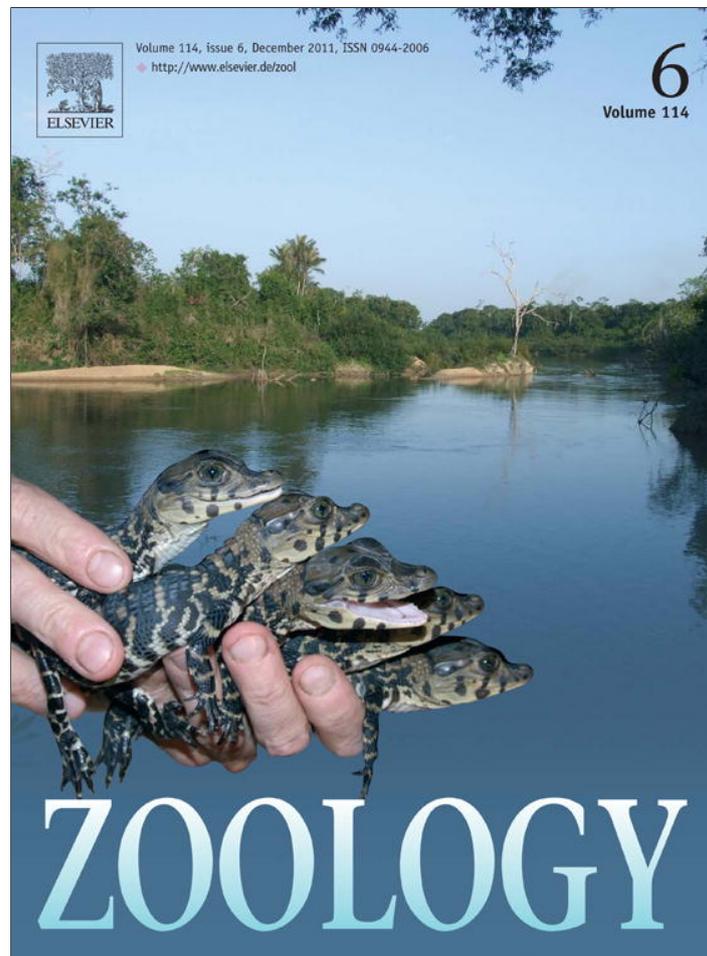


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Acoustic signals of baby black caimans

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ABSTRACT

In spite of the importance of crocodylian vocalizations for the understanding of the evolution of sound communication in Archosauria and due to the small number of experimental investigations, information concerning the vocal world of crocodylians is limited. By studying black caimans *Melanosuchus niger* in their natural habitat, here we supply the experimental evidence that juvenile crocodylians can use a graded sound system in order to elicit adapted behavioral responses from their mother and siblings. By analyzing the acoustic structure of calls emitted in two different situations ('undisturbed context', during which spontaneous calls of juvenile caimans were recorded without perturbing the group, and a simulated 'predator attack', during which calls were recorded while shaking juveniles) and by testing their biological relevance through playback experiments, we reveal the existence of two functionally different types of juvenile calls that produce a different response from the mother and other siblings. Young black caimans can thus modulate the structure of their vocalizations along an acoustic continuum as a function of the emission context. Playback experiments show that both mother and juveniles discriminate between these 'distress' and 'contact' calls. Acoustic communication is thus an important component mediating relationships within family groups in caimans as it is in birds, their archosaurian relatives. Although probably limited, the vocal repertoire of young crocodylians is capable of transmitting the information necessary for allowing siblings and mother to modulate their behavior.

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1. Introduction

Among the possible communication channels, acoustics is widely employed by vertebrates (Sebeok, 1977; Bradbury and Vehrencamp, 1998). Some species are vocal specialists, having developed large repertoires of signals and even cultural transmission, such as songbirds and humans (Marler and Slabbekoorn, 2004). Others, such as amphibians or fishes, use a more limited number of sound signals (Hauser, 1996). Within the polyphyletic group of reptiles, apart from some exceptions such as geckos and tortoises during mating (Galeotti et al., 2005), only crocodylians are known to communicate using vocalizations (Campbell, 1973; Herzog and Burghardt, 1977; Garrick et al., 1982; Britton, 2001; Wang et al., 2009). However, and in spite of its importance for the understanding of the evolution of sound communication, the study of crocodylian vocal communication has been almost completely

neglected (for a review on acoustic communication in crocodylians, see Vergne et al., 2009). Adult crocodylian vocalizations have been reported to occur during courtship and territorial defense (Garrick and Lang, 1977). While still in the egg, calls by the embryo induce the mother to open the nest and help to synchronize hatching (Vergne and Mathevon, 2008). Juveniles also vocalize, emitting a variety of calls that have been named according to their emission contexts, e.g., 'distress' or 'contact' calls (Campbell, 1973; Herzog and Burghardt, 1977; Britton, 2001; Vergne et al., 2007, 2009). However, the acoustic structure and biological function of most crocodylian vocalizations remain largely unknown (Britton, 2001; Vergne et al., 2009).

