf, 2020). QGIS and the R-package "leaflet" were used to generate the maps (Cheng, Karambelkar and Xie, 2021).

2.4.1 Home range estimations

Home ranges were estimated using two methods for each species and season. Minimum Convex Polygons (MCP), accounting for 95% of the locations, were estimated in order to obtain the minimum boundary that the turtles used. Then 95% and 50% Fixed Kernel Density Estimates (KDE) were calculated, representing the probable area of occupancy and core home range (50%). By only using 95% of locations, any remaining outliers could be filtered out. KDE was chosen as the most robust estimate for these turtles, but MCP estimates were also produced for comparison (Appendix Table 4). The KDE creates a probability matrix from the locations and then draws boundaries based on the probability matrix of any given number of locations. KDE estimates can thereby more accurately represent where the animals move, and not include large areas that are in reality unavailable, like MCPs can do in complex habitats, like the Amazon. While KDEs can be prone to overestimation, the relatively high frequency of location fixes enables estimation of movement corridors and routes, and is therefore presented in the results. Because of the large extent of the location fixes, the preferred method of using Least Squares Cross-validation (LSC) did not work. LSC works best on tight clusters, and a fixed reference grid was instead used and set to 250, with extent set to 3 (Gitzen, Millspaugh and Kernohan, 2006). A T-test was then used to test for differences in seasonal home range sizes between the two species.

2.4.2 Seasonal movements

With large data sets, projections of locations and trajectories over several years can easily become cluttered and difficult to interpret. In order to generalise where and when animals move, distances from each location fix to the nearest important spatial object were calculated (main river, oxbow lakes, and nesting beaches). This allowed for a simple visualisation of seasonal movement patterns and triangulation of what kind of location the turtles inhabit for a given month. Nesting beaches were identified by tracking the animals fitted with VHF. This also revealed that only the heavier animals (111365, 111369, and 111363) stayed close to the nesting beaches until hatching.

Shapefiles of the main river and large oxbow lakes were cut to fit the study area in QGIS, and the sites of the nesting were marked. These files were then imported to R and used to calculate the shortest distance between all the locations and the spatial objects. The shapefile for the lakes was incomplete, and so additional lakes were manually included at the norther end of the location fixes using satellite imagery (ESRI, 2021).

2.4.3 Habitat selection

Habitat selection was analysed by overlaying the spatial points of the turtles with shapefiles of the main river, oxbow lakes, and forest (Appendix Figure 8). The underlying habitat for each point was then summarised for each species. A random sample was then simulated within the 95% Fixed Kernel Density Estimate, simulating a random distribution where the movement and habitat selection is random. The shapefiles for the river and lakes were buffered to 600 m, in order to fit the width of the river and lakes. This was done to account for any inaccuracies in the location fixes and to account for the increased inaccuracy of GPS units under the forest canopy (Guilhon *et al.*, 2011). These files did however only map the main river and larger lakes. Smaller channels, streams and lakes covered by forest were not obtainable and could therefore not accounted for.

3 Results

The tracking effort from 2011 to 2016 resulted in a total of 6,726 location fixes for 7 individuals of *P. expansa* (n = 4,714; 70.1%) and 3 of *P. unifilis* (n = 2,012; 29.9%), after filtering out erroneous data and obvious outliers (Figure 4A). The average number of location fixes per animal (mean ± SD) was 673 ± 632 (range = 52-1,800). Of these were 58.6% (n = 3,942) of the locations registered during the high-water season and 41.4% (n = 2,784) during the low-water season. Most location fixes were registered in 2014 (n = 251; Figure 4B), with the highest number of location fixes registered in January-March (range = 893-1,082), and fewest from April to July (range = 74-292; Figure 4C). The total number of location fixes per day for both species throughout the study period ranged from 121-314 (Figure 4D), while the number of daily location fixes was lowest between 11:00-12:00 and 22:00-23:00 (Figure 4E).

