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PAULO BRAGA MASCARENHAS JÚNIOR

**PADRÕES DE ECOLOGIA POPULACIONAL DE *Caiman latirostris*  
(ALLIGATORIDAE) EM AMBIENTE LÊNTICO COM FRAGMENTOS DE MATA  
ATLÂNTICA, NORDESTE DO BRASIL**

Recife  
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Tese apresentada ao Programa de Pós-Graduação em Biologia Animal da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de doutor em Biologia Animal. Área de concentração: Biologia Animal

Orientador (a): Pedro Ivo Simões

Coorientador (a): Jozélia Maria de Sousa Correia

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Ao meu pai (*in memoriam*). Chegamos onde sonhávamos!  
À minha família, que tanto me apoia e dá forças,

Dedico.

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“Houve um tempo, num passado não muito distante, que o número de especialistas em crocodilianos brasileiros era menor que o número de espécies identificadas para o país – seis espécies! Felizmente, este tempo ficou no passado [...]”. Coutinho, 2021, p. 22).

## RESUMO

O estudo da ecologia de populações animais é fundamental para entender sua dinâmica demográfica e suas interações com elementos do hábitat circundante. Fatores como o clima, atividades antrópicas e características das paisagens podem moldar a distribuição, o tamanho e a estrutura das populações. Crocodilianos são predadores semi-aquáticos longevos e seu monitoramento em longo prazo têm permitido a elaboração de hipóteses sobre fatores que afetam sua distribuição e o planejamento de estratégias de conservação. Nesta tese, estudei a ecologia espaço-temporal do jacaré-de-papo-amarelo (*Caiman latirostris*) em um reservatório artificial formado pelo barramento do rio Tapacurá, no município de São Lourenço da Mata, Pernambuco, Brasil. A tese está dividida em quatro capítulos: O primeiro consiste em uma revisão bibliográfica de estudos envolvendo o rastreamento de crocodilianos por meio de telemetria. A maioria dos estudos concentra-se nos EUA e Austrália, com as espécies *Alligator mississippiensis* e *Crocodylus porosus*. Dentre os métodos mais utilizados nos estudos, a tecnologia VHF foi a mais utilizada, seguida da GPS/Satélite e acústica. No segundo capítulo, avalio os fatores que influenciam a detecção e distribuição dos jacarés do reservatório durante censos baseados em contagens noturnas. A temperatura da água, umidade relativa do ar, precipitação diária, percentual de nuvens e a profundidade local da água foram variáveis que afetaram a detecção dos jacarés. Além disso, os jacarés encontravam-se predominantemente no curso do rio e próximos aos fragmentos de floresta, associados à presença de redes de pesca. Também identificamos um aumento no número de indivíduos adultos detectados ao longo do estudo. No terceiro capítulo, descrevo o padrão sazonal e espacial da atividade pesqueira no reservatório e avalio sua influência na distribuição espacial dos jacarés. A pesca é uma atividade anual em Tapacurá, com crescimento significativo após o início da pandemia de COVID-19. Há uma correlação entre a distribuição dos jacarés e das redes de pesca no reservatório, principalmente nas áreas margeadas por floresta. Não há diferença na proporção de emalhe acidental entre diferentes classes etárias. No quarto capítulo estudei os padrões de movimentação e seleção de hábitat, e a influência do sexo dos indivíduos sobre estes padrões, utilizando dados de captura e rastreamento por telemetria via GPS. A população de jacarés em Tapacurá é formada em sua maioria por machos, que acessam áreas mais distantes da floresta no período chuvoso, quando apresentam

maiores escores corporais. A movimentação dos jacarés adultos foi principalmente noturna, com áreas de uso geralmente menores do que um quilômetro quadrado. Os manuscritos aqui apresentados trazem de forma pioneira informações robustas sobre a ecologia de populações do jacaré-de-papo-amarelo, úteis nas tomadas de decisão conservacionistas e no manejo da espécie e seus habitats.

**Palavras-chave:** conservação; contagem noturna; crocodilianos; distribuição espaço-temporal; pesca artesanal; telemetria.

## ABSTRACT

Understanding animal population ecology is crucial for unveiling their demographic dynamics and interactions with elements of the surrounding habitat. Factors such as climate, anthropogenic activities, and landscape characteristics can shape the distribution, size, and structure of populations. Crocodylians are long-lived semi-aquatic predators, and long-term monitoring has allowed hypotheses formulation about factors affecting their distribution and the planning of conservation strategies. In this dissertation, I investigated the spatiotemporal ecology of the broad-snouted caiman (*Caiman latirostris*) in an artificial reservoir formed by the damming of the Tapacurá River in São Lourenço da Mata, Pernambuco, Brazil. The dissertation is divided into four chapters: The first consists of a literature review of studies involving crocodylian tracking through telemetry techniques. Most studies focus on the USA and Australia, especially in the species *Alligator mississippiensis* and *Crocodylus porosus*. VHF technology was the most used technology, followed by GPS/Satellite and acoustic methods. In the second chapter, I evaluate the factors influencing the detection and distribution of caimans in the reservoir during night counts. Water temperature, air humidity, daily rain, cloud cover percentage, and water depth were variables that affected caiman detection. Additionally, caimans were preferentially found in the river course and near forest fragments, associated with the presence of fishing nets. We also identified an increase in the number of adult individuals detected throughout the study. In the third chapter, I describe the seasonal and spatial pattern of fishing activity in the reservoir and assess its influence on the spatial distribution of caimans. Fishing is a year-round activity in Tapacurá, with significant growth after the onset of the COVID-19 pandemic. There is a positive correlation between the distribution of caimans and fishing nets in the reservoir, especially in areas bordered by forest. There is no difference in the accidental entanglement ratio between different age classes. In the fourth chapter, I studied caiman's movement and habitat selection patterns, and the influence of individuals' sex on these patterns, using capture and telemetry tracking data via GPS. The population in Tapacurá is mostly composed by male individuals, which accessed areas farther from forest fragments during the wet season, period when they reached higher body scores. The movement of adult caimans was mainly nocturnal, with home ranges generally smaller than one square kilometer. The manuscripts presented here provide pioneering and robust information about the

ecology of broad-snouted caiman populations, useful in conservation decision-making and the management of the species and its habitats.

**Keywords:** conservation; spotlight counts; crocodylians; spatiotemporal distribution; artisanal fishing; telemetry.

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**Supplementary file 5** – Model selection results of habitat features predicting *Caiman latirostris* movements (m) 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  $\Delta$  Aikake’s Information Criteria (AICC) distance  $< 2$  are presented. All covariates were scaled (mean = 0, Standard error = 1). Rv: Reservoir volume; Rf: Daily rainfall; T: Water surface temperature. np: Number of parameters, logLik: Log likelihood of the model; AICc: Aikake’s Information Criteria;  $\Delta$ AICC: Distance from the best model; Weight: Weight of each model in the models with  $\Delta$ AICC  $< 2$  (values from 0 to 1).

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## 1 INTRODUÇÃO

O estudo da ecologia espaço-temporal de populações selvagens oferece ferramentas importantes para a conservação da biodiversidade e a compreensão dos processos biológicos. Ao avaliar a distribuição das espécies, torna-se possível identificar seus habitats preferenciais, entender os ciclos sazonais e estimar tendências nos índices de abundância (McGarigal *et al.*, 2016; Moreno-Fernández *et al.*, 2016). Essas informações são essenciais para guiar a gestão sustentável dos recursos naturais e na definição de áreas prioritárias para a conservação das espécies, bem como a proteção de seus habitats (Fletcher; Fortin, 2018).

Os crocodilianos são predadores semi-aquáticos importantes na manutenção dos ecossistemas, potencialmente regulando as teias tróficas, facilitando o transporte de nutrientes entre diferentes habitats e atuando como engenheiros ambientais (Somaweera *et al.*, 2020; Strickland *et al.* 2023). No entanto, mais de 60% das espécies encontram-se ameaçadas devido a fatores antrópicos como perda de habitats, mudanças climáticas, caça e poluição (Griffith *et al.*, 2022; Lourenço-de-Moraes *et al.*, 2023). Estudos sistemáticos vêm buscando desvendar como as populações respondem a essas alterações ou às dinâmicas ambientais naturais, avaliando tendências na distribuição e na estrutura populacional, incluindo aspectos sexuais e etários (Nifong; Silliman, 2017; Pereira; Portelinha; Malvasio, 2022; Strickland; Vilella; Flynt, 2018). Para isso, são empregados métodos como contagens noturnas com feixe de luz concentrado (Barão-Nóbrega; González-Jaurégui; Jehle, 2022), captura, marcação e recaptura de indivíduos (Balaguera-Reina *et al.*, 2018), e rastreamento por telemetria *Very High Frequency* (VHF), satélite ou acústica (Baker *et al.*, 2022; Marioni *et al.*, 2022; Strickland *et al.*, 2021).

O jacaré-de-papo-amarelo *Caiman latirostris* (Daudin, 1801) é uma espécie de crocodiliano de médio porte que atinge em média de 2,5 metros de comprimento, distribuído na América do Sul entre os paralelos de 8° S a 22° S e 5° O a 34° O (Siroski *et al.*, 2020). São predadores oportunistas e generalistas, com preferência por habitats lânticos, como açudes, lagos e planícies alagadas (Filogonio *et al.*, 2010). Aproximadamente 70% de sua população global está concentrada no território brasileiro, sobretudo em áreas com alta densidade de

populações humanas (Coutinho *et al.*, 2013). Nesses ambientes, o jacaré-de-papo-amarelo está sujeito à severas ameaças como urbanização, caça e fragmentação de seus habitats (Mascarenhas-Junior *et al.*, 2021; Yves *et al.*, 2018; Zucoloto *et al.*, 2021), com populações apresentando índices de abundância menores que um indivíduo por quilômetro (Fusco-Costa; Castellani; Tomás, 2008; Mascarenhas-Júnior *et al.*, 2020; Passos; Coutinho; Young, 2014). No entanto, a espécie é atualmente classificada como "Pouco Preocupante" (LC) em relação ao nível de ameaça de extinção global, de acordo com os critérios estabelecidos pela IUCN - União Internacional para a Conservação da Natureza (Siroski *et al.*, 2020). Além disso, as populações brasileiras foram recentemente incluídas no Apêndice 2 da CITES - Convenção sobre o Comércio Internacional de Espécies da Fauna e da Flora Selvagens Ameaçadas de Extinção, o que permite o manejo das populações selvagens sob estritas regulamentações (CITES, 2023).

Dentre os domínios fitogeográficos nos quais o jacaré-de-papo-amarelo se distribui, destaca-se a Mata Atlântica. Esta região abrange a segunda maior floresta úmida da América do Sul, estendendo-se por uma área de mais de um milhão de km<sup>2</sup> (Souza; Wagner; Vasconcellos, 2012). Porém, ao longo dos séculos, o desflorestamento contínuo reduziu a cobertura original da Mata Atlântica em cerca de 90%, restando apenas pequenos fragmentos pouco conectados (Ribeiro *et al.*, 2009). Ainda assim, a Mata Atlântica é reconhecida como um *hotspot* de diversidade global, abrigando cerca de 3% da diversidade de tetrápodes do mundo, por exemplo (Figueiredo *et al.*, 2021).

Nas últimas décadas, o crescimento das populações urbanas tem aumentado a demanda por recursos, levando ao represamento de vários rios na Mata Atlântica para suprir a demanda por água (Padial *et al.*, 2021). As modificações nos cursos d'água têm impactado a hidrologia desses ambientes, alterando as características físico-químicas da paisagem, o que pode resultar em processos de disrupção ecossistêmica (Vörösmarty; Sahagian, 2000). Redução nos processos migratórios, diminuição de áreas de reprodução, aumento na competição por recursos e introdução de espécies exóticas são algumas das consequências do represamento (Akama, 2017; Orr *et al.*, 2012). Nestes ambientes, também, atividades antrópicas como a pesca artesanal vêm

crescendo nos últimos anos (Stokes *et al.*, 2020), o que potencializa o conflito entre humanos e jacarés (Mascarenhas-Júnior *et al.*, 2018; Pooley *et al.*, 2020).

O jacaré-de-papo-amarelo, assim como outras espécies de crocodilianos, são animais longevos, com expectativa de vida de várias décadas (Stokes *et al.*, 2008). Alterações nos padrões de distribuição e estrutura populacional podem levar anos para serem detectadas, o que demanda esforços em longo prazo para obter resultados sólidos sobre sua distribuição espaço-temporal. Nesse contexto, realizei um dos mais extensos monitoramentos de uma população natural de jacaré-de-papo-amarelo no Brasil, com o objetivo de compreender aspectos da distribuição, movimentação e ocupação de habitats pelos jacarés no reservatório de Tapacurá, um importante manancial na Mata Atlântica do nordeste do Brasil.

## 2 OBJETIVOS

### 2.1 Objetivo geral

Investigar aspectos da distribuição e dinâmicas populacionais de *C. latirostris* no Reservatório de Tapacurá (São Lourenço da Mata - PE, Brasil), um ambiente lêntico contendo fragmentos de Mata Atlântica no Nordeste do Brasil, associando os padrões observados a fatores ambientais e antrópicos.

### 2.2 Objetivos específicos

- a) Estimar o tamanho da população de jacarés no reservatório de Tapacurá e a sua tendência ao longo do tempo.
- b) Determinar a estrutura (etária e sexual) da população de jacarés no reservatório de Tapacurá.
- c) Avaliar se fatores abióticos (temperatura da água, umidade relativa do ar; profundidade; luminosidade lunar, percentual de nuvens, precipitação diária e volume do reservatório) afetam a distribuição e detectabilidade dos jacarés;
- d) Avaliar se fatores ambientais do hábitat (vegetação aquática, fragmentos florestais, áreas lênticas ou lólicas, pesca e moradias) afetam a distribuição e detectabilidade dos jacarés;

- d) Testar se os padrões de distribuição estão relacionados à atividade pesqueira;
- f) Descrever padrões de movimentação e área de uso de indivíduos adultos;
- g) Evidenciar a importância de proteção dos habitats naturais na manutenção da população de jacarés na Mata Atlântica.

### 3 ESTRUTURA DA TESE E HIPÓTESES

No primeiro capítulo da tese, conduzi uma revisão sistemática da literatura sobre a aplicação da telemetria no rastreamento de crocodilianos. Nesta revisão, explorei os aspectos históricos relacionados ao uso das diversas tecnologias disponíveis, como VHF, GPS/Satélite e acústica, além de destacar as espécies e os países com maior representatividade nos estudos publicados até então. Abordei também os vieses e as limitações do conhecimento existente. Além disso, examinei a importância da adoção de protocolos adequados para a fixação dos transmissores, enfatizando a seleção do método mais apropriado com base nas questões de pesquisa e nos recursos financeiros disponíveis. Este estudo foi publicado no periódico *Animal Biotelemetry* (Mascarenhas-Junior *et al.*, 2023).

No segundo capítulo, meu objetivo foi investigar como variáveis climáticas, vegetação aquática e tipos de habitat (como regime lótico, lântico, presença de fragmentos de floresta e atividades de pesca) influenciam a detecção de jacarés e se houve alterações no tamanho da população ao longo dos últimos anos. Eu examinei as hipóteses de que variáveis abióticas e de habitat devem afetar a distribuição dos jacarés, uma vez que são organismos ectotérmicos, cuja fisiologia e comportamento são influenciados pela sazonalidade e pela disponibilidade de recursos (ex: proteção e abundância de alimento), além das experiências negativas com humanos em áreas historicamente impactadas (Da Silveira *et al.*, 2008; Portelinha *et al.*, 2022; Aguilera *et al.*, 2008). Além disso, eu antecipei que a população seria estruturada principalmente por indivíduos imaturos, condição característica de populações historicamente sujeitas à pressão de caça (Pereira *et al.*, 2022).

No terceiro capítulo, busquei correlacionar a distribuição da pesca em Tapacurá com a presença de jacarés no reservatório. Espero encontrar mais jacarés em áreas com maior atividade pesqueira, já que crocodilianos são oportunistas e podem ser atraídos por peixes emalhados nas redes de pesca

(Pooley et al., 2021). Adicionalmente, pescadores e jacarés podem selecionar áreas com maior abundância de peixes, o que potencializa a correlação espacial positiva entre a atividade de pesca e os jacarés (Wallace et al., 2011).

No terceiro capítulo, busquei estabelecer uma correlação entre a distribuição da atividade de pesca em Tapacurá e a presença de jacarés no reservatório. Minha hipótese é de que os jacarés devem ser mais encontrados em áreas com atividades pesqueira mais intensa, considerando que os crocodilianos são animais oportunistas e podem ser atraídos por peixes capturados nas redes de pesca (Pooley et al., 2021). Além disso, tanto pescadores quanto jacarés podem preferir áreas com uma maior abundância de peixes (Wallace et al., 2011), o que pode fortalecer a correlação espacial positiva entre a atividade de pesca e a presença de jacarés.

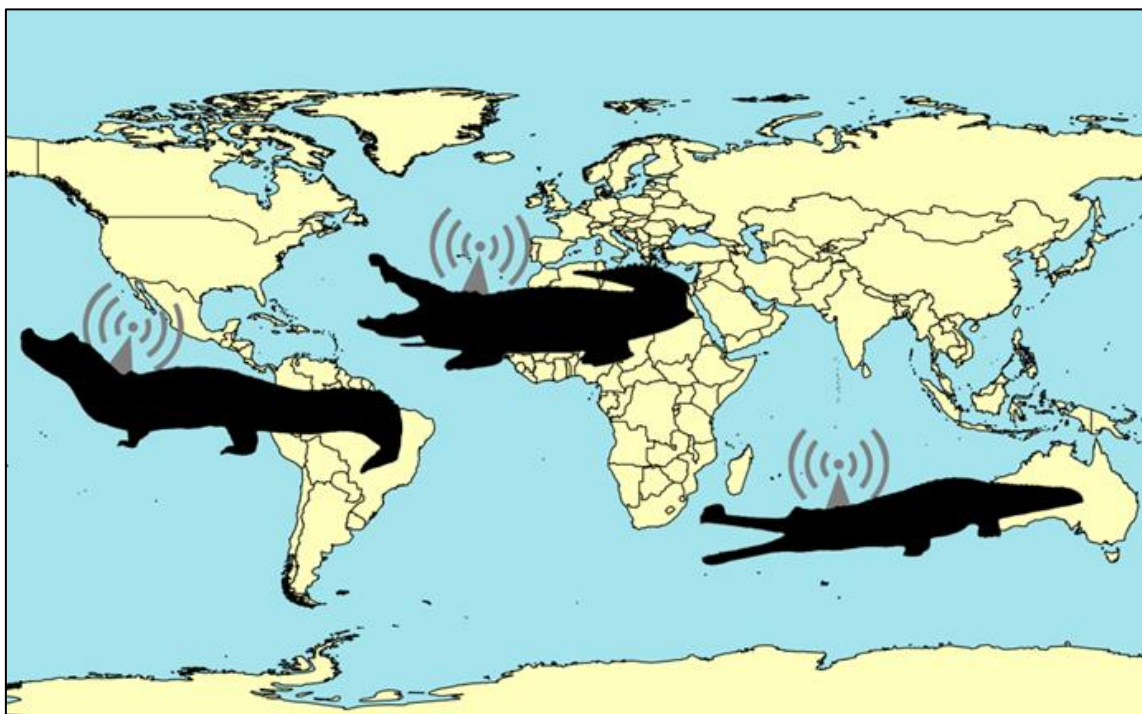
No quarto capítulo, avaliei a estrutura sexual da população de jacarés em Tapacurá e como a sazonalidade e variáveis abióticas podem influenciar a escolha de habitats, padrões de movimentação e área de uso. Espero que a população de jacarés seja formada majoritariamente formada por indivíduos machos em comparação com as fêmeas, a partir da hipótese de que o sexo de *C. latirostris* é determinado pela temperatura de incubação e a proporção de machos formados por ninho é maior sob temperaturas de incubação mais elevadas (Simoncini et al., 2019). Como em Tapacurá o período reprodutivo está relacionado aos meses mais quentes (Barboza et al., 2021), espero um maior número de machos nas ninhadas, refletindo na razão sexual da população. Além disso, acredito que os machos estejam espacialmente segregados no reservatório, já que são territoriais e tendem a proteger haréns formados por fêmeas e controlar acesso à áreas de mais recursos alimentares (Drews et al., 1990). Neste sentido, espero que indivíduos machos apresentem maior mobilidade espacial do que as fêmeas (Moreno-Arias; Ardila-Robayo, 2020). Adicionalmente, acredito que as áreas de uso sejam relativamente pequenas, o que corrobora com o descrito até então para outras espécies de jacarés na América do Sul (Quintana et al., 2020; Marioni et al., 2023) e a pouca capacidade de dispersão observada em jacarés-de-papo-amarelo (Zucolotto et al., 2021).

No quarto capítulo, avaliei a estrutura sexual da população de jacarés em Tapacurá e investiguei como a sazonalidade e variáveis abióticas podem

influenciar a escolha de habitats, padrões de movimentação e área de uso desses animais. Minha expectativa é que a população de jacarés seja majoritariamente composta por machos em comparação com as fêmeas, já que o sexo em *C. latirostris* é determinado pela temperatura de incubação, resultando em uma maior proporção de machos em ninhos incubados em temperaturas mais elevadas (Simoncini *et al.*, 2019). Considerando que o período reprodutivo em Tapacurá está associado aos meses mais quentes (Barboza *et al.*, 2021), antecipo uma predominância de machos nas ninhadas, o que provavelmente se refletirá na razão sexual da população. Além disso, acredito que os machos estejam espacialmente segregados no reservatório, pois são territoriais e tendem a proteger haréns formados por fêmeas, controlando o acesso a áreas com maior disponibilidade de recursos (Drews *et al.*, 1990). Nesse contexto, espero observar que os machos apresentem maior mobilidade espacial do que as fêmeas (Moreno-Arias; Ardila-Robayo, 2020). Adicionalmente, prevejo que as áreas de uso dos jacarés sejam relativamente pequenas, corroborando com o descrito até então para outras espécies de jacarés na América do Sul (Quintana *et al.*, 2020; Marioni *et al.*, 2023). Áreas de vida reduzida também devem estar relacionadas à limitada capacidade de dispersão observada em jacarés-de-papo-amarelo (Zucolotto *et al.*, 2021).

#### 4 CAPÍTULO 1 – Tracking crocodylia: a review of telemetry studies on movements and spatial use

Figura 1. Mapa mundi com representação das três famílias existentes da Ordem Crocodylia (Alligatoridae à esquerda, Crocodylidae no centro, Gavialidae à direita) ilustrando trabalhos de rastreamento por telemetria.



Este capítulo foi publicado no formato de artigo científico no periódico *Animal Biotelemetry* em 17 de maio de 2023 (APÊNDICE A).

O rastreamento por telemetria é uma importante ferramenta no monitoramento de populações de crocodilianos (Ordem Crocodylia). O uso dessas tecnologias auxiliam a elucidar aspectos da ecologia do movimento das espécies (Mascarenhas-Junior *et al.*, 2023). Ao longo do tempo, estudos com telemetria vêm sendo desenvolvidos em todos os continentes em que crocodilianos se distribuem (Figura 1), apesar de algumas famílias apresentarem grandes lacunas no conhecimento relacionado à ecologia do movimento.

## Abstract

Crocodylians are top predators that play key ecological roles in aquatic ecosystems. As in other groups of large predators, crocodylian populations are often impacted by habitat loss, habitat degradation or direct exploitation for commercial purposes or subsistence. Hence, understanding their spatiotemporal ecology can provide valuable information for conservation planning. We reviewed the published scientific literature on telemetry-tracking in crocodylians, combining the terms “telemetry”, “track” or “tag” and variations; “VHF”, “UHF”, “satellite”, “GPS”, “radio”, “acoustic” or “transmitters”; and “caiman”, “alligator”, “crocodile”, “gharial” or “Crocodylia”. Publications retrieved by our search were carefully reviewed for information on study length, geographic location, sample size, taxonomy, and telemetry technology used. We identified 72 research articles in indexed journals and 110 reports available from the IUCN’s Crocodile Specialist Group, published between 1970 and 2022. Publications included 23 of the 27-living described crocodylian species. We identified strong geographic and taxonomic biases, with most articles proceeding from the USA (21.2%) and Australia (14%), with *Alligator mississippiensis* and *Crocodylus porosus* as the main target species in studies conducted in these countries, respectively. Despite representing 22% of IUCN’s reports, *Gavialis gangeticus* was referred in a single indexed research article. VHF telemetry was the prevalent tracking method, followed by GPS and acoustic transmitters. Studies using VHF devices were generally shorter in length when compared to alternative technologies. Transmitter weight represented less than 2% of the body mass of the carrying individual in all studies. Although attachment site of transmitters was notified in all research papers, few described anaesthetic or clinical procedures during attachment (33%). Our review highlights the need to encourage publication of crocodylian telemetry studies in non-English speaking countries in Asia, Africa, and Latin America, where many endemic species are threatened. We also highlight the need for detailed information on methods and results to facilitate the choice and implementation of appropriate protocols in future telemetry-tracking studies.

Keywords: Crocodylians, Electronic tagging, Remote monitoring, Reptiles, Spatial ecology, Transmitters

## Background

Crocodylians figure among the largest predators in fresh and brackish water ecosystems in the tropical and subtropical regions of the world. They potentially play a fundamental role on defining local trophic webs, influencing population growth rates of their prey (Heithaus *et al.* 2008; Grigg & Kirshner 2015), and linking ecosystems by moving energy and nutrients between the aquatic and terrestrial habitats (Subalusky *et al.* 2009). However, when compared to other large predators in terrestrial or marine environments (e.g.: sharks, dolphins, seals, or bears), or even other large reptiles (e.g.: snakes and turtles), the spatial ecology and movement patterns of crocodylians are relatively less explored, with taxonomic and geographic gaps often jeopardizing their conservation (Hammerschang *et al.* 2019; Somaweera *et al.* 2020; Crane *et al.* 2021).

Traditionally relying on mark-recapture and observation/count techniques (Taylor 1984; Hutton & Woolhouse 1989), research on the spatial ecology of crocodylians has increasingly benefited from new technologies, among which telemetry tracking emerged as a promising tool for monitoring these large, yet secretive animals (Joanen & McNease 1970; Hutton 1989; Rootes & Chabreck, 1993; Read *et al.* 2007; Lang & Whitaker 2010; Quintana *et al.* 2020). Pioneering studies first estimated movement patterns of crocodylians based on mark-recapture, as well as by direct observations of the specimens in the field (Chabreck 1965; Modha 1968). Eventually, remote tracking allowed new approaches, reducing potential observer effects on the behavior of individuals during the length of the studies (Jacob & Rudran 2012).

Telemetry studies addressing the space-time ecology of crocodylians frequently included the estimation of parameters such as home range and patterns of seasonal or diel movements. These were often summarized in statistics including Kernel Density Estimator (KDE), Minimum Convex Polygons (MCP), and Brownian Bridge Movement Models (BBMM), for example. KDE calculates an individual's home range and core areas by placing a kernel function on each relocation point and summing them up to create a smooth probability

density surface (e.g., Caut *et al.* 2019); MCP is used to represent home range by a polygon created by connecting the outmost relocations (e.g., Balaguera-Reina *et al.* 2016); BBMM estimates the probability of an individual's distribution given its previous movements (e.g., Strickland *et al.* 2021). Some studies also use movement route analysis to describe the timing, direction, and length of movement routes (Thomas *et al.* 2010). Spatial data are then evaluated for associations with intrinsic and environmental factors, such as landscape seasonality (Campos *et al.* 2006; Nifong & Silliman 2017), habitat type (Marques *et al.* 2020), anthropogenic pressures (Campos *et al.* 2019), hunting behavior (Evans *et al.* 2017), sex (Fujisaki *et al.* 2014) or age (Lewis *et al.* 2014). Additionally, telemetry methods have been applied to a diverse set of research themes in crocodylian ecology, such as the study of thermoregulation, physiology, territoriality, and reproduction (Magnusson & Lima 1991; Campos *et al.* 2003; Campos *et al.* 2006; Da Silveira *et al.* 2011; Stegmann *et al.* 2017).

The first telemetry tracking studies took place in the USA (LeMunyan *et al.* 1959; Eliassen 1960) and were soon applied to the study of crocodylians. In the early 1970's, researchers investigated movements and habitat use of the *Alligator mississippiensis* (Daudin, 1802) in the USA (Joanen & McNease 1970; Joanen & McNease 1972; McNease & Joanen 1974) and of the saltwater and freshwater crocodiles, *Crocodylus porosus* Schneider, 1801 and *Crocodylus johnstoni* Schneider 1801, respectively (Johnson 1973; Yerbury 1977) using VHF telemetry. Along the 1970's, telemetry tracking expanded to additional populations of *A. mississippiensis* (Taylor *et al.* 1976; Goodwin & Marion 1979) and *C. porosus* (Webb & Messel 1978), and to a Florida population of the American crocodile, *Crocodylus acutus* (Cuvier, 1801) (Ogden 1978). In the 1980's, telemetry research spread to other continents, with additional studies being conducted in Central America (Rodda 1984b), Asia (Singh 1985), South America (Ouboter & Nanhoe 1988) and Africa (Hutton 1989).

Throughout the decades, technologies applied in telemetry tracking improved, providing more efficient methods to collect position and movement data. Earlier works relied on VHF transmitters attached to the animals, which were later followed by field observers carrying portable tracking receivers coupled to handheld antennae (Joanen & McNease 1970; Joanen & McNease 1972;

McNease & Joanen 1974; Taylor *et al.* 1976). It was only in the 21<sup>st</sup> century that crocodylian telemetry started to benefit from new technology that allowed for the remote tracking of animals tagged with GPS or GPS/GSM transmitters, able to emit signals at pre-defined time intervals (Read *et al.* 2004; Read *et al.* 2007; Campbell *et al.* 2013; Combrink *et al.* 2017; Marques *et al.* 2020; Moreno-Arias & Ardila-Robayo 2020). More recently, passive acoustic telemetry was added to the toolbox of crocodylian spatial ecology research, allowing sound signals emitted by transmitters attached to focal animals to be detected by hydrophones distributed throughout the area of the study or actively (Campbell *et al.* 2010; Rosenblatt & Heithaus 2011; Hanson *et al.* 2015; Campbell *et al.* 2015). Today, transmitter modules containing combinations of different technologies are not uncommon (Strauss *et al.* 2008; Brien *et al.* 2010; Campbell *et al.* 2010; Beauchamp *et al.* 2018; Baker *et al.* 2019).

The high cost and casual inefficiency of custom-made telemetry gear, in addition to the need of carefully choosing the right technology for a study's scale and habitat, have been suggested as possible factors hindering telemetry studies from reaching a larger number of research groups (Jacob & Rudran 2012; Skupien *et al.* 2016). Until now, no study summarized telemetry-tracking research on crocodylians over time or described geographic, taxonomic, or methodological gaps or biases. Understanding the operational viability and the quality of data acquired with distinct technologies or distinct sampling efforts is essential in applied ecology, whereas detection of taxonomic and geographic gaps is key to species conservation planning. Hence, we conducted a thorough review of published literature and of documentation published by IUCN's Crocodile Specialist Group to evaluate geographic, taxonomic, and technological trends in telemetry studies involving wild crocodylians, from their outset in 1970 to the present. Additionally, we summarized information on the application of different telemetry methods and related parameters such as body size of carrying individuals, battery life and transmission period. Lastly, we discuss our results highlighting potential barriers to telemetry implementation by a larger number of research groups, the most effective telemetry methods for potential research questions and the potential value of data reported in newsletters and short communications.

## Material and Methods

Until January 2023, we conducted systematic searches on the online databases Scopus, Web of Science, PubMed and Scielo using multiple combinations of the keywords “telemetr\*”, “track\*” “tag\*”, “VHF”, “UHF”, “satellite”, “GPS”, “radio”, “acoustic”, “transmitter”, “caiman”, “alligator”, “crocodile”, “gharial”, “Crocodylia”, “crocodylan”. We used the Boolean Operators ‘\*’ to indicate variations of keywords, ‘AND’ to create terms combinations, and ‘OR’ to find at least one of the terms in the search. After preliminary inspection of returned articles, we selected all that dealt with the evaluation of the temporal or spatial distribution of crocodylians, the ones which described their movement patterns, and those which described territories or home ranges. Replacing search terms with their equivalents in Spanish and Portuguese language did not retrieve any additional documents. In order to avoid biases generated by differences in availability and access to unpublished academic and technical studies in our sample, we removed unpublished monographs, dissertations, reports, books, and meeting abstracts from our database prior to review and to quantitative analyses described below. Additionally, we removed duplicate records (i.e., unpublished, and published versions) of the same studies.

In addition, we searched all documents available in the IUCN’s Crocodile Specialist Group’s website (CSG - <http://www.iucncsg.org/>) for non-peer reviewed short communications and articles reporting the use of telemetry for tracking crocodylians. We compared the number, taxonomic coverage, and geographic location of projects developed in the field in relation results published as articles in indexed journals. We also excluded any report of potential duplicates in the same document. At the time of our search, the CSG website contained 105 documents under their “CSG Proceedings” publication, covering works published from 1971 to 2018. Additional 163 documents containing reports, communications, and research papers were available in the “CSG Newsletter”, all published between 1979 and 2022. All abstracts, reports, communications, and papers were accessed through the “Regional Reports” section of the CSG’s website. We searched using the same keywords described

above. The complete list of works returned in our search and used in this review is presented in Supporting Information (S1).

We carefully reviewed all papers, reports and communications and, for each, we recorded the following information: (1) journal name; (2) type of publication; (3) year of publication; (4) country where telemetry tracking was applied; (5) species studied; (6) body attachment position of transmitters; (7) use of anesthetics during transmitter attachment; (8) tracking technology (VHF, GPS/Satellite and Acoustic); (9) number of specimens tracked; (10) study duration; (11) sex, weight, and total length of studied specimens (when publication presented snout-vent length, we made an estimation of total length); (12) Transmitter weight and lifespan. Due to the limitation of information in CSG's documents, data related to items 6 to 11 were obtained only from manuscripts published in peer-reviewed journals. We summarized data resulting from this review using descriptive statistics (percentages, means, standard deviations, range), which were calculated and plotted in R (R Core Team 2020).

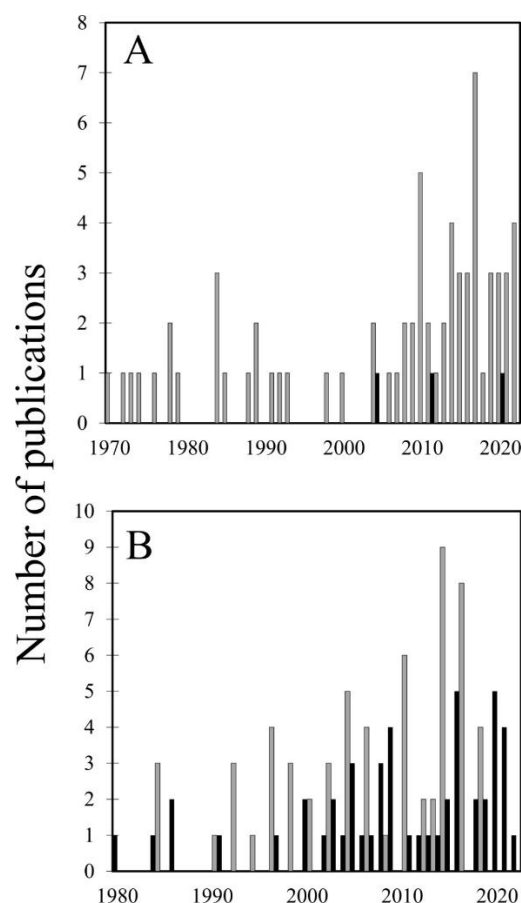
We adapted CSG's regional division criteria to quantify publications, which includes the USA, Latin America and the Caribbean, Africa, Asia, and Oceania. We created a map using the *sf* package in R (Pebesma 2018) and QGIS (QGIS Development Team, 2022) to illustrate the frequency distribution of telemetry studies on crocodylians worldwide. We used a density map with buffer zones of 350 km radius to visually evaluate geographic patterns in frequency of studies.

## Results

Our survey of online databases returned 104 items reporting studies on telemetry tracking of crocodylians, of which 32 consisted of unpublished monographs, dissertations, conference abstracts or duplicate versions of published studies. The remaining 72 documents were peer-reviewed publications, which covered a time span of over 52 years (Fig. 1 A), the first paper published in 1970 and the most recent in 2022. These publications included research articles ( $n = 69$ ) and short communications ( $n = 3$ ). Most papers were published in scientific journals (94.6%), whereas only three papers (5.4%) were published in compilations derived from scientific conferences.

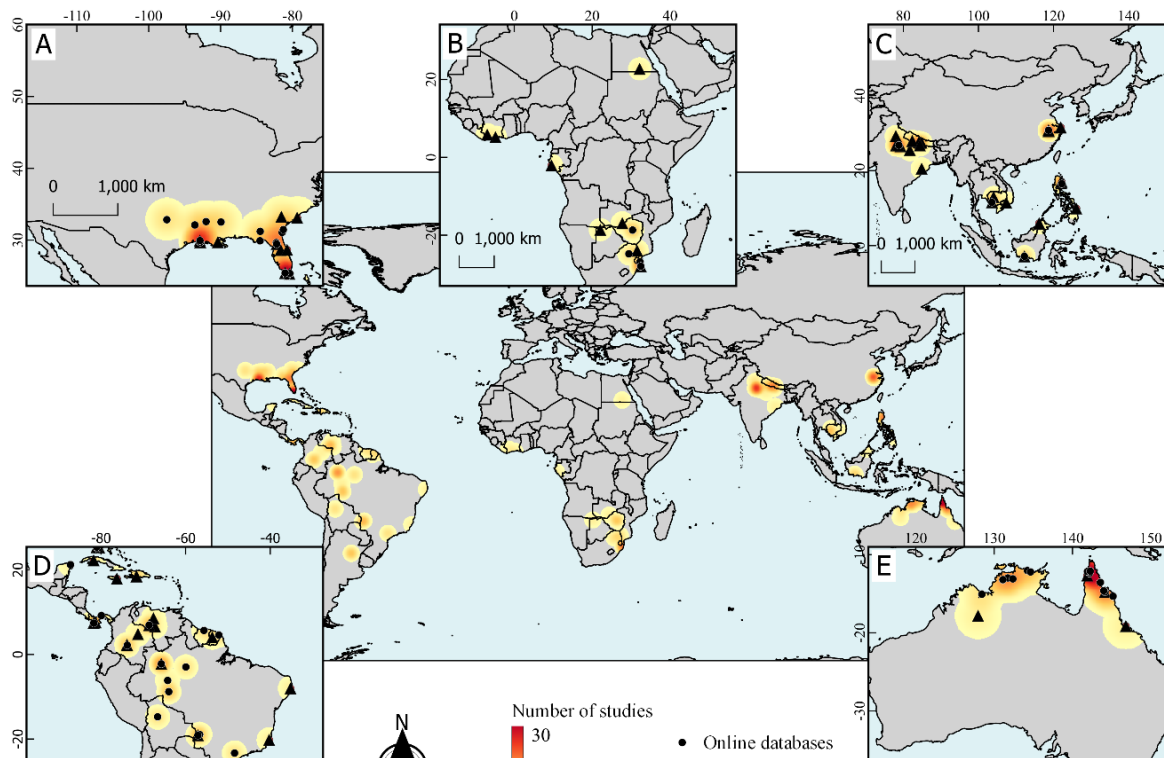
Our searches of the IUCN's Crocodile Specialist Group publications returned a total of 110 documents related to telemetry tracking. Out of these, 61 were published in the CSG Proceedings between 1984 and 2018, while the remaining 49 were published in the CSG Newsletter between 1980 and 2022. Documents in the CSG Proceedings included short abstracts (39.3%), technical reports (32.8%) and non-peer reviewed research articles (27.9%). Documents published in the CSG Newsletter comprised only technical reports (Fig. 1 B).

Surveys in online publication databases and in the CSG's archives showed a temporal trend of increase in the number of publications addressing telemetry tracking of crocodylians after 2000, with publication peaks between 2010 and 2016 (Fig. 1 A, B).



