

Vocalizations in two rare crocodylian species: A comparative analysis of distress calls of *Tomistoma schlegelii* (Müller, 1838) and *Gavialis gangeticus* (Gmelin, 1789)

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Abstract. We analysed 159 distress calls of five individuals of *T. schlegelii* for temporal parameters and obtained spectral parameters in 137 of these calls. Analyses of *G. gangeticus* were based on 39 distress calls of three individuals, of which all could be analysed for temporal and spectral parameters. Our results document differences in the call structure of both species. Distress calls of *T. schlegelii* show numerous harmonics, whereas extensive pulse trains are present in *G. gangeticus*. In the latter, longer call durations and longer intervals between calls resulted in lower call repetition rates. Dominant frequencies of *T. schlegelii* are higher than in *G. gangeticus*. *T. schlegelii* specimens showed a negative correlation of increasing body size with decreasing dominant frequencies. Distress call durations increased with body size. *T. schlegelii* distress calls share only minor structural features with distress calls of *G. gangeticus*.

Key words: *Tomistoma schlegelii*, *Gavialis gangeticus*, distress calls, temporal parameters, spectral parameters.

Introduction

Communication takes place whenever a signal is emitted by one individual and leads to changing behaviour of another individual (Wiley 1983). Thus, communication is based on interactions between at least one “signaller” and a “receiver”, but can also incorporate multiple signallers and receivers (Pough 2001, Wiley 2006). Communication is not restricted to conspecifics and can occur between members of different species (Pough 2001). Interspecific communication occurs further in mimicry systems used by various vertebrates (e.g. caudal luring by various snake species and the alligator snapping turtle *Macrochelys temminckii*), invertebrates (e.g. pheromone emission and attraction of bolas spider *Mastophora* spp.) and plants (e.g. orchid bee mimicry either to attract pollinators or to function as defensive Batesian mimicry) (Pasteur 1982, Lev-Yadun & Ne’eman 2012, Jackson & Cross 2013, Wickler 2013). Signalling modalities in animal communication are complex, including acoustic, chemical, electrical, tactile and visual signals (Pough 2001). While electroreception is limited to aquatic environments, all other signalling systems occur in both terrestrial and aquatic habitats (Bradbury & Vehrencamp 1998). Animal communication systems distinctly differ in operating distances. While the efficiency of visual signals is restricted to relatively short distances, acoustic signals are able to perform over long dis-

tances since sound propagation works fast and efficient in air or water (Pough 2001). In the case of infrasound, which by popular definition covers frequencies below 20 Hz (Leventhall 2007), acoustic signals are able to spread out over large kilometre distances. Infrasound communication is applied by various animals from insects to birds and mammals (Naguib & Haven Wiley 2001) and occurs further in crocodylians (Dinets 2013). Even though acoustic communication is well developed in most vertebrates, it is only marginally present in reptiles (Vergne et al. 2009). Tortoises limit their sound emission mainly to courtship behaviour while geckos vocalize in the context of territory advertisement and female attraction (Pough 2001). Crocodylians by contrast use vocalizations in a broader variety of contexts for long-range and short-range communication (Pough 2001, Vergne et al. 2009). Like in their sister group, birds, acoustic communication in crocodylians is highly developed, even though they are lacking a specialized vocal structure comparable to the syrinx of birds (Vergne et al. 2009). Vocalization among Crocodylia plays a key role during all life stages, especially during the breeding season at the time of hatching and juvenile development (Brien et al. 2013, and references therein, see also key references in Appendix S1).

Tomistoma schlegelii is an endangered large freshwater crocodile which mainly is restricted to fragmented parts of peat swamp forests in South-

east-Asia (Stuebing et al. 2006). Here we describe distress call analyses of *T. schlegelii* which were analysed for variance relating to body size. Additionally, we analysed distress calls of *G. gangeticus* for similarities and dissimilarities in temporal and structural parameters. There is some published provisional data on distress calls of *G. gangeticus* (Gramentz 2012a) and *T. schlegelii* (Gramentz 2012b) but in the case of *T. schlegelii* the data available must be regarded insufficient to display distinct structural patterns.

This study aims to analyse distress call structures of *T. schlegelii* in more detail, based on individuals of varying size, larger samples and the interspecific comparison to other Crocodylian species, particularly *G. gangeticus*.

Methods

Study site

Study sites were the Sekonyer River and the Sekonyer Kanan River of the Tanjung Puting National Park (Central Kalimantan, Indonesia). The Sekonyer River shapes the north-western boundary of the Park whereas the Sekonyer Kanan River forms a tributary of the Sekonyer and leads off to Camp Leakey, a world famous rehabilitation centre for Orangutans established by Biruté Galdikas in 1971 (Galdikas & Shapiro 1994). From the junction at the Sekonyer River, the Sekonyer Kanan River spans a distance of approximately 7.5 kilometres to Camp Leakey. The Pondok Ambung Tropical Forest Research station provided accommodation and survey vessels for the study and is located halfway between the rivers junction and Camp Leakey.

Capture sites of and capture techniques for *T. schlegelii*

The entire area surveyed encompassed 64.7 river kilometres and was subdivided into 6 transects, each covering a distance between 7.6 and 15.7 kilometres. Distress calls suitable for sound analysis were recorded of 5 specimens. Hereof two specimens were recaptured on the 8th and 12th September 2009 as part of mark-recapture approach of the entire study carried out in Tanjung Puting. Distress calls of recaptured individuals were additionally recorded, but analysed separately due to varying recording conditions (e.g. capture circumstances, weather conditions, background noise). Specimens were either captured by hand or by means of a snare-pole. GPS coordinates, water temperatures and body proportions [total length (TL); body weight (BWt)] were recorded on the spot. Data is compiled in Table 1.

