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Habitat use and movement patterns of broad-snouted caimans (*Caiman latirostris*) in an impacted Atlantic forest environment in Brazil

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Abstract

Background Animal habitat use can be influenced by a suite of factors including intraspecific interactions and resource availability. The broad-snouted caiman (*Caiman latirostris*) is the largest crocodylian species distributed in freshwater environments of the Brazilian Atlantic Forest, where it inhabits many types of human-impacted and preserved habitats. Despite their ability to occupy ecologically different water bodies, little is known about their movement patterns and their habitat use. We investigated the variation in movements and space use of adult caimans relative to sex, body condition, and environmental conditions in northeastern Brazil.

Methods We conducted long-term capture surveys from 2013 to 2022 and used GPS telemetry from 2021–2022 ($n = 12$ individuals) to assess movement patterns and home ranges of caimans and their habitat use based on Brownian Bridge Movement Modeling (BBMM) and Generalized Linear Mixed Modeling (GLMM).

Results Females ranged farther from reservoir's forested margins, exploring a greater diversity of habitats during the wet/non-reproductive season. During the dry/reproductive season, females remained close to nesting sites within forest fragments. The body condition of caimans did not change significantly over the wet and dry season, indicating that resources are available year-round. Caimans moved more at night than during daytime, likely due to nocturnal foraging and possibly avoiding periods of increased human activity. Female movement rates were positively associated with rainfall, in a pattern likely linked to nest attendance in the dry season. Male movement was positively correlated with reservoir volume in the wet season, possibly due to increased availability of habitats in comparison to dry periods and to decreased overlap with territories controlled by other males. Home ranges estimated as 95% utilization distributions were relatively small in both sexes, averaging 0.64 km^2 (range: 0.001–1.4 km^2), as were their core areas estimated as 50% utilization distributions, which averaged 0.12 km^2 (range: 0.0003–0.12 km^2). Small core areas may indicate that caimans remain most of their time in a specific habitat, suggesting abundant resource availability or territoriality.

Conclusions Our work reveals the complexity of social interactions and how caimans select their habitats in a highly altered environment.

Keywords Spatial ecology, Crocodylian, GPS-tracking, Capture–recapture, Habitat selection, Home range, Telemetry

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Background

Documenting how animals move across their habitats and define their home range is crucial to a better understanding of their behavior and demography, in addition to informed conservation planning. This becomes particularly urgent in areas subject to imminent effects of habitat fragmentation, climate change and biological invasions [62]. Individuals select their habitats based on a variety of factors and these choices involve innate and learned behaviors [36]. Decisions about movements and habitat use are often driven by essential needs such as foraging, mating, nesting, or protection from predators and human disturbance [40, 60, 82]. Cumulatively, these decisions affect the distribution and density of populations [7]. Habitat selection is a dynamic process that can vary, for example, across different spatial and temporal scales, across the diel cycle, across seasons, or through ontogeny [56]. Nonetheless, knowing how an animal makes movement and space use decisions can improve species management and conservation efforts.

Sex differences in habitat use and movement are common across many taxa. For instance, females may require more energy during the breeding seasons, engaging in foraging excursions around the period of egg maturation or embryo nutrition and moving to habitats which are safest for their offspring when nesting or nursing [28, 81]. In contrast, males may select habitats and maintain territories that maximize mating opportunities. In some species, males establish dominance hierarchies or defend territories to monopolize access to females or to prey resources, thereby relegating subordinate males to suboptimal habitats [30, 32, 89]. Dynamics related to sex-specific differences in space use can affect population dynamics and overall individual survival probabilities [83].

Crocodylians are semi-aquatic predators inhabiting freshwater and brackish environments, establishing crucial connections that span across terrestrial and aquatic ecosystems [85]. They present complex social systems, and although poorly studied, evidence does exist of considerable inter-individual variation in habitat use and movements within sexes [78, 86, 88]. During the breeding season, their movement tactics are influenced by choosing more suitable habitats for mating and for nesting [4, 15]. Additionally, as ectotherms, crocodylians respond to abiotic conditions, adjusting their movements in response to change in air or water temperatures, for example, by seeking out specific areas to bask in or cool down their body temperature [24, 63].

The broad-snouted caiman (*Caiman latirostris* Daudin, 1801) is a medium-sized crocodylian found in large water bodies in Brazil, Argentina, Bolivia, Paraguay, and Uruguay [84]. Across its geographic distribution, it is more abundant in lentic environments and in densely vegetated wetlands, using these areas for foraging, nesting, or protection [49, 69]. Nearly 70% of the global population is found within Brazil [22], with multiple populations impacted by human disturbance such as urbanization, agriculture, illegal hunting, fishing, and pollution [48, 52, 90]. Genetic assessments revealed the presence of three distinct lineages of broad-snouted caiman in Brazil, potentially isolated in the basins of the São Francisco, Rio Doce, and Paraná rivers [74]. Even within the same basins, there appears to be a limited number of breeding individuals and genetic connectivity among populations, suggesting that the broad-snouted caiman exhibits a strong site fidelity or limited migratory behavior [91].

Broad-snouted caiman distribution is concentrated in the eastern portion of Brazil, especially within the Atlantic Forest [22]. This phytogeographic domain stands as one of the most important biodiversity hotspots in the world and the second largest rainforest in South America, harboring 2.8% of global tetrapod diversity [26]. However, historical resource exploitation and deforestation have dramatically fragmented and diminished its coverage area, with estimates suggesting that only 28% of its original cover remains, distributed in small and isolated fragments [73]. Additionally, within the Atlantic Forest, multiple water sources have been dammed for water supply in neighboring cities, altering hydrological systems [65]. Here, we investigate the habitat use and movements of broad-snouted caiman in a human-impacted Atlantic Forest habitat. Specifically, we use a 9-year time series of caiman captures (2013–2022) to investigate the role of sex in habitat use patterns, and environmental factors influencing adult caiman habitat preferences. Moreover, we made the first-ever telemetry-tracking investigation conducted for the species in this region (2021–2022), addressing aspects of diel and seasonal patterns in caiman movements, and home range sizes of adult individuals.

