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SPACE USE AND HOME RANGE SIZE OF THE FRESHWATER TURTLE *HYDROMEDUSA MAXIMILIANI* (TESTUDINES: CHELIDAE) IN SOUTHEASTERN BRAZIL

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Abstract.—**Identifying the habitat area used by animals is vital for understanding species-level life-history traits and ecological requirements. The Maximilian's Snake-necked Turtle (*Hydromedusa maximiliani*) is an endemic and endangered freshwater turtle from the Atlantic Rainforest in Brazil. We tracked 14 adult *Hydromedusa maximiliani* (seven males and seven females) with radio-transmitters at the Parque Estadual Carlos Botelho, southeastern Brazil. We also monitored 22 turtles (11 males and 11 females) with thread-bobbins to evaluate habitat use and selection. We calculated movement distances with linear measurements and estimated home ranges sizes using five home range estimators: (1) Brownian Bridge Movement Models (BBMM), (2) dynamic Brownian Bridge Movement Models (dBBMM), (3) Autocorrelated Kernel Density Estimator (AKDE), (4) Minimum Convex Polygons (MCP), and (5) Kernel Density Estimators (KDE). Home range sizes varied between 0.4 and 137.4 ha throughout a year of monitoring. These estimates differed depending on the estimator method applied, with BBMMs showing larger areas overall. Home range sizes did not differ between sexes; however, males were more likely to overlap either with females or other males. *Hydromedusa maximiliani* used stream-bank burrows as refuge, showing the importance of shelter for this turtle species. We observed small individuals occupying shallow pool habitats more often than adults. Our estimates of home range size are the first reported for this species.**

Key Words.—Autocorrelated Kernel Density Estimator (AKDE); Brownian Bridge Movement Models (BBMM); burrows; radio-tracking; refuge; shelter; thread-bobbins.

INTRODUCTION

The comprehension of habitat use by animals holds significance in ecology and natural history due to its association with home ranges, distribution patterns, abundances, individual interactions, and resource partitioning (Carter et al. 1999; Conner et al. 1999; Calenge 2006; Cordero et al. 2012; Wariss et al. 2012). Thereby, individual patterns of habitat use stem from behavioral decisions shaped by the interplay of landscape features and individual traits (Ofstad et al. 2019). This implies that intraspecific variations such as age, sex, and body size are likely to influence the habitat and resources choices, shaping the area and configuration of the home range (Ofstad et al. 2019; Tavares et al. 2019). Yet, the connections between individual variations in home range size, habitat use, and selection of turtles remain poorly understood, particularly for those species within the Chelidae family distributed in the Neotropical region (Forero-Medina et al. 2011).

The Maximilian's Snake-necked Turtle (*Hydromedusa maximiliani*; Fig. 1) is a small, semiaquatic Chelidae species (< 200 mm straight-line carapace length), endemic to coastal mountainous regions of the Atlantic Forest in Brazil (Costa et al. 2015; Muller et al. 2024). The species is restricted to parts of southern, eastern, and southeastern coastal regions, with registered occurrence in the states of Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, and São Paulo (Costa et al. 2015; Muller et al. 2024). Given its limited distribution in a biome experiencing gradual yet persistent degradation (Pinto et al. 2024), *H. maximiliani* has recently been assessed and is in the process of being categorized as Endangered on the Red List of Threatened Species of the International Union for Conservation of Nature (Famelli et al. In press).

Hydromedusa maximiliani thrives in freshwater ecosystems, favoring clear mountain streams with

Figure 1. Maximilian's Snake-necked Turtle (*Hydromedusa maximiliani*) showing its long, slender neck with conical protuberances. (Photographed by Shirley Famelli).

sandy or rocky beds, using the aquatic and terrestrial habitats, often seeking shelter amongst submerged debris, rocks, or logs (Famelli et al. 2016). The habitat of this species spans elevations of 4–1,499 m above sea level (Muller et al. 2024), with factors like temperature, rainfall, and slope gradient of the terrain determining the distribution of the species (Costa et al. 2015; Muller et al. 2024). The dense understory and canopy common in the ridges and valleys inhabited by the species, however, restricts sunlight in the streams. Consequently, aerial basking is only feasible in forest gaps along the stream course (Souza and Martins 2006, 2009). In fact, *H. maximiliani* does not commonly exhibit basking behavior (Souza and Martins 2009; Famelli et al. 2016). To regulate body temperature, *H. maximiliani* uses a thermoconformity strategy that consists primarily in using the shallow waters of the stream, which showcases the strong association and dependence of this species on aquatic habitats (Souza and Martins 2006). This dependence is further substantiated by its feeding habits, with the diet mainly consisting of small macroinvertebrates such as aquatic insect larvae, crabs, and small terrestrial invertebrates that fall in the water (Souza and Abe 1995; Novelli et al. 2013).

Their activity season correlates with reproductive behavior; males exhibit greater movements in search of mating opportunities from August to November, while females display more pronounced movements associated with egg-laying from December to February (Famelli et al. 2014, 2016). Females reach sexual maturity with a minimum plastron size of 103 mm, typically around 13 y, and males at approximately 102 mm, at 14 y (Famelli et al. 2014; Martins and Souza 2008). Both sexes are estimated to have a lifespan of around 100 y (Martins and Souza 2008), although an alternative study suggested a lifespan of approximately 22.3 y, which considered the number of years from the age of first reproduction until 95% of adults in a specific cohort had die, rather than relying on the age of the longest-lived individual (Reinke et al. 2022).

