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ORIGINAL ARTICLE

Gharial acoustic signaling: Novel underwater pops are temporally based, context-dependent, seasonally stable, male-specific, and individually distinctive

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Abstract

Gharials (*Gavialis gangeticus*) produce a sudden, high amplitude, pulsatile, underwater sound called a POP. In this study, gharial POPs ranged from 9 to 55 ms, and were clearly audible on land and water, at ≥500 m. POPs were only performed underwater by adult males possessing a sex-specific, cartilaginous narial excrescence, termed the ghara. We recorded 130 POP events of seven wild adult males in 115 km stretch of the Chambal River during 2017–2019, using hydrophones and aerial mics. A POP event occurs when a male produces a single or double or triple POP, each with a specific duration and timing. A POP event was incorporated into a complex, multi-modal breathing display, typically performed by each male during the breeding season. Key features of this novel gharial POP signal are documented here for the first time. These include its incorporation into a complex breathing display, its reliance on temporal rather than spectral elements, its dependence on a specific social context, its stability within an individual, and its individually distinctive patterning specific to a particular male. The breathing display consisted of sub-audible vibrations (SAV) preceding each POP, then a stereotyped exhalation–inhalation–exhalation sequence, concluding with bubbling and submergence. In our study, 96% of the variation in POP signal parameters was explained by POP signal timings (92%) and number of POPs (4%), and only 2% was related to spectral features. Each POP event was performed in a specific social setting. Two behavioral contexts were examined: ALERT and PATROL. In each context, male identities were examined using Discriminant Function Analysis (DFA). Within each context, each of the seven males exhibited distinctive POP patterns that were context-specific and denoted a male's identity and his location. POP signal features were stable for individual males, from 1 year to the next. Overall, the seven males showed POP patterns that were individually specific, with minimal overlap amongst males, yet these were remarkably diverse. The stereotypy of POP patterns, based on temporal versus frequency difference was best characterized statistically using DFA metrics, rather than Beecher's Information Statistic, MANOVA, or Discriminant Score computations. Our field observations indicated that audiences of gharial, located nearby, and/or in the distance, responded immediately to POPs by orienting in the signal direction. Extensive auditory studies of crocodylians indicate that their capacity for auditory temporal discrimination and neural processing in relation to locating a sound target is on par with that of birds. How the POP sound is produced and broadcast loudly in both water and air has received little study to date. We briefly summarize existing reports on ghara anatomy, ontogeny, and paleontology. Finally, preliminary observations made in a clear underwater zoo enclosure indicate that jaw claps performed entirely underwater produce POP sounds. Simultaneous bubble clouds emanating from the base of the ghara are suggestive of cavitation phenomena associated with loud high volume sounds such as shrimp snaps and seal/walrus claps. We discuss the likelihood that the adult male's ghara plays an essential role in the production of the non-vocal underwater POP, a sexually dimorphic acoustic signal unique to gharial.

KEYWORDS
acoustic communication, archosaur, cavitation, crocodylian, Gavialis, ghara, gharial, temporal identity

1 | INTRODUCTION

In many vertebrates, acoustic communication plays a fundamental role in mate selection, parental care, and important aspects of behavioral ecology, but its evolutionary origins are still being debated (Chen & Wiens, 2020; Jorgewich-Cohen et al., 2022; Odom et al., 2021; Wilkins et al., 2013). For example, until recently, turtles were assumed to be non-vocal, but now over half of all genera and more than 14% of extant species are known to communicate acoustically. It now appears that acoustic communication is not only an homologous trait, but also a conserved feature of choanate vertebrates (Jorgewich-Cohen et al., 2022). This contention gains support when considered in light of a common neurobiological framework of sound production and reception related to commonalities of vocal-acoustic and pectoral-gestural signaling systems in all vertebrates, including fishes (Barkan & Zornik, 2020; Bass & Chagnaud, 2012).

The ability of extant Crocodylia to vocalize is now well documented in many of the 28+ species (Doody et al., 2021; Grigg & Kirshner, 2015). Relative to the other reptiles, this extraordinary capability appears to be universal, as well as one that is distinctive for the group (Capshaw et al., 2020). At every life stage, from a hatchling still inside its egg through to its adulthood, a crocodylian's vocalizations play a crucial role in mediating social encounters with conspecifics (Reber, 2018). These interactions include complex parental care, predator avoidance, breeding and reproduction, territorial defense, and social grouping (Doody et al., 2021). The crocodylian vocal repertoire is varied and consists of both short-range and long-distance signals, features shared most closely with the sophisticated repertoires of many birds (Vergne et al., 2009, 2011, 2012).

The common ancestry of these archosaur relatives is reflected in the many striking similarities in the auditory architecture, the neural processing of sound, and the vocal behaviors of the two groups (Carr & Christensen-Dalsgaard, 2015; Kettler & Carr, 2019). Birds and crocodylians also share ancestral archosaur pulmonary features, principally unidirectional airflow, and multiple-chambered lungs with complex branching (Farmer, 2015; Schachner et al., 2021). These similarities contrast with their diverse respiratory and contrasting metabolic strategies (Brocklehurst et al., 2020). Also, both groups exhibit diverse vocal repertoires employing very different mechanisms of sound production, for example, syrinx in birds versus simple larynx in crocodylians (Riede et al., 2019; Russell & Bauer, 2021).

To date, studies of acoustic communication in crocodylians have focused primarily on air-borne vocal calls and associated behaviors, including their production and reception (Reber, 2020). Species-specific sounds are produced by expelling air across a simple larynx, resulting in calls of variable frequencies with a low-frequency range (100–8000 Hz) (Riede et al., 2011, 2015). Bellowing in alligators and roaring in some crocodiles and similar postural-vocal displays communicate relevant information about location, size, sex, and possibly identity about the performer via frequency-dependent formants (Garrick & Lang, 1977; Jensen et al., 2024; Reber et al., 2015). Spectral cues are also contained in hatchling calls that mediate protective behavioral responses of guarding adults toward groups of young (Chabert et al., 2015).

In addition, other sounds within the human audible and sub-audible hearing range (<20 Hz), consisting of a variety of head-slaps, jaw claps, narial geysering, bubbling, and tail-wagging, are produced by representative species (Reber, 2020). Included here are sub-audible vibrations (referred to as SAVs), which is infrasound that either accompanies bellowing or roaring or occurs without an audible signal. Specialized mechanoreceptors, unique to crocodylians, termed integumentary sense organs (ISOs), may play an important role in detecting water borne vibrations (Leitch & Catania, 2012), as does the saccule in alligators (Todd, 2007, 2015).

Most studies have focused on frequency characteristics, rather than temporal components in analyses of crocodilian acoustic signaling. Consequently, the roles of temporal patterning in their sound production and reception remains an enigma, despite the demonstrated importance of temporal features in avian acoustic communication (Dooling & Prior, 2017; Elie & Theunissen, 2016; Fishbein et al., 2021).

As apex predators, modern crocodylians are amphibious, operating on land, at the water's edge as well as in the water, either at the air–water interface or underwater. In water, pressure waves (sounds/vibrations) propagate faster (4–5×) and over longer distances (>10 km) than in air (Ladich & Winkler, 2017). Consequently, in aquatic vertebrates, communication in water vs. air has resulted in various modes of sound production, including the use of ultrasound at short range (e.g., dolphin clicks; Madsen et al., 2023) and infrasound over long distances (e.g., baleen whale songs; Elemans et al., 2024). Fishes and aquatic frogs favor low frequencies (50–2500 Hz) and/or short, pulsatile sounds, for example, clicks or pulse trains, that depend on temporal patterning rather than frequency-based signaling. Alligators, caiman, and various crocodile species are known to communicate underwater with low-frequency bellows and roars, non-vocal headslaps and bubbling, as well as sub-audible vibrations (infrasound). Certain of these water-borne sounds are thought to function primarily as long-distance signals, providing location cues associated with loud, sudden, abrupt sounds (Dinets, 2013; Hopp et al., 2011). However, in the two gharial species (*Tomistoma* and *Gavialis*), evidence for long-distance signaling is lacking (Dinets, 2013; Senter, 2008a; Staniewicz et al., 2022). But, in water as well as in air, studies of crocodylian acoustics have paid more attention to frequency/spectral parameters, rather than temporal features. Overall, in crocodylians, aquatic acoustic communication is less understood, regarding both production and reception.

Unlike other crocodylians, both gharial species are reported to be unusually quiet, except as newly hatched young (Bonke et al., 2015; Gramentz, 2012). The *Tomistoma* acoustic repertoire consists primarily of six short-range vocal calls and bubbling non-vocal during courtship (Staniewicz et al., 2022). In the gharial, *Gavialis gangeticus*, a wide variety of acoustic sounds have been described, anecdotally or opportunistically. These consist of groaning, hissing, and bubbling, at close range to 1 km away (Rao & Singh, 1993; Singh & Rao, 1990; Whitaker et al., 2007; Whitaker & Basu, 1982). Senter (2008a, 2008b) noted the absence of infrasound, and questioned whether gharial headslapping would be a loud signal, due to the gharial's narrow snout and fragile skull. Dinets (2013) reported that gharial lacked infrasound production, and rarely jawclapped or headslapped.

In extant crocodylian phylogenies, both gharial species align separately, distinct from the short snouted alligators and caiman, as well as from the long snouted crocodiles and their close allies (summarized in Iijima et al., 2021). Functionally, based on the species' ecological traits, gharials are by far the most distinctive representative of the living Crocodylia (Griffith et al., 2023). Gharials have long been the subject of scientific fascination and scrutiny, from the early investigations of Geoffroy Saint-Hilaire (1825) to present day, because large adult males are adorned with a "ghara," a soft tissue elaboration of the external nares referred to as a "narial excrescence" (Martin & Bellairs, 1977). In addition to its role as a marker of "maleness," for example, a visual sexual dimorphism, the gharial "ghara" has been presumed to serve an acoustic function, primarily as a vocal signal modifier or resonator.

Osteological features, evident in the skulls of large gharials, include (1) an enlarged narial opening (to provide an attachment site for the base of the ghara) and (2) a pair of enlarged pterygoid bullae (Hone et al., 2020; Iijima et al., 2022; Martin & Bellairs, 1977). Because modern birds and crocodylians share an archosaur ancestry with dinosaurs, paleontologists as well as anatomists have had a keen interest in understanding, what might be the role, if any, of the "ghara" in gharial sound production, and how a functional understanding of the gharial "ghara" might translate into further insights about the acoustic capabilities of fossil crocodylian forms, as well as provide possible clues about dinosaurian acoustics. In this regard, knowledge of anatomical features in fossil forms and their soft tissue counterparts based on extant representatives are central to accurate interpretations and realistic reconstructions of fossil forms (Bourke & Witmer, 2023; Witmer, 1997). It is noteworthy that extant *Gavialis gangeticus* specimens have recently been used for baseline comparisons of facial, neuroanatomical, and endocranial details in fossil forms (Bona et al., 2015; Burke & Mannion, 2023; Pierce et al., 2017; Witmer, 1995).

Two centuries ago, gharials (*Gavialis gangeticus*) were common and widespread along the major large rivers and their tributaries in south Asia. Today, the species survives in less than 5% of its former range, with an adult breeding population estimated globally at less than 1000, 1/20th or less than the historical numbers (Singh et al., 2024). The largest remnant wild population resides along ~450 kms in the National Chambal Sanctuary and consists of an estimated 650 adults, producing ~500 nests resulting in ~15,000 hatchlings annually (Lang et al., 2019). Initiated in 2008, following a mass die-off of 110+ gharials in the lower Chambal, the Gharial Ecology Project has been focused during the past 17 years on studying the behavioral ecology of this last and largest population for its conservation and protection (Lang, 2018; Lang & Kumar, 2013, 2016).

In this context, we initially tagged individual wild resident gharials of all sizes, ages, and sexes, and made detailed behavioral observations, using still and video photography to document our findings. We observed that a breeding male gharial, possessing a mature "ghara" which was individually distinctive in size and shape, on occasion produced very loud underwater sounds in a variety of social group settings (Jailabdeen et al., 2018). In this report, we describe this distinctive acoustic signal, termed a "POP," and outline a number of the key features related to POP production and reception. Because the gharial's "ghara" is such a distinctive morphological addition to the nasopharyngeal architecture of mature males in this species, we discuss our findings not only in light of current knowledge about crocodylian acoustic communication but particularly with reference to what is known about the possible role of the ghara in sound production. We hypothesize that the POP signal described herein is produced within the gharial's ghara, by a mechanism yet to be determined, and that the sound is transmitted directly to the surrounding water through the ghara. In short, our detailed investigation of the gharial "POP" signal suggests that it is likely the product of a novel sound-producing mechanism, located inside a modified bulbous knob, the ghara, at the tip of the gharial's snout.

2 | METHODS

2.1 | Study site and animals

Audio recordings and behavioral observations were conducted during the breeding seasons of 2017–2019, resulting in 3 consecutive years of data collected in the National Chambal Sanctuary containing a large (~2000) self-sustaining population of gharial (*Gavialis gangeticus*) (Gharial Ecology Project, 2022). Six study sites and the associated seven males were: Rhea (=RH 26.826290°N, 78.275556°E; Rhea dominant = RHD), Maghera (=MG 26.788923°N, 78.688251°E; Maghera dominant = MGD, Maghera challenger = MGC), Dinnupura (=DN 26.789471°N, 78.727930°E; Dinnupura dominant = DND), Garhaita (=GR 26.764543°N, 78.810825°E; Garhaita dominant = GRD), Khera KH (=KH 26.672475°N, 78.972689°E; Khera channel dominant = KCD), and Kasaua (=KS 26.640732°N, 78.993197°E: Kasaua dominant = KSD) along a protected 115 km stretch of the Chambal River (locations shown in map, Figure S1). These wild resident males, each with a prominent ghara, were associated with established breeding areas in which the dominant male had an exclusive breeding arena, from which challenger males were excluded. The subject males were 5.5–5.7 m length, ~660–720 kg weight.

2.2 | Behavioral observations

During breeding season (Mid Feb to Early Mar; ~3–4 weeks), at each locality, a mature dominant male gharial resided in an established breeding area consisting of ~0.5–1 km of sand bank with a shoreline depth of 1 m, where adult females congregate for basking and courtship. At most sites, this concentrated group of females attracted one or more potential challenger males. In each breeding area, social interactions peaked in late afternoons into early night time (1600–2300 h), and again in late night through early mornings (0300–0700) before daytime basking prevailed (0800–1500). The riverside habitats were open, devoid of obscuring vegetation. Frequent activities of people at the riverside, engaged in grazing livestock, washing clothes, and bathing resulted in the gharial habituating to human presence. This feature facilitated documentation of behaviors at close range (<50–500 m), with gharial living in nature in the wild.

2.3 | Direct observation versus passive monitoring

Direct behavioral observations are made by an observer assisted by continuous video documentation, using tele-zoom point and shoot cameras in conjunction with manually placed hydrophones to simultaneously record POP events. In addition, passive monitoring was used at the GR locality to make continuous, unattended hydrophone recordings, typically 24 h/7 days a week, when observers were absent. The invariant timing, for example, virtually no variation in the millisecond duration, of POPs allowed grouping of sample POPs collected using both direct observation and passive monitoring methodologies, as illustrated in Figure S2. For each POP pattern, the temporal and frequency parameters were identical (Table 2). Consequently, the acoustic recordings for the GRD male were combined for further analyses. For all the other males, direct observations accompanied acoustic records.

2.4 | Sound recording

Aerial and underwater sound records were made with a setup that facilitated comprehensive documentation of the BR display and POP signals. A pair of matched hydrophones were placed in shallow water (25–75 cm depth) on the riverbank opposite the breeding area under observation. These were D-series hydrophones (−177 ± 9 dB re V/μPa, Flat frequency range – 1 Hz to 1 kHz; https://jezrileyfrench.co.uk/hydrophones.php; tested at National Institute of Ocean Technology, Chennai). These were connected to Zoom digital recorders, that is, Zoom H1 & H6 (https://www.zoom.co.jp). Simultaneous aerial tracks were recorded using Zoom SGH-6 directional mic (sensitivity: −37 dB, 1 kHz at 1 Pa, Input gain: −∞ to 42.5 dB). Sampling rate was at 44.1 kHz /16 Bit depth resolution in WAV format. Sounds were produced by subject males within <1–500 m recorder distance. The focal area for recordings was the breeding arena (~30 m of shoreline), usually at the same location in multiple years. For the GRD male, with a large sample size, some simultaneous recordings at close range were made with the male's midbody <1 m from the submerged hydrophone, and <3 m from the aerial shotgun microphone, in the center of his breeding arena.