Methods

Study site

The Tapacurá Reservoir (hereafter "Tapacurá") is an artificial lake created by the damming of the Tapacurá River, in the eastern State of Pernambuco, northeastern Brazil (8.043856° S, 35.195710° W) (Fig. 1A). The reservoir was created in the 1970s, to increase the water supply to densely populated cities near the coast of Pernambuco [80]. The reservoir covers *ca.* 9 km^2, and is under tropical humid climate, with a rainy period during autumn/winter, with *ca.* 1300 mm of rainfall [75]. The peak of the wet season is typically observed from March to August, when annual temperatures are lower. Tapacurá has undergone a series of pronounced

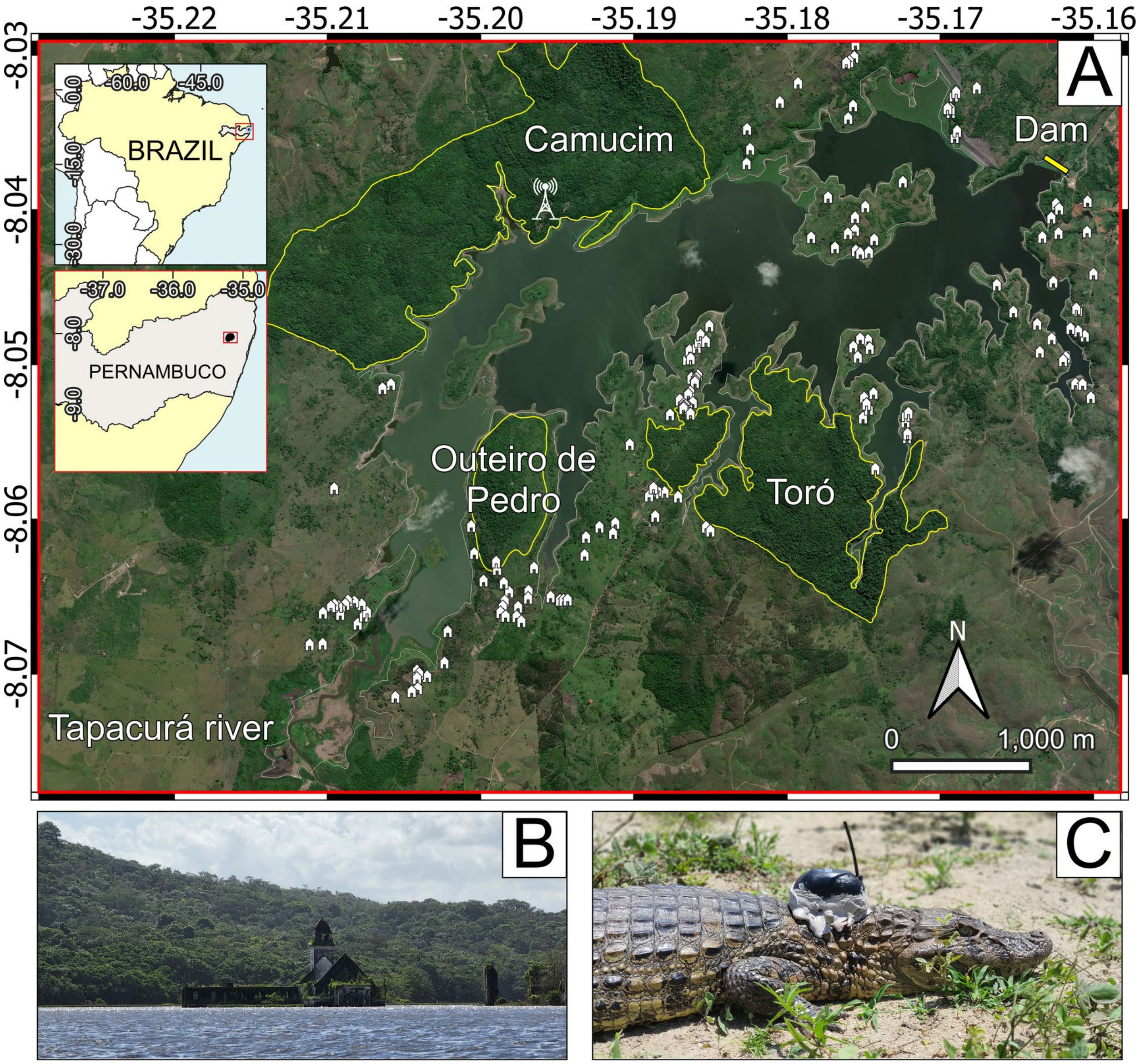

Fig. 1 **A** The Tapacurá reservoir, an reservoir formed by damming of the Tapacurá River in São Lourenço da Mata, northeastern Brazil; **B** overview of the wildlife refuge Mata do Camucim, an Atlantic Forest fragment located in the north sector of Tapacurá; **C** GPS transmitter attached to an adult broad-snouted caiman (*Caiman latirostris*). The reservoir area is represented by the white line and forest fragments limits by yellow lines. Houses icons represents human habitations near reservoir's margins and antennae icon indicate the location where the telemetry receiver station was installed

droughts and flood events. According to Pernambuco's water monitoring agency (APAC, https://www.apac.pe.gov.br/), water levels have historically exhibited considerable fluctuations, ranging from 3% capacity during the 1990s to 130% during 2011. At 100% capacity, water flows over spillways.