In the present study, our aim was to investigate the acoustic communication in the black caiman *Melanosuchus niger* after newborns have left the nest and the young crocodylians stay under the protection of their mother. The black caiman belongs to the Alligatoridae family, which includes both alligators and caimans. Although some populations are threatened with extinction, this species remains common in parts of northern South America. As in other species of Alligatoridae and Crocodylidae, the mother–newborn bond is strong in black caimans: mother and

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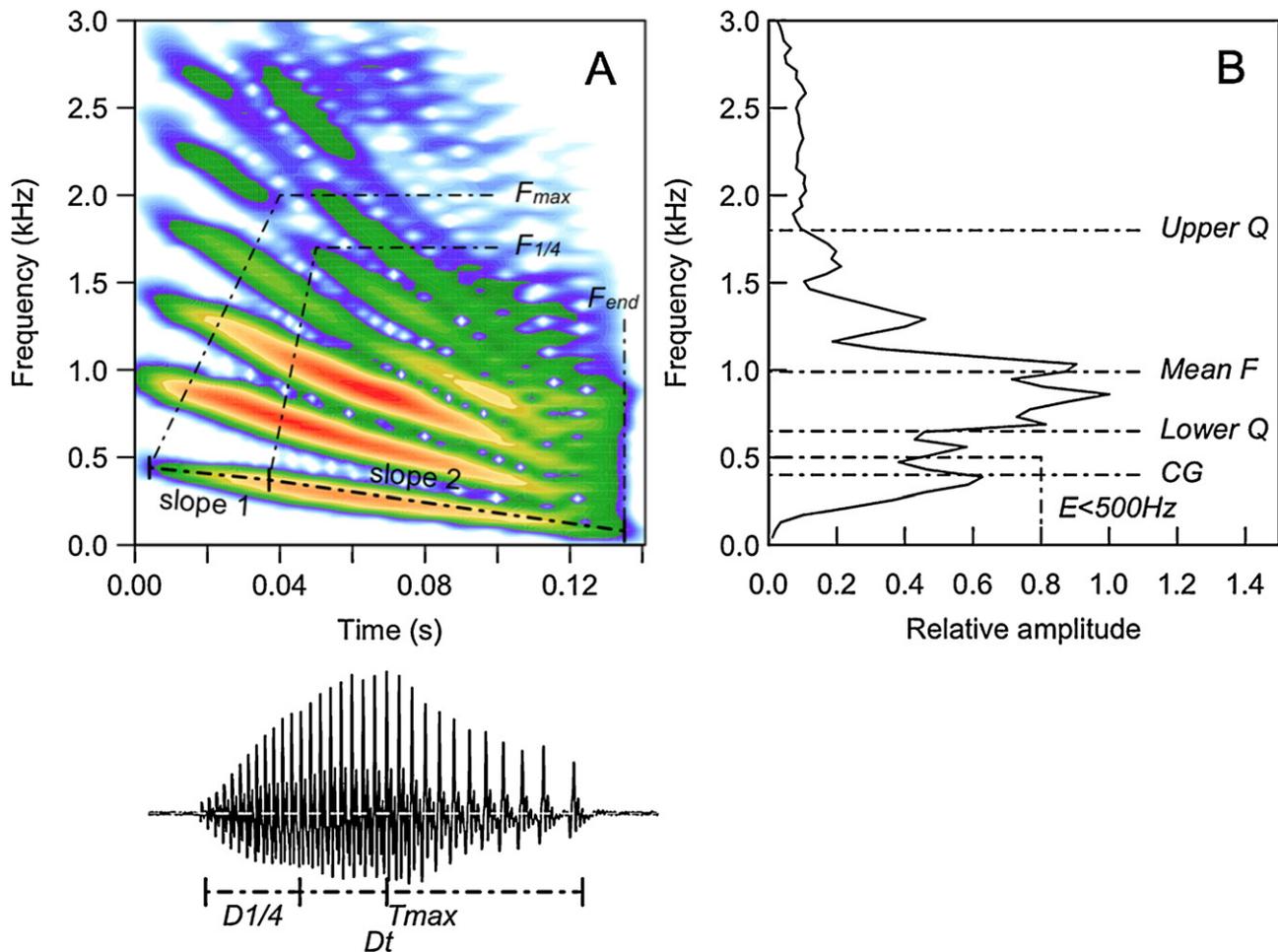


Fig. 1. Acoustic parameters used for the analysis of calls of juvenile black caimans. (A) Spectrogram (above) and oscillogram (below). (B) Frequency spectrum. See Section 2 for details.

juveniles stay close together after hatching. The black caiman is thus a representative model for the study of sound-based information transfer between familial relatives in crocodylians.

Here we provide experimental evidence that juvenile black caimans use graded sounds to target either their siblings or mother, which both respond accordingly. Using sound analysis and playback experiments, we thus show the existence of two functionally different types of juvenile calls.

2. Materials and methods

2.1. Animals and study site

The study was performed in the Rupununi river region (near Yupukari village, Republic of Guyana). In the Rupununi river, family groups of black caimans (an adult female accompanied by 20–30 juveniles, aged 10–30 days) are present along the river and remain sedentary for several weeks after hatching. For sound recordings, we focused on 10 family groups. Playback experiments were performed on 8 out of these 10 groups. The mother stayed in the water at viewing distance (mean distance \pm SD: 35 ± 27 m, min–max: 0–80 m, $N=8$) from her offspring who generally gathered on one bank of the river. Usually, no other adult was present within 200 m of the family group (mean distance between groups \pm SD: 1.37 ± 1.4 km; min–max: 0.2–4.6 km, $N=8$).