Snouts of aggressively behaving specimens and those exceeding 100cm total length (TL) were secured with duct tape immediately after capture. As a consequence distress call emission was affected. Therefore, we built two subsets for spectral parameter analyses: subset 1 [distress calls unaffected (snouts kept open during call emission /

$n=48$)] / subset 2 [distress calls affected (snouts kept shut during call emission / $n=89$)].

Sound recording and analysis

Distress calls of *T. schlegelii* were recorded during an autoecological study as part of a PhD thesis of the corresponding author carried out in Tanjung Puting National Park. Sound recordings were obtained by the aid of a German filming crew which accompanied the study in parts. Recordings were performed using a Røde NTG1 Condenser shotgun microphone (frequency range 20 Hz-20 kHz) connected to a Sony PMW EX3 professional video camera (32 bit digitization at 44.1 kHz sampling rate). Audio files were extracted from the video sequences and saved as .wav files. Recordings were performed in a distance of approximately one meter to *T. schlegelii* specimens.

Distress calls of three juvenile *G. gangeticus* hatched in 2008 were recorded by the second author at Madras Crocodile Bank Trust (S. India). Morphometric data of these specimens is summarized in Table 1. Recording equipment was similar as reported by Gramentz (2012a) and comprised a Shure SM58 dynamic microphone (frequency range 15 Hz- 15 kHz) connected to a Line 6 Toneport UX-2 using Line 6 Gearbox software (kHz 32 bit digitization at 44.1 kHz sampling rate). Audio files were recorded as .wav files. To reduce background noise, recordings were performed in a room on 24th October 2009 with comparable acoustic properties. Air temperatures were measured at approximately 30°C, no water temperature of the *G. gangeticus* enclosure was recorded. Recording distance was approximately 50 cm. All individuals were held during the recording procedure without taping the snouts.

For both species distress call recordings were cut and analysed for temporal properties (call lengths / intervals between calls) using Audacity software (V. 2.0.0 / <http://audacity.sourceforge.net/>). Spectral parameters were obtained using *seewave* (Sueur et al. 2008) for Cran R 2.15.2 (R Core Team 2012). Spectrograms (75 % overlap) with attached oscillograms were performed using the Fast Fourier Transformation (Hanning window / 512 points resolution). Spectrogram plots were limited to 20 kHz. Fundamental and dominant frequencies were tracked across the calls and calculated as average values for each call. Frequency tracks were plotted on the respective spectrograms. For interspecific comparisons between *G. gangeticus* and *T. schlegelii* we used distress calls of *T. schlegelii* of subset 1 only.

Results

In total, 159 distress calls of *T. schlegelii* were analysed for temporal parameters. Heavy background noise in some recordings limited spectral analyses to 137 distress calls. Spectral parameters were calculated for both subsets of the *T. schlegelii* dataset. Subset 1 included distress calls of specimens Ts1,

Table 1. Data relating to *G. gangeticus* (Gg) and *T. schlegelii* (Ts) morphometrics / Ts4* = recaptured specimen / Ts3* = recaptured specimen.

ID number	Capture Date	Capture Time	Coordinates	Water temperature(°C)	TL (cm)	BWt (kg)
Gg1	-	-	-	-	89.9	1.3
Gg2	-	-	-	-	73.5	0.7
Gg3	-	-	-	-	85.4	1.1
Ts1	24 th July 08	20:15	S2°44'10.2 E111°53'27.8	25.9	56.3	0.299
Ts2	27 th July 08	21:00	S2°47'54.3 E111°49'37.2	25.6	134	5.35
Ts3	28 th August 09	20:30	S2°44'50.8 E111°55'21.5	26.6	61.5	0.396
Ts4	04 th September 09	22:55	S2°44'16.2 E111°53'26.6	27.2	70	0.532
Ts4*	08 th September 09	21:25	S2°44'15.7 E111°53'26.0	26.4		
Ts3*	12 th September 09	20:50	S2°44'49.6 E111°55'21.2	25.9		
Ts5	16 th September 09	20:00	S2°45'09.6 E111°55'24.8	26.2	134	5.38

Ts3, Ts3* and Ts4*, subset 2 included distress calls of specimens Ts2, Ts3, Ts3*, Ts4, and Ts4*. Distress calls of specimen Ts5 were heavily affected by background noise and thus excluded from detailed spectral analyses. However, a combined spectrogram / oscillogram of an exemplary distress call of Ts5 was created to provide a rough structural overview. Total lengths (TL) of captured specimens emitting distress calls varied between 56.3 cm and 134 cm (cf. Table 1).

Call durations / Intervals between calls

Lengths of distress calls of *T. schlegelii* ranged between 0.262 – 3.805 s [mean 0.511 (SD: 0.443) / $n=159$]. Longest call durations were observed in Ts2 [0.499 – 0.917 s / mean 0.754 (SD: 0.098) / $n=19$] and Ts5 [1.714 – 3.805 s / mean 2.711 (SD: 0.89) / $n=5$], the two largest specimens (both 134 cm TL) studied. Distress call durations of Ts1 [0.347 – 0.528 s / mean 0.445 (SD: 0.057) / $n=10$], Ts3 [0.28 – 0.566 s / mean 0.408 (SD: 0.056) / $n=54$], Ts3* [0.289 – 0.44 s / mean 0.359 (SD: 0.043) / $n=18$], Ts4 [0.275 – 0.499 s / mean 0.384 (SD: 0.061) / $n=33$] and Ts4* [0.262 – 0.586 s / mean 0.386 (SD: 0.069) / $n=20$] were shorter as observed in Ts2 and Ts5.