There are three fragments of Atlantic Forest surrounding the reservoir, named "Mata do Camucim", "Mata do Toró" and "Mata do Outeiro de Pedro" (Fig. 1B). These fragments collectively cover an area of 5.4 km^2 of native forest and are categorized as wildlife refuges by the Brazilian government [67]. Within fragments, vegetation is mostly lowland semideciduous forest (Seasonally Dry Atlantic Forest—Pereira-Silva et al., [66]). Other regions surrounding Tapacurá are occupied by human settlements, agriculture, or ranching. Artisanal fishing conducted by local communities is common in the reservoir and hunting has also been documented alongside its forested margins [54, 79].

Nocturnal surveys and captures

We conducted nocturnal eyeshine surveys [45] to detect and capture caimans from 2013 to 2022. These surveys occurred yearly, on a quarterly basis (two during the dry season and two during the wet season), spanning two to four nights in a week, starting just after sunset (*ca.* 6:30 pm). We navigated the whole reservoir, covering all accessible areas using a 6.2-m boat fitted with a 15-hp engine that maintained an average speed of 8 km/h. At times, certain areas were inaccessible because of dense floating aquatic vegetation (mainly the common water hyacinth *Pontederia crassipes*), shallow water depths or the presence of many gillnets. Surveys were not conducted under adverse weather conditions, such as heavy rainfall, thunderstorms, or intense fog.

Using a hand-held spotlight, we detected caimans at up to 600 m distance. We conducted caiman captures using locking cable snares, and restrained individuals with adhesive tapes or ropes, immobilizing their limbs, jaws, and covering their eyes with a cloth. We weighed each caiman using a 40,000 *g* scale, determined sex by cloacal inspection [8] and measured their snout–vent length (SVL) using measure tapes. We considered as adults individuals with SVL > 67.9 cm, following the classification proposed by Leiva et al. [42].

We recorded the geographic position of each captured individual with a hand-held GPS (Garmin eTex), and collected information on habitat features in the field or based on updated satellite images. These were: the distance to the nearest forest fragment (in meters), distance to the nearest human residence (in meters), distance to the nearest reservoir's margin (measured at the water edge; in meters), gillnet frequency in the area where we captured the caiman (see Mascarenhas-Junior et al., [53] for details; percentage), and water depth (in meters).

Telemetry

From July 2021 to July 2022, we tracked 12 adult caimans (eight females and four males) using transmitters with GPS technology (Nortronic Ltda, Natal). Transmitters weighed 220 g and measured 4.5 × 9 × 5 cm (24 months of lifespan estimated) and were programmed to log data every six hours (400 mW of power and 6,500 mAh of autonomy). Transmitters used the LoRa Network system, a wireless communication technology designed for long-range and low-power communication between devices (including Internet of Things [IoT] technology), to receive GPS data. On the reservoir's north margin, we installed a waterproof station connected to an omnidirectional antenna (see Fig. 1A), designed to receive the data stored in each transmitter operating in an ultra-high frequency (UHF) range of 903–918 MHz. Under optimal conditions and without physical barriers, the antennae's range could extend up to 10 km. The station was powered by an external 12 V/3 A power supply. All data collected by the receiver station were subsequently uploaded to the Tago IO online platform (https://tago.io/) for further processing.

We attached transmitters onto the nuchal scutes of caimans using the methods of Brien et al. [10]. All transmitters weighed less than 2% of an animal's body mass to minimize potential effects on their natural behavior [51]. We subcutaneously injected a NaCl solution infused with 2% lidocaine (1 ml of lidocaine per 7 ml of NaCl) into the dermal bones of the nuchal rosette of the caimans, located on the dorsal portion of the neck. After 10 min, we used a 2-mm drill to perforate the dermal bones. We then secured the transmitter with 2 mm nylon wire passing through three pairs of bone holes. We filled the gaps between the transmitter and caimans' skin with Epoxy (Sikadur), maximizing the area of contact between the transmitter and the nuchal rosette. To mitigate pain and risk of inflammation, we administered a solution of 3% Meloxicam (0.2 mg/kg) in the forelimb muscles. Images of procedures are in Supplementary file 1. After 24 h of clinical observation, we released caimans at their location of capture (Fig. 1C).

During telemetry monitoring, we also collected abiotic variables associated with each GPS-transmitter location. We obtained values for the air temperature (Celsius degree) from a thermometer sensor attached in the transmitters and obtained daily reservoir volume (percentage of total reservoir's water capacity) and rainfall (millimeters) from a database provided by APAC.

Data analysis

We used the R program [72] to conduct statistical analysis and QGIS 3.28 to create maps [70]. When appropriate, we conducted Shapiro–Wilk (SW) tests to verify data normality. We report quantitative results as mean values ± standard deviation (mean ± SD) and alpha level of 0.05 as statistically significant (p value < 0.05).

To compare the values of habitat features between the dry and wet seasons for each sex separately, we conducted Wilcoxon tests (Supplementary File 2). We also adapted Fulton's relative condition index (Kn) for assessing caiman body condition, considering the relationship between weight and SVL. We used the formula $\mathrm{Kn} = (W/L^b]10^n)$, where W represents the individual's mass, L denotes SVL, b is calculated through ordinary least squares regression of W and L, and 10^n is a multiplier to achieve a unit [64]. Kn is used as proxy for crocodylian fitness when interpreted by quartile system because skeletal length and volumetric measurements are positively correlated [64, 92]. For the specific purpose of comparing differences in body condition between seasons, we opted to proceed with the analysis using values from the solution of Kn equation, as all captured individuals were adults, reducing potential size class biasing. We made the Kn seasonal comparison performing a T-test (males SW = 0.99, *p* value = 0.991; females SW = 0.95, *p* value = 0.15).

