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GPS-telemetry as a method to assess nest attendance by a female broad-snouted caiman *Caiman latirostris*

Paulo B. Mascarenhas-Junior^{1,3}, Rafael S.L. Barboza^{2,3}, Malu Caminha³, Gabriela Lucena³, Carlos F. Rodrigues³, Pedro Ivo Simões¹ & Jozelia Maria de Sousa Correia³

¹Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

²Programa de Pós-Graduação em Biodiversidade, Universidade Federal Rural de Pernambuco, Recife, Pernambuco, Brazil

³Laboratório Interdisciplinar de Anfíbios e Répteis, Universidade Federal Rural de Pernambuco, Recife, Pernambuco, Brazil

Crocodylians exhibit parental care, guarding their eggs during incubation to ensure offspring survival. We present the first description of nest attendance of a wild broad-snouted caiman using GPS-telemetry. During the reproductive season of 2022, we tracked a 1.8-metre female in the Tapacurá reservoir, a water source bordered by Atlantic Forest remnants and human settlements in north-eastern Brazil. Telemetry data revealed that 75.8% of the female's position records were near the nest, suggesting parental care and nest protection. However, the female periodically returned to water. We observed no differences in proximity to the nest between day and night-time, which could be possibly related to different egg predators in the area foraging at different times of the day. Furthermore, the period when the nest was unattended could be associated with either feeding activities or avoidance of human presence. This research brings light on an important part of the reproductive behaviour of broad-snouted caimans in their natural environment, highlighting the importance of GPS-telemetry as a tool for monitoring reproductive behaviour of crocodylians, while contributing to understanding their biology under human-influenced settings.

Keywords: Atlantic Forest, crocodylian, movement, parental care, reproductive biology

Parental care is a common behaviour observed in animals and is characterised by parents investing effort in order to enhance offspring survival and growth, sometimes at the cost of their own survival or health (Smiseth et al., 2012). In oviparous species, adults have developed specific strategies for attending their nests and protecting the eggs. This often benefits maintenance of the whole population, for example, by allowing egg maturation and juvenile survival, contributing to a higher number of reproductive adults (Klug & Bonsall, 2010). Crocodylians are egg-laying organisms, distinguished from most reptiles by consistently exhibiting parental care (Grigg & Kirshner,

2015). They typically lay eggs in excavated holes in the ground or in mounds of vegetation, with females often guarding their nests during incubation period (Thorbjarnarson, 1996). Their main behaviours while attending the nest include repeatedly approaching the nest, positioning themselves near or above it, directly attacking intruders and, in some cases, retreating to the water for self-protection (Kushlan & Kushlan, 1980). Females may also repair their nests after disturbance by predators (Charruau & Hénaut, 2012; Platt et al., 2024).

Several factors affect nest attendance in crocodylians, in addition to their natural behaviour. For instance, species that nest in holes excavated in the ground tend to be less territorial and less prone to defend the nest when compared to mound nesters, as the former possibly build communal nests more frequently (Murray et al., 2020). Another factor influencing parental care is sunlight. During daylight hours, females may also use the area over or near the nest for basking or resting (Grigg & Kirshner, 2015). Nest attendance during night-time has also been widely documented, and generally attributed to milder temperatures, protection of eggs against nocturnal predators, or increased activity after daytime basking (Balaguera-Reina et al., 2015; Campos et al., 2016; Combrink et al., 2017). The distance of water bodies also plays a role in female nest attendance, as they may return to the water for foraging more frequently when the nest is located near a water source, or experience starvation when nests are located farther from water bodies (Villamarín et al., 2011). Additionally, human disturbance including hunting, habitat loss or nest manipulation can negatively affect female attendance (Kushlan & Mazzotti, 1989; Simoncini et al., 2016; Mazzotti et al., 2022).