In home range studies, body size is a crucial factor, as larger sizes may increase energy demands, potentially necessitating larger areas for food collection unless resources are abundant (McNab 1963; Harestad and Bunnell 1979; Müller et al. 2019). Turtle body size has been identified as a predictor of microhabitat preferences in *H. maximiliani*, with males, which are larger than females, favoring deep and fast water systems compared to females and juveniles (Souza and Abe 1998). Previous research has also often noted the presence of *H. maximiliani* at the periphery of stream near the riverbank or using burrows alongside the stream margins (Famelli 2005; Famelli et al. 2016). Burrows represent a crucial refuge for reptiles in general (Silva et al. 2018; Averill-Murray et al. 2020) and for *Hydromedusa* species in particular. This behavior was reported by Semeñiuk et al. (2020) for the South-American Snake-headed Turtle (*H. tectifera*), especially during extremely cold or hot seasons in urban streams in Argentina, while *H. maximiliani* displays what is called a zigzag movement that allows them to use both stream margins where they access burrows and tunnels under the stream margins to find refuge (Famelli et al. 2016).

We used VHF radio-transmitters and thread-bobbins to determine space use and home range size of *H. maximiliani*. We tested the influence of sex stage and body size on their home range size and evaluated how the resource partitioning and availability drive habitat use by these turtles. We expected that males and females would show different home range sizes and partitioning of resources, primarily due to variations in their reproductive strategies. We also expected a decrease in home range size in the dry season, driven by a reduction in activity during this period. We anticipated that the home range estimate aligned with the ecology of *H. maximiliani* will result in a compact core area size, influenced by the frequent use of shelters along the edge of streams, given what is already known about the extensive use of bank refuges along the stream margin for the species. Research on the home range and habitat use of turtles has important implications for species and habitat management, thus providing important knowledge for the conservation of these long-lived organisms.

Materials and Methods

Study area.—We studied turtles from October 2007 to April 2010 at the Parque Estadual Carlos Botelho (PECB), an Atlantic Forest protected area in the state of São Paulo, southeastern Brazil. We sampled turtles in an approximately 250 ha area, comprising of about 7 km of clear and cold-water streams, 5–100 cm deep water, with sandy and rocky bottoms (Souza and Martins 2009; Fig. 2). The average annual temperature and mean daily air temperature range are key factors influencing the distribution of *H. maximiliani* (Costa et al. 2015), reflecting its thermoconformity and dependence on cold-water streams (Souza and Martins 2006). During the study period, the monthly rainfall ranged from 6 mm (July 2008) to 391 mm (January 2008) and monthly temperature between 13.1° C (July 2010) and 25.6° C (January 2008).

Capture.—We located turtles visually during diurnal searches along the streams. When turtles were detected, we hand-captured and individually marked them by notching marginal scutes (Cagle 1939). We measured the straight-line carapace length (CL) and midline plastron length (PL) with calipers to the nearest 5 mm and body mass (BM) with a spring scale to the nearest 5 g. We determined the sex of each turtle from external morphology, such as plastral concavity (an indicator of a male turtle), tail length (typically longer in males), and body size (with males typically larger than females; [Souza 1995a,b]).

Radio-tracking.—To confirm reproductive status, females were X-rayed with a portable X-ray machine (80 kV; Gibbons and Greene 1979; Famelli et al. 2014). We selected 10 gravid females and 10 males to equip with VHF radio-transmitters (TXE-125G Wildlife tracking; Telanex, Santiago de Querétaro, Mexico), and we used epoxy to attach the transmitter to the carapace (see Famelli et al. 2016). We ensured that the final weight of the device (approximately 5.5 g) was < 7% of the body mass of an individual to avoid impacting its movements (Jacob and Rudran 2003). We radio-tracked turtles diurnally every two weeks from September 2009 to December 2010 using a portable receiver (RX-TLNX) and a four-element Yagi antenna (Telenax). We used a directional antenna to locate the turtles when the signal was strong, which provided visual contact with individuals, eliminating triangulation errors. We recorded fixes using a Global Positioning System (GPS) Garmin 60 CSx and later plotted on GPS TrackMaker (Geo Studio Tecnologia Ltda; Belo Horizonte, Brazil). Owing to the loss of some radio-transmitters, we only included turtles with > 15 fixes in the analyses (seven males and seven females).

Figure 2. Study area showing a typical habitat for Maximilian's Snake-necked Turtles (*Hydromedusa maximiliani*) in the Parque Estadual Carlos Botelho, São Paulo State, southeastern Brazil. (Photographed by Shirley Famelli).

Thread-bobbins.—Although we tracked turtles using radio-transmitters and thread-bobbins at the same time (from September 2009 to December 2010), we did not simultaneously fit the same individual with both devices. Eight turtles that we tracked by thread-bobbins between 2007 and 2008 received the radio-tracking device only in 2009. On one occasion, a turtle received a thread-bobbins after losing the radio-tracking device (Famelli et al. 2016).

From October 2007 to November 2008 and October 2009 to December 2010, we equipped 22 individuals (11 females and 11 males) with thread-bobbins (Hiltex Indústria e Comércio de Fios Ltda, Itatiba, Brazil). Three of the females we tracked were gravid (detected after X-ray radiographs; Famelli et al. 2014). We fitted the turtles with two spools linked by their ends, giving a total of 600 m of thread that could be deployed. We decided to connect two spools because we experienced some devices releasing a large quantity of line after getting wet. We wrapped the two-spool device in transparent plastic film and attached it to the carapace with duct-tape (Tozetti and Toledo 2005; Tozetti et al. 2009). The final device weighed < 7% of the body mass of a turtle (Schubauer 1981). We tracked the trail left by the line for three consecutive days and mapped the trail using a compass, reel tape, and a paper grid. We transferred the distances between the points and the angles of the displacement to graph paper and transformed distances into Cartesian coordinates (Famelli et al. 2016). We ensured that the turtles were not disturbed during the data collection to avoid affecting their natural behavior (Tozetti et al. 2009).