**Figure 1** Number of publications of telemetry-tracking in crocodylians between 1970 and 2022 in (A) online databases and (B) in IUCN'S Crocodile Specialist Group documents. Grey bars indicate full articles (A) and CSG proceedings (B) and black bars indicates short communications (A) and CSG newsletter reports (B).

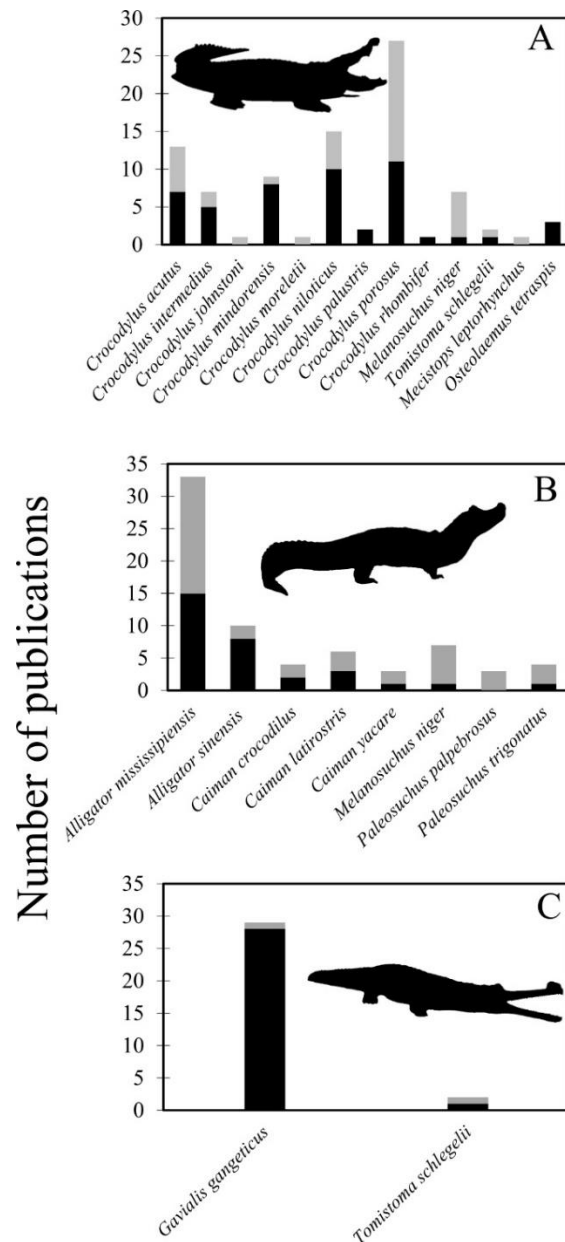
Considering papers retrieved in the online database survey, most published studies (59.7%) were conducted in the Americas (27.8% in Latin America and the Caribbean, Fig. 2 D, and 31.9% in the USA, Fig. 2 A). Studies in Oceania were conducted exclusively in Australia, which accounted for 22.2% of all publications (Fig. 2 E), followed by studies conducted in Asia (9.7%, Fig. 2 C) and Africa (8.4%, Fig. 2 B). Considering the pooled records of reports, articles, and communications available in the CSG Proceedings and the CSG Newsletter, most published studies took place in Asia (46.4%, Fig. 2 C), where India and Nepal accounted for most studies (18 and 10 studies, respectively). Studies conducted in the Americas accounted for 32.4% of the IUCN CSG's documents (19.8% in Latin American and the Caribbean, Fig. 2 D, and 13.6% in North America). The USA accounted for most of publications (15 studies, Fig. 2 A). IUCN CSG's documents also reported studies conducted in Africa (12.7%, Fig. 2 B) and Oceania (8.5%, Fig. 2 E), which mainly took place in South Africa (five studies) and Australia (nine studies), respectively.



**Figure 2** Geographic distribution of telemetry-tracking publications on crocodylians between 1970 and 2022. The number of publications increases from yellow to red shades. Buffer zones represent a 350 km radius. Black dots represent studies published in indexed journals. Black triangles represent research projects conducted in the field and reported in IUCN's CSG publications. A: the USA; B: Africa; C: Asia; D: Latin America and the Caribbean; E: Oceania.

Most of the studies (44.5%) focused on telemetry tracking research in crocodiles (family *Crocodylidae*). *Crocodylus porosus*, *C. niloticus* (Cuvier, 1807), and *C. acutus* were the most frequently studied species, accounting for 28, 15 and 13 studies, respectively (Fig. 3 A). Alligators and caimans (Family *Alligatoridae*) were the second most frequently studied group, accounting for 34.7% of the pooled survey results. Alligator *mississippiensis* ( $n = 34$ ), the Chinese alligator *Alligator sinensis* Fauvel, 1879 ( $n = 10$ ) and the black caiman *Melanosuchus niger* (Spix, 1825) ( $n = 7$ ) were the most frequently studied species (Fig. 3 B).

Gharials (Family *Gavialidae*) were comparatively less studied, accounting for 14.8% of the papers, reports, and communications. Studies covered the two species in the family, the gharial *Gavialis gangeticus* Gmelin, 1789, ( $n = 25$ ), and the false gharial *Tomistoma schlegelii* Müller (1838) ( $n = 2$ ) (Fig. 3 C).



**Figure 3.** Number of publications related to telemetry tracking in species of (A) Crocodylidae, (B) Alligatoridae, and (C) Gavialidae, between 1970 and 2022 in online databases and IUCN's Crocodile Specialist Group documents. Grey bars represent publications in the CSG, while black bars represent publications in online databases.

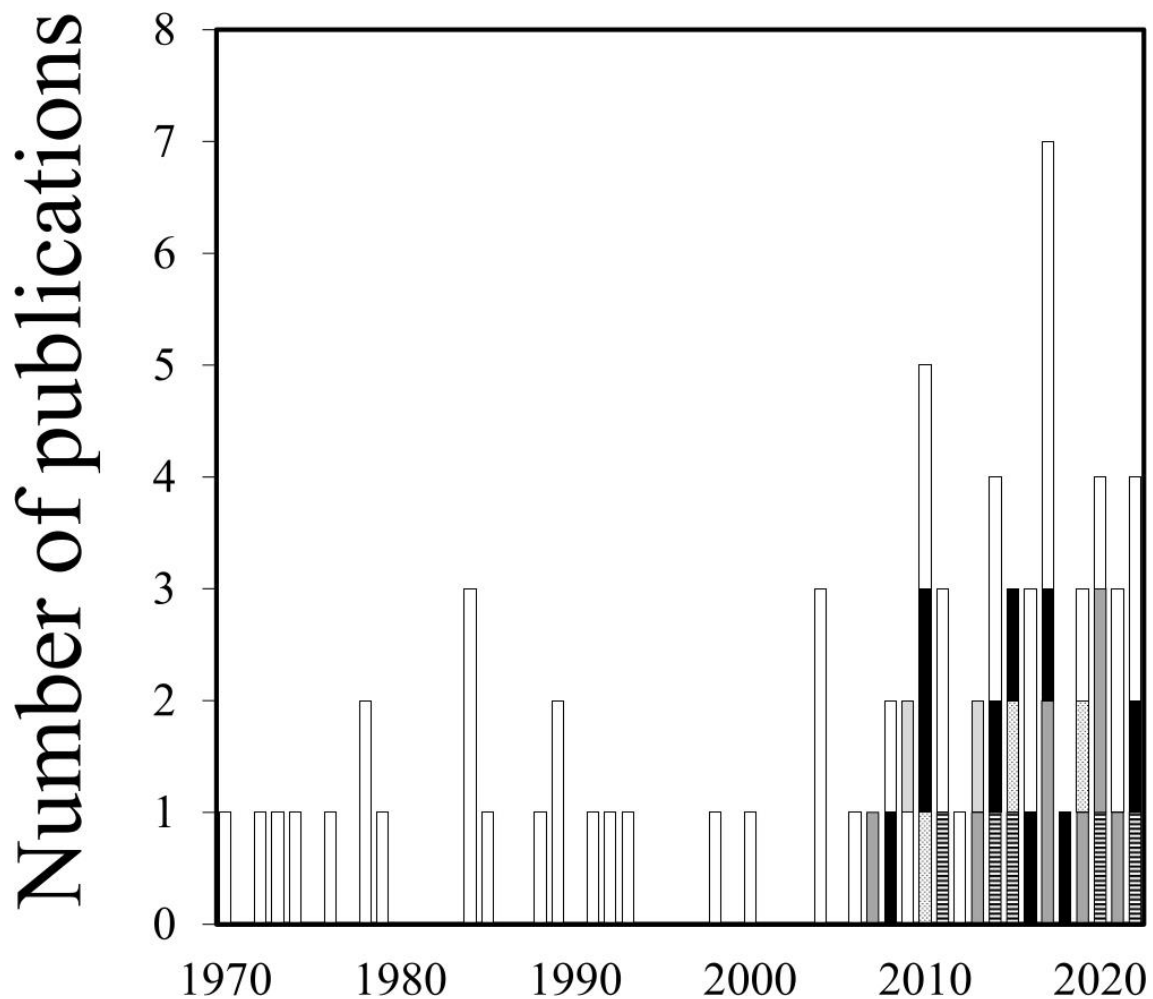
Several studies have utilized telemetry tracking to monitor multiple species. Among these studies, four have included species from different families (Gavialidae + Crocodylidae = 2.2%), while seven have focused on species within the same family (Alligatoridae = 2.2%; Crocodylidae = 1.6%). Hence, the total

amount of studies involving different taxa is slightly larger than the number of manuscripts evaluated.

In 69 peer-reviewed papers, transmitter attachment procedures were described in detail. Most studies used transmitters attached to the dorsal scales of the neck (43.1%), followed by attachment to the scales of the tail (25.0%) or to the dorsal surface of the head (1.4%). Subcutaneous transmitters were used less frequently, generally implanted in the forelimbs (4.2%), in the anterior region of dorsum (2.8%) or in the abdominal cavity (2.8%). In 16.5% of the studies transmitters were attached to more than one part of the body (e.g., Dwyer *et al.* 2015), or attachment site varied among studied specimens (e.g., Kouman *et al.* 2021).

Most papers reported the method of transmitter attachment (87.5%). Drilling dermal bones (tail or neck) was adopted in 54.2% of studies, followed by external attachment of collars or wires tied to the tail or dorsal surface (19.4%) and by intramuscular or intraperitoneal implant of subcutaneous transmitters (19.4%) (in four studies, two or more methods were used, hence pooled frequencies exceed 100%). Importantly, 66.7% of the publications did not report using anaesthetics when attaching transmitters to animals. Among studies that reported the use of anaesthesia, 87.5% used lidocaine solution, 2.1% used procaine hydrochloride and 2.1% used alfaxalone solution. Some papers that reported using anaesthetic drugs during transmitter attachment did not specify which drug or concentrations were used (8.3%).

Technologies applied to telemetry tracking of crocodylians diversified with time. Most peer-reviewed studies (62.5%) used VHF telemetry to sample spatial position of marked individuals. Studies based on alternative methods started to be published in 2007, and those included GPS (11.1%) and acoustic telemetry (6.9%). In some studies, hybrid transmitters (GPS + VHF) or complementary methods were applied, to minimize errors in the estimation of geographic position of sampled individuals or to allow direct comparisons between different telemetry approaches. The most frequent combination was VHF + GPS telemetry (n = 11.1% studies), followed by GPS + acoustic telemetry (n = 4.2%) and by the combination of VHF + GPS + acoustic telemetry (n = 4.2%) (Fig. 4).



**Figure 4** Technologies used in crocodylians telemetry-tracking studies in publications available on online databases between 1970 and 2022. Each different type of bar represents a different technology or combination of technologies. White: VHF; Dark grey: GPS; Black: GPS and VHF; Light grey: VHF, GPS and acoustic; Black dots: GPS and acoustic; Horizontal black lines: Acoustic.

Acoustic telemetry tracking allowed for the largest number of sampled specimens among all peer-reviewed studies (Table 1), with  $36 \pm 25$  individuals tagged per study. Studies that applied VHF and GPS methods had  $13 \pm 9$  and  $8 \pm 6$  tracked individuals, respectively. VHF studies generally spanned longer time frames ( $1.7 \pm 1.9$  years), but with large variation, ranging between 0.02 and 10 years. Studies involving GPS telemetry lasted  $2.3 \pm 1.5$  years (0.4 to 4.3 years) and studies involving acoustic telemetry lasted  $2.6 \pm 2.1$  years (1.7 to 9.8 years).

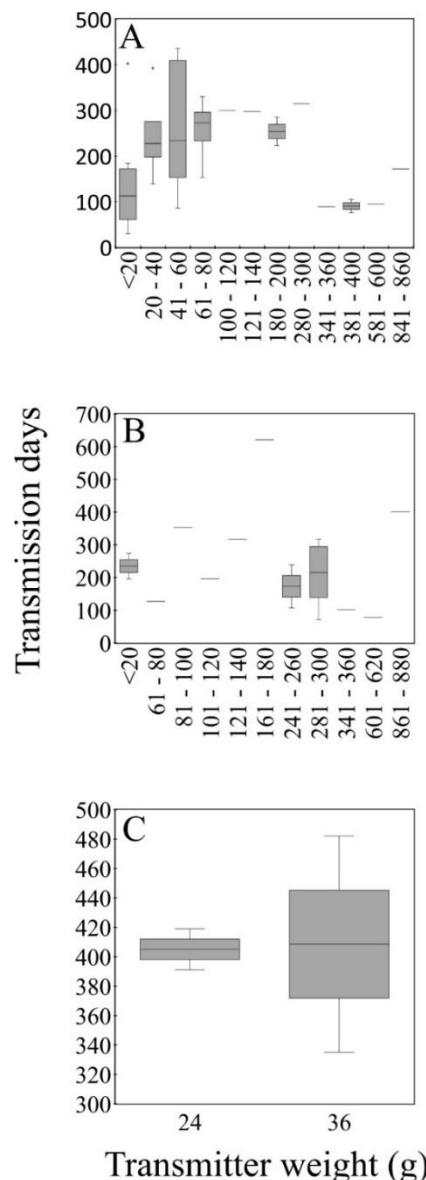
**Table 1** Sampling effort to monitor crocodylians with different telemetry-tracking technologies in publications available on online databases between 1970 and 2021. N: Number of crocodylians monitored; Pub: Number of publications; Mean: Mean number of crocodylians monitored; Max: Maximum number of crocodylians monitored; Min: Minimum number of crocodylians monitored; RLD: Research with longer duration (days).

<b>Technology</b>	<b>N</b>	<b>Pub</b>	<b>Mean</b>	<b>Max</b>	<b>Min</b>	<b>RLD</b>
<b>Acoustic</b>	425	10	55	105	2	>3997
<b>GPS</b>	141	17	8	30	1	>1584
<b>VHF</b>	658	50	13	47	1	>3470
<b>GPS + VHF</b>	50	6	8	15	2	>1337

Considering papers which precisely reported the transmission period of attached transmitters, tracking period of individuals ranged between one and 3997 days ( $1.2 \pm 1.06$  years). Acoustic telemetry transmitters were reported as the ones achieving the longest transmission periods, ranging from 18 to 3997 days ( $2.18 \pm 1.78$  years;  $n = 426$  individuals) (Fig. 5 C). VHF transmitters were reported to be functional from one to 1258 days ( $0.66 \pm 0.6$  years;  $n = 626$  individuals) (Fig. 5 A), and GPS transmitters from three to 1209 days ( $0.8 \pm 0.69$  years;  $n = 117$  individuals) (Fig. 5 B). Hybrid GPS + VHF devices transmitted from four to 744 ( $0.55 \pm 0.5$  years;  $n = 44$  individuals). The proportion of transmitters lost because of detachment from the carrying individual, malfunction or because the monitored individual moved away from the study area varied from 0 to 100% (mean = 22%;  $n = 28$  studies).

Body-size of individuals carrying transmitters were informed in 93,1% studies and varied from 0.28 to 4.86 m. Body mass of monitored specimens was presented only in 34.7% studies. In studies that provided information on body mass of the carrying individual and on transmitter weight (22.2%), transmitters corresponded to 1% to 13.25% of the body mass of the carrying individual (mean = 1.5%,  $n = 246$  specimens). VHF transmitters were generally lighter than GPS transmitters, varying between 3.9 and 850.0 g (mode = 50.0 g;  $n = 26$  studies) (Fig. 5 A). Weight of GPS transmitters ranged between 100 and 880 g (mode = 300 g;  $n = 10$  studies) (Fig 5 B). Acoustic transmitters were much lighter, ranging

between 24 and 36 g (mode = 24 g; n = 5 studies) (Fig 5 C). Transmitter modules carrying mixed technologies, or the total weight of different transmitters attached to a single individual ranged from 65 to 374 g (mode = 300 g; n = 7 studies). Males were more frequently monitored than females, accounting for 42.5% of the specimens monitored. Females represented 33% of monitored specimens. Sex was not determined for approximately 24.5% of all crocodylian specimens monitored in telemetry studies.



**Figure 5** Average transmission period of telemetry-tracking transmitters used in crocodilians based on publications available in online database between 1970 and 2022. Each category considers a 20 g range of transmitters weight, except for Acoustic (C), which only two different weights were informed in the publications. A: VHF; B: GPS; C: Acoustic.

## Discussion

From its outset in the early 1970's, the rate of publication of studies addressing telemetry tracking in crocodylians increased, both as scientific articles and communications published in indexed journals and as non-peer reviewed shorter scientific reports published by the IUCN's Crocodile Specialist Group. The number of publications per year increased steadily, peaking between 2010 and 2018, potentially reflecting the development of less costly tracking technologies (Kenward 2001) and their consequent deployment in crocodylian research (e.g., Read *et al.* 2007; Campbell *et al.* 2010; Calverley & Downs 2015; Strickland *et al.* 2020). From the early 2000's on, improvement in the performance and size of transmitters and the dramatic reduction in production costs, especially of GPS/satellite units, favored the spread of telemetry studies all over the world (Rodgers, 2001).

Despite the increasing trend in the rate of publication in the past 20 years, our review disclosed a considerable difference between the number of studies published in indexed journals and the actual number of studies developed in the field, as inferred by data recovered from IUCN's CSG Proceedings and CSG Newsletter. Published articles on telemetry tracking of crocodylians are geographically biased, with the USA and Australia accounting for more than half of the populations studied. Conversely, surveys that took place in countries fairly represented in the CSG's reports were either underrepresented in (e.g., India, China, Argentina) or completely absent from (e.g., Cuba, Nepal) indexed journals. India and Nepal objectively illustrate how studies in developing countries are severely underrepresented in indexed journals. In India, research in the Chambal National Park has been reported since the early 1980's (Singh 1984). However, the first article in this area was published in 2010, based on sampling efforts conducted between 2007 and 2009 (Lang & Whitaker 2010). In Nepal, telemetry tracking has played a key part of an important reintroduction program of gharials in the Royal Chitwan National Park since 2002 (Cadi *et al.* 2002; Maskey *et al.* 2006; Aufrey & Cadi 2009; Griffith *et al.* 2020), but results have not yet been published in indexed journals.

In addition to the early origin of telemetry tracking studies in English-speaking countries, structural issues in the scientific publication process may

help to explain the disproportionate number of peer-reviewed articles towards species distributed in the USA and Australia which, importantly, is not mirrored by the research effort in the field, as evidenced by our quantitative analysis of IUCN's CSG reports. Historically, researchers non-native to English-speaking countries face disadvantages in reaching scientific publications when compared to native English speakers, essentially because English is the main language in international journals. Authors are frequently discouraged along the editing process, or their manuscripts are rapidly rejected by editors due to grammatical deficiencies (Fergusson *et al.* 2011). Therefore, much of the scientific production from Africa, Latin America, Middle East, and Asia are published in local journals, in languages other than English, often ranked as of little impact (Ramírez-Castañeda 2020). To mitigate such biases, some measures could be applied, such as the provision of review services by international journals (Benfield & Feak 2006), the possibility of publishing both in English and in the researcher's native language (Meneghini & Packer, 2007) or enhancement of free English-writing courses at universities (Ferguson *et al.* 2011). Associated to the linguistic issue, national government investment in research directly influences academic production (Man *et al.* 2004). Journals with publication charges should provide fee waivers to authors from low- or mid-income countries (Lawson 2015) as a strategy to boost publication of high-quality scientific content, often produced in countries that concentrate most species of conservation concern.

Nearly half of the crocodylian telemetry papers published in indexed journals had the American alligator or the saltwater crocodile as research subjects, also indicating taxonomic biases on information available for conservation. The ecology and natural history of these species are well-known today. For example, telemetry tracking of *A. mississippiensis* has been used to assess individual movement, territoriality, and home range (Joanen & McNease 1970; Joanen & McNease 1972; McNease & Joanen 1974; Taylor *et al.* 1976; Goodwin & Marion 1979; Rodda 1984a; Taylor 1984), as well as habitat characteristics and responses to environmental changes (Fujisaki *et al.* 2014; Strickland *et al.* 2016; Nifong & Silliman 2017). On the other hand, threatened species (e.g., the False Gharial, the Gharial, the Chinese Alligator, the Siamese crocodile *Crocodylus mindorensis* Schmidt, 1935, and the Phillipine crocodile

*Crocodylus siamensis* Schneider, 1801) are often represented by one or a few papers, generally addressing movement patterns at relatively small geographic scales (Ding *et al.* 2004; Lang & Whitaker 2010; Wang *et al.* 2011; Eam *et al.* 2017; Van de Veen *et al.* 2017).

Effective planning of conservation strategies and management of highly elusive, long-lived species depend on long-term monitoring and data collection, thus the importance of increased access to results of earlier studies published as scientific articles by current researchers. Valuable information on individual and population-level responses have been evaluated in a few crocodylian species by telemetry tracking approaches, and it should be encouraged in those of high conservation concern, considering threats such as illegal hunting (Bezuijen *et al.* 2014), invasive species (Lang *et al.* 2019), water pollution (Jiang & Wu 2018), bycatch on fishing nets (Van Weerd *et al.* 2016; Mascarenhas-Junior *et al.* 2018), and habitat fragmentation (Bezuijen *et al.* 2012).

Movement patterns of crocodylians can vary between wet and dry periods, reproductive and non-reproductive seasons, or even between sexes, as male and female conspecifics can occupy and move across their environment in diverse ways (Kay 2004b; Brien *et al.* 2008; Balaguera-Reina *et al.* 2016; Marques *et al.* 2020). For example, male saltwater crocodiles can exhibit a greater site fidelity than females (Baker *et al.* 2022), while in other species, such the Orinoco crocodile, males can move far distances than females and occupy larger home ranges (Moreno-Arias & Ardila-Robayo 2020). Our survey revealed telemetry studies of crocodylians are slightly male-biased, potentially influencing metanalyses of movement and spatial ecology parameters across populations or across species.

Regarding field and sampling protocols, attached transmitters should not compromise individual behavior, whereas transmitter design and composition should minimize the risk of damage and loss of data (Jacob & Rudran 2012). The hard and keeled scales on the dorsal surface of the neck (the “nuchal rosette” area) was the most common transmitter attachment site in crocodylians, allowing for increased stability of the transmitter and facilitating signal transmission when individuals are positioned at the water surface (Kay 2004a; Franklin *et al.* 2009; Brien *et al.* 2010).

Researchers should consider that some transmitters are only functional when their antennae are exposed above the water surface and oriented vertically to improve signal transmission (Kenward 2001, Kay 2004a; Brien *et al.* 2010). In complex habitats such as swamps or riverine systems, neck-attachment could not be suitable, because they can potentially snag on vegetation or debris (Rothmeyer *et al.* 2002; Han *et al.* 1998; Kay *et al.* 2004a). In these cases, a streamlined attachment package in the tail surface is an option to reduce detachment (e.g., Bonke *et al.* 2014; Campos *et al.* 2017; Marques *et al.* 2020), if damage or injuries to the tail surface due to agonistic interactions are not common in the focal population (Strauss *et al.* 2008). Subcutaneous implantation is a promising option to prevent equipment loss due to detachment; however, it should be carefully considered, since GPS and VHF transmitters typically have larger batteries and may experience signal attenuation when submerged underwater (Franklin *et al.* 2009; Dwyer *et al.* 2015; Strickland *et al.* 2020). Therefore, this procedure is recommended for subaquatic acoustic transmitters. Malfunctioning or the loss of transmitters occurs not only by detachment, but also because of natural mortality (Kushlan & Mazzotti 1989; Da Silveira *et al.* 2010), illegal hunting (Muñoz & Thorbjarnarson 2000), technical issues inherent to transmitter hardware and batteries (Strauss *et al.* 2008), or failure of signal reception (Martin & Silva 1998). Depending on the ecological question being addressed, some studies can concentrate sampling efforts in short periods (e.g., during a specific season of the year), reducing the chance of data loss while collecting useful demographic data, such as dispersion, hatchling survival, territorial behavior, and short-term movement patterns (Taylor *et al.* 1976; Read *et al.* 2007; Campos *et al.* 2012).

Most of all published studies on crocodylian telemetry did not mention the use of anesthetic or prophylactic procedures during attachment of transmitters. Since the 1960's, ethics committees have been used to regulate and protect animals in research (Schuppli & Fraser, 2007), but countries deal with scientific permits differently. In the USA, which accounted for most of the studies in our survey, animal regulations have been reinforced in the last decades of the 20<sup>th</sup> century (National Research Council Committee to Update Science, Medicine, and Animals, 2004) and this is reflected on the poor description of clinical or

anesthetic procedures in papers published between the 1970's and 1990's. The first report of anesthetics use was published in 1990's by Hocutt *et al.* (1992), and it was the only research prior to 2000's reporting the use of drugs during transmitter-attachment procedures (see Supplementary file for further details). In addition, the small number of papers describing anesthetic procedures may be also due to committees considering some procedures as a little invasive. Nevertheless, some studies support the use of anesthesia and prophylactic procedures to minimize pain and reduce the risk of infections or necrosis in studied specimens (Brien *et al.* 2010; Manolis & Webb, 2016).

Lidocaine solution was the most used anesthetic solution for research involving invasive procedures. Lidocaine is a local anesthetic, widely available in veterinary suppliers and recommended for anesthesia in reptiles (Sladky & Mans 2012). However, toxic, and lethal doses are highly unknown for several species, including most crocodylians (Read 2004; Chatigny *et al.* 2017), which could be potentially related to the absence of such practice in most of the published studies. This should be thoroughly described in the resulting publications, allowing for the discussion and development of safer methods for transmitter attachment among different research teams.

Battery life of transmitters is a key feature limiting the length of telemetry tracking studies. Most of the weight of a transmitter can be attributed to its power source. Some authors argue that transmitter weight should not exceed 6% of the weight of the carrier individual, minimizing effects on foraging and other ecological interactions (Jacob & Rudran 2012). Our survey highlights that transmitters used in telemetry tracking of crocodylians are normally light, generally representing 2% of their body weight, with a few exceptions. A trend towards lighter transmitters is also evident from our results, with the first VHF transmitters weighting 300–850 g and allowing for study lengths of approximately 300 days (Joanen & McNease 1972; Goodwin & Marion 1979), to recent acoustic transmitters weighting 24–36 g, which were functional for over two years (Rosenblatt *et al.* 2013; Hanson *et al.* 2015; Baker *et al.* 2022). Importantly, many of the studies failed to report the causes that led to the end of monitoring of individuals (e.g., battery malfunction, transmitter detachment or achieving sufficient data for analyses). Hence, the apparent lack of relationship between

transmitter size and monitoring time uncovered in our review most probably reflects the lack of information on different causes determining the end of a study.

Reduction of the weight and size of transmitters is key to the development of monitoring protocols that include juvenile and subadult individuals, or that improve analyses based on long-term data, thus minimizing risk of transmitter loss in external attachment procedures (Gaby *et al.* 1985; Hocutt *et al.* 1992; McMichael *et al.* 2010; Baker *et al.* 2019) and refining important population parameters. To obtain accurate answers to ecological questions, it is essential to choose statistical methods that are appropriate to the type and quality of telemetry data collected in the field. For example, BBMM is a sophisticated statistical tool for predicting paths and core areas but requires discrete locations to be sampled over short periods of time (Horne *et al.* 2007). This type of analysis may not be suitable for VHF studies due to limits in spatial resolution imposed by constraints on data collection. Instead, it is recommended for studies based on GPS or acoustic telemetry data. Methods such as KDE and MCP can provide important clues about individual home range and movement patterns, but results can sometimes be misleading or biased (Crane *et al.* 2021). MCP data can overestimate an individual's home range by not considering areas with a higher frequency of relocations (Börger *et al.* 2006). On the other hand, traditional KDE methods do not consider the autocorrelation nature of animal movement, only evaluating the spatial clustering of relocations (Row & Blouin-Demers, 2006). Therefore, we recommend VHF technology for short-term analysis or in evaluating animal behavior, dispersion, site fidelity and survival rates. As for home ranges and movement patterns, combining GPS or acoustic telemetry with BBMM approaches can potentially predict an individual's spatial distribution probability and area of use more precisely.

Transmitters and other items (e.g., antenna and signal receiver) also vary greatly in referring to their cost, GPS transmitters being frequently the most expensive considering equipment acquisition (Skupien *et al.* 2016). Otherwise, costs in field expeditions, such as fuel, food and other services for VHF tracking studies can equalize or exceed the amount invested in GPS technology (Hebblewhite & Haydon, 2010). VHF telemetry is often advised as the method for direct observation of foraging and reproductive behavior, whereas GPS telemetry

is suggested in studies targeting at collecting spatial position data of individuals inhabiting landscapes which are difficult to access (Skupien *et al.* 2016), potentially providing more relocations records during the study. However, GPS signals are more sensitive to attenuation than VHF when transmitters are submerged (Lawson *et al.* 2018) or blocked by dense vegetation (Horak *et al.* 2010).

Emerging technologies like acoustic telemetry represent interesting alternatives in deep, vertically stratified aquatic habitats, because acoustic signals can be transmitted and received while tracked animals are submerged (Hartog *et al.* 2009; Strickland *et al.* 2020). Acoustic transmitters also benefit from extended battery life, light weight allowing for data collection along many consecutive years (Baker *et al.* 2019), and it is a useful low-cost option, mainly in limited of confined areas (Dwyer *et al.*, 2015). Transmission of acoustic signals can, however, be masked by background noise or by topographic barriers in underwater environments (DeCelles & Zemeckis 2014) and cannot be used to record information outside the water, such as nesting females in the land. To overcome technical limitations inherent to each tracking technology, combinations of telemetry methods (hybrid transmitters or use of different technologies in the same study) are suggested (Brien *et al.* 2010; Calverley & Downs 2015; Baker *et al.* 2019).

In the past two decades, the increase in the number of telemetry studies of crocodylians worldwide is notable, potentially associated with the increased access to new technologies. Even so, much of the scientific knowledge produced is restricted to developed English-speaking countries. We stress that there is an urgent need for investment in research and scientific production in countries in Africa, Asia, and Latin America, along with policies that warrant publication of studies conducted in these countries in international journals, especially because many species distributed in these continents are at risk (Targarona *et al.* 2008; Shirley 2014; Jiang & Wu 2018). We also encourage researchers to report in their manuscripts the methodological details of their work, such as the exact duration of transmission, size and weight of specimens and transmitters, as well as attachment procedures. We suggest that any difficulties found during fieldwork (e.g.: limitations in the signal range or transmitter loss/detachment) should be

reported, to guide the implementation of future studies and increasingly improve telemetry-tracking methods.

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**5 CAPÍTULO 2 – Factors influencing detection, distribution and population dynamics of the broad-snouted caiman (*Caiman latirostris*) in an altered environment in north-eastern Brazil**

**Figura 2.** Espécime de jacaré-de-papo-amarelo (*Caiman latirostris*) sob vegetação aquática.



O jacaré-de-papo-amarelo habita ambientes lênticos no nordeste do Brasil e geralmente estão associados à vegetação aquática abundante (Figura 2). Estes microhabitats funcionam ambientes protetivos contra ação antrópica e predadores, além de apresentarem de abundante disponibilidade de recursos alimentares (Mascarenhas-Junior *et al.*, 2020).

## ABSTRACT

Nocturnal spotlight surveys have been historically used to determine patterns in crocodylians' space-time ecology. This approach provides reliable insights about their conservation, especially when is based on long-term monitoring. We assessed how weather, habitat features, and anthropogenic factors influence distribution and population trends of broad-snouted caiman (*Caiman latirostris*) in an altered Atlantic Forest habitat in north-eastern Brazil. From 2015 to 2022, we conducted night counts to detect caimans, measure several abiotic variables and assess human activity. To account for changes in encounter rates based on abiotic variables, we employed a Generalized Linear Modeling approach and a single-species occupancy model to predict caiman probability of occurrence within the reservoir. Average caiman encounter rate in the reservoir was 1.3 ind/km, consistent with estimates conducted in other locations in Brazil. The population size remained relatively stable over the study period, although adults encounter rates increased. Water temperature and humidity positively affected caiman detection, whereas rainfall and cloud coverage had a negative influence on counts. Caimans were distributed throughout the reservoir, with a preference for the river channel and forested sectors. The presence of gillnets was positively correlated with caiman distribution. Our findings comprise the first long-term study of a broad-snouted caiman population dynamics in Brazil and provide useful guidelines for determining priority areas for caiman conservation within the highly threatened Atlantic Forest biome. Abiotic factors impact caiman metabolism and foraging behavior and on observer detection ability. The river channel and forested margins probably provide greater resources availability, while vegetated areas provide protective habitats against human pressures. Caiman distribution in fishing zone areas may be explained by their opportunistic feeding on tangled fish. Our findings comprise the first long-term study of a broad-snouted caiman population dynamics in Brazil and provide useful guidelines for determining priority areas for caiman conservation within the highly threatened Atlantic Forest biome.

Keywords: Atlantic Forest, crocodylian, detectability, encounter rates, spotlight counts.

## INTRODUCTION

Accurate assessment and precise predictions about population dynamics and the spatial distribution of individuals are needed to understand their underlying ecological drivers and to ensure effective planning of management and conservation strategies. Detecting an organism is key to estimate species occurrence and abundance by replicated surveys in long-term studies (Christy *et al.*, 2010; Franklin 1989; Joseph *et al.*, 2009). Although estimates are susceptible to biases due to observer imperfect detection, the incorporation of multi-variable frameworks with abiotic, habitat and human factors enhance biological and ecological comprehension of population trends (Guillera-Aroita *et al.*, 2010; McRae *et al.*, 2008).

Crocodylians play key roles in their habitats by potentially acting as top predators, modifying riparian habitats, and mediating nutrient flows by foraging across ecosystem boundaries (Hanson *et al.*, 2015; Somaweera *et al.*, 2020; Strickland *et al.*, 2023). Multiple studies have focused on estimating distribution of crocodylians through eyeshine detection by spotlight on nocturnal surveys (Barão-Nóbrega *et al.*, 2022; Peña *et al.*, 2003; Woodward and Marion 1978). This approach is considered an important tool for elucidating seasonal and long-term changes in demographic parameters (Woodward and Moore 1993) and offer valuable insights on the effectiveness of conservation efforts targeted at crocodylians and their habitats (Bishop *et al.*, 2009; Fukuda *et al.*, 2015; Ortiz *et al.*, 2020).

The abiotic conditions, biological interactions and anthropogenic factors that influence crocodylian counts and population dynamics have been well-studied, but their relative importance is still unclear. For example, water temperature, wind speed, cloud coverage, rainfall, moonlight, and water volume may be important predictors of crocodylian abundance and detection (Ahizi *et al.*, 2021; Da Silveira *et al.*, 2008; Strickland *et al.*, 2018). These variables can exert varying effects within the target population, exhibiting distinct influences at different ontogenetic stages. For instance, large crocodylians exhibit greater thermostability and are less susceptible to temperature fluctuations compared to small ones (Grigg *et al.*, 1998). Juveniles may prefer shallow areas due to

differences in feeding and survival strategies (Green *et al.*, 2014), while adults access open deep waters more often for mating (Joanen and McNease 1970).

Habitat features, including vegetation cover and food availability (Aguilar-Olguín *et al.*, 2020; Marioni *et al.*, 2008), as well as human disturbances such as boat traffic, poaching, farming, or fishing (Aguilera *et al.*, 2008; Mascarenhas-Júnior *et al.*, 2020; Rebelo and Lugli 2001), can also influence detection of crocodylians. Pressures originating from human activities are particularly associated with impacts on crocodylians' population size, age structure, and spatial distribution, as well as with behavioral responses as increased individual wariness of human presence (Borteiro *et al.*, 2008; Pacheco 1996a; Ron *et al.*, 1998). Considering possible combinations among such environmental and ecological drivers, and the existing variation in biology and natural history of different crocodylian species, it is extremely hard to predict how different uses and management of water bodies and riparian areas will affect population size, structure, and spatial distribution at the long term.

The broad-snouted caiman, *Caiman latirostris* is a medium-sized caiman distributed in central-eastern South America, ranging from northern Argentina and southern Bolivia to south- and north-eastern Brazil (Siroski *et al.*, 2020). It is a diet generalist, feeding on invertebrates and small vertebrates, such as birds and fishes (Borteiro *et al.*, 2009; Diefenbach 1979). Although some local populations are severely endangered (Fraga *et al.*, 2019), the species is listed as "Least Concern" in the International Union for Conservation of Nature's (IUCN) Red List of threatened species (Siroski *et al.*, 2020). While most of the geographic distribution of the broad-snouted caiman currently overlaps with highly altered watersheds threatened riverine landscapes, more accurate assessments of its conservation status are hindered by the lack of data on population trends. For instance, little is known about long-term changes in dynamics of populations, as the existing studies were mostly based on limited or non-continuous sampling efforts (Carvalho and Verás-Batista 2013; Filogonio *et al.*, 2010; Fusco-Costa *et al.*, 2008; Marques *et al.*, 2016; Mascarenhas-Júnior *et al.*, 2020; Passos *et al.*, 2014).

Despite historically fragmented and degraded, the Brazilian Atlantic Forest harbors several populations of the broad-snouted caiman (Coutinho *et al.*, 2013).

Recognized as one of the most important global biodiversity hotspots (Ribeiro *et al.*, 2011), the Atlantic Forest has experienced significant degradation, with only 10% of the native forest remaining due to rampant deforestation, habitat fragmentation, and extensive human land-use (Diniz *et al.*, 2022; Ribeiro *et al.*, 2009). Within the region, many rivers have been dammed to serve as water reservoirs (Padial *et al.*, 2021), resulting in significant changes in chemical and physical attributes of river basins, and in the associated ecological processes (Almeida *et al.*, 2009; Bouvy *et al.*, 2003; Zhao *et al.*, 2012). Such transformations also affected human activities related to the subsistence of local populations, for example, by limiting fish abundance and distribution (Akama, 2017; Gehrke *et al.*, 2002). These consequences potentially increase negative interactions between humans and caimans, often as a result of reduction in target fish populations, overlap of fishing areas or habitat loss (Mascarenhas Júnior *et al.*, 2018; Pooley *et al.*, 2021).