2.2. Sound recordings and analysis

To assess the information coded in juvenile vocalizations, we considered two situations: (1) 'undisturbed context', during which spontaneous calls of juvenile caimans were recorded without perturbing the group (with the microphone located at approximately 50 cm from a juvenile); (2) simulation of a 'predator attack', during which calls were recorded while shaking juveniles and pinching their legs or tails, as a natural predator like the jabiru stork, *Jabiru mycteria*, might do. The 10 juveniles to be recorded were captured by hand and kept in the boat for less than 10 min. When recording, one researcher was handling the recorded juvenile while another researcher held the microphone at 50 cm distance from the juvenile. The recorded individual was then released on the river bank. Recordings in the 'undisturbed context' were always made before capturing any individual.

Recordings were made using a Sennheiser ME64 microphone (frequency response = 40–20,000 Hz \pm 2.5 dB; Sennheiser electronic, Wedemark, Germany) connected to a Marantz PMD670 solid state recorder (sampling frequency = 44,100 Hz, frequency response = 0–20,000 Hz \pm 0.5 dB; Marantz, Kanagawa, Japan).

For both 'predator attack' and 'undisturbed context', a total of 100 calls/context was analyzed (one call randomly selected per recorded juvenile; $N=100$ individuals from 10 different familial groups). To describe the calls' structure, 13 acoustic parameters were measured in both temporal and frequency domains using Syntana software (Aubin, 1994), SaslabPro version 4.40 and Praat

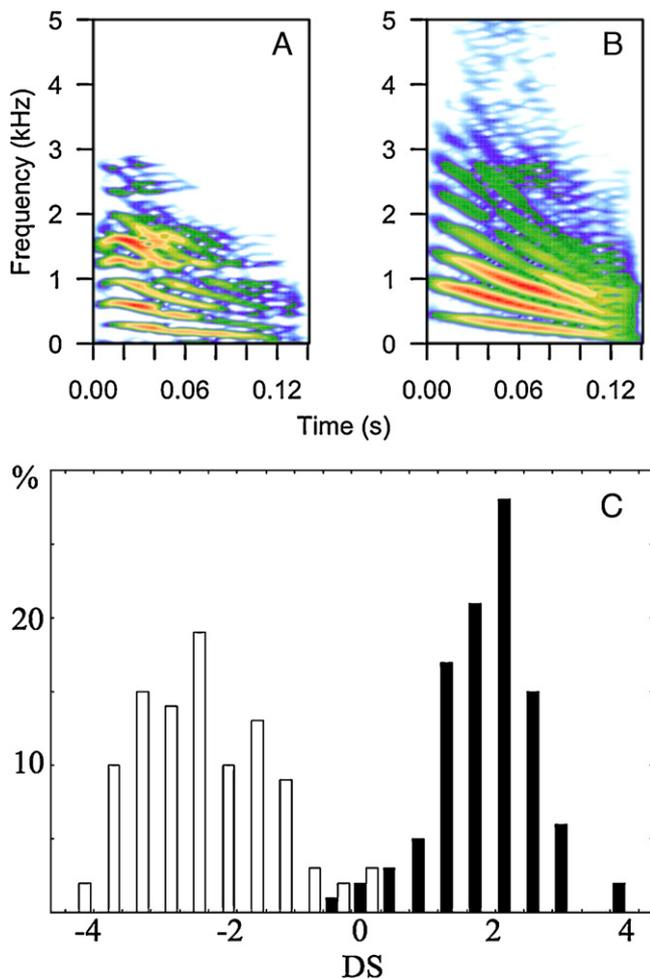


Fig. 2. Comparison of context-dependent calls of juvenile black caimans. (A) Spectrogram of an 'undisturbed context' call. (B) Spectrogram of a 'predator attack' call. (C) Frequency distribution of discriminant scores (DS) as derived from the acoustic analysis of the calls. In dealing with the two recording conditions, the discriminant function analysis assigns one discriminant score to each analyzed sound. We used the discriminant score in which the multivariate variability of calls is collapsed into a single number as a measure of acoustic similarity (Fischer et al., 2001). Calls in the overlapping region are indistinguishable by the analysis. Open bars = 'undisturbed context' calls; filled bars = 'predator attack' calls.

version 4.0.19 (Fig. 1). We performed a spectrographic analysis (window size: 1024) and measured three variables related to the fundamental frequency: the maximal frequency value (F_{\max} , Hz), the frequency value at the first quartile of the call ($F_{1/4}$, Hz), and the final frequency value (F_{end} , Hz). Three temporal variables were measured from the oscillogram: the total duration of the call (D_{t} , s), the temporal position of $F_{1/4}$ ($D_{1/4}$, s), and the time at which the highest amplitude in the calls occurs (T_{max} , expressed as percentage of the total call duration). To describe the frequency modulation, we calculated the slope of the first quartile of the call (slope 1, Hz/s, calculated as $(F_{1/4} - F_{\max})/D_{1/4}$) and the slope of the last three quartiles of the call (slope 2, Hz/s, calculated as $(F_{\text{end}} - F_{1/4})/(D_{\text{tot}} - D_{1/4})$). To describe the spectral energy distribution, six variables were measured from the power spectrum: the lower quartile (lower Q, Hz; 25% of the total energy is below this frequency), the mean frequency (mean F, Hz; 50% of the total energy is below this frequency), the upper quartile (upper Q, Hz; 75% of the total energy is below this frequency), the fraction of the total energy that is allocated below 500 Hz ($E < 500$ Hz, expressed in %), and the center of gravity (CG, Hz; a measure for how high the frequencies in a spectrum are on average).

A discriminant function analysis using the 13 measured acoustic variables and validated by cross-validation provided a classification procedure that assigned each call either to its appropriate emission context (correct assignment) or to the other one (incorrect assignment). For the subsequent analysis of single acoustic variables we used a one-way ANOVA using call context as categorical predictor variable. Statistical analyses were conducted with Statistica version 6 (StatSoft, Tulsa, OK, USA). The spectrograms were realized with the software Seewave R (Sueur et al., 2008).