The broad-snouted caiman *Caiman latirostris* (Daudin, 1801), is a widely distributed South American crocodylian species, ranging from Argentina to north-eastern Brazil. Most of its global population is distributed within Brazilian territory (Coutinho et al., 2013), threatened by urbanisation, hunting and pollution (Yves et al., 2018; Mascarenhas-Junior et al., 2021;

Correspondence: Paulo Braga Mascarenhas-Junior (paulo.bragamascarenhas@ufpe.br)

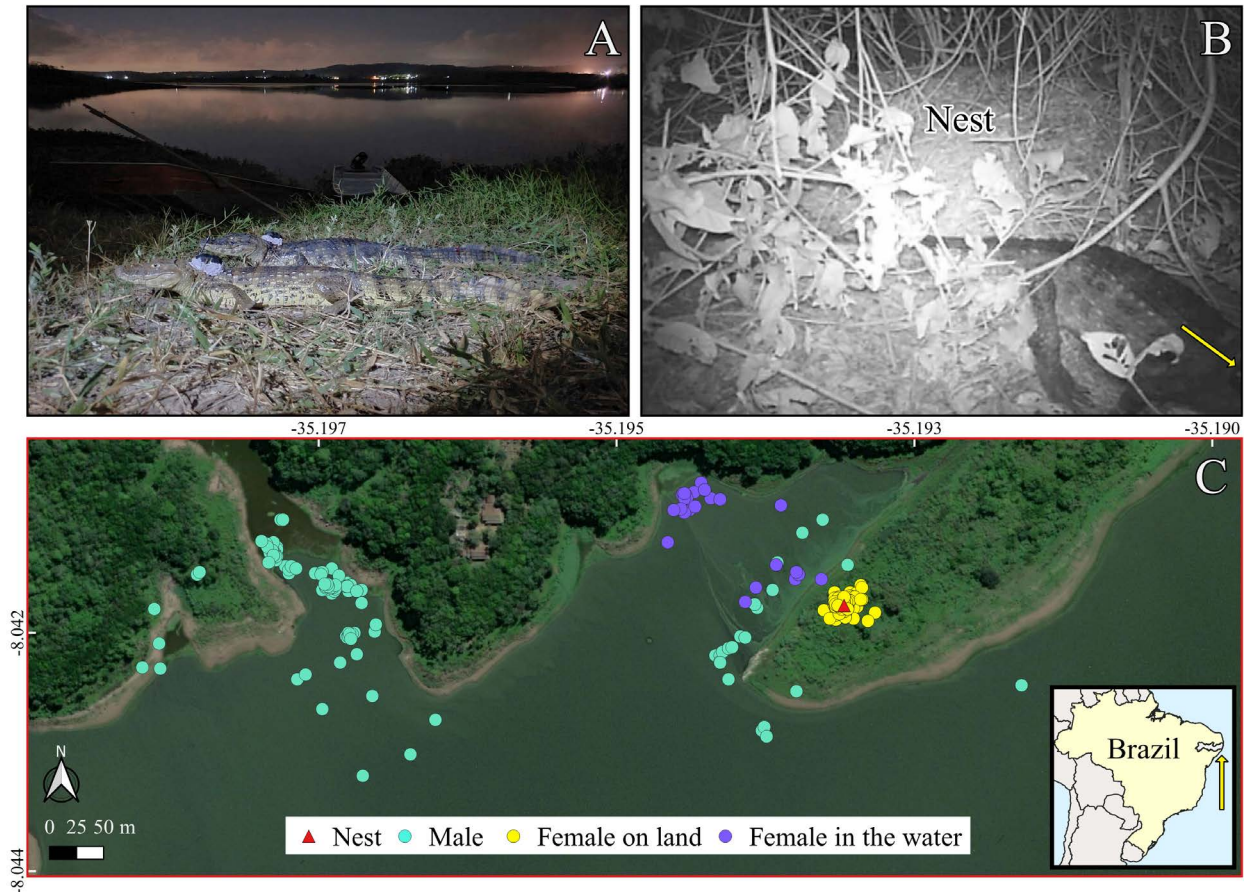


Figure 1. **A.** Deployment of GPS-telemetry transmitters on adult male (front) and female (behind) broad-snouted caimans *Caiman latirostris* in the Tapacurá Reservoir, São Lourenço da Mata City, Pernambuco, Brazil. **B.** Camera trap image with evidence of GPS-telemetry tracked female situated above a nest mound, with a yellow arrow indicating the transmitter attached to her neck. **C.** Geographic positions of GPS-telemetry tracked male (turquoise dots), female on land (yellow dots) and in the water (purple dots). Female's geographic position presented represents the period between the first access to the land (6 January 2022) until transmitter detachment (15 March 2022), and male's geographic position represents full monitoring (25 November 21 to 4 July 2022). Red triangle indicate nest geographic position.