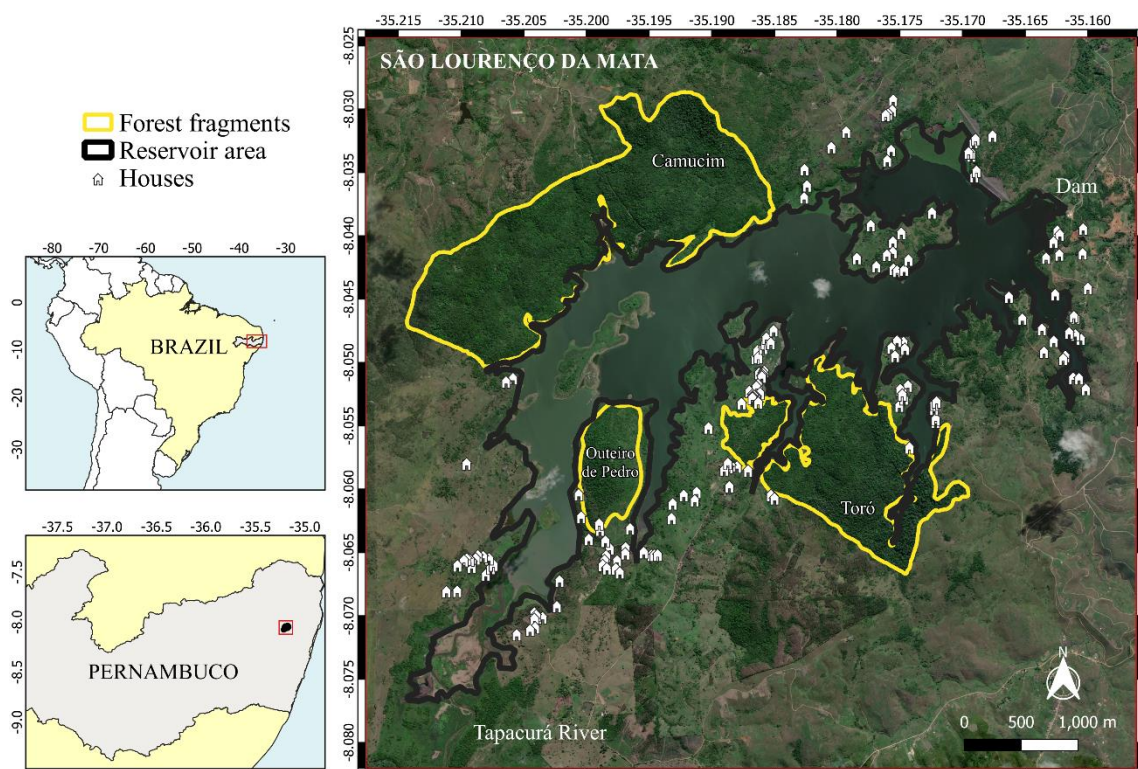
Broad-snouted caiman's populations in Brazil often small and isolated, mostly because of habitat fragmentation and specie's reduced dispersion patterns (Zucoloto *et al.*, 2021). In this study, we undertook the longest spotlight monitoring ever conducted for a wild broad-snouted caiman population and evaluated the temporal and spatial dynamics of a population of broad-snouted caiman inhabiting a large water reservoir in north-eastern Brazil, subjected to different regimes of human use, both of its lake and of its surrounding terrestrial landscapes. We investigate how weather conditions, water temperature, habitat, and human variables influence the detectability of caimans during surveys, describe variation in population age-structure, and distribution in a highly impacted Atlantic Forest reservoir.

## **METHODS**

### **Study area**

The Tapacurá reservoir was formed by damming of the Tapacurá River in 1973, near the municipality of São Lourenço da Mata, State of Pernambuco, north-eastern Brazil (8.043856° S, 35.195710° W) (Fig. 1). It is one of the largest freshwater sources in eastern Pernambuco, supplying more than a third of the

state's urban population (Santos *et al.*, 2021). The region's climate is tropical humid, with average rainfall of 1300 mm in the wet season (March–August) and less than 100 mm in the dry season (Rodal *et al.*, 2005). The average surface area of the reservoir is 8 km<sup>2</sup>, but it varies greatly between dry and rainy seasons, when water volume may retract to less than 3% (e.g., 1994) and expand to over 130% (e.g., 2011), when water flows through dam spillways.



**Figure 1.** Tapacurá Reservoir located in São Lourenço da Mata city, Pernambuco, Brazil. Atlantic Forest fragments are a common habitat within the reservoir and local communities are distributed around the forest.

Adjacent to the reservoir, along its north, south and southwest sectors, there are three conservation units encompassing remnants of semi-deciduous Atlantic Forest vegetation: Mata do Camucim, Mata do Toró, and Mata do Outeiro de Pedro (Rodal *et al.*, 2005) - which are categorized as “Wildlife Refuge” by Brazilian laws (Pernambuco 2011). Roughly 5.4 km<sup>2</sup> of native forest cover the margins of the reservoir, with legally protected areas comprising 1.7 km<sup>2</sup>. The remaining margins are surrounded by open fields, agriculture, and livestock areas

(Mascarenhas-Júnior *et al.*, 2020). Deforestation, illegal hunting, and intense fishing activity (including in areas bordered by forest) have been documented in Tapacurá (Mascarenhas Júnior *et al.*, 2018; Santos *et al.*, 2020).

## Study Design

From April 2015 to June 2022, we carried out 50 spotlight surveys, at least quarterly, to count and capture caimans. Surveys started after sunset (*ca.* 18:30). We moved through accessible areas in the reservoir in a 6.2-meter boat with a 15 hp engine at a speed of 8 km/h, recording all track distances. Not all areas of the reservoir were accessible because of shallow water depth, dense aquatic vegetation (mainly the common water hyacinth *Pontederia crassipes*), and fishing gillnets that tangled in engine's propeller. Otherwise, survey routes comprised a complete survey of the reservoir and river sections. We did not perform surveys during intense rain or foggy conditions.

We used a spotlight attached to an external battery to locate caimans by eyeshine (Magnusson, 1982). Spotlights were able to detect caimans positioned roughly 600 m away in ideal conditions. All counts were conducted by the same observer, who had previous experience in nocturnal caiman detection. For each caiman observation, we recorded the GPS position using a Garmin eTex hand GPS and the general habitat of the detection: near forested margin (north and south sectors), in open water (dam and river sectors), or among floating aquatic vegetation. To determine the size class, we estimated total length (TL) and snout-vent length (SVL) by a visual assessment of head size. We categorized observations into juveniles (SVL < 25 cm), subadults (SVL 25 cm – 67.9 cm) or adults (SVL > 67.9 cm), following size-cutoffs given by Leiva *et al.*, (2019). We categorized some caimans as unknown size class because of difficulties approaching to estimate their head size. All size estimates were made by the same observer, so any bias would be consistent across all surveys. To calibrate the accuracy of size estimates, we captured 60 specimens (all without tail injuries) using locking cable snares. Captured individuals were restrained with adhesive tapes to allow collection of biometric data (SVL and TL). We performed linear regressions to determine the accuracy of the observer's size estimations, which were made before capture. Observer size estimation was highly accurate ( $r^2 = 97.14$ ,  $P < 0.01$ ; Online Resource 1).

Every 30 min during surveys we measured abiotic variables: water temperature, air relative humidity, estimated percentage of cloud cover and percentage of lunar luminosity. Additionally, for each survey occasion, we obtained the percentage of the reservoir's water volume (100% represents the maximum capacity before it leaks through the spillways) and daily rainfall, both provided by Agência Pernambucana de Águas e Clima ([www.apac.pe.gov.br](http://www.apac.pe.gov.br)). We also obtained location-specific reservoir bathymetric values (measured in quota, a proxy for depth) provided by Companhia Pernambucana de Saneamento ([servicos.compesa.com.br](http://servicos.compesa.com.br)). We recorded and georeferenced the presence of fishing gillnets during spotlight surveys using the same hand-held GPS.

## **Data analysis**

### *Data standardization*

To account for differences in area travelled because of changes in water volume, shorelines, and inaccessible areas over the study, we standardized all counts by dividing counts by distance traveled, producing encounter rates (raw counts/km traveled). We also created a 62,500 m<sup>2</sup> grid of our study area by gridding the reservoir in 250 m x 250 m cells, spatially grouped in three different sectors: river (western sector), forest (north and southern sections) and dam (eastern sections). The size of grid cells was defined considering caimans are expected to be essentially sedentary and their nocturnal movements should not exceed grids size. Hence, the same individual is unlikely to move among different cells within the same survey occasion. We quantified the number of surveys we visited each grid cell.

### *Population structure and size*

In order to estimate population size and age structure, we used the methods described in Messel *et al.*, (1981) and King *et al.*, (1990), which incorporate the indirect spotlight method based on population visible fraction ( $vf$ ). To enhance the accuracy of our estimations, we assumed that: 1) samples are representative of the population; 2) unknown size-classes were proportionally distributed across all size classes in relation to their frequencies in the population; and 3) the ability of observers to detect each size class is equal and does not

change through time (Woodward and Moore 1993). Messel *et al.*, (1981) estimated  $vf$  in crocodylian spotlight surveys as:

$$vf = \frac{\underline{x}}{\sum^{sc} \max} \quad (1)$$

where  $\underline{x}$  represents the average number of caimans spotted per survey and  $\max$  is the maximum number of sightings for each size class. King *et al.*, (1990) proposes estimating  $vf$  as:

$$vf = \frac{\underline{x}}{(2SD + \underline{x})1.05} \quad (2)$$

where SD is the standard deviation considering each survey. To calculate population size (N) with a 95% confidence interval using  $vf$ , both methods define N as

$$N = \frac{\underline{x}}{vf} + \frac{[1.96(SD)]^{0.5}}{vf} \quad (3)$$

We performed a time-series analysis to address annual variations in population size estimates for both Messel *et al.*, (1981) and King *et al.*, (1990) approaches. First, we transformed population estimates into a time-series data starting in 2015 with annual frequency. We then calculated stationarity tendency of the temporal data using the Kwiatkowski-Phillips-Schmidt-Shin (KPSS) test, available in the *tseries* package (Trapletti and Hornik 2023) of R program. Subsequently, we employed a Box-Jenkins Auto-Regressive Integrated Moving Average (ARIMA) modeling utilizing the built-in *stats* package in R to capture trends within temporal observations. To validate the absence of significant population size changes over our study period, we conducted a Shapiro-Wilk test to assess the normality of residuals obtained from the ARIMA models. We repeated the analysis for encounter rates values, considering data on a quarterly basis. It is worth noting that we conducted only two surveys in 2019 and 2020

because of logistic issues related to the onset of the Covid-19 pandemic, so we did not consider these years in time-series analysis.

### *Seasonal and abiotic effects*

We conducted a chi-squared test to compare caiman detection in areas with or without floating aquatic vegetation, considering different sectors of the reservoir. We classified each observation as either "presence" or "absence" of vegetation in each reservoir sector based on the exact moment of detection to build the contingency table. We repeated the analysis for total counts and each size class separately.

We used Student's T-test to compare caiman encounter rates in the dry and wet seasons, after verifying data normality ( $W = 0.99$ ,  $p$  value = 0.99) and confirmed homogeneity of residuals by a Levene's test ( $F = 4.19$ ,  $df = 47$ ,  $p$  value = 0.05).

We used a Gaussian Generalized Linear Model (GLM) framework to determine the effects of covariates on encounter rate, our response variable (Zuur *et al.*, 2009). We created models for total encounter rates, as well as for encounter rates at each size class. First, we scaled all continuous variables by subtracting the mean and dividing by the standard error of each variable. To check overdispersion, we used the ratio between the sum of squares of residual deviance and degrees of freedom (Gardner *et al.*, 1995). We checked for multicollinearity between explanatory variables by using the Variance Inflation Factor ( $VIF < 5$ ) (Shrestha 2020). In our modeling framework, we built models using water temperature, daily rainfall, air relative humidity, percentage of clouds in the sky, percentage of moonlight, reservoir volume, depth, and date variables as fixed effects. We converted the date of survey into numerical format using the number of days since the start of the study period. We also included a null and global covariates model. To rank models, we used Aikake's Information Criteria ( $AIC_c$ ), defining the best models as those with  $\Delta AIC_c < 2$  (Burnham and Anderson 2002). We used the parameter estimates from models within  $\Delta AIC_c < 2$  to calculate an averaged model using the *lme4* package in R (Bates *et al.*, 2015).

We conducted the multi-model inference with the package *MuMIn* (Bartoń 2023), and graphics created with *ggplot2* package (Wickham 2016).

### *Occupancy and detectability*

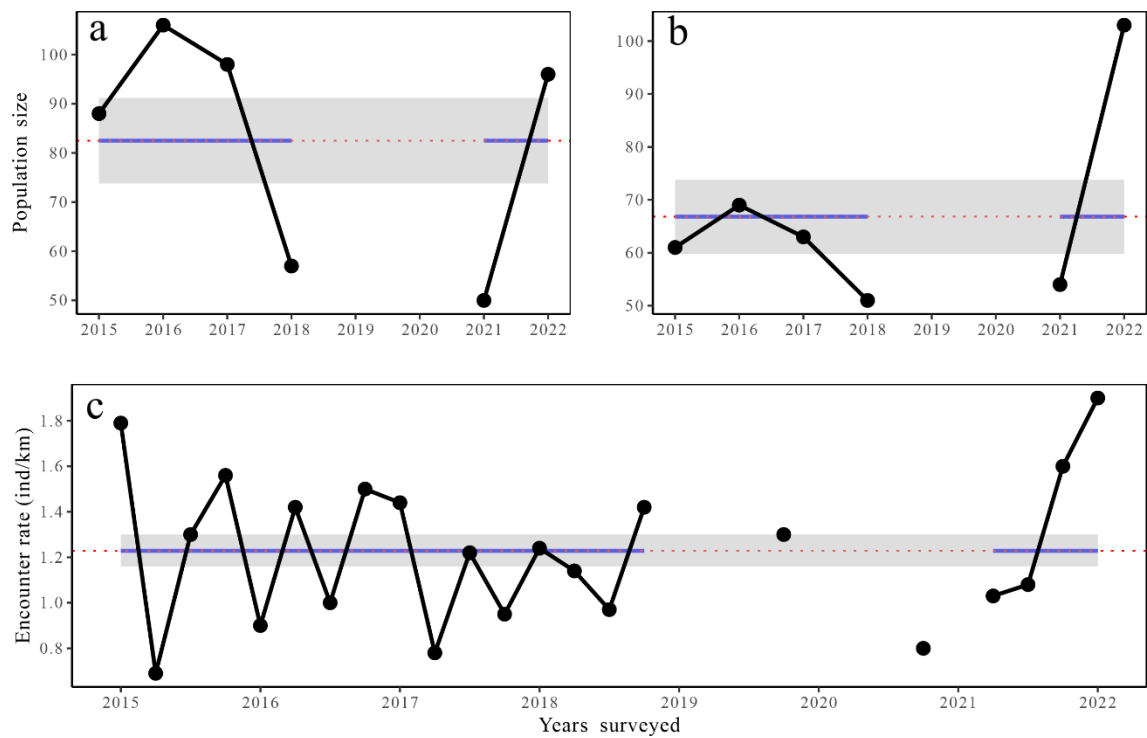
We built single-species and single-season models to predict caiman occupancy in the reservoir ( $\Psi$ ), considering imperfect detection ( $p$ ) in spatially and temporally replicated survey data (Mackenzie *et al.*, 2006). We analyzed the data at the scale of individual grid cells. We included the significant covariates present in GLM's best-ranked models as fixed terms for determining the predictors of total counts of each survey as observation-level covariates in the occupancy model excluding water depth, which we decided to use as a site-level covariate, considering the average depth of each grid cell. We also incorporated site-level covariates, including the frequency of encounter of fishing nets (number of gillnets divided by the number of surveys) and the distance of each grid cell to the closest forest fragment (measured from the centroid of each grid cell). We repeated model selection based on AIC<sub>c</sub> (see above) to estimate the probability of occupancy in each site and calculated the detection probability for site-level covariates once a grid cell had been occupied by at least one caiman. To calculate differences between occupancy probability in grid cells of river, dam and forest sectors, we performed a Kruskal-Wallis analysis, followed by a Dunn's *post hoc* test between each pair of sectors, after confirming data distribution was non-normal (River:  $W = 0.72$ ,  $p$  value  $< 0.01$ ; Forest:  $W = 0.77$ ,  $p$  value  $< 0.01$ ; Dam:  $W = 0.77$ ,  $p$  value  $< 0.01$ ). We used the R package *unmarked* (Fiske and Chandler 2011) to calculate occupancy and detectability estimation, and the R package *dunn.test* (Dinno 2017) to calculate differences in occupancy probability between each sector.

For all analyses, we assumed an alpha level of 0.05 as statistically significant and presented means using standard deviation (mean  $\pm$  SD) as a measure variation. We used the Shapiro-Wilk test to verify normality when appropriate. All data analyses were performed in R (R Core Team 2022) and maps were built in QGIS 3.28 software (QGIS Development Team 2023).

## **RESULTS**

At each survey night, we traveled an average of  $34.5 \pm 5.1$  km. We spent a total of 222:36 h in the field (average of  $04:45 \pm 01:37$  h of duration), varying according to reservoir's water level. The average encounter rate was  $1.3 \pm 0.7$  ind/km, varying between surveys from 0.4 to 4.94 ind/km. We counted an average of  $41.6 \pm 16.4$  caimans (max = 84, min = 6) per survey, with population size estimated in  $82 \pm 24$  caimans (min = 49, max = 106) according to Messel *et al.*, (1981)'s method and  $67 \pm 19$  (min = 51, max = 103) according to King *et al.*, (1990)'s method. The *vf* varied from 40% to 90% in the approach by Messel *et al.*, (1981) and ranged between 50% and 90% in the approach by King *et al.*, (1990). Detailed information on population size and annual *vf* estimates broken down by size classes are available in Online Resource 2.

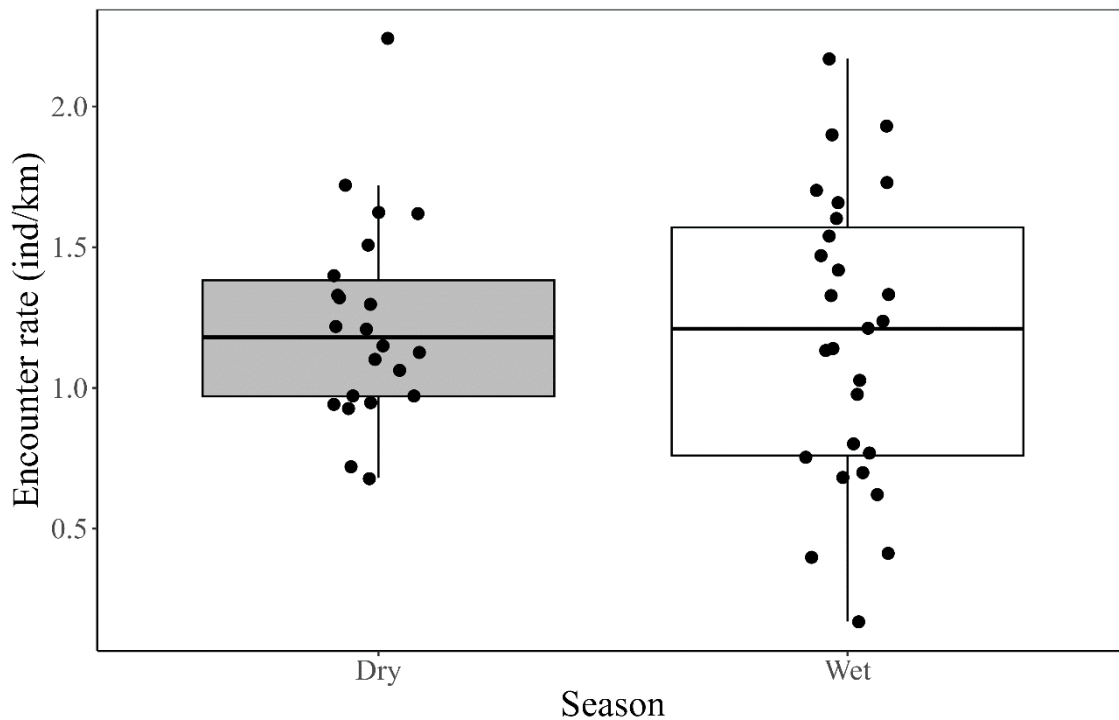
Our time-series analysis indicated a stationary trend in population size changes for both Messel *et al.*, (1981) (KPSS level = 0.17, truncation lag parameter = 2, *p* value = 0.10; Fig. 2a) and King *et al.*, (1990) (KPSS level = 0.22, truncation lag parameter = 2, *p* value = 0.10; Fig. 2b) approaches. Residuals from ARIMA models residuals followed a normal distribution (Messel *et al.*, [1981]: *W* = 0.86, *p* value = 0.18, CI = [65.49, 99.51]; King *et al.*, [1990]: *W* = 0.81, *p* value = 0.07, CI = [53.06, 80.60]), meaning no significant oscillations on population size estimates. Encounter rates changes also exhibited a stationary trend (KPSS level = 0.00, truncation lag parameter = 2, *p* value = 0.10) and we did not detect significant changes throughout our study period (*W* = 0.97, *p* value = 0.86, CI = [1.09, 1.36]) (Fig. 2c).



**Figure 2** Time-series analysis for estimating annual trends in caiman's population size based on Messel *et al.*, (1981) (a) and King *et al.*, (1990) (b) visible fraction approaches and for estimating trends in encounter rates on a quarterly basis (c) in Tapacurá Reservoir between 2015 and 2022. Blue lines indicate the stationary average tendency in the models, grey shadings indicate the standard error and red dotted lines indicate gaps in survey efforts (2019 and 2020).

Immature individuals (juveniles and subadults) were more representative in 88% of surveys, exceeding 60% of detections in these surveys (juveniles =  $13.9 \pm 8.4$ ; subadults =  $8.4 \pm 7.6$ ). Adults' average detection was  $7.8 \pm 4.9$  individuals and have been increasingly representative in our surveys from 2021, representing 70% of our counts by early 2022. We defined 28% of counts as unknow size class. Most caiman detections were associated with floating aquatic vegetation (71%;  $\chi^2 = 17.71$ ,  $df = 2$ ,  $p$  value  $< 0.01$ ), including those unknow size class. Adult and subadult counts did not reveal differences between areas with and without aquatic vegetation ( $\chi^2 = 1.877$ ,  $df = 2$ ,  $p$  value = 0.40 and  $\chi^2 = 5.485$ ,  $df = 2$ ,  $p$  value = 0.06, respectively), while juvenile detections were mostly associated with floating vegetation (75%;  $\chi^2 = 16.652$ ,  $df = 2$ ,  $p$  value  $< 0.01$ ).

Modeling encounter rates with GLM revealed correlations with environmental covariates, although we did not detect differences in encounter rates between seasons ( $t = 0.42$ ,  $df = 45.96$ ,  $p$  value = 0.67, CI: [0.20, 1.18] Fig. 3). We did not detect multi-collinearity in models' covariates ( $VIF \leq |3.30|$ ) nor was overdispersion observed for total or single size class counts ( $\leq 0.40$ ). From 256 candidate models, values of  $\Delta AIC < 2$  were seen only in one model for total encounter rates (overall  $R^2 = 0.42$ ), eight for models accounting only for juveniles (including null model; overall  $R^2 = 0.16$ ), five for subadults (overall  $R^2 = 0.20$ ), and six for adults (overall  $R^2 = 0.45$ ) (Table 1). Water temperature had a positive effect on detection after averaging parameters of best-ranked models in all size classes (except for the adult size-class model) but was only significant on total encounter rates (Fig. 4a;  $\beta = 0.18$ ,  $p$  value = 0.02, CI: [0.03, 0.32],  $R^2 = 0.10$ , Table 2). Humidity had a positive effect on encounter rate (Fig. 4b;  $\beta = 0.23$ ,  $p$  value < 0.01, CI: [0.10, 0.36],  $R^2 = 0.13$ ), while cloud coverage and daily rain had negative effects (Fig. 4c, d,  $\beta = -0.17$  and  $-0.16$ ,  $p$  value = 0.01 and 0.03, CI: [-0.29, 0.04 and -0.29, 0.03],  $R^2 = 0.06$  and 0.06, respectively) (Table 2). No covariates in the subadult models were significant, but water temperature and daily rain were present in four of five models with  $\Delta AICc < 2$  ( $\beta = 0.05$  and  $-0.05$ , respectively,  $p$  value = 0.09 and  $p$  value = 0.09, respectively, CI: [-0.01, 0.10] and CI: [-0.10, 0.01], respectively) (Table 2). Date had a positive effect in adults encounter rate (Fig. 4e;  $\beta = 0.015$ ;  $p$  value < 0.01, CI: [0.07, 0.23],  $R^2 = 0.34$ ) (Table 2), meaning that more adult caimans were spotted at the latter surveys of the study period. The null model was ranked as the best model for encounter rates of juveniles, indicating a potential lack of effect of our selected covariates on counting at this age class (Table 2).



**Figure 3.** Seasonal variation in *Caiman latirostris* encounter rate in the Tapacurá Reservoir between 2015 and 2022.

**Table 1.** Model selection results of abiotic covariates predicting *Caiman latirostris* counts in the Tapacurá reservoir between 2015 and 2022. Along with the global and null models, only models with  $\Delta$  Aikake's Information Criteria ( $AIC_c$ ) distance  $< 2$  are presented. All covariates were scaled (mean = 0, Standard error = 1). C: Clouds; R: Daily rain; D: Depth; H: Humidity; Wt: Water temperature; M: Moonlight; Dt: Date; Rv: Reservoir volume. np: Number of parameters, logLik: Log likelihood of the model;  $AIC_c$ : 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 2).

Total					
Model	np	logLik	$AIC_c$	$\Delta AIC_c$	Weight
C + R + D + H + Wt	4	25.15	-41.3	0.00	0.07
Global	10	27.09	-27.5	13.76	$< 0.01$
Null	2	21.13	-38.0	3.30	0.01
Juvenile					

<b>Model</b>	<b>np</b>	<b>logLik</b>	<b>AIC<sub>c</sub></b>	<b>ΔAIC<sub>c</sub></b>	<b>Weight</b>
Null	2	-28.28	60.85	0.00	0.21
Wt	3	-27.64	61.86	1.02	0.13
M	3	-27.68	61.94	1.10	0.12
R	3	-27.69	61.96	1.12	0.12
R + Dt	4	-26.50	62.01	1.16	0.12
Dt	3	-27.76	62.11	1.27	0.11
R + Dt + H	5	-25.39	62.33	1.48	0.10
H	3	-28.01	62.61	1.76	0.09
Global	10	-23.69	73.85	13.01	< 0.01

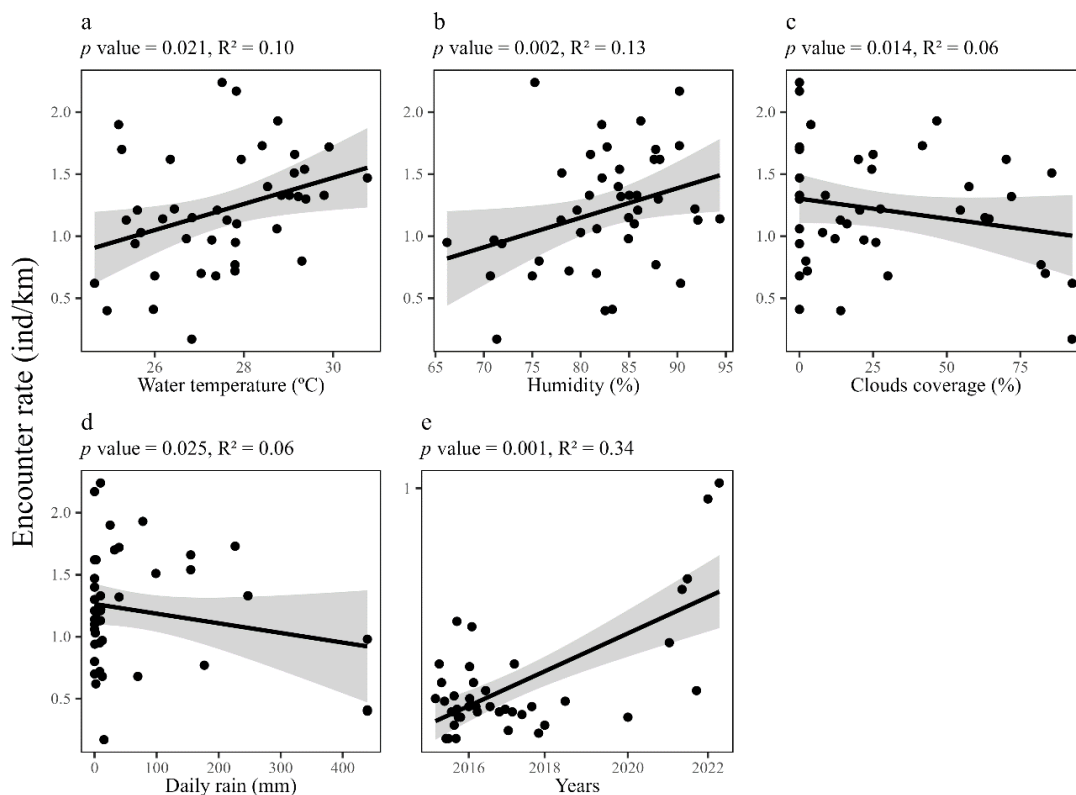
#### Subadult

<b>Model</b>	<b>np</b>	<b>logLik</b>	<b>AIC<sub>c</sub></b>	<b>Δ AIC<sub>c</sub></b>	<b>Weight</b>
R + Wt	4	25.15	-41.3	0.00	0.34
Wt	3	23.34	-40.1	1.19	0.19
R + M + Wt	5	25.79	-40.0	1.26	0.18
R	3	23.12	-39.6	1.62	0.15
C + R + Wt	5	25.50	-39.4	1.86	0.14
Global	10	27.09	-27.5	13.76	< 0.01
Null	2	21.13	-38.0	3.30	0.01

#### Adult

<b>Model</b>	<b>np</b>	<b>logLik</b>	<b>AIC<sub>c</sub></b>	<b>ΔAIC<sub>c</sub></b>	<b>Weight</b>
Dt + C	4	18.75	-28.4	0.00	0.27
Dt	3	17.38	-28.1	0.28	0.23
Dt + C + Rv	5	19.31	-27.0	1.45	0.13

Dt + C + D	5	19.29	-26.9	1.50	0.13
Dt + D	4	17.94	-26.8	1.62	0.12
Dt + Rv	4	17.92	-26.8	1.65	0.12
Global	10	19.84	-12.6	15.82	< 0.01
Null	2	5.04	-5.77	22.64	< 0.01



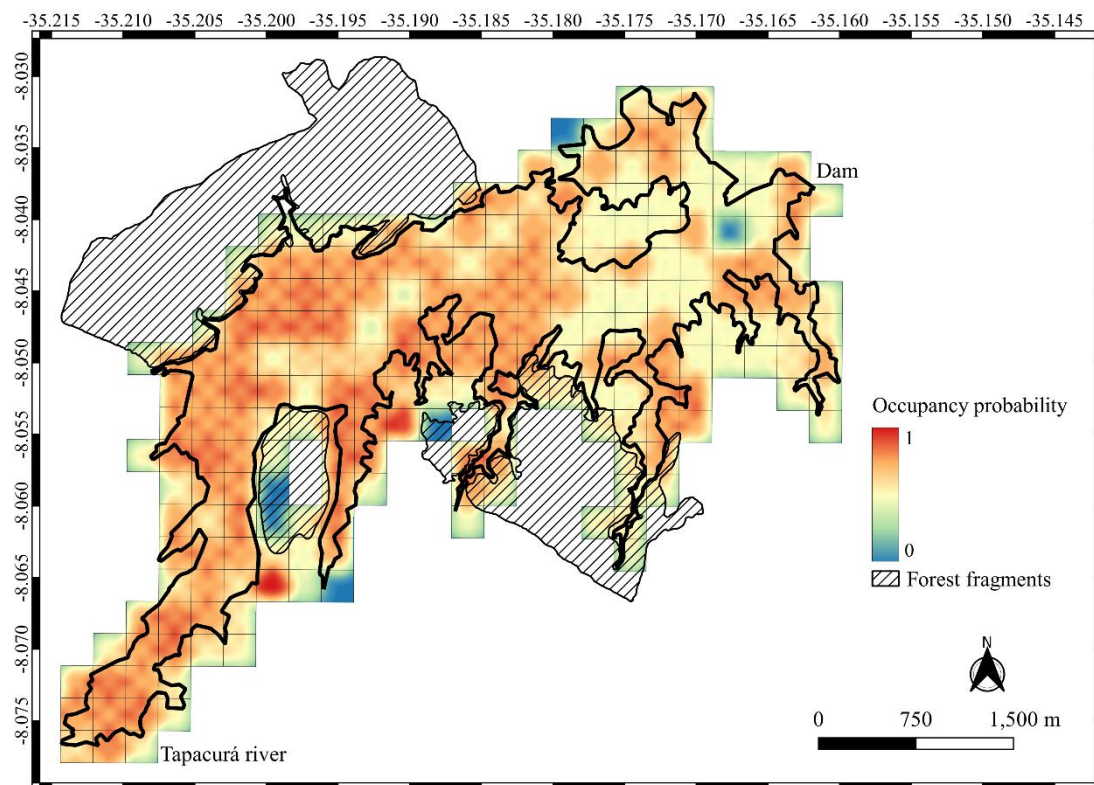
**Figure 4.** Univariate linear regressions of significant covariates that predicted total encounter rates (individuals/kilometer) of caiman determined through a multi-model framework, represented by individuals per kilometer. The four most important covariates for total encounter rate were (a) water temperature, (b) humidity, (c) cloud coverage and (d) daily rain, and (e) survey year was the most important covariate for adult's encounter rate. Gray shading indicates the standard error.  $p$  value: Statistical significance;  $R^2$ : Coefficient of determination.

**Table 2.** Gaussian generalized linear model averaged parameters of the covariates predicting *Caiman latirostris* counts in the Tapacurá reservoir between 2015 and 2022. Covariates were scaled (mean = 0, Standard error = 1). Models with  $\Delta\text{AICC} < 2$  were averaged.  $\beta$ : Coefficients estimate; SE: Standard Error; W. temp.: Water temperature; Moon: Moonlight percentual; R. vol.: Reservoir volume.

Total						
Parameter	$\beta$	SE	t value	p value	CI 2.5%	CI 97.5%
Intercept	1.21	0.06	21.01	< 0.001	1.10	1.32
Daily rain	-0.20	0.07	-2.35	0.025	-0.29	-0.03
Humidity	0.23	0.07	3.43	0.002	0.10	0.36
Clouds	-0.20	0.06	-2.60	0.014	-0.29	-0.04
W. temp.	0.18	0.07	2.42	0.021	0.03	0.32
Depth	0.24	0.12	1.98	0.056	0.00	0.48
Juveniles						
Parameter	$\beta$	SE	t value	p value	CI 2.5%	CI 97.5%
Intercept	0.44	0.07	6.48	< 0.001	0.31	0.58
Date	-0.10	0.10	-1.54	0.132	-0.36	0.04
Daily rain	-0.10	0.08	-1.79	0.083	-0.30	0.01
Humidity	0.08	0.08	1.72	0.095	-0.02	0.30
W. temp.	0.08	0.09	0.75	0.457	-0.10	0.23
Moon	-0.10	0.07	-0.72	0.475	-0.20	0.09
Subadults						
Parameter	$\beta$	SE	t value	p value	CI 2.5%	CI 97.5%
Intercept	0.24	0.02	10.86	< 0.01	0.20	0.28
Daily rain	-0.10	0.03	-1.76	0.090	-0.10	0.01
W. temp.	0.05	0.03	1.73	0.090	-0.01	0.10

Clouds	0.02	0.02	-0.66	0.52	-0.06	0.03
Moon	0.03	0.02	1.31	0.200	-0.02	0.08
<b>Adults</b>						
<b>Parameter</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>t value</b>	<b>p value</b>	<b>CI 2.5%</b>	<b>CI 97.5%</b>
Intercept	0.26	0.03	9.78	< 0.001	0.21	0.38
Date	0.15	0.04	3.80	0.001	0.07	0.23
Clouds	-0.04	0.03	-1.38	0.176	-0.10	0.02
R. vol.	0.03	0.05	0.75	0.461	-0.06	0.13
Depth	0.03	0.05	0.15	0.880	-0.09	0.10

The occupancy and detection single-season model estimated an occupancy probability of  $0.91 \pm 0.03$  and  $0.16 \pm 0.01$  detection probability considering all visited sectors of the reservoir pooled. We found differences in occupancy among reservoir sectors ( $\chi^2 = 30.022$ ,  $df = 2$ ,  $p$  value < 0.01). Grid cells of river and forest habitats had high rates of occupancy ( $0.95 \pm 0.02$  and  $0.92 \pm 0.03$ , respectively; forest x river difference:  $Z = -1.22$ ,  $p$  value adjusted = 0.33) and occupancy at the dam sector was slightly lower ( $0.87 \pm 0.04$ ; river x dam difference:  $Z = -5.11$ ,  $p$  value adjusted < 0.01 and forest x dam difference:  $Z = -4.20$ ,  $p$  value adjusted < 0.01) (Fig. 5). All site-level covariates were included in models with  $\Delta AIC < 2$  (Table 3), with the presence of fishing nets exhibiting a strong positive effect on caiman occupancy and detection ( $c = 1.05$ ;  $p$  value < 0.01; CI: [0.24, 1.88]; Table 4, Fig. 6).



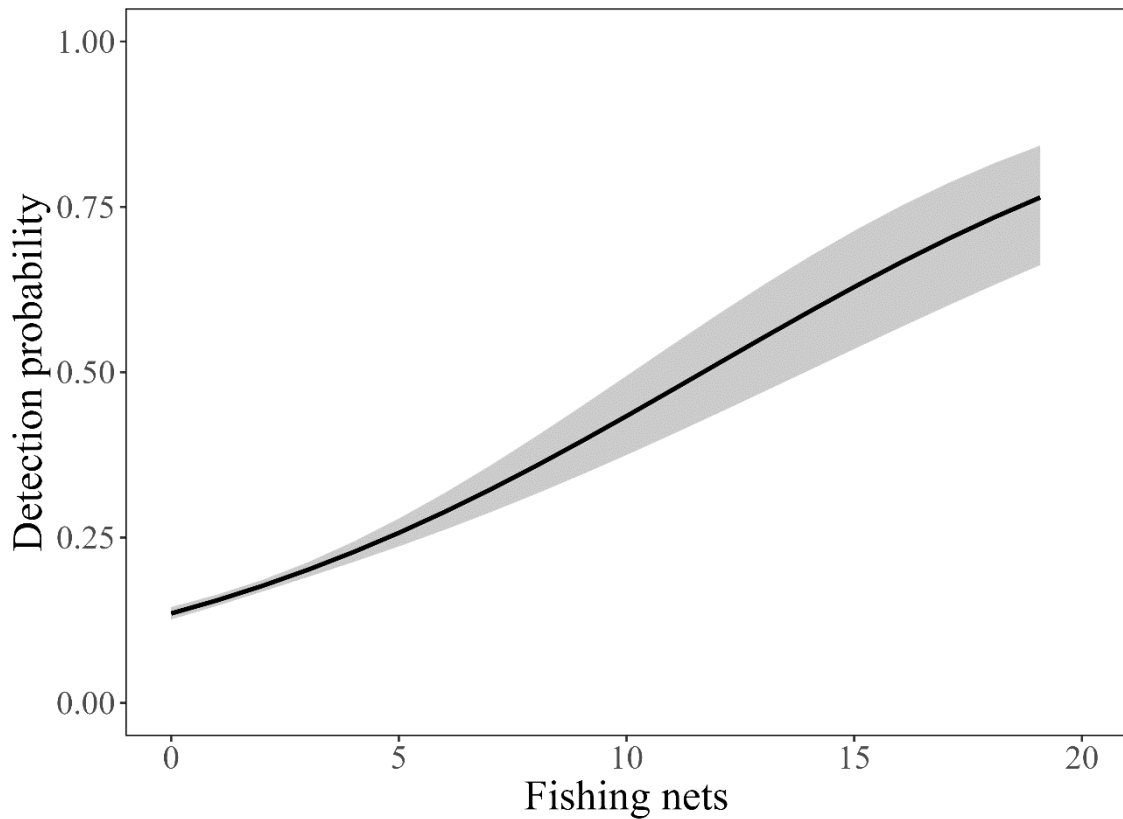
**Figure 5.** Predicted occupancy of *Caiman latirostris* based on single-species and single-season occupancy and detection model in the Tapacurá Reservoir between 2015 and 2022 (from 0 to 1). Values were obtained averaging best-ranked models following  $AIC_c < 2$ . The 225 grid cells were 250 m x 250 m.

**Table 3.** *Caiman latirostris* occupancy ( $\Psi$ ) best-ranked models in following  $AIC_c < 2$ . Global ( $\Psi$  [F + D + Dfo], p [C + H + R + Wt]) and null models were included as reference. Models included all observation-level covariates as detection (p) criteria. F: Fishing nets; D: Depth; Dfo: Distance from grid's centroid to the forest; C: Clouds; H: Humidity; Wt: Water temperature; R: Daily rain; np: Number of parameters, logLik: Log likelihood of the model;  $AIC_c$ : Aikake's Information Criteria;  $\Delta AIC_c$ : Distance from the best model; Weight: Weight of each model in the models with  $\Delta AIC_c < 2$ .