2.3. Propagation experiments

Series of 'undisturbed context' calls and 'predator attack' calls (1 series = 20 calls; 1 call = 2 s) were broadcasted from a Marantz PMD 670 recorder connected to a 10W amplifier and an Audax loudspeaker placed on the river edge (frequency response of the emission chain varied less than ± 4 dB within the 1–9 kHz range; emission intensity adjusted to the natural intensity of calls: 73 ± 1.5 and 77 ± 1.5 dB for 'undisturbed context' and 'predator attack' calls, respectively, measured at 1 m from the loudspeaker with a SL-4001 sound level meter (Digital Instruments, Tonawanda, NY, USA)). The sounds were recorded through a Sennheiser ME64 microphone, maintained 5 cm above water and connected to a Marantz PMD 670 recorder (transmission distances from the loudspeaker: 1 m (=control), 4, 16, 32, 64, and 128 m). For analysis, we selected the first six replicates of each call that were not masked by transient external noise such as vocalizations of birds, frogs or insects. The selected sounds were then band-pass filtered using sound-specific filter bandwidths that matched the frequency range of each call. For each propagation distance, we also recorded the stationary background noise. The spectrograms, power spectra and amplitude envelopes of the selected propagated signals were averaged for each propagation distance and compared with the 1 m control sounds using Bravais–Pearson product–moment correlations.

2.4. Playback experiments

We tested whether mothers recognized juvenile vocalizations by assessing their behavioral response to the playback of both call types. Each one of 8 caiman females attending their offspring was successively challenged by the playback of three series of calls: 'predator attack', 'undisturbed context' and 'control noise'. Mothers were always silent and motionless during the minute before any test.

We also assessed juveniles' behavior during playback tests to see whether it was affected by the broadcasted signals. As it was not possible to measure the individual response of each juvenile, we recorded movements and vocal activities of the entire group ($N=8$ groups, each comprising 20–30 individuals) and compared them before and during playback tests.

Before playback, the positions of the female and the juveniles were assessed and the loudspeaker was set up on the river bank near the water at 10 m from the juvenile group, with the female on the other side of the loudspeaker. After 20 min, the three experimental series – 'predator attack', 'undisturbed context' and 'control noise' – were played back (30 calls/series; interval between calls = 2 s; duration of series = 1 min on average; interval between two series = 15–25 min to let the mother return to the approximate position she had occupied before the playback; emission intensity adjusted to the natural intensity of calls; order of series balanced across family groups; each family group was challenged only once with each of the three playback series; the 'predator attack' and 'undisturbed context call' stimuli were built from recordings of the juveniles of the tested group). The characteristics of the noise signal were chosen to be in the range of those of 'predator attack' calls (duration = 0.09 s; frequency range = 100–5000 Hz;