Habitat use and availability.—For all animals captured and monitored by radio-tracking and thread-bobbins, we measured water depth (cm) and speed (cm/s), the distance to the nearest river margin (cm), substrate type (sandy; rocky; sandy/rocky; presence or absence of decomposing and clay material), and movement angle. We marked the percentage of substrate type after drawing the microhabitats onto a paper grid. We measured the water speed by releasing a styrofoam ball with 3 cm in diameter and we measured the speed of the ball while traveling a 30 cm distance. We measured these same habitat characteristics at each point of change in the angle of direction along the line left by the animals monitored by thread-bobbins and at the radio-tracking fixes.

To analytically investigate the use of shelter and terrestrial habitat use along the riverbank and the position of the turtle within the stream, we measured the distance of the turtle to the nearest stream margin. We considered the distance to the margin equal to zero when turtles were using streambank burrows. We also indicated the water speed and depth as < 1 in case of turtles using burrows as refuge. In turtles that we found inland (terrestrial habitat), we indicated the distance to the stream as a negative value. This method helped us to categorize the habitat use and selection along the path of the turtle. To allow comparison between turtle habitat use and availability, we measured water depth, water speed, margin width, and stream substrate type every 50 m along the streams in the study area. To determine the margin distance, we used half of the width of the stream to define the midpoint, which represented the farthest distance a turtle could be from burrows and shelters along the stream margin.

Data analysis.—We performed all analyses in program R 4.2.1 (R Development Core Team 2022). Using the software GPS TrackMaker, we obtained the Minimum Straight-Line Distance between fixes (MSLD) and the Distance Between Fixes considering the watercourse (DBFW) (Sexton 1959; Plummer et al. 1997). Then we calculated five home range estimators using R 4.2.1 (R Development Core Team 2022): (1) Minimum Convex Polygon (MCP); (2) Kernel Density Estimator (KDE); (3) Autocorrelated Kernel Density Estimator (AKDE); (4) Brownian Bridge Movement Models (BBMM), and (5) the dynamic Brownian Bridge Movement Models (dBBMM). To compare these estimates, we used conventional MCP (including 95% of the fixes) and the KDE using the adehabitatHR package in R (Calenge 2006). KDE provides information on how intensely animals use different areas within their home range (utilization distribution or UD). It also offers a description of home range overlap, displaying centers of activity associated with critical ecological zones for chelonians, such as mating or nesting zones (Leão et al. 2019), but as a counterpoint to this, KDE ignores the temporal structure of animal tracking data (Fieberg 2007). KDE is widely adopted because it incorporates information on the spatial distribution of use with smoothing parameters by estimating the likelihood of finding the animal at any particular location within its home range (Worton 1995; Seaman et al. 1998). The size of the kernel is determined by the bandwidth optimizer or smoothing parameter, which influences how tightly KDEs conform to the data (Bauder et al. 2015; Worton 1995). We used the function plotLSCV in adehabitatHR to adjust the smoothing factor so that the 95% KDE is equal to the MCP area as suggested by Row and Blouin-Demers (2006). This not only offers an objective approach to select the smoothing factor but also enables us to determine the consistency of kernel estimators in producing home-range sizes (Row and Blouin-Demers 2006). To achieve this, we examined the results of Least Square Cross Validation (LSCV) minimization, obtaining an average value of 6.475, which we adopted as the defined bandwidth for all turtles. We labelled this parameter and estimator method as KDE^{def} (defined by the user). We also use KDE^{def} to determine home range overlap among individuals (adehabitatHR package; Calenge 2006).

To address the challenges posed by the highly autocorrelated nature of animal tracking data, irregular sampling intervals, or the three-dimensional aspect of animal movements, a range of estimation methods has emerged as alternative approaches. These methods integrate spatial and temporal information to estimate home range area based on animal movements (Silva et al. 2018; Crane et al. 2021). They are known as movement-based KDE (Horne et al. 2007; Benhamou 2011), such as the autocorrelated KDE (AKDE; Fleming et al. 2015) and the BBMM (Horne et al.

2007; Kranstauber et al. 2012). Therefore, AKDE and BBMM represent advanced KDE approaches designed to address and mitigate the inherent challenges of high autocorrelation and uncertainty in tracking data collected over time and space for individual animals (Horne et al. 2007; Crane et al. 2021). Specifically, AKDE considers the processes underlying animal movements and long-term space-use (Horne et al. 2019), while BBMM, especially the dynamic BBMM (Kranstauber et al. 2012), examines the occurrence distribution, providing insights into a movement trajectory of an animal and its core region (Kranstauber et al. 2012; Silva et al. 2020).

We also analyzed our VHF turtle data using these approaches that account for spatial and temporal dependence: (1) the AKDE (ctmm R package; Calabrese et al. 2016); (2) the BBMM, and (3) the dBBMM (bbmm R package; Nielson et al. 2013). The movement-based estimators require a time-stamped series of animal locations, which we obtained using the R packages amt, ctmm, and move (Calabrese et al. 2016; Signer et al. 2019; Smolla et al. 2022). The first estimator approach, AKDE, calculates the optimal bandwidth matrix of movement data (Crane et al. 2021). We used AKDE to estimate home range sizes in the wet season (September to February) and the dry season (March to August). Regarding BBMM and dBBMM, the main difference between the two is that dBBMM allows variation in response to underlying shifts in the behavior of the animal, while BBMM assumes a constant mean variance along an entire movement trajectory of an animal (Horne et al. 2007; Kranstauber et al. 2012). We prepared 50% and 95% BBMM and dBBMM to represent the core area of use (50%) and the standard size of the residential area (95%).

