

REVIEW

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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 sub-tropical 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, 1987)

[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 “telemetri*”, “track*” “tag*”, “VHF”, “UHF”, “satellite”, “GPS”, “radio”, “acoustic”, “transmitter”, “caiman”, “alligator”, “crocodile”, “gharial”, “Crocodylia”, “crocodylian”. 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. 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

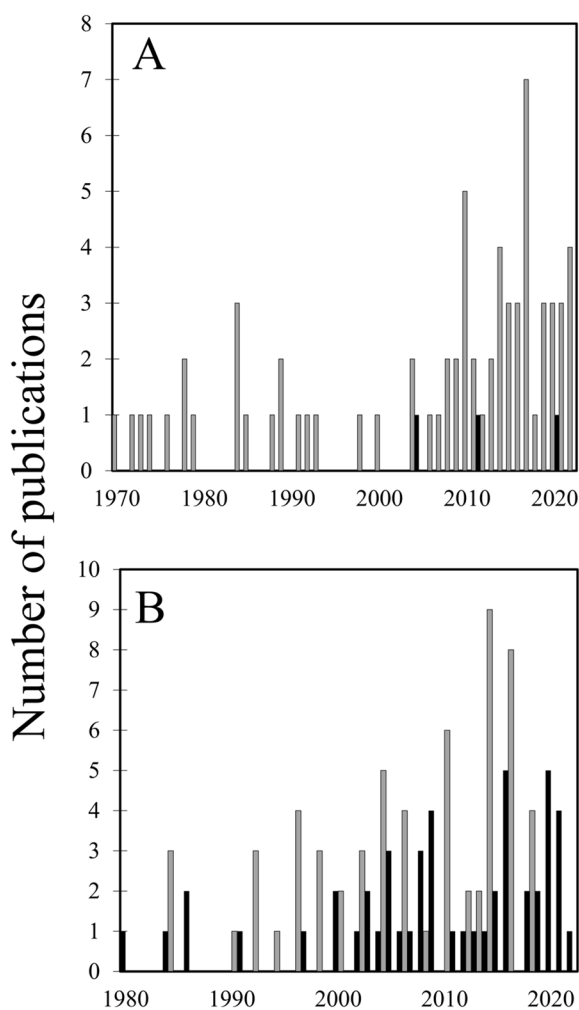


Fig. 1 Number of publications of telemetry-tracking in crocodylians between 1970 and 2022 in **A** online databases and **B** in IUCN'S Crocodile Specialist Group documents. Grey bars indicate full articles (**A**) and CSG proceedings (**B**) and black bars indicates short communications (**A**) and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