Occupancy	np	logLik	$AIC_c$	$\Delta AIC_c$	Weight
$\Psi$ (F + D)	8	-3397.92	6812.50	0.00	0.39
$\Psi$ (F)	7	-3399.18	6812.87	0.37	0.32
Global	9	-3397.71	6814.26	1.76	0.16
Null	6	-3406.46	6825.30	12.80	< 0.01

**Table 4.** Coefficients ( $\beta$ ) of the covariates in occupancy models to predict *Caiman latirostris* counts in the Tapacurá reservoir between 2015 and 2022. Covariates values were obtained averaging best-ranked models following  $AIC_c < 2$ . W. temp.: Water temperature; D forest: Distance from the nearest forest fragment; SE: Standard Error; CI: Confidence interval.

Occupancy (logit-scale)						
Parameter	$\beta$	SE	z value	p value	CI 2.5%	CI 97.5%
Intercept	2.31	0.67	3.47	0.001	1.01	3.73
D. forest	< 0.01	< 0.01	0.37	0.709	-0.01	0.01
Fishing nets	1.03	0.38	2.74	0.006	0.32	2.12
Depth	-0.23	0.14	-1.61	0.108	-0.55	0.04
Detection (logit-scale)						
Parameter	$\beta$	SE	z value	p value	CI 2.5%	CI 97.5%
Intercept	-6.64	0.75	-8.88	< 0.001	-7.96	-5.06
Clouds	< 0.01	< 0.01	-1.28	0.200	0.00	0.00
Humidity	0.02	0.01	3.35	0.001	0.01	0.03
Rain	< 0.01	< 0.01	-2.07	0.038	0.00	0.00
W. temp.	0.13	0.02	6.23	< 0.001	0.08	0.16



**Figure 6.** *Caiman latirostris*'s detection probability based on fishing nets presence in the Tapacurá Reservoir, São Lourenço da Mata, Pernambuco, Brazil, between 2015 and 2022. Results were obtained from single-species and single-season occupancy and detection model after averaging best-ranked models following  $AIC_c < 2$ . Grey shading indicates prediction interval.

## DISCUSSION

Our modeling approaches indicate that, in Tapacurá Reservoir, caiman detectability is influenced by combinations of abiotic factors, habitats and fishing practices. This study represents the longest dataset of spotlight counts for a broad-snouted caiman population. Most studies for the species are based on estimates of population structure and distribution are limited to surveys spanning less than two years (Carvalho and Verás-Batista 2013; Fusco-Costa *et al.*, 2008; Mascarenhas-Júnior *et al.*, 2020; Mourão and Campos 1995; Passos *et al.*, 2014). Our present evaluation stands out for its comprehensive approach and long-term perspective. Long-term monitoring is fundamental for revealing reliable population and demographic trends and patterns in wild crocodylians (Woodward and Moore 1993). Crocodylians are long-lived and slow-growing animals, meaning that it could take several years to unveil how changes in landscape,

abiotic conditions and human disturbance influence their population parameters and distribution (Charruau *et al.*, 2022; Fujisaki *et al.*, 2011; Ortiz *et al.*, 2020). For instance, broad-snouted caimans reach sexual maturity at five years in captivity (Verdade *et al.*, 2003), but competition and resources availability in the wild can delay the onset of breeding until ca. 10 years (Moulton *et al.*, 1999; Simoncini *et al.*, 2013). To our knowledge, our assessment is the first broad-scale study allowing a better understanding of how broad-snouted caimans respond to environmental and human factors and how such responses influence their autecology and demography.

The average encounter rate of caimans we found in Tapacurá was about one caiman per kilometer, within the range of encounter rates observed for broad-snouted caimans in other regions of Brazil, which vary between 0.07 and 11.3 caimans per kilometer (Marques *et al.*, 2016; Mourão and Campos 1995). However, most population assessments revealed encounter rates less than one individual per kilometer (Fusco-Costa *et al.*, 2008; Carvalho and Batista, 2013; Passos *et al.*, 2014; Mascarenhas-Junior *et al.*, 2020). In comparison to other species of the genus, the broad-snouted caiman has a relatively lower encounter rate, likely as a result of lower population abundance. For example, estimates based on populations of the Yacaré (*Caiman yacare*), resulted in more than 1,000 individuals per kilometer in some central-South America wetland areas (Campos, *et al.*, 2020a), and studies of wild populations often present encounter rates higher than 10 individuals per kilometer (Aguilera *et al.*, 2008; Coutinho and Campos 1996; Mourão *et al.*, 2000). Demographic estimates of the Spectacled Caiman (*Caiman crocodilus*) have also reported encounter rates higher than five individuals per kilometer (Balaguera-Reina *et al.*, 2021; Cartagena-Otálvaro *et al.*, 2020; Parra-Torres *et al.*, 2020), even in disturbed areas (Hernández *et al.*, 2021; Pereira *et al.*, 2022). The low detection probability observed during our study, combined with the fact that approximately one-third of caimans submerged upon boat approach, indicates a notable level of wariness within the population (Brazaitis *et al.*, 1996; Rebelo and Lugli 2001), which may also affect encounter rates. Crocodylians exhibit elusive behavior in areas experiencing human pressures including boat traffic, illegal hunting, or fishing activities (Grant and Lewis 2010; Tellez *et al.*, 2016). In Tapacurá Reservoir, high levels of intense

fishing practice and hunting pressure are suspected to increase caiman wariness (Mascarenhas-Júnior *et al.*, 2020; Rodrigues *et al.*, 2021).

The population size of broad-snouted caimans in Tapacurá showed fluctuations over the study period, but without significant changes since the beginning of monitoring (2015). Such relative stability could be attributed to stable birth and survival rates (Barboza *et al.*, 2021; Briggs-Gonzalez *et al.*, 2017), or to high site fidelity and poor dispersal patterns, which are not uncommon in broad-snouted caimans (Borges *et al.*, 2018; Verdade *et al.*, 2002; Zucoloto *et al.*, 2021). Moreover, the reservoir has abundant food supply, including both native and nonnative fish (El-Deir *et al.*, 2012), so the prevalence of agonistic interactions may be minimal and death rates by cannibalism (Campos and Mourão 2021; Drews 1990) may be low. Notably, data from interviews suggest that local human communities in Tapacurá perceive caiman population has not substantially decreased or increased in recent years (Bezerra, *et al.*, 2019a).

Although we did not find significant trends in population size over the years surveyed, we documented potential shifts in population structure. Juveniles and subadults make up most of the population, but the increasing number of adults is noteworthy. The relatively high number of immature caimans have been suggested as an indication of potential impacts of illegal hunting for other caiman populations (Balaguera-Reina and González-Maya 2009; Pereira *et al.*, 2022), as larger individuals are often targeted for meat in areas where subsistence activities are prevalent (Cook *et al.*, 2022). Furthermore, they may be killed by fishermen, who perceive them as competitors for fish resources or as retaliation for damage caused to fishing gears (Hilevski and Velasco 2020). An additional possibility is that adult caimans are harder to count, as individual wariness is often positively correlated with caiman size, as result of past negative interactions with humans (Pacheco 1996b). This may influence size-class estimation during surveys, as large caimans tend to dive in advance to observer approaching, resulting in many records unassigned to any size-class, and biasing counts towards larger numbers of small individuals (Aguilera *et al.*, 2008; Briggs-Gonzalez *et al.*, 2017; Flores-Escalona *et al.*, 2021). However, the number of adults spotted in Tapacurá has increased with time, with major changes between 2021–2022. Detecting a greater proportion of larger caimans, even with no significant reduction on counts

in smaller size classes, could be an indicative of high survival and growth rates (Campos, *et al.*, 2020b), and these changes could be attributed to recent conservation efforts targeting caiman populations (Borteiro *et al.*, 2008; Joanen *et al.*, 2021; Piña *et al.*, 2010). For instance, since 2018, multiple educational initiatives were implemented in Tapacurá, mostly trying to engage fishermen and the local community in conservation efforts and reduce hunting and poaching pressure (Bezerra, *et al.*, 2019b). Effects on population size from these programs may only be apparent after many years, but changes to size-class structure may be more immediate and detectable.

Most detections were made near or among floating aquatic vegetation, which provide protection to caimans against predators and human disturbances (Mascarenhas-Júnior *et al.*, 2020), while harboring more prey items than open water, including small fish and invertebrates (Borteiro *et al.*, 2009). However, excluding unknown size class, this pattern was observed only among juveniles. Due to their limited interactions with humans and potential predators, juvenile caimans tend to exhibit less wary behavior (Pacheco 1996b), and are less likely to dive or seek refuge within aquatic vegetation when boat approached. We suspect subadult and adult individuals tend to conceal themselves behind macrophyte banks (Portelinha *et al.*, 2022), decreasing detection and accurate size estimates.

Seasonality did not predict changes in caiman encounter rates. When surveyed areas are fixed, crocodylian counts often increase when water level and rainfall decrease, because the scarcity of available areas forces them to congregate in smaller territories (Lance *et al.*, 2011; Ouboter and Nanhoe 1988; Pantoja-Lima *et al.*, 2010). Still, in regions where floodplains are small or inaccessible, such as in Tapacurá, where the margins are relatively steep, it may be difficult to detect an effect of water level on counts (Wood *et al.*, 1985). Furthermore, we anticipate that the absence of other major neighboring rivers or reservoirs downstream of Tapacurá will lead to a reduction in emigration and immigration processes. As a result, encounter rates are expected to remain relatively stable across seasons.

Water temperature had positive effects on total encounter rate, while daily rainfall had the opposite effect. In crocodylians, warmer conditions lead to higher metabolic rates, increasing foraging, reproduction, or territorial behavior (Hutton and Woolhouse 1989; Mazzotti *et al.*, 2019; Nifong and Silliman 2017). They also increase prey availability and abundance, influencing crocodylian foraging tactics and movements (Rosenblatt and Heithaus 2011; Somaweera *et al.*, 2011). During our surveys, water temperature varied between 24.6–30.8°C, a range sufficient to increase movement rates in other crocodilian species (Fujisaki *et al.*, 2014; Goodwin and Marion 1979; Nifong and Silliman 2017). Interestingly, temperature was present in most of juvenile and subadult best-ranked models, but not in the adult models. As larger individuals have greater thermostability than smaller ones, they could be less affected by changes in temperature (Grigg and Kirshner 2015). Also, juvenile and subadult broad-snouted caimans have higher metabolic rates than mature individuals (Mascarenhas-Junior *et al.*, 2021), and metabolism and movements are probably more sensitive to changes in temperature. Conversely, adverse weather conditions and rain may impact crocodylian behavior, for example, by limiting their opportunities for feeding or hindering emergence from shelters (Ahizi *et al.*, 2021; Strickland *et al.*, 2018). Heavy rainfall can also limit habitat availability for smaller individuals (Herrera *et al.*, 2015). However, recent studies on West African crocodile (*Crocodylus suchus*) suggest that precipitation can have positive effects on counts, possibly due to effects on prey availability, increasing crocodylians' foraging movements (Velo-Antón *et al.*, 2014); Nifong and Silliman 2017).

Cloud coverage and air relative humidity were both significant factors in predicting caiman encounter rate. Cloud coverage in our study and others had a negative effect on counts, possibly because of its association to increased wind speed, which can limit caiman emergence and feeding (Pacheco 1996a; Sarkis-Gonçalves *et al.*, 2004; Strickland *et al.*, 2018). Overcast skies can reduce the amount of moon and starlight, which can disorient smaller individuals by visibility reduction (Murphy 1981), and prompt their movements towards open waters. Conversely, humidity positively affected counts, mainly because it is closely correlated to the decrease in air temperature. Due to specific heat properties, water tends to remain warmer for longer periods compared to the air. As a result,

when the water temperature exceeds air temperature, evaporation processes occur, consequently increasing the air relative humidity. Crocodylians often bask on the land or logs, even during the night (Nordberg and McNight 2023) but retreat to the water when the air temperature drops, potentially increasing their detectability (Hutton and Woolhouse 1989). It is important to note that dense fog can limit spotlight reach and can negatively impact counts (Woodward and Moore 1990).

Our study and others have failed to find an association with moonlight and water depth (Caut *et al.*, 2019; Da Silveira and Magnusson 1999; Villamarín *et al.*, 2017), though the effect of water depth may be marginally significant, and some authors have identified its significant influence on crocodylians counts (Nifong and Silliman 2017; Flores-Escalona *et al.*, 2021). Shallow waters in the Tapacurá Reservoir are found mostly near the margins, creating an ecotone between terrestrial and aquatic habitats. This ecological interface generally has a high species richness, influencing prey abundance (e.g., invertebrates and fishes) and thereby caiman detection (Caut *et al.*, 2019; Da Silveira and Magnusson 1999; Villamarín *et al.*, 2017). Moreover, these shallow areas often have extensive coverage of aquatic vegetation on the water surface (Mascarenhas-Júnior *et al.*, 2020), providing a protective habitat for caimans. Effects of moonlight are controversial between studies and can be site dependent (Da Silveira *et al.*, 2008). During dark nights, invertebrates can increase their activity due to lower predation risk, possibly increasing prey consumption by crocodylians (Eversole *et al.*, 2015; Perry and Fisher 2006). Nevertheless, intense moonlight can negatively affect observer visibility by dimming eyeshine reflection, reducing detection rate (Sarkis-Gonçalves *et al.*, 2004).

Although caimans occupied all sectors of the reservoir, predicted occupancy was higher in forested areas and the river course. Forested areas are the most protected habitats with the lowest levels of boating traffic and illegal hunting. Forested fragments also provide ideal nesting sites, offering protection from high solar radiation and human interference, while providing organic material for mounts due to dense vegetation cover (Banon *et al.*, 2019; Cintra 1988; Rodrigues *et al.*, 2021). In Tapacurá, nests are located away from human settlements and only found within the forest (Barboza *et al.*, 2021). Additionally,

forested areas are expected to harbor a greater abundance of prey items due to habitats complexity and nutrient cycling (Arantes *et al.*, 2018; Harper *et al.*, 1997; Lo *et al.*, 2021). The river sector likely has high prey availability from nutrient influences and continuous water flow, compared to stagnant water close to the dam (Maavara *et al.*, 2020). The decreased occurrence of caimans in the dam sector could be associated to a reduced availability of prey, due to hydrological alterations. These changes have the potential to disrupt habitat functioning by reducing spawning sites and creating barriers for species dispersion, reducing prey richness and abundance (Gehrke *et al.*, 2002). Moreover, the dam area presents reduced chemical features such as nitrogen and carbon (Bouvy *et al.*, 2003), which may reduce primary productivity and consequently the prey abundance for caimans. While occupancy is lower in habitats close to the dam, the average occupancy within the sector remains relatively high at over 80%, indicating that resources are still available in this area.

Fishing activity was positively correlated with an increase in caiman occupancy. The overlap between gillnets and caiman distributions has two potentially linked explanations: 1) Both caimans and fishers choose areas with higher fish abundance and compete for resources, and/or 2) caimans may be attracted to fish entangled in gillnets given that they are opportunistic and generalist feeders (Borteiro *et al.*, 2009). In both scenarios, bycatch and entanglement can be detrimental to caimans as they may sustain injuries, such as body compression and limb amputation (Mascarenhas-Junior *et al.*, 2018). Furthermore, entangled crocodylians can damage gillnets impacting subsistence activity (Amarasinghe *et al.*, 2015; Cook *et al.*, 2022). The presence of caimans in fishing areas can result in negative perceptions among local communities, potentially increasing in intentional killing of entangled individuals for retaliation (Pooley *et al.*, 2021). Although fishing activity does not appear to impact the overall population size of caimans in Tapacurá so far, the potential increase in negative interactions highlights a conservation concern.

## CONCLUSIONS

Our study yields several novel insights into the ecology of the broad-snouted caiman with implications to the species' conservation: 1) There are no significant changes in the population size of caimans in the Tapacurá Reservoir during our study, but observations include an upward trend in the number of adult individuals recorded in recent years. This observation potentially indicates a positive recovery trend following a period of significant human pressures; 2) Weather conditions are significant covariates impacting the detectability of caimans. These abiotic factors have the potential to influence crocodylians ecological dynamics, physiological stress, and the accuracy of observer detection. Nevertheless, effects vary across different size classes and interact with habitat characteristics, individual wariness, and human disturbance; 3) While all reservoir general habitat sectors were found to be suitable for caimans, river and forested areas exhibited greater occupancy compared to the dam. The availability of resources and level of protection may be influential factors that shape the preference of caimans; 4) A compelling correlation exists between fishing activity and the distribution of caimans. This relationship can be attributed to both selecting areas with abundant fish resources and/or caimans being attracted by fishes entangled in fishing nets.

Enhancing our comprehension of how alterations in habitats and environmental factors impact caiman populations is of utmost importance in formulating effective strategies for species conservation and management in Atlantic Forest. The protection of caiman's habitats in Tapacurá aligns with Pernambuco's law for conservation of natural resources, especially in areas integrally protected by state laws (Pernambuco, 2009). We are confident that our findings and the continued monitoring of broad-snouted caiman in the Atlantic Forest of Brazil will not only be useful for regional managers, conservationists, and decision-makers, but will also provide insights into which aspects affect the detectability, distribution the population dynamics of an important predator in a fluctuating environment. We expect our approach here presented to also be applied to other less studied and perhaps more threatened crocodylians.

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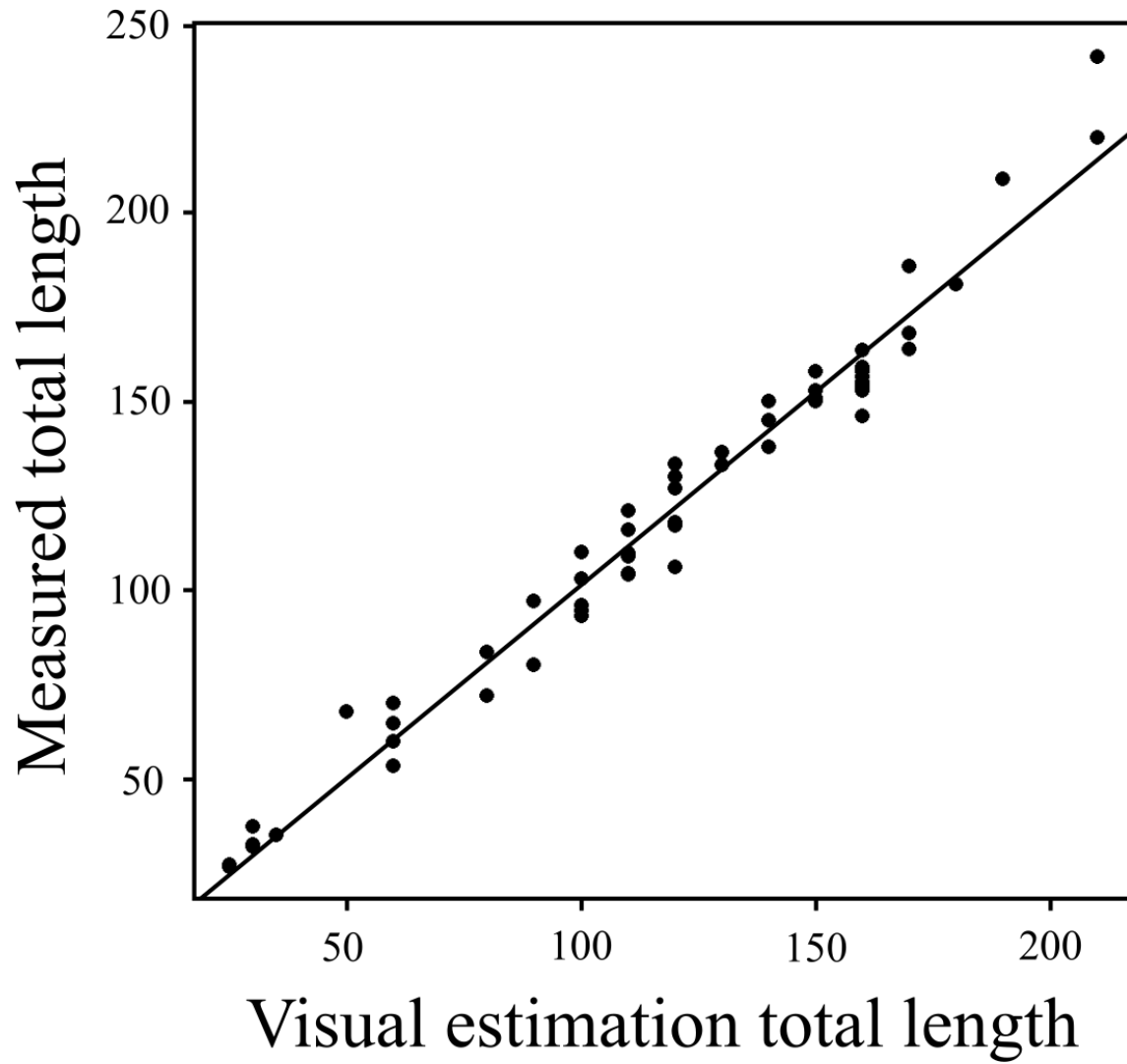
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**Supplementary File 1.** Estimate of measured total length (cm) of *Caiman latirostris* based on visual estimation (cm) by head width in surveys performed between 2015 and 2022 in Tapacurá Reservoir, São Lourenço da Mata, Pernambuco, Brazil. Accuracy of the observer to the nearest cm was 97%.

**Supplementary File 2.** Estimates of *Caiman latirostris* population size in Tapacurá reservoir based on Messel *et al.*, (1981) and King *et al.*, (1990) visible fraction (*vf*) equations. The estimated population size within each size class, *N*, is estimated by size-specific encounter rate for each survey.

<b>Messel <i>et al.</i>, (1981)</b>						
<b>Year</b>	<b>Juvenile</b>		<b>Subadult</b>		<b>Adult</b>	
	<b><i>vf</i></b>	<b><i>N</i></b>	<b><i>vf</i></b>	<b><i>N</i></b>	<b><i>vf</i></b>	<b><i>N</i></b>
2015	0.6	39	0.5	25	0.5	24
2016	0.5	48	0.5	30	0.4	28
2017	0.5	45	0.5	32	0.5	21
2018	0.7	31	0.7	11	0.7	15
2019*	1	34	1	8	1	4
2020*	1	18	1	18	1	6
2021	0.8	13	0.8	11	0.8	26
2022	0.6	21	0.9	20	0.8	55

<b>King <i>et al.</i>, (1990)</b>						
<b>Year</b>	<b>Juvenile</b>		<b>Subadult</b>		<b>Adult</b>	
	<b><i>vf</i></b>	<b><i>N</i></b>	<b><i>vf</i></b>	<b><i>N</i></b>	<b><i>vf</i></b>	<b><i>N</i></b>
2015	0.8	27	0.7	18	0.7	16
2016	0.8	31	0.7	20	0.7	18
2017	0.8	25	0.7	23	0.7	15
2018	0.8	27	0.8	10	0.8	14
2019*	1	36	1	9	1	4
2020*	1	19	1	19	1	7
2021	0.7	14	0.7	12	0.8	28
2022	0.9	15	0.5	35	0.9	53

\*Only one spotlight survey was performed in 2019 and 2020.

## 6 CAPÍTULO 3 – Effects of fishing activities on the broad-snouted caiman (*Caiman latirostris*) population in a Brazil reservoir

**Figura 3.** Espécime de jacaré-de-papo-amarelo (*Caiman latirostris*) emalhado em uma rede de pesca.



O jacaré-de-papo amarelo habita regiões intensamente impactadas por ações antrópicas, incluindo práticas de pesca para subsistência. No nordeste do Brasil, há registros de emalhes acidentais de jacarés em redes de pesca (Figura 3), o que pode lesionar os indivíduos ou destruir os equipamentos de pesca (Mascarenhas-Junior et al., 2018).

## ABSTRACT

Fishing is an important subsistence practice worldwide, but threatens the conservation of several non-target species, including crocodylians. We investigated the effects of artisanal fishing on the distribution of a remaining population of broad-snouted caiman (*Caiman latirostris*) inhabiting the Tapacurá reservoir, within the Atlantic Forest biome. We conducted spotlight surveys to detect caimans and gillnets deployed in the reservoir from April 2015 to June 2022. We evaluated temporal differences in gillnet encounter rates and the relationship between caimans and gillnets distribution. Gillnet encounter rates remained consistent year-round, which is aligned with subsistence practices. Gillnets positively predicted caiman detection, especially in the river channel and in forested margins. Caimans are opportunistic predators attracted by tangled fish in gillnets and may also prefer habitats similar to fishers due to the increased fish abundance. Future conservation plans must establish fishing zones to reduce human-caiman conflicts, benefiting species conservation, fishing stock and subsistence.

Keywords: Atlantic Forest; bycatch; crocodylians; encounter rates; gillnets; fisheries; human-wildlife conflict; spotlight surveys; subsistence.

## INTRODUCTION

Inland waters encompass land-locked rivers, channels, streams, lakes, and reservoirs, and comprise about 40% of the world's fish diversity and 20% of vertebrate diversity (Lévêque *et al.* 2008). Despite constituting merely 0.01% of Earth's water volume, these habitats contribute 41% to global fish production (Stiassny 1996; Lynch *et al.* 2016). Although inland fisheries have high socioeconomic relevance, they are often unregulated, unreported, illegally conducted within protected areas (Vince, Hardesty, and Wilcox 2021). Consequences of these practices pose significant threats to species conservation by facilitating biological invasions, pollution, depletion of fish stocks, and the inadvertent capture of non-target species (Raj *et al.* 2021; Constantino *et al.* 2022).

In freshwater habitats, fishing has direct or indirect impacts on species that are not the primary targets. For instance, overexploitation of fish can escalate competition for limited food resources among aquatic organisms, as well as between wildlife and fishers (Demaster *et al.* 2001; Wolfshaar *et al.* 2012). Fish are prey to several species

of aquatic non-fish vertebrates in freshwater ecosystems (Magnusson, Vieira Da Silva, and Lima 1987; Brum *et al.* 2021), and the reduction of their availability can disrupt natural predator-prey dynamics and trophic web interactions (Allan *et al.* 2005). Fisheries can also influence habitat selection by non-target species, as organisms can either be attracted by fish entangled on fishing nets or avoid fishing areas due to potential negative interactions with fishers or fishing gear, such as accidental entanglement (bycatch) or poaching (Morteo *et al.* 2012; Chávez-Martínez *et al.* 2022).

Crocodylians are particularly susceptible to impacts resulting from inland fishing practices. Fish constitutes a prominent component of the diet of crocodylians, with many species exhibiting opportunistic feeding behavior (Grigg and Kirshner 2015). In addition, their global distribution often overlaps with freshwater ecosystems characterized by high productivity and intense fishery, resulting in resource competition with fishers (McIntyre, Liermann, and Revenga 2016; Lourenço-de-Moraes *et al.* 2023). At the local scale, conflicts between humans and crocodylians may take place in the context of fishing activities, sometimes marked by negative interactions such as attacks on people or on domestic animals, which can elicit revengeful actions by fishers or local communities (Cook *et al.* 2022; Bitencourt and Maschio 2023). Also, bycatch of crocodylians in fishing nets may result in injuries or drowning (Platt and Thorbjarnarson 2000; Amarasinghe *et al.* 2015). These interactions may have varying effects on the spatial distribution of crocodylian individuals and populations depending on the intensity of pressure exerted by fishing activity. For instance, crocodylians may either avoid areas explored by fishermen due to previous negative experiences, or they may increase activity in these areas because of facilitated access to food resources, such as entangled fish (Ahizi *et al.* 2021; Caldicott *et al.* 2005).

The broad-snouted caiman, *Caiman latirostris* (Daudin, 1802), is a medium-sized crocodylian reaching an average length 2.5 meters, distributed in the central-eastern portion of South America, where it inhabits rivers, lakes, and lagoons (Siroski *et al.* 2020). Most of its geographic range overlaps with the Brazilian Atlantic Forest, where artisanal fishing is widely practiced. In recent years, there have been local records of broad-snouted caimans becoming entangled in fishing nets, frequently leading to severe injuries (Mascarenhas Júnior *et al.* 2018). These records were made in an artificial water reservoir in the north-eastern Atlantic Forest of Brazil, where different areas of the lake are subject to distinct conservation policies, varying from strict conservation purpose to areas open to farming and artisanal fishing. The latter

generally deploys gillnets, transported on small motorboats or canoes, and fish catch is mainly consumed or sold locally (Mascarenhas-Júnior *et al.* 2020). The outbreak of the COVID-19 pandemic in 2020, and the consequent reduction of the population's average income, have led more people to resort to alternative subsistence strategies (Stokes *et al.* 2020). If an increased demand for artisanal fishing occurred during the pandemic, we predict that the spatial distribution pattern of broad-snouted caimans and the rate of interactions between caimans and fishing gear was also affected during that time.

In regions with artificial dams, several studies have examined the repercussions of alterations in landscape and hydrology on fisheries (Marmulla 2001; Orr *et al.* 2012; Yoshida *et al.* 2020). Concomitantly, other studies provided valuable information on the population structure and distribution of crocodylians within similar lentic habitats (Saalfeld *et al.* 2008; Combrink *et al.* 2011; Campos *et al.* 2020). However, how fisheries predict crocodylians distribution or even impact in their survival and conservation in these altered environments is still unclear. In this study, we investigate the effects of fishing activity on the spatial and temporal distribution of caimans in a reservoir within the Brazilian Atlantic Forest biome based on survey data collected along seven years. Specifically, we investigate whether caiman detection is associated with fishing effort in space and time, and whether the COVID-19 outbreak possibly affected caiman interactions with fishing gear due to increased fishing effort. Additionally, we test if these associations vary among caimans in different body-size classes. Given the recent history of conflicts between caimans and fishers in Brazil, (Bitencourt and Maschio 2023), we discuss our results from a conservation perspective, delineating strategies that could potentially mitigate harmful interactions between them.

## **MATERIAL AND METHODS**

### **Ethics statement**

Caiman counts and handling when found entangled followed permits authorized by the Ethics Committee and Animal Use (CEUA) of Federal Rural University of Pernambuco (license #8606200622) and the Brazilian Biodiversity Authorization and Information System (SISBIO) from the Chico Mendes Institute for Biodiversity Conservation (ICMBio) (license #63030-4).

## Study site

We conducted surveys in the Tapacurá Reservoir (hereafter, Tapacurá), located in the municipality of São Lourenço da Mata, in the state of Pernambuco, Brazil (8.043856° S, 35.195710° W, Figure 1A). It is an artificial lake formed by a dam installed on the Tapacurá River in 1973. It supplies water to about a third of Pernambuco's urban population (Santos *et al.* 2021). Domestic sewage and effluents from the sugar cane industry flow into the reservoir, resulting in degraded water quality and high levels of eutrophication (Gunkel *et al.* 2003).

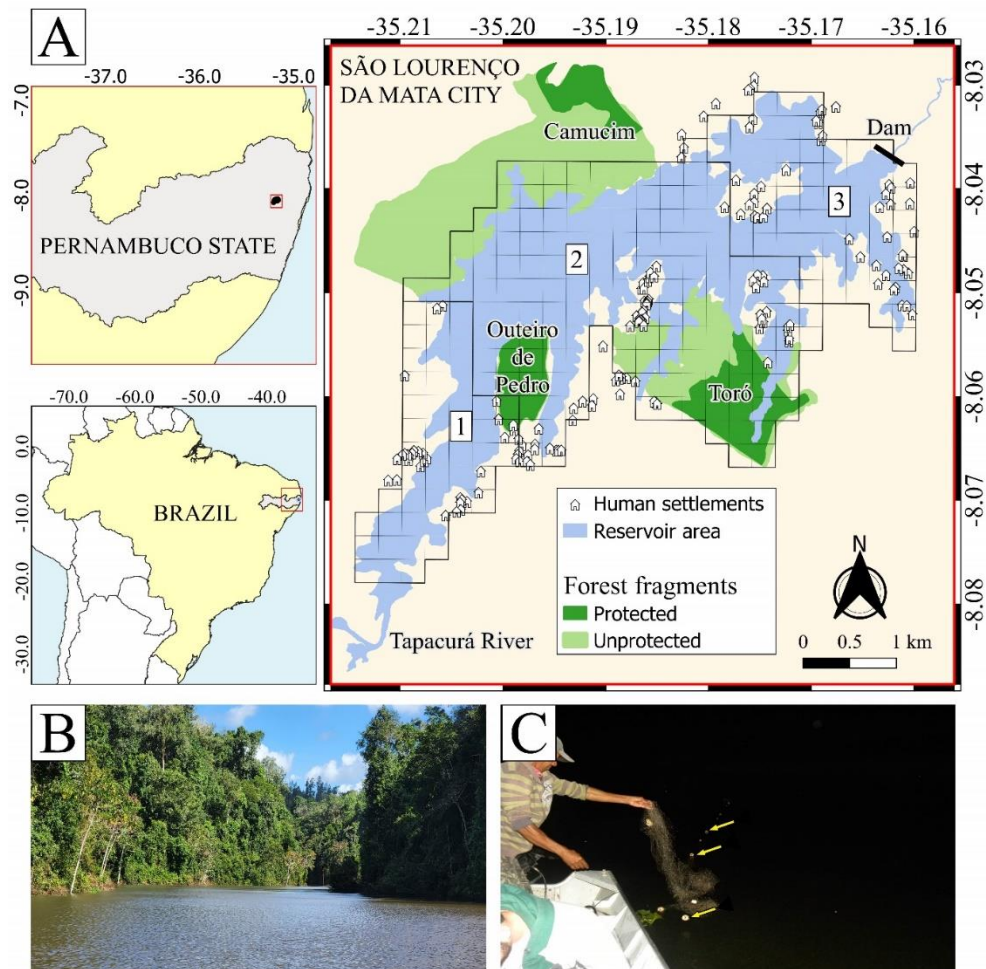
Tapacurá covers more than 8 km<sup>2</sup> with a volume of ca. 105,000.00 m<sup>3</sup> and it is part of the Capibaribe basin, a 470 km<sup>2</sup> watershed in the eastern portion of Pernambuco (Gunkel *et al.* 2003; Mascarenhas-Júnior *et al.* 2020). The climate in the area is Tropical Humid, receiving 1,300 mm of average annual rainfall, with a marked wet season between March and August (Rodal, Lucena, and Melo 2005). The water level of the reservoir can vary seasonally, ranging from 2% to 132% of its volume because of drought and floods, according to data available on Pernambuco's water management agency (*Associação Pernambucana de Águas e Clima* – APAC; <https://www.apac.pe.gov.br/>).

The reservoir's margins are covered by approximately 5.4 km<sup>2</sup> of lowland semi-deciduous Atlantic Forest fragments in its north, south and southwest sectors (Figure 1 A). These are, in part, legally protected as part of the forest fragments “Mata do Camucim” (north sector), “Mata do Toró” (Figure 1 B) and “Mata do Outeiro de Pedro” (both in the south sector) (Pernambuco 2011). These fragments are important wildlife corridors for native and endemic species, but also are impacted by deforestation, invasive species, and fire, according to data available on Pernambuco's environmental state agency ([www2.cprh.pe.gov.br/uc/](http://www2.cprh.pe.gov.br/uc/)). Seasonal vacation homes, ranches and communities occupy the remaining sectors of Tapacurá. Practices such as agriculture, ranching, poaching (Supplementary File 1), and artisanal fishing are common alongside the reservoir, mainly as means subsistence of the local human population (Correia *et al.* 2021).

## Fishing activity

Fishing is an important subsistence activity in Tapacurá, mainly practiced by local residents. Most fishing is by gillnets (Bezerra *et al.* 2019), a gear that stretch a

considerable distance, generally ca. 50 m, with some gillnets sets reaching between 200–300 m and extending from the surface to the pelagic zone (Figure 1 C). The deployment of gillnets is typically carried out using motorboats or canoes. Occasionally, fishers use other methods, such as casting nets or hook and line (Bezerra *et al.* 2019). Of the 16 fish species recorded in the reservoir (El-Deir *et al.* 2012), fishers most commonly target the nonnatives Nile Tilapia (*Oreochromus niloticus*) or the South American Silver Croaker (*Plasgiocion squamosissimus*), along with native Piaba (*Astyanax* spp.) and Trahira (*Hoplias malabaricus*) (Bezerra *et al.* 2019). Additionally, Tucunaré (*Cichla* spp.), another nonnative species, are often entangled in gillnets (Supplementary File 2).



**Figure 1.** Study area showing Tapacurá Reservoir (A), located in São Lourenço da Mata city, Pernambuco State, Brazil. The reservoir was divided into (1) river, (2) forest and (3) dam sectors. Example of Atlantic Forest fragment, a common habitat bordering the reservoir, named Mata do Toró

(B) in the southern section of Tapacurá Reservoir. Gillnets (C) are the most common fishing gear used in the reservoir and are often identified by buoys (depicted by yellow arrows).

### **Data collection**

We carried out 50 field expeditions in Tapacurá from April 2015 to June 2022 (at least one per quarter) to count and capture caimans, and account for gillnets deployed in the reservoir. Surveys started just after the sunset (ca. 06:30 pm), and we moved through the reservoir following the entire perimeter as much as we could using an engine boat (8 km/h of average speed), aiming to detect caimans by their eyeshine using a 600 meters-reach spotlight (Magnusson 1982). Occasionally, some areas could not be accessed because of dense floating vegetation (generally the common water hyacinth, *Pontederia crassipes*), shallow water depth, or fishing nets that would damage the boat's engine propeller. We recorded all track distances during the surveys. It's worth mentioning that we could only perform one survey in 2019 (March) and one in 2020 (February) because of logistic issues and restrictions imposed by the COVID-19 pandemic, respectively.

We estimated snout-vent length (SVL) of caimans by visual assessment of head size, and we categorized all sights into different size classes based on life stages of the broad-snouted caimans proposed by Leiva *et al.* (2019): Juveniles: SVL < 25.0 cm; Subadults: SVL 25.0 – 67.9 cm; Adults: SVL > 67.9 cm). All size class estimates were made by the same observer. During our surveys, we recorded all gillnets detected, usually identified by surface buoys. Rarely, gillnets were in poor condition and did not have floats. These nets were only identified when tangled in the boat's propeller. Caimans recorded at a distance shorter than 50 m to a gillnet were registered as "near gillnet" and those recorded at distances larger than 50 m were registered as "not near gillnet". All caimans and gillnets identified had their coordinates recorded. When possible, we captured the caiman using locking cable snares and restrained them with adhesive tape, in order to collect biometric data. We noted any direct negative interactions between caimans and gillnets during counting and measurements, and categorized them as 1) Entangled, if the specimen was wrapped in the net, but without any injury; 2) Injury, when tissue of forelimbs or/and hindlimbs was wrapped and damaged by netting or if a net or wire compressed specimen's trunk or/and abdomen;

4) Death, if we could confirm that *causa mortis* was directly related to fishing nets. We also observed whether caimans were in proximity to gillnets, but without negative interactions, when the distance was < 50 m.

### Data analysis

Our survey routes were designed to be adaptative to accessible areas within the reservoir (i.e., survey length varied slightly due to seasonal variation in the reservoir's water level). Hence, we calculated gillnet raw encounter rates by dividing the number of records per kilometer traveled. We also divided the study area into cells of 250 m x 250 m ( $n = 221$  cells) to understand the relationship between gillnets and caiman encounters. Grid cell size was determined considering the maximum length registered for gillnet sets in the reservoir. We calculated separately the values for gillnet and caiman encounter frequencies in each grid cell by dividing the number of surveys that were conducted within a grid cell by the number of surveys at which at least one caiman or gillnet was detected in that grid cell.