We tested for differences among home range size estimators and sexes ($\mathrm{MCP}^{95\%}$, KDELSCV, KDE^{def}, AKDE, BBMM, dBBMM) using Analysis of Variance (ANOVA) followed by Tukey-Kramer multiple comparisons. We also tested the difference between linear measurements (MSLD and DBFW) using Student *t*-tests. We performed Linear Regressions to examine relationship among the home range sizes data and body mass (g), followed by ANOVA. We considered the body mass as a fixed effect (independent variable), and the home range sizes as responses. We used a log-transformation (log10) on the data estimated with KDE^{def} and dBBMM to mitigate data skewness. Home range overlap among individuals was determined with KDE^{def} in R 4.2.1 (R Development Core Team 2022) using the adehabitatHR package (Calenge 2006). We compared habitat characteristics measured along the path of a turtle (radio-tracking, thread-bobbins, and manual capture) using Linear Mixed-effects Models (LME) in R (package lme). LME is a modelling approach that allows minimizing the implicit error in the same group of data in simultaneous and non-independent collections that can be highly correlated and/or have unequal variances (Pinheiro et al. 2021). In this case, we used the function to investigate the serial autocorrelation values of habitat use collected for the same individual along the trajectories travelled, either by thread-bobbins, radio-tracking, or capture-recapture throughout the study. We considered the method (radio-tracking; thread-bobbins; and capture) as the fixed effects, and the response was the habitat use data (depth; velocity; and margin-distance) given the different sexes (only adults). All habitat variables underwent a logarithmic transformation. We added the value 0.5 to the data obtained before the logarithmic transformation because of the presence of zeroes in the data (Yamamura 1999). We applied the random effects formula repeated for all levels of grouping (random = approximately 1 per individual). We also used Linear Regression to test if the habitat use (mean depth and mean water speed per individual) was affected by turtle body size (body mass and carapace length).

To investigate whether individuals selected pool depth, water speed, and substrate type according to their availability in the study area, we compared habitat used to the random values collected within the study area (availability) using a Chi-square Goodness-of-fit Test. The use of burrows along the stream margin was represented by comparing the difference between the stream width and the animal distance to the stream margins with values equal to zero represented animals using burrows, and negative values representing animals in the terrestrial habitat. This representation was made using density plots followed by the Kolmogorov-Smirnov Test.

The use of substrates by males, females, and juveniles was represented by the quality on the factor map (cos2), using Multiple Correspondence Analysis (MCA). The MCA summarizes a data set of categorical variables or groups of individuals with similar profiles to reveal the most important variables contributing to explain the association and variation among them in terms of correlation ratio (Husson et al. 2017). The results are displayed in terms of dimensions (Dim1: Dimension 1 and Dim2: Dimension 2), which highlight the categories

Table 1. Mean home range size (ha; ± standard error) and range of values (in parentheses) of Maximilian's Snake-necked Turtles (*Hydromedusa maximiliani*) estimated by Minimun Convex Polygon (MCP) with 95% of re-locations and Kernel Density Estimator (KDE^{def}), Minimum Straight-Line Distance (MSLD), the distance between fixes considering the river course (DBFW), the Autocorrelated Kernel Density Estimator (AKDE), the Brownian Bridge Movement Models (BBMM 50 and 95%), and the dynamic Brownian Bridge Movement Models (dBBMM).

Home range estimator	Females (n = 7)	Males (n = 7)
MCP$^{95\%}$ (ha)	0.43 ± 0.20 (0.19–0.715)	1.70 ± 1.54 (0.18–4.37)
KDE^{def} (ha)	0.56 ± 0.13 (0.40–0.75)	0.66 ± 0.43 (0.36–1.61)
MSLD (m)	140 ± 30 (90–190)	330 ± 230 (70–720)
DBFW (m)	230 ± 50 (150–310)	340 ± 220 (70–760)
AKDE (ha)	2.45 ± 1.77 (0.27–5.42)	4.60 ± 1.1 (0.17–9.02)
BBMM$^{50\%}$ (ha)	16 ± 20 (0.54–77.9)	8.5 ±5.6 (0.45–21.5)
BBMM$^{95\%}$ (ha)	34.9 ± 42 (15–183.35)	16.2 ± 10.6 (15–42.5)
dBBMM$^{50\%}$ (ha)	32.1 ± 71.32 (1.9–193.7)	37.76 ± 45.3 (1.9–107.1)
dBBMM$^{95\%}$ (ha)	118.44 ± 256.3 (9.6–699)	137.4 ± 162.4 (9.3–386.6)

that contribute the most and account for the largest portion of the total variance in the data. We used the packages FactoMineR (for the analysis) and factoextra (for data visualization) to complete MCA in R (Husson et al. 2017). MCA analysis uses the Gaussian distribution, and correlations were checked by the v-test (Husson et al. 2017).

Results

Home range and space use.—We located turtles equipped with radio-transmitters 468 times (average 33.4 locations per individual) during a period of 15 mo. Mean home range sizes ranged from 0.40 to 137.40 ha, with significant differences among estimators ($F_{6,91}$= 4.118, $P = 0.001$; Table 1). Mean home range size varied between 0.40 and 118.44 ha in females and 0.66 to 137.4 ha in males, with no significant difference between the sexes based on any method (t = 2.414, df = 6, $P = 0.532$; Table 1). KDE^{def} predicted the smallest areas, while the dBBMM$^{95\%}$ predicted the largest sizes, but sizes based on dBBMM$^{50\%}$ were similar to those areas predicted by BBMM$^{95\%}$.

We found a positive relationship between body mass and home range size in two estimators: MCP ($F_{2,11}$ = 7.101, $r^2 = 0.35$, $P = 0.026$), and KDE^{def} ($F_{2,11}$ = 8.467, $r^2 = 0.41$, $P = 0.013$; Fig. 3). There was no relationship between body size and home range in any other estimators (AKDE: $F_{2,11}$= 3.52, $P = 0.52$; BBMM$^{95\%}$: $P = 0.630$; dBBMM$^{95\%}$: $P = 0.455$; Fig. 3). Minimum Straight-Line Distance (MSLD or linear home range) was 236.0 ± 193.4 m (standard deviation) and the distance between fixes following the watercourse (DBFW) was 299.6 ± 172.0 m, which were significantly different (t = -3.545, df = 13, $P < 0.05$), although these measures did not differ significantly between males and females in either measure (MSLD: t = -2.136, df = 6, $P = 0.078$; DBFW: t = -1.395, df = 6, $P = 0.212$). The home range size of *H. maximiliani* did not differ significantly between wet and dry seasons (t = 0.946, df = 6, $P = 0.436$). In the wet season, turtles used a mean area of 2.77 ± 3.56 ha and in the dry season 1.98 ± 1.70 ha, which were not significantly different between sexes (t = -1.584, df = 6, $P = 0.144$).

