INNSPUB

Journal of Biodiversity and Environmental Sciences (JBES)
ISSN: 2220-6663 (Print) 2222-3045 (Online)
Vol. 23, No. 1, p. 52-61, 2023
http://www.innspub.net

REVIEW PAPER OPEN ACCESS

Review of crocodilian communication: A research gap in acoustic and chemical signals in Gharial (*Gavialis gangeticus*)

Jailabdeen Ajjim[1,2], G. Archunan[*1,3]

[1]*Department of Animal Science, Bharathidasan University, Tiruchirappali, Tamil Nadu, India*

[2]*Gharial Ecology Project, Madras Crocodile Bank, Mamalapuram, Tamil Nadu, India*

[3]*Dean-Research, Marudupandiyar College, Thanjavur, Tamil Nadu, India*

Article published on July 11, 2023

Key words: Crocodilian, Communication, Acoustic signal, Chemical signal, Gharial

Abstract

Crocodilians are a diverse group of reptiles that have been extensively studied for their morphology, behaviour, and ecology. However, the communication and signalling mechanisms in crocodilian species, especially for the critically endangered gharial, remain poorly understood. Acoustic communication in crocodilians is relatively well-documented, but the production and reception of acoustic signals remain understudied. The application of new technological advancements, such as the acoustic camera used in frogs, could greatly advance acoustic research in various species of crocodilians. In contrast, chemical communication research is comparatively more limited for all species of crocodilians, and has been limited to sampling captive animals, primarily in zoos. Studying both acoustic and chemical signalling in gharials could significantly contribute to the understanding of their behavioural ecology and aid conservation aspects. Furthermore, it would considerably enlarge the representation of contemporary crocodilians since gharials in captivity are few and largely unstudied. This review summarizes current understanding of acoustic and chemical communication in crocodilians and highlights the need for future research.

***Corresponding Author:** G. Archunan ✉ garchu56@yahoo.co.in

Introduction

Crocodilians, like other reptiles, use visual, acoustic, chemical, and tactile signals for communication. However, acoustic, and chemical signalling in crocodilians is difficult to study due to the challenges involved in recording and studying such signals (Doody *et al.,* 2021). Pioneering work in complex communication behaviour in crocodilians was done in the 1970s-1980s by Leslie D Garrick, Jeffrey W Lang, (Garrick & Lang 1977; Garrick *et al.,* 1978) and Kent A Vliet (Vliet 1989), followed by Valdimir Dinets (Dinets 2010, 2011, 2013a, 2013b) and Stephan A. Reber (Reber *et al.,* 2015, 2017, 2020). Acoustic signals in crocodilians are mostly vocal, but there are exceptions. Previously, it was reported that the gharial (*Gavialis gangeticus*; family: Gavialidae) rarely vocalizes and does not produce infrasound (Dinets 2013a). However, recent studies have shown that acoustically matured male gharials with a grown "ghara" can produce "POP" preceded by SAVs (AjjiM J *et al.,* 2018, 2023).

On the other hand, chemical signals are the oldest method of communication, dating back to the earliest days of life in the Earth's oceans, where even single-celled organisms possess the ability to produce and detect chemical signals (Wyatt 2014). Reptiles have granular glands in the anal region, and some lizards have four types of these glands near the vent (Martín & López 2011). In crocodilians, in addition to the glands near the vent, they have a row of glands along the back called “Dorsal gland” and two large glands under the lower jaw called "Gular gland" (Reese 1915, 1921). However, there have only been preliminary studies conducted in the field of chemical signalling communication of crocodilians because of the difficulties inherent in sampling, especially with wild populations. The critically endangered gharial, once widespread across the Indian subcontinent, is now restricted to India and Nepal only. National Chambal sanctuary holds the last strong hold population of wild gharials. Globally above 80% of wild gharials resides in National Chambal Sanctuary the only protected river sanctuary in India (Lang *et al.,* 2019). This review attempts to summarize research on the acoustic and chemical communication of crocodilians, while also identifying notable research gaps and challenges. Our focus is on the acoustic and chemical signalling systems of the critically endangered gharial, in an effort to understand the species' behavioural ecology for conservation. Furthermore, detailed study of wild resident gharial will likely expand our knowledge about the complexity and diversity of crocodilian signalling systems. In this review, we present the information available in aspect of acoustic and chemical signals of different families within Crocodilia order.

Acoustic signal:

Sound signalling is an efficient form of communication that is easily transmitted and contains biological information for receivers without leaving permanent traces (Bradbury & Vehrencamp 1998). The common ancestors of extinct dinosaurs, pterosaurs, and extant birds and crocodilians are the Archosaurs. The larger species of extant pterosaurs have diverse structures such as crests, frills, and horns that are likely used in sexual dimorphism, mating displays, and ritualized combat (Bennett 1992; Knell *et al.,* 2012; Hone & Naish 2013). Some crest-like structures have labyrinthine air passages that may be used for intraspecies communication calls (Wiman 1931; Diegert & Williamson 1998).