Santos et al., 2021). Adults reach an average length of 2.5 metres (Siroski et al., 2020), and although their reproductive biology has been well studied in captivity (Verdade & Sarkis, 1998; Verdade, 2001; Bassetti et al., 2014), information on reproductive behaviour from Brazilian wild populations is relatively scarce. Studies on reproductive ecology of wild crocodylians traditionally utilise camera traps to investigate parental care, but information is limited to sensor and image capture range limit (Caravaggi et al., 2017). The employment of telemetry techniques could be an ally to improve data collection robustness (Campos, 2019; Mascarenhas-Junior et al., 2023). In this sense, we present novel information on nest attendance by a wild female broad-snouted caiman, revealed by GPS-telemetry data. This study is part of a systematic monitoring program aimed at unveiling critical aspects of broad-snouted caimans' reproductive ecology in the Atlantic Forest of Brazil (Barboza et al., 2021).

From July 2021 to July 2022, we started a telemetry-tracking program focused on adult caimans inhabiting the Tapacurá Reservoir (hereafter 'Tapacurá'), a lentic water body formed by damming of the Tapacurá River, in São Lourenço da Mata, State of Pernambuco,

Brazil (8.043856 °S, 35.195710 °W). The surrounding landscape comprises fragments of native Atlantic Forest and open fields where local communities practice agriculture and ranching. On 25 November 2021, we fitted GPS transmitters (Nortronic, Brazil) to an adult female caiman measuring 89 centimetres of snout-vent length (SVL) (24.5 kg) and an adult male caiman measuring 101 centimetres of SVL (> 40.0 kg) (Fig. 1A). Transmitters weighed less than 2% of individuals body mass, to avoid interference in their natural behaviours (Mascarenhas-Junior et al., 2023). The attachment procedure followed the protocol proposed by Brien et al. (2008). We programmed the transmitters to collect and transmit geographic co-ordinates by a flexible antenna at every six-hour interval, and both caimans were subsequently released at the same location where they were originally captured, 24 hours after attachment procedures. Preliminary tests indicated that the transmitter's error range was within a radius of five metres.

During the monitoring period, we observed a spatial and temporal overlap in the geographic position data for both individuals on 4 January 2022, the only spatial overlap between these two individuals during