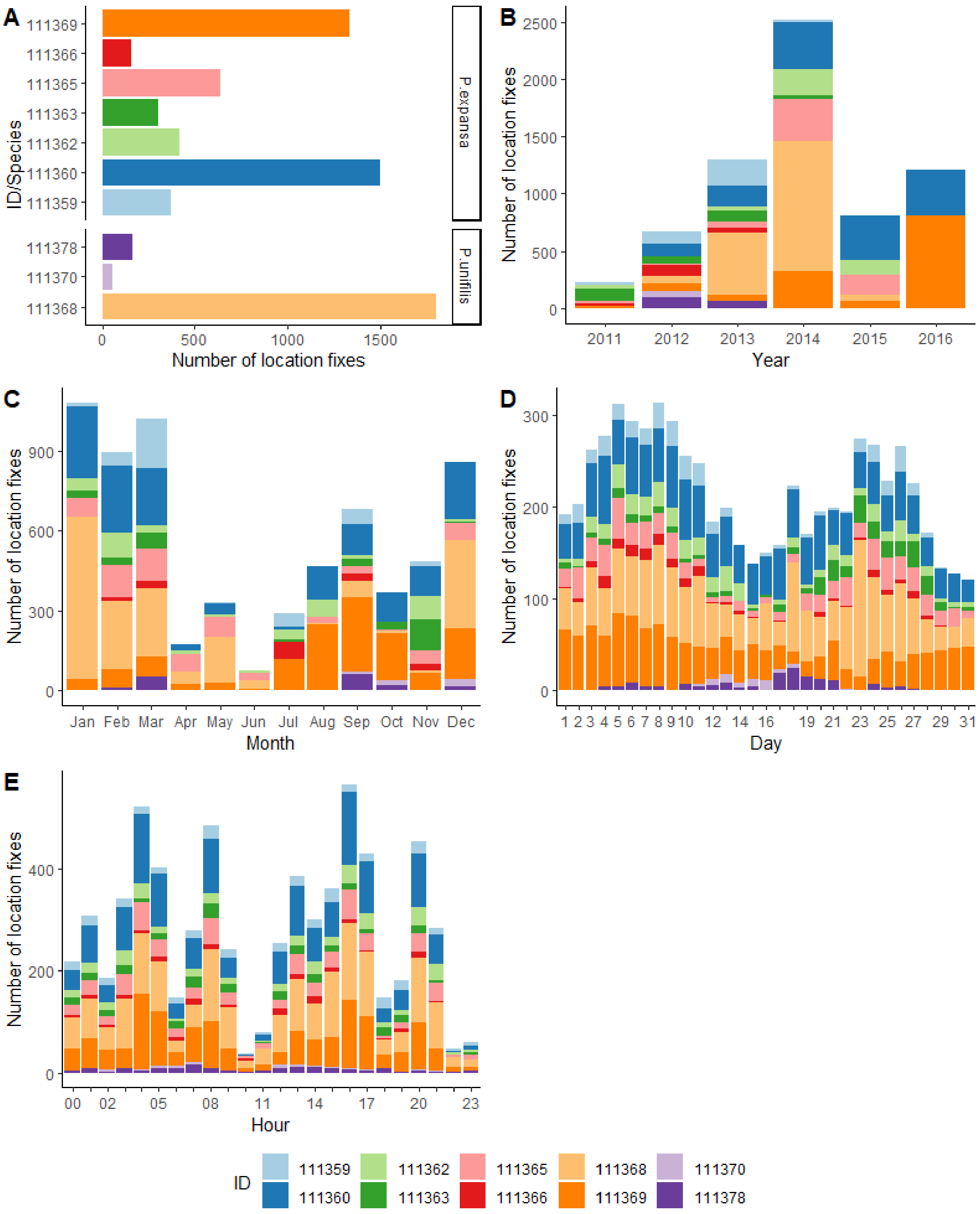

Figure 4: Tracking effort as number of location fixes per A) individual, B) year, C) month, D) day, and E) hour of each location fix.

3.1 Home range estimates

P. expansa has an estimated home range size of 74,881ha (± 81,453 SD) and 9,639ha (± 9,980 SD), using a Fixed KDE at 95% and 50%, respectively (Table 1). The home range estimates and variation were higher in the low-water period, but did not differ significantly between low and high-water seasons for either estimate (95%: t = 1.53, p = 0.17; 50%: t = 1.82, p = 0.11; Appendix Table 5).

P. unifilis utilizes a home range noticeably smaller than *P. expansa* – 31,167 ha (± 27,550 SD) using 95% KDE (Table 1). The core home range (KDE 50%) is also considerably smaller at 5,859 ha ± 4,013 SD. There was no significant difference between the seasonal home range size for *P. unifilis* (95%: t = -1.01, p = 0.42; 50% t = -1.00, p = 0.42), despite the home range and variation estimates being considerably larger during high-water.

The analysis of the effect of location fixes on home range size show that an asymptote is reached for most of the animals at roughly 200-300 location fixes (Appendix Figure 9).

Table 1: Kernel Density Estimates of home range for P. expansa and P. unifilis for low-water, high-water, and the entire year.

	P. expansa		*P. unifilis*	
	95% KDE (ha)	***50% KDE (ha)***	***95% KDE (ha)***	***50% KDE (ha)***
Low-water	*113.178 ± 146.659*	*20.424 ± 23.051*	13.877 ± 5.551	1.634 ± 508
High-water	*26.831 ± 28.149*	*3.955± 6.291*	47.074 ± 56.566	11.332 ± 16.774
All year	**74.881 ± 81.453**	**9.639 ± 9.980**	**31.167 ± 27.550**	**5.859 ± 4.013**

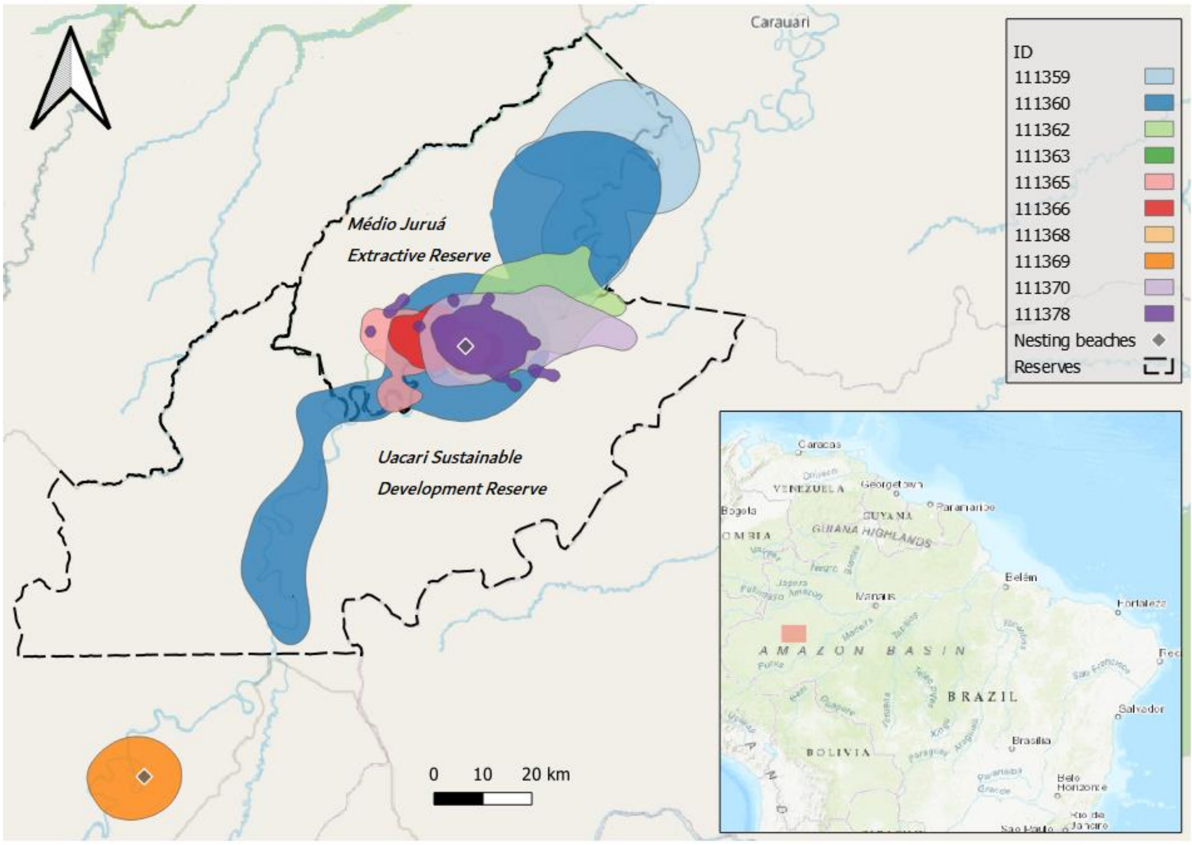

Figure 5: Map of the study area showing 95% Kernel Density Estimated home ranges for each freshwater turtle individual tracked along the Juruá River, western Amazonia, Brazil.

3.2 Movements

3.2.1 P. expansa

P. expansa shows great mobility, as well as large individual variation in its movements. Location fixes were in some extreme cases registered more than 60 km away from the nesting beaches (Figure 6A), and nearly 10 km away from the main river (Figure 6B). However, the furthest mean distances were lower, with *P. expansa* venturing approximately 24 km from the nesting beaches in March, and 4 km from the river in April. Their proximity to oxbow lakes was somewhat higher (1-2 km on average) in these months than during the rest of the year (Figure 6C).