Intervals between calls lasted from 0.265 to 44.82 s [mean 3.03 (SD: 5.249) / $n=142$]. Similar to distress call durations, intervals between calls of specimen Ts5 were longer [3.588 – 44.82 s / mean 26.752 (SD: 18.856) / $n=4$] and differed distinctly from Ts1 [0.299 – 1.983 s / mean 1.234 (SD: 0.561) / $n=9$], Ts2 [0.466 – 4.065 s / mean 1.973 (SD: 1.287) / $n=18$], Ts3 [0.265 – 7.273 s / mean 2.512 (SD: 1.426) / $n=48$], Ts3* [1.093 – 3.546 s / mean 1.723 (SD: 0.66) / $n=15$], Ts4 [0.601 – 7.725 s / mean 2.438 (SD: 1.578) / $n=31$] and Ts4* [1.137 – 17.165 s / mean 3.130 (SD: 3.934) / $n=18$].

Compared to *T. schlegelii*, distress calls of *G. gangeticus* were characterized by longer mean durations. Distress call lengths of Gg1 [0.492 – 2.604 s / mean 1.016 (SD: 0.614) / $n=28$], Gg2 [0.613 – 2.306 s / mean 1.413 (SD: 0.54) / $n=9$] and Gg3 [0.858 – 2.155 s / mean 1.506 (SD: 0.917) / $n=2$] exceeded distress call lengths of *T. schlegelii* with the exception of Ts5. Intervals between calls calculated for Gg1 [0.476 – 18.744 s / mean 6.403 (SD: 3.906) / $n=26$], Gg2 [2.982 – 40.328 s / mean 11.052 (SD: 12.485) / $n=8$] and Gg3 [7.218 s] were much longer as in *T. schlegelii* leading to lower call repetition rates. Again, specimen Ts5 differed markedly. Both datasets are summarized in Fig. 1.

Distress call structures

T. schlegelii (Subset 1)

Distress calls of *T. schlegelii* can roughly be divided into two call patterns. Both patterns are strongly modulated in frequency, express complex harmonics and develop slightly visible pulses towards call ends. Pattern 1 (Fig. 2A/B) differs from pattern 2 (Fig. 2C/D) by its amplitude envelope attack phase which is less abrupt. Distress call bandwidth of subset 1 is wide, occasionally extending over 15 kHz. Dominant frequencies of Ts1 [2.604 – 3.280 kHz / mean 2.847 (SD: 0.216) / $n=9$], Ts3 [1.526 – 3.330 kHz / mean 2.225 (SD: 0.527) / $n=18$], Ts3* [1.994 – 2.665 kHz / mean 2.319 (SD: 0.182) / $n=8$] and Ts4* [1.596 – 2.476 kHz / mean 2.309 (SD: 0.228) / $n=13$] are relatively low. Fundamental frequencies of Ts1 [0.315 – 0.338 kHz / mean 0.324 (SD: 0.007) / $n=9$], Ts3 [0.315 – 0.404 kHz / mean 0.358 (SD: 0.020) / $n=18$], Ts3* [0.325 – 0.383 kHz / mean 0.356 (SD: 0.020) / $n=8$] and Ts4* [0.292 – 0.371 kHz / mean 0.342 (SD: 0.021) / $n=13$] show only minor differences in spectral range among each other.

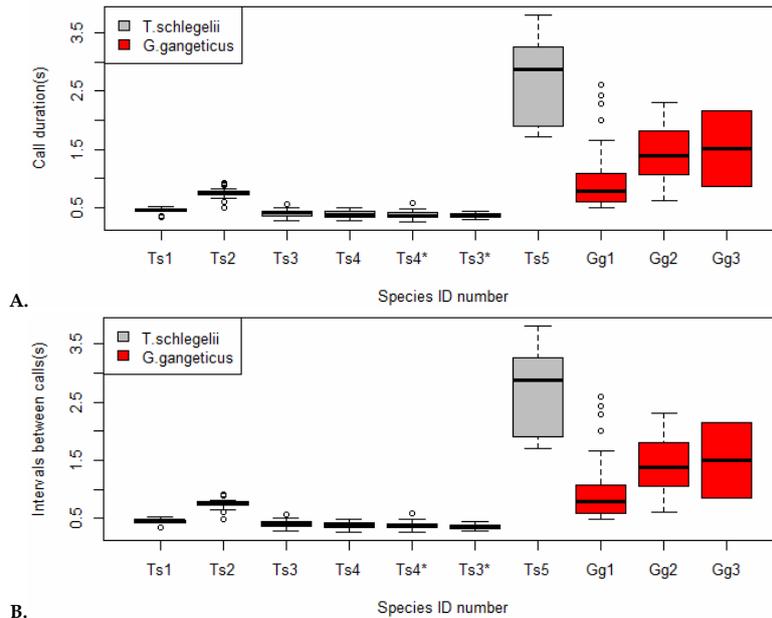


Figure 1. (A) Distress call durations of *T. schlegelii* and *G. gangeticus*
(B) Intervals between distress calls of *T. schlegelii* and *G. gangeticus*.