Acoustic signalling is widespread among modern vertebrates, including mammals, birds, amphibians, and fishes (Bradbury & Vehrencamp 1998). Reptiles, however, are known to be more vocal in nature (Young 2003), and crocodilians are likely the most vocal among non-avian reptiles (Campbell 1973; Britton 2001). Within the order Crocodylia, there are three families: Alligatoridae (alligators and caimans), Crocodylidae (true crocodiles), and Gavialidae (gharials and tomistoma), of which about 28 species are recognized (Stevenson 2019; Griffith *et al.* 2022).

Alligatoridae and Crocodylidae

Crocodilians vocalize more during their early stages of life and diminish as they mature (Neill 1971; Campbell 1973).

Adults can produce a variety of acoustic signals, and these signals generally intensify during mating/courtship, nesting/incubation, and hatching/post-hatch/parenting/guarding seasons (Garrick and Lang 1977; Dinets 2013a). Across all species, crocodilians use three major sound types in various combinations with respect to the species: bellowing/roaring, infrasounds, and headslaps/jawslaps (Doody *et al.,* 2021).

Bellowing/roaring is vocal and produced above water, and it can easily be observed by humans (Garrick and Lang 1977; Dinets 2013a). Recent studies show that crocodilians produce around four types of vocal signals during the courtship/mating season (Staniewicz 2020). Infrasounds or sub-audible vibrations (SAVs) are produced below the water surface at frequencies below the hearing range (-10Hz), but the integumentary sensory organ (ISOs) in crocodilians helps them perceive these signals (Gridd & Kirshner 2015). The "water dance" effect caused by this infrasound has a coded signal of the size and physical power of the signalled individual (Urra *et al.,* 2019). The last signal, headship/jawslap, is a sharp onset signal often used to advertise location and used in combination with infrasound signals (Dinets 2013a,b).

Most of these signals are produced in the head oblique tail arched (HOTA) posture, making it easy to see from afar (Garrick *et al.,* 1978; Dinets 2013a). During the HOTA posture, there is evidence of chemical signals released and everted gular glands during displays (Garrick and Lang 1977). These chemical signals produced by gular glands and paracloacal glands possibly carry information about the animal's species, sex, and sexual maturity (Weldon and Wheeler 2001). In many species of crocodilians, these features are primarily produced by adult males, and adult females occasionally produce roars/slaps but without infrasounds and not in HOTA posture (Vliet 1989).

Acoustic signalling in crocodilians have been extensively studied and experimented upon, with a particular focus on smaller animals, especially juveniles, as the risks and management are negligible when compared to adults (Reber *et al.,* 2020). Juvenile calls have been classified into different categories, including hatching calls, contact calls, distress calls, and threat calls (Vergne *et al.,* 2009). Within the category of distress calls, juvenile calls can be further classified into two: "screech", which is always loud and high pitched and produced when the palatal valve is open, and "moan", which is always softer and low pitched and produced when the palatal valve is closed (Herzog and Burghardt 1977). Similar calls were also observed in a field study on spectacled caiman in Western Amazonia, Brazil (Roberto and Botero-Arias 2013).

Within a few days of hatching, young Nile crocodiles change the fundamental frequency in their calls, and attendant females adjust their responses as they grow (Vergne *et al.,* 2007; Chabert *et al.,* 2015). Black caiman hatchlings showed two functionally different context-based calls, and both the mother and juveniles could differentiate between distress calls and contact calls (Vergne *et al.,* 2011). Experimental studies conducted by Reber's team revealed cognitive and evolutionary aspects of crocodilian communication. In two different studies, it was shown that Chinese alligators and American alligators provide information about body size in the formants of their bellow signals (Reber *et al.,* 2015, 2017).

A comparative study of American alligators and spectacled caiman hatchlings suggested opposite ontogenetic development in behavioural predisposition. While alligators and true crocodiles are apex predators capable of protecting their offspring against most dangers, adult caimans, such as the spectacled caiman species, frequently become prey themselves (Reber 2020). However, most of these studies are based on captive or semi-captive populations, and it is essential to understand wild populations. Some studies conducted in the wild are mostly based on smaller size classes, mostly juveniles.

Gavialidae:

The signalling system of the gharial (*Gavialis gangeticus*) is unique among crocodilians, but information on this species' vocal communication is scarce.