We utilized a Tweedie generalized linear mixed modeling (GLMM) framework to assess seasonal (wet/dry) differences in movements between males and females and the effects of abiotic covariates (air temperature, reservoir volume, and daily rainfall) on caimans' movements. We chose the Tweedie family for its flexibility in dealing with positively skewed and zero-inflated data [38], as on many occasions, caimans maintained their positions between consecutive valid transmissions. We averaged the values recorded for each abiotic variable between consecutive valid transmissions to obtain covariates values. We tested multicollinearity between abiotic variables using a variance inflation factor (VIF) implemented in the *car* package [27] in R. Before modeling, we standardized covariate data by centering each covariate on its mean and scaling by its standard error. We tested whether the effects of abiotic covariates on movement are different for females and males separately and whether the seasonal effect on movement differs between males and females (fixed effects). We also incorporated individual ID to account for individual-level variability in movement (random effects). The base model structure was: Movement ~ Air temperature:Sex + Reservoir volume:Sex + Daily rainfall:Sex + Sex*Season + (1|individual ID). For multi-model inference, we used the 'dredge' function of the MuMIn package [5], combining all covariates and ranking models based on Akaike's Information Criteria (AIC_C). We considered models with $\Delta AIC_C < 2$ as the best models [12]. To calculate the averaged model, we used the 'model.avg' function in MuMIn, which considered parameter estimates from models within $\Delta AIC_C < 2$. In assessing model performance, we used conditional effects (conditional R^2) to measure the proportion of variance in the response variable explained by both fixed and random effects, and marginal effects (marginal R^2) to evaluate the variance in the response variable explained only by fixed effects. We performed the Tweedie GLMM analysis using the package *glmmTMB* [11] in R using the function 'glmmTMB'.

We applied the Brownian bridge movement model (BBMM) to evaluate the trajectories of caimans. The BBMM method considers consecutive discrete locations in a straight line-distance recorded in short-time periods to estimate the animals' movement paths and probability of movement occurrence [37]. To calculate caimans' trajectories, we used the 'ltraj' function from the *adehabitatLT* package in R [14]. Our data fulfilled the assumptions of Trajectory type II, in which relocations include information about time. Thus, we were able to calculate the number of distance-based bursts, defined as segments (in our case, in meters) of consecutive valid relocations within a short-time period (in our case, a maximum interval of 12 h), during which movement is relatively homogeneous. We further divided bursts into daytime intervals (with sunlight) and nighttime intervals (without sunlight) to calculate daily movements. To account for differences in general movements during daytime and nighttime, we conducted a Wilcoxon test (SW = 13, *p* value = 0.014). For this specific analysis, we removed individuals F2 and F8 from daytime analysis, and F4 and F8 from nighttime analysis because transmitters did not provide more than five valid coordinates.

We also used BBMM to calculate the area of use of caimans using the function 'kernelbb' in *adehabitatHR* package in R [13] to create a Utilization Distribution area (UD) based on kernels produced by the caimans' trajectories and relocations. We set two smoothing parameters to implement the connection between relocations and build the UDs: 1) Sig1, which compute the individual's motion variance parameter, associated to their individual speed [37], calculated by the function 'liker' to find parameter's maximum likelihood, 2) Sig2, representing the imprecision of the relocations and that should be previously known (in our case, five meters). We considered the 95% UD contour as the overall home range (HR) and the 50% UD contour as core area activity (CA) [41]. To ensure the robustness of our results, we included only individuals with a minimum of 30 valid relocations in the analysis. After obtaining HR and CA values, we determined the size of the overlapping areas for males and females, separately.

Results

Over 101 surveys, we spanned 07:34 ± 1:28 h in the field and covered a distance of 50.1 ± 7.4 km per night. We successfully captured 75 adults, including 14 recaptures. We did not find significant differences in the values of each habitat feature when comparing sexes and seasons, except for females' distance to the closest forest fragment, which was higher during the wet season (523 ± 609 m) when compared to the dry season (209 ± 579 m) (W = 27, *p* value = 0.020, Fig. 2). We did not observe any significant seasonal differences in Kn among females (t = − 1.08, df = 22.36, *p* value = 0.291), averaging 2.14 ± 0.25 in the wet season and 2.25 ± 0.26 in the dry season. Males also did not present differences in Kn (t = − 0.54, df = 33.69, *p* value = 0.593), averaging 2.55 ± 0.43 in the wet season and 2.47 ± 0.39 in the dry season.

Individuals tagged with GPS transmitters in 2021 were tracked over a total of 355 days. During this period, we

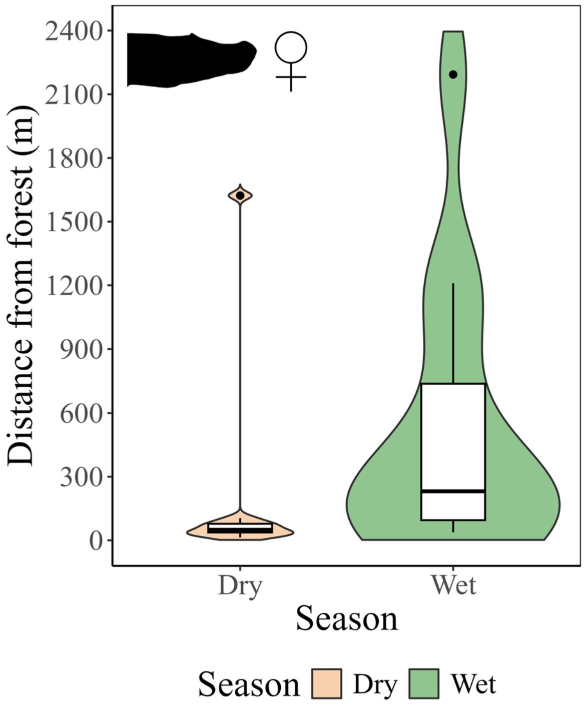

Fig. 2 Seasonal differences in the average distance (meters) from the closest forest fragment of captured adult female broad-snouted caimans (*Caiman latirostris*) between August 2013 and June 2022 in Tapacurá Reservoir, São Lourenço da Mata, Brazil. White boxes: range between the first and third quartiles of the data; black whiskers: variability outside the upper and lower quartiles; horizontal black lines: data median; black dots: outliers; brown and green violins: data distribution