We calculated temporal variation in the average encounter rates of gillnets in the reservoir across four quarters of the year: (1) January–March; (2) April–June; (3) July–September; (4) October–December. We opted for the quarter system because the first three months of the year coincide with the Easter Christian Holiday, when fish consumption is higher in the region. Moreover, the second and third quarters correspond essentially to the wet season. We performed a non-parametric Kruskal-Wallis test to investigate differences in the encounter rates between year quarters because the fourth quarter presented non-normal data distribution ( $W = 0.72$ ,  $P = 0.01$ ). Additionally, we used the non-parametric Wilcoxon test to calculate changes in the average gillnet encounter rates before and after the onset of COVID-19 pandemics after detecting non-normal distribution in post pandemic data ( $W = 0.78$ ,  $p\text{-value} = 0.04$ ).

In order to calculate the relationship between gillnets and caimans encounter frequency, we performed two separate analyses. For the first analysis, we assigned each cell a binary value for presence (1) or absence (0) of a gillnet and separately a caiman to consider potential areas of interactions. We then calculated the spatial tetrachoric correlation between nets and caimans (Muthén *et al.*, 1988). In the second analysis, we used a logistic regression with a quasibinomial Generalized Linear Model

(GLM) to predict the frequency of encounter a caiman using gillnet frequency of encounter as a predictor in each grid cell, and modeling parameters by the maximum-likelihood method (Zuur *et al.* 2009). We chose a quasibinomial distribution because of overdispersion and confirmed model fits by log-likelihood (Pseudo  $R^2 = 0.12$ , Hemmert *et al.* 2018), and identified a significant improvement in the model over the base model (likelihood ratio p-value  $< 0.01$ , (Archer, Lemeshow, and Hosmer 2007). Areas not surveyed were excluded from our analysis.

We partitioned the reservoir into river (west), forest (north and south), and dam wall (east) sectors to investigate differences in encounter frequencies of gillnets and caimans between distinct sectors in the reservoir. After confirming non-normal distribution of encounter frequency in all reservoir sectors for both gillnets (dam wall:  $W = 0.65$ , p-value  $< 0.01$ ; forest:  $W = 0.85$ , p-value  $< 0.001$ ; river:  $W = 0.65$ , p-value  $< 0.001$ ) and caimans (dam:  $W = 0.95$ , p-value  $= 0.01$ ; forest:  $W = 0.91$ , p-value  $< 0.01$ ; river:  $W = 0.80$ , p-value  $< 0.01$ ), we proceeded to conduct a Kruskal-Wallis test to assess variation of frequencies among grid cells and to test for differences among sectors. Subsequently, we conducted a *post hoc* test using Dunn's method to further investigate specific pairwise differences. We calculated the spatial correlation between fishing and caimans encounter frequency overlaying each grid cell by the values of gillnets and caiman encounter frequency, creating coefficients ranging from -1 (high negative correlation) and +1 (high positive correlation).

We used the Wilcoxon test to calculate the differences between the average caimans sighted near to gillnets per quarter before and after the onset of COVID-19 pandemic, after confirming non normal distribution of both pre and post pandemic data ( $W = 0.86$ , p-value  $= 0.02$  and  $W = 0.65$ , p-value  $= 0.02$ , respectively). To evaluate the rates of entanglements or injuries, we conducted a chi-square test to examine whether the proportion of negative interactions with gillnets among different age classes was similar to that in overall observations of caimans near gillnets. We calculated the proportion of negative interactions dividing the number of entanglements and injuries by the total number of caiman observations made  $< 50$  m from gillnets.

We performed all statistical analyses in R (R Core Team 2023), using the packages *psych* for tetrachoric correlation (Revelle 2022), *rms* for logistic regressions (Harrell Jr 2022), *dunn.test* to calculate differences between gillnets and caimans encounter frequency in reservoir sectors (Dino 2017), and *raster* for spatial correlation

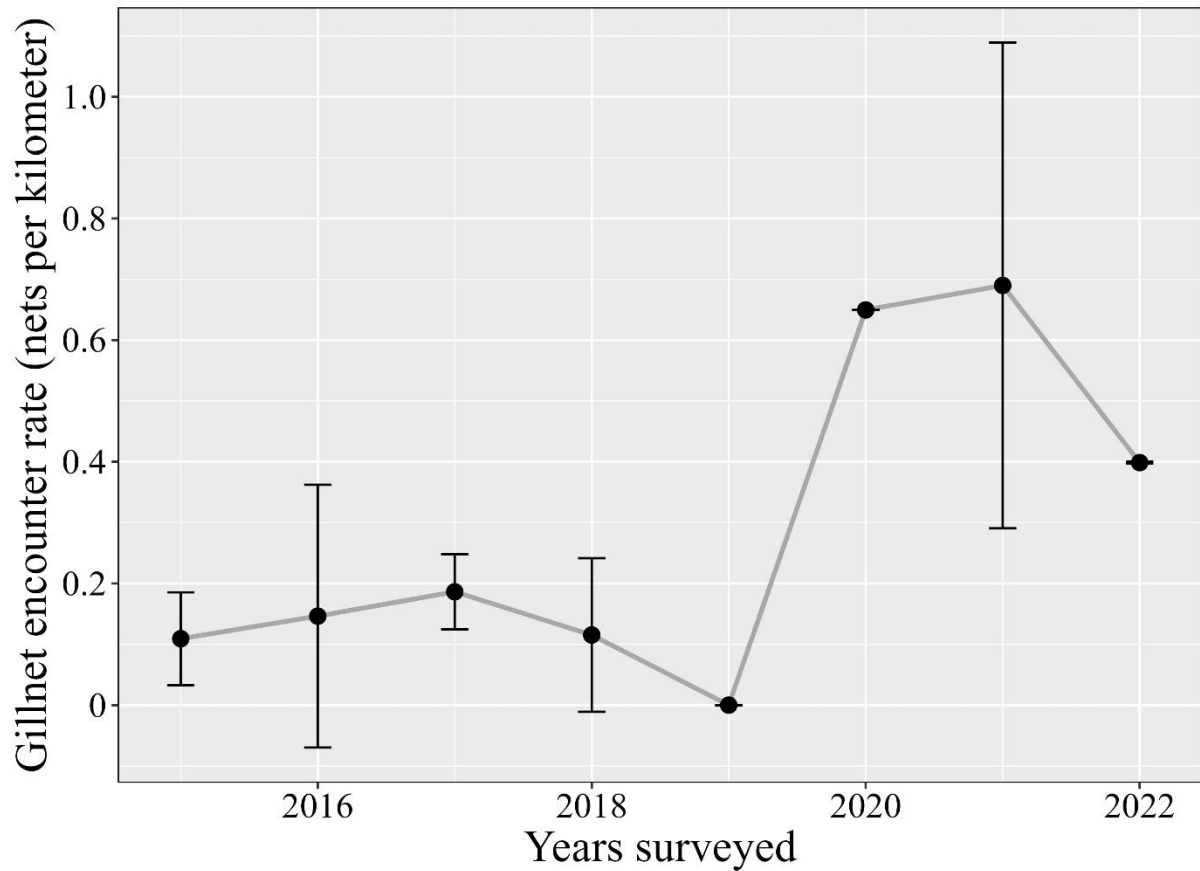
(Hijmans 2023). We used the *ggplot2* package of R to produce graphics (Wickham 2016) and developed the study area map using QGIS software (QGIS Development Team, 2022).

We considered  $\alpha = 0.05$  (alpha level) as statistically significant level in our analysis and reported standard deviation (mean  $\pm$  SD). When appropriate, we used Shapiro-Wilk test to verify normality assumptions.

## RESULTS

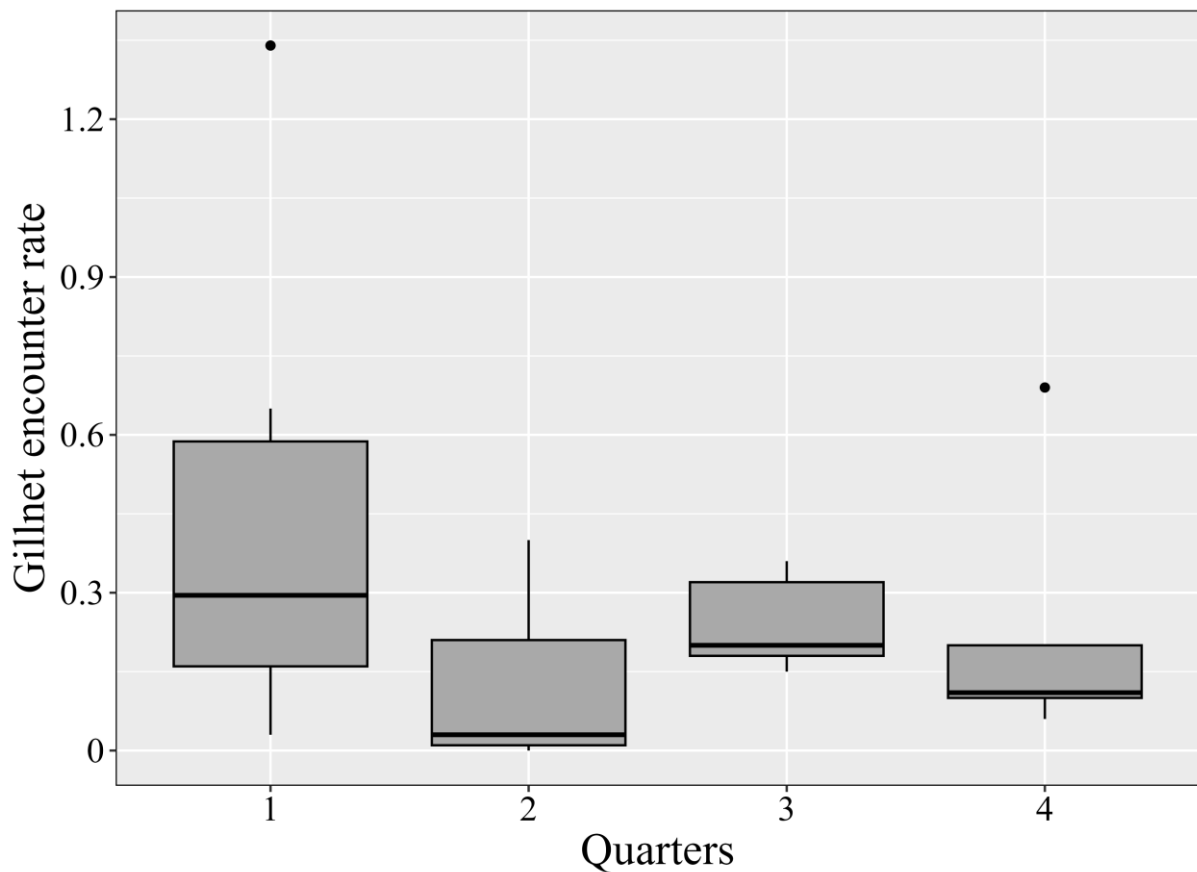
Our surveys routes averaged  $34.5 \pm 5.1$  km and we spent a total of 223:36 hours (04:45  $\pm$  01:37) in the reservoir across 50 nocturnal field surveys over seven years. We spotted  $42 \pm 16$  caimans (min = 6, max = 84) per survey, with detections structured as  $14 \pm 8$  juveniles,  $8 \pm 8$  adults,  $8 \pm 5$  subadults. We could not determine the size class of 28% of sights because individuals submerged prior boat approximation. The average frequency of encountering a caiman was  $0.19 \pm 0.18$  per grid cell.

We detected  $6 \pm 7$  (min = 0, max = 38, total = 312) gillnets per survey (Figure



**Figure 2.** Average raw encounter rates of gillnets (nets detected per kilometer traveled) during each year surveyed in the Tapacurá Reservoir, Pernambuco, Brazil, between 2015 and 2022. Black bars indicate standard deviation. It's worth noting that one survey was performed in 2019 and one survey was performed in 2020.

2). Gillnet encounter rate did not statistically differ among seasons of the year ( $\chi^2 = 2.788$ ,  $df = 3$ ,  $p\text{-value} = 0.43$ , Figure 3), but was higher after the onset of the COVID-19 pandemics (before:  $0.13 \pm 0.09$ ; after:  $0.64 \pm 0.34$ ;  $W = 90$ ,  $p < 0.01$ ). Considering all grid cells, the average frequency of encountering a gillnet was  $0.04 \pm 0.08$ .



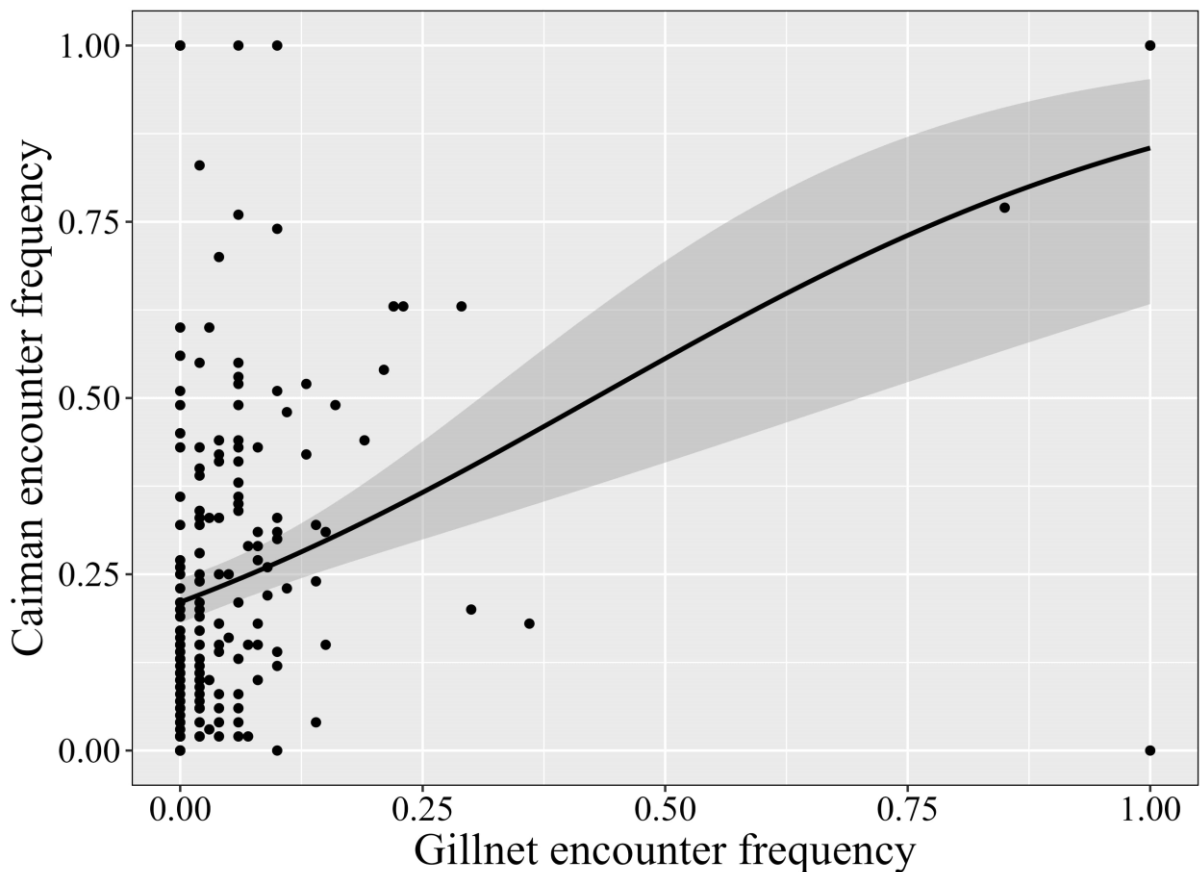
**Figure 3.** Seasonal differences between raw encounter rate of gillnets (nets detected per kilometer traveled) based on a non-parametric Kruskal-Wallis test over surveys in the Tapacurá Reservoir, Pernambuco, Brazil, between 2015 and 2022. Each number in x axis indicates one quarter of the year. 1: January to March; 2: April to June; 3: July to September; 4: October to December.

The correlation coefficient between the presence or absence of fishing nets and caimans in different cells was 0.71, which indicates a strong positive relationship between potential cooccurrence areas. We also identified that gillnets encounter frequency is a strong predictor of caiman encounter frequency (T-value = 4.71, p-value < 0.01; Table 1. Figure 4).

**Table 1.** Parameters from a quasi-binomial Generalized Linear Model predicting the frequency of encounter a caiman associated to the encounter frequency of gillnets the presence of a gillnet in the Tapacurá Reservoir, Pernambuco, Brazil, between 2015 and 2022.  $\beta$ : coefficient estimate; SE: Standard error.

	$\beta$	SE	T-value	p-value
Intercept	-1.32	0.10	-13.83	<0.01
Gillnets	3.09	0.66	4.71	<0.01

**Figure 4.** Frequency of caiman occurrence relative to gillnet encounter probability based on a quasibinomial logistic regression model from night surveys in Tapacurá Reservoir (2015 to 2022). Dark grey shading indicates standard error.



We found significant differences for both gillnet and caiman encounter frequencies among different sectors of the reservoir ( $\chi^2 = 26.80$ ,  $df = 2$ ,  $p\text{-value} < 0.01$  and  $\chi^2 = 9.82$ ,  $df = 2$ ,  $p\text{-value} = 0.007$ , respectively). Gillnets encounter frequency was higher in forest and river sectors than in the dam wall sector (forest x dam wall: Diff =

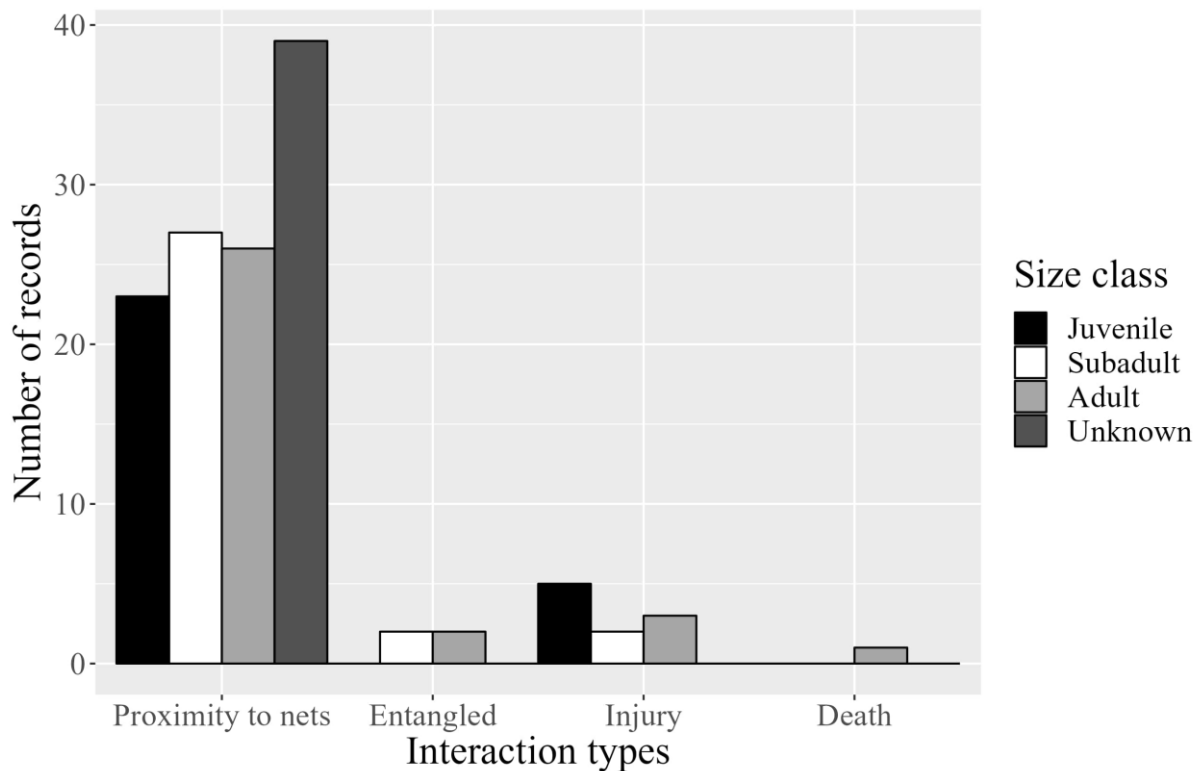
-3.97,  $p$ -value < 0.01; River x Dam: Diff = -4.78,  $p$ -value < 0.001) and the caimans encounter frequency was higher in forested areas than in the dam wall sector (forest x dam wall: Diff = -3.08,  $p$ -value < 0.01) (Table 2). The spatial correlation across grid cells in the reservoir was essentially positive ( $R = 0.32 \pm 0.41$ ).

**Table 2.** Dunn's *s post hoc* test for comparing gillnets and caimans encounter frequency in river, dam, and forest sectors of Tapacurá Reservoir, São Lourenço da Mata, Brazil. Surveys were conducted between April 2015 and June 2022. Diff: differences between means of groups compared.

<b>Gillnet encounter frequency</b>				
<b>Sector</b>	<b>Mean</b>	<b>SD</b>	<b>Diff</b>	<b>p-value</b>
Forest	0.04	0.04	-	-
River	0.10	0.12	-	-
Dam	0.01	0.04	-	-
Forest x Dam	-	-	-3.97	< 0.01
Forest x River	-	-	-1.27	0.31
River x Dam	-	-	-4.78	< 0.01
<b>Caiman encounter frequency</b>				
<b>Sector</b>	<b>Mean</b>	<b>SD</b>	<b>Diff</b>	<b>p-value</b>
Forest	0.24	0.18	-	-
River	0.20	0.19	-	-
Dam	0.12	0.20	-	-
Forest x Dam	-	-	-3.08	< 0.01
Forest x River	-	-	1.84	0.10
River x Dam	-	-	-0.93	0.53

We detected 130 caimans near fishing nets, representing 6.2% of overall observations ( $n = 2,080$ ), with most sights of unknow size class ( $n = 39$ ). We did not find differences between the average sights near gillnets before and after the COVID-19 onset ( $W = 70.5$ ,  $p$ -value = 0.18). Only 3.1% of captured individuals presented injuries or were wrapped in gillnets (14 of 455). A total of 17.9% (five of 28) of juvenile caimans in areas distant < 50 m from gillnets were entangled or injured, compared to 15.6% (five of 32) and 12.9% (four of 31) of adults and subadults, respectively (Figure

5). All age classes had similar proportions of entanglements and injuries compared to the overall proportion of observed individuals near gillnets (juveniles:  $\chi^2 = 0.53$ ,  $df = 1$ ,  $p\text{-value} = 0.465$  subadults:  $\chi^2 = 0$ ,  $df = 1$ ,  $p\text{-value} = 1$ ; adults:  $\chi^2 = 0.81$ ,  $df = 1$ ,  $p\text{-value} = 0.37$ ). Importantly, we recorded one death directly related to gillnets; an adult male suffocated after a nylon wire obstructed its trachea.



**Figure 5.** Records of proximity or negative interactions between caimans and gillnets in the Tapacurá Reservoir, Pernambuco, Brazil, during surveys between 2015 and 2022. Records were divided into different size classes (Juvenile, Subadult, Adult and Unknown).

## DISCUSSION

This is the first study addressing the impact of fishing on the distribution of broad-snouted caimans. Most studies about conflicts between humans and crocodylians aim to understand factors that influence co-existence, including the perception of local communities about attacks on people or livestock, or about conflicts originating from sharing fish resources (Dunham *et al.* 2010; Brackhane *et al.* 2018; Khan *et al.* 2020). Fishing threatens several crocodylians species across the world (Shirley, Oduro, and

Beibro 2009; Pooley *et al.* 2021; Panda *et al.* 2023), but it is still unclear how fisheries impact the population ecology and distribution of crocodylians. The growing spatial overlap between humans and crocodylians has significant implications for their interactions, underscoring the potential negative effects on species conservation (Cook *et al.* 2022). In regions characterized by subsistence practices and high conservation priorities, such as the Atlantic Forest, understanding patterns of fishing activity can guide habitat and species protection as well as fisheries management strategies (Begossi 2010).

Over the seven years surveyed, the caiman population in Tapacurá is structured towards young individuals. Multiple studies suggest that the prevalence of immature individuals within crocodylian populations may serve as an indicator of population rebound, following declines influenced by historical habitat fragmentation and degradation, illegal hunting, and intense fishing activity, common threats to crocodylians in South America (Aguilera *et al.* 2008; Balaguera-Reina, Vargas-Castillo, and Densmore 2021; Pereira, Portelinha, and Malvasio 2022). However, recent assessments in Tapacurá indicated there have been a population shift towards more adults (Mascarenhas-Junior *et al.*, forthcoming), raising concerns about potential conflicts with local communities. For instance, larger crocodylians more often destroy gillnets when they accidentally become entangled while foraging or dispersing (Harris *et al.* 2023). Consequently, fishers often turn to killing or retaliating against these animals due to the detrimental effects on their fishing efficiency and the associated economic losses (van der Ploeg, van Weerd, and Persoon 2011; Dagostino *et al.* 2023). Moreover, fishers retaliate against caimans when attacks on livestock or pets are discovered (McGregor 2005; Pierre *et al.* 2023), although there are few reported incidents of which those are mostly non-fatal to livestock or pets (Pooley *et al.* 2021). Fishers take advantage of the moment of deployment or removal of gillnets to practice illegal hunting, and crocodylians are especially their target when observed near gillnets (Platt and Thorbjarnarson 2000; Dunham *et al.* 2010). They can also be inadvertently caught in passive traps, such as a bait suspended from a branch attached to a fishing hook (See Supplementary file 1 C).

We saw through our gillnet surveys that fishing is a year-round activity by local residents, likely driven by its role in subsistence. In Brazil, fish consumption experiences a surge during the first three months of the year attributed to the Easter tradition (as per Christian Holiday) (Louis, Filho, and Flores 2022). It can also be

seasonally-dependent and affected by rainfall, water level, river inflow or seasonal livelihoods (Patrick 2016; Than, Zaw, and Hughes 2022). However, inland small-scale fishing takes place throughout the year as it serves as a source of income for local markets and food for consumption (Bartley, De Graaf, and Valbo-Jørgensen 2015). Considering that gillnets encounter rates remained consistent across seasons, aligned with no significant variations in caiman seasonal encounter rates observed in the Tapacurá, reported in another study (Mascarenhas-Junior *et al.*, chapter one), it is likely that the effects of fishing in caimans' distribution are consistent across all year.

Since 2021, there has been an upward trend in the average encounter rates of gillnets in Tapacurá, coinciding with the onset of the COVID-19 pandemic. The reduction in enforcement efforts is thought to contribute to the escalation of illegal and unreported fishing practices, especially in low-income countries (Minahal *et al.* 2020). Certain areas have experienced a surge in fishing pressure since the start of the pandemic, primarily driven by a decline in available employment opportunities, which has compelled people to seek alternative sources of food and income (Stokes *et al.* 2020). In Tapacurá, residents typically take multiple jobs and fishing and livestock rearing serve as supplementary sources of income. While we observed a rise in fishing activities within the reservoir as seen through more gillnets, this increased trend may need further investigation particularly through a social science perspective.

The distribution of gillnets is positively correlated with caimans' distribution throughout the reservoir. Caimans exhibit opportunistic feeding behavior and are attracted to vibrations in the water caused by entangled fish in gillnets (Villamarín *et al.* 2017). Additionally, both caimans and fishers may seek areas with higher fish abundance, overlapping their distribution and increasing competition (Wallace, Leslie, and Coulson 2011). Some of the most significant fish genera (e.g., *Cichla* spp. and *Oreochromus* spp.) locally consumed and commercially valuable in Tapacurá have been observed as preyed by caimans (Borteiro *et al.* 2009; Bontemps *et al.* 2016). Several studies have indicated that fishers perceive crocodylians as direct competitors for fish, and habitat features associated to overexploitation can limit both fish abundance and areas for obtain food resources (Pierre *et al.* 2023; Dagostino *et al.* 2023). Nevertheless, other findings indicate negative effects of the presence of fishing nets on crocodylian detection, as individuals associate fishing to entanglement threats based on past experiences (Ahizi *et al.* 2021; Panda *et al.* 2023). Hence, the relationship between caiman distribution based on gillnet distribution appears to be

dependent on the level of human pressures exerted on the population. We expect that caimans avoiding human presence on the reservoir, but as gillnet is a passive-catch strategy for fishing, they may approach the nets when fishers are absent.

The river sector is one of the most used areas for gillnet deployment in Tapacurá. Water flow facilitates the influx of nutrients, which enhances productivity, leading to increased fish availability (Nunn, Tewson, and Cowx 2012; Broadley *et al.* 2022). Regions characterized by higher nutrient deposition and sedimentation harbor more diverse and more abundant fish communities (Dai *et al.* 2020). However, in the northeast corner of Tapacurá, construction of a major dam has resulted in local alterations to water flow and landscapes, contributing to the decline of native fish in the immediate area in long-term (Gehrke, Gilligan, and Barwick 2002). Physical barriers create lentic waters, altering hydrological dynamics and negatively impacting native fish populations by reducing spawning habitats and blocking migration processes, ultimately leading to a decrease in species richness and abundance (Wang *et al.* 2021). These alterations create favorable conditions for the establishment of nonnative species, which can compete for resources, modify habitats, and increase diseases dissemination (Cucherousset and Olden 2011; van der Veer and Nentwig 2015; Arantes *et al.* 2019). As a result, habitat functioning is disrupted, thus potentially affecting fish stocks and consequently the artisanal fishing (Tarkan *et al.* 2021). The negative impact of damming on changes in fish assemblages may be observed within a few decades (Agostinho and Gomes 2008; Loures and Pompeu 2019), and as Tapacurá was dammed about 50 years ago, we suspect that these alterations are already affecting the local fish community.

Both caimans and gillnets had higher encounter frequency in forested sector than in dam sector. Habitats bordering forest areas are also expected to have high productivity due to its heterogeneous features (e.g., complex vegetation structure, diverse abiotic conditions, and increased organism interactions), rising species abundance and richness by providing availability of food resources, protection against predators and suitable reproduction sites (Sarkar *et al.* 2013; Lobón-Cerviá *et al.* 2015; Kantharajan *et al.* 2022). As fish is one of the most important items in caiman's diet (Borteiro *et al.* 2008), areas with higher abundance may influence their distribution, and can also serve as a lure for artisanal fishing. However, fisheries are strictly prohibited in Atlantic Forest strictly protected areas, in accordance with Brazilian laws

(Brazil, 2000). Instances of illegal fishing have been documented in forested areas, resulting in negative impacts on caimans, such as entanglement, injuries, and drowning (Mascarenhas-Júnior *et al.* 2020; Mascarenhas Júnior *et al.* 2018). The presence of fishing practices in non-permitted zones affects caiman distribution, but also likely affects other more vulnerable species, such as freshwater turtles, with records of multiple individuals entangled in gillnets (Santos *et al.* 2020).

Few individuals were detected near or interacting with gillnets. Crocodylians often get accidentally entangled in gillnets during dispersion or foraging, with records of nets ingestion, body injuries or, in more severe instances, death by drowning (Mascarenhas Júnior *et al.* 2018; Rosenblatt *et al.* 2022; Platt and Thorbjarnarson 2000). In some regions, bycatch is recognized as one of the major threats for crocodylians conservation (Cedeño-Vázquez, Ross, and Calmé 2006; Katdare *et al.* 2011; Shirley *et al.* 2018). However, the relatively low incidence of entanglement/injuries and the equability in the proportion of entanglement of each size classes compared to the overall interactions observed in Tapacurá may be attributed to larger caimans being capable of destroying gillnets (as earlier mentioned), while smaller individuals can avoid being caught up by the gear because of their size (Aguilera *et al.* 2008). Although the number of gillnets in Tapacurá has increased after the onset of COVID-19 pandemic, there is not a clear change in the number of caimans near or interacting with gillnets during the same period. Other study indicated that population size of caimans in Tapacurá remained relatively stable in past seven years (Mascarenhas-Júnior *et al.*, forthcoming), suggesting that negative interactions with gillnets do not appear to have a significant impact on population dynamics thus far.

### **Conservation perspectives**

There is a significant overlap between the distribution of gillnets and caimans in Tapacurá. Understanding the full impact of fishing activities across the entire ecosystem is fundamental for effective management plans. We suggest that caimans are valuable indicators to identify areas with potential fisheries conflicts. Additionally, we highlight the urgent need for regulations and control of fishing activity in areas bordered by forest, especially during the first quarter of the year. This period is

particularly sensitive for caimans, as it corresponds to the nesting season, and nest sites exclusively occur within the forest fragments (Barboza *et al.*, 2021).

While the population size of caimans has not experienced a significant decline in recent years (Mascarenhas-Junior *et al.*, forthcoming), the growing presence of gillnets observed in Tapacurá raises valid concerns regarding caiman conservation and the potential for bycatch and overfishing. The compounded risks posed by bycatch, along with the possibility of fishers killing caimans due to competition for fish, fear, or damage to fishing gear, intensify threats for caimans and other crocodylians species. The increased practice of fishing following COVID-19 outbreak also shed light on the rise of human-crocodylian conflicts, posing risks to populations maintenance and species conservation worldwide.

Based on evaluations from The International Union for Conservation of Nature (IUCN) Red List ([iucnredlist.org](http://iucnredlist.org)), nearly half of all crocodylian species are currently categorized at some level of risk of extinction, and interactions with artisanal fishing is one of the most concerning threats. The broad-snouted caiman is globally listed as "Least Concern" according to IUCN's criteria (Siroski *et al.* 2020), and Brazilian populations were recently included in the appendix II of Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2023), which allows sustainable trade following strict regulations. However, the upward trend of artisanal fishing in areas inhabited by caiman populations, associated with the potential escalation of bycatch and illegal hunting, underscores significant conservation concerns, as the impacts of fishing over caiman populations have been poorly studied. In Brazil, the combination of increased threats, low encounter rates, limited number of breeding individuals and poor genetic connectivity (Zucoloto *et al.* 2021), means that broad-snouted caiman may need further investigation for species management.

Multiple regulatory strategies have helped mitigate diversity loss, declines in fish stocks, and impacts on ecological services in inland freshwater ecosystems. For instance, the implementation of a multi-zone approach for fisheries can be highly beneficial to designate fully protected areas alongside zones where land use and fishing activities are permitted (Linke, Hermoso, and Januchowski-Hartley 2019). Other strategies include regulations on fisheries by selecting target species and promoting subsistence practices over commercial purposes (Abell, Allan, and Lehner 2007;

Hermoso *et al.* 2018). This should be complemented by the implementation of regulations (e.g., fishers' registration and enforcements to avoid fishing in non-permitted forested areas), promotion of educational initiatives aimed at riverside communities, and continuity of research to further monitor the impact of intensified fishing on caimans.

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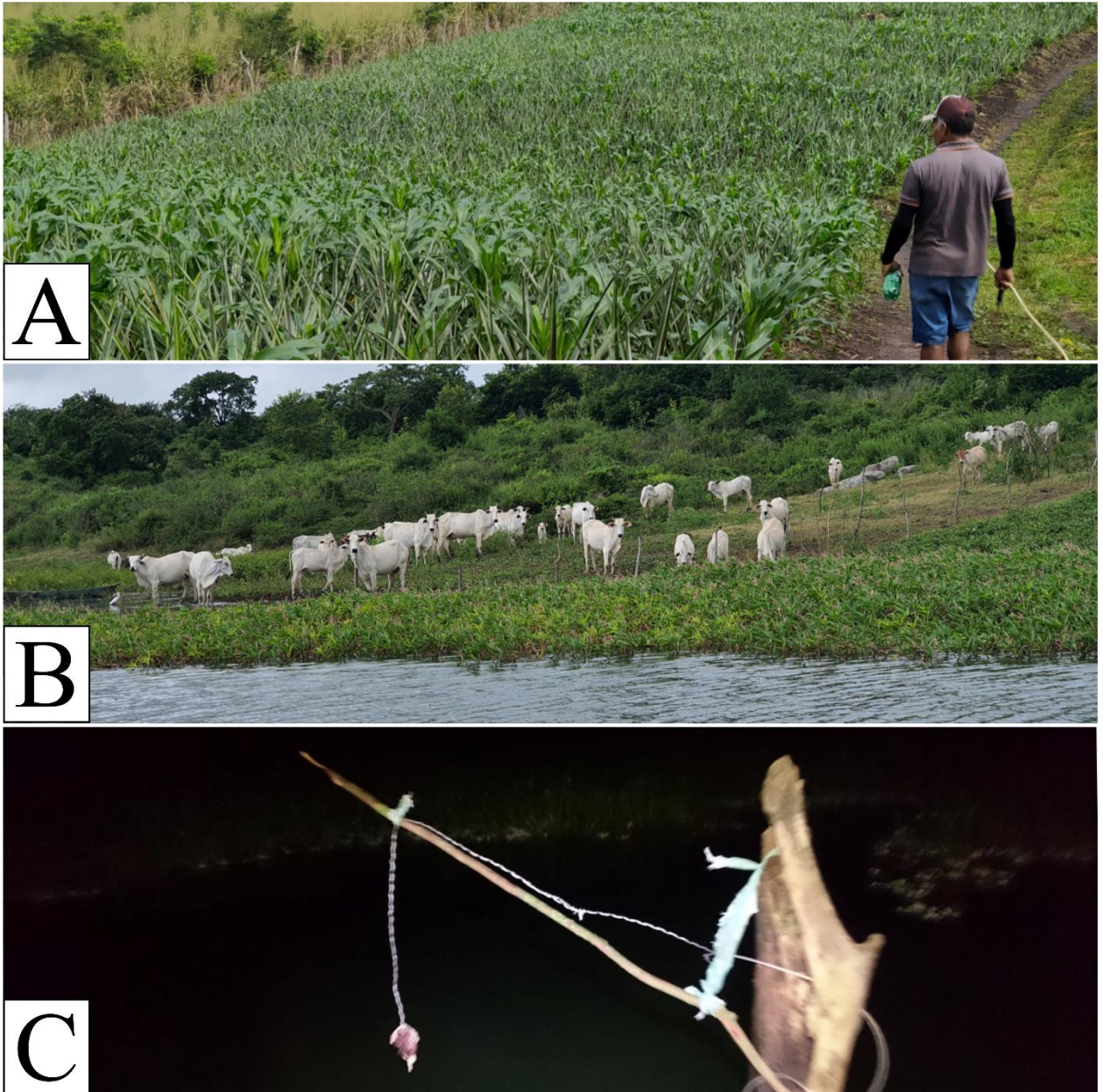
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**Supplementary File 1.** Human activities in Tapacurá reservoir, São Lourenço da Mata, Brazil. A: Pineapple agriculture made by residents; B: Cattle farming in the border of forest fragments; C: Suspended baited hook for capturing caimans. Photo A was taken by Author 5 and photos B and C by Author 1.



**Supplementary File 2.** Nonnative Tucunare (*Cichla* spp.) in the Tapacurá Reservoir, São Lourenço da Mata, Brazil. The species is originally distributed in the Amazon basin. Photo taken by Author 1.

## 7 CAPÍTULO 4 – Differential space use by broad-snouted caimans (*Caiman latirostris*) in a male-biased population of an impacted Atlantic Forest environment, Brazil

Figura 4. Transmissor para rastreamento via GPS acoplado em um jacaré-de-papo-amarelo (*Caiman latirostris*).



As populações naturais de jacarés-de-papo-amarelo são bastante fragmentadas, com pouca conectividade genética e dispersão reduzida (Zucoloto *et al.*, 2021). Apesar disso, pouco se sabe sobre os padrões de movimentação e área de uso dos jacarés na Mata Atlântica (APÊNDICE B), e técnicas de rastreamento por telemetria podem ser úteis na compreensão de aspectos relacionados à ecologia do movimento desses animais (Figura 4).