T. schlegelii (Subset 2)

Because snouts were kept shut during call emission, distress call structures of subset 2 differed from subset 1. Compared to subset 1 the amplitude envelope is relatively smooth. Fundamental frequencies of Ts2 [0.259 – 0.287 kHz / mean 0.273 / (SD: 0.008) / $n=19$], Ts3 [0.253 – 0.404 kHz / mean 0.345 (SD: 0.031) / $n=35$], Ts3* [0.321 – 0.386 kHz / mean 0.357 (SD: 0.025) / $n=5$], Ts4 [0.324 – 0.408 kHz / mean 0.360 (SD: 0.021) / $n=28$] and Ts4* [0.332 – 0.363 kHz / mean 0.348 (SD: 0.022) / $n=2$] were relatively low. Dominant frequencies were lower for Ts3 [0.544 – 1.193 kHz / mean 0.746 (SD: 0.137) / $n=35$], Ts3* [0.736 – 1.293 kHz / mean 0.916 (SD: 0.222) / $n=5$], Ts4 [0.532 – 0.816 kHz / mean 0.662 (SD: 0.069) / $n=28$] and Ts4* [0.779 – 0.866 kHz / mean 0.822 (SD: 0.061) / $n=2$] as observed in subset 1 and close to fundamental frequencies in the case of Ts2 [0.296 – 0.343 kHz / mean 0.321 (SD: 0.014) / $n=28$]. Similar to subset 1 call bandwidth sporadically exceeded 15 kHz, but for the most part there is hardly any spectral energy above 8 kHz (Fig. 3A-D).

A comparison of affected and unaffected distress calls is given for a series of three distress calls of specimen Ts3 (Fig. 4). Additionally, an exemplary distress call of Ts5 is illustrated in Fig. 5. This specimen exhibited the longest distress call

durations and intervals between calls of the entire *T. schlegelii* dataset. However, we interpret this as an exception as the capture procedure strongly affected the exhaustion level of this specimen. Distress calls of Ts5 were strongly amplitude modulated but detailed spectral parameters could not be obtained for this specimen.

G. gangeticus

Distress calls of *G. gangeticus* rarely show harmonics and are predominantly amplitude modulated. Four distress call patterns can be distinguished. The amplitude peak in pattern one is reached in the last third of the amplitude envelope wherein pattern two develops the amplitude peak after a short and steep attack phase of the amplitude envelope in the first fifth of call length (Fig. 6.A/C). Call patterns three and four display frequency modulated harmonics, either at the beginning of call emission or shortly after a series of pulses during the initial phase (Fig. 6.E/F). In all distress call patterns temporal pulse intervals increase towards call end. Fundamental frequencies of Gg1 [0.242 – 0.309 kHz / mean 0.277 (SD: 0.019 kHz) / $n=28$], Gg2 [0.251 – 0.337 kHz / mean 0.289 (SD: 0.025 / $n=9$) and Gg3 [0.248 – 0.278 kHz / mean 0.263 (SD: 0.021 / $n=2$)] covered only minor lower spectral regions as observed in *T. schlegelii*.

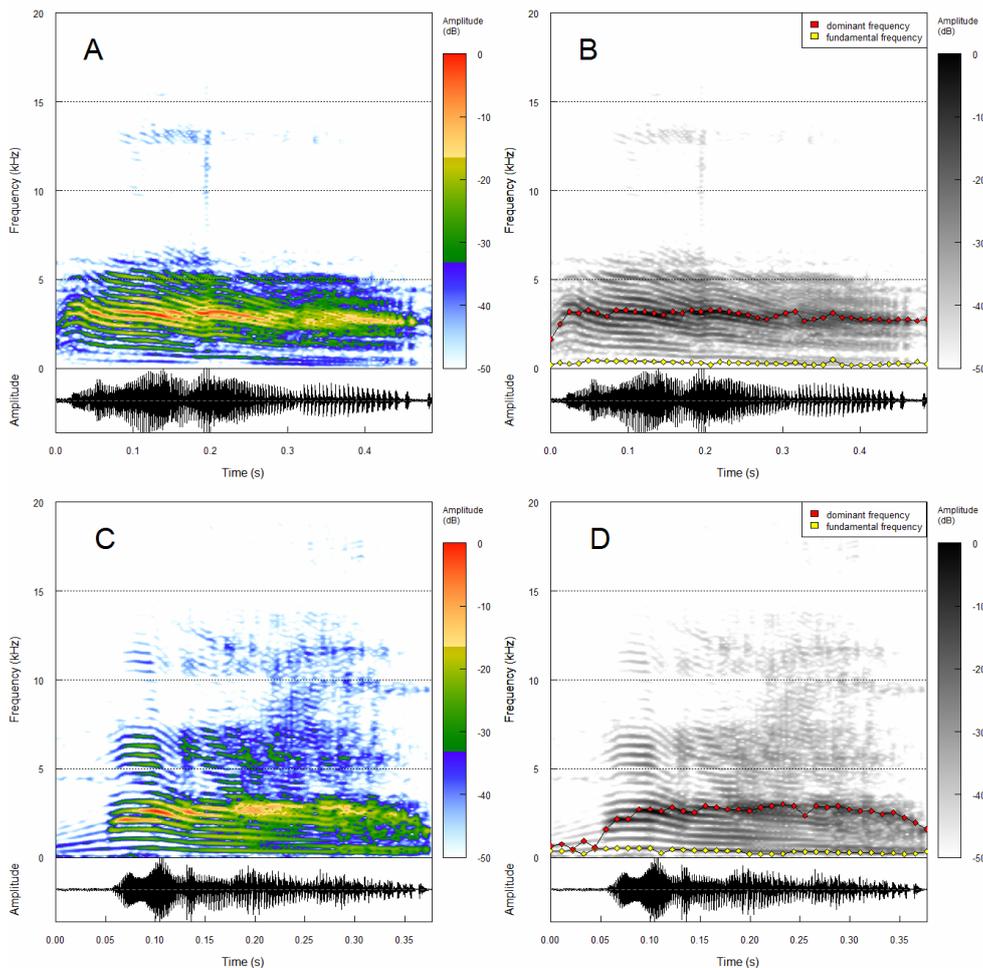


Figure 2. Spectrograms, oscillograms, fundamental and dominant frequency tracks of two exemplary distress calls of *T. schlegelii* (subset 1). (A) Spectrogram & oscillogram of distress call pattern 1 (B) Fundamental and dominant frequency track of distress call pattern (C) Spectrogram & oscillogram of distress call pattern 2 (D) Fundamental and dominant frequency track of distress call pattern 2.