2.5 | Acoustic analysis

We manually identified the POP and POP intervals (IPIs) (Gerhardt, 1998; Kershenbaum et al., 2016; Marler & Isaac, 1960) of the POP event of gharials using both Oscillogram and Spectrogram window (FFT size 512, Hann window, overlap 50%) using Raven Pro: Interactive Sound Analysis Software (Version 1.5; Computer software, Ithaca, NY: The Cornell Lab of Ornithology). The selections are verified by pulse train analysis feature in Avisoft-SASLAB PRO (Avisoft Bioacoustics, Berlin, Germany). The temporal parameters: delta time (Δt P and Δt IPI) and frequency parameters: peak frequency (PKFQ) and center frequency (CNFQ) are calculated using selection measurement feature in Raven Pro 1.5. (Figure 2). The terminology used to describe the measurement parameters is shown in Figure S3, and the description of acoustical parameters is shown in Table S1.

2.6 | Statistical analyses

In a preliminary analysis, the temporal versus frequency differences in the POP signals were readily detectable. Rstudio version 1.3.1093 (RStudio Team 2020) was used for all statistical analyses. A two-step approach was used initially for data transformation and then for variance analyses.

2.6.1 | Data transformation

Data were transformed to facilitate numerical sample comparisons with categorical data, that is, the number of POPs, single, double, or triple POPs per POP event (Catchpole, 1976). The minimum and maximum values of each of these parameters were designated as follows: Delta time of POP (Δt P), Delta time of Inter-POP interval (Δt IPI), Peak Frequency (PKFQ) and Center Frequency (CNFQ). This resulted in 4 parameters ×2 values (Min, Max) = 8 parameters in total (MinΔt P, MaxΔt P, MinΔt IPI, MaxΔt IPI, MinPKFQ, MaxPKFQ, MinCNFQ, MaxCNFQ). The categorical value for number of pops (single, double, or triple = NPOP) was included only in the DFA analyses.

2.6.2 | Variance analyses

Multiple variance statistics were computed to examine variation in the dataset: Discriminant Score (DS) (Linhart et al., 2019), Multivariate analysis (MANOVA) (Randall, 1989), Beecher's information statistic (HS) technique (Linhart et al., 2019; Linn et al., 2021) and Discriminant Function Analysis (DFA). The DFA is based on the function lda() (=linear discriminant analysis) of the R package library MASS (Barbosa et al., 2022; Carlson et al., 2020; Price et al., 2015). We used 70% for model training, and 30% to predict model efficiency, using the Confusion Matrix function available in R studio. For all statistical analysis, we have used data from two contexts: PA($n = 79$) and AL($n = 55$) from seven wild male gharial (RHD = 5, MGD = 15, MGC = 6, DND = 4, GRD = 87, KCD = 12, KSD = 5).

3 | RESULTS

Gharials produce a sudden, high amplitude, pulsatile, underwater sound, referred to hereafter as a POP. The gharial POP has durations ranging from 11 to 55 ms, and is clearly audible on land at distances of 200–500 m. POPs were performed only by adult males possessing a sex-specific, cartilaginous narial excrescence, the ghara. In this paper, we examine the acoustic features of the gharial POP signal. These include its incorporation as the initial component in a complex breathing display, its reliance on temporal rather than spectral elements, its dependence on a specific social context, its consistency within an individual, and its individually distinctive patterning which is specific to a particular male. For this analysis, 130 popping events performed by seven wild resident gharials, were recorded along a 115 km stretch of the Chambal River in the National Chambal Sanctuary in northern India during the three breeding seasons of 2017–2019, in February to March. Each POP signal was performed in a specific social context, either as part of an ALERT sentinel signal or when the adult male was on a PATROL within his breeding area.

3.1 | "POP-BREATHE" display

Adult male gharials performed a complex acoustic-visual display, designated here as a "pop-breathe" display and abbreviated as POP-BR. It consisted sequentially of a subaudible vibration (=SAV), then an underwater POP event (once, twice, or thrice; each POP preceded with an SAV), followed by an immediate exhalation at the water surface, followed by a prolonged inhalation, then a second exhalation, often concluded with bubbling as the animal submerges underwater (Figure 1). The underwater SAV-POP was invariably followed by an exhalation-inhalation cycle (as described and illustrated below), as the gharial surfaced. Invariably, each POP was preceded by a subaudible vibration, so when multiple POPs were produced in rapid succession, each individual POP followed a subaudible vibration, producing multiple preceding SAV events. The initial SAV-POP sequence described above, for a double POP, is illustrated in Figure 1. In the top panel, the gharial's body is shown inside view, positioned accurately relative to the water surface. An aerial recording from a microphone positioned on shore adjacent to the displaying male produced the waveform and spectrogram illustrated in the bottom panel (Figure 1).

3.2 | "BREATHE" display

Although the SAV-POP sequences were always followed by a breathe display (=BR) as shown in Figure 1, breathe displays were also performed in multiple variations in different social contexts without a preceding SAV-POP sequence. In fact, breathe displays, minus an initial SAV-POP sequence, were performed frequently during each breeding season of the 3 years study (Video S1). To illustrate the combinatorial aspect of the BR display involving various exhalation and inhalation sequences, we examined 215 BR displays performed by a single resident dominant male, the Garhaita male (GRD), during a representative breeding season for which we have extensive recordings (2017, 14 February to 7 March). Each BR display was categorized with respect to its sequence of components, the frequency of its occurrence, and the date when it occurred (Table 1). The most frequent sequence performed by the GRD male was a short exhalation, followed by a long inhalation, then a second brief exhalation, often followed immediately by bubbling (B) at the water surface, prior to and during eventual submergence underwater (Figure 1).

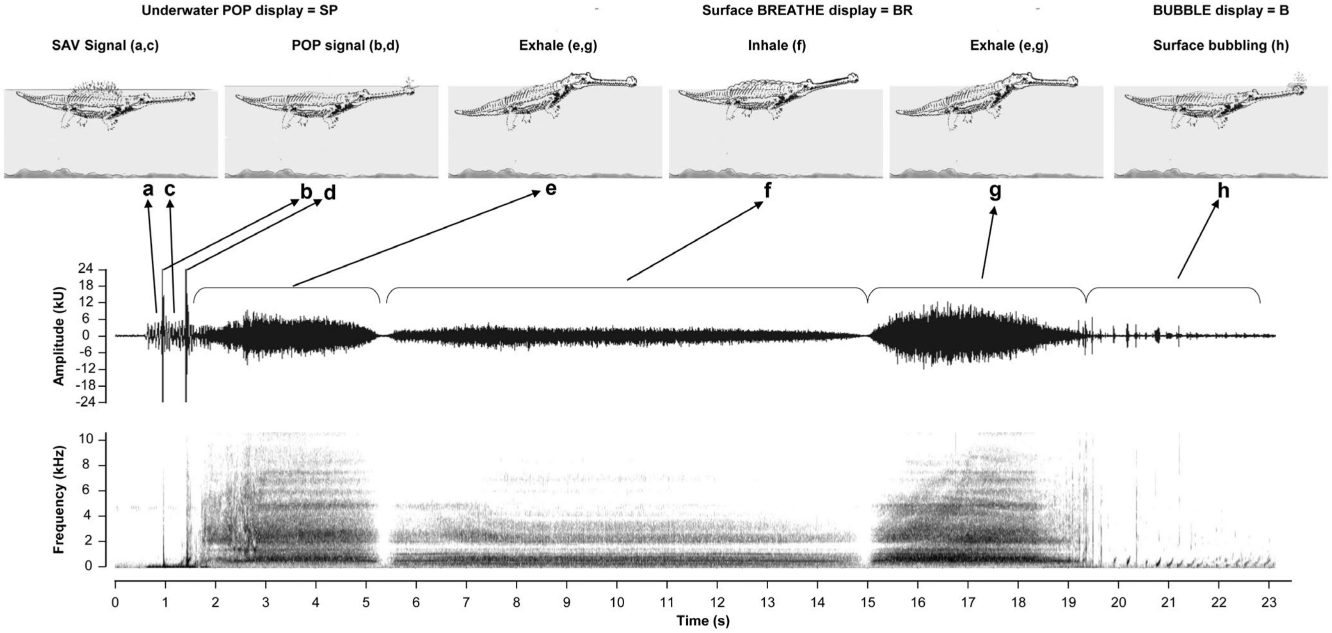

FIGURE 1 (top) Illustration of a "POP-BREATHE" display, as performed by an adult male gharial (top panel, side view) in the water near the surface (air-water interface; water shaded). Initially, a sub-audible vibration (SAV; panel "a") precedes the first POP performed underwater (panel "b"), and the SAV-POP sequence is repeated (panels "c" & "d"). This initial sequence is designated as "SP." It is followed immediately by a brief exhalation (panel "e"), then a prolonged inhalation (panel "f"), followed by a second exhalation (panel "g"), as the gharial's midbody floating at the water surface, lowers slightly on exhalations, and rises on inhalation. Then, at times, surface bubbling may occur (panel "h") as the gharial submerges, body first and finally its head and snout disappear underwater. This figure shows the sequence "SP + EIE + B" as denoted in top left, Table 1, which was the most frequent POP-BREATHE sequence noted for this animal ($n = 54$ instances). (bottom) Aerial recording of above sequence, showing waveform (amplitude in kilounits, kU on vertical axis, over time in seconds) for the various components, panels "a" through "h" and corresponding spectrogram (frequency, in kilohertz on vertical axis, over time in seconds) for the sequence. The total time for this SP-BR display was 22 seconds.

This sequence has been abbreviated here as EIE + B and occurred in 109 instances, or 51% of the total instances recorded (109/215).

Peak occurrence on 27 February corresponded to the first of 2 days (27–28 February) when the overall breathe display (=BR) frequency peaked at 37% (80/215). Overall, 126 instances occurred without a preceding SAV-POP, and this combination was the most frequent (59%) type of BR display that was performed. In 85 instances (39%), the BR display was preceded by the performance of an SAV-POP sequence. Peak performance of the preceding SAV-POP sequence occurred on 28 Feb, with 26 occurrences within 24 hours, more than double the number recorded on any other day. Overall, during this breeding season, this male performed seven variations of the BR display accompanied by SAV-POP plus bubbling, six variations of the BR + bubbling, and was observed to produce only one instance of a simple BR display, that is, exhalation-inhalation-exhalation (=EIE), without a SAV-POP or bubbling (Table 1).

Salient features of the BR include: (1) an initial exhalation (E) and a concluding exhalation (E), sometimes accompanied by bubbling (B), (2) exhalations were relatively short, whereas the inhalation (I) was prolonged, (3) these elements were variously combined, dependent on social context, (4) bubbling (B) was prolonged in the presence of a female, typically during courtship, and was brief or absent in other contexts, (5) multiples of the basic "EIE" breathing sequence occurred in 48 of the 215 sequences tallied (Table 1).

The BR display was quite variable in the number of exhalations and inhalations, and in the presence or absence of bubbling, and appeared to be a graded, rather than a stereotyped pattern of movements. During breeding (February to March), males perform the BR display in an exaggerated manner, relative to other times of year. Specifically, during breeding, more of the performer's mid body and tail were raised above the water surface, and the head was raised in an elevated, angled position. The inflow vs. outflow of air through the male's ghara produced distinctly different sounds (Figure 1). It is important to note here that these breathing sequences were relatively loud in air, easily heard by an observer sitting riverside, at 200 + m from the performer.

Exhalations and inhalations sounded different to an observer; and presumably, these sounds reinforced the visual features of the BR display. Hydrophone recordings indicated that the underwater sounds related to the BR display did not transmit at long distances, and were limited in range, <50 m or less, in contrast to the aerial signal. The breathing sounds are generated and propagated as air moves in and out of the nasal chamber, transmitting into the water with difficulty, due to high impedance at the air/water interface. Furthermore, because the BR display is usually performed at the water's edge, the resultant underwater sounds were muffled in the shallow water (<2 m), and readily absorbed in the sandy bottom sediment.

TABLE 1 Breathing signal summary 2017 ($n = 215$).

(a) Day-wise

		February											March					
	N	14	15	18	21	22	23	24	25	26	27	28	01	02	03	04	05	07
SP+BR+B (7, n=85)																		
SP+EIE+B	54	①	①	④				⑤	①	③	⑤	⑨	④	⑦	②	⑦	③	②
SP+EIEIE+B	19					②				②		⑦	③	③	①			①
SP+EIEIEIE+B	5											④	①					
SP+EIEIEIEIE+B	1											①						
SP+B+EIEIE	1											①						
SP+EIE+B+EIE	3											②	①					
SP+EIEIE+B+EIE	2											②						
BR+B (6, n=126)																		
EIE+B	109			1	1	2		2	1	10	23	10	21	11	7	12	4	4
EIEIE+B	8										3	3			2			
EIEIEIE+B	4									1	3							
EIEIEIEIE+B	2										1	1						
EIE+B+EIE	2										1	1						
EIEIE+B+EIE	1									1								
BR (1, n=4)																		
EIE	4						1				2	1						
Sub total SP+BR+B	*85*	1	1	4	0	2	0	5	1	5	5	26	9	10	3	7	3	3
Sub total BR+B	*126*	0	0	1	1	2	0	2	1	12	31	15	21	11	9	12	4	4
Sub total BR	*4*	0	0	0	0	0	1	0	0	0	2	1	0	0	0	0	0	0
Grand total	***215***	1	1	5	1	4	1	7	2	17	38	42	30	21	12	19	7	7

(b) Context-wise

Dates	AL	PA	MM	MF
14 Feb		1		
15 Feb		1		
18 Feb	1	1	2	
22 Feb			2	
24 Feb	1	1	2	1
25 Feb	1			
26 Feb	1	1	1	2
27 Feb		1	2	2
28 Feb	1	1	5	19
01 Mar		2	1	6
02 Mar		1	6	3
03 Mar	1	2		
04 Mar		1	4	2
05 Mar		1	2	
07 Mar		1	2	
Total	6	15	29	35

Abbreviations: ○, denotes number of BR episodes that incorporated a POP; AL, Alert; B, Bubbling; BR, Breathe signal; E, Exhale; I, Inhale; MF, Male–Female; MM, Male–male; N, Number of samples;P, POP signal; PA, Patrol; S, Sub-audible vibration.

3.3 | Social contexts

The POP-BREATHE display, as illustrated in Figure 1, was variably performed by individual males, in a variety of social settings. We identified four social contexts in which POP events occurred during the breeding seasons (February to March), based on behavioral observations in 2017–2019. These were: (1) alert, (2) patrol, (3) male–male communication, and (4) male–female communication. In this presentation, only the ALERT and PATROL contexts are considered, simply to illustrate the context-dependent nature of the POP signal, as it was employed by wild adult male gharials. Further comparison of POPs across all four contexts are presented elsewhere.

In the ALERT social context, any marked changes in the local riverine environment occupied by a group of gharials often triggered a POP event, which was performed underwater and typically without any prior overt behaviors by the male performing it. In this context, each POP event was sudden and unannounced. The presence of any potential disturbance, such as a group of sand miners walking with their camels to the shoreline, the appearance at the shoreline of fishermen using lines to fish, or the approach of a large group of villagers at the water's edge may be accompanied by a POP event. In this situation, the POP appeared to function as an "alert/attention" signal, typically performed in the direction of the disturbance. It served to alert not only gharial in the vicinity but resulted in responses from other riverside residents and visitors. In most instances, such a signal was performed well in advance, of any overt movements of gharials basking at shorelines. However, on occasion, soon after a POP was performed in this context, gharials on land moved into the water, interrupting an otherwise extended basking session. As noted above, the POP was always followed by a BR display of varying intensity, revealing visually as well as acoustically the performer's location in the water.