## ABSTRACT

Animal habitat use can be influenced by a suite of factors including intraspecific interactions and resource availability. Little is known about the movements and habitat selection of broad-snouted caiman (*Caiman latirostris*), especially in habitat fragments of the imperiled Atlantic Forest. We investigated variation in movements and space use of caiman relative to sex, body size, and environmental conditions in northeastern Brazil. We conducted long-term capture-recapture surveys from 2013-2022 and used GPS telemetry ( $n = 12$  individuals) and Brownian bridge movement modeling to assess fine-scale movements. The population was male-biased (1.9:1.0), and there existed a marked difference in space use between sexes. Males ranged farther from the forest and exhibited higher body condition scores during the wet season compared to the dry/mating season. This may be due to reduced resources or reproductive sites, increasing competition in the dry season. Male caimans are also territorial and sought foraging and mating areas when more habitats are available during the wet season. Individuals of a diverse range of body sizes were found in most habitats, suggesting that resource competition between large and small individuals may be relatively low or there are refuges for small individuals within our habitat designations. Caimans moved more at night than during the day, likely due to nocturnal foraging and possibly to avoid human activities that occur during the day. Female movement varied seasonally, with higher movement rates during the wet season. This pattern likely is linked to their need to defend nests during the dry season. Home ranges (95% UD) across both sexes and seasons were small, varying from 0.001 to 1.4 km<sup>2</sup>, as were core areas (50% UD, 0.0003 - 0.12 km<sup>2</sup>). Small core areas may indicate caimans remain most of their time in a specific microhabitat, suggesting resources availability or dominance over a territory. Our work reveals the complexity of social interactions and how caimans select their habitats in a highly-altered environment.

## INTRODUCTION

Understanding how animals move across their habitats and select preferable areas is crucial in the understanding of ecological and evolutionary processes. This becomes particularly urgent in scenarios of habitat fragmentation, climate changes and biological invasions, for instance (Nathan, 2008). Individual organisms select their habitats based on a variety of factors and these choices involve innate and learned

behaviors (Holbrook *et al.*, 2019). Decisions about movements and habitat use are often driven by essential needs such as foraging, mating, nesting, or protection from predators and human disturbance (Klaassen; Broekhuis, 2018; Morris, 2003; Šigutová *et al.*, 2021). Cumulatively, these individual decisions affect the distribution and abundance of populations (Boyce *et al.*, 2016). Habitat selection is a dynamic process that can vary across different spatial and temporal scales and may vary across the diel cycle, seasons, and through ontogeny (Mayor *et al.*, 2009). Nonetheless, understanding 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 breeding seasons to reproduce successfully by focusing foraging excursions around embryo nutrition and opting for habitats safest for their offspring during parental care periods (Garcia-Garcia, 2012; Saïd *et al.*, 2012). In contrast, males may select habitats to maximize mating opportunities. In some species, males may also establish dominance hierarchies or defend territories to monopolize access to females or prey resources thereby relegating subordinate males to suboptimal habitats (Gillingham; Carpenter; Murphy, 1983; Gordon, 1993; Wolf; Kauermann; Trillmich, 2005). Dynamics related to sex-specific differences in space use can affect population dynamics and overall individual survival probabilities (Silk, 1984).

Crocodylians are semi-aquatic predators inhabiting freshwater and brackish environments, forging crucial connections that span across terrestrial and aquatic ecosystems (Somaweera *et al.*, 2020). These movements across and within habitats are influenced by several factors. They present complex social systems, and although poorly studied, there exists considerable inter-individual variation in habitat use and movements within age/sex classes of crocodylians (Rosenblatt *et al.*, 2013; Strickland, Vilella; Belant, 2016; Waters; Bowers; Burghardt, 2017). During the breeding season, their movement tactics are influenced by choosing more suitable habitats for mating and for nesting (Campbell *et al.*, 2013; Baker *et al.*, 2023). Crocodylians also respond to abiotic conditions. As ectotherms, they may adjust their movements in response to changes in air and/or water temperatures, seeking out specific areas to bask in or cool down, to optimize physiological conditions (Dinets; Britton; Shirley, 2014; Nordberg; McKnight, 2023).

The broad-snouted caiman (*Caiman latirostris* Daudin, 1801) is a medium-sized South American crocodylian commonly found in lentic habitats and densely vegetated wetlands (Siroski *et al.*, 2020). The species often uses these habitats for foraging, nesting, or protection (Marques *et al.*, 2020; Portelinha; Verdade; Piña, 2022). Nearly 70% of the global population is found within Brazil, with multiple populations impacted by human disturbance such as agriculture, illegal hunting, fishing, and pollution (Marques *et al.*, 2016; Mascarenhas-Junior, *et al.*, 2021a; Yves *et al.*, 2018). 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 (Roberto *et al.*, 2020). 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 (Zucoloto *et al.*, 2021).

Although it is well-known that broad-snouted caimans prefer lentic areas with dense aquatic vegetation (Siroski *et al.*, 2020; Verdade; Larriera; Piña, 2010), aspects of size- and sex-dominance dynamics patterns of micro-habitat (patch) selection are unknown. Several distribution studies rely on nocturnal counts as a methodology approach, which only allows for the classification of individuals into size class, without sex assignment, especially in Brazil (Fusco-Costa; Castellani; Tomás, 2008; Mascarenhas-Júnior *et al.*, 2020; Mourão; Campos, 1995). The studies that involved captures and sexual determination generally are conducted over short periods (Carvalho; Verás-Batista, 2013; Marques *et al.*, 2016; Passos; Coutinho; Young, 2014), making it challenging to discern trends in seasonal habitat preferences. Nevertheless, the knowledge of broad-snouted caimans' movements activity and home range assessments is scarce, with few studies addressing telemetry approaches thus far (Marques *et al.*, 2020; Portelinha; Verdade; Piña, 2022; Viotto *et al.*, 2022).

Broad-snouted caiman distribution is concentrated in the eastern portion of Brazil, especially within the Atlantic Forest (Coutinho *et al.*, 2013). 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 (Figueiredo *et al.*, 2021). However, historical resource exploitation and deforestation has dramatically fragmented and diminished its coverage area, with estimates suggesting that only 11% of its original cover remains (Ribeiro *et al.*, 2009).

Additionally, within the Atlantic Forest, multiple water sources have been dammed for water supply in neighboring cities, altering hydrological systems (Padial *et al.*, 2021). Here, we investigate the habitat use and movements of broad snouted caiman in a human-impacted Atlantic Forest habitat. We make use of a nine-year time series of caiman captures and the first-ever telemetry-tracking investigation conducted for the species in the region. Specifically, we investigated: 1) sex structure of the population; 2) the role of sex and size in habitat use patterns 3) environmental factors influencing caiman habitat preferences; 4) diel and seasonal patterns in caiman movements; and 5) home range sizes of adult individuals.

## **MATERIAL AND METHODS**

### **Ethics statement**

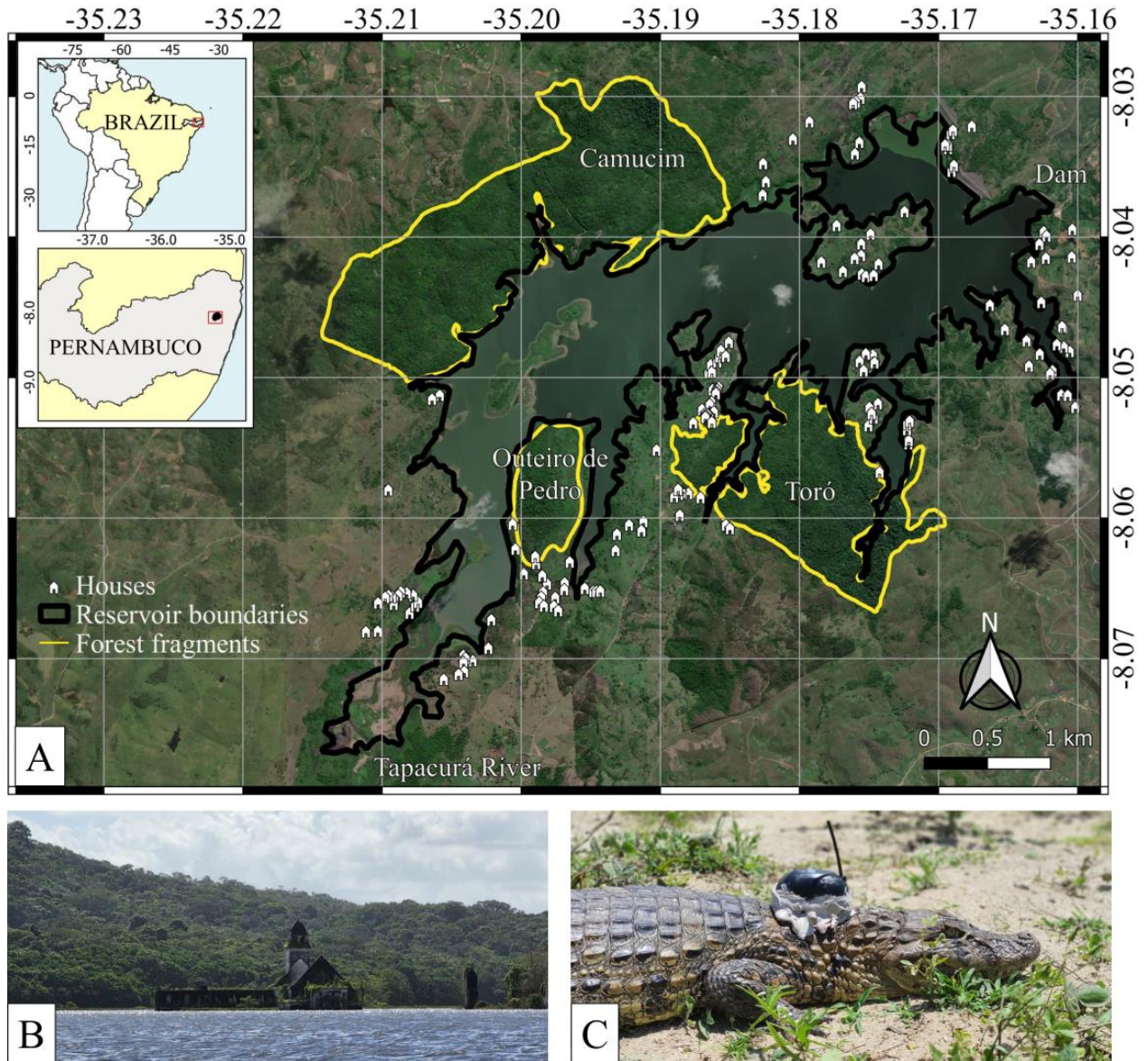
All procedures performed in this study follow legal permits authorized by the Ethics Committee and Animal Use (CEUA) of Federal Rural University of Pernambuco (license CEUA UFRPE #8606200622) and Brazilian Biodiversity Authorization and Information System (SISBIO) from the Chico Mendes Institute for Biodiversity Conservation (ICMBio) (license SISBIO #63030-4). We conducted transmitters attachment procedures and clinical observation of caimans in a sterilized environment under supervision of a specialized veterinarian.

### **Study site**

The Tapacurá Reservoir (hereafter “Tapacurá”) is an impoundment created by the construction of a dam along the Tapacurá River, situated in São Lourenço da Mata, Pernambuco state of Brazil (8.043856° S, 35.195710° W) (Figure 1 A). In the 1970s, the river was dammed to create the reservoir, primarily for water storage to supply Pernambuco’s urban population (Santos *et al.*, 2021). Tapacurá, which covers ca. 9 km<sup>2</sup>, is an integral component of the broader Capibaribe basin, an intricate network of water bodies spanning approximately 470 km<sup>2</sup> (Gunkel *et al.*, 2003). The climate is tropical humid, with a rainy period during autumn/winter that experiences ca. 1300 mm of rainfall (Rodal; Lucena; Melo, 2005). The peak of wet season is typically observed from March to August, when temperatures are lower. Tapacurá has undergone a series of pronounced droughts and flood events. According to Pernambuco’s water monitoring agency (APAC, <https://www.apac.pe.gov.br/>), its water levels have

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 (Figure 1A). Mata do Camucim (Figure 1B) in the northern sector (Figure 1B), Mata do Toró in the south and Mata do Outeiro de Pedro to the southwest. These fragments collectively cover an area of 5.4 km<sup>2</sup> of native forest, categorized as “Wildlife Refuge” by Brazilian laws (Pernambuco, 2011). The predominant vegetation type is a lowland semideciduous forest, one of the last remaining examples of seasonal dry Atlantic Forest within the state of Pernambuco (Pereira-Silva *et al.*, 2022). The other adjacent regions surrounding Tapacurá are occupied by human settlements and characterized by monoculture matrices (especially sugar cane). Local communities use these lands for livestock and agricultural purposes, and often engage in fishing within the reservoir. Illegal hunting and fishing have been documented in areas bordered by forest (Mascarenhas-Júnior *et al.*, 2020; Santos *et al.*, 2020).



**Figure 1.** Tapacurá reservoir, an artificial weir formed by the dam of Tapacurá River, situated in São Lourenço da Mata, northeastern Brazil (A). B: Atlantic Forest fragment named “Mata do Camucim”, in the north sector of Tapacurá reservoir; C: GPS transmitter attached to an adult broad-snouted caiman.

### Nocturnal surveys and captures

We conducted nocturnal eyeshine surveys (Magnusson, 1982) to detect and capture caimans from 2013 – 2022. These surveys occurred on a quarterly basis each year, spanning two to four nights in a week, starting just after sunset. Using an external battery, we could detect caimans at up to 600 m under optimal environmental and weather conditions. We navigated the entirety of the reservoir through 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. We avoided surveys under intense adverse weather conditions, such as rainfall, thunderstorms, or fog.

Captures occurred year-round with procedures varying based on animal size. For larger individuals, we used locking cable snares, while those < 1 m were captured by hand. We restrained caimans 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 and measured its snout-vent length (SVL) and determined sex using cloacal inspection (Brazaitis, 1969).

## Telemetry

From July 2021 – July 2022, we tracked 12 adult caimans (eight females and four males) using transmitters with GPS technology (Nortronic Ltda, Natal). The disproportionate number of females, twice that of males, was attributed to captures opportunities in the field. Transmitters, which were 220 g and measured 4.5 x 9 x 5 cm, had an estimated lifespan of 24 months, and were programmed to operate 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 margin, we installed a waterproof station connected to an omnidirectional antenna, designed to receive the data stored in each transmitter operating in an Ultra-High Frequency (UHF) range of 903.00 – 918.00 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 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.* (2010). All transmitters had a mass of less than 2% of an animal's bodyweight to minimize effects on natural behavior (Mascarenhas-Junior; Correia; Simões, 2023). We subcutaneously injected a NaCl solution infused with local 2% lidocaine (1 ml of lidocaine per 7 ml of NaCl) into the dermal bones of nuchal rosette

of the caimans, located on the dorsal portion of the neck. After 10-min, we used a rotary tool (Dremel) with a 2 mm drill to perforate the dermal bones. We then secured the transmitter with 2mm 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 hours of clinical observation, we released caimans at their location of capture (Figure 1 C).

We also collected abiotic variables associated with each GPS location. Temperature was measured onboard by transmitters. We decided to not include values of habitat features for the telemetry program due to physical barriers that could potentially attenuate or limit signal reception and transmission (e.g., dense vegetation, terrain elevation, or human constructions), thus biasing our results. We collected daily reservoir volume and rainfall data from APAC.

### **Data analysis**

We used the R program (R Core Team, 2023) to conduct statistical analysis and Qgis 3.28 to create the maps (QGIS Development Team, 2023). Before analyses, we conducted Shapiro-Wilk tests to verify normality (Supplementary file S2). We report mean values  $\pm$  standard deviation (mean  $\pm$  SD).

We calculated capture success by dividing the number of captured individuals by the total number of caimans observed. From captured individuals, we categorized the caimans into four distinct size classes as per the classification proposed by Leiva *et al.* (2019): Class I or juveniles (SVL < 25 cm); Class II or subadults (SVL 25 cm – 67.9 cm); Class III or adults (68 cm – 99.9 cm); and Class IV or larger adults (> 99.9 cm). We classified individuals < ca 25 cm as unknown sex. We compared the number of captured caimans across size classes across dry and wet seasons using a chi-squared test. After categorizing caimans' sex, we were able to perform an ANOVA test to compare the sex ratio (males:females) between seasons during years surveyed (S2.1). We decided to remove Class I individuals from sex ratio analysis due to the large amount of unknown sex. We also removed recaptures from analysis to avoid potential biases.

We employed a Negative Binomial Generalized Linear Mixed Modeling (GLMM) framework, using the 'glmer.nb' function from the *lme4* package (Bates *et al.*, 2015) to investigate how caiman SVL varied with habitat features (distance to the nearest forest fragment, distance to the nearest human residence, distance to the nearest margin, gillnet frequency, and water depth). We tested multicollinearity between habitat covariates using a Variance Inflation Factor (VIF) from the *car* package (Fox; Weisberg, 2019) in R. We then chose Negative Binomial distribution to deal with data overdispersion (Stoklosa; Blakey; Hui, 2022) and included habitat features as fixed effects. We constructed two separate models, one for the wet season and the other for the dry season, while including sex as a random effect in both seasons. Before modeling, we standardized covariates data by centering each covariate on its mean and scaling by its standard error. To validate for overdispersion, we used the *performance* package (Lüdtke *et al.*, 2021) in R. For multi-model inference, we used the 'dredge' function from the *MuMIn* package (Bartoń, 2023) in R, combining all covariates and ranking models based on Akaike's Information Criteria (AIC<sub>C</sub>). We considered models with  $\Delta AIC_C < 2$  as the best models (Burnham and Anderson, 2002). 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 determine the variance in the response variable explained only by fixed effects. To compare the values of habitat features between the dry and wet seasons for each sex, we conducted Wilcoxon tests (S2.2).

We adapted Fulton's Relative Condition Index (Kn) for assessing caiman body score, considering the relationship between weight and SVL. We used the formula  $Kn = ([W/L^b]10^n)$ , where  $W$  represents the individual's weight,  $L$  denotes SVL,  $b$  is calculated through ordinary least squares regression of  $W$  and  $L$ , and  $10^n$  is a multiplier to achieve a unit (Ojeda-Adame *et al.*, 2020). Kn is used as proxy for crocodylian fitness when interpreted by quartile system because skeletal length and volumetric measurements are positively correlated (Ojeda-Adame *et al.*, 2020; Zweig *et al.*, 2014). The index result from Kn equation may be useful for detecting periodic changes but does not show true nutritional condition of a population composed of individuals from different size classes (Ojeda-Adame *et al.*, 2020). For the specific purpose of

comparing differences in body condition between seasons and considering the consistent capture rate of all size classes during both dry and wet seasons (see Results), we opted to proceed with the analysis using values from the solution of Kn equation. We made the Kn seasonal comparison performing a Wilcoxon test (S2.3).

### *Telemetry data*

We applied the Brownian Bridge Movement Model (BBMM) to evaluate the trajectories of caimans. The BBMM method considers consecutive discrete locations obtained in short-time periods to estimate the animals' movement paths and probability of occurrence (Horne *et al.*, 2007). To calculate caimans' trajectories, we used the 'ltraj' function from the *adehabitatLT* package in R (Calenge; Dray; Royer, 2023). Our data fulfilled the assumptions of Trajectory type II, which relocations include information of time. We considered consecutive movements (bursts) of these relocations within a maximum interval of 12 hrs. We further divided movements into daytime intervals (with sunlight) and nighttime intervals (without sunlight) to calculate daily movements. Each movement was quantified as the distance traveled between bursts. To account for differences in general movements during daytime and nighttime, we conducted a Wilcoxon test (S2.4). Additionally, we used the same movement data to compare differences in movements between the dry and wet seasons for each sex, repeating the Wilcoxon test (S2.5). For this analysis, we only included individuals with a minimum of five bursts.

We utilized a Tweedie GLMM framework to assess the effects of abiotic covariates (temperature, reservoir volume, and daily rain) on caimans' movements. We chose the Tweedie family for its flexibility in dealing with positively skewed and zero-inflated data (Jorgensen, 1997), as all caimans remained with no movements for several times. We considered abiotic covariates as fixed effects and sex and individual ID as random effect. To determine values for abiotic covariates, we averaged the values obtained for each abiotic variable between bursts. We performed the Tweedie GLMM analysis using the package *glmmTMB* (Brooks *et al.*, 2017) in R using the function 'glmmTMB'. Covariates scaling, multicollinearity detection, model selection based on AIC and model averaging followed the same approach as described in Negative Binomial GLMM (see above).

We also used BBMM to calculate the area of use of caimans using the function 'kernelbb' in *adehabitatHR* package in R (Calenge; Fortmann-Roe, 2023) to create a Utilization Distribution area (UD) based on kernels produced by caimans' trajectories and relocations. We set two smoothing parameters to implement the connection between relocations and build the Uds: 1) Sig1, which compute animals' motion variance parameter, associated to their individual speed (Horne *et al.*, 2007), 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) (Laver; Kelly, 2008). To ensure robustness in our results, we included only individuals with a minimum of 30 relocations in the analysis. We decided to not compare the HR and CA of males and females because we did not monitor all caimans simultaneously (Table 4). We further computed the linear distance between the outermost boundaries of largest nucleus of HR and CA contours (defined as "boundary distance"). We then compared the boundary distances of HR and CA with the linear distance between the positions of capture and recapture (defined as "capture/recapture distance") of other adult specimens by t-test (S2.6) to validate the robustness of HR and CA modeling.

## RESULTS

### Capture data

Over 101 surveys, we spanned  $07:34 \pm 1:28$  hours in the field and covered a distance of  $50.1 \pm 7.4$  km per night. We successfully made 455 captures, including 45 recaptures. The overall capture success was nearly 10%. Individuals captured were 33.6% of class I ( $n = 153$  of 455), 49.9% of class II ( $n = 227$  of 455), 15.2% of class III ( $n = 69$  of 455), and 1.3% of class IV ( $n = 6$  of 455; Table 1). We did not find differences in the number of individuals captured per size class between the seasons for either males ( $\chi^2 = 0.09$ ,  $df = 2$ ,  $p\text{-value} = 0.955$ ) or females ( $\chi^2 = 0.08$ ,  $df = 1$ ,  $p\text{-value} = 0.778$ ). After excluding recaptures and individuals with unknown sex ( $n = 147$ ), the male:female ratio was 1.9:1, varying from 0.7:1 in 2014 ( $n = 20$  individuals) to 3.4:1 in 2018 ( $n = 57$  individuals). We did not find differences in the sex ratio between seasons

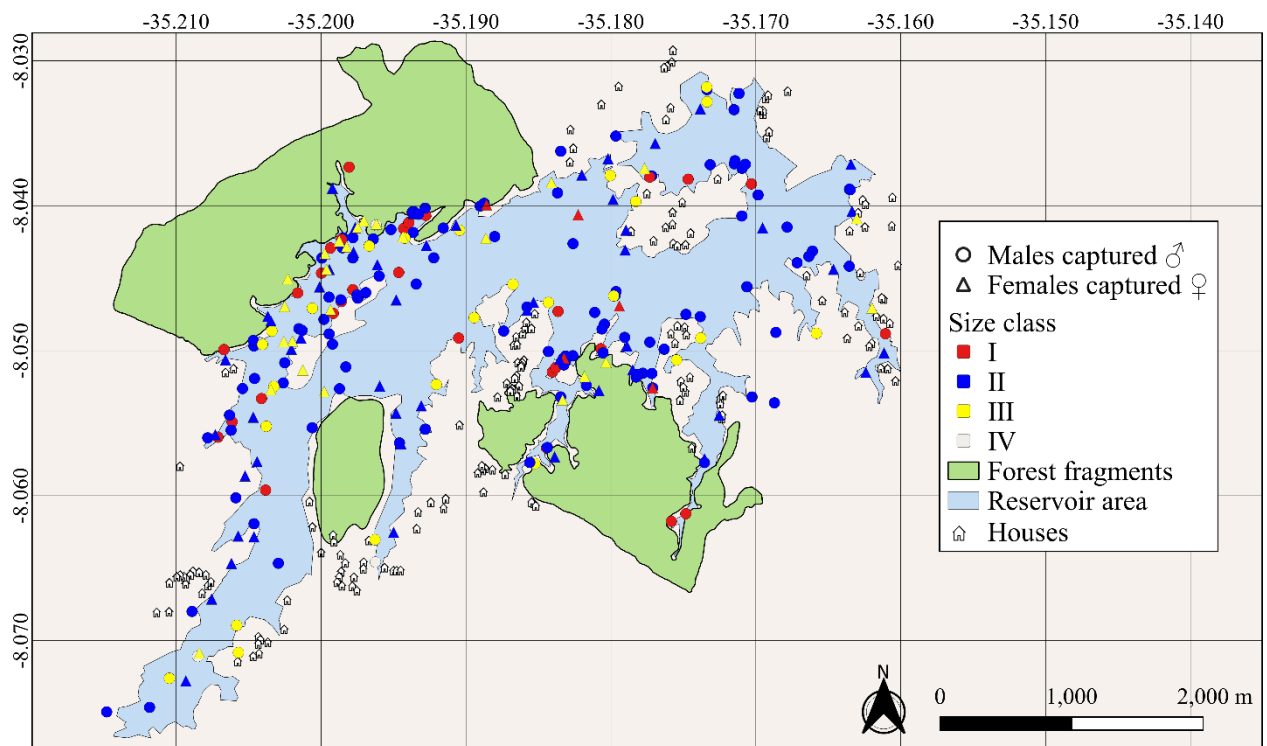
surveyed ( $F = 0.09$ ,  $df = 6$ ,  $p = 0.78$ ), averaging  $1.8 \pm 1.2$  males per female in the wet season and  $2.3 \pm 1.0$  males per female in the dry season.

**Table 1.** Number of *Caiman latirostris* captured per size and size class during surveys performed in Tapacurá Reservoir, São Lourenço da Mata, Pernambuco, Brazil, between August 2013 and June 2022. Individuals categorized as ‘Unknown’ are those for whom we were unable to determine their sex.

Year	Females			Males				Unknown	
	I	II	III	I	II	III	IV	I	II
<b>2013</b>	0	0	0	3	0	0	0	0	0
<b>2014</b>	0	4	1	3	9	2	1	6	1
<b>2015</b>	2	17	4	1	8	5	2	10	0
<b>2016</b>	3	15	1	8	12	2	0	16	4
<b>2017</b>	0	18	4	7	31	3	0	6	2
<b>2018</b>	5	3	5	15	21	8	0	39	3
<b>2019</b>	0	11	8	9	28	2	0	11	1
<b>2020</b>	0	2	2	2	7	0	0	0	0
<b>2021</b>	0	3	10	1	9	8	1	1	0
<b>2022</b>	0	6	1	3	12	3	2	2	0
<b>Total</b>	10	79	36	52	137	33	6	91	11

We found that SVL of caiman varied little with habitat features (see Figure 2) in either season, averaging  $47.1 \pm 23.2$  cm in wet season and  $36.4 \pm 20.6$  cm in dry season for males and  $52.1 \pm 20.6$  cm in wet season and  $52.5 \pm 19.6$  cm in dry season for females. We confirmed that there was no multicollinearity issue between covariates ( $VIF \leq |1.18|$ ) nor data overdispersion in wet season modeling (1.08). In dry season modeling, data was slightly overdispersed (1.36). We obtained 32 candidate models after modeling covariates, with values of  $\Delta AIC < 2$  presented in four models in wet season (marginal  $R^2 = 0.16$ , conditional  $R^2 = 0.16$ ) and five models (including null model) in dry season (marginal  $R = 0.16$ , conditional  $R^2 = 0.03$ ) (See model selection on Supplementary file 3). In the wet season, the distance to the margin and the

frequency of gillnets had positive although small effects on caimans' SVL ( $R^2 = 0.06$ ,  $\beta = 0.13$ ,  $z = 2.71$ ,  $p\text{-value} = 0.007$ , and  $R^2 = 0.08$ ,  $\beta = 0.13$ ,  $z = 3.43$ ,  $p\text{-value} < 0.001$ , respectively) (Table 2). However, SVL did not vary significantly with any covariates in the dry season (Table 2). The estimated variance for sexes were  $< 0.01$  in wet season ( $SD < 0.001$ ,  $CI [0.00 - 0.23]$ ) and  $0.3 \pm 0.17$  in dry season ( $CI: [0.06 - 0.75]$ ) (Table 2). We did not find significant differences in the values of each habitat feature when comparing sexes and seasons, except for males' distance to the closest forest fragment, which was higher during the wet season ( $521 \pm 534$  m) compared to the dry season ( $332 \pm 411$  m) ( $W = 2,732$ ,  $p\text{-value} = 0.007$ ) (See complete statistics and habitat features plots on Supplementary file 4).



**Figure 2.** Spatial distribution of captured females (triangles) and males (circles) caimans from all size classes based on surveys performed in Tapacurá Reservoir, São Lourenço da Mata, Pernambuco, Brazil between August 2013 and June 2022.

**Table 2.** Negative Binomial Generalized Linear Mixed Model averaged parameters of covariates predicting *Caiman latirostris* snout-vent length in the wet and dry seasons in the Tapacurá Reservoir, São Lourenço da Mata, Pernambuco, Brazil between August 2013 and June 2022. Covariates were scaled (mean = 0, standard error = 1). N obs = Number of observations; N groups = Number of groups for random effects; SD = Standard Deviation; SE = Standard Error; CI = Confidence Interval.

<b>WET SEASON</b>						
<b>Random effects:</b>						
Groups	N obs	N groups	Variance	SD	CI 2.50%	CI 97.50%
Sex	123	2	< 0.01	< 0.01	< 0.01	0.23
<b>Fixed effects:</b>						
Variables	Estimate	SE	z value	p value	CI 2.50%	CI 97.50%
Intercept	3.86	0.04	100.62	< 0.001	3.74	4.02
Distance to forest	0.03	0.06	0.48	0.633	-0.08	0.14
Distance to houses	-0.06	0.05	-1.10	0.273	-0.15	0.04
Depth	0.03	0.06	0.60	0.547	-0.08	0.15
Distance to Margin	0.13	0.05	2.71	0.007	0.04	0.23
Gillnets frequency	0.13	0.04	3.43	0.001	0.06	0.20
<b>DRY SEASON</b>						
<b>Random effects:</b>						
Groups	N obs	N groups	Variance	SD	CI 2.50%	CI 97.50%
Sex	126	2	0.03	0.17	0.06	0.75
<b>Fixed effects:</b>						
Variables	Estimate	SE	z value	p value	CI 2.50%	CI 97.50%
Intercept	3.76	0.13	29.78	< 0.001	3.34	4.20
Distance to forest	0.09	0.05	1.71	0.087	-0.01	0.18
Distance to houses	0.02	0.05	0.38	0.701	-0.07	0.11
Depth	0.00	0.05	0.08	0.940	-0.10	0.10

We did not observe any significant seasonal differences in the Kn index among females ( $W = 1,600$ ,  $p\text{-value} = 0.894$ ), averaging  $1.59 \pm 0.56$  in the wet season and  $1.58 \pm 0.64$  in the dry season. Conversely, males had higher body condition scores during the wet season, averaging  $1.49 \pm 0.84$ , 18% higher than the dry season ( $W = 2,745$ ,  $p\text{-value} = 0.01$ ).

### Telemetry data

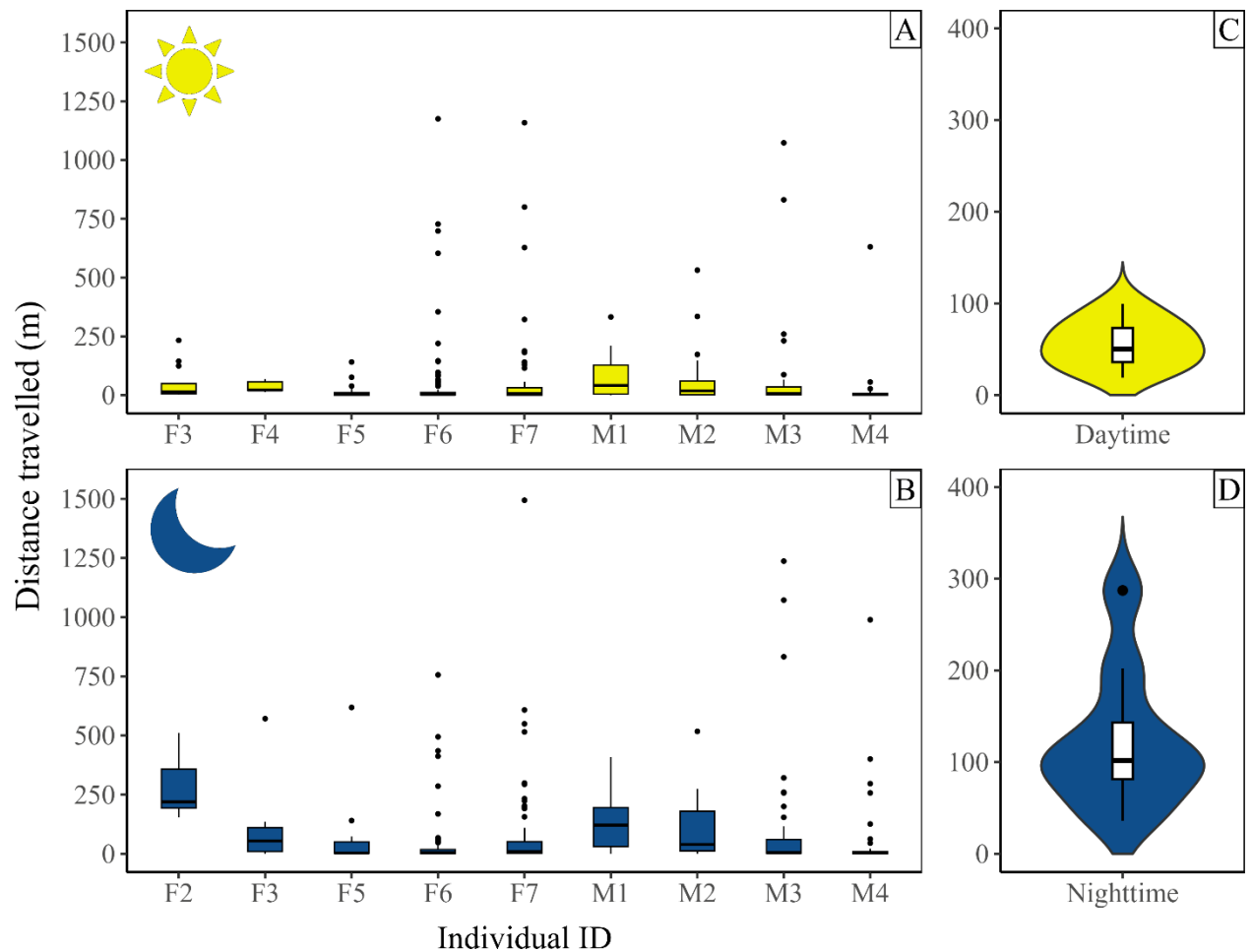
Individuals were tracked over a total of 355 days. During this period, we tracked individual adult caimans for  $86.8 \pm 72.4$  days (range 18 - 221 days). We recorded  $90.1 \pm 79.7$  (range 13 to 275) valid relocations for each caiman (Table 3). We collected a total of 647 bursts, ranging from 1-205 per individual, except for F1, which did not produce any consecutive movement data. For the daily movement analysis, we removed F2 and F8 from daytime analysis (total bursts = 300), and F4 and F8 from nighttime analysis (total bursts = 347) because transmitters did not provide more than five valid coordinates (Table 3). 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 Tagolo system. The other transmitters probably sank, and the signal was no longer transmitted.

**Table 3.** Data of *Caiman latirostris* tracked by GPS telemetry in the Tapacurá Reservoir, São Lourenço da Mata, Pernambuco, Brazil, from July 2021 and July 2022. ID: Individual identification ('F' represents females and 'M' represents males); SVL: Snout-vent length (cm); HR: Home range km<sup>2</sup> (95% utilization distribution); CA: Core area km<sup>2</sup> (50% utilization distribution).

ID	SVL	Weight (g)	Relocations	Date begin	Date end	Days	HR	CA
F1	83	18240	30	7/20/2021	8/22/2021	33	0.001	0.0003
F2	75	13040	23	7/14/2021	8/9/2021	26	-	-
F3	77	16300	38	7/14/2021	8/10/2021	27	0.50	0.03
F4	79	15080	18	7/27/2021	8/14/2021	18	-	-
F5	76	14410	52	9/2/2021	10/28/2021	76	0.42	0.07
F6	82	15120	275	9/2/2021	3/1/2022	180	0.88	0.13
F7	89	24540	204	11/25/2021	3/15/2022	110	1.05	0.08

F8	74	14060	13	11/24/2021	12/24/2021	30	-	-
M1	75	-	57	7/16/2021	8/21/2021	36	0.32	0.09
M2	78	12240	98	9/2/2021	11/18/2021	77	1.44	0.35
M3	78	14530	135	9/2/2021	3/29/2022	208	0.92	0.31
M4	101	40000	139	11/25/2021	7/4/2022	221	0.27	0.06

During nighttime, caimans displayed greater mobility, traveling  $81.4 \pm 193.8$  m, compared to  $58.8 \pm 163.1$  m during daytime ( $W = 46,500$ ,  $p$ -value = 0.019; Figure 3). Males traveled further ( $84.1 \pm 181.5$  m) than females ( $63.2 \pm 178.6$  m;  $W = 42,478$ ,  $p$ -value = 0.005). Movement patterns did not significantly change over seasons for the males ( $W = 7,741$ ,  $p$ -value = 0.337), while females moved further during the wet season ( $71.7 \pm 118.7$  m) than the dry season ( $61.8 \pm 186.7$  m) ( $W = 7,537$ ,  $p$ -value = 0.002).



**Figure 3.** Boxplots representing differences between the mean distance traveled (m) by caimans 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.

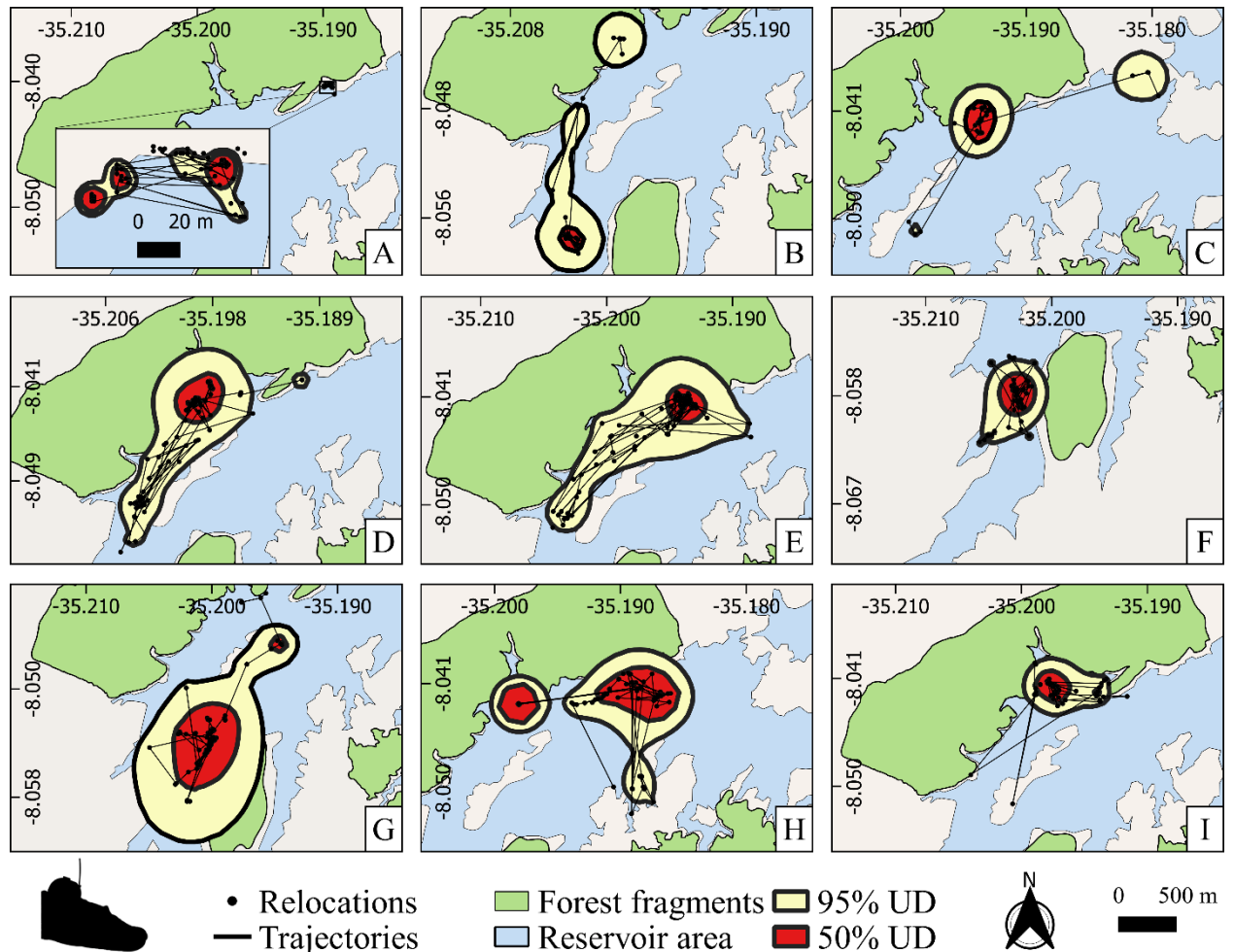
According to the Tweedie GLMM, abiotic covariates have small or negligible effects on the movement of caimans. We did not detect multicollinearity between covariates ( $VIF \leq |0.17|$ ). Among the eight candidate models resulting from the model selection process, three exhibited values of  $\Delta AIC < 2$  (marginal  $R^2 = 0.05$ , conditional  $R^2 = 0.14$ ; Supplementary file 5). The reservoir volume was the sole covariate with a significant and positive, albeit weak, effect on caimans' movements ( $R^2 = 0.04$ ,  $\beta = 0.27$ ,  $z = 3.44$ ,  $p\text{-value} = 0.001$ , see Table W). The estimate variance for individual ID random effect was  $0.15 \pm 0.39$  (CI: [0.20, 0.75]) while the sex random effect was negligible ( $< 0.01$ ,  $SD < 0.01$ , CI: [0.00 – 0.00]) (Table 4).