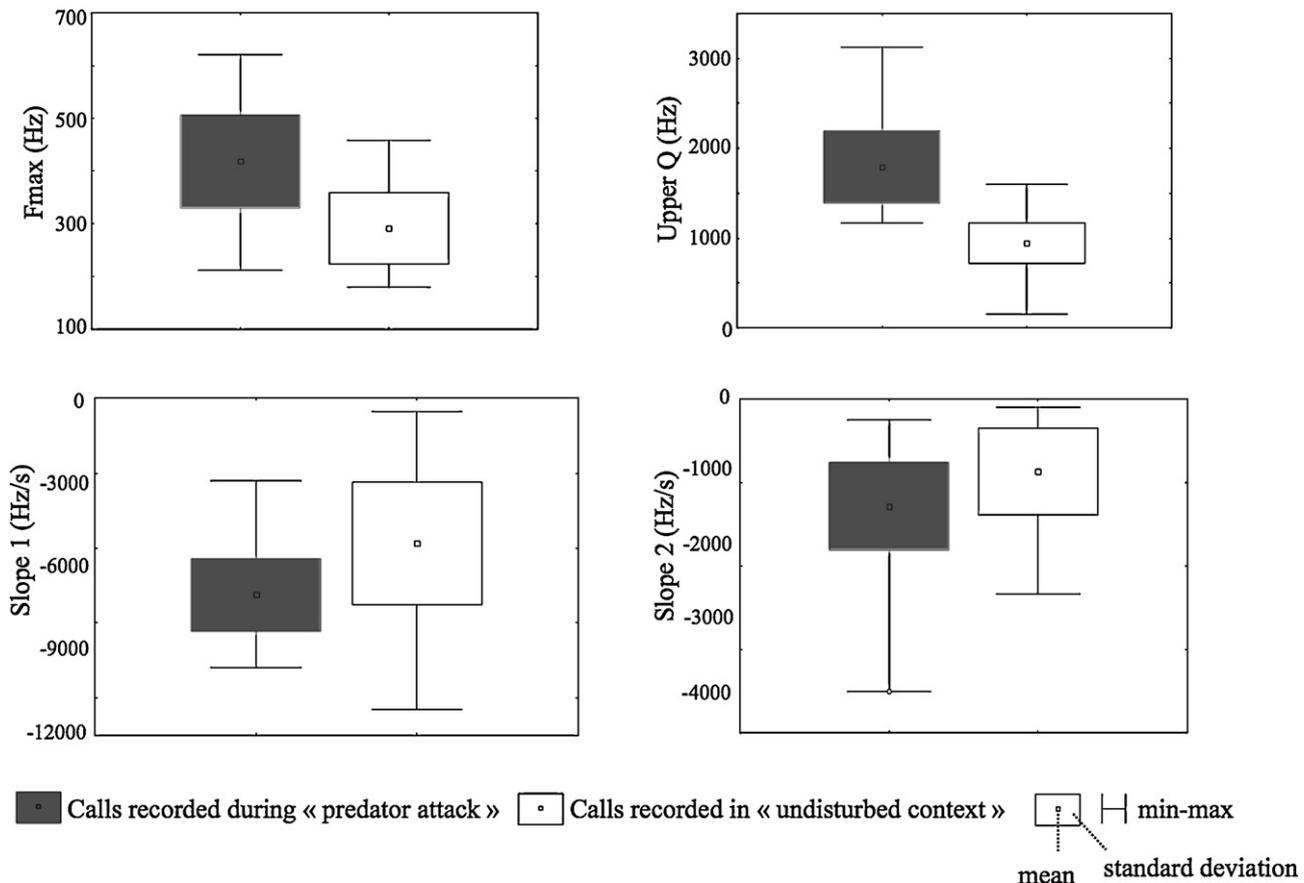


Fig. 3. Examples of acoustic parameters showing the grading between 'predator attack' and 'undisturbed context' calls of juvenile black caimans (mean \pm SD, min–max). F_{max} : maximal frequency (Hz); upper Q: upper quartile (Hz, 50% of the total energy is below this frequency); Slope 1 (Hz/s, frequency modulation slope of the first temporal quartile); Slope 2 (Hz/s, frequency modulation slope of the second temporal quartile).

intensity = 70 ± 2 dB SPL at 1 m). Responses of both the female and the juveniles were assessed by measuring their displacements and the number of vocalizations emitted before and during playbacks. As experiments were carried out at night, the positions of the animals were assessed preceding and following each experimental series by switching on an artificial light for 5 s—a method that appeared more efficient than the use of night-goggles since the eyes reflect light extremely well.

The positions of the mother were compared using a Friedman analysis followed by a post hoc Wilcoxon test for paired samples. The movement of the group of juveniles was assessed according to the following scale: 0 = no displacement, 1 = simple gathering (the individuals were closer to each other after than before the playback but did not approach the loudspeaker), 2 = weak approach (the group was located 5–10 m from the loudspeaker after playback), 3 = strong approach (the group approached to less than 5 m from the loudspeaker). A Friedman analysis followed by a post hoc Wilcoxon test for paired samples was used to compare the displacement response between tests. The number of vocalizations emitted by the juvenile group and the mother was counted 1 min before playback and during playback and compared using a Friedman analysis followed by a post hoc Wilcoxon test for paired samples.

2.5. Ethical note

Experiments were performed under the authorization no. 42-218-0901-38 SV 09 (ENES Lab) and were in agreement with the French and the Guyanese legislations regarding experiments on animals. After the experiments, the animals were monitored to

assess potential deleterious effects of our investigations. Two weeks after the end of the field work the caiman families were still there and no mortality was noticed.

3. Results

3.1. Sound analysis

In both 'predator attack' and 'undisturbed' contexts, caimans produced complex, frequency- and amplitude-modulated sounds with a fundamental frequency associated with several harmonics (Fig. 2; sound files 1 and 2 in the electronic supplement). The discriminant analysis revealed two signal categories that exhibited a transition, with an average correct assignment of 97.5% to the two emission contexts (cross-validated discriminant function analysis, Fig. 2). The vocalizations in the two contexts differed in almost all of the analyzed acoustic parameters. The most decisive differences were spectral cues (Table 1): calls emitted during 'predator attack' were higher pitched than 'undisturbed context' calls (fundamental maximal frequency, $F_{max} = 418 \pm 88$ Hz vs. 292 ± 68 Hz, one-way ANOVA, $F = 128$, $N_1 = N_2 = 100$ calls, $P < 0.0001$; 75% of spectral energy (upper Q) $< 1.79 \pm 0.40$ kHz vs. $< 0.95 \pm 0.22$ kHz, one-way ANOVA, $F = 337$, $N_1 = N_2 = 100$, $P < 0.0001$), and frequency modulation was more pronounced (slope 1 = -2623 ± 486 Hz/s for 'predator attack' calls vs. -1935 ± 819 Hz/s for 'undisturbed context' calls, one-way ANOVA, $F = 52$, $N_1 = N_2 = 100$, $P < 0.0001$; slope 2 = -3851 ± 1572 Hz/s for 'predator attack' calls vs. -2598 ± 1557 Hz/s for 'undisturbed context' calls, one-way ANOVA, $F = 32$, $N_1 = N_2 = 100$ calls, $P < 0.0001$). Each acoustic