Compared to fundamental frequencies, dominant frequencies of Gg1 [0.543 – 2.220 kHz / mean 1.093 (SD: 0.616) / $n=28$], Gg2 [0.458 – 2.056 kHz / mean 1.432 (SD: 0.551) / $n=9$] and Gg3 [0.424 – 1.134 kHz / mean 0.779 (SD: 0.502) / $n=2$] were located at lower spectral regions.

Discussion

All crocodylian species have a repertoire of acoustic signals and emit sounds in various situations (Neill 1971, Britton 2001, Vergne et al. 2009). To date, bioacoustic information for *G. gangeticus*

(Gramentz 2012a) and *T. schlegelii* (Gramentz 2012b) is scarce. Generally, detailed information regarding vocalization structures and particularly the juvenile vocal repertoire of crocodylians are yet poorly studied and understood (Vergne et al. 2009, Vergne et al. 2012). Juvenile crocodylian vocalizations can be distinguished in four main categories: hatching calls, contact calls, distress calls and hissing calls (Vergne et al. 2009). Distress calls of juvenile crocodiles are emitted in threatening situations, provoked by loud noises, rapid movements nearby, presence of a predator and when being seized (Neill 1971, Campbell 1973, Staton 1978). Britton (2001) documented significant effects of

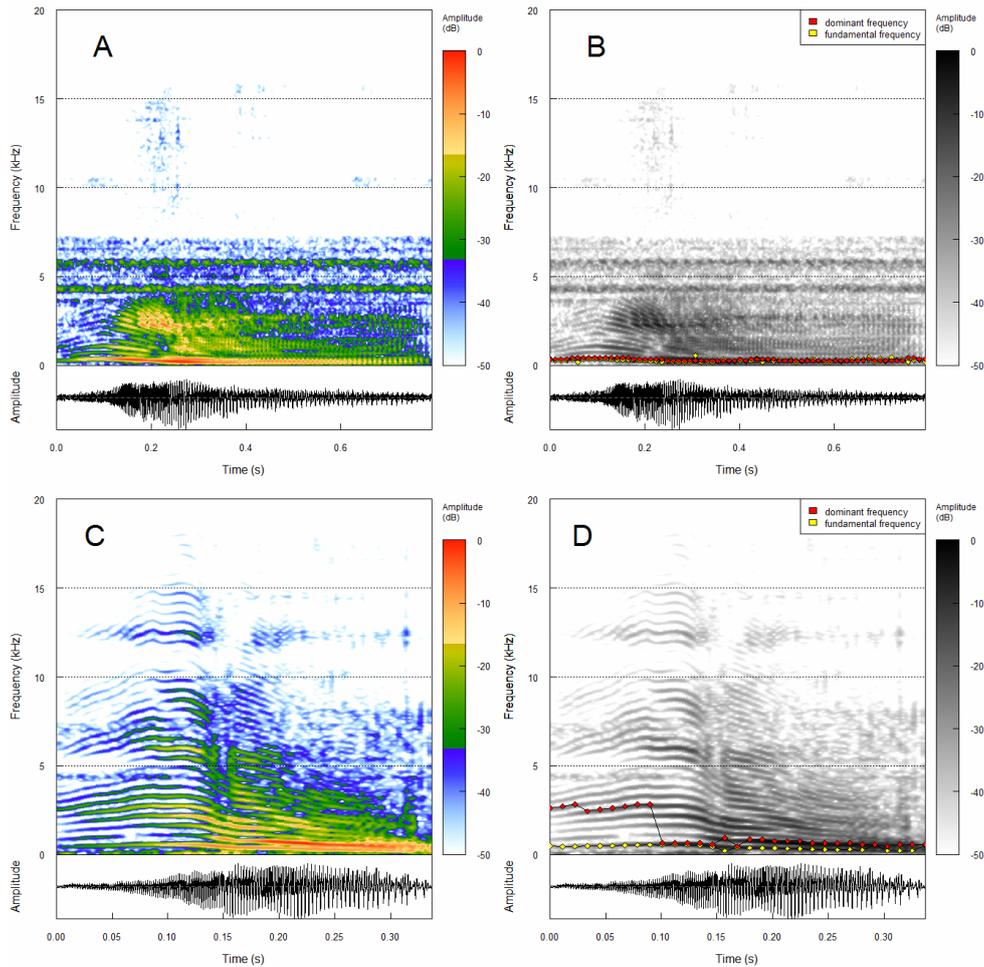


Figure 3. Spectrograms, oscillograms, fundamental and dominant frequency tracks of *T. schlegelii* (Ts2) compared to an exemplary distress call (Ts3) of subset 2. (A) Distress call of specimen Ts2 with slightly developed harmonics (B) Fundamental and dominant frequency track of specimen Ts2 showing the interference of both frequencies (C) Distress call with well pronounced harmonic frequencies up to 15 kHz (D) Fundamental and dominant frequency track with higher dominant frequency in the first third of distress call and subsequent convergence of frequencies.

the palatal valve in distress calls of *C. johnstoni* and Gramentz (2012b) observed effects of the palatal valve in distress calls of *T. schlegelii*.