**Table 4.** Tweedie Generalized Linear Mixed Model averaged parameters of covariates predicting *Caiman latirostris* movements (m) in the Tapacurá Reservoir, São Lourenço da Mata, Pernambuco, Brazil between August 2013 and June 2022. Covariates were scaled (mean = 0, standard error = 1). ID: Individual identification; N obs = Number of observations; N groups = Number of groups for random effects; SD = Standard Deviation; SE = Standard Error; CI = Confidence Interval.

<b>Random effects:</b>						
Groups	N obs	N groups	Variance	Std. Dev.	CI 2.50%	CI 97.50%
ID	647	11	0.15	0.39	0.20	0.75
Sex	647	2	<0.01	< 0.01	0.00	0.00
<b>Fixed effects:</b>						
Variables	Estimate	Std. Error	z value	Pr(> z )	CI 2.50%	CI 97.50%
Intercept	4.27	0.15	28.09	< 0.01	3.97	4.56
Temperature	0.01	0.08	0.09	0.93	-0.16	0.17
Reservoir volume	0.27	0.08	3.44	< 0.01	0.11	0.42
Daily rain	0.04	0.09	0.47	0.64	-0.13	0.21

We estimated HR and CA of nine individuals, excluding F2, F4, and F8 from the analysis due to their limited number of valid relocations (Table 3). HR varied between

0.001 - 1.444 km<sup>2</sup> ( $0.644 \pm 0.431$  km<sup>2</sup>) and CA ranged from 0.0003 to 0.346 km<sup>2</sup> ( $0.146 \pm 0.121$  km<sup>2</sup>) (Table 3, Figure 5).



**Figure 4.** Overall home range (HR) and core area (CA) of GPS-tracked *Caiman latirostris* based 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.

## DISCUSSION

We offer a novel assessment of seasonal habitat selection for males and females individuals of a broad-snouted caiman population, considering a nine-years systematic surveys, the most extensive systematic capture program published so far for the species in Brazil. Furthermore, we performed the first population-level telemetry study for the species in the Atlantic Forest. The caiman population in Tapacurá is male-

biased, with no clear spatial segregation by size or sex. Movements, however, varied with sexes. While both sexes moved more at night than during the day, males increased their movement rates in the wet season when they moved farther per day and night than females did. Somewhat surprisingly, we did not find movements to be affected greatly by any environmental factors. This may, in part, reflect their relatively small ranges. Understanding caiman's habitat selection and movements is particularly relevant for elucidating how their environment drives behaviors their inter- and intra-specific interactions.

Most captured individuals were immature. This corroborates our simultaneous eyeshine surveys conducted alongside this study, which indicate that the Tapacurá population is predominantly composed of juveniles and subadults (Mascarenhas-Junior *et al.*, 2020; Mascarenhas-Junior *et al.*, in prep). Consequently, our capture attempts are skewed towards smaller individuals due to their higher prevalence in the population. Although immature-biased populations are typical for crocodylians (Sai *et al.*, 2016, Wallace *et al.*, 2013), population-level studies on caiman in disturbed habitats in Brazil suggested that populations composed mainly by juvenile and subadult individuals may indicate areas impacted by hunting pressures, as adults are targeted for their meat (Marques *et al.*, 2016; Pereira; Portelinha; Malvasio, 2022). This could negatively affect reproductive processes, declining the number of breeders and subsequently reducing birth rates. However, recent assessments indicate an increase in the number of adults in Tapacurá without a significant decrease in the number of immature individuals (Mascarenhas-Junior *et al.*, in prep), which may imply in a reduction in harvesting and the continuity of reproductive cycles. Moreover, it is thought that smaller crocodylians exhibit lower levels of wariness compared to adults when exposed to threats like bycatch in gillnets, hunting attempts or retaliation by local fishers (Ahizi *et al.*, 2021; Ron; Vallejo; Asanza, 1998; Verdade, 1996). Under these conditions, larger individuals generally submerge or hide within vegetation banks when boat is approximating, making them less accessible to capture (Pacheco, 1996; Portelinha; Verdade; Piña, 2022). In Tapacurá, anthropogenic pressures persist consistently throughout the year, and the level of wariness of the population is considered elevated (Mascarenhas-Junior, in prep), possibly explaining the low capture rate in the reservoir.

Based on capture rates, this study population is male-biased (we caught nearly two times the number of males compared to females). Male-biased populations are not unusual for crocodylians. Males often exhibit higher dispersion rates while seek new territories, and recruitment into new areas are more likely compared to females (Murray *et al.*, 2015; Warner *et al.*, 2016). However, the population size remained relatively stable over the period of our surveys (Mascarenhas-Junior *et al.*, in prep), as well as the sex ratio between surveyed seasons. As there is no other larger river or water body neighboring Tapacurá, we do not expect immigration to be a determinant factor for prevalence of males. Moreover, crocodylians display temperature-dependent sex determination (TSD), meaning that embryo sex will be determined by incubation temperature (Deeming, 2004). Broad-snouted caimans usually produce viable embryos in temperatures between 28 to 34 °C, with male-skewed nests above 33 °C (Simoncini *et al.*, 2014, 2019). In Tapacurá, nesting season primarily occurs during warmer months (Barboza *et al.*, 2021; Rodrigues *et al.*, 2021), potentially increasing the proportion of males within the nests. While incubation temperature and sex determination of caimans' nests in Tapacurá are currently under investigation, several crocodylian species have shown males-biased populations when exposed to elevated temperatures (Bock *et al.*, 2020; Charruau, 2012; Marcó *et al.*, 2017). Effects of male-skewed populations include reduction of reproductive processes, inducing demographic collapse and potential local extinction in a long-term (Valenzuela *et al.*, 2019). However, it does not currently appear to significantly impact reproduction rates in our target population so far (Barboza *et al.*, 2021).

There is a positive correlation between caimans' size and their distance to the reservoir's margin in the wet season, but this relationship is relatively weak. Spatial segregation among size classes may arise from strategies to avoid agonistic interaction or fulfil dietary requirements. Smaller caimans are less common to access open waters far from the shoreline to mitigate predation risk (Ouboter; Nanhoe, 1988; Somaweera; Brien; Shine, 2013). Both adult male and female crocodylians can access open and deep waters, essentially for courtship or during dispersion processes (Herron, 1994; Hutton, 1989; Joanen; Mcnease, 1970, 1989). Nonetheless, marginal areas are typically situated at the interface of water and land, forming an habitat with increased prey availability for caimans of all size classes (Borteiro *et al.*, 2008; Duncan; Kubecka, 1995). Additionally, most of floating vegetation in Tapacurá congregates

around the margin, enhancing food availability and providing areas to refuge against human disturbance (e.g., poaching or boat traffic) or predation (Mascarenhas-Júnior *et al.*, 2020; Somaweera *et al.*, 2019). These protective habitats are also utilized by adult female caimans during maternal attendance, remaining near the nests during incubation (dry season) and to the hatchlings after their birth (wet season) (Barão-Nóbrega *et al.*, 2016; Cintra, 1988; Leiva *et al.*, 2019). Adult females in Tapacurá often present site-fidelity to their nesting site (unpublished data), and we expect that they rarely access open waters (see Figure 3A). In this context, we assumed that in marginal areas where food resources are abundant and habitats are protective larger caimans tolerate the presence of smaller conspecifics (Cherkiss; Romañach; Mazzotti, 2011; Eversole *et al.*, 2018).

Even though we captured caimans from all size classes in fishing zones, we found a weak, but positively significant correlation with caiman body size and areas with higher frequency of gillnets detected during the wet season. Crocodylians exhibit opportunistic feeding behavior at all size classes, possibly attracted by fish entangled in fishing gear (Dagostino *et al.*, 2023; Pooley *et al.*, 2021). In Tapacurá, areas preferred by fishers for gillnet deployment overlaps with habitats where caimans presented higher occupancy probability, which may indicate a competition for areas with higher fish availability (Mascarenhas-Junior *et al.*, in prep). Individuals of various sizes were found in gillnets areas, presenting similar rates of interactions with gillnets such as entanglement or injuries (Mascarenhas-Junior *et al.*, in prep 2). Larger crocodylians can destroy fishing gear when becoming entangled, whereas smaller individuals often manage to divert or disentangle from nets (Aguilera *et al.*, 2008; Harris *et al.*, 2023).

For males, distance from forest fragments was higher during the wet compared to the dry season. We presume that dominant adult males exercise control over resources in forested areas. In general, male crocodylians present territorial behavior (Drews, 1990; Garrick; Lang, 1977) by displaying dominance and excluding other males from mating, nesting sites, or access to food resources (Messel; Vorlicek, 1986). In response, subordinate males may strategically explore areas that are not under the control of other males to secure food, habitat, and mating resources (Campbell *et al.*, 2013; Fukuda *et al.*, 2022). In freshwater habitats bordered by forests, prey populations are expected to be abundant of complex vegetation structures, nutrient availability, and

a wider range of tolerable abiotic conditions (Harper *et al.*, 1997; Kovalenko; Thomaz; Warfe, 2012; Lo *et al.*, 2021; van Schalkwyk *et al.*, 2021). Additionally, caimans exhibit a propensity to select forested areas for nesting due to the protection against intense solar radiation and human disturbances and availability of material for constructing the nests (Banon *et al.*, 2019; Ferguson *et al.*, 2017; Rodrigues *et al.*, 2021). In Tapacurá, suitable caiman nesting sites are restricted to forested areas (Barboza *et al.*, 2021). During the dry season, the forested sectors of the reservoir remain inundated because of their significant depth and the substantial volume of water they contain (Lima; Moraes, 2019). Though drought events may reduce available habitats and potentially increase competition for resources. Tapacurá has marked seasonal peaks of primary productivity during the wet season (Hartman; Asbury; Coler, 1981), and regular flooding events may enhance prey availability (Talbot *et al.*, 2018), creating novel habitats within the reservoir. Consequently, we expect non-dominant males probably occupy these new areas farther from the forest.

Body condition in males presented lower values during dry season. During the wet season, feeding opportunities increase for caimans within their habitats, enhancing their growth rates (Gorzula, 1978). Body condition scores in crocodylians are dependent on temperature, diet, intraspecific competition, and habitat disturbance (Barham *et al.*, 2023; Brandt *et al.*, 2016; Mazzotti *et al.*, 2012; Pereira-Silva *et al.*, 2022). We anticipate that as resources become scarcer, inter-male competition will intensify, leading to negative impacts on body condition. Female caimans exhibited 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, female F7 constructed her nest during our monitoring period, intermittently accessing the water while attending to the nest. This finding may indicate that females in Tapacurá maintain access to food resources during nest attendance (Mascarenhas-Junior *et al.*, in prep).

In general, adult male mobility exceeded that of adult females. Moreover, during the wet season, adult females exhibited a tendency to disperse over greater distances compared to the dry season. A previous telemetry study involving broad-snouted caimans also found that male movements outpaced those of females, as males may seek areas unprotected by other males for accessing food resources or mating opportunities (Marques *et al.*, 2020). Similar movement patterns have been

documented in various other crocodylian species (Brien *et al.*, 2008; Campos *et al.*, 2006; Goodwin; Marion, 1979; Moreno-Arias; Ardila-Robayo, 2020). Females often remain near to their nesting sites and may fight or even cooperate with other females in parental care, including construction, maintenance, and vigilance of nests (Cunha; Barboza; Rebêlo, 2016; Pierini *et al.*, 2022; Rodrigues *et al.*, 2021). Our data also suggests that caimans present sedentary behavior, with most of monitored individuals exhibiting long-periods of limited movement. These findings corroborate existing studies that attribute this sedentarism to territorial behavior in males and nesting-related care in females (Drews, 1990; Magnusson; Lima, 1991; Marioni *et al.*, 2022). Given that the breeding season coincides with the dry season, it is expected that adult female movement rates would be lower during this period. While the reservoir's volume had minor impacts on caiman movements, the positive effect we observed suggests an augmentation of their mobility during periods of elevated water levels.

Adult caimans exhibit higher activity levels during nighttime compared to daytime, aligning with the role of most species as nocturnal predators (Grigg; Kirshner, 2015). Despite this nocturnal behavior, temperature fluctuations did not significantly predict their movements. Adult crocodylians may bask during warm daylight hours to elevate their metabolic rates (Aziz; Islam, 2018; Campos; Magnusson, 2011; Gorzula, 1978; Grigg *et al.*, 1998), and often increase their nocturnal movement activity for foraging or nest attendance (Caut *et al.*, 2019; Combrink; Warner; Downs, 2017; Merchant *et al.*, 2018; Moreno-Arias; Ardila-Robayo, 2020; Rosenblatt *et al.*, 2013). 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 (Watanabe *et al.*, 2013). Considering lower annual temperatures in Tapacurá rarely reaches 21 °C and stay within the range conducive for adult caiman metabolism (Bassetti *et al.*, 2014; Marcó; Piña; Larriera, 2009), we assume that adult movements are minimally affected by thermal changes (Mascarenhas-Junior *et al.*, in prep). 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 (Campbell *et al.*, 2015; Lewis; Cain; Denkhaus, 2014). Given our

assumption that Tapacurá's caiman population is wary, we expect increased movements during nighttime to avoid human disturbance.

Our evaluations of caiman home ranges (HR) and core areas (CA) were consisted with previous records documented for broad-snouted caiman and other caiman species, ranging from  $< 0.001$  to  $1.98 \text{ km}^2$  for HR and from  $< 0.001$  and  $0.42 \text{ km}^2$  for CA (Caut *et al.*, 2019; Marioni *et al.*, 2022; Marques *et al.*, 2020; Quintana; Aparicio; Pacheco, 2020). From monitored individuals, male M4 stood out as the only "larger adult" (size class IV). Yet exhibiting the lower value for both HR and CA among males. Larger adults display site-fidelity in their territories, patrolling resources access and females' HR (Barham *et al.*, 2023; Campbell *et al.*, 2013; Moreno-Arias; Ardila-Robayo, 2020). In contrast, subordinate adult males may be compelled to increase their movements and consequently expand their areas of use to mate and forage (Campbell *et al.*, 2013). Males M1, M2 and M3, classified as "adults" (size class III) had limited access to the northern forest fragment in Tapacurá, primarily occupied by male M4 and selected adjacent areas (Figure 5). Notably, male M3 was the only male overlapping CA with male M4, yet his behavior included frequent long-distance movements to the reservoir's southern sector. While territorial dominant adult males might tolerate the presence of other subordinate males when resources are plentiful (Baker *et al.*, 2023), it remains unclear whether M4 permitted M3's presence or if M3 traveled to northern forest fragment during M4's absence. Furthermore, there is an overlap between females' HR in areas bordering the forest at north, corroborating our previous hypothesis of female tolerance and/or cooperation. Females may also occupy larger areas to enhance the chance of mating with multiple males, improving offspring genetic structure (Goodwin; Marion, 1979; Kay, 2004; Muniz *et al.*, 2011; Rootes; Chabreck, 1993).

## CONCLUSIONS

Caimans in Tapacurá are predominantly male, with nocturnal movement preferences. Moreover, adult males had higher mobility than adult females, and tend to occupy areas farther from forests during wet season, when body scores are higher. Moreover, there is no discernible size class segregation within the reservoir. Our study encompasses the most extensive systematic capture program of a wild broad-snouted

caiman population in Brazil, contributing to the understanding of their spatial ecology in one of the most ecologically imperiled and important ecoregions of the planet. Furthermore, the integration of capture/recapture and telemetry must be imperative for a better understanding in caimans' movements and habitat selection in a long-term and promote suitable management strategies for the species.

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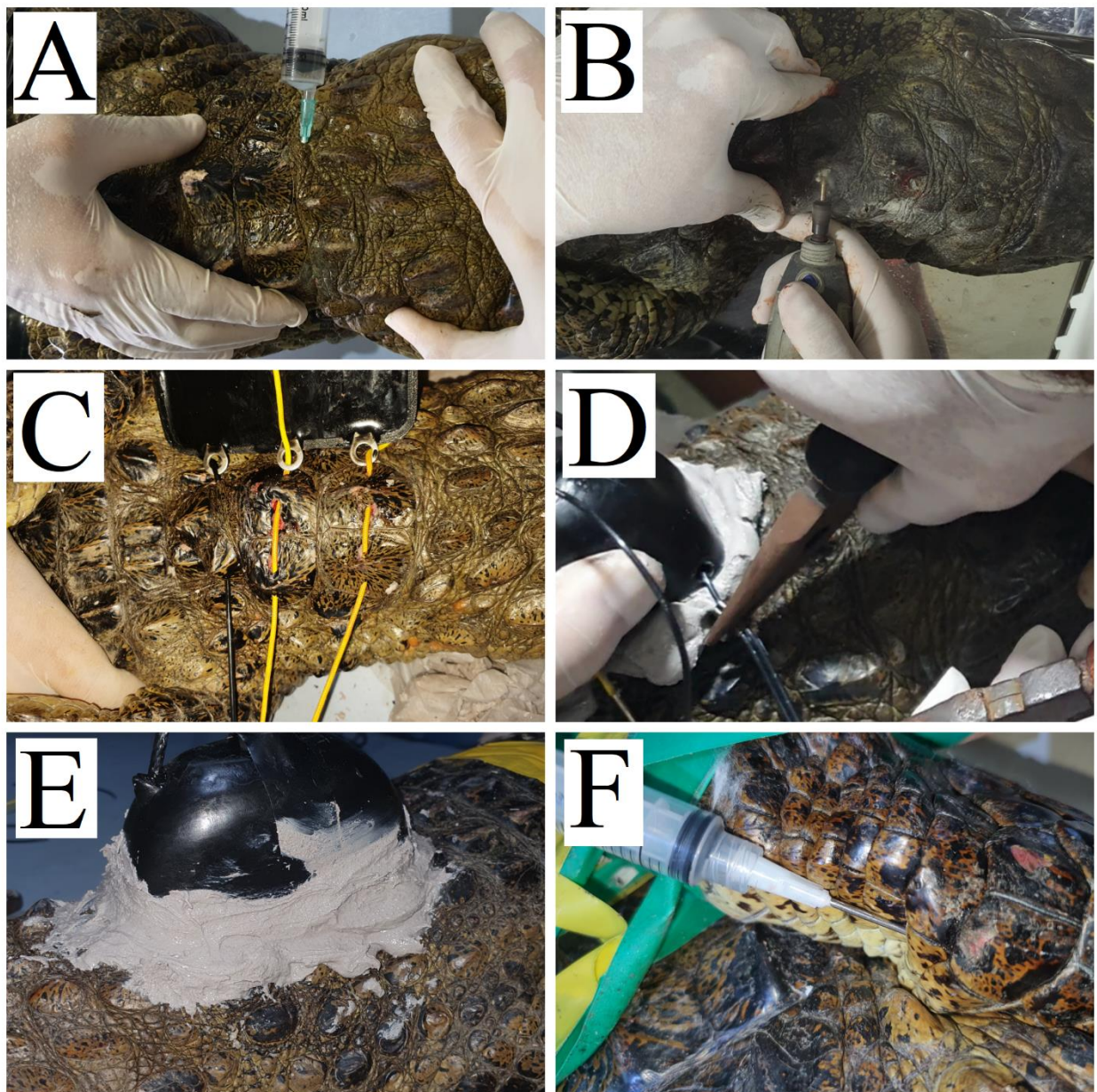
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Cranial direction 

**Supplementary File 1.** Procedures for GPS transmitter attachment. A: Infusing a 2% lidocaine NaCl solution (1 ml of lidocaine per 7 ml of NaCl) in the neck (nuchal rosette) to reduce individual's pain; B: Performing a transversal drilling of the dermal bones of the nuchal rosette using a rotary tool; C: Threaded transmitters through the holes in the dermal bones of the nuchal rosette using a nylon stainless wire and securing them with a washer using pliers to prevent wire slippage; D: Filling empty gaps with epoxy adhesive glue to maximize the contact area between the transmitter and the individual's skin; E: Administering muscle infusion (forelimbs) of 3% Meloxicam (0.2 mg/kg) to reduce the risk of inflammation.

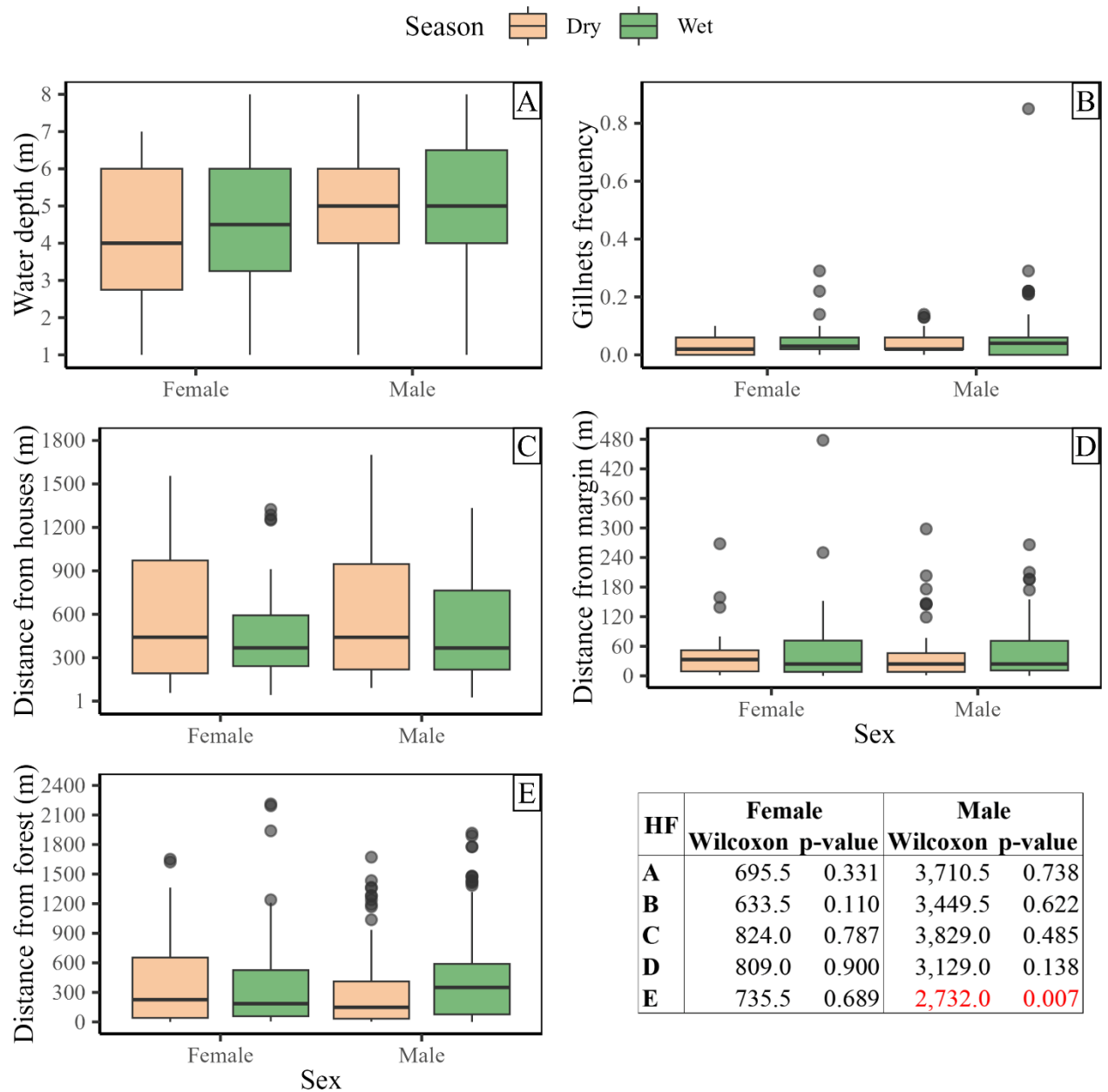
1	Captures in wet season				Captures in dry season					
	Females		Males		Females		Males			
	W	p-value	W	p-value	W	p-value	W	p-value		
	0.94	0.584	0.94	0.533	0.88	0.140	0.86	0.106		
2	Habitat feature females wet									
	depth		dist.for		dist.marg		houses		freq.nets	
	W	p-value	W	p-value	W	p-value	W	p-value	W	p-value
	0.94	0.031	0.72	< 0.001	0.61	< 0.001	0.87	< 0.001	0.73	< 0.001
	Habitat feature females dry									
	depth		dist.for		dist.marg		houses		freq.nets	
	W	p-value	W	p-value	W	p-value	W	p-value	W	p-value
	0.93	0.016	0.80	< 0.001	0.70	< 0.001	0.85	< 0.001	0.84	< 0.001
	Habitat features males wet									
	depth		dist.for		dist.marg		houses		freq.nets	
	W	p-value	W	p-value	W	p-value	W	p-value	W	p-value
	0.92	< 0.001	0.83	< 0.001	0.78	< 0.001	0.88	< 0.001	0.50	< 0.001
	Habitat features males dry									
	depth		dist.for		dist.marg		houses		freq.nets	
	W	p-value	W	p-value	W	p-value	W	p-value	W	p-value
	0.95	0.002	0.76	< 0.001	0.68	< 0.001	0.87	< 0.001	0.88	< 0.001
3	Kn index wet				Kn index dry					
	Females		Males		Females		Males			
	W	p-value	W	p-value	W	p-value	W	p-value		
	0.9217	0.001	0.89	< 0.001	0.94	0.007036	0.85	< 0.001		
4	Daily movement									
	Nighttime		Daytime							
	W	p-value	W	p-value						
	0.46	< 0.001	0.39	< 0.001						
5	Movements in dry season				Movements in wet season					

	Females		Males		Females		Males	
	W	p-value	W	p-value	W	p-value	W	p-value
	0.36	< 0.001	0.51	< 0.001	0.64	< 0.001	0.49	< 0.001

**Supplementary File 2.** Shapiro-Wilk tests performed for normality assumptions. dist.for: Distance to the closest forest fragment; dist.marg: Distance to the margin; freq.nets: Frequency of gillnets; Kn: Fulton's Relative Body condition index; HRBL: Overall Home Range Boundary Limits; CABL: Core Area Boundary Limits; CRL: Capture/Recapture Boundary Limits.

DRY SEASON					
Model	np	logLik	AICc	$\Delta AIC_c$	Weight
Df	3	-563.56	1,133.3	0.00	0.35
Null	2	-565.30	1,134.7	1.37	0.18
Df + H	4	-563.22	1,134.8	1.45	0.17
D	3	-564.34	1,134.9	1.57	0.16
Df + D	4	-563.43	1,135.2	1.87	0.14
Global	7	-562.97	1,140.9	7.58	0.00
WET SEASON					
Model	np	logLik	AICc	$\Delta AIC_c$	Weight
Dm + Gn	4	-543.77	1095.9	0.00	0.41
Dm + H + Gn	5	-543.15	1096.8	0.92	0.26
Df + Dm + Gn	5	-543.53	1097.6	1.70	0.18
D + Dm + Gn	5	-543.67	1097.9	1.97	0.15
Global	7	-543.00	1101.0	5.08	0.02
Null	2	-555.97	1116.0	20.15	0.00

**Supplementary File 3.** Model selection results of habitat features predicting *Caiman latirostris* snout-vent length in the Tapacurá Reservoir, São Lourenço da Mata, Pernambuco, Brazil, between August 2013 and June 2022. Null, Global and models with  $\Delta$  Aikake's Information Criteria ( $AIC_C$ ) distance  $< 2$  are presented. All covariates were scaled (mean = 0, Standard error = 1). Df: Distance to the closest forest fragment; H: Distance to the closest house; D: Depth; Dm: Distance to the margin; Gn: Frequency of gillnets. 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).



**Supplementary File 4.** Boxplots representing habitat features (HF) associated to capture location mean values across seasons for both female (f) and male (m) broad-snouted caimans captured in the Tapacurá Reservoir, São Lourenço da Mata, Pernambuco, Brazil, from August 2013 to June 2022. A: Local water depth (m); B: Frequency of encountering a gillnet; C: Distance from the closest residence (m); D: Distance to the closest margin (m); E: Distance from the closest forest fragment (m). Males' distance closest fragment was the only covariate presenting significant differences between seasons, highlighted in red.

Model	np	logLik	AICc	$\Delta AIC_c$	Weight
Rv	3	-4,273.0	8,552.0	0.00	0.48
Rv + Rf	4	-4,272.4	8,552.9	0.84	0.31
Rv + T	4	-4,272.8	8,553.7	1.68	0.21
Null	5	-4,272.3	8,554.7	2.70	0.11
Global	2	-4,277.8	8,559.7	7.67	0.01

**Supplementary File 5.** Model selection results of habitat features predicting *Caiman latirostris* movements (m) 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  $\Delta$  Aikake's Information Criteria (AIC<sub>c</sub>) distance < 2 are presented. All covariates were scaled (mean = 0, Standard error = 1). Rv: Reservoir volume; Rf: Daily rainfall; T: Water surface temperature. np: Number of parameters, logLik: Log likelihood of the model; AIC<sub>c</sub>: 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).

## 8 CONSIDERAÇÕES FINAIS

Os estudos de rastreamento de crocodilianos por telemetria são realizados principalmente em países desenvolvidos, como EUA e Austrália. Isso se dá principalmente porque nestes países o recurso disponível para pesquisa amplia as possibilidades de estudos. Além disso, a língua inglesa é nativa desses países, o que facilita a publicação em periódicos internacionais de alto fator de impacto. Consequentemente, a ecologia do movimento de espécies distribuídas nestes países, como o *Alligator mississippiensis* e o *Crocodylus porosus* é mais conhecida. A telemetria VHF foi historicamente mais utilizada, mas com limitações na coleta de dados. Desde os anos 2000, equipamentos via GPS vêm acessando áreas mais remotas, mas com custos de aquisição mais elevados. A telemetria acústica surge como um método mais recente e ainda pouco explorado, com a possibilidade de obtenção de um grande volume de dados, mas limitado a ambientes aquáticos. Compreender os vieses nos estudos com telemetria e as principais tecnologias são importantes para incentivar novos monitoramentos para crocodilianos ao longo da distribuição das espécies.

Com relação a ecologia espaço-temporal do jacaré-de-papo-amarelo, pouco ainda se sabe sobre as dinâmicas das populações em longo prazo, considerando sua extensa distribuição geográfica. Os resultados aqui obtidos evidenciam as respostas dos jacarés diante de mudanças na paisagem e parâmetros abióticos, bem como a influência antrópica sob sua distribuição:

- 1) O tamanho da população de jacarés em Tapacurá não sofreu mudanças significativas ao longo dos últimos sete anos, mas indicou um aumento na taxa de encontro de indivíduos adultos, o que sugere uma recuperação da população após períodos de caça, já que adultos são alvos preferidos desta prática. Variáveis climáticas (temperatura, umidade relativa do ar, nebulosidade e chuvas) impactam significativamente a detecção de jacarés, influenciando fatores ecológicos e fisiológicos dos indivíduos. Os jacarés estão ocupando principalmente nas áreas de floresta e no curso do rio, e estão positivamente correlacionados com atividades de pesca artesanal, possivelmente por serem atraídos por peixes emalhados ou pela maior abundância de recursos disponíveis. A ocupação maior nos ambientes

florestados e do rio podem indicar habitats com disponibilidade de recursos mais adequados para a distribuição dos jacarés;

2) Há uma sobreposição entre a distribuição de redes de pesca e jacarés em Tapacurá. Nos últimos anos, há uma tendência de crescimento da atividade pequena em Tapacurá. Mesmo sem detectar aumento significativo nos encontros de jacarés nos anos com maior taxa de encontro de redes de pesca, o crescimento da atividade pesqueira levanta preocupações sobre a conservação de jacarés, principalmente no que se refere ao risco de captura acidental e a sobrepesca. A pesca se não devidamente regulada e espacialmente zoneada, pode representar uma ameaça para o jacaré-de-papo-amarelo e para o estoque pesqueiro local;

3) O número de machos é quase o dobro de fêmeas em Tapacurá, com proporção sexual relativamente estável ao longo dos anos. Não há segregação de habitats entre classes de tamanho, indicando que jacarés de diferentes classes de tamanho estão distribuídos homogeneamente pelo reservatório. Machos tendem a ocupar áreas mais distantes da floresta no período chuvoso e apresentam escores corporais mais elevados, o que pode estar relacionado com o aumento de habitats e recursos alimentares disponíveis. As variáveis ambientais selecionadas apresentaram baixo poder preditivo relacionado à movimentação dos jacarés adultos, apesar da mobilidade ser maior durante à noite, possivelmente em função do forrageamento e diminuição no fluxo de embarcações. Estes dados colaboram com novas perspectivas sobre a seleção de habitats e movimentação de jacarés em ambientes alterados.

Este estudo estabelece uma base sólida para orientar as decisões de gestão e conservação, não apenas para o jacaré-de-papo-amarelo, mas também para outras espécies de crocodilianos que possam estar sujeitas a ameaças semelhantes. Tapacurá é um importante sistema e pode ser utilizado como modelo para outros corpos d'água na região, dado que as características de represamento e mudanças na paisagem são similares. Nesse contexto, os fragmentos de Mata Atlântica são elementos cruciais na distribuição dos jacarés, que utilizaram de forma significativa esses ambientes como sítos de reprodução, alimentação e proteção, mesmo que em fragmentos diminutos. Além disso, a relação entre pesca e jacarés não pode ser negligenciada. Torna-se imperativo investir em uma fiscalização mais eficaz da pesca em áreas não autorizadas e envolver a comunidade local como agentes ativos na conservação dos jacarés e dos recursos do reservatório.

A continuidade do monitoramento aqui apresentado e a inclusão de novas abordagens devem ser incentivadas. Métodos de estimativa de tamanho populacional por captura, marcação e recaptura, monitoramento aéreo por drones, participação dos pescadores locais no monitoramento e diagnóstico da pesca e ampliação do tempo e número de indivíduos rastreados por telemetria podem contribuir para uma melhor compreensão da ecologia espaço-temporal dos jacarés e promover práticas sustentáveis do uso dos recursos naturais.

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## APÊNDICE A – Tracking crocodylia: a review of telemetry studies on movements and spatial use

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Animal Biotelemetry

### REVIEW

### Open Access

## Tracking crocodylia: a review of telemetry studies on movements and spatial use



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### Abstract

Crocodylians are top predators that play key ecological roles in aquatic ecosystems. As in other groups of large predators, crocodylian populations are often impacted by habitat loss, habitat degradation or direct exploitation for commercial purposes or subsistence. Hence, understanding their spatiotemporal ecology can provide valuable information for conservation planning. We reviewed the published scientific literature on telemetry-tracking in crocodylians, combining the terms “telemetry”, “track” or “tag” and variations; “VHF”, “UHF”, “satellite”, “GPS”, “radio”, “acoustic” or “transmitters”; and “caiman”, “alligator”, “crocodile”, “gharial” or “Crocodylia”. Publications retrieved by our search were carefully reviewed for information on study length, geographic location, sample size, taxonomy, and telemetry technology used. We identified 72 research articles in indexed journals and 110 reports available from the IUCN's Crocodile Specialist Group, published between 1970 and 2022. Publications included 23 of the 27-living described crocodylian species. We identified strong geographic and taxonomic biases, with most articles proceeding from the USA (21.2%) and Australia (14%), with *Alligator mississippiensis* and *Crocodylus porosus* as the main target species in studies conducted in these countries, respectively. Despite representing 22% of IUCN's reports, *Gavialis gangeticus* was referred in a single indexed research article. VHF telemetry was the prevalent tracking method, followed by GPS and acoustic transmitters. Studies using VHF devices had generally shorter in length when compared to alternative technologies. Transmitter weight represented less than 2% of the body mass of the carrying individual in all studies. Although attachment site of transmitters was notified in all research papers, few described anaesthetic or clinical procedures during attachment (33%). Our review highlights the need to encourage publication of crocodylian telemetry studies in non-English speaking countries in Asia, Africa, and Latin America, where many endemic species are threatened. We also highlight the need of detailed information on methods and results to facilitate the choice and implementation of appropriate protocols in future telemetry-tracking studies.

**Keywords** Crocodylians, Electronic tagging, Remote monitoring, Reptiles, Spatial ecology, Transmitters

### Background

Crocodylians figure among the largest predators in fresh and brackish water ecosystems in the tropical and subtropical regions of the world. They potentially play a fundamental role on defining local trophic webs, influencing population growth rates of their prey [42, 48], and linking ecosystems by moving energy and nutrients between the aquatic and terrestrial habitats [113]. However, when compared to other large predators in terrestrial or marine environments (e.g., sharks, dolphins, seals, or bears), or even other reptiles (e.g., snakes and turtles), the spatial

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ecology and movement patterns of crocodylians are relatively less explored, with taxonomic and geographic gaps often jeopardizing their conservation [26, 43, 107].

Traditionally relying on mark-recapture and observation/count techniques [53, 115], research on the spatial ecology of crocodylians has increasingly benefited from new technologies, among which telemetry tracking emerged as a promising tool for monitoring these large, yet secretive animals [29, 52, 57, 65, 91, 96]. Pioneering studies first estimated movement patterns of crocodylians based on mark-recapture, as well as by direct observations of the specimens in the field ([79]. Eventually, remote tracking allowed new approaches, reducing potential observer effects on the behavior of individuals during the length of the studies [54].

Telemetry studies addressing the space–time ecology of crocodylians frequently included the estimation of parameters such as home range and patterns of seasonal or diel movements. These were often summarized in statistics including Kernel Density Estimator (KDE), Minimum Convex Polygons (MCP), and Brownian Bridge Movement Models (BBMM), for example. KDE calculates an individual's home range and core areas by placing a kernel function on each relocation point and summing them up to create a smooth probability density surface e.g., [23]. MCP is used to represent home range by a polygon created by connecting the outmost relocations e.g., [4]. BBMM estimates the probability of an individual's distribution given its previous movements (e.g., Strickland et al. 2021). Some studies also use movement route analysis to describe the timing, direction, and length of movement routes [117]. Spatial data are then evaluated for associations with intrinsic and environmental factors, such as landscape seasonality [18, 21, 83], habitat type [72], anthropogenic pressures [22], hunting behavior [35], sex [38] or age [68]. Additionally, telemetry methods have been applied to a diverse set of research themes in crocodylian ecology, such as the study of thermoregulation, physiology, territoriality, and reproduction [69] Campos et al. 2003; [18, 21, 27, 108].

The first telemetry tracking studies took place in the USA [34, 67] and were soon applied to the study of crocodylians. In the early 1970's, researchers investigated movements and habitat use of the *Alligator mississippiensis* (Daudin, 1802) in the USA [56, 57, 77] and of the saltwater and freshwater crocodiles, *Crocodylus porosus* Schneider, 1801 and *Crocodylus johnstoni* Schneider 1801, respectively [58, 122] using VHF telemetry. Along the 1970's, telemetry tracking expanded to additional populations of *A. mississippiensis* [40, 116] and *C. porosus* [121], and to a Florida population of the American crocodile, *Crocodylus acutus* (Cuvier, 1887)

[84]. In the 1980's, telemetry research spread to other continents, with additional studies being conducted in Central America [94], Asia [103], South America [85] and Africa [52].

