

*(b) Adult deep grunts*

After hatching, the mother stays with her juveniles for periods from several weeks to months, depending on the species (Hunt & Watanabe, 1982; Joanen & McNease, 1970; Neill, 1971; Reagan, 2000). During this period, females appear to use deep grunts to attract juveniles (Hunt & Watanabe, 1982; McIlhenny, 1935; Watanabe, 1980). During a recent field trip in Guyana, we observed a black caiman mother emitting a series of deep grunts while moving in water. Her group of young, situated about 20 m away, responded vocally and approached her (A.L. Vergne, T. Aubin, P. Taylor & N. Mathevon, unpublished observations).

Few recordings of deep grunts have been obtained. Garrick *et al.* (1982) recorded a single deep grunt from an adult alligator responding to juvenile contact calls. We recorded two sounds from a mother spectacled caiman in a similar context (Fig. 4B). It can be seen from Fig. 4B that these deep grunts are low-frequency sounds with a complex harmonic structure. Grunt duration is about 100 ms for both the alligator (Garrick *et al.*, 1982) and the spectacled caiman (Fig. 4B). While Garrick *et al.* (1982) described an alligator call with most of the spectral energy concentrated between 50 and 100 Hz, for the spectacled caiman call we found a clear contribution of frequencies at least up to 1 kHz (Fig. 4B). Further recordings and analyses are needed to characterize better this adult vocalization.

*(c) Hisses*

A hiss vocalization is widespread among crocodylians; it has been reported in the Nile crocodile (Cott, 1971), the black caiman (Neill, 1971), the American crocodile (Campbell, 1973), the American alligator (Garrick *et al.*, 1982; Watanabe, 1980), the Australian freshwater crocodile and saltwater crocodile (Britton, 2001) and the Chinese alligator (Wang *et al.*, 2007). This vocalization is used during female nest defence behaviour and territorial interactions among males (Garrick *et al.*, 1982; Neill, 1971). The hiss is characterized by a fundamental frequency below 1 kHz, a poorly defined harmonic structure and a duration of a few seconds (Garrick *et al.*, 1982; Wang *et al.*, 2007). This call seems to be a short-distance signal emitted at rather low intensity (e.g. around 60 dB at 2 m from the source in Chinese alligators; Wang *et al.*, 2007).

*(d) Other calls*

Crocodylians can utter a variety of short-distance signals in social interaction contexts. ‘‘Coughlike’’ calls are emitted by both sexes in the American alligator during pre-copulatory behaviours (Garrick & Lang, 1977). ‘‘Moos’’ in the Chinese alligator have a dominant frequency around 273 Hz and a duration of 1 s (Wang *et al.*, 2007). In response to moos, individuals swim away or submerge. Finally, it has been suggested that Nile crocodiles, American crocodiles, and American alligators produce infrasonic vibrations that pass through the water during courtship (Garrick & Lang, 1977).

**III. PRODUCTION AND DETECTION OF ACOUSTIC SIGNALS****(1) Sound production**

In birds the syrinx is a highly specialized apparatus devoted to the production of acoustic signals. Crocodylians have no specialized vocal organ and the mechanisms underlying sound production are poorly defined. Vocalizations are likely to involve the passage of air through the glottis, with muscles varying tension to control pitch and duration (Britton, 2001; Naifeh *et al.*, 1970).

*(a) The problem of sound production inside the egg*

Crocodylians are able to vocalize a few days before hatching (Lee, 1968; Magnusson, 1980; Vergne & Mathevon, 2008). Air must be present in the lungs at this point as airflow makes the glottis vibrate and thus allows sound production (Naifeh *et al.*, 1970). In birds (Vince, 1969), lung ventilation begins before hatching (up to 67 h pre-hatching in the bobwhite *Colinus virginianus*, and 48 h in the Japanese quail *Coturnix coturnix japonica*), as soon as the embryo has pierced the inner shell membrane. In some cases, e.g. the pied-billed grebe *Podilymbus podiceps*, embryos are able to emit vocalizations while the inner shell membrane is intact (Driver, 1967). True aerial respiration is said to occur only when the outer shell membrane is perforated by the beak (‘‘pipping’’ egg). As crocodylian calls have been heard from unpipped eggs (Britton, 2001; Lee, 1968; Magnusson, 1980), a mechanism allowing lung inflation within the intact egg must exist. Based on observations on saltwater and freshwater crocodiles, Britton (2001) suggested that the embryo could pierce the fibrous inner membrane with the egg tooth (caruncle) in front of its nostril, ‘‘allowing air to enter by inhalation or diffusion through the porous outer mineral layer’’. It is also possible that, as in megapod birds (Booth & Thompson, 1991; Seymour & Ackerman, 1980), the egg progressively loses water during incubation, forming an air bubble beneath the shell membrane and around the albumen (Ferguson, 1982). In the Australian freshwater crocodile (Whitehead, 1987), airspaces can appear between the calcareous shell and shell membranes or between the shell membranes and chorio-allantoic membranes.

*(b) Post-hatching call production*

Crocodylians possess a palatal valve, or gular flap, which is described as ‘‘an extension of the back of the tongue’’ (Britton 2001, Fig. 5A). In addition to preventing water from flooding the throat when the crocodile dives with an open mouth, it may also be used during sound production (Britton, 2001). The position of the palatal valve may be used to modulate the acoustic characteristics of the emitted sounds, for instance in the two forms of the distress calls: ‘‘moan’’ (palatal valve closed) and ‘‘screech’’ (open) (Herzog & Burghardt, 1977). The screech is a louder, higher pitched vocalization compared to the moan; total valve opening probably maximizes the active space of the distress call.