The tracking data shows that *P. expansa* move away from the nesting beaches in November-December. The distance away from the nesting beach and the main river then gradually increases with the rising water level until March/April when the water level is at its highest. The distance to the nesting beach and main river then drops with declining water levels. While the distance from the river increases gradually in December-January, the move back to the river in June-July is more abrupt (Figure 6B). The distance from the oxbow lakes shows the same slight decline from mean and median distances of 2-3 km in January to close to 0 km in June, before a rapid increase in July as the turtles move closer to the river and the nesting beaches (Figure 6C).

3.2.2 P. unifilis

P. unifilis travelled shorter distances than *P. expansa,* had markedly less variation between individuals, and showed a stronger site fidelity with a maximum distance from the nesting beaches of 4-5 km in November (Figure 6A). They also move up to 5 km away from the main river in November (Figure 6B). The furthest distance from oxbow lakes is 4 km in September, coinciding with the shortest distance from the nesting beach, while the shortest distance (1-2 km) occurs in November (Figure 6C).

Overall, *P. unifilis* remains closer to the nesting beach and river (<1 km) throughout most of the year (Figure 6). As the river level rises, *P. unifilis* moves away from their nesting beach and the river in October-November, while moving closer to the oxbow lakes, before returning to the river and nesting beach in December.

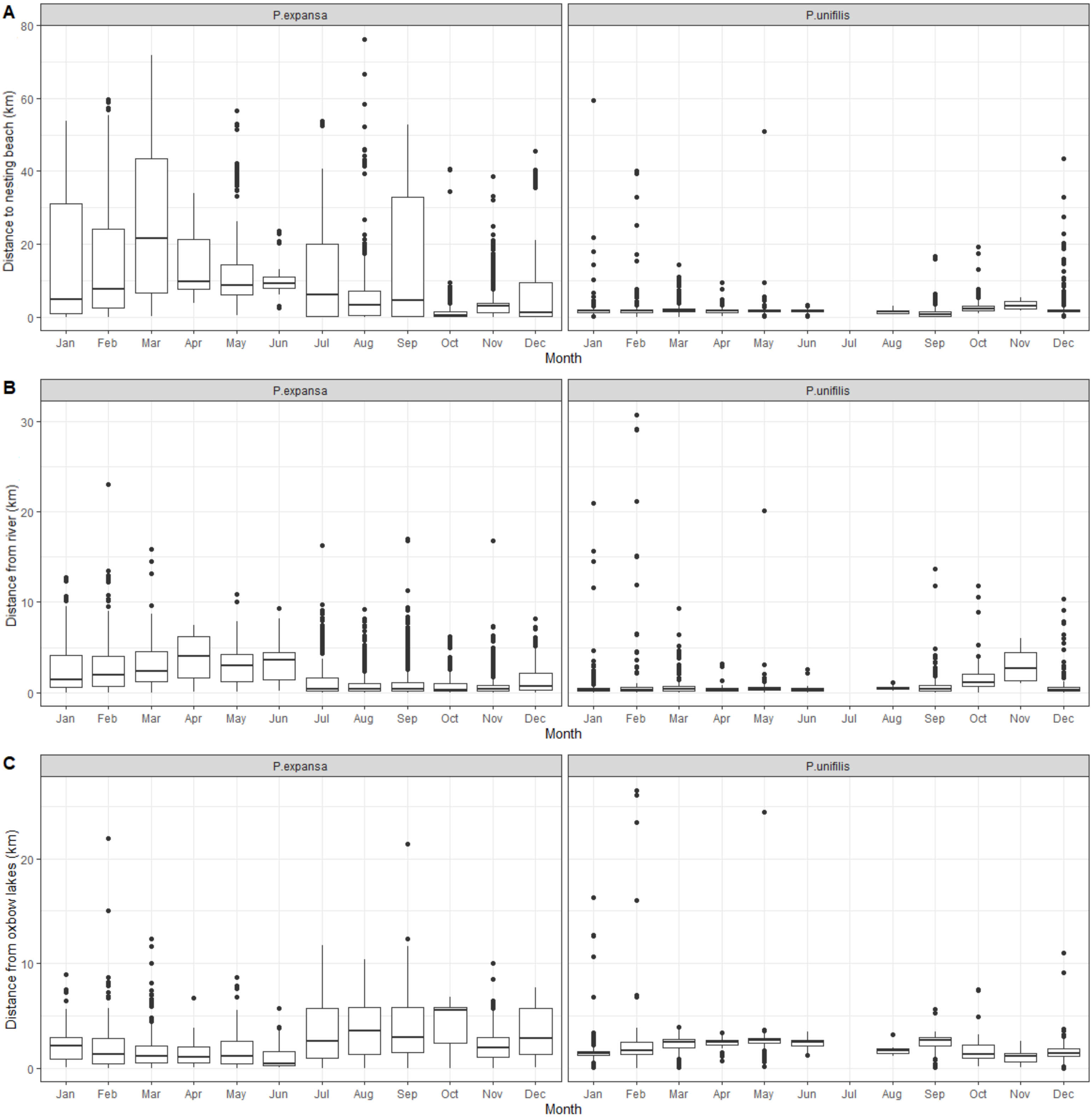

Figure 6: Distance from location fixes to the A) Nesting beach, B) the main river, C) oxbow lakes for P. expansa and P. unifilis. Boxplots represent first and third quartiles, lines the median, whiskers extend up to 1.5 times the inter-quartile range, points beyond are plotted individually.

3.3 Habitat use

The habitat use model suggests that *P. expansa* spends more time in the river throughout the year than in either the floodplain forest or oxbow lakes (Figure 7 A-C, Table 2). This affinity to the main river channel was highest in the low-water season, while lakes were more utilised as habitat during the high-water season. *P. unifilis* shows an even stronger affinity for the river than *P. expansa*, while the flooded forest is only moderately used, and the oxbow lakes were rarely used (Figure 7 D-E, Table 2). These results did not differ considerably between the seasons.