tracked individual caimans for an average of 87 ± 72 days (range 18–221 days). We recorded an average of 90 ± 80 (range 13–275) valid relocations for each caiman (Table 1). We collected a total of 647 bursts (300 during daytime and 347 during nighttime), ranging from 1–205 per individual, except for individual F1, which did not produce any consecutive movement data. All transmitters ceased operation before reaching their programmed lifespan, likely due to detachment or malfunction. We were able to recover two transmitters in the margins of reservoir following the coordinates available in Tago IO system. The other transmitters probably sank, and the signal was no longer transmitted.

We did not detect multicollinearity among abiotic covariates (VIF ≤|1.04|). Among 64 candidate models resulting from model selection process, one exhibited value of ΔAIC < 2 (marginal $R^2 = 0.13$, conditional $R^2 = 0.33$; Table 2), without air temperature as a contributing factor. According to Tweedie GLMM, overall mobility did not differ significantly between males and females ($\beta = -0.68$, $z = -1.46$, *p* value = 0.145), but males traveled further than females in the wet season ($\beta = 1.36$, $z = 2.78$, *p* value = 0.005) (Table 3). Daily rainfall had a significant and positive, albeit weak, effect on female's movements ($R^2 = 0.01$, $\beta = 0.42$, $z = 2.81$, *p* value = 0.005) (Table 3), while males' movements were slightly positively affected by the reservoir volume ($R^2 = 0.04$, $\beta = 0.31$, $z = 3.33$, *p* value 0.001) (Table 3). The estimated variance for individual ID random effect was 0.33 ± 0.57 (CI [0.29, 1.12]) (Table 3).

Considering daily movements, caimans displayed greater mobility during nighttime, traveling 81.4 ± 193.8 m, compared to 58.8 ± 163.1 m during daytime (W = 46,500, *p* value = 0.019; Fig. 3). We estimated

Table 1 Data of broad-snouted caimans (*Caiman latirostris*) tracked by GPS telemetry in the Tapacurá Reservoir, in São Lourenço da Mata, Pernambuco, Brazil, from July 2021 and July 2022

ID	SVL	W	Reloc	Date begin	Date End	Days	HR	CA
F1	83	18,240	30	7/20/2021	8/22/2021	33	0.001	0.0003
F2	75	13,040	23	7/14/2021	8/9/2021	26	–	–
F3	77	16,300	38	7/14/2021	8/10/2021	27	0.50	0.03
F4	79	15,080	18	7/27/2021	8/14/2021	18	–	–
F5	76	14,410	52	9/2/2021	10/28/2021	76	0.42	0.07
F6	82	15,120	275	9/2/2021	3/1/2022	180	0.88	0.13
F7	89	24,540	204	11/25/2021	3/15/2022	110	1.05	0.08
F8	74	14,060	13	11/24/2021	12/24/2021	30	–	–
M1	75	–	57	7/16/2021	8/21/2021	36	0.32	0.09
M2	78	12,240	98	9/2/2021	11/18/2021	77	1.44	0.35
M3	78	14,530	135	9/2/2021	3/29/2022	208	0.92	0.31
M4	101	40,000	139	11/25/2021	7/4/2022	221	0.27	0.06

ID: Individual identification ('F' represents females and 'M' represents males); SVL: snout–vent length (centimeters); W: weight (grams); Reloc: number of valid relocations; HR: home range in km^2 (95% utilization distribution); CA: core area in km^2 (50% utilization distribution)

Table 2 Model selection results of covariates predicting broad-snouted caimans (*Caiman latirostris)* movements (meters) in the Tapacurá Reservoir, São Lourenço da Mata, Pernambuco, Brazil, based on GPS-telemetry data between July 2021 and July 2022. Null, global and models with ΔAikake's Information Criteria (ΔAIC_C) distance < 2 are presented

Model	np	logLik	AICc	ΔAIC_C	Weight
S + Sx + Rv:Sx + Rf:Sx + S*Sx	10	− 3265.09	6550.50	0.00	1.00
Global	12	− 3264.38	6553.30	2.73	0.00
Null	3	− 3285.06	6576.10	25.62	0.00

All covariates were scaled (mean = 0, standard error = 1)

Rv: reservoir volume (percentage); Rf: daily rainfall (millimeters); Sx: sex (female/male); S: season (dry/wet). np: number of parameters; logLik: log likelihood of the model; AICc: Aikake's Information Criteria; $\Delta AIC_{C:}$ distance from the best model; Weight: weight of each model in the models with $\Delta AIC_C < 2$ (values from 0 to 1)

HR and CA of nine individuals, excluding F2, F4, and F8 from the analysis due to their limited number of valid relocations (Table 1). HR averaged 0.644 ± 0.431 km^2 (range: 0.001–1.444 km^2) and CA averaged 0.146 ± 0.121 km^2 (range: 0.0003–0.346 km^2) (Table 1, Fig. 4). The average overlap in HR among females was 0.128 ± 0.184 km^2 (range: 0–0.605 km^2), nearly four times higher that of the males, whose overlap averaged 0.028 ± 0.058 km^2 (range: 0–0.158 km^2). Female's overlap in CA averaged 0.006 ± 0.019 km^2 (range: 0–0.064 km^2), the double that of the males, averaging 0.003 ± 0.005 km^2 (range: 0–0.01 km^2).