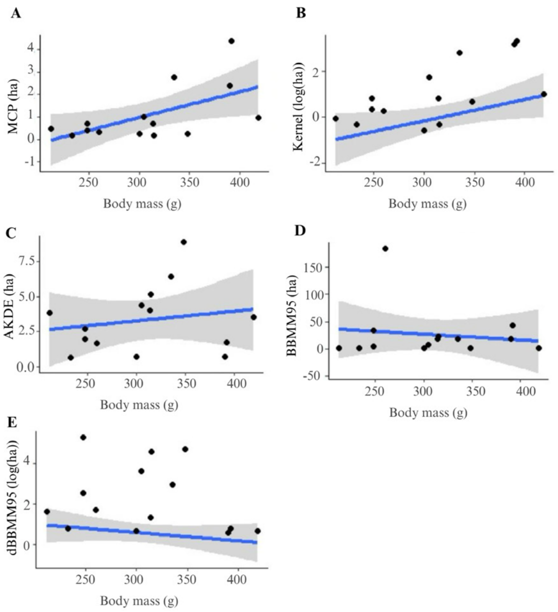

Figure 3. Relationships between body mass (g) and home range size (ha) of Maximilian's Snake-necked Turtles (*Hydromedusa maximiliani*) estimated by (A) Minimum Convex Polygon (MCP$^{95\%}$), (B) Kernel Density Estimator (KDE^{def}), (C) Autocorrelated Kernel Density Estimator (AKDE), (D) Brownian Bridge Movement models (BBMM$^{95\%}$), and (E) dynamic Brownian Bridge Movement models (dBBMM$^{95\%}$). The grey areas around the regression lines indicates the 95% confidence interval of the linear regressions.

All turtles monitored overlapped their home range areas with at least one other conspecific of the opposite sex. The percentage overlap of KDE home ranges between sexes varied from 2–100% (33 ± 0.39%). The maximum number of turtles overlapping their areas was three. All females overlapped with at least one other female. The proportion of areas overlapping

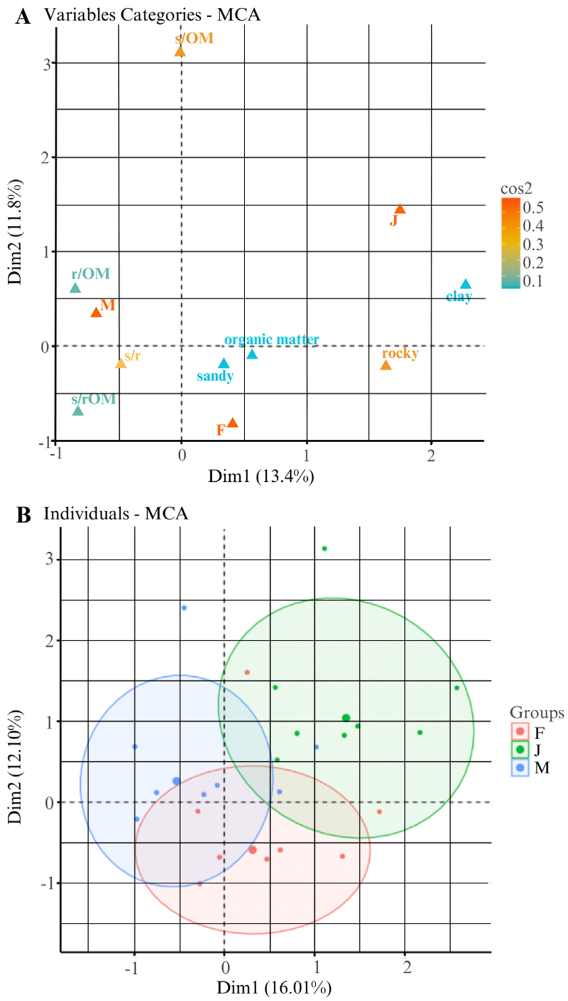

Figure 4. Multiple Correspondence Analysis (MCA) plots of (A) substrate type used by Maximilian's Snake-necked Turtles (*Hydromedusa maximiliani*) and (B) the difference in MCA plots among juveniles (J), females (F), and males (M) monitored at the Parque Estadual Carlos Botelho, São Paulo State, southeastern Brazil. Dim1 and Dim2 indicate the average position (dimension) of each variable. Abbreviations are OM = organic matter and s/r = sandy/rocky.

among females ranged from 0.5–67% (5.2 ± 0.23% standard deviation) and among males, the range of overlapping areas was between 38% and 90% (42.4 ± 0.34%). The number of males overlapping the home range areas with other males varied from one to two. There was a significant difference between same-sex overlapping proportions ($t = 2.529$, df = 13, $P < 0.05$).