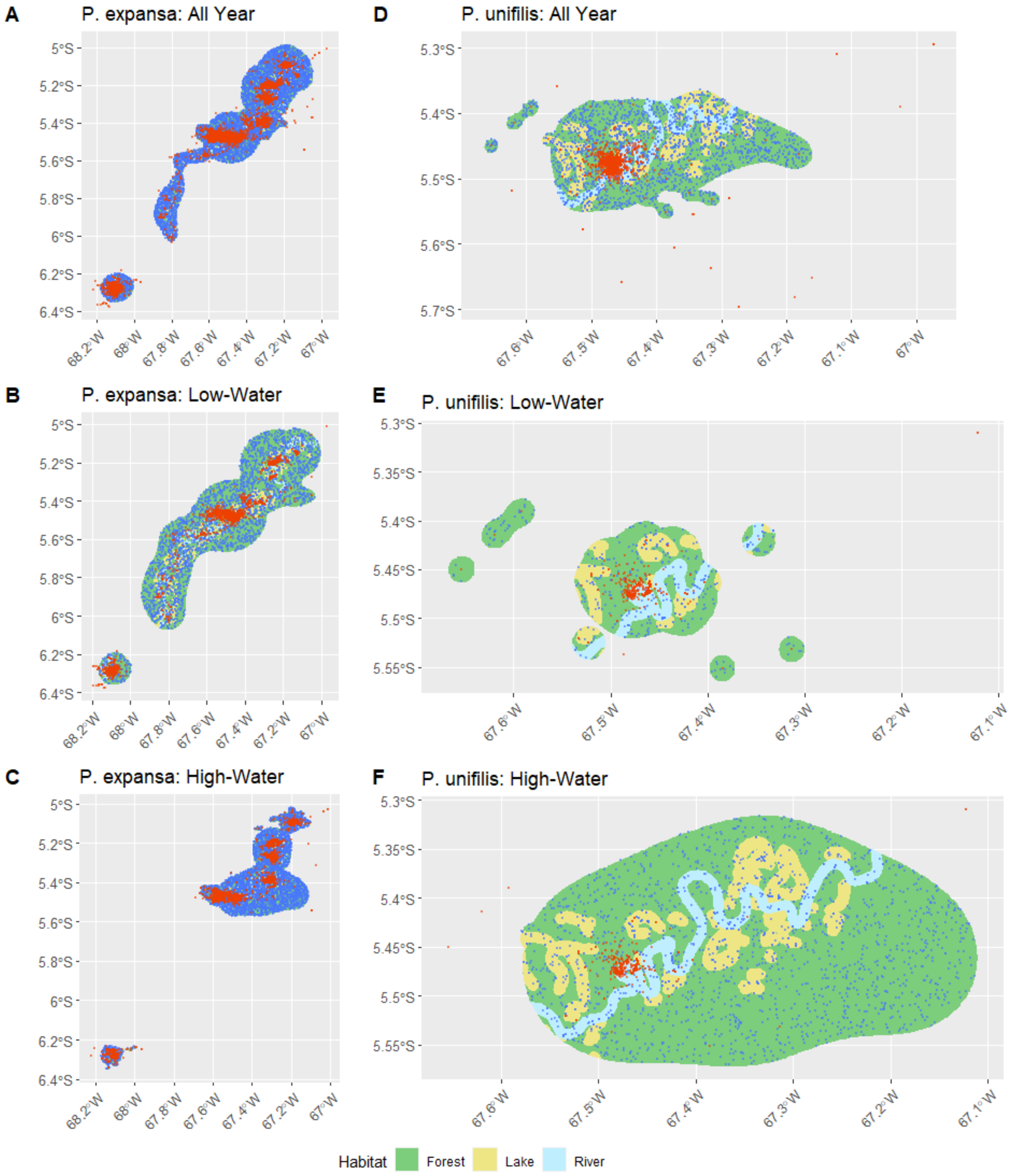

Figure 7: Visualisation of habitat analysis of P. expansa and P. unifilis. Habitat data is attributed to the real (red) and random simulated locations (blue) within the estimated home ranges.

Table 2: Summary the number of locations in the selected habitats comparing the actual locations versus a random distribution of locations in the same estimated home range for P. expansa and P. unifilis.

	All year			***Low water level***			***High water level***		
	Forest	**Lake**	**River**	**Forest**	**Lake**	**River**	**Forest**	**Lake**	**River**
P. expansa *Random locations*	4,797	1,064	794	2,132	399	256	3,440	666	478
P. expansa *Real locations*	2,714	1,011	1,951	1,038	300	1,547	1,675	711	404
P. unifilis *Random locations*	1,611	538	248	271	78	67	1,438	345	161
P. unifilis *Real locations*	818	77	1,515	164	29	210	654	48	1,305

4 Discussion

This study tracked 7 individuals of *P. expansa* and 3 *P. unifilis* between 2011 and 2016 using ARGOS GPS technology. While most animals were tracked for approximately one year, some of the GPS units lasted up to 62 months, and thus yielded data through several years and seasons. The high number of location fixes obtained and the long tracking duration outperform most previous studies that were largely dependent on very high frequency (VHF) radio transmitters for manual tracking (Souza, 2012; Naveda-Rodríguez, Cueva and Zapata-Ríos, 2018; Ponce De Leão, Famelli and Vogt, 2019). Previous studies may have tracked more individuals but for durations shorter than a year (5-11 months), and most only yielded 21-25 location fixes per animal (176.2 ± 91.8 in the case of Souza, 2012). The current study therefore allows a more robust analysis of home range and habitat use, in terms of tracking duration, than previous work.

4.1 Seasonal movement patterns

4.1.1 *P. expansa*

P. expansa appears to reside in front of the nesting beaches from early September to November-December, perhaps waiting for the hatchlings to emerge and the water level to rise. This is consistent with reports from studies on the nesting behaviour of *P. expansa*, which suggest that adults congregate in front of nesting beaches waiting for hatchlings to emerge and then utilise sound to communicate and move together with their offspring (Ferrara *et al.*, 2014). Indications of such behaviour can be observed in the current study as, shortly after the expected hatching in November-December, *P. expansa* adults appear to venture into the flooded forest (Smith, 1974; Ferrara, Vogt and Sousa-Lima, 2013). Here, they are known to spend time feeding on leaves and seeds (Cunha, Bernhard and Vogt, 2020).

Most of the flooded period from December to June is spent away from the oxbow lakes, but the distance from the oxbow lakes makes a sudden drop in June, while the distance from the river remains at around 2-4 km. This could suggest that *P. expansa* use the lakes as a last stop before returning to the main river in July through the complex network of floodplain channels (Pádua

1981, cited in Ferrara *et al.*, 2014). Such behaviour resembles previously described behaviour where turtles have been observed to utilise connections between lakes and the main river as the water level in the forest drops rapidly (Alho and Pádua, 1982a).

There is large variation in the distance of the turtles from their nesting beaches in July-September, when they are expected to return to the main river channel. This could correspond to movement to and from nearby lakes (Pádua, 1981, cited in Ferrara *et al.*, 2014), but this movement is not detected in relation to the distances recorded from the river or the oxbow lakes. It therefore appears, in this case, as though the smaller individuals of *P. expansa* which were not observed to reside near the nesting beaches, mostly moves within the main river. Then, in October and November most of the nesting animals appear to wait close to the nesting beaches for the emerging hatchlings to reach the water.