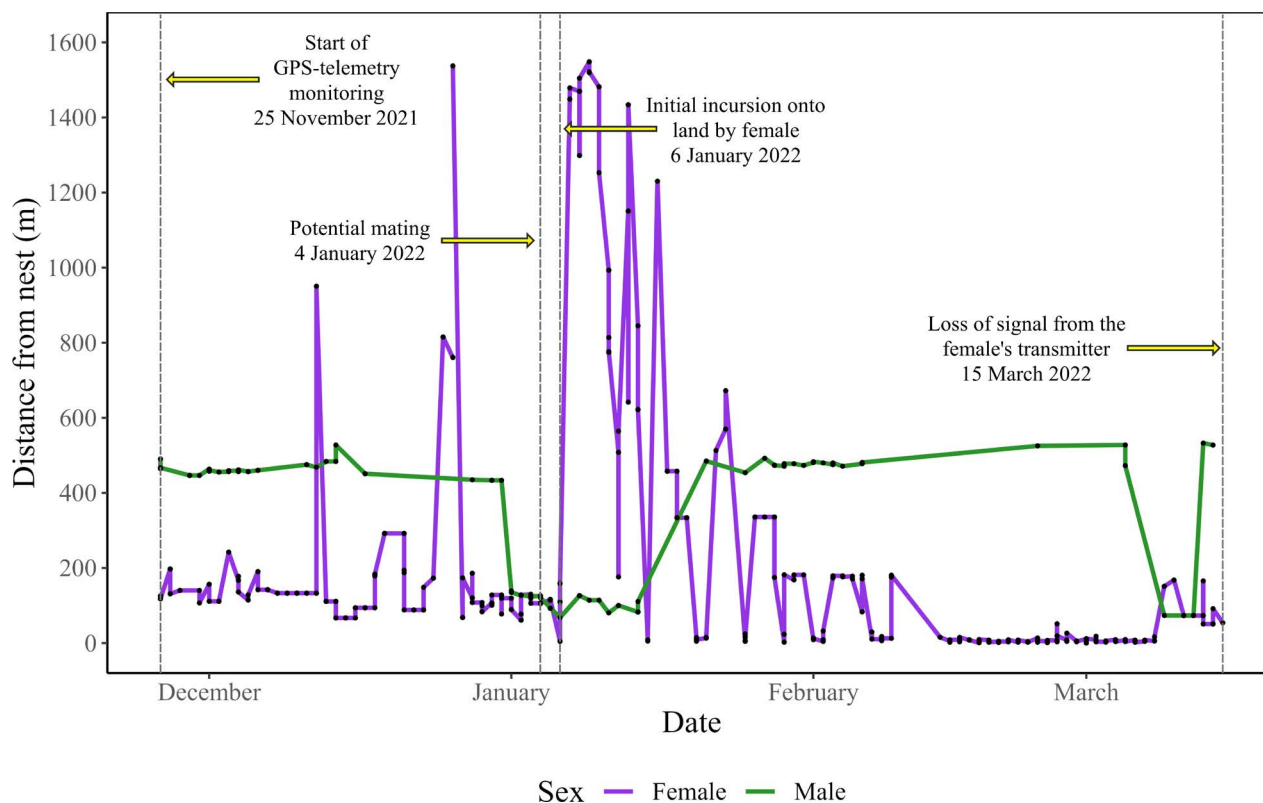


Figure 2. Daily distance from the nest of adult male (green line) and female (purple line) broad-snouted caimans *Caiman latirostris* based on GPS-telemetry monitoring between 25 November 2021 and 15 March 2022 in the Tapacurá Reservoir, São Lourenço da Mata City, Pernambuco, Brazil. Important events are highlighted by dark grey dashed lines: Potential mating between male and female (4 January 2022); Female's initial visit to the nesting site on land (January 6, 2022); Termination of female monitoring due to transmitter signal loss (15 March 2022).

monitoring, suggesting a potential mating. From 6 January 2022, GPS position data indicated that the female caiman started making incursions onto land. These were made in a small stretch of Tapacurá, in an area covered by grass and shrub vegetation. On 8 March 2022 we visited the same co-ordinates and found the female in the shrub vegetation, 4.7 m distant from a newly constructed nest. The nest was built under an emerging tree, protected from direct solar radiation, composed by a combination of branches, leaf litter and ground material, with 2.75 m of height and 56 metres distance from the water. We opened the nest and verified that the opaque band filled about 70% of egg's size, leading us to suspect that oviposition occurred about 30 days earlier (lungman et al., 2008). In the same day (8 March 2022), we installed a camera trap two metres from the nest, and directed at it. We used photos obtained from the next weeks to confirm nest attendance by the female (Fig. 1B).