We distinguished between distress calls of *T. schlegelii* either emitted with snouts kept open (subset 1 / unaffected distress calls) or with snouts kept shut during distress call emission. (subset 2 / affected distress calls). The abrupt drop in dominant frequency of affected distress calls in *T. schlegelii* (cf. Fig. 4) can be well explained by the “source-filter theory of speech” which can also be applied to nonhuman vocalizations (Fitch & Fritz 2006). This theory describes vocal signal produc-

tion as a two-stage process in which the generation of a sound source is subsequently filtered in the vocal tract (Taylor & Reby 2010). Compared to the results obtained by Gramentz (2012b) the amplitude envelope of our subset 1 resembled distress calls with the palatal valve opened, whereas subset 2 looked similar to distress calls with the palatal valve closed. In accordance with Gramentz (2012b) we found that distress calls of *T. schlegelii* regularly display harmonics. Basic acoustic structures in juvenile crocodile vocalization comprise a fundamental frequency with several harmonics which are strongly modulated in frequency

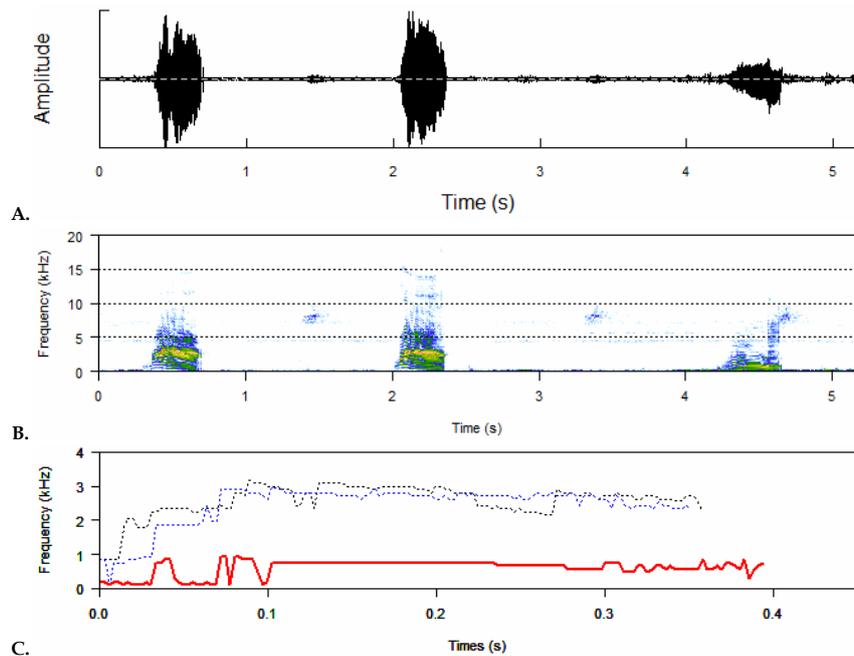


Figure 4. (A) Oscillogram of *T. schlegelii* (Ts3) distress call series with the first two calls (unaffected) and the last call (affected) (B) Spectrogram of the call series described in figure 4 (A) with blue colour representing the lowest spectral energy and red colour indicating the highest spectral energy of calls. (C) Comparison of dominant frequencies of the call series described in figure 4 (A) with blue-dotted line representing distress call 1 (unaffected), black-dotted line representing distress call 2 (unaffected) and solid red line representing distress call 3 (affected).

(Vergne et al. 2009). Frequency modulation in *T. schlegelii* are similar to distress calls of *Crocodylus niloticus*, *Crocodylus johnstoni* and *Caiman yacare* partly showing a “circumflex” shape (Britton 2001, Sicuro et al. 2013) caused by frequency modulated upsweeps and downsweeps of harmonics. This “circumflex” shape has been slightly indicated in one distress call of *G. gangeticus* but compared to *T. schlegelii*, harmonics are rarely present and pulses are prominent. In contrast to Gramentz (2012b), we found notable pulses in both *T. schlegelii* subsets, but much less pronounced than in *G. gangeticus*. We trace back these findings to the poor dataset used by Gramentz (2012b), which comprised only one individual of smaller body size than our study animals and thus pulses may just have been overlooked.

Considerable differences in call lengths, intervals between calls, fundamental and dominant frequency range were found between *G. gangeticus* and *T. schlegelii*. In accordance with Gramentz (2012a) we found longer call durations and lower repetition rates in distress calls of *G. gangeticus*.

Fundamental and dominant frequencies were lower in *G. gangeticus* than in *T. schlegelii*. Gramentz (2012a) discussed a possible relationship between the elongated, narrow snout of *G. gangeticus* and distress call duration, whereupon the snout seems worse suited to repel against predators and thus stronger emitted signals may have evolved to ensure intraspecific protection over longer time periods. In our opinion this assumption seems unlikely as *G. gangeticus* produces the largest eggs of all extant crocodylians (Trutnau & Sommerlad 2006) and hatchlings are comparatively large. Therefore, defending should not be more disadvantageous compared to other crocodylian species. To us it seems more plausible, that distress call lengths and their frequency range may form an adaption to the natural habitat of *G. gangeticus*. Post-natal maternal care exists in this species (Stevenson & Whitaker 2010) but juveniles and adults prefer different microhabitats (Neill 1971, Whitaker 1983). Consequently, an alarming system of juveniles needs to perform over long distances to ensure maternal protection. Prime