Habitat characteristics.—Apart from turtles monitored with thread-bobbins and radio-tracking, we collected habitat use data for 150 turtles captured, marked, and recaptured by active search (61 juveniles, 58 females, and 31 males) with 307 recapture events (110 juveniles, 138 females, and 59 males). We found turtles using shelters in rocks and burrows present along the riverbank in 69% of the captures by active search, 75% of observations made using thread-bobbins, and 85% of observations made using radio-tracking. We observed males, females, and juveniles using different substrate types (Fig. 4). Turtles were more often in sandy/rocky substrates (57%) with a uniform distribution in the remaining types of substrates, except clay (1%) and sandy (3%), which were the least common substrate types used by turtles (Table 2). Males had the lowest use of rocky substrate in comparison to any of the categories (only 4%), similar to females in relation to sandy organic material (only 5%; Fig 4, Table 2). Juveniles were less specialized, using all types of substrates in comparison to adults. There was a significant difference in substrate use among females, males, and juveniles (Substrate: $\chi^2 = 83.49$, df = 7, $P < 0.001$). In the MCA results, both dimensions were statistically significant, with Dim1 and Dim2 making notable contributions to the variance (Dim1: $r^2 = 0.603$, $P < 0.001$; Dim2: $r^2 = 0.532$, $P < 0.001$; Fig. 4). We also found a significant difference in the substrate use measured by different monitoring methods (Dim1: $r^2 = 0.647$, $P < 0.001$; Dim2: $r^2 = 0.585$, $P < 0.001$).

Table 2. Percentage (%) of female, juvenile, and male Maximilian's Snake-necked Turtles (*Hydromedusa maximiliani*) associated with the percentage availability of each type of substrate in the streams of the Parque Estadual Carlos Botelho, São Paulo, Brazil. Substrate abbreviations are OM = organic matter and S/R = sandy/rocky.

Substrate	Availability	Female	Juveniles	Males
Sandy	4%	4	5	3
Rocky	7%	10	17	4
OM	3%	9	12	7
Sandy/ Rocky	52%	56	44	60
Sandy OM	3%	5	11	7
Rocky OM	4%	6	5	9
S/R OM	22%	9	4	10
Clay	4%	1	2	0

Adults also used streams with faster water flow and deeper pools significantly more than juveniles (Depth: $F_{1,33} = 45.03$, $P < 0.001$; Speed: $F_{1,33} = 8.47$, $P = 0.004$), with significant differences between the sexes also ($F_{2,313} = 8.14$, $P < 0.001$; Table 2). There were significant differences in the use of habitats based on their availability ($\chi^2 = 22.40$, df = 63, $P < 0.005$).

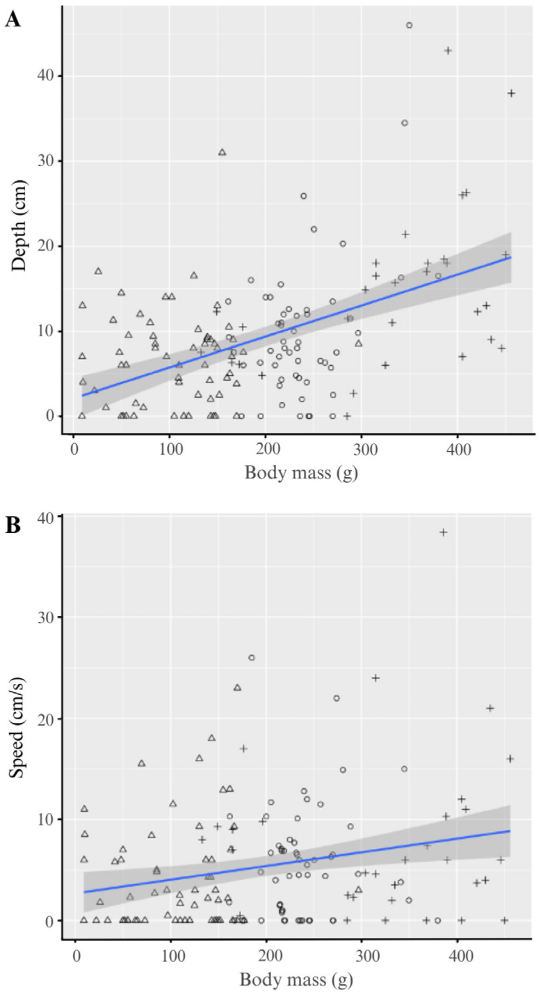

Figure 5. Relationship between body mass (g) and (A) depth and (B) water speed used by juvenile (triangles), female (circles), and male (crosses) Maximilian's Snake-necked Turtles (*Hydromedusa maximiliani*) at the Parque Estadual Carlos Botelho, São Paulo State, southeastern Brazil. The grey area around the regression line indicates the 95% confidence interval of the linear regressions.

Turtles used shallow and lentic pools more frequently than expected based on their availability in the study area (Depth: $D = 0.18$, $P < 0.05$; Speed: $D = 0.76$, $P < 0.05$; Fig. 5). The size of juveniles ranged from 45–124 mm carapace length (CL), females from 125–168.2 mm CL, and males 116.1–203 mm CL (Table 3), and the relationship between use and availability of shallow and calm water pools was stronger for smaller animals (juveniles) than for adult females and males, as indicated by the significant effect of their size on Depth ($F_{1,63} = 33.39$, $P < 0.001$) and Speed ($F_{1,63} = 7.92$, $P = 0.005$). Using bobbins, we found turtles in deeper pools (< 1–110 cm) compared to radio-tracking (< 1–53 cm) and capture-recapture (< 1–56; Table 3) and these differences were significant (Depth: $F_{1,148} = 102.4$, $P < 0.001$; Speed: $F_{1,148} = 4.64$, $P < 0.001$; Fig. 5). Turtles commonly made use of shelters, which consist of a complex network of roots, burrows, and overhanging vegetation along the riverbank. We observed a significant number of animals using burrows (Fig. 6), or closer to the stream edges/river margin distances ($D = 0.87$, $P < 0.05$).