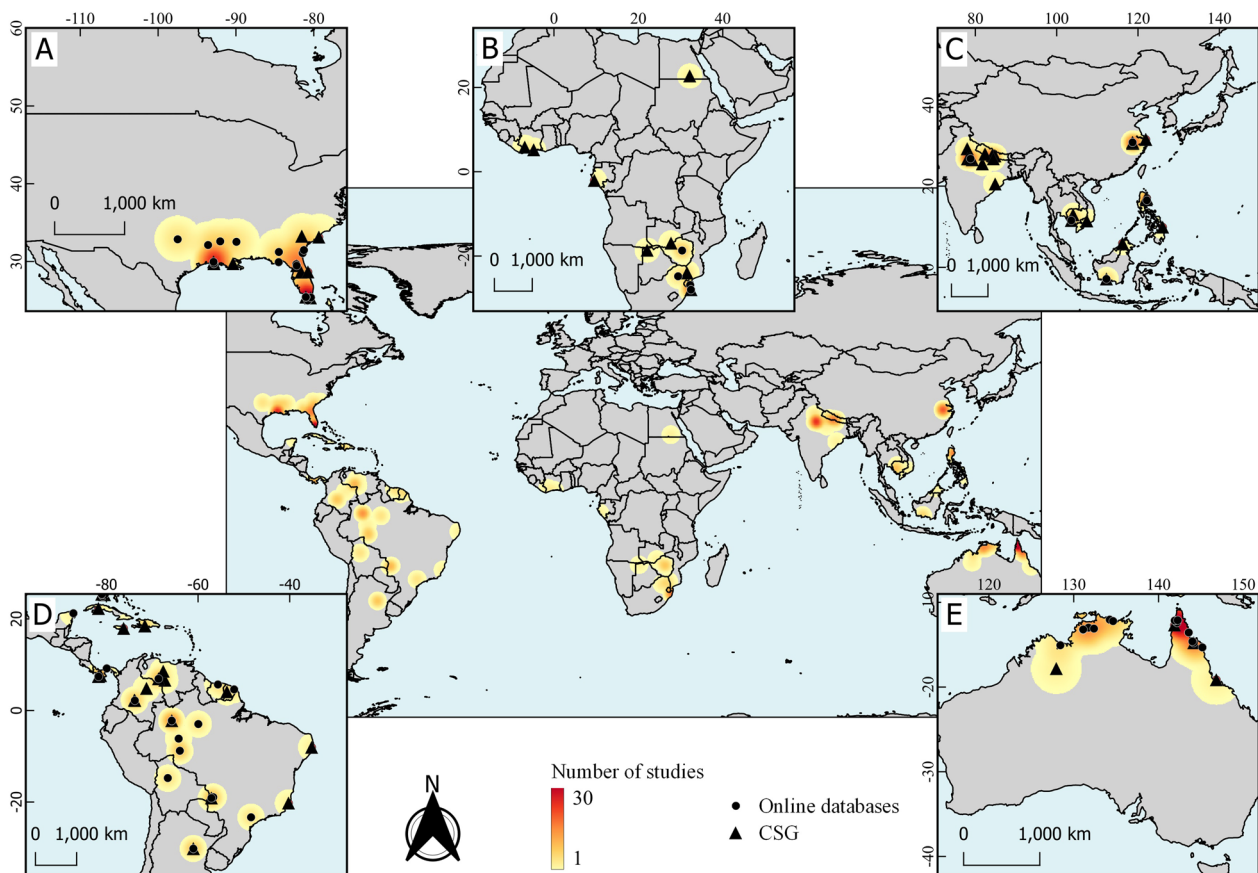


Fig. 2 Geographic distribution of telemetry-tracking publications on crocodylians between 1970 and 2022. The number of publications increases from yellow to red shades. Buffer zones represent a 350 km radius. Black dots represent studies published in indexed journals. Black triangles represent research 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 ± 25 individuals tagged per study. Studies that applied VHF and GPS methods had 13 ± 9 and 8 ± 6 tracked individuals, respectively.

VHF studies generally spanned longer time frames (1.7 ± 1.9 years), but with large variation, ranging between 0.02 and 10 years. Studies involving GPS telemetry lasted 2.3 ± 1.5 years (0.4–4.3 years) and studies involving acoustic telemetry lasted 2.6 ± 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 ± 1.06 years). Acoustic telemetry transmitters were reported as the ones achieving the longest transmission periods, ranging from 18 to 3997 days (2.18 ± 1.78 years; $n=426$ individuals) (Fig. 5C). VHF transmitters were reported to be functional from one to 1258 days (0.66 ± 0.6 years; $n=626$ individuals) (Fig. 5A), and GPS transmitters from three to 1209 days (0.8 ± 0.69 years; $n=117$ individuals) (Fig. 5B). Hybrid GPS+VHF devices transmitted from four to 744 (0.55 ± 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