In the PATROL social context, the dominant male living with a social group of adult and near-adult females, patrolled the shoreline where the group was basking, including upstream and downstream adjacent areas. The POP-BR display was performed at various times of day and night throughout the area, punctuating the dominant male's slow, deliberate cruising, at times with his back exposed at the water surface, as he moved back and forth along the entire shoreline. At other times, the male would disappear from view, swimming rapidly underwater through the breeding area, and then perform a POP announcing his presence suddenly and loudly at a considerable distance from where he was last on the surface. Typically, each male patrolled a length of shoreline in the early morning as basking was initiated, and then again in the late afternoon, as basking sessions were ending, when individual animals moved into water.

3.4 | POP acoustic structure

Adult male gharials produced a single POP, a double POP, or a triple POP. The nomenclature of the POP structure is shown diagrammatically in cartoon waveforms, illustrating the terminology used to identify the POP parameters presented here (Table S1). The examples in Figures 2–5 are representative POP recordings via hydrophone for a single dominant male, GRD male, for whom 87 POPs were documented in the ALERT and the PATROL social contexts during three breeding periods in 2017–2019 (supplementary videos).

In the ALERT context, responding to an external disturbance, this male performed two distinct POP patterns. He produced a single POP with a duration of 22 ms, and a peak frequency of 8.269 kHz, at peak power of 78.7 dB (Figure 2; Table 2). Or he performed a double POP, which showed identical pulse durations of 0.022 s for both the first and second POP, with an inter-syllable interval (ISI) of 0.482 s. The single POP and the double POP had similar frequency and power values (Figures 2 and 3; Table 2). Overall, 26 POP events were recorded for this male in the ALERT context. Of these, 7 were single POPs and 19 were double POPs.

3.5 | POP structure is context-dependent

In the PATROL social context, the same GRD male produced three distinct POP patterns, all three differing from the single and double POPs produced in the ALERT context (Figure 5a–c) = POPs in PATROL contexts; (Figure 4a,b), top = POPs in ALERT context, for comparison = composite of Figures 2 and 3. In the PATROL context, his POP pattern consisted of a single POP of slightly longer duration, 35 ms, than the single POP of 22 ms in the ALERT context. In addition, in the PATROL context, there were two other distinct double POP patterns, differing primarily in the POP duration, 29 ms repeated twice, or 43 ms repeated twice, with a similar inter-syllable interval (0.369–0.370 s) between the first and second POP (Figure 5b,c). These slightly longer double POPs in the PATROL context contrasted with the shorter POP duration of 0.022 s evident in the ALERT double POP produced by this male. In addition, the inter-POP interval (IPI) was shorter in the PATROL context.

A total of 61 instances of POP events in the PATROL context were recorded for the GRD male, of which 17 were a single POP (Figure 5a), 15 were short double POPs (Figure 5b), and 29 were long double POPs (Figure 5c; for values for all three types, see Table 2). In brief, within a given context, this individual's POP timing, that is, ALERT = 0.022 s, PATROL = 0.029 s or 0.043 s, did not vary and was repeatable and identical in its timing dimension, and the number of POPs in a given POP event was consistent. However, the POP patterns were context-dependent, differing in PATROL vs. ALERT contexts. Overall, for these two social contexts examined, this single individual male produced a total of five different, repeatable POP patterns, for example, distinctive POP events, consisting of different numbers of POPs, of different durations and/or inter-POP intervals, dependent upon social context (Figures 2–5).

3.6 | POP structure is stable across years

A detailed comparison of the POP signal parameters across breeding seasons was facilitated by the large number of recorded POPs

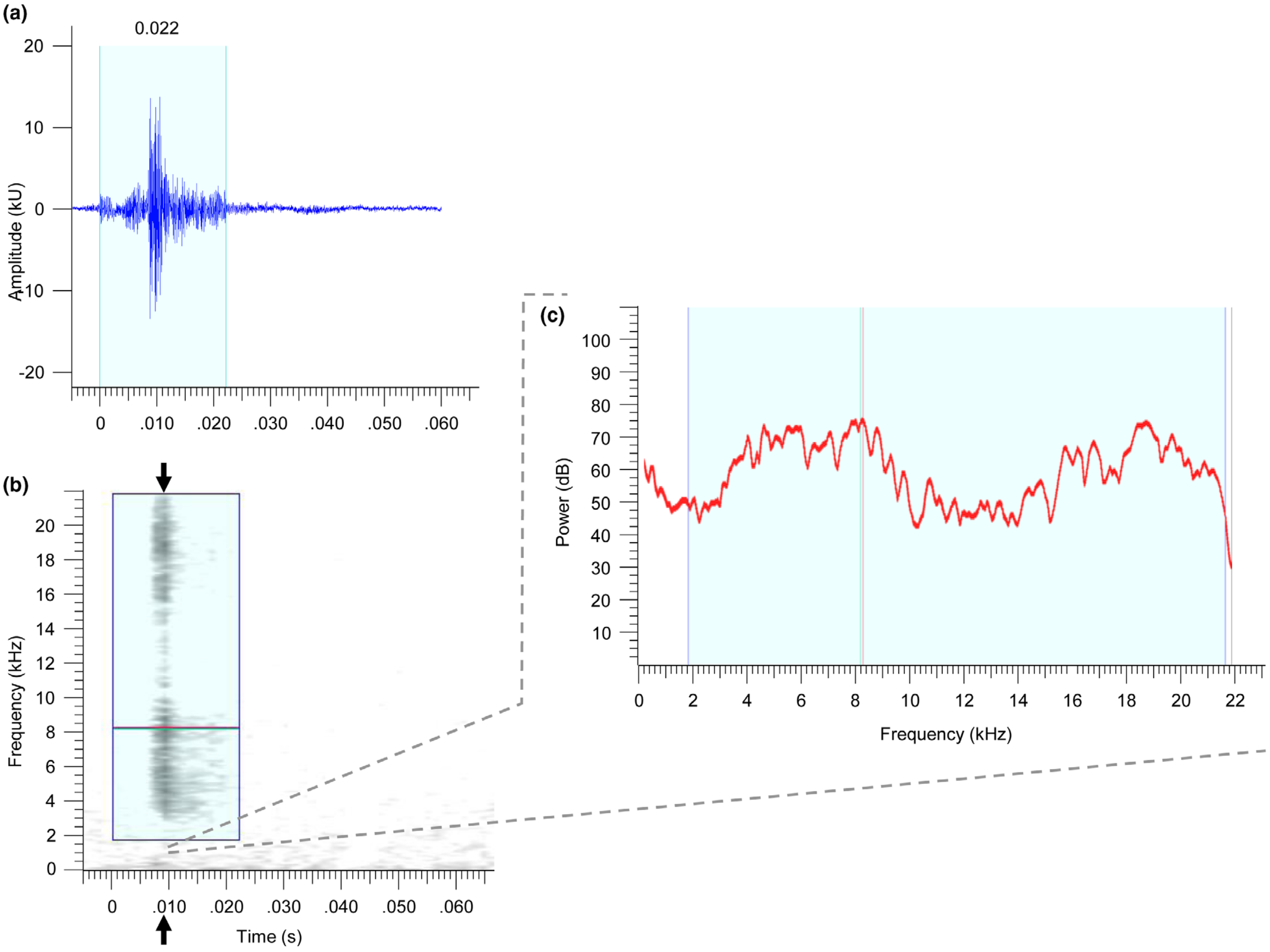

FIGURE 2 Example of a single POP, in the ALERT context, performed underwater and recorded by hydrophone, by the GRD male, depicted as a waveform (a; top panel with relative energy in kilounits, kU, over time in seconds), as a spectrogram (b; left bottom panel with frequency in kilohertz, over time in seconds), and power spectrum slice (c; right panel in decibels, over frequency in kilohertz) at peak frequency (denoted by arrows, top and bottom on spectrogram). Acoustic parameters of 7 single POPs recorded for this male are shown in Table 2 (GRD male, ALERT context, single POP, *n* = 7).

(*n* = 87) produced during the 3 years study by the GRD male, in the same location, during the breeding seasons of 2017, 2018, and 2019. As above, the two social contexts for this inter-annual comparison were restricted to ALERT and PATROL. For ALERT, the GRD male samples include 26 instances, namely 8 in 2017 and 18 in 2018. Of these 26 POPs in the ALERT context, all 8 in 2017 were double POPs; and in 2018, 11 were identical double POPs, and 7 were identical single POPs. Each individual POP in this context had the same exact syllable timing, namely 22 ms (Table 2).

For the PATROL context, total samples numbered 61, namely 20 in 2017, 38 in 2018, and 5 in 2019. Of these 61 POPs, both single (*n* = 5) and double (*n* = 10) POPs were performed in 2017. In 2018, 38 POPs in this context consisted of 12 single POPs, 12 short double POPs, and 14 long double POPs. In 2019, the five recorded POPs in this context consisted of two single POPs and three short double POPs (Table S1). Although this individual male did not exhibit every version of a context-dependent POP pattern in every year monitored, each POP pattern, whether single or double POPs, was performed identically across the 3 years of recording.

With respect to the year-wise distribution of POPs for the seven males considered here, two had samples from all 3 years in both contexts (ALERT & PATROL; MGC, MGD), three had samples from 2 years of the three-season study (ALERT & PATROL: KSD, GRD, and KCD), and the remaining two individuals had samples for two of the 3 years in the ALERT context only (RHD, DND). To further test the stability of POP structure within an individual male across three breeding seasons, a DFA model was created with the 2018 dataset and tested with the 2017 and 2019 datasets. The model accuracy was 79%; confusion matrices for 2017 and 2019 were 72% and 89% respectively. This result indicates that the features of an individual male POP signals were stable and did not change appreciably from year to year, as described above for the GRD male in the ALERT and PATROL contexts.

TABLE 2 Consolidated data of pop signal for males having more than three samples for Alert (AL) and Patrol (PA) context.

Context	Male ID	N = total	Number of POPs	POPs by category	Δt 1P (A, B, D) s	Δt 2P (C, E) s	Δt 3P (F) s	Δt 1IPI (BC, DE) s	Δt 2IPI (EF) s	PKFQ kHz	CNFQ kHz	DO	PM
ALERT	GRD	26	~~I~~	7	0.022	-	-	-	-	8.269	8.183	4	3
			~~II~~	19	0.022	0.022	-	0.482	-	8.269	8.183	8	11
	MGD	8	~~I~~	2	0.036	-	-	-	-	1.895	2.670	2	-
			~~II~~	4	0.018	0.018	-	0.559	-	3.359	3.359	4	-
			~~III~~	2	0.018	0.018	0.018	0.559	0.675	3.359	3.359	2	-
	MGC	6	~~II~~	3	0.026	0.026	-	0.338	-	4.134	4.737	3	-
			~~II~~	1	0.018	0.018	-	0.191	-	1.550	1.550	1	-
			~~II~~	1	0.018	0.018	-	0.132	-	1.637	1.637	1	-
			~~II~~	1	0.023	0.023	-	0.372	-	0.172	0.172	1	-
	KCD	6	~~II~~	5	0.025	0.027	-	0.382	-	2.842	2.326	5	-
			~~II~~	1	0.026	0.026	-	0.377	-	2.326	2.412	1	-
	RHD	5	~~II~~	2	0.018	0.018	-	0.190	-	0.086	0.086	2	-
			~~III~~	3	0.036	0.036	0.036	0.369	0.538	1.550	1.550	3	-
	DND	4	~~III~~	2	0.046	0.046	0.046	0.253	0.487	2.326	3.101	2	-
			~~III~~	1	0.055	0.055	0.055	0.249	0.443	2.240	2.412	1	-
			~~III~~	1	0.011	0.009	0.012	0.253	0.487	1.292	1.206	1	-
PATROL	GRD	61	~~I~~	17	0.035	-	-	-	-	0.948	0.775	3	14
			~~II~~*	15	0.029	0.029	-	0.369	-	2.929	5.426	5	10
			~~II~~**	29	0.043	0.043	-	0.370	-	2.842	2.842	12	17
	MGD	7	~~II~~	1	0.028	0.028	-	0.319	-	4.134	4.048	1	-
			~~III~~	6	0.028	0.028	0.028	0.319	0.522	4.134	4.134	6	-
	KCD	6	~~II~~	6	0.017	0.017	-	0.257	-	4.048	4.048	6	-
	KSD	5	~~II~~	5	0.023	0.023	-	0.372	-	0.172	0.258	5	-

Note: N – Number of samples, Δt 1P – Delta time of 1st POP, Δt 2P – Delta time of 2nd POP, Δt 3P – Delta time of 3rd POP, Δt 1IPI – Delta time of 1st Inter POP interval, Δt 2IPI – Delta time of 2nd Inter POP interval, PKFQ – Peak frequency, CNFQ – Center frequency, DO – Direct observation, PM – Passive monitoring, ALERT – Alert, PATROL – Patrol, Male IDs: GRD – Garhaita dominant, MGD – Maghera dominant, MGC – Maghera challenger, KCD – Khera channel dominant, RHD – Rhea dominant, DND – Dinnupura dominant, and KSD – Kasaua dominant.

3.7 | Temporal vs. spectral acoustic components

The individual male-specific POP patterns were examined further using Discriminant Function Analysis (DFA) as well as other statistical measures conventionally used to characterize acoustic signals. The values used in these analyses were $n = 130$ total samples from seven males (RHD = 5, MGD = 15, MGC = 6, DND = 4, GRD = 87, KCD = 12, KSD = 5). By examining the individual contributions of each variable in the DFA models to the overall variation observed, it was possible to evaluate the relative importance of the temporal vs. the spectral components evident in the POP signals. For the ALERT context, the temporal parameters accounted for 89% of the overall variation, whereas spectral parameters accounted for only 4% of the overall variation observed. For the PATROL context, the temporal parameters accounted for 99% of the overall variation observed, and spectral parameters contributed only 1% of the overall variation noted. Taken together, in both contexts, 94% of the total variation was explained by POP signal timing, whereas only 2% of the variation was attributable to frequency (spectral) differences. In this analysis, the number of pops was treated as a categorical variable and accounted for the other 4% of overall variation, not attributed to temporal or spectral variables.

3.8 | POP patterns are individually distinctive

A comprehensive summary of the acoustic parameters is presented in Table 2, for six individual males in the ALERT context, and for four males in the PATROL context. Overall, these records reveal distinct differences in the number of POPs, the POP delta time (Δt P), the IPIs delta time (Δt IPI), the peak frequencies (PKFQ), and the center frequencies (CNFQ). Using these metrics, these males ($n = 7$) performed POP patterns that were (1) individually consistent, (2) different across individuals, and (3) clearly context-dependent.

The POP patterns of four different males for which >4 samples of each pattern type were recorded are illustrated for the two social contexts presented earlier for the single GRD male. For the ALERT context, the POPs produced by two additional males are shown graphically in Figure 6a–c for direct comparison with each other, as well as with the GRD male's patterns shown in Figure 4a,b. In the PATROL context, the corresponding comparisons for two additional males are shown in Figure 7a,b, relative to those shown for the GRD male in Figure 5a–c.

The individual specificity of the characteristic POP patterns of each male are summarized in Figure 8, in which the delta time POP values are plotted for these males in the ALERT and PATROL contexts.