4.1.2 *P. unifilis*

P. unifilis has a markedly different behaviour compared to *P. expansa*. While there are a few outliers in the location fixes, *P. unifilis* spends most of the year near the nesting beach and close to the river. *P. unifilis* only temporarily move further than a few km (>4 km) from the nesting site or river. In October and November, approximately one month before *P. expansa, P. unifilis* briefly moves away from the nesting beaches and river. During this period, *P. unifilis* appears to move closer to the lakes before rapidly returning closer to the river and nesting beach, gradually increasing their distance from the lakes. This is concordant with other records of *P. unifilis* hatchlings emerging roughly a month before *P. expansa*, when they leave the river and venture into the flooded forest as the water level rises (Ferreira and Castro, 2010; Ponce De Leão, Famelli and Vogt, 2019).

The smaller size of *P. unifilis* likely makes it capable of utilising the forest earlier through smaller channels may therefore feed in the flooded forest and lakes earlier than *P. expansa*. Records report that *P. unifilis* utilise backwaters, lagoons and streams during high-water (Pritchard and Trebbau, 1984; Peñaloza *et al.*, 2013). However, they do not appear to have the same affinity to the large lakes included in this analysis, but rather utilise smaller floodplain lakes closer to the nesting beach and river that are more difficult to detect and map. This is also in accordance with other tracking studies reporting short travel distances and a high site fidelity in *P. unifilis* (Naveda-Rodríguez, Cueva and Zapata-Ríos, 2018).

P. unifilis also has less variation in the movement estimates compared to *P. expansa*. This is likely a result of the lower number of animals tracked, and relatively few observations for two out of three animals. The true variation may thus be larger and would likely be more apparent if more animals were tracked. However, the findings of this study may also suggest that *P. unifilis* has a more predictable and consistent behaviour. The behaviour of *P. unifilis* is known to be bimodal, with different behavioural responses to lower water levels. Whereas some of the animals may move to the river and nesting beaches to lay eggs, other stay in drying lakes and nest in clay soil at the perimeter of the channels or lakes (R.C. Vogt, unpublished data, cited in Fachín-Terán, Vogt and Thorbjarnarson, 2006). The three individuals tracked in this study appear to nest on a sandy beach along the river. However, they may be buried in mud at some point between April and June when the number of location fixes are fewer, or completely lacking (June). Further studies should therefore analyse movement patterns of more individuals at various locations for longer periods, to obtain an even better estimate of home range size and use by *P. unifilis*.

4.2 Habitat selection

P. expansa shows a strong affinity to the main river, higher than to the oxbow lakes or forest, particularly in the low-water period. The period of higher water level has a similar number of locations in the river as the random sample, suggesting that the river is less actively used in this period, while the forest is used to some degree. This is concordant with observations of *P. expansa* leaving the river as the hatchlings emerge and water level increases in December (Ferrara, Vogt and Sousa-Lima, 2013). However, the habitat analysis suggests a weaker affinity to the forest than the movement analysis indicates. Whereas *P. expansa* seems to spend half of the year away from the river, the habitat analysis shows that a large proportion of the locations are found in or near the main river. This could be a result of the nesting, where tracked individuals residing close to nesting beaches have good satellite reception for GPS fixes for several months in or near the river. However, the number of location fixes were fairly evenly distributed between seasons. The number of locations obtained from lake environments appears to be relatively similar to the random locations, with the period of high-water being most distinguished with 15% more locations in lakes. This may suggest that *P. expansa* use lakes briefly in a transitional stage before returning to the river, like the seasonal movement indicates.

Habitat use of *P. unifilis* differs from *P. expansa* with a strong affinity to the river throughout the year, while the affinity for the flooded forest and oxbow lakes is weaker. This supports the finding of *P. unifilis* spending most of the time near the river, with limited activity in the forest and lakes. This agrees with previous studies describing *P. unifilis* as a short-distance seasonal migrant (Naveda-Rodríguez, Cueva and Zapata-Ríos, 2018). However, lakes and flooded forest have been reported as important habitat for *P. unifilis* during the period of high water level (Ponce De Leão, Famelli and Vogt, 2019). It therefore seems plausible that *P. unifilis* use smaller lakes, streams and backwaters rather than the larger oxbow lakes included in this analysis.

4.3 Home range

4.3.1 *P. expansa*

The home range estimates for *P. expansa* presented in this study are among the first available for the species, and indicate that *P. expansa* utilises vast areas of river and floodplain habitat on a seasonal basis. Previous studies of *P. expansa* consist largely of linear ranges from recaptured individuals, or simply statements of an assumed large range and movements of hundreds of kilometres (Forero-Medina *et al.*, 2019). Souza (2012) estimated the 95% Fixed Kernel home range for *P. expansa* to be 370 ha in the eastern Amazon (Trombetas River, Pará State; Souza, 2012). However, this estimate does not appear to reflect the vast distances *P. expansa* has been recorded to travel elsewhere. Carneiro and Pezzuti (2015) tracked *P. expansa* for 143-320 days using GPS/ARGOS technology, revealing that each individual travelled 401 km on average (range = 196-725, n = 7; Carneiro and Pezzuti, 2015). Other mark and recapture studies have reported similar distances (von Hildebrand et al. 1997, as cited in Fachín-Terán, Vogt and Thorbjarnarson, 2006), with adults displaying short two-day movement bursts covering more than 45 km (Moreira and Vogt, 1990, as cited in Souza, 2012). Even juveniles have been recorded 38.47 km upstream nine months after having hatched (Fagundes *et al.*, 2017). The large home range estimates (KDE) in this study therefore seem plausible (Carneiro and Pezzuti, 2015).

However, the KDE presented in this study show considerable variation, with a large standard deviation. This deviation might result from a low sample size (7 individuals) and the mix of different ages and sizes among the *P. expansa* individuals tracked. Similar studies on *P. unifilis* and other species in the Amazon have also yielded standard deviations as large as the mean, despite using manual VHF tracking, which should give more accurate locations (Leite *et al.*, 2018; Ponce De Leão, Famelli and Vogt, 2019). These studies also had relatively small sample sizes. Individual differences would in such cases have a large impact and contribute to the variation observed. The tracking effort and duration also differ between the animals in these studies and could contribute to some of the variation. However, even with larger sample sizes (e.g. 63 individuals; Naveda-Rodríguez et al., 2018) there can be considerable variation in home range estimates. Considering the findings above, the home range estimates presented here likely reflect the area used reasonably well and make an important contribution to the knowledge about *P. expansa*, highlighting its mobility.