We GPS-tracked the female's movements over a span of 110 days, obtaining 207 geographic positions from 25 November 2021 to 15 March 2022. Over the 42 days preceding the initiation of female nesting activities on the land, from 25 November 2021 to 5 January 2022, we obtained 81 geographic positions. Notably, we documented all these records (100%) within the water. The average $\pm$ SD distance of the female from the chosen nest construction site was 203 ± 272 metres, ranging from 61 to 1,629 metres (Fig. 2). In the remaining 68

days, from 6 January 2022 to 15 March 2022, after the female starting to access the land, the average distance of female from the nest was 36 ± 57 metres, ranging from 0 metres to 182 metres (Fig. 2). During this time, we obtained a total of 126 valid geographic position records. Among these, 75.8% were located on land, in proximity with the nest (Fig. 1C), averaging 8 ± 5 metres (Fig. 2). The remaining 24.2% records occurred in the water (Fig. 1C), averaging 128 ± 53 metres, with 182 metres as maximum distance (Fig. 2). We confirmed by a Wilcoxon test that the female remained closer to the nest upon initiating access to the land compared to the period before starting to visit the nesting site ($W = 1,547$, $p < 0.001$). We were also able to track the male for 221 days until 4 July 2022, when we lost transmitter signal. The male remained in the water during all of the monitoring period (100% of geographic positions recorded) but continued patrolling the breeding site even after mating (Fig. 1C). Prior to mating, the male remained 414 ± 124 metres distant from the constructed nest, which slightly increased to 432 ± 168 metres after mating (Wilcoxon test: $W = 3,386$, $p < 0.001$; Fig. 2).

Our data revealed that 39.3% of the land-based geographic positions occurred during daylight hours, while 60.7% occurred during night-time. Geographic positions in the water were almost evenly distributed between daytime (45.6% of records) and night-time (54.4%). There was no significant difference in distance from the nest during daytime (44 ± 65 metres) and

night-time (30 ± 51 metres) (Wilcoxon's test: $W = 3,926$, $p = 0.912$). On five distinct days, the female alternated between water and land in different periods of the day. During the monitoring, she went onto land eight times, typically staying for a duration of 5 ± 8 days, with a maximum consecutive stretch of 23 days, between 14 February 2022 and 8 March 2022. In the water, the female spent an average of 2 ± 2 days, with a maximum of six consecutive days, observed from 8 March 2022 to 15 March 2022. The transmitter ceased operation on 15 March 2022 due to detachment from female's neck. After detachment, the female continued nest attendance in the land, but eggs failed to hatch due to predation by black-and-white tegu *Salvator merianae*, confirmed by camera trap data. The last record of the female on the nest was on 27 March 2022, 80 days after she initiated accessing the land. Raw data obtained from telemetry is available in the Supplementary Material.

The female altered her movement patterns upon accessing the land for the first time. Prior to starting movements towards the nesting site, she maintained farther from the land, remaining exclusively in the water. Female crocodylians typically relocate to deeper waters for mating but retract to smaller ponds or shallow areas after copulation (Joanen & McNease, 1989). Our tracked female first accessed the nesting site two days after the potential mating. We suspect that copulation occurred during the period of spatial overlap between the tracked individuals, as no additional records have been documented since the beginning of study (25 November 2021). Nevertheless, it remains plausible that the female was fertilised before this encounter. The duration between copulation and the initiation of nesting activities can vary, occurring either immediately or after a few days, as observed in wild American alligators (Lance, 1989), or even preceding mating, as documented in captive Philippine crocodiles *Crocodylus mindorensis* (Schneider et al., 2014). However, the interval between copulation and oviposition may extend over a more prolonged period. Studies on wild Nile crocodiles and spectacled caimans suggest that egg laying typically occurs a month after mating (Kofron, 1990; Thorbjarnarson, 1994). We presumed our telemetry monitoring occurred during the phases of nest construction and attendance, extending until approximately halfway through the incubation period. This assumption was based on the understanding that the incubation period for broad-snouted caimans spans about two months (Simoncini et al., 2019; Barboza et al., 2021), and the egg's embryologic stage based on opaque band suggested one month of oviposition. Hence, our tracked female caiman probably laid her eggs in either the first or second week of February.