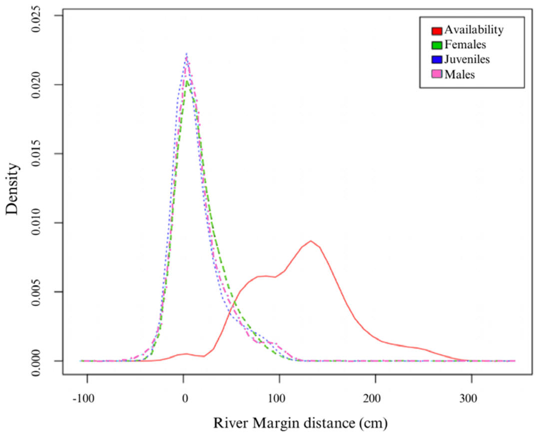

Figure 6. Margin-distance of Maximilian's Snake-necked Turtles (*Hydromedusa maximiliani*) to the riverbank used by all turtles at the Parque Estadual Carlos Botelho, São Paulo State, southeastern Brazil with indication of burrows (values = zero) and terrestrial use (negative values).

Discussion

Hydromedusa maximiliani commonly made use of shelters, which consist of a complex network of roots, burrows, and overhanging vegetation along the riverbank. These burrows provide refuge not only for turtles but also for a diverse range of other animals, including species of herpetofauna (Rocha et al. 2008, Bertoluci et al. 2021), crustaceans (Onda and Itakura 1997), mammals (Linley et al. 2024, Santos et al. 2024), etc. The use of burrows also influenced their home range size as the turtles tracked repeatedly use the same shelters along the stream margin, a common behavior of herpetofaunal species (Row and Blouin-Demers 2006; Famelli et al. 2016). Over a year, *H. maximiliani* used a mean area of 0.4 to 137.4 ha depending on the estimator applied. With a mean home range size of 2.7 ha in the wet and 2.0 ha in the dry season, we found no significant difference between the seasons in home range sizes even with a decrease in activity during the cold/dry season (see Famelli et al. 2016). The broad ranges of home range sizes observed were due to the different estimators providing different information about space use

Table 3. Mean carapace length (CL), body mass (BM), and depth and water speed of habitats used by Maximilian's Snake-necked Turtles (*Hydromedusa maximiliani*) at the Parque Estadual Carlos Botelho, Brazil. Data show means ± standard deviation and range of values in parentheses. An asterisk (*) indicates difference between adults and juveniles ($P < 0.05$). In range of values in Habitat Use, < 1 corresponds to use of shelter or stagnant water (speed).

				Habitat Use	
		CL (mm)	BM (g)	Depth (cm)	Speed (cm/s)
Captured	Females	141 ± 9.9	237 ± 45.9	9.6 ± 8.1	6.1 ± 7.2
(n=150)	(n=57)	(125–168.2)	(161–380)	(< 1–46)	(< 1–30)
	Males	165 ± 23.9	324.4 ± 100.3	13.7 ± 9.5	6.2 ± 6.9
	(n = 31)	(122–203)	(133–456)	(< 1–51)	(< 1–31)
	Juveniles	101.1 ± 21.2	101.3 ± 48.5	7.4 ± 7.7*	4.6 ± 7.2
	(n = 62)	(45–124)	(9–177)	(< 1–46)	(< 1–18.4)
Bobbins	Females	143.1 ± 6.2	249.6 ± 28	10.3 ± 8.9	5.2 ± 5.6
(n=22)		(135–155.5)	(205–287)	(< 0–90)	(< 1–30)
	Males	164.1 ± 21.9	331.8 ± 88.7	12.8 ± 10	7.8 ± 7.1
		(116.1–203)	(137–450)	(< 1–110)	(< 1–30)
Radio (n=14)	Females	143.7 ± 7.8	256.2 ± 34.5	4.9 ± 9.1	2.5 ± 5.3
		(132.7–155.5)	(212–314)	(< 1–56)	(< 1–32.3)
	Males	170.8 ± 8.0	359.2 ± 40.2	2.8 ± 8.4	2.0 ± 8.4
		(156.5–181.3)	(305–419)	(< 1–53)	(< 1–20)

patterns.

Essentially, a valuable estimator will produce an output with ecological relevance for its studied species (Silva et al. 2018), enclosing key areas crucial for activities like feeding, mating, and seeking refuge. Linear home range is one of the simplest ways to represent the home range of aquatic animals in streams as it is computed from a single line (Ouellette and Cardille 2011). The linear home range was described for an Australian chelid, Irwin's Turtle (*Elseya irwini;* Freeman et al. 2018), which has a mean carapace length of 207 mm, similar to *H. maximiliani*. The mean linear home range of 299 m we found for *H. maximiliani* was smaller than observed for *E. irwini* (Freeman et al. 2018), which varied between 387 and 1,128 m. Nevertheless, substantial variation in linear home range was observed in the larger chelid, Geoffroy's Side-necked Turtle (*Phrynops geoffroanus)* living in an urban area of Brazil with linear home ranges varying from 14 to 1,360 m (Müller et al. 2019). Linear home range expresses the intrinsic connection between the studied species and its aquatic habitat where they feed (Souza and Abe 1997b, Novelli et al. 2013), find refuge (Famelli et al. 2016), and thermoregulate (Souza and Martins 2006). Nevertheless, this method is problematic in a multiple-channel river and lacks representation of the terrestrial habitat used (Ouellette and Cardille 2011). For that, other more robust home range estimators based on movements, space use, and activity are more likely to encompass terrestrial uplands (Noonan et al. 2019) and other areas critical for the life cycle of aquatic turtles (Steen et al. 2012).