The home range estimates show that *P. expansa* cover large areas through its movements. However, the core home ranges are concentrated in a smaller area and the large estimate is therefore likely a result of the extensive seasonal movements. The seasonal KDE for *P. expansa* did not differ significantly, although this has been observed in *P. unifilis* (Ponce De Leão, Famelli and Vogt, 2019). While the movement analysis shows an annual movement pattern, the lack of a seasonal difference in home range size could be due to a relatively high activity in both the high- and low-water period. Whereas the movements in the flooded forest could be large, the seasonal movement along the main river could increase the home range size of the low-water period, and thus make it difficult to detect a significant difference in home range size. The small sample size and large standard deviations would also make it difficult to detect differences in the seasonal home range size.

4.3.2 *P. unifilis*

Both the estimated home range for *P. unifilis* and the relative standard deviation for the 95% home range estimate are considerably smaller than that of *P. expansa*. This is concordant with previous literature describing *P. unifilis* as a short distance seasonal migrant with relatively high site fidelity (Naveda-Rodríguez, Cueva and Zapata-Ríos, 2018). However, the home range estimate obtained in the current study is considerably larger than previous studies estimating mean home range size from 77-520 ha (range from 0.6 - 1,300 ha; Naveda-Rodríguez, Cueva and Zapata-Ríos, 2018; Ponce De Leão, Famelli and Vogt, 2019). However, these studies are limited by a short study period during lower water levels (Ponce De Leão, Famelli and Vogt, 2019), or have few location fixes (mean of 21 locations; Naveda-Rodríguez, Cueva and Zapata-Ríos, 2018). Previous studies also suggest that the home range size of turtles varies depending on habitat quality, productivity, and availability, as well as body size, feeding preferences, and sex (Plummer, Mills and Allen, 1997; Galois *et al.*, 2002; Slavenko *et al.*, 2016). Such factors, combined with a relatively high number of locations from different periods may thus be factors enlarging the home range estimates of this study.

The seasonal home range did not differ significantly between the seasons for *P. unifilis*, despite previous studies detecting a difference using a different home range estimator methodology (Ponce De Leão, Famelli and Vogt, 2019). The lack of a significant seasonal difference in home range is maintained although the movement analysis shows that *P. unifilis* performs a short displacement during the rising water. The lack of a significant difference is likely caused by the large variation in estimates leading to an overlap, and a result of the small sample size. How the seasons were defined could also affect this outcome. The coarse distinction between low- and high-water level may have been too broad and thus included a high number of locations outside of the time of movement. With a high number of locations in each season, the movements that could increase the home range size would thus be diluted by the movement in each assigned season.

The home range estimates for both *P. expansa* and *P. unifilis* are considerably larger than previous studies. Although ARGOS and GPS positions can have errors ranging up to kilometres and have difficulty acquiring positions in concealed locations, the number of location fixes they can provide helps including habitats that VHF might not detect, and tend to give larger, but more accurate estimates (Hays *et al.*, 2001; Skupien, Andrews and Norton, 2016). A common denominator for previous studies is a shorter tracking duration and a considerably lower number of location fixes. Studies on the effect of the number of location fixes on home range size suggest that 100-300 locations are needed to reach an asymptote in home range size and thus obtain reliable estimates (Girard *et al.*, 2002). This is also supported by the analysis of the home range accumulation rate by location fixes in this dataset, suggesting that most of the area used by the animals in this study were captured (Appendix Figure 9). The home range estimates in this study are therefore an important contribution to the knowledge base of *P. expansa* and *P. unifilis*. However, home range size for both species varied considerably, and future studies should track a higher number of individuals for a longer period of time in order to obtain a better understanding of how the home range size varies with location, season, and individual morphometric differences.

4.4 Implications for conservation

P. expansa and *P. unifilis* share many aspects of their life histories but differ somewhat in habitat use and ranging behaviour. Conservation of the two species will therefore need to incorporate measures considering these differences.

The protected area (PA) network is important for the conservation of Amazonian biodiversity (Sobral-Souza *et al.*, 2018). However, the effectiveness of PAs can vary considerably (Pfaff *et al.*, 2015). Targeted action for single species or a suite of species may therefore strengthen and support the conservation of vulnerable populations. The most common and widespread conservation effort for Amazonian freshwater turtles has been protection of nesting beaches in order to prevent massive natal loss from overharvesting of eggs or capture of nesting females (Cantarelli, Malvasio and Verdade, 2014). Since both species in this study show a high fidelity to the nesting beaches, continuation of these measures will likely continue to be important. This study does, however, highlight that both *P. expansa* and *P. unifilis* utilize areas larger than previous home range estimates suggest and confirm that *P. expansa* in particular has extensive seasonal movements where it could be vulnerable to exploitation and habitat loss. Actions to mitigate poaching for trade and uncontrolled exploitation are therefore likely to be important measures, especially during the low-water period when *P. expansa* is largely confined to the main river. *P. unifilis* seems to utilise the adjacent flooded forest only briefly as the water level rises, and protection of adjacent forest 3-5 km from the nesting beaches could be an effective way to protect this species. In sum, protection of nesting beaches and the adjacent river, together with flooded várzea forest will therefore be important for the long-term survival and recruitment of both *P. expansa* and *P. unifilis*. This should be considered in the design and implementation of PAs.

In order to ensure the survival of endangered species, conservation actions must also be effectively implemented and enforced. However, the protection of species and habitats is a major challenge in many areas where funding is limited and staff are responsible for huge areas (Campos-Silva *et al.*, 2017). Another problem is more ethical; anti-poaching measures may harm smallholders and economically marginalised people dependent on these resources for their survival and annual income (Cooney *et al.*, 2017). An effective tool to deal with these challenges is community-based management (CBM; Franco *et al.*, 2021). CBM is a scheme where local people are empowered to take control of resources in a more sustainable and appropriate way than states or larger corporations (Brosius, Tsing and Zerner, 1998; Franco *et al.*, 2021). In the Juruá region and elsewhere, recent evaluations of CBM have demonstrated a positive effect on local wildlife population recoveries, while simultaneously supporting local food security and socio-economic welfare (Campos-Silva and Peres, 2016; Campos-Silva *et al.*, 2018). As a result, several turtle species, such as *P. expansa*, *P. unifilis*, and *P. sextuberculata* have experienced positive effects of CBM across the Amazon (Miorando *et al.*, 2013; Campos-Silva *et al.*, 2018; Norris, Michalski and Gibbs, 2018b), both inside and outside PAs (Franco *et al.*, 2021). For example, CBM of *P. expansa* in the Juruá has yielded an 11-fold increase in numbers (Campos-Silva *et al.*, 2018), highlighting how CBM can be a relatively simple, yet highly effective conservation tool. CBM can in this way protect species and benefit local people, instead of implementing measures targeting poachers that could harm marginalised people depending on bushmeat. CBM therefore pose a great opportunity to empower PAs and increase connectivity and protection of species and habitats. Utilising the knowledge from this study to guide where and when to focus efforts could facilitate sustainable use of both *P. expansa* and *P. unifilis*, while likely also benefit other riverine fauna and yield socio-economic benefits for local communities.