Discussion

Our results revealed that movement patterns of broad-snouted caimans varied between sexes, with males presenting higher mobility during the wet season than females. Caimans moved more at night than during the day. Females increased their movement rates in rainy periods and remained close to the forest during the driest months, while males enhanced movements under higher water levels. However, these movements and habitat use were slightly affected by environmental factors (habitat features and abiotic variables) considered in our study. This may, in part, reflect their relatively small utilization areas. Our results offer a novel assessment of seasonal habitat selection by male and female broad-snouted caimans, based on data collected systematically over a long time series and including telemetry-tracking information, previously unavailable for Atlantic Forest populations of this species. We discuss our results in the light of possible factors associated with sexual differences in movement patterns and habitat use.

Female broad-snouted caimans generally were captured far from forest fragments during the wet season. Moreover, during rainy periods, they also exhibited a tendency to disperse over greater distances, when compared to their movements during drier periods. Female crocodylians often remained near nesting sites during part of the year, when they engaged in activities related to nest construction, maintenance, and vigilance, or in parental care, which can be done alone or in association with neighbor females [23, 68, 76]. Given that the breeding season of caimans coincides with the driest

Table 3 Tweedie generalized linear mixed model (GLMM) averaged parameters of covariates predicting broad-snouted caimans (*Caiman latirostris*) movements (meters) in the Tapacurá Reservoir, São Lourenço da Mata, Pernambuco, Brazil between August 2013, and June 2022

Fixed effects	β	SE	z	*p*	CI 2.5%	CI 97.5%
Intercept	4.84	0.35	13.68	< 0.001	4.14	5.53
Reservoir volume:female	0.31	0.23	1.32	0.188	− 0.15	0.76
Reservoir volume:male	0.31	0.09	3.33	0.001*	0.13	0.50
Daily rainfall:female	0.42	0.15	2.81	0.005*	0.13	0.71
Daily rainfall:male	− 0.09	0.08	− 1.14	0.255	− 0.23	0.06
Sex(male)	− 0.69	0.47	− 1.46	0.145	− 1.61	0.24
Sex(male)*Season(wet)	1.36	0.49	2.78	0.005*	0.40	2.32
Random effects	**N gr**	**N obs**	**Var**	**SD**	**CI 2.5%**	**CI 97.5%**
ID	11	647	0.33	0.57	0.29	1.12

Covariates were scaled (mean = 0, standard error = 1)

GLMM framework: Movement ~ Reservoir volume:Sex + Daily rainfall:Sex + Sex*Season. Male sex and wet season were used as reference categories to present modeling results

ID, individual identification; N obs., number of observations; N gr., Number of groups for random effects; Var., variance; SD, standard deviation; β, parameter estimate; SE, standard error; z, z-statistic value; *p*, statistical significance level; CI, confidence interval

*p value statistically significant (< 0.05)

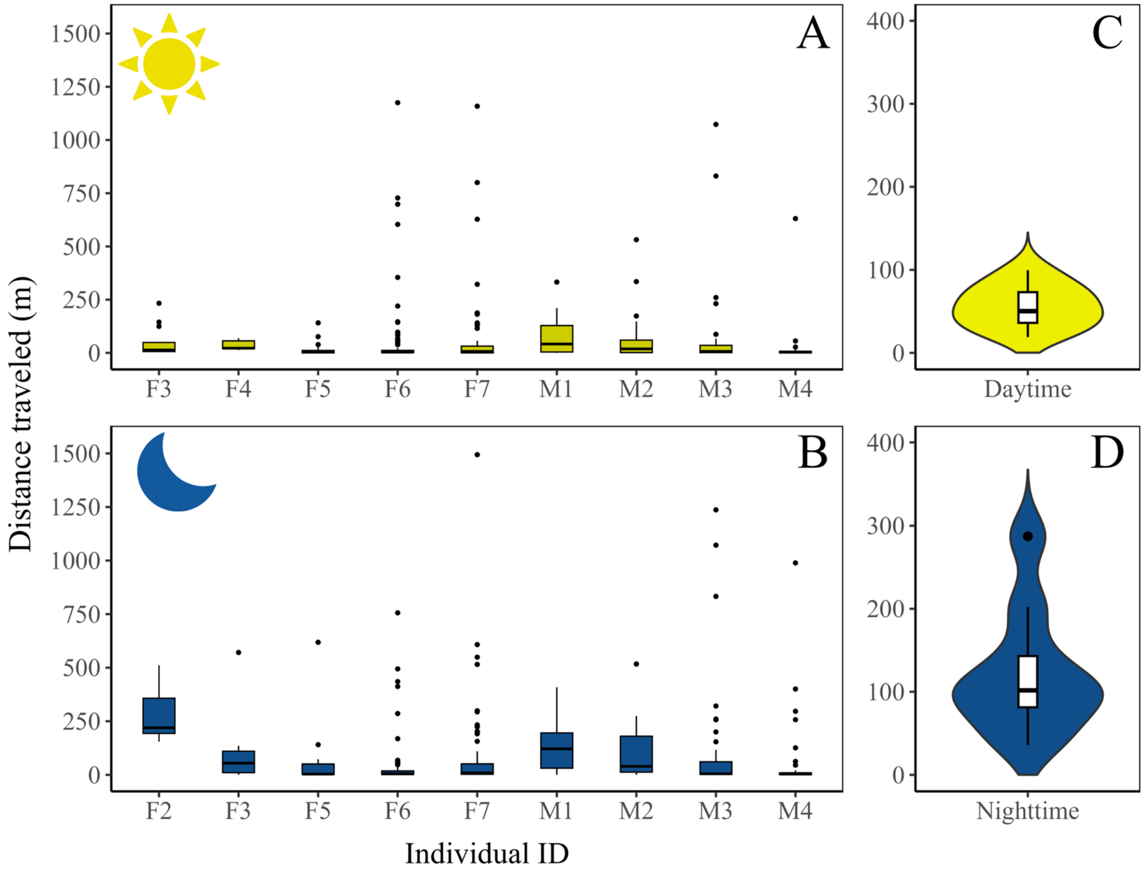

Fig. 3 Differences between the distance traveled (meters) by broad-snouted caimans (*Caiman latirostris*) tracked by GPS telemetry during (**A**) daytime and (**B**) nighttime in Tapacurá Reservoir, located in São Lourenço da Mata, Pernambuco, Brazil from 07/14/2021 and 07/04/2022. Plots **C** and **D** represent the median distance traveled across all individuals. White, blue and yellow boxes: range between the first and third quartiles of the data; black whiskers: variability outside the upper and lower quartiles; horizontal black lines: data median; black dots: outliers; yellow and blue violins: data distribution