KDE provided a home range area estimate similar to MCP, as expected, because we selected KDE bandwidth to approximate the home range size estimation of MCP$^{95\%}$. Yet, KDE^{def} showed the smallest home range sizes, which could be due to isolation of core area sites leading to unstable home range estimates (Row and Blouin-Demers 2006, Byer et al. 2017, Mitchell et al. 2019). We defined the KDE^{def} bandwidth by Least Square Cross Validation, which exacerbated the autocorrelation in the movement data, inducing an underestimation of home range areas (Blundell et al. 2001; Hemson et al. 2005). Furthermore, conventional KDE values are highly affected by fix rates and often substantially overestimate home range sizes for herpetofaunal species (Row and Blouin-Demers 2006; Mitchell et al. 2019). Our KDE estimates fit tightly to the data. In contrast, the autocorrelated and movement-based estimates (AKDE and BBMMs) added some predictions of future space use, accommodating a more honest account of uncertainties (Silva et al. 2020); however, that approach led to the large dBBMM estimates in our study. The values of dBBMM$^{50\%}$ were similar to those of BBMM$^{95\%}$, however, suggesting that both methods covered the core areas of activity and underlying shifts in the behavior of these turtles (mainly the intense use of refuge), which inflated the size of these areas. Silva et al. (2019), highly supported the use of BBMMs (especially dBBMMs) for studies of reptiles, focusing on identification of temporal shifts in animal movement patterns. Yet, in our study, BBMM methods did not appear to accurately represent the home range of a relatively sedentary turtle species and might have induced an error because of small sample sizes.

The areas obtained through BBMM reflect more of the uncertainty surrounding the locations of turtles rather than their actual area of use or home range size (Averill-Murray et al. 2019; Fleming et al. 2015; Fleming and Calabrese 2017), primarily influenced by the use of burrows. This is because BBMMs take into consideration the trajectory between reported locations and the level of uncertainty in the recorded locations (Horne et al. 2007; Kranstauber et al. 2012), estimating the probability distribution of an animal during the observed timespan (Horne et al. 2007; Kranstauber et al. 2012). In contrast, the areas estimated by AKDE exhibit smaller errors while mitigating sampling bias (Fleming et al. 2015). AKDE predictions captured the use of shelters along the stream margin while accommodating any increase in autocorrelation among locations. Overall, AKDE demonstrates superior performance compared to other estimators used in our study, particularly considering the relatively sedentary behavior of *H. maximiliani*.

Although each method had its ability to provide different information about space use patterns and home range size, only the MCP and KDE estimators indicated a positive correlation between body size and home range size. Home range size is commonly associated with body size in many turtle species, feasibly reflecting higher demand for resources to attend to metabolic requirements (Slavenko et al. 2016), or simply differences in locomotor capabilities (e.g., greater rate of limb movement; Rowe and Dalgarn 2010). Even though male *H. maximiliani* are larger than females, the size dimorphism did not reflect in a significant difference in their home range size in our study. Sexual differences in home range size are found among some chelonians (Harless et al. 2009; Leão et al. 2019), particularly for species with sexual size dimorphism, such as Spiny Softshells (*Apalone spinifera*; Galois et al. 2002) and species of Podocnemididae (Leão et al. 2019). In a concurrent study, both male and female *H. maximiliani* engaged in activities that demanded mobility over long distances, represented by nesting season for females and the mating season for males (Famelli et al. 2016); still the overall distances moved were not significantly different between the sexes (Famelli et al. 2016), which we now see is reflected in no difference in home range sizes.

In our data, the only significant difference between sexes was the magnitude of home range overlap, with males engaging in social encounters more frequently than females. Home range overlaps represent centers of activity and reveal critical areas for maintaining turtle populations (Leão et al. 2019). While nesting areas are still unknown for *H. maximiliani*, in our study, the center of activity of the population is suggestive of areas where mating occurs. We occasionally observed a female and male sharing the same burrow (see Famelli et al. 2016), suggesting that burrows may play a role in social interactions. The overall importance of shelters for such encounters remains unclear and requires further investigation. Additional studies are needed to determine whether burrows and tunnels are associated with key behaviors such as mating and nesting, particularly during their respective seasons.

Partitioning of resources was previously reported by Souza and Abe (1998) in the same population and study area. Adult and juvenile *H. maximiliani* exhibited different habitat exploration modes (Souza and Abe 1997a,b; Souza and Abe 1998). In previous studies, males often used greater water current and deeper areas compared to females and younger individuals (Souza 1995a, Souza and Abe 1998). Our data showed relationships between water depth and speed to turtle body size. Small individuals remain in shallow and calm areas where they thermoregulate and are protected from being carried away by strong currents (Souza and Abe 1998, Souza and Martins 2006). Souza and Abe (1998) also observed that juveniles used a broader diversity of food items compared to adults and suggested that juveniles would also be more generalists in substrate use, which agrees with our findings. The partitioning of observed habitat use may reduce intraspecific competition and helps to protect juveniles from fast water currents and predation (Bury and Germano 2003; Souza and Abe 1998).

Our results indicated that variation in water depth and speed and the high availability of shelter affected space use by *H. maximiliani*. The cryptic coloration of *H. maximiliani* has often been stated as a factor that increases the difficulty of finding these turtles in the wild (Guix et al. 1992; Souza and Abe 1997a; Famelli et al. 2011). The simultaneous use of tracking methods helped us find animals in the wild and secured data on their behavior, habitat use, and resource partitioning. Our study presents a preliminary investigation of home range size using AKDE and BBMM in preference to other traditional estimators, plus a detailed habitat selection study for the endangered *H. maximiliani*. Our data indicated that turtles tracked over the study period were mostly sedentary in their annual home ranges with intense use of refuges among the rocks and in the stream banks, with AKDE showing superiority in estimation of their home range sizes. Burrows in the stream margins represent a crucial refuge for *Hydromedusa* species in all size classes and for both sexes throughout the year. Because low activity sites do not necessarily correlate with low use or least preferred areas in reptiles, it is important for researchers to properly identify refuge and core areas of use (Silva et al. 2018).

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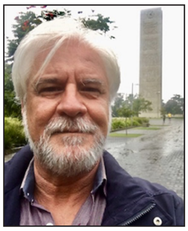

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