CBM pose an important solution to direct threats like exploitation. However, climate change and construction of hydroelectric dams pose major threats for long-term survival for riverine species such as freshwater turtles (Castello *et al.*, 2013; Zulkafli *et al.*, 2016; Fagundes *et al.*, 2018). Both dams and climate change are expected to alter the natural flow of water and thus the seasonal fluctuations in water level (Castello and Macedo, 2016; Norris, Michalski and Gibbs, 2018a). This can cause altered timing of nesting or flooding of nests, and may alter the dynamics of the flooded forest, which in turn could interrupt feeding opportunities (Forero-

Medina *et al.*, 2019). The future of *P. expansa* and *P. unifilis* is therefore paved with challenges ranging from direct exploitation through habitat loss, all the way to large-scale alterations of weather and seasonal rhythms. Insight into the way these species move and utilise their ecosystem can thus guide development and conservation efforts to safeguard the future survival of *P. expansa* and *P. unifilis*.

4.5 Conclusion

This study sheds new light on the spatio-temporal movements of *P. expansa* and P. *unifilis* through long-term tracking of several individuals of each species. The habitat analysis highlights the importance of the main river and use of the flooded forest. However, the movement analysis provides more detail and shows that *P. expansa* ventures further from the river into the flooded forest during the flooded period than *P. unifilis*, which only exploits the flooded forest for a brief period, shortly after hatching, when the water level rises. The home ranges of *P. expansa* and P. *unifilis* presented here are substantially larger than previous home range estimates. These observations emphasise that both movement patterns and home range estimates should be considered when implementing conservation measures, in order to focus efforts at the right time and location. Protecting both nesting beaches and flooded várzea forest is clearly key, but this study also highlights the importance of considering the vast areas these freshwater turtles utilise on a seasonal basis and hence the extent of required actions. Future research should focus on obtaining data from additional locations, preferably including more individuals of both sexes for multi-year tracking periods, in order to improve our knowledge of the behavioural diversity among Amazonian freshwater turtles.

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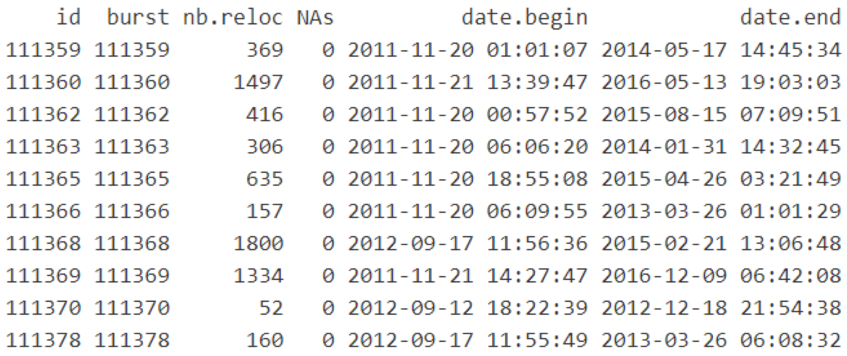
6 Appendix:

Table 3: Tracking effort and duration for each animal showing number of location fixes and start and end date.



```
    id  burst nb.reloc NAs          date.begin            date.end
111359 111359      369   0 2011-11-20 01:01:07 2014-05-17 14:45:34
111360 111360     1497   0 2011-11-21 13:39:47 2016-05-13 19:03:03
111362 111362      416   0 2011-11-20 00:57:52 2015-08-15 07:09:51
111363 111363      306   0 2011-11-20 06:06:20 2014-01-31 14:32:45
111365 111365      635   0 2011-11-20 18:55:08 2015-04-26 03:21:49
111366 111366      157   0 2011-11-20 06:09:55 2013-03-26 01:01:29
111368 111368     1800   0 2012-09-17 11:56:36 2015-02-21 13:06:48
111369 111369     1334   0 2011-11-21 14:27:47 2016-12-09 06:42:08
111370 111370       52   0 2012-09-12 18:22:39 2012-12-18 21:54:38
111378 111378      160   0 2012-09-17 11:55:49 2013-03-26 06:08:32
```

Table 4: Minimum Convex Polygon Home range estimates (mean ± SD) for P. expansa and P. unifilis for the whole period, and for each season.

	***P. expansa* *95%* MCP (ha)**	***P. unifilis* *95%* MCP (ha)**
Low waterlevel	*57.681 ± 87.198*	*4.563 ± 1.760*
High waterlevel	*57.681 ± 87.198*	*10.573 ± 6.420*
All year	***62.168 ± 70.202***	***13.254 ± 8 655***

Table 5: Result of T-test on the difference in home range size between the seasons.

	95% MCP	*95% KDE*	*50% KDE*
P. expansa	t = 1.11, p = 0,30	t = 1.53, p = 0,17	t = 1.82, p = 0.11
P. unifilis	t = -1.56, p = 0,24	t = -1.01, p = 0.42	t = -1.00, p = 0,42