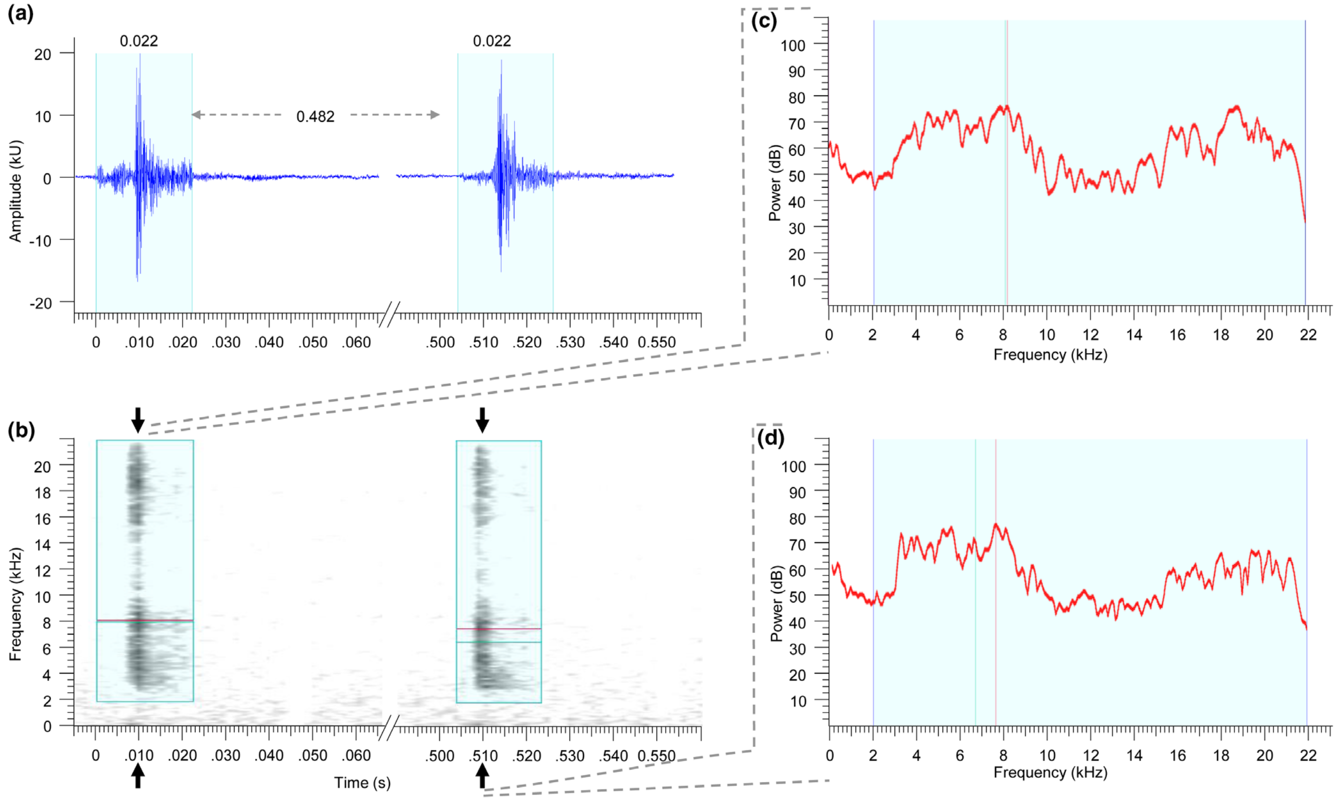

FIGURE 3 Example of a double POP, in the ALERT context, performed underwater and recorded by hydrophone, by the GRD male, depicted as a waveform (a; top panel with relative energy in kilounits, kU, over time in seconds), as a spectrogram (b; left bottom panel with frequency in kilohertz, over time in seconds), and respective power spectrum slices (c + d; right panel in decibels, over frequency in kilohertz) at peak frequency (denoted by arrows, top and bottom on spectrogram). Acoustic parameters of 19 double POPs recorded for this male are shown in Table 2 (GRD male, ALERT context, double POPs, $n = 19$).

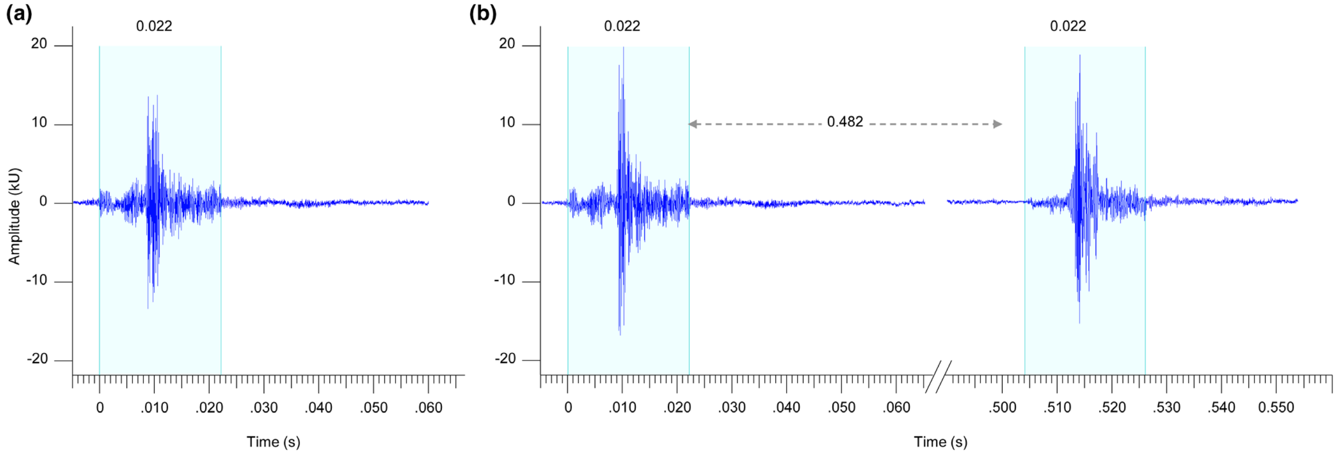

FIGURE 4 Example of a single POP (a; left panel) and a double POP (b; right panel), in the ALERT context, performed underwater and recorded by hydrophone, by the GRD male, depicted as waveforms (with relative energy in kilounits, kU, over time in seconds). Acoustic parameters for a total of 26 POPs (single = 7, double = 19) recorded for this male in the ALERT context are shown in Table 2.

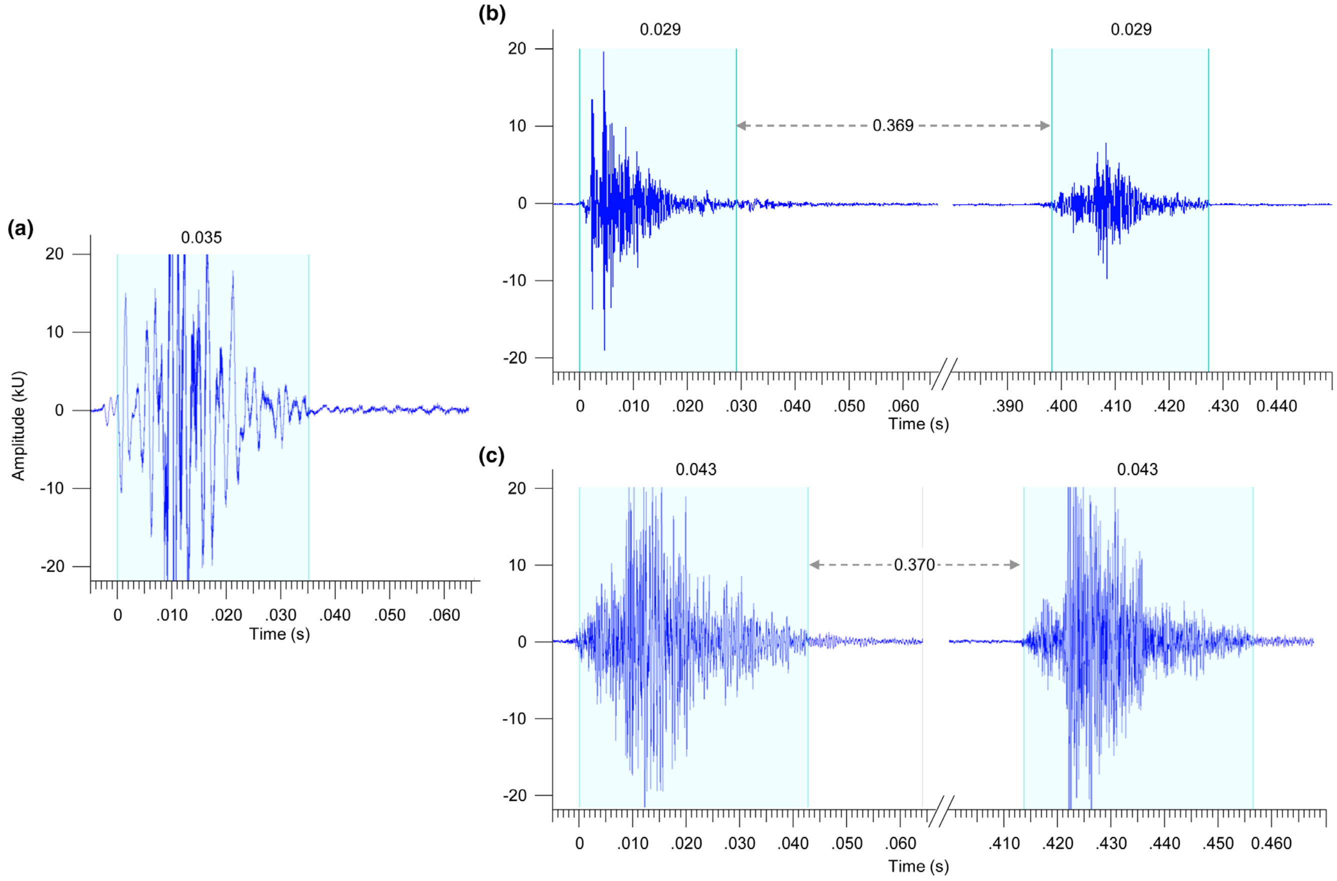

FIGURE 5 Examples of a single POP, (a; left side) and two versions of double POPs (b; right side, top) (c; right side, bottom), in the PATROL context, performed underwater and recorded via hydrophones by the GRD male, depicted as waveforms (relative energy in kilounits, kU, over time in seconds). Acoustic parameters for a total of 61 POPs, in the three versions above (a, *n* = 17; b, *n* = 15; c, *n* = 29), are shown in Table 2 for the GRD male, in PATROL context.

All of the values are based on direct observations in conjunction with the acoustic recordings for six of these (DND, RHD, KCD, MGC, MGD, and KSD) and for both direct observations (DO) and passive monitoring (PM) for the GRD male. It is important to note two features: (1) the diversity of POP patterns exhibited by these males and (2) the individually specific POP patterns across males, as evidenced by minimal overlaps of POP patterns amongst males. Additional POP parameters for all seven individuals are listed in Table 2.

3.9 | POP pattern discrimination among males

For the ALERT context, the DFA model explained 94.86% of the variation, based on a DF1 of 82.66% and a DF2 of 12.20% (Figure 9, ALERT context = left panel). In this context, the confusion matrix was 94.6%. Three males (GRD, MGD, and DND) showed tightly clumped, distinct clusters, whereas the other four males showed distinct, but less clumped groupings, with minimal overlap. The only direct overlap occurred for the MGC and RHD males, but these males occupied geographically distant breeding sites, separated by >80 km of river shoreline. Although two of the males with tightly clumped POP patterns were represented by relatively large sample sizes (GRD = 87; MGD = 15), it is noteworthy that even with a much smaller sample size of *n* = 4, the DND male's pattern was distinct and tightly clustered (Figure 9, AL context, left panel).

For the PATROL context, the DFA model explained 99.98% of the variation, based on a DF1 of 98.61% and a DF2 of 1.37% (Figure 9, PA context, right panel). In this context, the confusion matrix was 100%. The DF1 axis clearly showed tight patterns for all four males (KCD, MGD, GRD, and KSD), with further separation between the GRD and KSD males on the DF2 axis.

The stereotypic nature of the POP signals produced by these males, with virtually no variation in the temporal parameters of a distinctive POP pattern within a given social context led us to use DFA metrics to adequately characterize comparisons statistically. Nevertheless, the Beecher's Information Statistic, MANOVA, and a Discriminant Score were also computed to further characterize the *n* = 130 sample of POPs, within each context as well as overall (Table 3a,b, respectively). The closest approximation to the DFA analysis was MANOVA which discriminated amongst the seven males ($p < 0.05$) but failed to highlight the temporal vs. frequency components in both individual contexts as well as overall (Table 3a,b). Likewise, Beecher's Information Statistic and the Discriminant Score showed overall discrimination amongst males but failed at the context level of analysis (Table 3a,b).

4 | DISCUSSION

Gharials produce a sudden, high amplitude, pulsatile underwater sound, referred to as a POP. POPs were performed only by large (>4 m total length) males possessing a sex-specific, cartilaginous narial excrescence, the ghara. The POP signal has a duration of

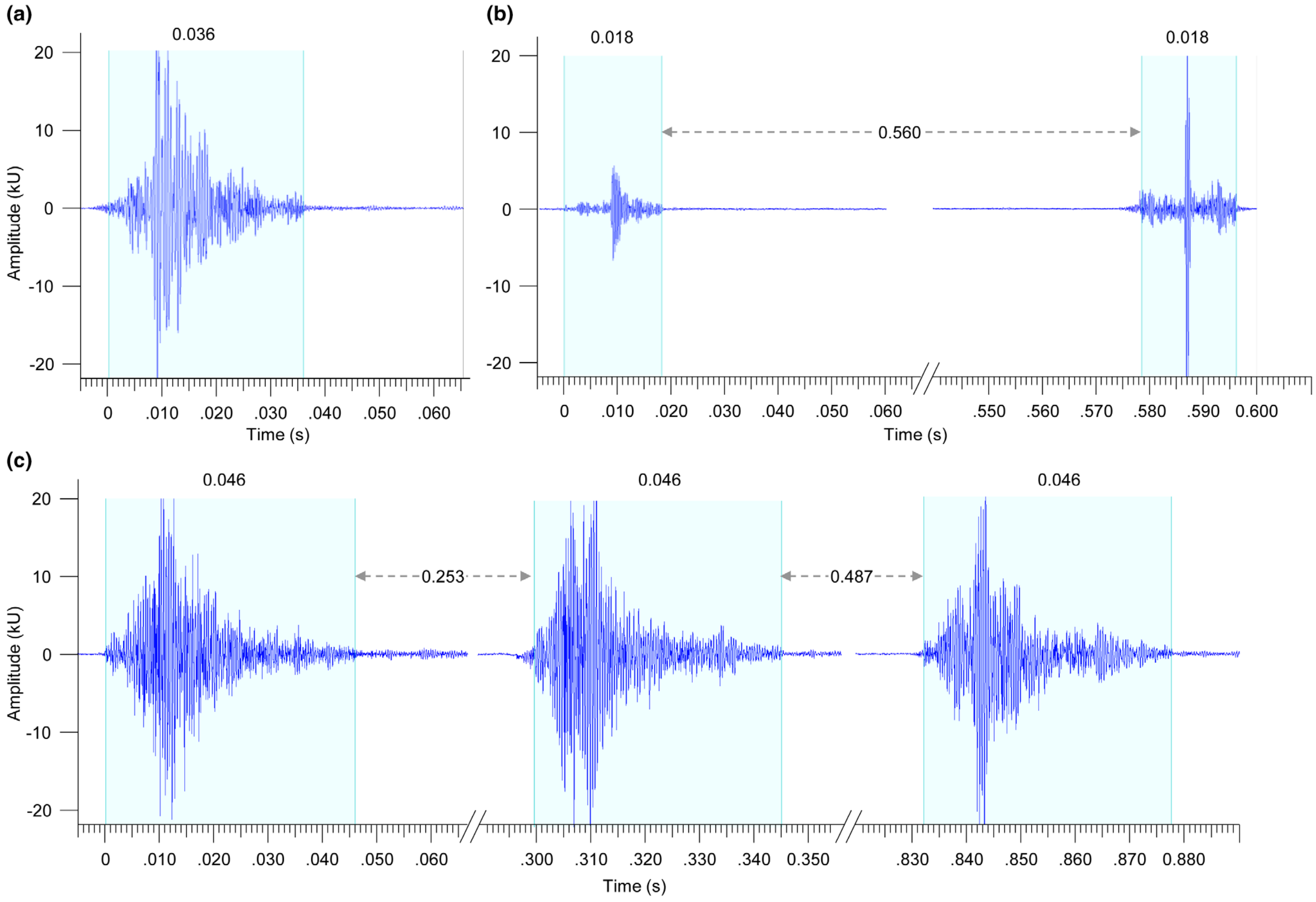

FIGURE 6 Examples in the ALERT context, of the POPs performed by other males, for comparison with Figure 4. Male MGD performed a single POP (a; top left) and also a double POP (b; top right) in the ALERT context, while male DND performed a triple POP (c; bottom). Waveform axes as in Figure 4. Acoustic parameters for MGD (*n* = 8; ALERT context) and for DND (*n* = 4, ALERT context) are shown in Table 2.