Adult male gharials with bulbous growth at the tip of their snouts, known as "ghara," modify their HOTA posture as a head-up posture on land, which is considered a territorial display (Singh & Rao 1990; Dinets 2013a). Mature males with ghara produce soft buzzes, and both males and females produce incredibly loud jawslaps, both underwater and occasionally above the water surface (Whitaker & Basu 1982; Dinets 2013a). However, these observations are based on only a few observations.

Over the last six years, we have been conducting acoustic field studies on the largest wild gharial population in the National Chambal Sanctuary through Gharial Ecology Project (under Madras Crocodile Bank Trust, Chennai), yielding valuable insights into gharial acoustic communication. Mature male Gharials produce 1-3 loud, short burst POP signal events underwater throughout the year, but these signals intensify during social behaviour seasons. Earlier these POP signal events are often misidentified as jawslaps (Dinets 2013a). The primary characteristics of the POP signal event include: (1) each male produces a unique and consistent set of patterns for its popping event; (2) these patterns appear to relate to the context of the environment during the production of the pop event; and (3) the increase in the production of POP events during the mating season can be used to estimate the synchrony in the mating/courtship season. These are the four different contexts of the POP signal events were initially observed: (I) Alert (AL), (II) Patrol (PA), (III) Male-Male (MM), and (IV) Male-Female (MF) (AjjiM *et al.,* 2018, 2023).

In addition to POP signals, observations of gharial hatchlings and females have revealed the production of clicks. Vocalizations between inter-nest and intra-nest hatchlings are also evident, and their possible communication mechanisms will be investigated in future studies.

Chemical signal:

Chemical signalling is one of the oldest forms of communication, having evolved over 3.5 billion years and is widely used by many organisms (Ache and Young. 2005). Insect chemical ecology has received much attention and has been extensively studied when compared to vertebrate chemical ecology (Eisner & Meinwald 1995). One of the key differences between insect and vertebrate chemical signals is that many insect species use chemical signals alone for mate choice, whereas in vertebrate species, social communication is often multi-sensory in nature (Mason 1992; Müller-Schwarze 2006; Wyatt 2014). In mammals, feces and body fluids such as urine, saliva, vaginal mucus, and glandular secretions are the main sources of chemical signals, which play a major role in manifesting effective maturity, reproduction, and social behaviours (Archunan 2009). However, chemical communication in reference to reptiles are limited.

Lizards and Testudines

All reptiles, especially lizards, have granular glands in the anal region involved for chemical signalling (Quay 1986). Lizard chemical signalling is one of the most extensively studied systems in the last 40 years (Martín & López 2011). Some of the chemical compounds from these gland secretions serve as signals and are volatile in nature, making them efficient for airborne transport in arid conditions (Alberts 1990; Bruinjé *et al.,* 2020). Several lizard taxonomic groups have been studied, and the ability to discriminate the volatile compounds of male and female conspecifics has been experimentally demonstrated (Cooper & Vitt 1984; Mason & Gutzke 1990; Cooper 1996; Cooper & Steele 1997; Labra & Niemeyer 1999; López & Martín 2001; Cooper & Pérez-Mellado 2002).

After lizards, chemical signalling in turtles has also been well-studied in detail. Terrestrial tortoises of the Testudinidae family have mental/chin glands that express male aggression and cloacal glands that express species and sex recognition (Mason 1992). A study by Bill Belzer (Belzer 2002) found that males of eastern box turtles were able to find females by the visible and moving latter and not by any chemical cues. In contrast, most male species of turtle sniff female's cloaca while social bonding (Legler & Vogt 2013).

The Rathke glands secrete through the pores on the shell bridge of the axillary or inguinal areas and are present in most turtle species except for some Testudinidae and Emydidae (Ehrenfeld & Ehrenfeld 1973; Solomon 1984). Mental/chin glands are common in all Emydidae, Geoemydidae, Platysternidae, and Testudinidae (Winokur & Legler 1975). Most of these glands become active only in adults and only during the breeding season, which underscores their critical role in reproduction (Rose *et al.,* 1969).

Crocodilians

Crocodilians possess three primary glands for chemical signalling: (i) Dorsal glands, which are rows of glands located on their back; (ii) Gular glands, which are a large pair of glands situated under their lower jaw; and (iii) Paracloacal glands located on either side of the inner wall of the cloaca or vent (Grigg & Kirshner 2015). Although many studies have been conducted on the structure and chemical composition of these glands (Weldon & Wheeler 2001; Weldon *et al.,* 2008), there has been relatively little research on the ecological and behavioural characteristics associated with them due to practical difficulties in studying crocodilians (Weldon & Ferguson 1993).