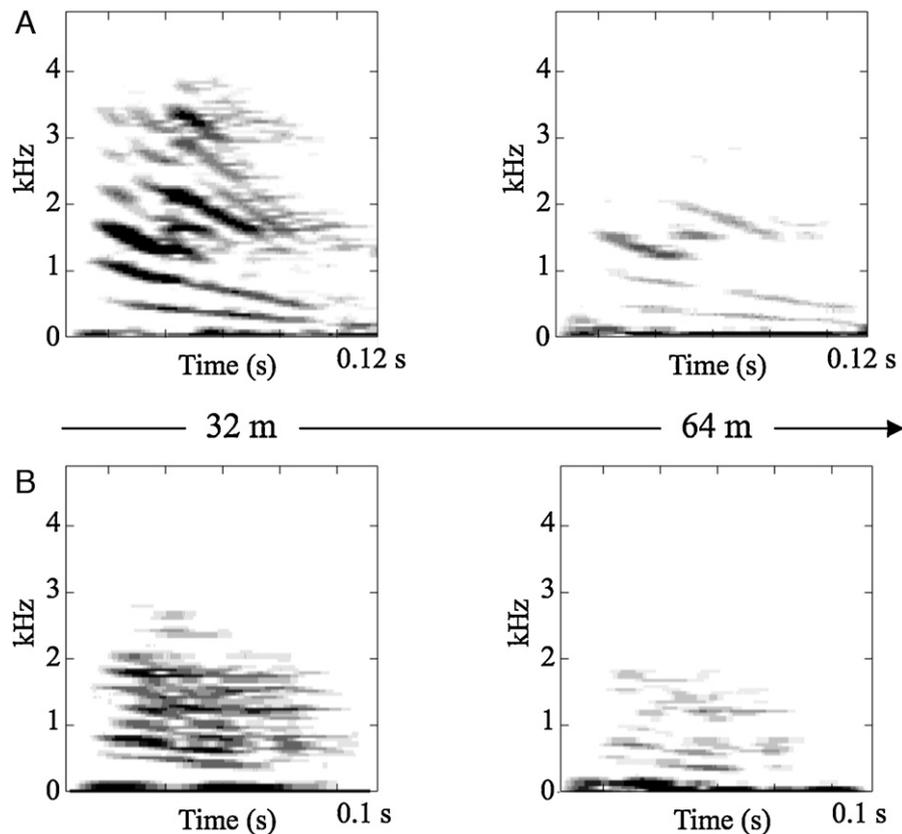


Fig. 4. Spectrograms of propagated caiman sounds. (A) 'Predator attack' call. (B) 'Undisturbed context' call. Both calls are still in the same frequency domain after long-range transmission.

parameter showed a continuum between both call categories (Fig. 3), explaining the transition found by the discriminant analysis. This is typical of a graded vocalization, in which the emitter can encode information by varying the acoustic properties of its signal along a gradient (Marler, 1961).

3.2. Propagation experiments

Results show that the intensity as well as the correlation values of spectrograms, power spectra and amplitude envelopes between propagated and control sounds decreased with distance for both

types of calls (Tables 2 and 3). In terms of intensity, both calls were at the level or below the level of mean background noise (44 ± 2.5 dB) after 32 m of propagation. However, the harmonic structure of both calls seems quite conserved at this distance as shown by correlation values of spectrograms and power spectra (all correlations ≥ 0.66 ; Table 3) and illustrated by spectrograms of the propagated sounds showing the emergence above the background noise in the frequency domain (Fig. 4). Both types of calls thus experience propagation-induced modifications in a comparable way, transmitting well across the water surface, even at a relatively long range (32–64 m).

Table 1

Acoustic parameters of 'undisturbed context' and 'predator attack' calls of juvenile black caimans.

Acoustic parameters	Mean \pm SD		One-way ANOVA	
	Undisturbed context (n = 100)	Predator attack (n = 100)	P	F
F_{\max} (Hz)	292 \pm 68	418 \pm 88	0.00	128
D_t (s)	0.08 \pm 0.09	0.1 \pm 0.02	0.21	1.6
$D_{1/4}$ (s)	0.02 \pm 0.03	0.02 \pm 0.01	0.21	1.6
$F_{1/4}$ (Hz)	246 \pm 54	323 \pm 54	0.00	102
F_{end} (Hz)	144 \pm 37	133 \pm 27	0.00	5.69
Slope 1 (Hz/s)	-1935 \pm 819	-2623 \pm 486	0.00	32.1
Slope 2 (Hz/s)	-2598 \pm 1557	-3851 \pm 1572	0.00	52.2
T_{\max} (%)	38 \pm 32	36 \pm 11	0.52	0.41
CG (Hz)	415 \pm 216	894 \pm 237	0.00	222
Lower Q (Hz)	242 \pm 153	647 \pm 112	0.00	458
Mean F (Hz)	540 \pm 196	988 \pm 277	0.00	174
Upper Q (Hz)	946 \pm 223	1792 \pm 404	0.00	337
$E < 500$ Hz (%)	47 \pm 15	15 \pm 4	0.00	467

3.3. Behavioral responses to signals

While females never responded to the 'control noise', they reacted during both of the other stimuli. The 'predator attack' calls elicited a stronger behavioral response (approach to the loudspeaker: Friedman ANOVA, $N=8$, $F=19.5$, $P<0.016$, post hoc Wilcoxon paired test, $N=8$, $Z=2.52$, $P=0.012$; 4 females out of 8 calling, number of calls: Friedman ANOVA, $N=8$, $F=17.9$, $P<0.031$, post hoc Wilcoxon paired test, $N=8$, $Z=1.83$, $P=0.068$; Fig. 5A and B) than the 'undisturbed context' calls (approach to the loudspeaker: post hoc Wilcoxon paired test, $N=8$, $Z=2.20$, $P=0.028$; only 1 female emitting a single call; Fig. 5A and B).