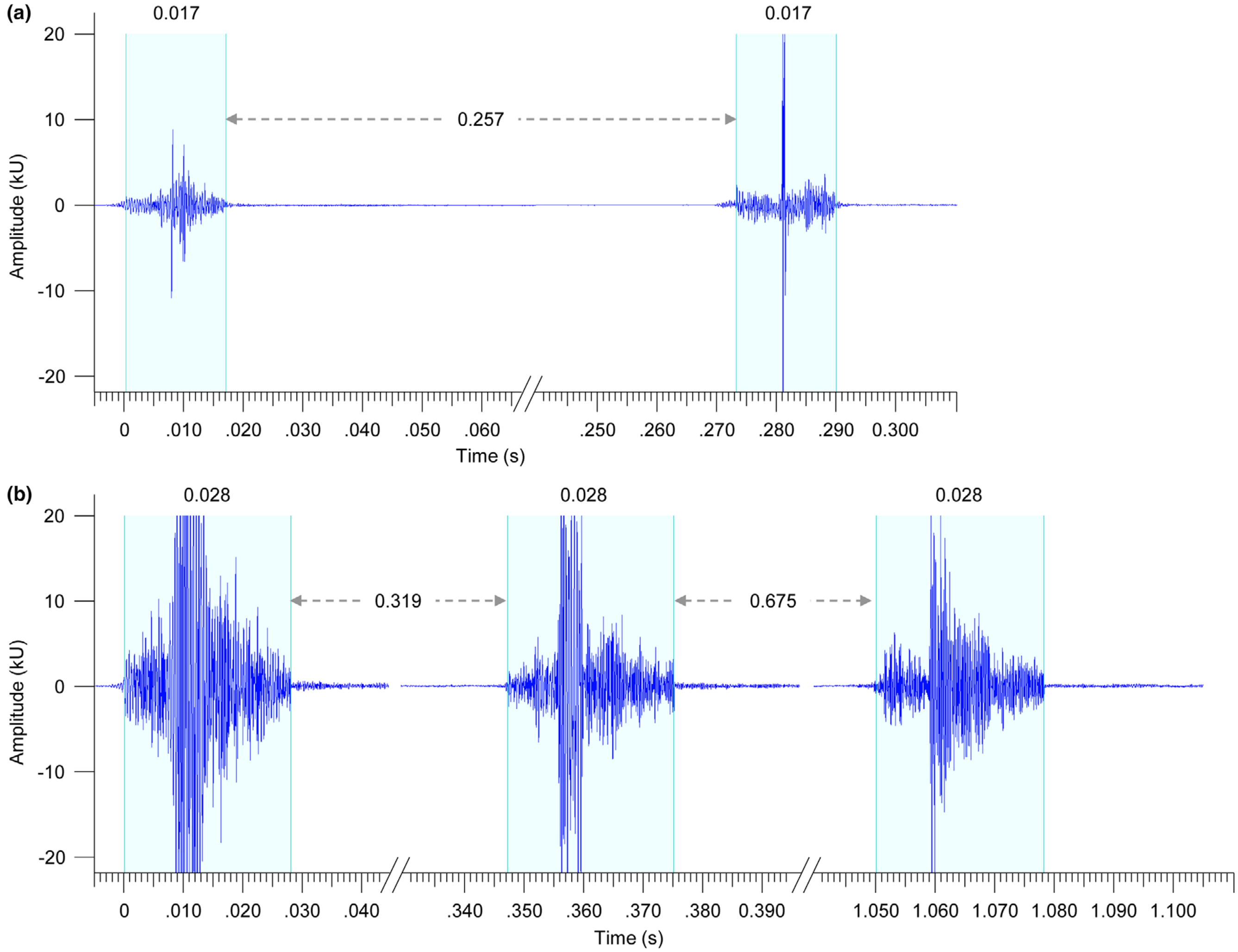

FIGURE 7 Examples in the PATROL context, of POPs performed by other males, for comparison with Figure 5. Male KCD performed one version of a double POP (a; top) on 6 occasions, and male MGD performed a triple POP (b; bottom) on 6 occasions. Acoustic parameters for KCD ($n = 6$; PATROL context) and MGD (n = 6; PATROL context) are shown in Table 2.

0.011 to 0.055 s and is clearly audible on land at distances of ~500 m. Here, we discuss the acoustic features of the gharial POP, including its reliance on temporal vs. spectral (frequency) elements, its incorporation into a complex breathing display, its dependence on a specific social context, its stability within an individual over time, and its distinctive patterning which is individual-specific.

4.1 | Temporal versus spectral features

In our study, 96% of the total variation in POP signal parameters was explained by POP signal timings (92%) and the number of POPs (4%), whereas only 2% of the variation was related to frequency (spectral) differences. This result contrasts strongly with the results in all other species of crocodylians examined to date in which, the principal component of acoustic signaling is based on frequency characteristics. Without exception, in all other species, relatively low frequency vocalizations make up a large proportion of acoustic signaling, with only a minor role played by a limited repertoire of non-vocal sounds, for example, headslaps, jawclaps, bubbling, and related sounds.

In comparison with other crocodilian species, the most notable and studied acoustic sound is the bellowing display of American alligators, consisting of a complex, multi-modal, contagious advertisement call, prominently performed by both males and females during seasonal breeding (summarized in Vergne et al., 2009). An alligator bellow is a loud, low-pitched pulsating rumble, dominated by a series of low-frequency vocalizations. Resonant frequencies known as formants broadcast “honest” information about the caller's body size, with lower frequencies indicating larger animals (Reber, 2018; Reber et al., 2015; Reber et al., 2017). Less studied, but likely similar in structure and function are the vocal “roars” of crocodiles, caiman, and other crocodilians (Garrick & Lang, 1977; Reber, 2018; Vergne et al., 2009). In all species examined, low-frequency vocalizations dominate the acoustic repertoire, with temporal vocal features and non-vocal acoustic sounds playing only minor roles (Reber, 2020).

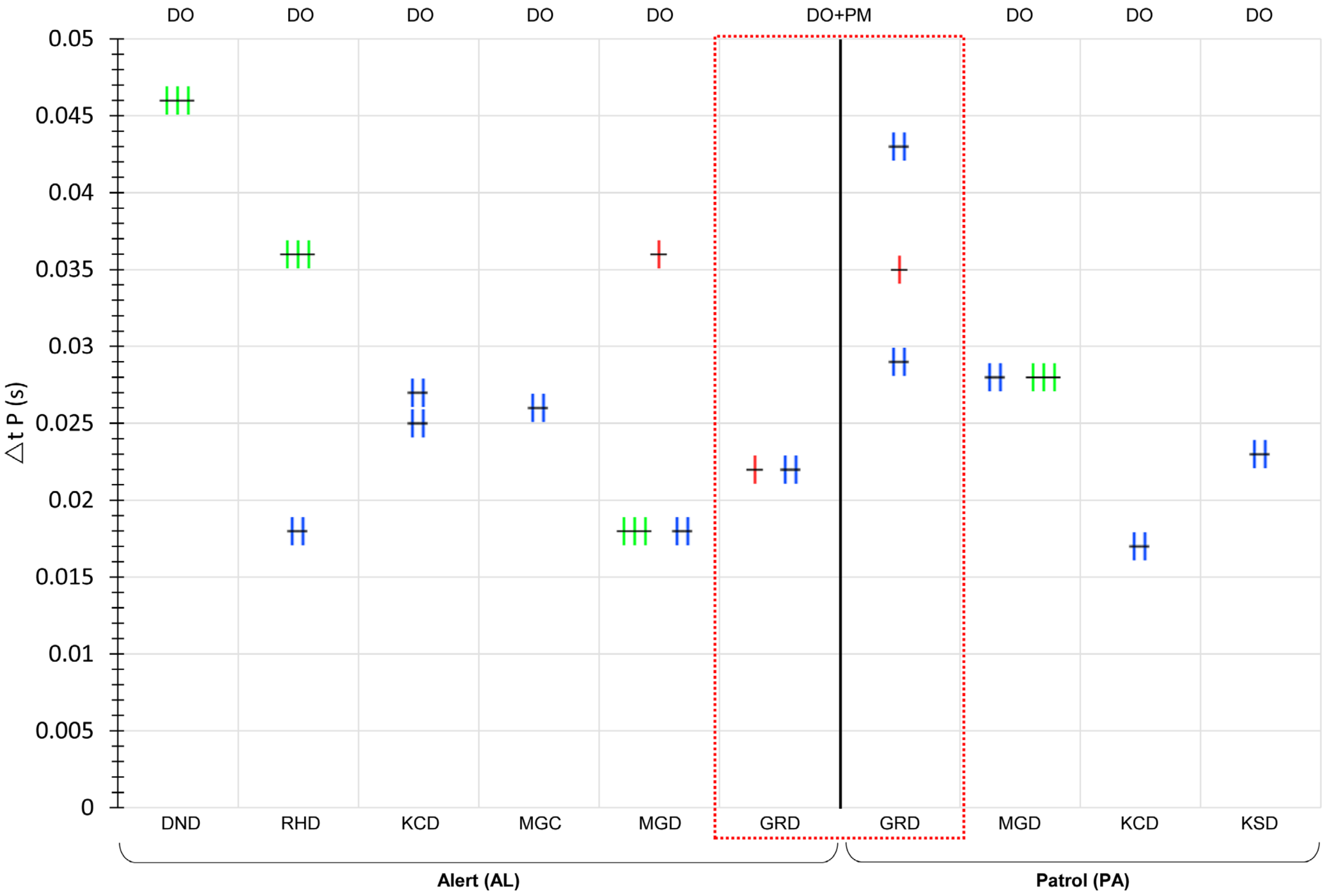

FIGURE 8 Schematic showing POP event parameters for seven different male gharials, in two behavioral contexts, ALERT and PATROL. POP duration, in seconds, (=delta time syllable value) is shown on the vertical axis, and the number of POPs (single, double, or triple) are depicted as vertical bars on each symbol. For example, the GRD male performed two versions of POPs in the ALERT context, both at POP durations of 0.022 seconds, namely a single POP and a double POP (left column within dashed line box). The symbols correspond to the waveforms shown in Figure 4. In the PATROL context, GRD male (right column within dashed line box) performed a single POP at 0.035 seconds, and two versions of double POPs, one at 0.029 seconds and the other at 0.043 seconds (as shown in waveforms in Figure 5). DO = direct observations; PM = passive monitoring—see Methods and also Supplementary figure B.

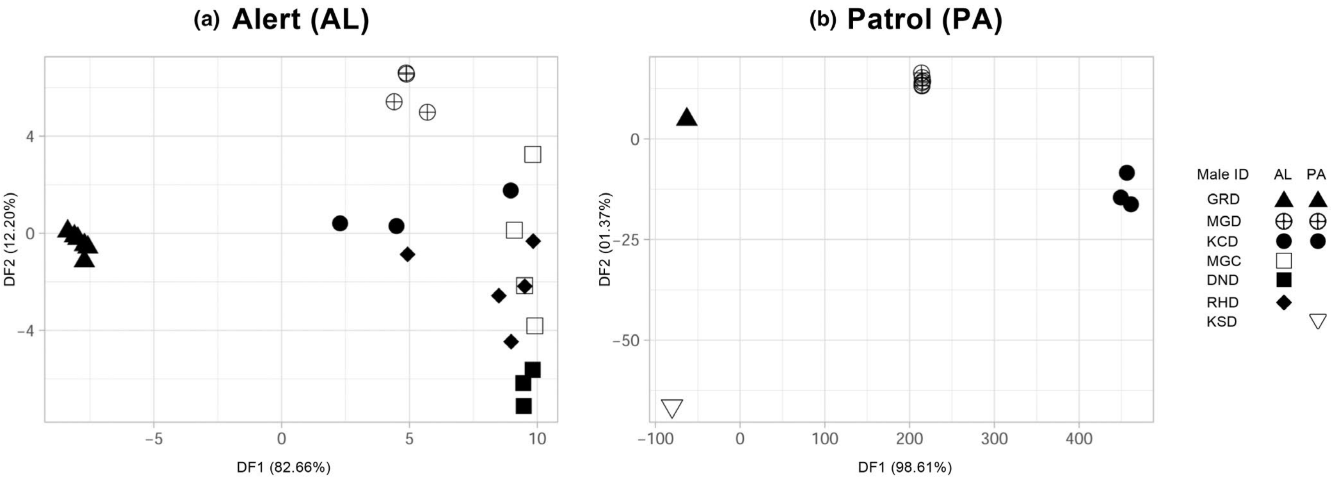

FIGURE 9 In the ALERT context (left panel), the DFA plot showed 3 males (GRD, MGD, DND) tightly clumped in distinct clusters (black triangles, black squares, crossed circles). The model explained 94.86% of the variation, with a confusion matrix of 94.6%. In the PATROL context (right panel), the DFA plot separated all four males (KCD, MGD, GRD, KSD) into tight clusters, with the model explaining 99.98% of the variation, and a confusion matrix of 100%.

TABLE 3 MANOVA, Discrimination score, Beecher's information statistic, and Discriminant Function Analysis (DFA) summary.

(a) MANOVA, Discrimination score, Beecher's information statistic summary for AL and PA context by individual parameters

	Df value		F value		*p* value		PIC value		DS		H_S	
Parameters	**AL**	**PA**	**AL**	**PA**	**AL**	**PA**	**AL**	**PA**	**AL**	**PA**	**AL**	**PA**
Temporal parameters												
Δt P	5	3	6.63145	32.192	0.00014	1.906E-13	1.40	2.2	0.635	0.78	0.345	0.680
Δt IPI	5	3	0.81725	4.354	0.547	0.213	1.25	2.8	0.205	0.14	−0.015	0.105
Frequency parameters												
PKFQ	5	3	108.87	29.389	2.2e-16	8.7895E-12	1.40	3.8	0.69	0.64	1.84	0.64
CNFQ	5	3	76.86	16.158	2.2e-16	7.685E-05	1.45	4.1	0.64	0.58	1.60	0.39

(b) Discrimination score, Beecher's information statistic and DFA overall summary for AL and PA context

	Discriminant function analysis (DFA)	Beecher's information statistic (H_S)	Discrimination score (DS)
AL	94.9%	7.52	0.72
PA	99.9%	3.63	0.28

Abbreviations: Δt IPI, Delta time of Inter POP interval; Δt P, Delta time of POP; AL, Alert; CNFQ, Center frequency; Df, degree of frequency (MANOVA); DS, Discrimination score metrics; F value, value two mean square values (MANOVA); H_s, Beecher's information statistic metrics; P value, Probability (MANOVA); PA, Patrol; PIC value, potential of individual coding (Beecher's information statistic); PKFQ, Peak frequency.

A possible exception is the African dwarf crocodile, a small, highly terrestrial, forest-dwelling species. In captive and wild individuals, low-frequency "drums" (<31 Hz) were the most frequent call type. Drums consisted of 1–5 pulses, ~0.09 s in duration, without a visible harmonic structure; their function is unknown (Staniewicz et al., 2023). A similar pulsatile, short duration (~0.10s) sound without harmonic structure, referred to as a "drum", has also been described in captive false gharials (*Tomistoma schlegelii*). These drums were performed in single, double, or triple bouts during the breeding season, but no sex-specific information or behavioral context was recorded (Staniewicz et al., 2022).

In general, acoustic studies of bird and mammal vocalizations have identified frequency parameters as the primary informative communication channel, as opposed to accompanying temporal components. Likewise, in other reptiles, vocalizations have been characterized largely with respect to frequency vs. temporal elements. Interesting exceptions to the above are the diverse non-vocal acoustic signals produced by mechanical manipulations of body parts such as feathers and bills in birds, or constrictions in the respiratory tract producing hissing, snorting, and whispering sounds in other vertebrates. For example, temporal parameters predominate in the drumming displays of woodpeckers (Budka et al., 2018) and ruffed grouse (Garcia et al., 2012). Seal "claps" and kangaroo rat "drumming" are other examples of sound production beyond phonation which typically employ temporal versus frequency elements (Clark, 2016; Verga & Ravignani, 2021).