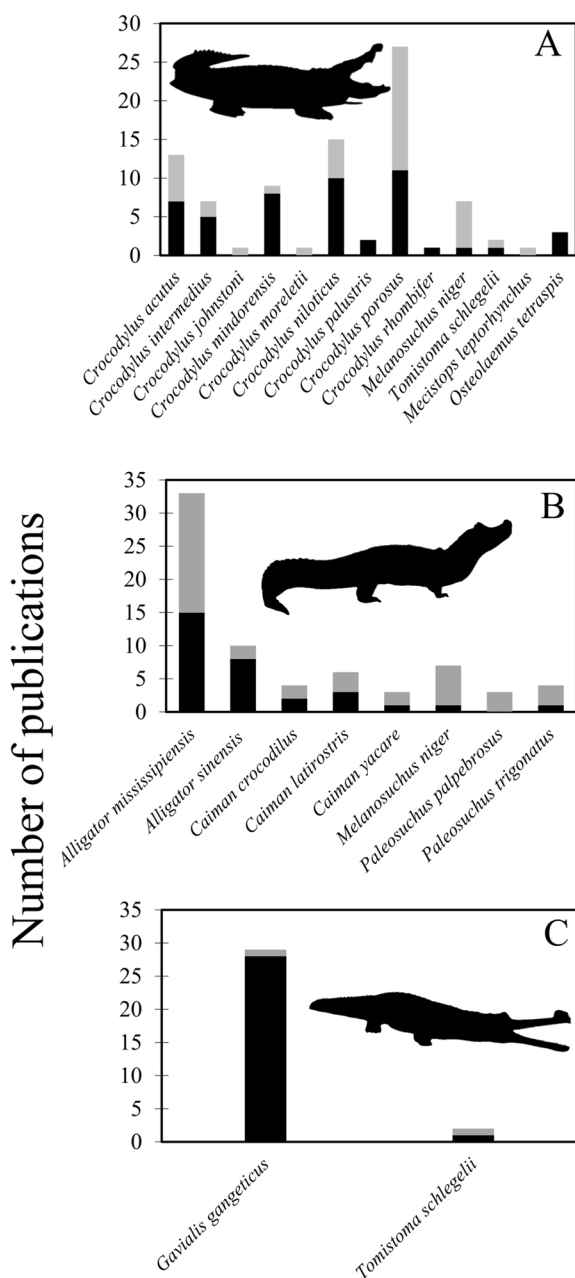


Fig. 3 Number of publications related to telemetry tracking in species of **A** Crocodyliidae, **B** Alligatoridae and **C** Gavialidae, between 1970 and 2022 in online databases and IUCN's Crocodile Specialist Group documents. Grey bars represent publications in the CSG, while black bars represent publications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

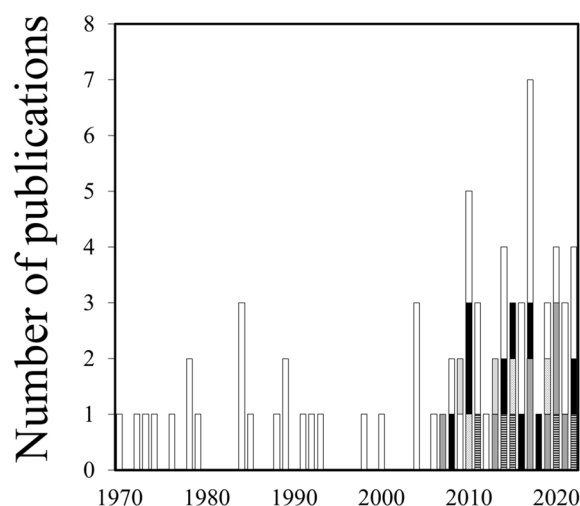


Fig. 4 Technologies used in crocodylians telemetry-tracking studies in publications available on online databases between 1970 and 2022. Each different type of bar represents a different technology or combination of technologies. White: VHF; Dark grey: GPS; Black: GPS and VHF; Light grey: VHF, GPS and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

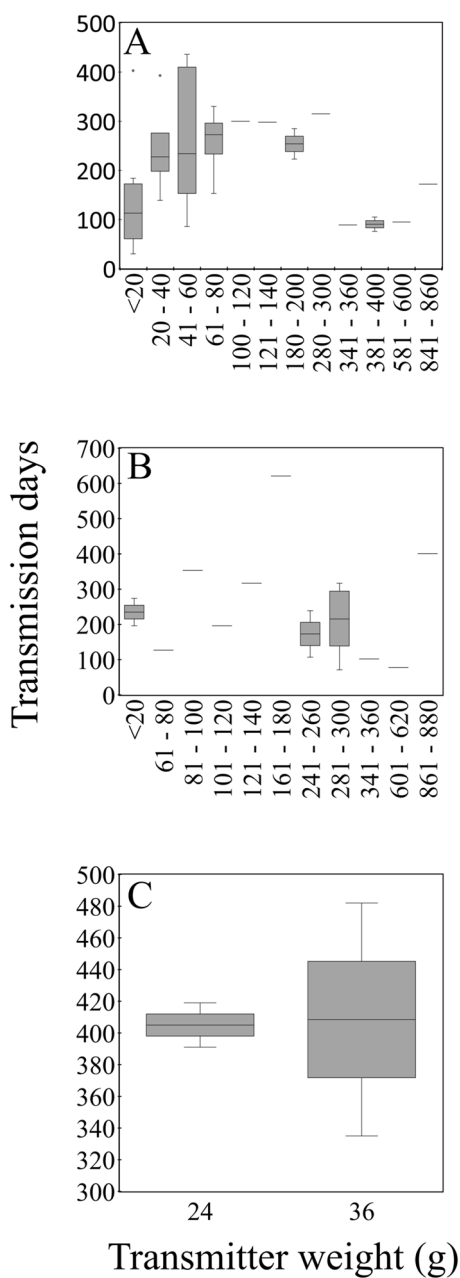


Fig. 5 Average transmission period of telemetry-tracking transmitters used in crocodylians based on publications available in online database between 1970 and 2022. Each category considers a 20 g range of transmitters weight, except for Acoustic (C), which only two different weights were informed in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

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Competing interests

The authors declare that they have no competing interests.

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