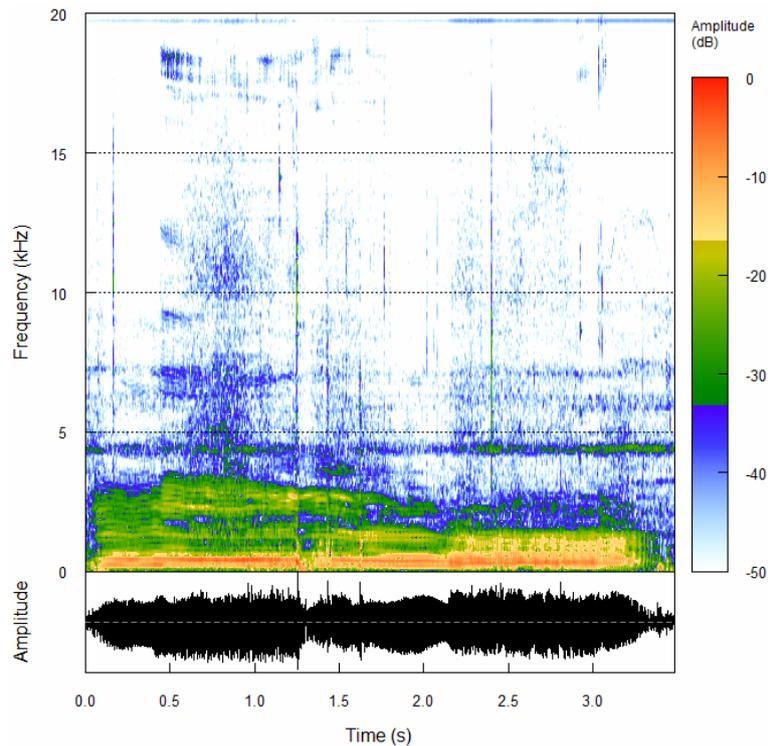


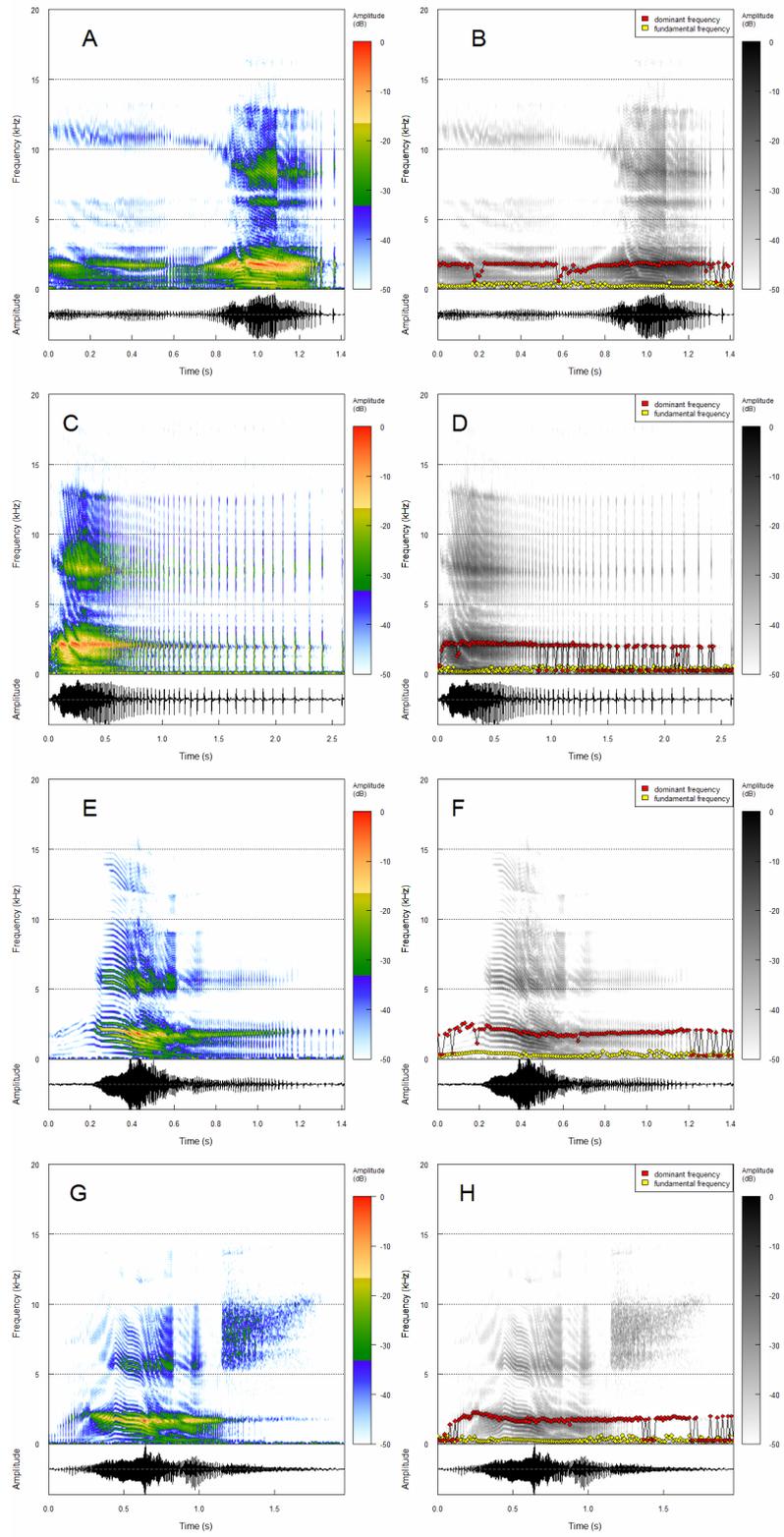
Figure 5. Amplitude modulated distress call of *T. schlegelii* (Ts5). Call duration was measured at 3,805 s.