4.2 | Incorporation into breathing display

When it is performed, the gharial POP is an integral part of a complex, multi-modal "breath" display (BR). We have never observed a POP performance that was not followed by a BR display. Not only does the BR display contain other acoustic cues but also is multi-modal, incorporating visual, tactile, vibratory, and likely chemical signals as well. Additional acoustic elements include the initial subaudible vibration (SAV) which precedes each POP, singly or in sequences. Also included are the prolonged inhalation–exhalation cycle(s) and the optional "bubbling" at the end of the BR display. Each POP is preceded by a distinct SAV (Figure 1). If the performer is in shallow water (1–2 m depth), the SAV is evident as a vibratory disturbance of water in the thoracic region dorsally, as the male emerges at the water surface from an underwater position (Figure 1). Visualization of a SAV is very similar to the "water dance" effect that accompanies an alligator bellowing in shallow water. Although prior reports have suggested the absence of SAVs in gharial, our results indicate otherwise. SAVs are an integral feature of every BR sequence containing POP signal(s) in gharial, and SAVs may occur associated with other behaviors as well.

Other acoustic elements incorporated into the multi-modal BR display include the respiratory cycle(s) and the concluding "bubbling" sequences. In aerial recordings, the respiratory cycle(s) is distinct acoustically, and each phase is clearly distinguishable, on the basis of amplitude and frequency (Figure 1). Bubbling sometimes occurs at the end of the BR display and is audible on aerial and on hydrophone recordings. The male's up and down movements at the water surface during respiration appear to be exaggerated and provide strong visual cues that accompany the corresponding sounds. These movements are visible at moderate distances (~50 to 300 m across open water/land). In contrast, bubbling is only visible at close range, ~5 to 50 m, when the male submerges underwater, as a disappearing trail of bubbles on the water surface. It is audible on close-range hydrophone records as a gurgling sound, similar to an empty bottle filling with water when it is placed below the surface of the water.

The gharial BR display is a long-distance advertisement call, as in other crocodylian species, based on Dinet's criteria (2013). Specifically, it occurs primarily during the breeding season, in early morning or late evening. It has been observed in captive isolates, as well as in captive and in wild social groupings. With the incorporation of the POP signal, it is the loudest call in the gharial acoustic repertoire. The gharial BR is an elaborate, multi-modal display, categorized appropriately as a "call", albeit a complex one, based on multiple criteria articulated by Marler (2004) and Kondo and Watanabe (2009). It is species-specific, stereotypic, and largely innate, but without intensive learning.

In gharial, the BR display (with or without the preceding POP) is used in agonistic as well as affiliative contexts and is most appropriately viewed as a generic "announcement" display, proclaiming simultaneously the location and identity of the performer (see below sections for further explanation/elaboration). It is analogous to a "contact" call, encoding information about distance, group membership, and identity (Kondo & Watanabe, 2009). In its performance, the gharial BR display is similar to an alligator bellow, minus the booming, low frequency vocalizations in series, as described previously (Garrick et al., 1978; Reber, 2018, 2020; Vliet, 1989). With the addition of the preceding POP, the POP+BR display is context-specific, as well as context-dependent (see next section).

In the gharial BR, the head-oblique, tail-arched posture (HOTA) described in bellowing alligators (Garrick et al., 1978) and roaring crocodiles (Garrick & Lang, 1977) is replaced by a body posture that raises the midbody to an emergent position at the water surface, that is, head, back, and tail emergent (HBTE). In effect, this posture results in the performer's entire body from tail tip to snout tip being fully visible at the water surface. The exhalation–inhalation–exhalation cycle(s) further emphasize body size, as the animal periodically emerges and then submerges its body.

The presence of sub-audible vibrations (SAVs) in the gharial acoustic repertoire has been previously open to question, with their apparent absence noted anecdotally (Dinets, 2013; Senter, 2008a). We have documented SAVs performed by adult male gharial, immediately preceding the POP signal in the initial phase of the POP+BR sequences. In our study, SAVs were recorded with hydrophones and aerial mics, and are illustrated in Figure 1. In other crocodilian species, SAVs are produced in bellowing and roaring contexts (Reber, 2020) and appear to be male-specific in alligators (Vliet, 2001). The sound energy is concentrated at very low frequencies, resulting in infrasound in the range of 16–25 Hz during alligator-bellowing sequences (Todd, 2007). SAVs are visible as a "water dance" on the performer's dorsum and flanks in shallow water; and at close range, SAVs are sensed as powerful sub-sonic vibrations, detectable on land and in the water. In instances we have videotaped, small fish nearby the performer jump out of the water (Video S2), submerged turtles quickly emerge and look around, and spoonbills standing nearby in shallow water suddenly flap their wings, as vibrations in the animal's midback become visible, an instant before the underwater POP is audible on land.

4.3 | Context-dependency

In this study, the acoustic structure of a gharial POP was clearly dependent on the behavioral context in which it was performed. Single, double, and triple POPs constituted a POP event, termed here as a POP pattern. Each POP pattern was incorporated into a multi-modal BR display, as noted above in detail. In this presentation, the POP patterns of each male were recorded across two social contexts during seasonal breeding in late February and early March. Each male displayed one or more distinctive POP patterns, each pattern specific for the Alert (AL) context, and another set of different POP patterns that were associated with the Patrol (PA) context. A visualization of these context-dependent, male-specific POP patterns is presented in Figure 8, for six of the seven males in the Alert context, and for four of the seven males in the Patrol context.

In other words, none of the POP patterns ($n=18$; seven males) performed by these males were common to all, or even to some of these gharials. None of the seven males shared a POP pattern. This result pertained to both social contexts examined. Within a given context, each male exhibited one to three unique POP patterns. Within an individual across these two contexts, each male showed one to five unique patterns (Figure 8). Such a finding is in strong contrast to the typical "alarm call" setting in which at least some key acoustic elements are shared in common among members of a social group, and presumably perceived with a common meaning, with or without the addition of individually specific identifiers.

In fact, we examined the context-dependency of these POP patterns in a total of four behavioral contexts in another forthcoming study, in which the context-dependency of POP patterns is analyzed in further detail and compared in terms of signal specificity and possible signal function. Nevertheless, on the basis of evidence presented here, the POP signals used by these seven males were not only context-dependent but were also context-specific. In other words, each POP pattern not only denoted a particular context but also provided information about the identity of the male sender. As noted above, in most instances, each male performed several versions of POPs within a context, but our categorization of behavioral context does not permit us, at this point, to do a fine scale analysis of the significance of these within-context differences in POP patterns. Contextual flexibility, in the sense of gradations proportionately scaled to the social setting, such as changes in emission rates, modifying notes, or changes in syntax have been demonstrated in some birds (e.g., Montes-Medina et al., 2016) and mammals (Díaz López, 2022; Keenan et al., 2020), but was not apparent in the POP patterns we observed.

4.4 | Signal stability over multiple breeding seasons

Another notable acoustic feature of the gharial POP patterns observed in this study is the stability of POP signal parameters of individual males over three breeding seasons, in 2017, 2018, and 2019. In the Alert context, POP patterns were recorded over all 3 years for two males (MGC and MGD) and over two seasons for the remaining four males (GRD, DND, RHD, and KCD). In the Patrol context, POP patterns were recorded over all 3 years for three males (GRD, MGD, and MGC), over 2 years for KSD, and over a single season for KCD. For the GRD male, for which a large sample of POPs in each context were examined in detail (see "Results" section), the POP patterns he exhibited in both contexts (AL and PA) were remarkably consistent. Little to no variation was evident from one breeding season to the next, spanning the three annual breeding seasons.

Vocal stability is thought to be fundamental in social species, especially those showing mate and/or site fidelity over multiple breeding seasons. In effect, each animal produces the same call, year after year. This trait has been increasingly well-documented in many species of birds and mammals, including those that are not vocal learners as well as those that are (Calcari et al., 2021). Call stability may contribute to social grouping, especially in species that are long-lived, colony breeders by promoting individual recognition over a prolonged time. In birds, this feature is associated with seabirds, owls, cranes, and songbirds. In mammals, it has been documented in primates, deer, squirrels, and whales (refs in Calcari et al., 2021). In contrast, loons shifting territories from 1 year to the next, switch their territorial vocalizations accordingly, and may even switch back to a prior pattern upon return subsequently (Walcott et al., 2006).

Presumably, signal stability of non-vocal acoustic sounds, such as the drumming seen in woodpeckers and grouse is likewise an important feature of non-vocal systems of communication, but are less well-documented with regard to within-individual variation, particularly over seasons (Budka et al., 2018; Garcia et al., 2012). Signal stability is of paramount importance in passive-acoustic monitoring (PAM) schemes to document and census populations for management and conservation (Budka et al., 2018). The present study indicates that it should be possible to detect the presence or absence of gharial, specifically males, at any given locality using PAM to screen for POP features (Kirsch et al., 2023) but the varied nature of the POP signals within individuals, as well as among individuals will confound attempts to census numbers of males accurately, unless combined with behavioral observations to identify individuals.

In our study, individually marked, breeding male gharial resided in a small section of river, ~1–2 km, year after year, even after making brief 1–2 month seasonal migrations up or downstream during the monsoonal high water. Consequently, a resident male was closely associated with a well-defined, small stretch of river, year after year, at times for a decade or more. In contrast, breeding females were surprisingly mobile, with dynamic shifts in breeding and/or nesting sites chosen from 1 year to the next; at times, these distances exceeded 350 km in a single season (Gharial Ecology Project, 2022).

In discussing how little within-individual variation was evident in the POP patterns of each male we studied, we have chosen to use the term "stable" rather than "consistent." Vocal consistency has been narrowly defined with respect to repeatability of birdsong specifically, as follows: "the ability to consistently produce spectral structure of a song element (syllable) or phrase across multiple renditions, including its dominant/fundamental frequency, note shape, and duration" (Sakata & Vehrencamp, 2012). In this framework, the focus has been on song learning and vocal practice, especially in relation to age-dependency and seasonal changes.

4.5 | Distinctive POP patterns

As noted above, not only were POP patterns context-dependent, but also were male-specific. Each male performed his own distinctive repertoire of POPs, with a high degree of individual specificity. POP timings (Δt P) of the seven males across both contexts ranged from 0.009 to 0.055 s. Yet, the range of timings for each individual were similar, approximating an equivalent span, that is a range of ~0.045 s. Within a single behavioral context, for example, Alert, each of the six males exhibited one or more POPs that had distinctive features that differed from those of any of the other males. The same held true for the four males for which POPs were recorded in the Patrol context (Figure 8; both contexts).

In both contexts examined, the DFA model explained the POP signal variation (>94–99%) in the two contexts, on the basis of temporal vs. spectral features. Because the POP signal was strongly stereotypic, commonly used metrics, namely MANOVA, Beecher's Information Statistic, and Discriminant Score, all showed limited abilities to discriminate amongst males, as detailed in the Results section. An important feature that emerged in our analyses is that relatively small sample sizes, for example, 15 versus 87 (MGD vs. GRD, respectively) were sufficient to allow discrimination, in large part because each POP pattern was distinct and tightly clustered in the DFA analyses.

In the ALERT context, the performer was responding to a perceived change in the immediate riverine environment, on land as well as in the water. For example, during festivals, a large group of worshipers might appear at the river's edge, to celebrate and bathe in the river, remaining onshore briefly, or for hours. If the group approached a sandbar near where gharials were basking, the resident male gharial moved toward the human intruders, orienting in their direction, and then he performed a POP-BR display while in the water offshore facing the visitors. Individual gharial, primarily females, basking in a social group nearby, responded immediately to the POP-BR by lifting their heads slightly and/or orienting toward the nearest water, but otherwise did not respond overtly. In this example, the POP signal appears to function as a long-distance signal, alerting most, if not all, of the gharial within 50–200 m that a disturbance is nearby. Thus, the POP signal reached a general audience within the immediate vicinity of the disturbance, signaling the presence of the disturbance as well as its location. Such a disturbance may constitute a threat and require further response from one or more group members.

On the other hand, in the PATROL context, the resident male actively swam along the residential shoreline, moving up and down to the limits of his breeding area. He would periodically submerge, disappearing briefly, only to emerge some distance away unannounced.

On occasion, his re-emergence was announced with a POP-BR display. This performance was typically directed at a challenger male that had entered the resident male's breeding area. In effect, although the POP signal was directed at the intruder male, it was still perceived by nearby members of the social group, assembled close together while basking on land. In this context, the POP signal acted over both short and long distances. There were two audiences, the primary one being the intruder male, and the other being the entire social group as witnesses to the directed signaling of the resident male toward the intruder.

In the two contexts outlined above, the resident male produced one or more POP patterns specific to either the ALERT or PATROL context, and also unique to him only as a specific, presumably recognizable, breeding male, residing in that particular stretch of river (see Figure 8 for a schematic showing unique POP patterns of seven males). In effect, the POP signal indicated the social setting (ALERT vs. PATROL), the individual male, and by association not only his location but also the likely location of either a potential threat or possibility of an encounter.

If we assume that each POP pattern had a communicative function, then potentially the signal recipient would be able to extract relevant information about the behavioral context of the sender, as well as his identity. But this would imply that the receiver has prior information about both features, presumably based on memorization of such an association, namely learning a specific context-male association based on prior experience. It is especially noteworthy that each male had a series of unique POP patterns that were essentially exclusive to a specific behavioral context, as well as capable of denoting his identity. Because each male resided in a small stretch of river, the performance of each unique POP pattern was tightly associated with a specific location, during the breeding season each year.

In a related study, Jensen et al. (2024) have recently presented evidence of individuality encoded in the vocal bellowing of young alligators. Individual discriminations were 66% correct based primarily on spectral features which varied on land versus in water but also provided information about animal sizes. These authors suggest that identity cues may be contained in the roars and bellows of other species, and may provide ways to monitor and/or manage captive and wild crocodylian populations.

4.6 | Sound reception

Behavioral observations of conspecifics within the vicinity of a POP performer clearly indicated that the POP signal produced underwater was perceived by gharial positioned on land, or floating on the water surface, or submerged underwater. On land, gharial responded with a quick slight lifting of the head, from a characteristic resting posture. If an individual was head emergent at the water surface, it would turn its snout/head directionally toward the sound. A submerged individual would quickly appear at the water surface from underwater. Typically, response times for these actions were immediate, within 1–2 s if not sooner.

Sound reception in crocodylians is highly developed, with many important features on a par with birds. There are marked similarities not only in the mechanics of the middle and inner ear of both groups, but also in the neural pathways for auditory processing (reviewed in Vergne et al., 2009; Reber, 2020). Crocodylians perceive sound primarily at the air-water surface, while positioning the upper head above the water in air, as well as on land with the head entirely out of the water (Higgs et al., 2002; Papet et al., 2019). Underwater hearing via the tympanum may be reduced by the bony exterior earlid covering. However, bone conduction and/or the integumentary sense organs (ISOs) may contribute to sensing sounds/vibrations underwater (Grigg & Kirshner, 2015; Higgs et al., 2002; Reber, 2020).

With regard to spectral sensitivity, the audiograms of representative crocodylians tested in air are closely comparable to those of birds, with a notable shift to lower frequencies with sensitives (100–300 Hz, peak sensitivity ~1 kHz, range 0.1–8 kHz; Higgs et al., 2002; Vergne et al., 2009; Papet et al., 2019). Underwater, with sound traveling 4.4× faster, auditory capabilities in alligators shifts to predominately low frequencies (100–2000 Hz in range, peak sensitivity at 800 Hz), with higher sensitivity (=lower thresholds) than goldfish, a species considered to be a hearing specialist among fishes (Higgs et al., 2002). In our study, in the two contexts presented, POP signal frequencies ranged from 82 to 8269 Hz for peak frequency measurements, and from 86 to 8183 Hz for center frequencies recorded (Table 2).

With regard to temporal sensitivity, temporal reception and perception/processing of sound/pressure waves is of special importance to understanding how gharials communicate via POP signals. In this study, the POP signal we detected had durations of 0.011 to 0.055 s (=11 to 55 ms), with inter-POP intervals of 0.130 to 0.675 s (Table 2). The temporal sensitivity of crocodylians via auditory/vibratory channels remains enigmatic. In contrast, in birds, auditory temporal resolution is of paramount interest, particularly as it relates to fine structure discrimination of calls/songs (Dooling & Prior, 2017; Prior et al., 2018). In zebra finches, small temporal/spectral differences (pitch, duration, amplitude) encode biologically important details about sex, call type, and individual identity (Elie & Theunissen, 2016; Fishbein et al., 2021). Earlier studies of temporal acuity in zebra finches indicated discrimination abilities as short as 1–2 ms (Dooling et al., 2002; Dooling & Lohr, 2006). Other songbirds show temporal discrimination abilities in the 1–10 ms range, as well as evidence of species-specific responses mediated by season and also spectral-temporal trade-offs in sensitivity (Gall et al., 2012; Henry et al., 2011).