Throughout the decades, technologies applied in telemetry tracking improved, providing more efficient methods to collect position and movement data. Earlier works relied on VHF transmitters attached to the animals, which were later followed by field observers carrying portable tracking receivers coupled to handheld antennae [56, 57, 77, 116]. It was only in the twenty-first century that crocodylian telemetry started to benefit from new technology that allowed for the remote tracking of animals tagged with GPS or GPS/GSM transmitters, able to emit signals at pre-defined time intervals [15, 25, 72, 80, 90, 91]. More recently, passive acoustic telemetry was added to the toolbox of crocodylian spatial ecology research, allowing sound signals emitted by transmitters attached to focal animals to be detected by hydrophones distributed throughout the area of the study or actively [16, 17, 45, 98]. Today, transmitter modules containing combinations of different technologies are not uncommon [2, 5, 11, 17, 109].

The high cost and casual inefficiency of custom-made telemetry gear, in addition to the need of carefully choosing the right technology for a study's scale and habitat, have been suggested as possible factors hindering telemetry studies from reaching a larger number of research groups [54, 105]. Until now, no study summarized telemetry-tracking research on crocodylians over time or described geographic, taxonomic, or methodological gaps or biases. Understanding the operational viability and the quality of data acquired with distinct technologies or distinct sampling efforts is essential in applied ecology, whereas detection of taxonomic and geographic gaps is key to species conservation planning. Hence, we conducted a thorough review of published literature and of documentation published by IUCN's Crocodile Specialist Group to evaluate geographic, taxonomic, and technological trends in telemetry studies involving wild crocodylians, from their outset in 1970 to the present. Additionally, we summarized information on the application of different telemetry methods and related parameters such as body size of carrying individuals, battery life and transmission period. Lastly, we discuss our results highlighting potential barriers to telemetry implementation by a larger number of research groups, the most effective telemetry methods for potential research questions and the potential value of data reported in newsletters and short communications.

## Material and methods

Until January 2023, we conducted systematic searches on the online databases Scopus, Web of Science, PubMed and Scielo using multiple combinations of the keywords “telemetry”, “track”, “tag”, “VHF”, “UHF”, “satellite”, “GPS”, “radio”, “acoustic”, “transmitter”, “caiman”, “alligator”, “crocodile”, “gharial”, “Crocodylia”, “crocodylan”. We used the Boolean Operators’<sup>o</sup> to indicate variations of keywords, ‘AND’ to create terms combinations, and ‘OR’ to find at least one of the terms in the search. After preliminary inspection of returned articles, we selected all that dealt with the evaluation of the temporal or spatial distribution of crocodylians, the ones which described their movement patterns, and those which described territories or home ranges. Replacing search terms with their equivalents in Spanish and Portuguese language did not retrieve any additional documents. To avoid biases generated by differences in availability and access to unpublished academic and technical studies in our sample, we removed unpublished monographs, dissertations, reports, books, and meeting abstracts from our database prior to review and to quantitative analyses described below. Additionally, we removed duplicate records (i.e., unpublished, and published versions) of the same studies.

In addition, we searched all documents available in the IUCN’s Crocodile Specialist Group’s website (CSG—<http://www.iucncsg.org/>) for non-peer reviewed short communications and articles reporting the use of telemetry for tracking crocodylians. We compared the number, taxonomic coverage, and geographic location of projects developed in the field in relation results published as articles in indexed journals. We also excluded any report of potential duplicates in the same document. At the time of our search, the CSG website contained 105 documents under their “CSG Proceedings” publication, covering works published from 1971 to 2018. Additional 163 documents containing reports, communications, and research papers were available in the “CSG Newsletter”, all published between 1979 and 2022. All abstracts, reports, communications, and papers were accessed through the “Regional Reports” section of the CSG’s website. We searched using the same keywords described above. The complete list of works returned in our search and used in this review is presented in Additional file 1: Table S1).

We carefully reviewed all papers, reports and communications and, for each, we recorded the following information: (1) journal name; (2) type of publication; (3) year of publication; (4) country where telemetry tracking was applied; (5) species studied; (6) body attachment position of transmitters; (7) use of anesthetics during transmitter attachment; (8) tracking technology (VHF, GPS/Satellite and Acoustic); (9) number of specimens tracked; (10) study duration; (11) sex, weight, and total length of

studied specimens (when publication presented snout-vent length, we made an estimation of total length); (12) Transmitter weight and lifespan. Due to the limitation of information in CSG’s documents, data related to items 6 to 11 were obtained only from manuscripts published in peer-reviewed journals. We summarized data resulting from this review using descriptive statistics (percentages, means, standard deviations, range), which were calculated and plotted in R [88].

We adapted CSG’s regional division criteria to quantify publications, which includes the USA, Latin America and the Caribbean, Africa, Asia, and Oceania. We created a map using the *sf* package in R [86] and QGIS [87] to illustrate the frequency distribution of telemetry studies on crocodylians worldwide. We used a density map with buffer zones of 350 km radius to visually evaluate geographic patterns in frequency of studies.

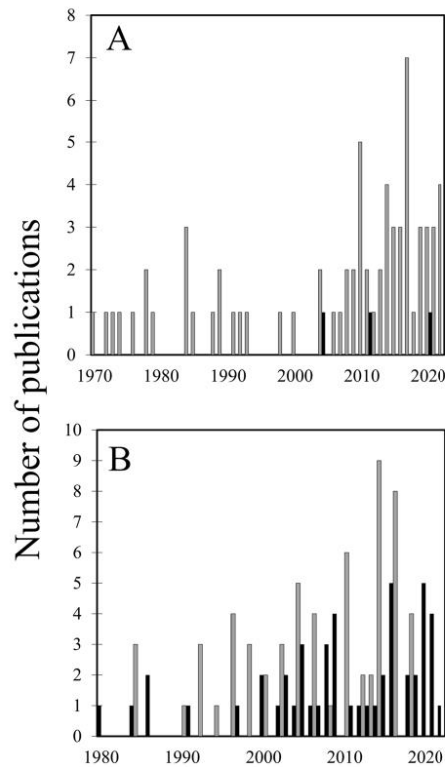
## Results

Our survey of online databases returned 104 items reporting studies on telemetry tracking of crocodylians, of which 32 consisted of unpublished monographs, dissertations, conference abstracts or duplicate versions of published studies. The remaining 72 documents were peer-reviewed publications, which covered a time span of over 52 years (Fig. 1A), the first paper published in 1970 and the most recent in 2022. These publications included research articles ( $n=69$ ) and short communications ( $n=3$ ). Most papers were published in scientific journals (94.6%), whereas only three papers (5.4%) were published in compilations derived from scientific conferences.

Our searches of the IUCN’s Crocodile Specialist Group publications returned a total of 110 documents related to telemetry tracking. Out of these, 61 were published in the CSG Proceedings between 1984 and 2018, while the remaining 49 were published in the CSG Newsletter between 1980 and 2022. Documents in the CSG Proceedings included short abstracts (39.3%), technical reports (32.8%) and non-peer reviewed research articles (27.9%). Documents published in the CSG Newsletter comprised only technical reports (Fig. 1B).

Surveys in online publication databases and in the CSG’s archives showed a temporal trend of increase in the number of publications addressing telemetry tracking of crocodylians after 2000, with publication peaks between 2010 and 2016 (Fig. 1A, B).

Considering papers retrieved in the online database survey, most published studies (59.7%) were conducted in the Americas (27.8% in Latin America and the Caribbean, Fig. 2D, and 31.9% in the USA, Fig. 2A). Studies in Oceania were conducted exclusively in Australia, which accounted for 22.2% of all publications (Fig. 2E), followed by studies conducted in Asia (9.7%, Fig. 2C) and



**Fig. 1** Number of publications of telemetry-tracking in crocodylians between 1970 and 2022 in **A** online databases and **B** in IUCN's Crocodile Specialist Group documents. Grey bars indicate full articles (**A**) and CSG proceedings (**B**) and black bars indicates short communications (**A**) and CSG newsletter reports (**B**)

Africa (8.4%, Fig. 2B). Considering the pooled records of reports, articles, and communications available in the CSG Proceedings and the CSG Newsletter, most published studies took place in Asia (46.4%, Fig. 2C), where India and Nepal accounted for most studies (18 and 10 studies, respectively). Studies conducted in the Americas accounted for 32.4% of the IUCN CSG's documents (19.8% in Latin American and the Caribbean, Fig. 2D, and 13.6% in North America). The USA accounted for most of publications (15 studies, Fig. 2A). IUCN CSG's documents also reported studies conducted in Africa (12.7%, Fig. 2B) and Oceania (8.5%, Fig. 2E), which mainly took place in South Africa (five studies) and Australia (nine studies), respectively.

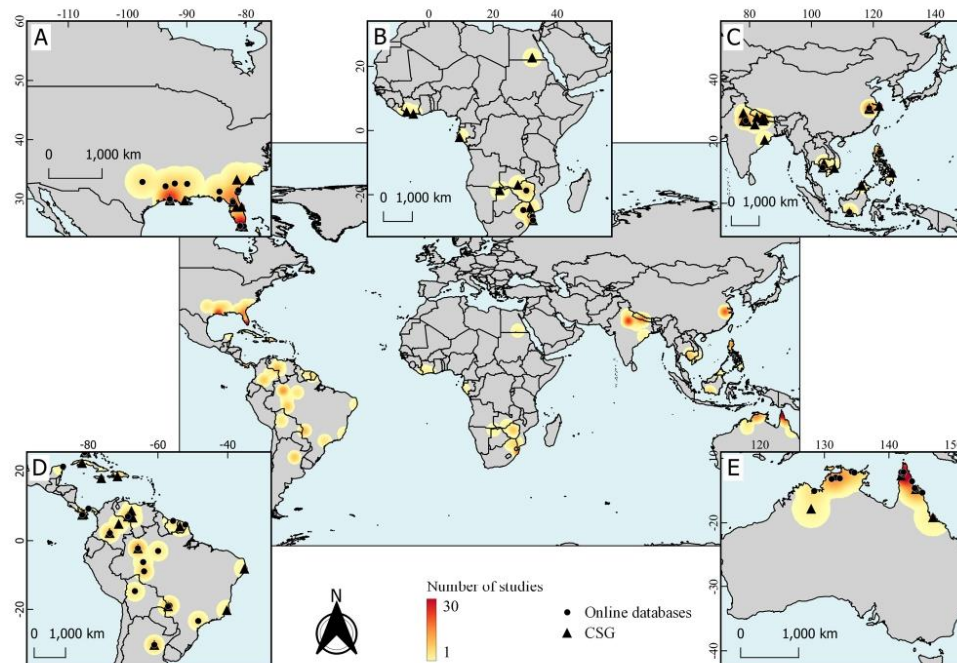
Most of the studies (44.5%) focused on telemetry tracking research in crocodiles (family *Crocodyliidae*). *Crocodylus porosus*, *C. niloticus* (Cuvier, 1807), and *C. acutus* were the most frequently studied species, accounting for 28, 15 and 13 studies, respectively (Fig. 3A). Alligators and caimans (Family *Alligatoridae*) were the second most frequently studied group, accounting for 34.7% of the pooled survey results. *Alligator mississippiensis* ( $n=34$ ), the Chinese alligator *Alligator sinensis* Fauvel, 1879 ( $n=10$ ) and the black caiman *Melanosuchus niger* (Spix, 1825) ( $n=7$ ) were the most frequently studied species (Fig. 3B).

Gharials (Family *Gavialidae*) were comparatively less studied, accounting for 14.8% of the papers, reports, and communications. Studies covered the two species in the family, the gharial *Gavialis gangeticus* Gmelin, 1789, ( $n=25$ ), and the false gharial *Tomistoma schlegelii* Müller (1838) ( $n=2$ ) (Fig. 3C).

Several studies have utilized telemetry tracking to monitor multiple species. Among these studies, four have included species from different families (*Gavialidae* + *Crocodyliidae* = 2.2%), while seven have focused on species within the same family (*Alligatoridae* = 2.2%; *Crocodyliidae* = 1.6%). Hence, the total amount of studies involving different taxa is slightly larger than the number of manuscripts evaluated.

In 69 peer-reviewed papers, transmitter attachment procedures were described in detail. Most studies used transmitters attached to the dorsal scales of the neck (43.1%), followed by attachment to the scales of the tail (25.0%) or to the dorsal surface of the head (1.4%). Subcutaneous transmitters were used less frequently, generally implanted in the forelimbs (4.2%), in the anterior region of dorsum (2.8%) or in the abdominal cavity (2.8%). In 16.5% of the studies transmitters were attached to more than one part of the body [32], or attachment site varied among studied specimens [62].

Most papers reported the method of transmitter attachment (87.5%). Drilling dermal bones (tail or neck) was adopted in 54.2% of studies, followed by external attachment of collars or wires tied to the tail or dorsal surface (19.4%) and by intramuscular or intraperitoneal implant of subcutaneous transmitters (19.4%) (in four studies, two or more methods were used, hence pooled frequencies exceed 100%). Importantly, 66.7% of the publications did not report using anaesthetics when attaching transmitters to animals. Among studies that reported the use of anaesthesia, 87.5% used lidocaine solution, 2.1% used procaine hydrochloride and 2.1% used alfaxalone solution. Some papers that reported using anaesthetic drugs during transmitter attachment did not specify which drug or concentrations were used (8.3%).



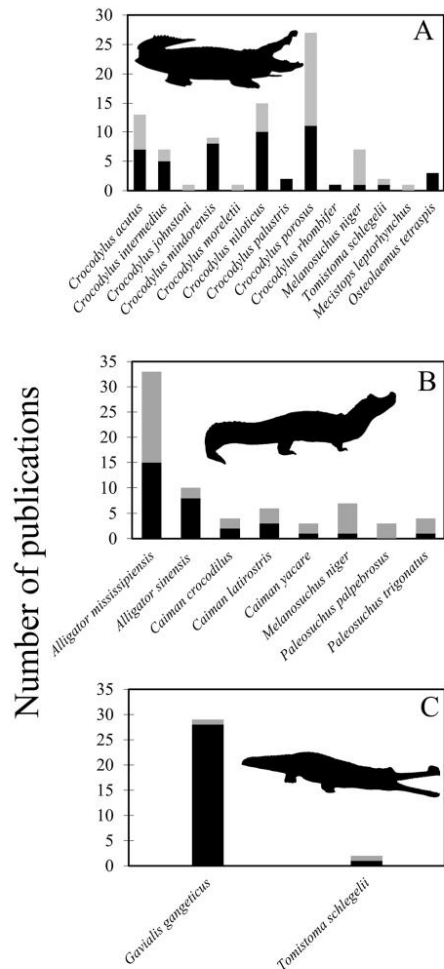
**Fig. 2** Geographic distribution of telemetry-tracking publications on crocodylians between 1970 and 2022. The number of publications increases from yellow to red shades. Buffer zones represent a 350 km radius. Black dots represent studies published in indexed journals. Black triangles represent research projects conducted in the field and reported in IUCN's CSG publications. **A:** the USA; **B:** Africa; **C:** Asia; **D:** Latin America and the Caribbean; **E:** Oceania

Technologies applied to telemetry tracking of crocodylians diversified with time. Most peer-reviewed studies (62.5%) used VHF telemetry to sample spatial position of marked individuals. Studies based on alternative methods started to be published in 2007, and those included GPS (11.1%) and acoustic telemetry (6.9%). In some studies, hybrid transmitters (GPS+VHF) or complementary methods were applied, to minimize errors in the estimation of geographic position of sampled individuals or to allow direct comparisons between different telemetry approaches. The most frequent combination was VHF+GPS telemetry ( $n=11.1\%$  studies), followed by GPS+acoustic telemetry ( $n=4.2\%$ ) and by the combination of VHF+GPS+acoustic telemetry ( $n=4.2\%$ ) (Fig. 4).

Acoustic telemetry tracking allowed for the largest number of sampled specimens among all peer-reviewed studies (Table 1), with  $55 \pm 25$  individuals tagged per study. Studies that applied VHF and GPS methods had  $13 \pm 9$  and  $8 \pm 6$  tracked individuals, respectively.

VHF studies generally spanned longer time frames ( $1.7 \pm 1.9$  years), but with large variation, ranging between 0.02 and 10 years. Studies involving GPS telemetry lasted  $2.3 \pm 1.5$  years (0.4–4.3 years) and studies involving acoustic telemetry lasted  $2.6 \pm 2.1$  years (1.7–9.8 years).

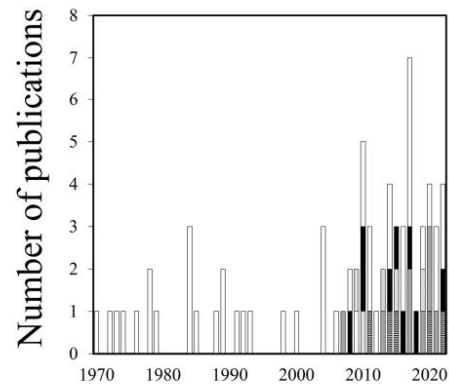
Considering papers which precisely reported the transmission period of attached transmitters, tracking period of individuals ranged between 1 and 3997 days ( $1.2 \pm 1.06$  years). Acoustic telemetry transmitters were reported as the ones achieving the longest transmission periods, ranging from 18 to 3997 days ( $2.18 \pm 1.78$  years;  $n=426$  individuals) (Fig. 5C). VHF transmitters were reported to be functional from one to 1258 days ( $0.66 \pm 0.6$  years;  $n=626$  individuals) (Fig. 5A), and GPS transmitters from three to 1209 days ( $0.8 \pm 0.69$  years;  $n=117$  individuals) (Fig. 5B). Hybrid GPS+VHF devices transmitted from four to 744 ( $0.55 \pm 0.5$  years;  $n=44$  individuals). The proportion of transmitters lost because of detachment from the carrying individual, malfunction or because the monitored individual moved away from



**Fig. 3** Number of publications related to telemetry tracking in species of **A** Crocodylidae, **B** Alligatoridae and **C** Gavialidae, between 1970 and 2022 in online databases and IUCN's Crocodile Specialist Group documents. Grey bars represent publications in the CSG, while black bars represent publications in online databases

the study area varied from 0 to 100% (mean = 22%;  $n = 28$  studies).

Body-size of individuals carrying transmitters were informed in 93.1% studies and varied from 0.28 to 4.86 m. Body mass of monitored specimens was presented only in 34.7% studies. In studies that provided information on



**Fig. 4** Technologies used in crocodylians telemetry-tracking studies in publications available on online databases between 1970 and 2022. Each different type of bar represents a different technology or combination of technologies. White: VHF; Dark grey: GPS; Black: GPS and VHF; Light grey: VHF, GPS and acoustic; Black dots: GPS and acoustic; Horizontal black lines: Acoustic

body mass of the carrying individual and on transmitter weight (22.2%), transmitters corresponded to 1–13.25% of the body mass of the carrying individual (mean = 1.5%,  $n = 246$  specimens). VHF transmitters were generally lighter than GPS transmitters, varying between 3.9 and 850.0 g (mode = 50.0 g;  $n = 26$  studies) (Fig. 5A). Weight of GPS transmitters ranged between 100 and 880 g (mode = 300 g;  $n = 10$  studies) (Fig. 5B). Acoustic transmitters were much lighter, ranging between 24 and 36 g (mode = 24 g;  $n = 5$  studies) (Fig. 5C). Transmitter modules carrying mixed technologies, or the total weight of different transmitters attached to a single individual ranged from 65 to 374 g (mode = 300 g;  $n = 7$  studies). Males were more frequently monitored than females, accounting for 42.5% of the specimens monitored. Females represented 33% of monitored specimens. Sex was not determined for approximately 24.5% of all crocodylian specimens monitored in telemetry studies.

## Discussion

From its outset in the early 1970's, the rate of publication of studies addressing telemetry tracking in crocodylians increased, both as scientific articles and communications published in indexed journals and as non-peer reviewed shorter scientific reports published by the IUCN's Crocodile Specialist Group. The number of publications per year increased steadily, peaking between 2010 and 2018, potentially reflecting the development of less costly tracking technologies [61] and their consequent deployment in crocodylian research [14, 17, 91, 111]. From the

**Table 1** Sampling effort to monitor crocodylians with different telemetry-tracking technologies in publications available on online databases between 1970 and 2022

Technology	N	Pub	Mean	Max	Min	RLD
Acoustic	425	10	55	105	2	> 3997
GPS	141	17	8	30	1	> 1584
VHF	658	50	13	47	1	> 3470
GPS + VHF	50	6	8	15	2	> 1337

N Number of crocodylians monitored, Pub Number of publications, Mean Mean number of crocodylians monitored, Max Maximum number of crocodylians monitored, Min Minimum number of crocodylians monitored, RLD Research with longer duration (days)

early 2000's on, improvement in the performance and size of transmitters and the dramatic reduction in production costs, especially of GPS/satellite units, favored the spread of telemetry studies all over the world [95].

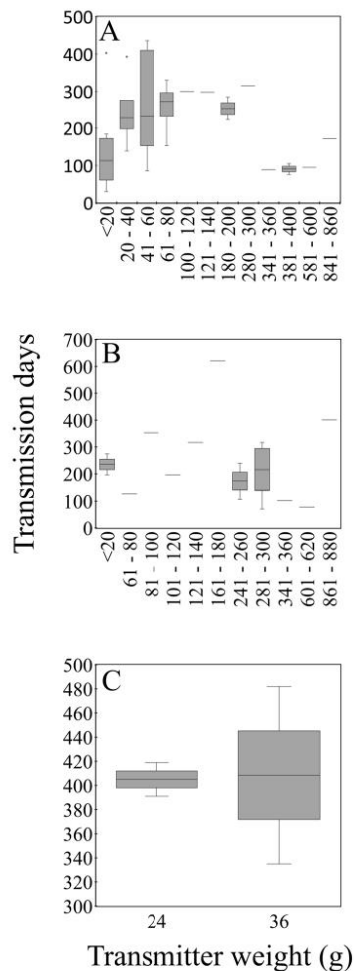
Despite the increasing trend in the rate of publication in the past 20 years, our review disclosed a considerable difference between the number of studies published in indexed journals and the actual number of studies developed in the field, as inferred by data recovered from IUCN's CSG Proceedings and CSG Newsletter. Published articles on telemetry tracking of crocodylians are geographically biased, with the USA and Australia accounting for more than half of the populations studied. Conversely, surveys that took place in countries fairly represented in the CSG's reports were either underrepresented in (e.g., India, China, Argentina) or completely absent from (e.g., Cuba, Nepal) indexed journals. India and Nepal objectively illustrate how studies in developing countries are severely underrepresented in indexed journals. In India, research in the Chambal National Park has been reported since the early 1980's [104]. However, the first article in this area was published in 2010, based on sampling efforts conducted between 2007 and 2009 [65]. In Nepal, telemetry tracking has played a key part of an important reintroduction program of gharials in the Royal Chitwan National Park since 2002 [1, 13, 41, 75], but results have not yet been published in indexed journals.

In addition to the early origin of telemetry tracking studies in English-speaking countries, structural issues in the scientific publication process may help to explain the disproportionate number of peer-reviewed articles towards species distributed in the USA and Australia which, importantly, is not mirrored by the research effort in the field, as evidenced by our quantitative analysis of IUCN's CSG reports. Historically, researchers non-native to English-speaking countries face disadvantages in reaching scientific publications when compared to native English speakers, essentially because English is the main language in international journals. Authors are frequently discouraged along the editing process, or their manuscripts are rapidly rejected by editors due to grammatical

deficiencies [36]. Therefore, much of the scientific production from Africa, Latin America, Middle East, and Asia are published in local journals, in languages other than English, often ranked as of little impact [89]. To mitigate such biases, some measures could be applied, such as the provision of review services by international journals [6], the possibility of publishing both in English and in the researcher's native language [78] or enhancement of free English-writing courses at universities [36]. Associated to the linguistic issue, national government investment in research directly influences academic production [70]. Journals with publication charges should provide fee waivers to authors from low- or mid-income countries [66] as a strategy to boost publication of high-quality scientific content, often produced in countries that concentrate most species of conservation concern.

Nearly half of the crocodylian telemetry papers published in indexed journals had the American alligator or the saltwater crocodile as research subjects, also indicating taxonomic biases on information available for conservation. The ecology and natural history of these species are well-known today. For example, telemetry tracking of *A. mississippiensis* has been used to assess individual movement, territoriality, and home range [40, 56, 57, 77, 93, 115, 115], as well as habitat characteristics and responses to environmental changes [38, 83, 112]. On the other hand, threatened species (e.g., the False Gharial, the Gharial, the Chinese Alligator, the Siamese crocodile *Crocodylus mindorensis* Schmidt, 1935, and the Philippine crocodile *Crocodylus siamensis* Schneider, 1801) are often represented by one or a few papers, generally addressing movement patterns at relatively small geographic scales [31, 33, 65, 118, 120].

Effective planning of conservation strategies and management of highly elusive, long-lived species depend on long-term monitoring and data collection, thus the importance of increased access to results of earlier studies published as scientific articles by current researchers. Valuable information on individual and population-level responses have been evaluated in a few crocodylian species by telemetry tracking approaches, and it should be encouraged in those of high conservation concern,



**Fig. 5** Average transmission period of telemetry-tracking transmitters used in crocodilians based on publications available in online database between 1970 and 2022. Each category considers a 20 g range of transmitters weight, except for Acoustic (C), which only two different weights were informed in the publications. **A:** VHF; **B:** GPS; **C:** Acoustic

considering threats such as illegal hunting [8], invasive species [64], water pollution [55], bycatch on fishing nets [74, 119], and habitat fragmentation [7].

Movement patterns of crocodilians can vary between wet and dry periods, reproductive and non-reproductive seasons, or even between sexes, as male and female

conspecifics can occupy and move across their environment in diverse ways [4, 12, 60, 72]. For example, male saltwater crocodiles can exhibit a greater site fidelity than females [3], while in other species, such as the Orinoco crocodile, males can move far distances than females and occupy larger home ranges [80]. Our survey revealed that telemetry studies of crocodylians are slightly male-biased, potentially influencing meta-analyses of movement and spatial ecology parameters across populations or across species.

Regarding field and sampling protocols, attached transmitters should not compromise individual behavior, whereas transmitter design and composition should minimize the risk of damage and loss of data [54]. The hard and keeled scales on the dorsal surface of the neck (the “nuchal rosette” area) was the most common transmitter attachment site in crocodylians, allowing for increased stability of the transmitter and facilitating signal transmission when individuals are positioned at the water surface [11, 37, 59].

Researchers should consider that some transmitters are only functional when their antennae are exposed above the water surface and oriented vertically to improve signal transmission [11, 59, 61]. In complex habitats such as swamps or riverine systems, neck-attachment could not be suitable, because they can potentially snag on vegetation or debris [44, 59, 99]. In these cases, a streamlined attachment package in the tail surface is an option to reduce detachment [9, 19, 72], if damage or injuries to the tail surface due to agonistic interactions are not common in the focal population [109]. Subcutaneous implantation is a promising option to prevent equipment loss due to detachment, however, it should be carefully considered, since GPS and VHF transmitters typically have larger batteries and may experience signal attenuation when submerged underwater [32, 37, 111]. Therefore, this procedure is recommended for subaquatic acoustic transmitters. Malfunctioning or the loss of transmitters occurs not only by detachment, but also because of natural mortality [28, 63], illegal hunting [81], technical issues inherent to transmitter hardware and batteries [109], or failure of signal reception [73]. Depending on the ecological question being addressed, some studies can concentrate sampling efforts in short periods (e.g., during a specific season of the year), reducing the chance of data loss while collecting useful demographic data, such as dispersion, hatchling survival, territorial behavior, and short-term movement patterns [20, 91, 116].

Most of all published studies on crocodylian telemetry did not mention the use of anesthetic or prophylactic procedures during attachment of transmitters. Since the 1960's, ethics committees have been used to regulate and protect animals in research [101], but countries deal with

scientific permits differently. In USA, which accounted for most of the studies in our survey, animal regulations have been reinforced in the last decades of the twentieth century [82] and this is reflected on the poor description of clinical or anesthetic procedures in papers published between the 1970's and 1990's. The first report of anesthetic use was published in 1990's by Hocutt et al. [49], and it was the only research prior to 2000's reporting the use of drugs during transmitter-attachment procedures (see Additional file 1 for further details). In addition, the small number of papers describing anesthetic procedures may be also due to committees considering some procedures as a little invasive. Nevertheless, some studies support the use of anesthesia and prophylactic procedures to minimize pain and reduce the risk of infections or necrosis in studied specimens [11, 71].

Lidocaine solution was the most used anesthetic solution for research involving invasive procedures. Lidocaine is a local anesthetic, widely available in veterinary suppliers and recommended for anesthesia in reptiles [106]. However, toxic, and lethal doses are highly unknown for several species, including most crocodylians [24, 92], which could be potentially related to the absence of such practice in most of the published studies. This should be thoroughly described in the resulting publications, allowing for the discussion and development of safer methods for transmitter attachment among different research teams.

Battery life of transmitters is a key feature limiting the length of telemetry tracking studies. Most of the weight of a transmitter can be attributed to its power source. Some authors argue that transmitter weight should not exceed 6% of the weight of the carrier individual, minimizing effects on foraging and other ecological interactions [54]. Our survey highlights that transmitters used in telemetry tracking of crocodylians are normally light, generally representing 2% of their body weight, with a few exceptions. A trend towards lighter transmitters is also evident from our results, with the first VHF transmitters weighting 300–850 g and allowing for study lengths of approximately 300 days [40, 56], to recent acoustic transmitters weighting 24–36 g, which were functional for over 2 years [3, 45, 97]. Importantly, many of the studies failed to report the causes that led to the end of monitoring of individuals (e.g., battery malfunction, transmitter detachment or achieving sufficient data for analyses). Hence, the apparent lack of relationship between transmitter size and monitoring time uncovered in our review most probably reflects the lack of information on different causes determining the end of a study.

Reduction of the weight and size of transmitters is key to the development of monitoring protocols that include juvenile and subadult individuals, or that improve

analyses based on long-term data, thus minimizing risk of transmitter loss in external attachment procedures [2, 39, 49, 76] and refining important population parameters.

*'To obtain accurate answers to ecological questions, it is essential to choose statistical methods that are appropriate to the type and quality of telemetry data collected in the field. For example, BBMM is a sophisticated statistical tool for predicting paths and core areas but requires discrete locations to be sampled over short periods of time [51]. This type of analysis may not be suitable for VHF studies due to limits in spatial resolution imposed by constraints on data collection. Instead, it is recommended for studies based on GPS or acoustic telemetry data. Methods such as KDE and MCP can provide important clues about individual home range and movement patterns, but results can sometimes be misleading or biased [26]. MCP data can overestimate an individual's home range by not considering areas with a higher frequency of relocations [10]. On the other hand, traditional KDE methods do not consider the autocorrelation nature of animal movement, only evaluating the spatial clustering of relocations [100]. Therefore, we recommend VHF technology for short-term analysis or in evaluating animal behavior, dispersion, site fidelity and survival rates. As for home ranges and movement patterns, combining GPS or acoustic telemetry with BBMM approaches can potentially predict an individual's spatial distribution probability and area of use more precisely.'*

Transmitters and other items (e.g., antenna and signal receiver) also vary greatly in referring to their cost, GPS transmitters being frequently the most expensive considering equipment acquisition [105]. Otherwise, costs in field expeditions, such as fuel, food and other services for VHF tracking studies can equalize or exceed the amount invested in GPS technology [47]. VHF telemetry is often advised as the method for direct observation of foraging and reproductive behavior, whereas GPS telemetry is suggested in studies targeting at collecting spatial position data of individuals inhabiting landscapes which are difficult to access [105], potentially providing more relocations records during the study. However, GPS signals are more sensitive to attenuation than VHF when transmitters are submerged (Lawson et al. 2018) or blocked by dense vegetation [50].

Emerging technologies like acoustic telemetry represent interesting alternatives in deep, vertically stratified aquatic habitats, because acoustic signals can be transmitted and received while tracked animals are submerged [46, 111]. Acoustic transmitters also benefit

from extended battery life, light weight allowing for data collection along many consecutive years [2], and it is a useful low-cost option, mainly in limited of confined areas [32]. Transmission of acoustic signals can, however, be masked by background noise or by topographic barriers in underwater environments [30] and cannot be used to record information outside the water, such as nesting females in the land. To overcome technical limitations inherent to each tracking technology, combinations of telemetry methods (hybrid transmitters or use of different technologies in the same study) are suggested [2, 11, 14].

## Conclusions

In the past two decades, the increase in the number of telemetry studies of crocodylians worldwide is notable, potentially associated with the increased access to new technologies. Even so, much of the scientific knowledge produced is restricted to developed English-speaking countries. We stress that there is an urgent need for investment in research and scientific production in countries in Africa, Asia, and Latin America, along with policies that warrant publication of studies conducted in these countries in international journals, especially because many species distributed in these continents are at risk [55, 102, 114]. We also encourage researchers to report in their manuscripts the methodological details of their work, such as the exact duration of transmission, size and weight of specimens and transmitters, as well as attachment procedures. We suggest that any difficulties found during fieldwork (e.g., limitations in the signal range or transmitter loss/detachment) should be reported, to guide the implementation of future studies and increasingly improve telemetry-tracking methods.

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40317-023-00333-2>.

**Additional file 1. Table S1.** Full list of publications on crocodylians telemetry-tracking in online databases and in IUCN's Crocodile Specialist Group (CSG) documents between 1970 and 2022.

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## Author contributions

All authors participated in writing and structuring the manuscript. Data Analysis was performed by PBMJ, and PIV and maps and figures designs were performed by PBMJ. All authors read and approved the final manuscript.

## Availability of data and materials

All data is available in supporting material or under reasonable request to corresponding author.

## Declarations

### Ethics approval and consent to participate

Not applicable.

### Consent for publication

All authors have read and approved the submission of the manuscript.

### Competing interests

The authors declare that they have no competing interests.

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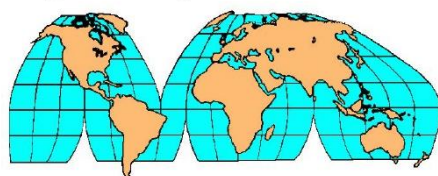
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## APÊNDICE B – Dawn of Telemetry Tracking of Caimans in the Atlantic Forest of Brazil

Nota publicada no IUCN/SSC Crocodile Specialist Group Newsletter (disponível em <http://www.iucncsg.org/pages/Publications.html>).

### Regional Reports



### Latin America and the Caribbean

#### Brazil

DAWN OF TELEMETRY TRACKING OF CAIMANS IN THE ATLANTIC FOREST OF BRAZIL. Tracking of crocodilians by telemetry date back to the 1970s (Joanen and McNease 1970), and since then it has been applied in all continents where crocodilians occur (eg Wang *et al.* 2011; Balaguera-Reina *et al.* 2016; Combrink *et al.* 2017; Baker *et al.* 2019; Campos 2019; Strickland *et al.* 2020; Fukuda *et al.* 2019). Over the past five decades, the technology used for describing and monitoring movement patterns and home ranges of aquatic organisms has evolved enormously (Franklin *et al.* 2009), including lighter and cheaper transmitters, increased battery life and the introduction of satellite and GPS-based transmissions. Such improvements have, to some extent, allowed for an increase in the number of population and behavioural studies of crocodilians based on telemetry, especially in developing countries.

In Brazil, the first studies applying radio-telemetry were carried out in the 1990s by Magnusson and Lima (1991) and Martin and Silva (1998), who tracked *Paleosuchus trigonatus* and *Melanosuchus niger* in the Amazon forest, and described some of their movement patterns. Years later, radio-telemetry was also applied in the study of the movement patterns of *Caiman yacare* in the Pantanal floodplains of southwestern Brazil (Campos *et al.* 2006), the relationships between spatial ecology of *Caiman crocodilus* and *M. niger*, and predation pressure imposed by jaguars in floodplains of central Brazilian Amazonia (Da Silva *et al.* 2010). More recently, using GPS-tracking, Marques *et al.* (2020) studied the home range and movement patterns of *Caiman latirostris* in an area severely impacted by forestry in the Cerrado biome of Brazil.

Whereas telemetry-based studies shed light on many interesting aspects of the ecology of South American crocodilians, the vast majority of extant crocodilian populations in Brazil were never subject to evaluations of individual home range, movement patterns or territoriality. In the Brazilian Atlantic Forest, a highly impacted and fragmented biome currently covering only 8% of its original area (Cunha *et al.* 2019), monitoring of crocodilians by telemetry is still insipient, without any published information.

In a pioneering effort, the Projeto Caiman (Instituto Marcos Daniel; IMD) recently initiated the first monitoring study of *Caiman latirostris* movement and home ranges based on

GPS tracking of 7 individuals in protected Atlantic rainforest fragments. The methods involve GPS/GSM technology in association with a Sigfox mobile network. All gear was developed and adapted by Nortronic, a Brazilian company specializing in technology for animal tracking. The first caimans monitored by the IMD team were tagged with GPS transmitters (Fig. 1) and released in a protected area within the city of Serra, in southeastern Brazil, in April 2019 (Fig. 2). Data on home range and movement patterns of these caimans were presented in an undergraduate thesis elaborated by one of the authors (GGD), who is currently part of the IMD staff.



Figure 1. Fitting of GPS transmitters on *Caiman latirostris* by Eduardo Lázaro (veterinarian, Projeto Caiman), on the right. From left to right: Lucas Fraga (veterinary student, FAESA), Paulo Braga Mascarenhas Júnior (biologist, Projeto Jacaré); Gabriel Dias (biologist, Projeto Caiman), Thassiane Targino da Silva (Veterinarian, Projeto Caiman), Eduardo Lázaro.

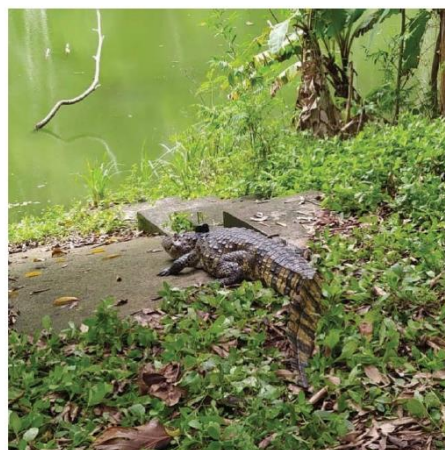


Figure 2. Release of a *Caiman latirostris* tagged with a GPS transmitter in a protected area in the Municipality of Serra, Espírito Santo.

Following these first steps, a research program was established to apply GPS tracking in the study of *Caiman latirostris* populations in the north Atlantic Forest of Brazil. The program (Projeto Jacaré) is currently integrated by students and faculty of the Universidade Federal Rural de Pernambuco (UFRPE) and the Universidade Federal de Pernambuco (UFPE). In August 2020, our research proposal to monitor caiman population in a water reservoir in the outskirts of the city of Recife was selected by the Rufford Foundation to receive a small grant of £5770. Research will be led by PBMJ as part of his doctoral thesis, and will focus on GPS tracking of caimans in both protected areas and areas subject to net fishing in the same reservoir. Most of the fund will be spent in fieldwork and in acquiring the GPS transmitters and receiver. All gear and protocols will follow those already in use by the IMD in southeastern Brazil, allowing for future exchange and comparison of results.

The partnership between IMD and Projeto Jacaré was greatly facilitated through the 2018 CSG Meeting in Santa Fe, Argentina. Since then, several collaborations have been articulated and consolidated between the two initiatives. We hope that spatial data collected in the forthcoming years will help us understand how *Caiman latirostris* populations occupy, move, feed and reproduce in such impacted environments as the periurban rivers and reservoirs of the Brazilian Atlantic forest. We also expect that home range and movement data will be useful in pointing out the main causes of disturbance and avoidance by caimans, thus providing guidelines for informed conservation action.

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