habitats of adults are deep rivers (Whitaker 1983), whereas dense vegetation with hiding places in shallows, backwaters and isolated floodplains is favoured by juveniles (Neill 1971, Singh 1976). Mean dominant frequencies of *G. gangeticus* calculated in the present study are concentrated at low dominant frequencies which have been documented to be well suited for long range communication in *A. sinensis* (Wang 2007). Further, a linkage of habitat structure and long range communication based on low frequency signals has been demonstrated for *A. mississippiensis* (Garrick & Lang 1977) including infrasound communication (Vliet 1989, Dinets 2011b, Dinets 2013). Although infrasound production in *G. gangeticus* has not yet been proven (Dinets 2013) and adult *G. gangeticus* inhabit large river systems, long range communication based on low frequency spectra seems likely due to ecological niche separation of adults

and juveniles. Prolonged distress calls of *G. gangeticus* at comparatively low dominant frequencies could thus enable intraspecific communication over large distances to reduce predation risks.

Distress call durations of *G. gangeticus* distinctly exceeded distress call durations of *T. schlegelii*. A negative correlation between increasing body size and decreasing dominant frequencies of distress calls has been documented for *T. schlegelii* (subset 2). Highest dominant frequency means were calculated for the smallest specimen of subset 2 [Ts3/Ts3* (61.5 cm TL / 0.746 kHz; 0.916 kHz)], lowest dominant frequency means were determined for the largest specimen [Ts2 (134 cm TL / 0.321 kHz)]. In animal vocalizations the increase of body size results in a decrease of call frequencies because body structures relevant for sound production get larger and vibrate at

Figure 6. *G. gangeticus* distress calls (A) Spectrogram / oscillogram of distress call pattern 1 (B) Fundamental and dominant frequency track of pattern 1 (C) Spectrogram / oscillogram of distress call pattern 2 (D) Fundamental and dominant frequency track of pattern 2 (E) Frequency modulation of harmonics in distress call pattern 3. (F) Fundamental and dominant frequency track of pattern 3 (G) Frequency modulation of harmonics in distress call pattern 4 (H) Fundamental and dominant frequency track of pattern 4.



lower frequencies (Collias 1960, Britton 2001). Acoustic signals at low frequencies play a key role during courtship and mating, especially in species inhabiting densely vegetated habitats (Garrick & Lang 1977, Dinets 2011a, Brien et al. 2013). As we have demonstrated for *G. gangeticus*, distress calls emitted at comparatively low frequencies occur also in crocodylian species inhabiting open habitats and may be appropriate if intraspecific niche separation between adults and juveniles exists. Further, we revealed distinctive differences in temporal and spectral parameters of distress calls of *G. gangeticus* and *T. schlegelii*. This finding is supported by Dinets (2011b) who pointed out apparent dissimilarities in the signalling system of *G. gangeticus* and *T. schlegelii*. However, our study solely focused on distress call analyses of both species and did not include analyses on the entire vocal repertoire. Furthermore, our results need to be regarded as preliminary since distress calls of both species were recorded under different conditions (e.g. recording equipment, distress level of specimens etc.) and thus no standardized analyses could be performed. The implementation of standardized distress call analyses for *G. gangeticus* and *T. schlegelii* is a drawback difficult to overcome because they are rarely kept in captivity and captive breeding successes are low. Nonetheless, we were able to provide valuable additional information on the vocal repertoire of both species but further investigations are urgently needed in order to understand key functions of crocodylian communication systems.

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Appendix S1: Overview on key references for bioacoustics of Crocodylians.

Bioacoustic information exists for *Alligator mississippiensis* (Beach 1944, Wever 1971, Campbell 1973, Garrick & Lang 1977, Herzog & Burghardt 1977, Hunt & Watanabe 1982, Vliet 1989, Higgs et al. 2002, Todd 2007, Dinets 2011a, 2011b, Riede et al. 2011), *Alligator sinensis* (Garrick 1975, Wang et al. 2006, 2007, 2009a, 2009b), *Caiman crocodilus* (Wever & Vernon 1957, Maley 1970, Wever 1971, Campbell 1973, Herzog & Burghardt 1977, Hödl 1977, Garrick & Garrick 1978, Smolders & Klinke 1984, Vergne et al. 2012), *Caiman yacare* (Sicuro et al. 2013), *Crocodylus acutus* (Wever 1971, Campbell 1973, Garrick & Lang 1977, Benko & Perc 2009, Dinets 2011b), *Crocodylus johnstoni* (Britton 2001), *Crocodylus niloticus* (Garrick & Lang 1977, Herzog & Burghardt 1977, Vergne et al. 2007, Vergne & Mathevon 2008, Dinets 2011a, 2011b, Vergne et al. 2012), *Crocodylus palustris* (Dinets 2011b), *Crocodylus porosus* (Gramentz 2009), *Crocodylus rhombifer* (Gramentz 2010), *Crocodylus siamensis* (Herzog & Burghardt 1977, Gramentz 2010), *Melanosuchus niger* (Campbell 1973, Dinets 2011b, Vergne et al. 2011, Vergne et al. 2012) and *Osteolaemus tetraspis* (Berger 1924).