Since nesting, and throughout monitoring, the female exhibited a marked preference for terrestrial areas near the nesting site. This behaviour is commonly observed among crocodylians, when breeders typically stay close to their nests for defence (Murray et al., 2020). Proximity to the nest may reduce predation attempts on the eggs, as egg predators refrain from

foraging when females are near (Hunt & Ogden, 1991; Eversole & Henke, 2022). In Tapacurá, several species have been identified as potential threats to caiman eggs and hatchlings, such as *S. merianae* and the South American coati *Nasua nasua*, with records of females actively repelling these animals from their nesting areas (Barboza et al., 2021). The presence of female broad-snouted caimans near their nests has been associated with lower predation rates and offspring survival (Simoncini et al., 2016), similar to observations made on black caimans *Melanosuchus niger* in the Brazilian Amazon (Torralvo et al., 2017). However, outcomes of nest attendance by female crocodylians are variable, and the presence of females did not enhance eggs survival in other crocodylian species and areas (Vergne & Mathevon, 2008; Platt et al., 2021), suggesting they may be species- or site-specific. Moreover, during nest attendance, females have limited opportunities to feed, potentially reducing their body condition and overall nutritional conditions (Barão-Nóbrega et al., 2018). Consequently, some individuals occasionally return to the water to forage (Barão-Nóbrega et al., 2016). While we were unable to recapture the tracked female to confirm the body score, we suspect that regular access to water likely contributed to the maintaining of nutritional condition during nest attendance, as observed in other adult females captured in Tapacurá (unpublished data). Alternatively, another hypothesis for females moving into the water might be associated with human disturbances, particularly in wary populations (Ron et al., 1998). Crocodylians likely learn from previous negative experiences, such as hunting attempts and fishing, activities that are common in Tapacurá (Mascarenhas-Junior et al., 2020). In such situations, females may leave their nests unattended, as widely recorded in our target population (Barboza et al., 2021; Rodrigues et al., 2021).

Nest attendance occurred both during daylight and at night. Studies on American alligators *Alligator mississippiensis*, American crocodiles *Crocodylus acutus* and smooth-fronted caimans *Paleosuchus trigonatus* suggest that females may visit their nests at night for protecting eggs against nocturnal predators (Charruau & Hénaut, 2012; Balaguera-Reina et al., 2015; Campos et al., 2016; Merchant et al., 2018). However, primary predators of caiman's eggs in Tapacurá present diurnal foraging habits (Emmons & Helgen, 2016; Srbek-Araujo et al., 2020), indicating that daytime nest attendance could also serve as a protective measure. In contexts with multiple predators with varying daily foraging behaviours, crocodylians may adjust their diel visits to the nest (González-Desales et al., 2023). Furthermore, female caimans may also visit their nests at night because human disturbance is lower during this period (Charruau & Hénaut, 2012). The presence of females near the nest during daylight hours may also be associated with basking or resting, a behaviour observed in other crocodylian species during the nesting care, such as the Nile crocodile *Crocodylus niloticus* and the spectacled caiman (Cott, 1971; Marioni et al., 2007). Crocodylians

often return to the top of the nest during the night to increase protection and remain near the nest in nearby vegetation-covered areas for protection from intense sunlight during daytime (Combrink et al., 2016), which aligns with our findings.

GPS-telemetry revealed that the breeder female spent most of the monitoring time near the nest, especially after oviposition. We suspect the infrequent access to the water was likely for feeding or to avoid human disturbance. This is the first description of movements of a broad-snouted caiman nesting female, providing valuable insights into the species' reproductive biology. We assumed that our tracked individual was an experienced breeder, considering that caimans typically attain sexual maturity with a SVL of 75 cm in Tapacurá (Barboza et al., 2021). Further studies considering different sizes of reproductive females should clarify the generality of the movement patterns described here and allow a better understanding of broad-snouted caiman's reproductive ecology. The utilisation of integrated methods, such as camera trap and telemetry, must be imperative to investigate nesting behaviour in broad-snouted caimans, and effectively addresses gaps that are frequently overlooked by traditional research methods.

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Author contributions

Research conceptualisation: PBMJ. Data collection: All authors. Data analysis: PBMJ. Data interpretation: PBMJ, RSLB, PIS, JC. Writing: All authors. Formatting: PBMJ, MC, GL, CFR.

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