period in Tapacurá, and that nests are built within forest fragments [3], it is expected that adult female movement rates would be lower as they remain closer to the forest for nest attendance. Moreover, female caimans also had consistent body condition scores between seasons, indicating that they likely do not undergo longer periods of starvation, even during nest attendance in the dry season. Notably, one female (F7) constructed her nest during our monitoring period, intermittently accessing the water while attending to the nest. We suspect that females in Tapacurá may return to the water to access food resources, regulate their body temperature during warmer periods, or seek refuge from human disturbance [50].

None of the selected habitat features were associated with differences in males' habitat use between dry and wet season, but movements slightly increased when reservoir volume was higher. In general, dominant male crocodylians present territorial behavior [25, 29] by excluding subordinate males from mating, nesting sites, or access to food resources [58]. When water level is high, we presume that subordinate males may seek out habitats for mating or foraging, likely avoiding territories that are actively controlled by dominant males. However, in areas where species density is relatively low and habitat availability is more abundant, dominance hierarchy may not be observed on a large spatial scale [86]. In Tapacurá, caiman encounter rates (averaging 1.3 ind/km, [53]) is lower than observed in other congeneric caiman populations in Brazil, such as those observed in populations of Yacares (*Caiman yacare*) and spectacled caimans (*Caiman crocodilus*) [1, 21]. Since males did not show a preference for any specific habitat throughout the year and body condition scores did not significantly change between the dry and wet seasons, we anticipate that resources are available in most of reservoir's habitats [53].

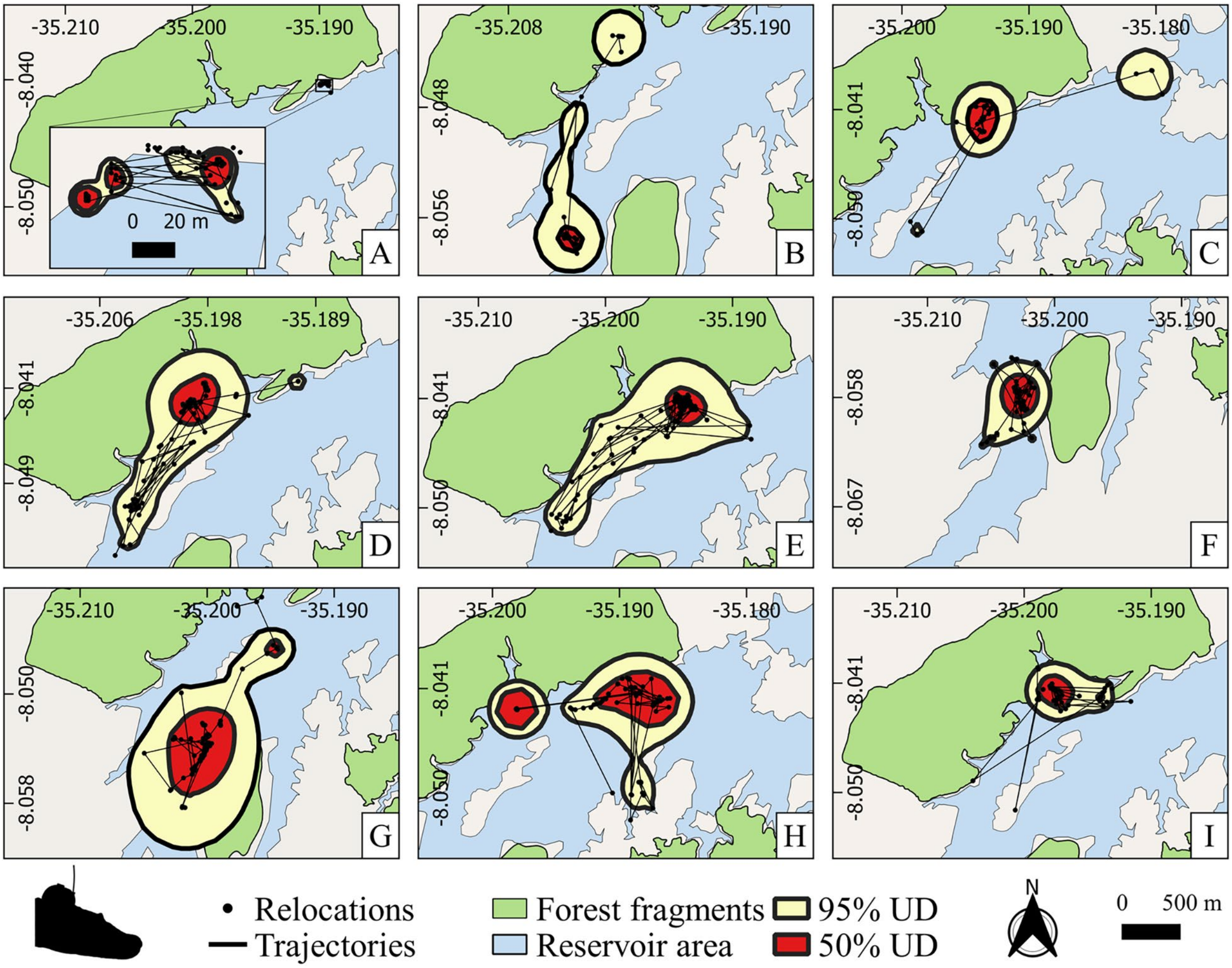

Fig. 4 Overall home range (HR) and core area activity (CA) of GPS-tracked broad-snouted caimans (*Caiman latirostris*) based on Brownian bridge movement models (BBMM) analysis (minimum 30 relocations) in Tapacurá Reservoir, São Lourenço da Mata, Pernambuco, Brazil, between 07/14/2021 and 07/04/2022. Females were represented by **A** F1, **B** F3, **C** F5, **D** F6, **E** F7 and males by **F** M1, **G** M2, **H** M3 and **I** M4