Temporal discrimination of sounds within hearing range is especially well developed in crocodylians as evidenced by their ability to precisely locate potential targets (e.g., prey, conspecifics, and test speakers) via interaural time differences (ITDs) together with sound level differences (ILDs) (Bierman & Carr, 2015; Carr & Christensen-Dalsgaard, 2015). In air, signal arrival time and/or amplitude at the two ears provide potentially critical information for sound source localization via interaural differences which, in turn, also depend on skull size and acoustic coupling via an interaural canal (Papet et al., 2019). Subsequent experiments, using Nile crocodiles trained to swim in an arena with airborne sounds via speakers, showed that ITDs were the predominant cues for sound source localization, especially at low frequencies, even though ILDs facilitated directional orientation at frequencies above 1500 Hz (Papet et al., 2020). Underwater, alligators showed directional responses to underwater sounds (Beach, 1944; Dinets, 2013), but the mechanistic bases for underwater localization of target sounds/vibrations remains unresolved (but see Delbosc et al., 2023 discussed below).

Overall, target localization strategies, whether for prey or conspecifics, that utilize sound cues have been compared in owls, alligators, and geckos (Carr & Christensen-Dalsgaard, 2015). Striking similarities were noted in the ITD/ITL neural coding processes of owls and alligators, in contrast to that of geckos. Distinctive features shared by owls and alligators, with their common archosaur lineage, suggested both relatives encode neural ITD information using a "place map" vs. a metering system involving firing rates as was apparent in geckos. Other birds, for example, chickens and emus, use a similar place code (Köppl & Carr, 2008; MacLeod et al., 2006), in contrast to the two-channel hemispheric model posited for some mammals, for example, gerbils and cats (Karino et al., 2011; Pecka et al., 2008). Kettler and Carr (2019) measured the ITD responses in the auditory brainstem of alligators and showed that alligators form neural maps very similar to neural coding seen in birds. This result further reinforced the very close correspondence of these archosaur relatives, birds and crocodylians, in their temporal auditory capabilities.

In addition, recent studies indicate that crocodylians appear to employ spatial release from masking to improve sound scene analyses and target detection, effectively filtering out background noise, to more precisely locate a target (Thévenet et al., 2022). Crocodylians also use sound categorization, compartmentalizing a sound continuum into discrete categories, as a way to facilitate learning and decision-making (Thévenet et al., 2023). Furthermore, localization strategies may not only rely on aerial and/or aquatic cues but also vibration cues in water or on land, or multiple sensory channels detecting pressure waves in tandem (Delbosc et al., 2023).

4.7 | POP sound levels

Samples of gharial POPs from our study were shared with a research team at Applied Ocean Sciences in order to study acoustic propagation modeling in a river environment (Kirsch et al., 2023). Sound pressure amplitude or source levels (SL) of gharial POPs were computed assuming spherical and cylindrical spreading, and resulted in values of 196 dB 1 µPa and 188 dB 1 µPa, respectively. The average of these values, 192 dB 1 µPa, characterized the gharial POPs, while the ambient Chambal River background sounds averaged 45 dB re 1 µPa. For the gharial POP signal, propagation loss was ~30% across the width of the river (~350 m), and dropped to ~60% at a river length of >2000 m. POP signal distances traveled tens of kms in a model river channel that was straight, with depths of 9–10 m, but bends in the river channel limited propagation distances.

In general, high sound pressures in air do not exceed 120 dB_{peak} re 20 µPa at 1 m whereas in water, values approach 240 dB_{peak} re. 1 µPa. Source levels and maximum radiated pressures for two species of alligators bellowing in air (Todd, 2007; Wang et al., 2007) are among the loudest recorded values for any reptiles (Jakobsen et al., 2021). In water, the loudest group of animals are the toothed and baleen whales (Jakobsen et al., 2021) and seals and walruses (Hocking et al., 2020; Larsen & Reichmuth, 2021). For these, sound levels >200 dB_{peak} re 1 µPa are routinely recorded. The gharial POPs we recorded were very loud, entirely underwater impulse sounds, which at an average of 192 dB 1 µPa, exceeds reported values of 183 dB_{peak} re. 1 µPa at 1 m, for the loudest teleost fish (Locascio & Mann, 2011) or pistol shrimp (Au & Banks, 1998).

4.8 | Ghara anatomy, ontogeny, and paleontology

At present, detailed studies of ghara internal anatomy/histology are likely to be informative in order to identify relevant structural and functional components contributing to POP sound production, as well as the flow dynamics of water and/or air within the snout and skull during sound production. To date, reports on ghara anatomy and development are scarce. Two centuries ago, in 1825, Geoffroy Saint-Hilaire illustrated the external features of a mature ghara in side view (Figure 10a) as well as internal cavities in a longitudinal cross section (Figure 10b), showing multiple, interconnected chambers. A century and a half later, Martin and Bellairs (1977) provided additional details on ghara anatomy by examining two examples, namely a mature ghara removed from a British Museum specimen (total length = 4.83 m) presumably wild-caught in 1897, and a smaller immature ghara from a zoo specimen (total length = 3.43 m; Zoological Society of London, 1972). These authors describe the gharial ghara to be an entirely cartilaginous excrescence positioned in a bony depression surrounding the narial fossa on the dorsal tip of the snout, with a single opening (fossa) at its base and another opening at its posterior base (Figure 10c). The narial muscle bundle, responsible for opening and closing the nares, are folded into the interior of the mature ghara, and no longer function to close off the ghara at its posterior base (Figure 10d).

Importantly, these authors point out that the mature excrescence does not exhibit any mechanism for shutting off any or all of its cavities from the surroundings (Figure 10d, see small arrow, right side). Whereas Geoffroy Saint-Hilaire (1825) incorrectly posited that the ghara was an accessory respiratory structure that inflated and deflated to aid in breathing underwater, Martin and Bellairs (1977) suggested that the mature ghara and associated enlarged pterygoid bullae evident in large male gharial played some vocal role. Specifically, in their discussion, they focused on the ghara and bullae primarily as vocal tract modifiers or resonators of an airborne vocal signal, originating from the larynx, as in a typical crocodylian vocalization.

Martin and Bellairs (1977) also suggested the probable mode of development of the mature ghara, based on two examples they described in detail. They postulated the progressive upward growth of a ridge of tissue located just anterior to the nares, which is eventually bent backward and folded inward on itself to form the fully formed ghara, as shown in their illustration of a mature ghara, in longitudinal cross section (Figure 10d here; adapted from Figure 4d, Martin & Bellairs, 1977). A ventral view of the excised ghara examined by Martin and Bellairs (1977) is shown in Figure 10c (adapted from Figure 3, Martin & Bellairs, 1977), showing the posterior of the ghara as a ridged channel (top half, center of Figure 10c here), terminating in a lip not capable of closure, and a complex, interconnected series of internal chambers filling the anterior of the ghara (=ANTR; bottom half of Figure 10c here). The excised ghara (ventral view, Figure 10c) measured 13.5 cm from front to back and 11.8 cm across its base. Photographs of the dorsal and ventral views of the excised ghara were illustrated in Plate III in Martin and Bellairs (1977), as well as a side view and longitudinal dissected view plus an X-ray image of the ghara interior showing interconnected chambers. Recent images of gharial with gharas, including representative examples of those on males of differing sizes, are included in Figure 1, a-f in Hone et al., 2020.

Based on our direct field observations with the Chambal gharial population, the mature gharas of representative males generally measure approximately 10 cm X 10 cm X 10 cm, and are either cuboid in shape or are sloped backward, as in the illustration (Figure 10a), with an anterior central lobe, situated between two lateral lobes which are angled posteriorly. Development of the ghara, from an initial frontal ridge, is illustrated in the various views shown in Figure 11 a-f. Ghara formation starts with an elevated ridge just anterior to the external nares, which are undivided in gharial (in contrast to other crocodylians; see Grigg & Kirshner, 2015), as shown in Figure 11a (top down) and Figure 11b (front view). As this ridge grows upward and rearward, the anterior lobe enlarges as a dark mass of tissue, evident in Figure 11c (side view), Figure 11d (top down), Figure 11e (frontal view), and Figure 11f (head shot) on a 4.3 m young male captured and radio tagged in late November 2013. In this male, subsequent ghara development was documented photographically in April 2014 (Figure 12a), in June 2015 (Figure 12b), and June 2016 (Figure 12c), and in April 2018 (Figure 12d). In 2018, this male's ghara size and shape were stable and did not exhibit any further changes, and bore a remarkable resemblance to the ghara figured in side view in 1825 (shown here as Figure 10a, for comparison with ghara evident in Figure 12d). Consequently, in this male which was monitored while living in the wild, a full ghara developed from a nub within a brief period of 14–18 months. This observation was consistent with other examples of relatively rapid ghara development

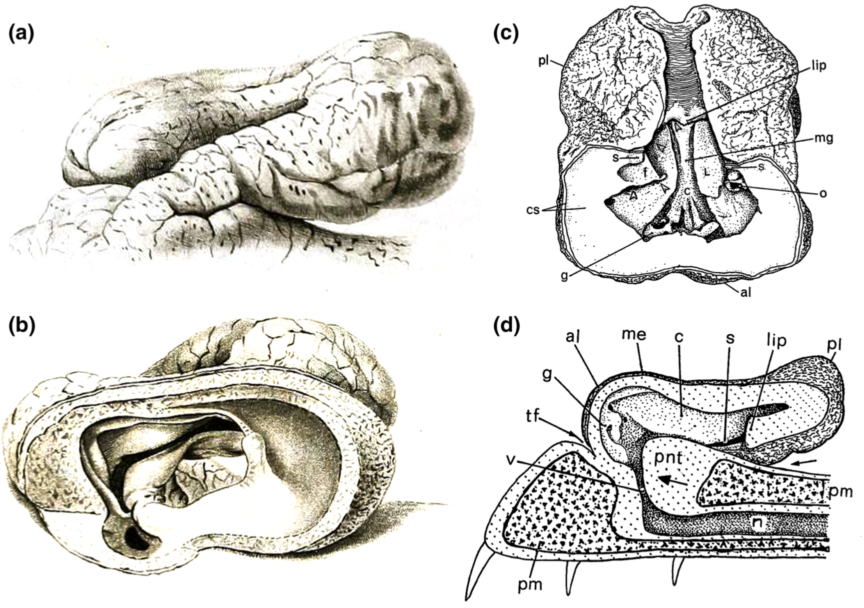

FIGURE 10 Ghara depictions of Geoffroy Saint-Hilaire (1825) a and b, and Martin and Bellairs (1977) c and d, showing exterior and interior views based on dissection and histological studies. Mature ghara in side view (a) positioned on the snout-tip (left = front of specimen) and in longitudinal cross-section (b), revealing interior chambers and structures. An excised ghara, cut off the snout tip at its base, is shown in ventral view (c), with the cut surface indicated by "cs," from a mature male gharial, with the unrestricted rear channel (shown in top half of c, as an open, ridged trough) clearly visible, and the multi-chambered interior of the ghara revealed from underneath (bottom half of c; "al" on c corresponds to same designation on (d). Shown in longitudinal cross-section diagramatically (d), the ghara is positioned atop the snout tip, as a cartilaginous bulbous structure with multiple internal chambers. Al, anterior lobe; c, central cavity; cs, cut skin and superficial tissue; d, depression in premaxilla; en, external nostril; f, flap of tissue; g, glandlike structure; L, ledge of tissue; me, median eminence; mg, median groove; n, nasal cavity (caum); o, opening into lateral passage thru folded flap; pl, posterior lobe; pm, premaxilla; pnt, post narial tissue containing narial muscles (not shown); s, slitlike opening into hollows of posterior lobes; tf, transverse tissue; v, vestibule.

over 1–2 years in maturing males in the Chambal population at total lengths of 4–4.5 m. In captivity, ghara growth appears to be more variable. At 10 years of age, a long-time captive male gharial at the Madras Crocodile Bank Trust began to develop a ghara which grew steadily to full size ~5–6 years later, by 16 years of age (Whitaker & Whitaker, 1989).

Martin and Bellairs (1977) included an illustration of the fossil skull of a giant Pliocene gavialoid *Rhamphosuchus* and pointed out the presence of a bony depression surrounding the narial opening, a skeletal feature similar to that found in the skulls of mature male gharial known to have possessed a fully developed gharas. Subsequent paleontological descriptions of fossil gavialoids have detected additional instances of skeletal signatures indicative of an attachment site for the soft tissue narial excrescence, that is, the ghara as previously described (Langston & Gasparini, 1997). Recently, skeletal evidence of a narial excrescence has been tallied by Iijima et al. (2021) for at least 10 extinct gharial relatives, with four to seven co-occurrences of associated enlarged pterygoid bullae in these ten taxa. Several recent studies have focused on this close association of the male-specific ghara and the enlarged pterygoid bullae, particularly in large adult gharial (Bourke et al., 2021; Hone et al., 2020). Following Martin and Bellairs (1977) comment on a possible vocalization role, it has been suggested that Bernoulli effects in the airflow between anterior and posterior chambers of the enlarged pterygoid bullae in male gharial may be responsible for the POP signal we describe (Bourke et al., 2021, citing a preliminary report of Jailabdeen et al., 2018).

4.9 | Sound production

Our field observations indicate that gharials are capable of vocalizing in a typical crocodylian manner. Gharials apparently utilize a simple larynx, distinctively crocodylian (Riede et al., 2015), to produce a species-specific variety of low-frequency contact and distress calls as hatchlings, yearlings, and juveniles (Bonke et al., 2015; Gramentz, 2012). As subadult and adults, gharials exhibit a limited repertoire of calls, including growls, groans, and roars (Rao & Singh, 1993; Singh & Rao, 1990; Whitaker et al., 2007; Whitaker & Basu, 1982). Sometimes, individuals of either sex vocalize when handled or restrained. However, as multiple previous observers have noted, gharials generally vocalize much less frequently than most other species (Dinets, 2013; Senter, 2008a). We have observed that wild Chambal gharial transition rapidly from frequent vocalizing as hatchlings living in creche groups during their first several months to only infrequent vocalizing by 3 months of age when they are usually dispersed post-monsoon. In nature, juveniles, subadults, and adults rarely vocalize except when disturbed. Clearly, gharial can vocalize, but typically do not appear to use this capability often. As is common in other species, gharials employ species-specific non-vocal acoustic sounds, such as jaw-claps, tail-wagging, hissing, and bubbling in conspecific encounters, as well as in some inter-specific interactions. In our study, mature adult males always produced sub-audible vibrations (SAVs) immediately before a POP, but no audible vocalizations, as mentioned above, accompanied any of the POP-BREATHE displays we documented. Gharials in different age/size classes may produce sound/vibration

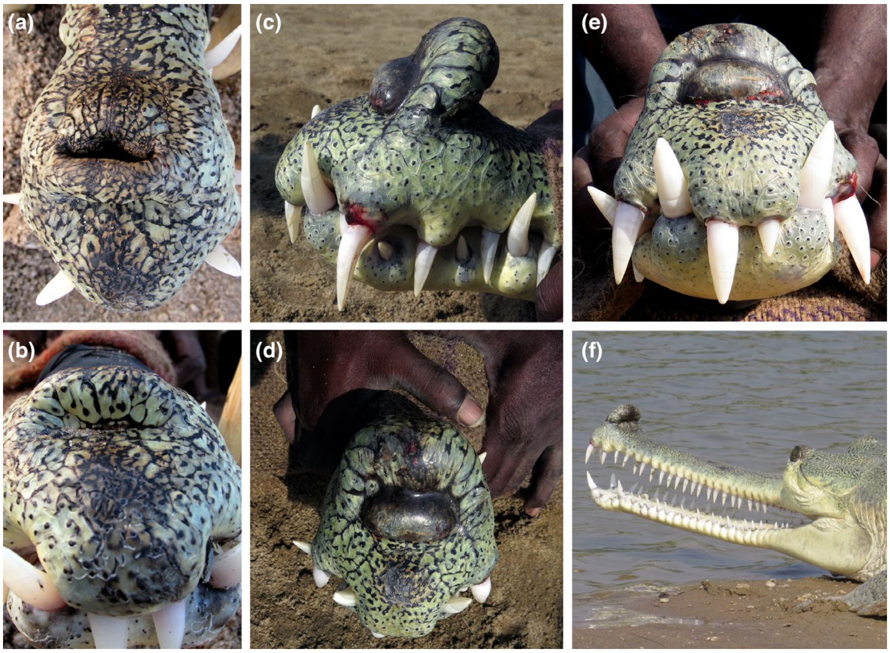

FIGURE 11 (a) dorsal view, snout tip showing ridge just anterior to nares and narial musculature posterior to the narial opening, showing undivided single narial opening, (b) frontal view, same snout tip as in (a), showing prominant elevated ridge directly in front of narial opening. (c–f), views of snout tip of 4.3 m young adult male gharial captured in late November 2013 and radio-tagged. Note tissue growth (visible as darkened knob in front of elevated ridge of tissue) above former narial opening and backward-leaning aspect of enlarged ridge of tissue above former narial opening.

