Table 2. Mean ± S.D. and results of one-way analysis of variance (ANOVA) of acoustic variables of contact and distress calls in the Nile crocodile *Crocodylus niloticus* (five individuals, five calls/individual, 1–2 weeks old). Acoustic variables are defined in Fig. 3. Intensity is measured at 15 cm from the source.

Acoustic parameters	Contact call ($N = 25$)	Distress call ($N = 25$)	F	P
DT (s)	0.195 ± 0.029	0.184 ± 0.031	1.80	0.19
$F0_{max}$ (Hz)	506 ± 115	733 ± 177	28.55	< 0.01
F_{end} (Hz)	211 ± 61	253 ± 61	6.12	0.02
Bandpass	3924 ± 760	8553 ± 1522	185	< 0.01
Slope 1 (Hz/s)	-1292 ± 429	-2024 ± 866	14.38	< 0.01
Slope 2 (Hz/s)	-2225 ± 1536	-4585 ± 3212	10.99	< 0.01
PicF (Hz)	912 ± 138	3564 ± 501	649.65	< 0.01
Intensity (dB)	59.8 ± 5.6	67.4 ± 7.2	12.99	< 0.01

Burghardt, 1977). Besides functioning in group cohesion, Campbell (1973) suggests that crocodilian contact calls may serve to alert group members about environmental features of interest such as the presence of food. Further experiments are clearly required to clarify the biological function(s) of juvenile crocodilian contact calls.

(*c*) *Distress calls*

In the presence of a predator or when seized, juvenile crocodilians emit distress calls that may correspond to the 'screech' given when a bird is held by a predator (Marler & Slabbekoorn, 2004). The acoustic structure of distress calls appears similar to contact and hatching calls: a complex sound with multiple harmonics showing a downsweeping frequency modulation over the duration of the call (Britton, 2001; Fig. 2C). However, there are few published data and authors disagree about the extent to which distress and contact calls differ. It has been shown that distress calls of American alligators have a greater amplitude, and use larger amounts of energy at higher frequencies than contact calls (Herzog & Burghardt, 1977; see also Britton, 2001). Our acoustic measurements on Nile crocodile distress calls (Table 2, Fig. 2C) show that these vocalizations, while having the same overall structure as contact calls, exhibit particular features like more pronounced frequency modulation slopes, a higher pitched energy spectrum (see Bandpass and *PicF* in Table 2) and a greater amplitude (Intensity in Table 2). In some species, including the Nile crocodile (Campbell, 1973; Herzog & Burghardt, 1977; Vergne *et al.*, 2007) and the Australian freshwater crocodile *Crocodylus johnstoni* (Britton, 2001), the frequency-modulated downsweep can be preceded by a frequency-modulated upsweep giving a "circumflex" shape (Fig. 2C). Moreover, young crocodilians are able to modulate the intensity and pitch of their distress calls depending on their mouth aperture (see Section III. 1 for details). Thus, Herzog & Burghardt (1977) differentiated two kinds of distress calls: the "screech", a loud and high pitched vocalization, and the "moan", a more soft and low pitched distress call.

The primary function of distress calls is to solicit the protection of an adult (Britton, 2001; Gorzula, 1978; Romero, 1983; A.L. Vergne, T. Aubin, P. Taylor & N. Mathevon, unpublished data). Since crocodilian pods, at least early in life, consist mostly or entirely of siblings, Staton (1978) suggested that kin selection could act as an evolutionary pressure on the emission of distress calls. It is also possible that acoustic cues are used by the mother for offspring recognition. In numerous species of birds and mammals, parents are able to use acoustic cues to discriminate their young from aliens, this ability is more pronounced in animals living in colonies (Aubin & Jouventin, 2002; Charrier, Mathevon & Jouventin, 2001). In some crocodilians, close nest proximity (Woodward *et al.*, 1984) implies that mixing of juveniles of different clutches occurs. However, a recent study on 0–4 day old juvenile Nile crocodiles found that calls are poorly individualized, making acoustic recognition of hatchlings by their mother unlikely (Vergne *et al.*, 2007). This could be tested experimentally using playback experiments.

In birds, distress calls are known to elicit cross-species responses (Aubin, 1991). In crocodilians different species share a similar repertoire of analogous calls (Britton, 2001) and it is possible that crocodilians also do not restrict their responses to calls from their own species (Campbell, 1973).

(*d*) *Threat calls*

In response to a perceived threat, juveniles occasionally emit hisses or snarls (Britton, 2001). As underlined by Britton (2001), "such behaviour should be more common in larger juveniles than smaller ones and is often accompanied by other aggressive behaviour like inflating the body and lunging toward the threat". The acoustic structure of snarls and hisses is relatively noisy, with no clear harmonic content; they are broadband signals (>15 kHz, Britton, 2001) of highly variable intensity and repetition rate (Fig. 2D). Hissing calls are produced by some hole-nesting birds in response to a predator (Marler & Slabbekoorn, 2004), and these defensive calls are remarkably convincing imitations of a snake.

Britton (2001) separated distress and threat calls from "annoyance calls". These loud and high-pitched vocalizations, heard when juvenile crocodiles are seized, appear distinct from distress calls (larger frequency band, higher peak frequency) and are usually accompanied by aggressive biting behaviour.