However, an early behavioural study demonstrated evidence of the spread of odour and the visual eversion of gular glands during social displays of crocodilians (Garrick and Lang 1977). This indicates that the combination of chemical, visual, acoustic, and tactile signals has encoded the species, sex, and sexual maturity of the animal (Weldon & Wheeler 2001). Gular gland secretions have been found to contain a variety of lipid family compounds such as fatty acids, squalene, cholesterol, alcohols, and α-tocopherol. These compounds are involved in advertising sexual and individuality information and have been shown to be used by females to mark nest sites (Weldon *et al.,* 1987; Weldon & Sampson 1988; Weldon *et al.,* 1990; Weldon & Tanner 1991; Weldon & Ferguson 1993; Weldon & Wheeler 2001).

On the other hand, paracloacal gland secretions contain hydrocarbons, fatty acids, alcohols, tricylglycerols, steroids and their esters, and phospholipids. This mixture of compounds has been evidenced in the communication of mating and nesting behaviour (Weldon *et al.,* 1988; Shafagati *et al.,* 1989; Weldon *et al.,* 1990; Weldon & Tanner 1991; Dunn *et al.,* 1993; Weldon & Ferguson 1993; Wheeler *et al.,* 1999; Weldon & Wheeler 2001; García-Rubio *et al.,* 2002). Despite the evidence of these chemical signals, there is a lack of behavioural research on their detection except for one study on Caiman *crocodylus* that showed prolonged sniffing behaviour (Huggins *et al.* 1968) and a study on yearling Alligator *mississippiensis*, which reacted to exposure of conspecific scents (Johnsen & Wellington 1982).

In gharials (*Gavialis gangeticus*), evidence exists for the presence of both gular and paracloacal glands (Grigg & Kirshner 2015). However, to date, only one study has examined both gland secretions comparatively using thin layer chromatography (Weldon & Tanner 1991).

Conclusion

In conclusion, crocodilians, particularly the gharial, have been understudied in terms of their communication and signalling. Acoustic communication is well documented in various species of crocodilians, but little is known about the production and reception of the signals. Additionally, chemical communication research is even more limited, especially in gharials, due to their critically endangered status and limited availability of individuals in captivity. In reference to acoustic signals, Crocodilians exhibit diverse vocalization patterns throughout their life stages, with juveniles being more vocal and vocalizations diminishing as they mature. Adult crocodiles and alligators produce various acoustic signals during mating, nesting, and parenting seasons, including bellowing/roaring, infrasounds, and headslap/jawslap. As far as chemical signals are concerned, Crocodilians have three main glands: dorsal glands, gular glands, and paracloacal glands which produce compounds that convey information about species, sex, and sexual maturity.

Overall, the research on crocodilian acoustic and chemical communication is still in its infancy, with many research gaps yet to be filled. Future studies should utilize new technologies and focus on understudied species like the gharial to gain a more complete understanding of crocodilian communication. This information can be used to inform conservation management plans and aid in the preservation of these remarkable and ecologically important species.

Recommendations

In crocodilian species, studies related to the characteristics and properties of acoustic signals are well-documented. However, the mechanisms of signal production and reception remain a less explored topic. New technical advancements, such as the acoustic camera used in frogs to locate the source of signals (Beeck *et al.* 2022; Calsbeek *et al.,* 2022), could be applied in various species of crocodilians to advance acoustic research. Morphological studies in gharials are not well-established, which is a major limitation for interpreting the source and reception of any acoustic signal production. While acoustic communication research is more advanced than chemical communication research in crocodilians, species particularly gharials have not been studied well in terms of both acoustic and chemical communication. Preliminary research on gharial communication suggests that male gharials produce POP signals carrying individual signatures in the temporal characteristics (AjjiM *et al.,* 2018, 2023), while acoustic communication in other crocodilian species is based on frequency characteristics. Furthermore, there is a scope for studying hatchling calls, female and hatchling clicks, inter-nest, and intra-nest communication in gharials.

Similarly, the chemical signals in gharials are less studied, mainly due to the small number of individuals in captivity and the risks involved in working with wild populations due to their critically endangered status. However, studying both acoustic and chemical signalling in gharials would greatly benefit our understanding of their behavioural ecology. The results from such research could directly contribute to conservation actions and management.

Acknowledgment

We extend our sincere acknowledgement to Gharial Ecology Project/Madras Crocodile Bank Trust and their funding supporters mainly Zoo Praha (Prague, Czech Republic), Crocfest 2018, 2021, Bronx Zoo (Wildlife Conservation Society) and Astral Foundation.

Conflict of interest

The authors declare that there is no conflict of interest related to this article.

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Abbreviation

SAVs- sub-audible vibrations

HOTA- Head Oblique Tail Arched

ISOs- Integumentary Sensory Organs