Overall, mobility did not differ between males and females, but male's movements exceeded that of females during the wet season. A previous telemetry study involving broad-snouted caimans found that male movements outpaced those of females, as males may seek unpatrolled areas by other males [49]. Similar movement patterns have been documented in other crocodylian species [9, 17, 31, 59]. The increase in male movement during the wet seasons corroborate with the positive association observed between movement and reservoir water levels. Moreover, our data suggest that broad-snouted caimans present sedentary behavior, with most monitored individuals exhibiting long-periods of limited movement. These findings align with existing studies that attribute this sedentarism to territorial behavior in males and nesting-related care in females [25, 44, 47].

Adult caimans exhibit higher activity levels during nighttime compared to daytime, aligning with their role as nocturnal predators [34]. Furthermore, crocodylians may move from areas protected by vegetation to open channels during nighttime to evade potential human threats like poaching or boat traffic, considering the reduced human activity during these hours [16, 43]. Despite this nocturnal behavior, temperature fluctuations did not predict their movements in our study system. Adult crocodylians may bask during warm daylight hours to elevate their metabolic rates [2, 18, 33, 35], and often increase their nocturnal movement activity for foraging or nest attendance [78, 59, 19, 20, 57]. However, the overall impact of temperature on their movement might be dependent on seasonal variations. During cold winters, crocodylians may shift their activities to the daytime when temperatures better suit their metabolic processes, whereas the opposite could be valid in hot summers [87]. Broad-snouted caimans often seek warmer habitats to keep their body temperature above 30 °C, increasing their metabolism functioning, growth and nutritional conversion rates [6, 46]. Considering average annual temperatures in Tapacurá is *ca*. 27 °C and often exceeds 30 °C, we assume that adult movements are minimally affected by local thermal changes [55].

Our evaluations of caiman home ranges (HR) and core areas (CA) were similar with previous records documented for broad-snouted caimans and other caiman species, ranging from < 0.001 to 1.98 km^2 for HR and from < 0.001 and 0.42 km^2 for CA [49, 47, 19, 71]. From all monitored individuals, male M4, the largest tracked specimen, had the lowest HR and CA estimated among males. Larger adults frequently display site-fidelity, patrolling their territories to protect resources and their access to females [4, 15, 59]. Consequently, smaller males must increase their movement and expand their areas of use to find unpatrolled territories to mate and forage [15]. Smaller males tracked in our study (M1, M2 and M3) generally occupied adjacent areas, with limited access to the forest areas in the north margin of the reservoir, which were primarily occupied by M4, and (Fig. 4).

Females exhibited a HR overlap four times greater than that of males, particularly in the northern forested sector of the reservoir (Fig. 4). Typically, multiple females cohabit within a dominant male's territory [34]. Additionally, females may move across different territories to enhance their chances of mating with multiple males, thereby improving offspring genetic diversity [31, 39, 61, 77], and consequently increasing the spatial overlap with other females.

Conclusions

In Tapacurá, caiman's movement patterns appear to be more influenced by the species' behavioral ecology, such as male territoriality and dominance and female nesting and parental care, than by habitat structure or abiotic variables. Since some of these ecological factors remain relatively stable in the study area during our study, future research should investigate these movement patterns in environments with significant variations in water flow (e.g., lotic systems) and seasonality (e.g., higher latitudes with greater temperature ranges). Additionally, future studies should account for individual differences in movement patterns, rather than focusing solely on the population level and include quantification of resources availability (e.g., fish abundance or primary productivity level) to predict their movements and habitat use.

Our study found that telemetry and capture methods complemented each other effectively, and future spatial ecology studies may benefit from using these two methods in association. Despite the benefits of telemetry, significant advancements in hardware and transmitter adjustments are needed to better suit caimans and study systems which are naturally obstructed by dense aquatic vegetation. In our study, all transmitters presented lifespans much shorter than expected, due to malfunction or detachment. Future studies should explore alternative technologies or attachment procedures (e.g., subcutaneous or intracoelomic attachment of acoustic tags) and more durable batteries to enhance the longevity and reliability of telemetry data.

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Author contributions
All authors contributed for manuscript conceptualization. PBMJ, JMSC and PIS wrote proposals for funding acquisition. PBMJ, JMSC and PIS participated in field surveys and developed research methods. PBMJ, BAS, MRH and PIS interpreted and analyzed the data. PBMJ prepared figures and tables. All authors participated in manuscript writing. All authors approved the final version.

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Availability of data and materials
The datasets analyzed in this study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
All procedures performed in this study followed were authorized by the Ethics Committee and Animal Use (CEUA) of Universidade Federal Rural de Pernambuco (license CEUA UFRPE #8606200622) and Brazilian Biodiversity Authorization and Information System (SISBIO) from the Chico Mendes Institute for Biodiversity Conservation (ICMBio) (license SISBIO #63030–4). Transmitter attachment procedures and clinical observations of caimans were conducted in a sterilized environment by a specialized veterinarian.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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