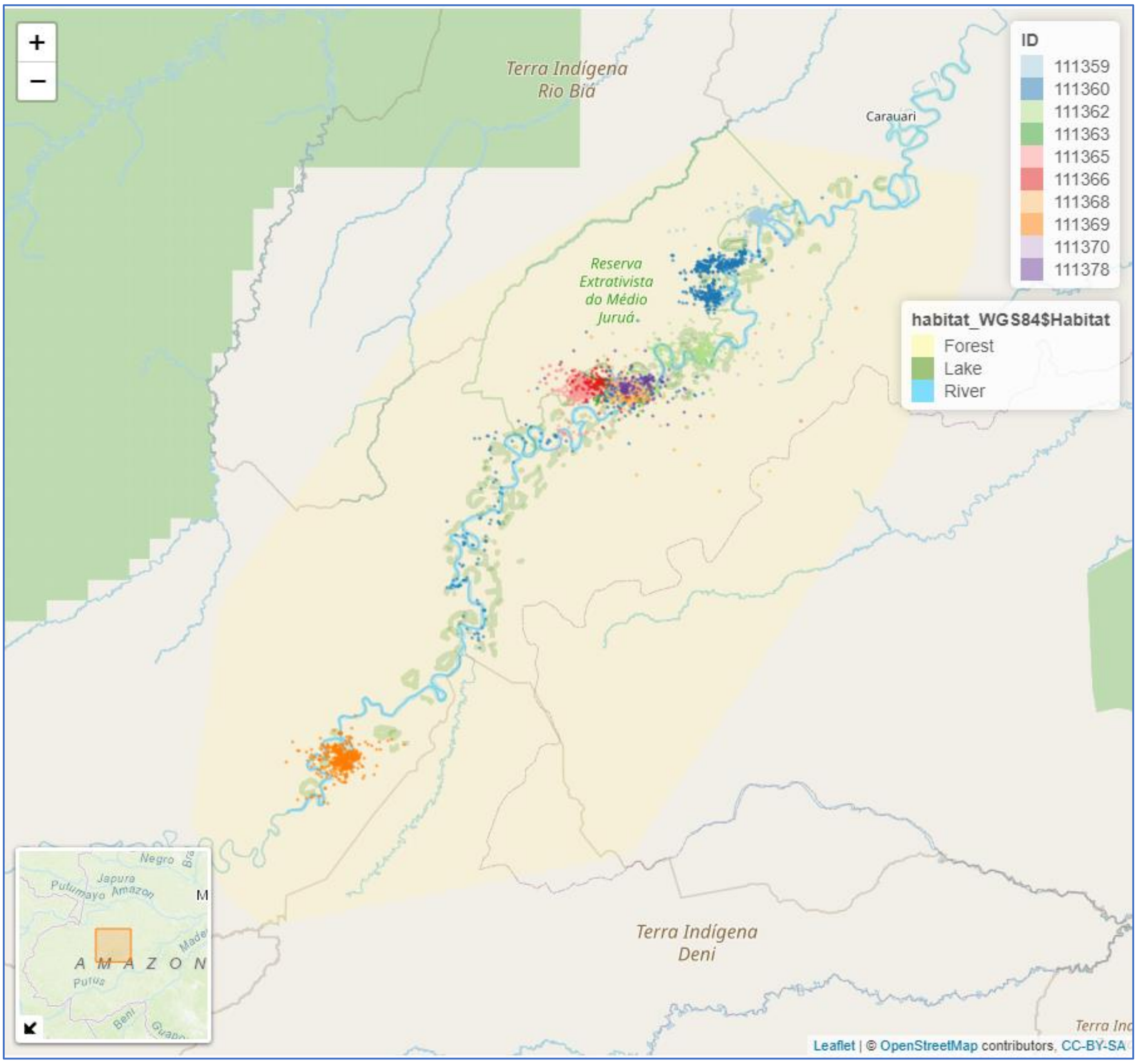


Figure 8: Visualisation of the spatial attributes used in the habitat analysis. Forest is cut along the river and lakes.

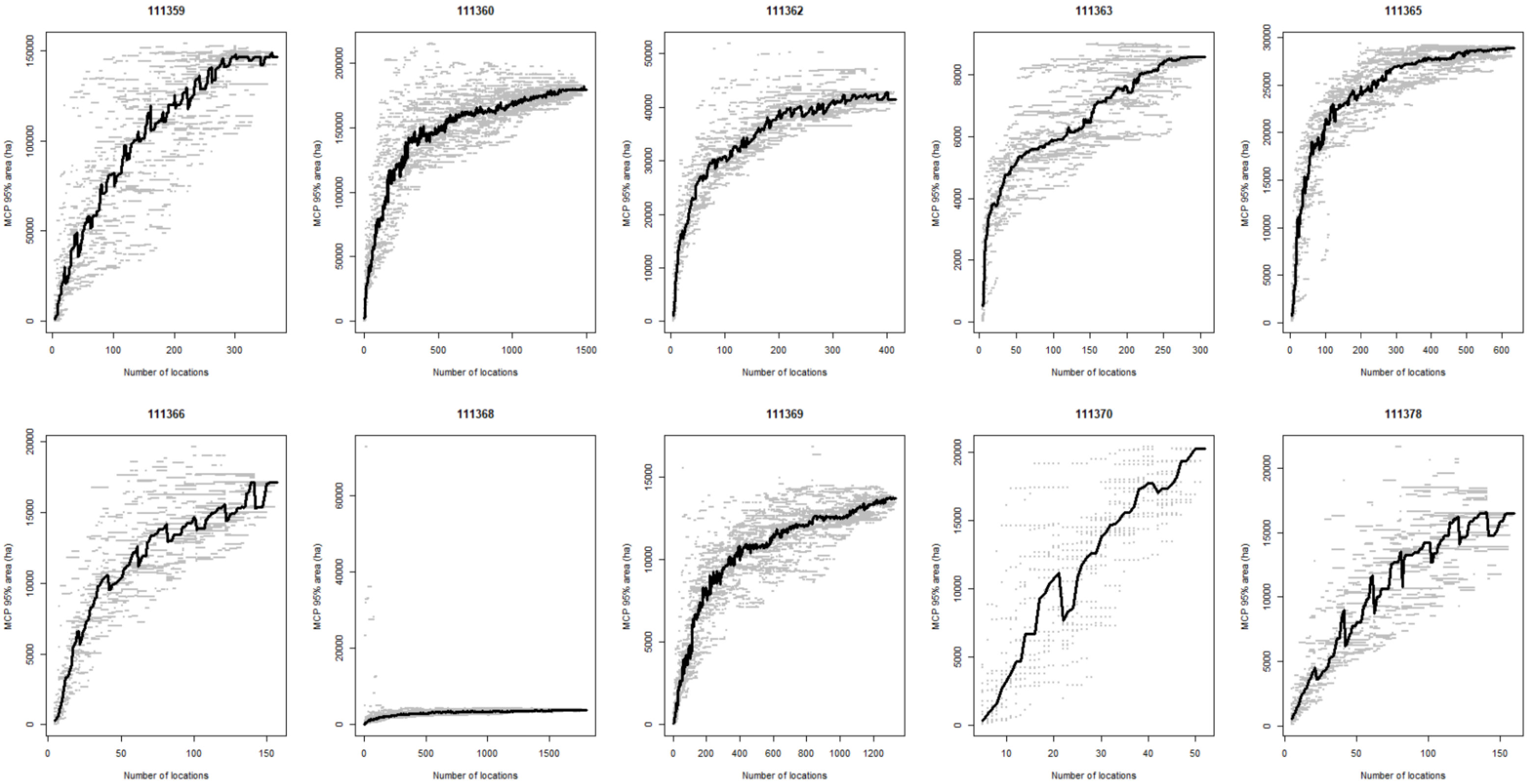


Figure 9: The size of the Minimum Convex Polygons with increasing location fixes. The size reaches an asymptote at about 100-300 locations.

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