Control noise as well as 'predator attack' calls never elicited group movements in juveniles, whereas 5 out of the 8 groups moved during playback of 'undisturbed context' calls (Friedman ANOVA, $N=8$, $F=10.0$, $P<0.007$; post hoc Wilcoxon paired test, $N=8$, $Z=2.02$, $P=0.043$; Fig. 5C). Conversely, only 'predator attack' calls elicited a significant increase in juveniles' vocal activity (Friedman ANOVA, $N=8$, $F=16.3$, $P<0.006$; 'predator attack': post hoc

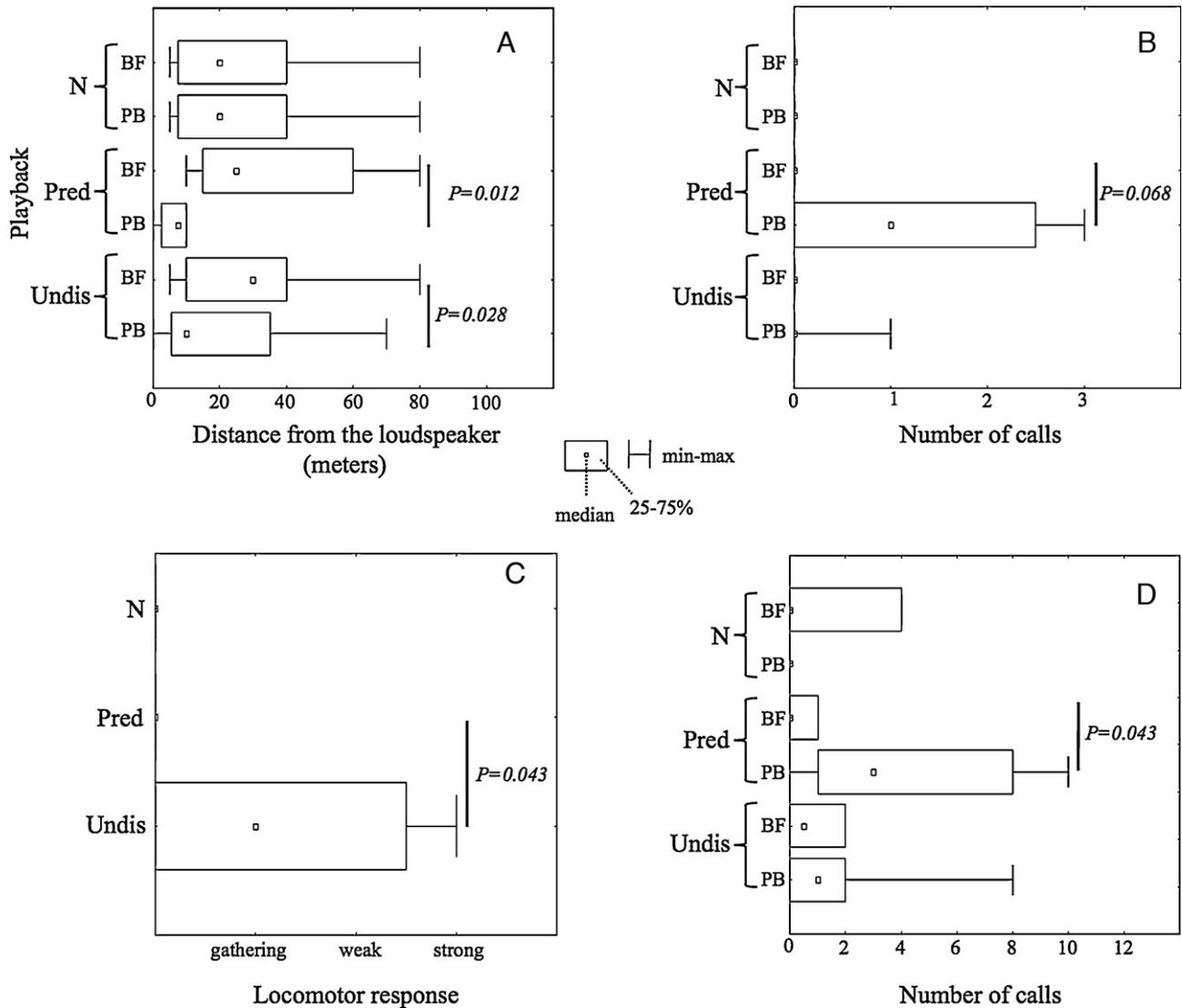


Fig. 5. Behavioral reaction of mother and juveniles to playback of experimental signals. (A) Distance between the tested female and the loudspeaker before (BF) and after playback (PB). (B) Number of female calls emitted during the minute before playback and during playback. (C) Juvenile locomotor response as a result of playback (0 = no displacement, 1 = simple gathering of the individuals, 2 = weak approach to the loudspeaker, 3 = strong approach; before playback, the loudspeaker was set up at 10 m from the juvenile group). (D) Number of juvenile calls emitted during the minute before playback and during playback. Experimental signals: N ('control noise'), Pred (calls recorded in the 'predator attack' context), Undis (calls recorded in the 'undisturbed context').

Table 2

Average intensity of propagated signals in 'undisturbed context' and 'predator attack' calls of juvenile black caimans (mean \pm SD).

Propagation distance	4 m	16 m	32 m	64 m	128 m
'Undisturbed context' calls (N=6)	61 \pm 1 dB	49 \pm 1 dB	43 \pm 1.5 dB	40 \pm 2 dB	41 \pm 3 dB
'Predator attack' calls (N=6)	65 \pm 0.3 dB	53 \pm 1.5 dB	47 \pm 2 dB	42 \pm 3 dB	43 \pm 2.6 dB

Table 3

'Undisturbed context' and 'predator attack' calls of juvenile black caimans. Pearson product–moment correlations (*r* values) between a control signal (recorded at a distance of 1 m from the loudspeaker) and signals propagated at different distances for averaged spectrograms, averaged power spectra and averaged amplitude envelopes (N=6 replicates for each propagation condition).