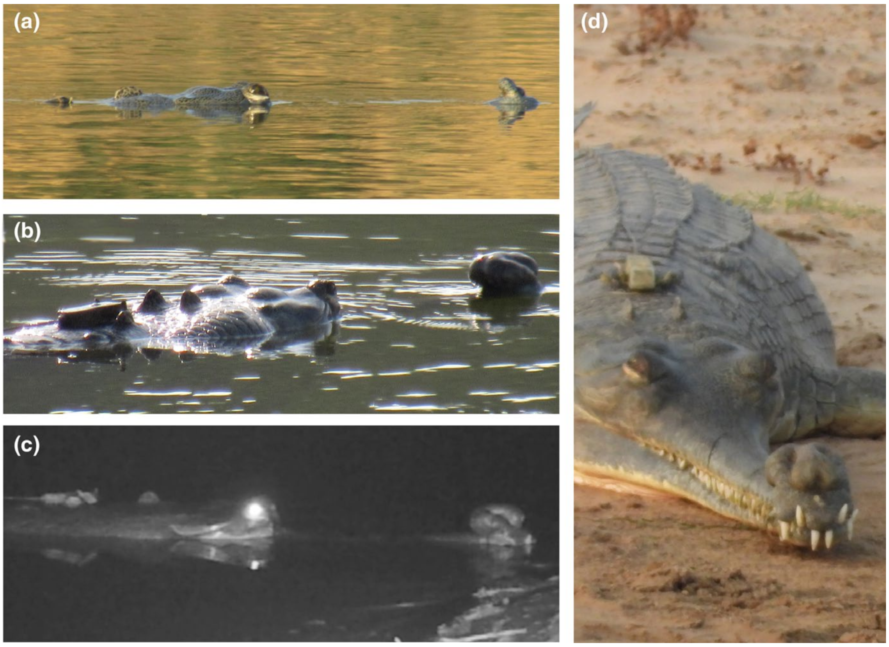

FIGURE 12 Profile views taken subsequently of 4.3 m male shown in Figure 11. Profile views of the same male shown in Figure 11c–f, in April 2014 (a), in June 2015 (b), in June 2016 (c), and in April 2018 (d). In later years (2018 thru 2022), there were no further changes in the ghara depicted in Figure 12(d) here for this male. Note the rapid ghara development evident when comparing (a) versus (b), between 2014 versus 2015. This change occurred in ≤14 months for this male living as a wild resident in Chambal River.

signals that are not strictly vocalizations produced in the vocal tract, but further study is warranted.

Exactly how the gharial POP, described here in detail, is produced is unknown. Clearly, it is tightly coupled to the intermittent exhalation–inhalation cycles performed periodically by an adult male possessing a ghara, but the POP signal appears to be a non-vocal acoustic sound, rather than a laryngeal vocalization per se. Here we note important features associated with POP sound production. First, POPs are not produced in the absence of a ghara; an intact ghara that is not visibly damaged is a prerequisite. In captivity, at the Madras Crocodile Bank, near Chennai, where a captive breeding group of gharials has been maintained for decades, when a mature male with ghara lost his snout tip-ghara assemblage due to fighting with other large males, he was no longer able to POP, as he had demonstrated earlier with an intact ghara. On several occasions, males had gharas damaged, by visible punctures or rips. The POPs produced by these males with torn or punctured gharas were low volume, muffled, and distorted relative to POPs produced prior to injury; in these instances, audible broadcast distances in air were limited to <50 m post injury versus 250–1500 m pre-injury. Similar scenarios and observations were observed in wild resident adult males at multiple localities, during field work on the Chambal River, upstream as well as downstream.

Second, POPs were always performed underwater, and no air bubbling and/or water disturbances were evident at the water surface directly above the submerged snout at the moment the POP sound was heard. This observation strongly suggests that water is likely moving thru the ghara, rather than air, and is partly responsible for producing the POP sound. On occasion, as the male's snout tip with attached ghara emerged at the water surface, immediately following a POP, a jet of water was ejected from the exterior narial opening at the posterior base of the ghara. In other instances, a spray of water, rather than a stream of water, was observed exiting the rear of the ghara, at its base at the moment of emergence following a POP.

Third, audible “bubbling” sounds typically accompanied the visual presence of bubbles at the water surface directly behind the ghara, at the external narial opening of the ghara, as the male submerged at the end of an exhalation-inhalation cycle (BR = breathe display). The characteristic sound that accompanied the appearance of bubbles at the water surface is easily replicated by slowly submerging a long-necked bottle underwater, with the bubbling produced at the tip of the bottle as water enters the bottle and air is expelled. Our detailed observations, documented with many video-audio recordings, indicated that water was flowing into the submerging nasal passage for ~1–3 s as the snout was submerged (e.g., see sequence finale, Figure 1h and Video S3).

A backflow of water, rather than air, into the elongated nasal chamber in the snout for some distance, is consistent with the interpretation of Martin and Bellairs (1977), based on their detailed examination of ghara anatomy/morphology. These authors concluded that the mature ghara, with its chambers and cavities, was essentially open to its surroundings because it lacked a closure mechanism. This nonoccluded opening at the caudal base of the mature ghara is evident in Figure 10c,d which clearly show the opening at the top of Figure 10c, and at the small arrow in Figure 10d.

In the normal crocodylian condition, the narial constrictor and dilator muscles are positioned dorsally on the nares to open and close the narial opening (Klassen et al., 2020). Within the ghara, these "open-close" muscles have been repositioned within folded tissue inside the ghara (Figure 10d). The narial muscles are no longer in an exterior position, and so do not function as an exterior value. As a consequence, the ghara is not able to be sealed off at its posterior base, but remains open to the exterior, with an unsealed backward opening, directly facing the gharial's eyes (Martin & Bellairs, 1977). When an adult male with ghara exhales, he literally expels air from the caudal base of the ghara backwards into his eyes. In adult female gharial, the exterior nares are not obviously modified during maturation, but do exhibit the atypical single (rather than "double" as in all other crocodylians; Grigg & Kirshner, 2015) narial opening characteristic of gharial at any age (Bourke et al., 2021).

4.10 | Underwater jaw claps + ghara = POPs

On rare occasions, mature male gharials with fully developed gharas bite forcefully in air or at the air-water interface. Such jaw claps, typically 1–3× in rapid succession, produce loud percussive sounds, with an explosive impact at the water surface (Video S4). The timings associated with the few recorded jaw claps we have observed on the Chambal River coincide closely with POP timings, for individual POPs as well as POP intervals (Figure S4). Taken together, these observations suggested that this same behavior, if made underwater, may be an important component of POP production, but one that would require a fully functional ghara to generate the impressively high sound pressures, averaging 192 dB 1 μPa (196–188 dB spherical and cylindrical, respectively; Kirsch et al., 2023). In other words, a rapid jaw clap, made underwater by a gharial bearing a fully developed, intact ghara would produce a single POP with the features we have described. Multiple jaw claps in rapid succession would produce the series of POPs recorded, for example, double or triple.

Fortunately, we have obtained multiple video recordings of a mature male gharial residing in a large enclosure with underwater viewing tanks at the Fort Worth Zoo, Texas. This male produced underwater jaw claps which, upon analyses, have acoustic features that are similar to the POP timings that we have documented for the wild Chambal River gharial population (Figure S4). A frame by frame examination of a sample double POP by this male is shown in Figure 13, with 3 sequential frames corresponding to the initial POP (frames 22, 23, 24; left to right, top panel Figure 13), and 3 sequential frames encompassing the second POP (frames 35, 36, 37; left to right, bottom panel Figure 13). A jaw clap underwater precedes each POP sound, with the entire open to closed mouth sequence taking place in less than 1/30th of a second (video shot at 30 fps), or less than 33 ms (Video S5). The bubble cloud visible at the posterior base of the ghara, in frame 24 (Figure 13), and the subsequent bubble clouds evident in frames 35–37 (Figure 13) are suggestive of cavitation bubble clouds forming in and around the ghara, as an intense impulsive sound is produced by each exceptionally rapid underwater jaw closure. Maximum possible cavitation sound pressure is 220 dB re 1μPa (Brennen, 2014).

These underwater observations in captivity of mature male gharials with intact and fully developed gharas are only preliminary, and systematic investigation with high resolution imagery and synchronous acoustic recordings will be required to document the precise mode of sound production and the possible role of cavitation phenomena in producing loud POPs. Specifically, a better understanding of the functional anatomy of the ghara as well as the flow dynamics within the ghara during jaw claps will likely be required to clarify how the POP sound is produced. Ultimately, it will be important to understand how the unique structure and shape of the ghara contributes to the extraordinarily loud, finely tuned POP signals that characterize each individual male gharial.

4.11 | Concluding comments

At this point, based on our direct observations as well as audio-video documentation of the POP signal, we suggest the following scenario for POP signal production, as a working hypothesis for further study. We contend that the POP signal is produced within the ghara while the snout is submerged underwater. Prior to sound production, the ghara and adjacent nasal chamber are filled with water as the animal disappears slowly below the water surface, with visible air bubbles emitted from the proximate base of the mature ghara, where the external nares are located. This pre-POP, water charging process may occur some minutes or longer before the POP signal is actually produced, dependent on the frequency of intermittent breathing by the performer. When a POP occurs, water residing in the anterior portion of the nasal canal is propelled at high pressure through the multi-chambered ghara to produce the POP signal. The SAVs that immediately precede the POP sound implicate direct involvement of the respiratory tract. Expired air within the lung would generate a propulsive force. In turn, air flow in the trachea / posterior nasal chamber at high pressure would propel a column of water at high velocity into and through the ghara. Because water, and not air, moves through the ghara immediately prior to emergence, no water surface disturbance of any kind is evident, becoming visible only when the snout tip-ghara reaches the air-water interface upon emergence. However, exhalation from the rear base of the ghara is evident as the gharial's snout tip breaks the water surface, accompanied with an audible "whizzing" sound, initiating the exhalation-inhalation–exhalation cycle(s) post POP production (Figure 1). Air is not expelled from the throat and/or gular flap. As noted, only occasionally, a very brief jet of water or spray has been observed as the snout is lifted out of the water upon emergence at the surface following a POP.

The actual sound producing mechanism, presumably dependent upon the functional morphology of the ghara with its multiple, complex arrangement of inter-connected cavities and flaps, remains elusive. Which components, acting in what fashion, are responsible for creating the POP sound? At present, cavitation

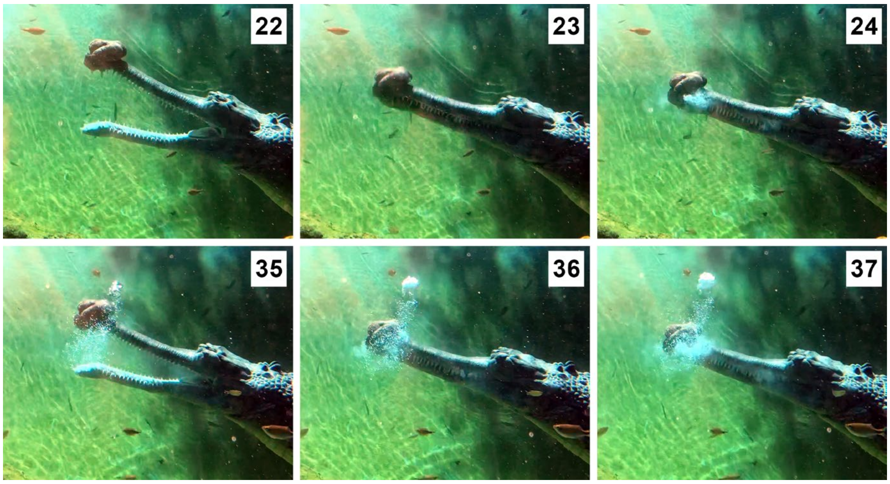

FIGURE 13 Individual frames, extracted from a video clip (at 30 frames per second), of a male gharial with a mature ghara, jaw clapping twice in rapid succession underwater at the Fort Worth Zoo. Frames 22–24 show the initial jaw closure, followed by a second jaw closure shown in frames 35–37 from the same video. The bubble cloud near the ghara, evident in Frame 24, is indicative of cavitation at the snout tip, presumably within the ghara, immediately following the rapid jaw closures evident in 22–23 and 35–36, <0.033 s (33 ms) in each instance. See text for additional explanation.

processes seem plausible. Notably, POP temporal features are in the millisecond range, rather than the microsecond range, as in the pistol shrimp claw closure example (Versluis et al., 2000). However, several recent reports of loud claps and "knocks" by walruses and seals have implicated cavitation phenomena, evident as momentary bubble clouds underwater associated with very loud sound pulses. These reports illustrate features similar to our depiction of bubble clouds produced by underwater jaw claps in a male gharial with a ghara (Figure 13).

The unusual "adhesive disc" separation mechanism, responsible for producing pipid frog "clicks" as a result of a modification of the laryngeal folds, occurs in milliseconds and at low frequencies (Kelley et al., 2020; Kwong-Brown et al., 2019). As such, a similar mechanism involving discs or flaps that snap open or shut might be consistent with the temporal patterning observed for the gharial POP signal, but considerable upscaling would be needed to make a similar system, for example, adhesive discs, workable in the gharial context. At present, detailed studies of ghara internal anatomy/histology are likely to be informative in order to identify the relevant structural and functional components contributing to POP sound production, as well as air-water flow dynamics within the snout and skull.

In this study, we have documented in detail a novel, non-vocal, underwater, acoustic signal, the gharial POP, that was performed only by adult ghara-bearing males in specific behavioral contexts in particular social settings. It appears that gharial POPs are akin to the strange sounds produced non-vocally by a wide variety of animals, from snapping shrimps to marine mammals (Patek & Longo, 2018; Verga & Ravignani, 2021). The precise timings of the gharial POPs appear to be the product of finely controlled muscle-driven jaw claps that can be varied consistently to exhibit only millisecond differences. How gharial POPs relate, if at all, to a performer's body features remains a question to be answered. In other words, are gharial POPs an honest signaling strategy, as articulated by Partan (2013) and by Garcia and Ravignani (2020)? Our observations suggest that various ghara architectures do not necessarily map directly to obvious differences in male features, such as body size. Finally, the gharial POP signals we have described are clearly important elements in a multi-modal communication of sexual identity, dependent on the presence of a ghara. This sexually dimorphic feature is unique among living crocodylians, and was likely present in fossil relatives, not only in crocodyliforms but possibly in other archosaur lineages (Holliday & Schachner, 2022; Hone et al., 2020; Iijima et al., 2021). The gharial ghara likely projects relevant information visually, acoustically, and haptically about maleness, its various qualities, its location, and potentially the identity of each individual male.

AUTHOR CONTRIBUTIONS

AJJIM J and LANG JW conceived & designed the study. LANG JW and AJJIM J analysed and interpreted the data and prepared the figures. LANG JW and AJJIM J reviewed the literature and wrote the manuscript. AJJIM J and LANG JW reviewed various drafts together and finalized the manuscript. AJJIM J conducted the field study, and LANG JW provided equipment & supplies, and organized funding for the project.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

All the acoustic and video recording data and statistical analyses data supporting this research are available upon reasonable request from JAILABDEEN AJJIM and JEFFREY W LANG at jaiwildlife@gmail.com and jeff.w.lang@gmail.com.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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