Propagation distance		4 m	16 m	32 m	64 m	128 m
Spectrogram	'Undisturbed context' calls	0.85	0.89	0.80	0.39	0.10
	'Predator attack' calls	0.90	0.88	0.80	0.49	0.22
Power spectrum	'Undisturbed context' calls	0.91	0.93	0.73	0.73	0.72
	'Predator attack' calls	0.88	0.88	0.66	0.51	0.50
Amplitude envelope	'Undisturbed context' calls	0.62	0.67	0.66	0.51	0.50
	'Predator attack' calls	0.71	0.72	0.57	0.60	0.33

Wilcoxon paired test, $N=6$, $Z=2.02$, $P=0.043$; 'undisturbed context': post hoc Wilcoxon paired test, $N=6$, $Z=0.53$, $P=0.59$, Fig. 5D).

On the basis of the same 13 acoustic parameters as above, the discriminant analysis classified 67% of the calls induced by 'predator attack' playbacks in the 'predator attack' category and the remaining 33% in the 'undisturbed context' category.

4. Discussion

Black caiman juveniles seem to modulate the structure of their vocalizations along an acoustic continuum as a function of the emission context, targeting the receiver. Under stressful conditions, siblings stay motionless and elicit maternal protection with a chorus of 'predator attack' vocalizations. Conversely, in a quiet situation, 'undisturbed context' calls seem mostly directed towards other juveniles, gathering the group. Following the classical denomination of crocodylian vocalizations (Britton, 2001; Vergne et al., 2009), these 'distress' and 'contact' calls thus constitute graded vocalizations that may serve to communicate variations in the sender's motivation, and our playback experiments demonstrated that both mother and juveniles discriminate between them. Although it was already known that young crocodiles emit a repertoire of different calls (Vergne et al., 2009), this is, to our best knowledge, the first experimental demonstration that juveniles of a crocodylian species can emit two functionally different types of calls. It is also the first experimental evidence that crocodylians can change the characteristics of their calls (e.g., the fundamental frequency). Moreover, these vocalizations show all the acoustic features required to facilitate localization of the emitter (slowly frequency-modulated sound with a wide frequency bandwidth and strong amplitude gaps; Aubin and Jouventin, 2002). Together with robust information coding, this may add to the efficiency of the communication within the caiman family group.

It is remarkable that juveniles vocalize in response to 'predator attack' calls emitted by their siblings. This may indicate that the increased potential of group calls to attract the mother's protection makes such group vocalizing beneficial despite potentially increasing the risk of predation. Synchronization of calling behavior between juveniles is well known in numerous bird species when siblings call their parents for food or protection (Wright and Leonard, 2002). In crocodylians, although food begging synchronization between siblings cannot exist since parents do not usually feed their young, our results show that juveniles could beg simultaneously in reaction to a danger, which probably increases the probability of the mother to react and defend the group.

Among acoustic communication systems of vertebrates, two major trends of information coding can be identified. The first is to use a repertoire of a discrete number of sounds that communicate information. Bird song is one example in which information about the sender such as sex, individuality, motivation and various "qualities" may be encoded by the succession of several notes (Marler and Slabbekoorn, 2004). Another example is human language, which is based on recursivity—the use of countless combinations of discrete sound units (Hauser et al., 2002). Besides using discrete sound units, a second trend is to use graded sounds that can be modulated in their acoustic structure by varying their intensity, the distribution of energy among the frequency spectrum and/or their time duration. These two ways of coding information are not mutually exclusive. As we experience in everyday life, the information contained in human words and sentences can be modified by grading acoustic features when speaking, substantially enriching the possibilities of information coding.

Our results show that juvenile black caimans use a simple graded system to encode what may be considered discrete information. One might wonder whether the species has failed to develop – or secondarily lost – the ability to use a repertoire of discrete signals. To answer this question more investigations on the crocodylian acoustic repertoire would be necessary.

Although some controversy persists (Wesolowski, 2004), the presence of parental care in crocodylians and birds is thought to be a homologous trait, derived from the common ancestor (Tullberg et al., 2002). As modern crocodylians stem from terrestrial and possibly endothermic ancestors (Summers, 2005), juvenile vocalizations could have had more functions in extinct species than in extant species (e.g., to signal hunger and thermal state to parents), in line with what is observed in modern birds (Leonard and Horn, 2001). Similarly to many birds, juvenile crocodylians use a call repertoire that supports anti-predator tactic, group cohesion, mother–juvenile localization and parental care. In some bird species, chicks are known to emit various kinds of calls, e.g., begging calls to solicit parental feeding, contact calls to keep in contact with parents and/or siblings, and lost or distress calls when a chick feels lost or threatened. In Tetraonidae, both contact and distress calls are immediately answered by the mother, either vocally or by approaching the young (Del Hoyo et al., 1994). Young ostriches (*Struthio camelus*) also produce distress and fear notes besides contact calls (Cramp et al., 1977). Although a detailed analysis of these calls has yet to be conducted, their acoustic structures differ. In a species like the ostrich, adults can provide effective protection against predators. The parallels to our observations on black caimans are striking. Therefore, it would now be interesting to compare the acoustic structure of the distress calls of bird chicks with that of the juvenile caimans' calls.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.zool.2011.07.003](https://doi.org/10.1016/j.zool.2011.07.003).

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