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Water-wave production in the Neotropical frogs *Physalaemus albonotatus* and *Pseudopaludicola mystacalis*: a seismic signal?

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Seismic signals in anuran amphibians may be conveyed either via the soil (Lewis & Narins 1985), plants (Narins 1990), or the water surface (Seidel et al. 2001). Lewis & Narins (1985) provided evidence of seismic communication in *Leptodactylus albilabris*, using geophones for the detection of vibratory waves, and registered the recipient's answer to the wave emission at the same magnitude. This species produces signals by beating the vocal sac against the ground (Lewis & Narins 1985), similar to *Hydrolaetare dantasi* (see Souza & Haddad 2003). Cardoso & Heyer (1991) proposed foot-pounding behaviour as a possible means of seismic signals during aggressive displays in *Leptodactylus syphax*. Seidel (1999), in field observations of *Bombina variegata,* interpreted the rhythmic wave patterns males were creating by strokes of their hind legs as a means of territory demarcation. Seidel et al. (2001) additionally reported on water-wave communication in *Bombina bombina* and *B. orientalis*. Cardoso & Heyer (1991) stated that seismic signalling in frogs may be much more common than currently believed. Furthermore, anurans are sensitive enough to perceive substrate vibrations as low-frequency waves, which are received at the body wall and vonveyed via the opercular system to the inner ear (Lewis et al. 2001).

This paper presents the possibility of intraspecific seismic communication on the water surface in two frog species: *Physalaemus albonotatus* and *Pseudopaludicola mystacalis*. *Physalaemus albonotatus* belongs to the *P. cuvieri* species group (Nascimento et al. 2005) and occurs in Mato Grosso, Mato Grosso do Sul, Brazil, and the Chaco regions of Bolivia and Argentina (Frost 2011). This species is usually found vocalizing on the surface of small puddles (Fig. 1D). During oviposition, couples build foam nests right above the water (Ávila & Ferreira 2004). The advertisement and territorial calls of *P. albonotatus* have been described by Duré et al. (2003). *Pseudopaludicola mystacalis* is a small diurnal frog, which reproduces in shallow water bodies (Diniz-Filho et al. 2004, Gordo & Campos 2003). This species is known from Chapada dos Guimarães, Mato Grosso, Brazil (Frost 2011). In both species, the natural history is poorly know.

Our observations were made in a flooded area of the northern Pantanal, in Poconé (16°29' S, 56°25' W) (*Physalaemus albonotatus*), and in a savannah at Cuiabá (15°19' S, 55°52' W), state of Mato Grosso, Brazil (*Pseudopaludicola mystacalis*).

The vocalization behaviour of *Physalaemus albonotatus* was documented on 28 November 2007, between 18:00 and 19:30 h, with a Nikon D40 camera. During this period, approximately ten individuals of *P. albonotatus* were observed calling in pools at the edge of a large flooded area besides a road. During the observation, a territorial encounter occurred, in which the resident expelled an invader male from its territory, utilizing territorial calls (Fig. 1E) followed by a leap on the invader's head. After that, the invader remained motionless at a distance of 80 cm from the resident.

The behaviour observed in *Physalaemus albonotatus* may be characteristic for many other anuran species vocalizing on the water surface, in which the individual initially takes air into the lungs by substantially enlarging its abdominal region (Fig. 1A). During calling, it contracts the trunk musculature (Fig. 1B) and pushes the air through the larynx into the vocal sac (Fig. 1C). Muscle contraction, as illustrated in Figure 1B, produces a surface vibration, which is propagated in water undulations. These waves potentially create a seismic signal that may reach other individuals. The same phenomenon can be observed in *Physalaemus ephippifer* and *Pleurodema diplolister* in footage submitted by W. Hödl, accessible in AmphibiaWeb (2012).

Water-wave production was also observed in *Pseudopaludicola mystacalis* males at a rivulet in May 2008. During fieldwork, the males were observed striking the water surface with the gular region by inflating the vocal sac with and without sound production. This behaviour produced waves that spread on the water surface. On one occasion, a male changed its body orientation when it received water waves produced by another male at a distance of 70 cm (Fig. 2). The waves apparently convey visual and seismic information and may trigger the recipient to move its body. A similar hypothesis was proposed by Seidel et al. (2001) to explain water-wave communication in the genus *Bombina*.

In a manner similar to *P. mystacalis'* mode of communication, Vliet (1989) demonstrated a comparable behaviour in *Alligator mississippiensis* (Crocodylia: Alligatoridae), which was termed "headslap display" and involved a rapid clapping shut of the jaws as the underside of the head hit the water surface. Vliet (1989) characterized the headslap display as a declaration of presence. *Alligator mississippiensis* also communicate via water waves produced by body vibrations (Vliet 1989). Many species of crocodilians use the water surface as a communication channel, because they are capable of detecting sound in both air and water (Vergne et al. 2009).

In the case of *P. albonotatus*, the signal broadcast on the water may serve to alert conspecific males to the presence of its sender and maybe advertise it to females looking for a reproductive partner. In *P. mystacalis,* the signals travelling on the water surface may help in the spatial orientation of the males within conspecific congregations and probably have a territorial function. Narins (1990) pointed out that the waves produced in seismic communication (or water-wave communication) could be useful for setting up and keeping spacing patterns in a chorus of conspecifics and have an increasing effect on the vocalization rate of the neighbourhood.

Meanwhile, there are basically three physical prerequisites for facilitating seismic communication: (1) presence of a channel through which information-bearing signals can be transmitted, (2) presence of a sender that is able to generate or encode signals and feed them into the channel, and (3) presence of a recipient that is able to extract signal energy from the channel and detect and decode the signals contained therein (Lewis & Narins 1985). The change in body orientation observed in *P. mystacalis* is a cue that may confirm the existence of water-wave communication.

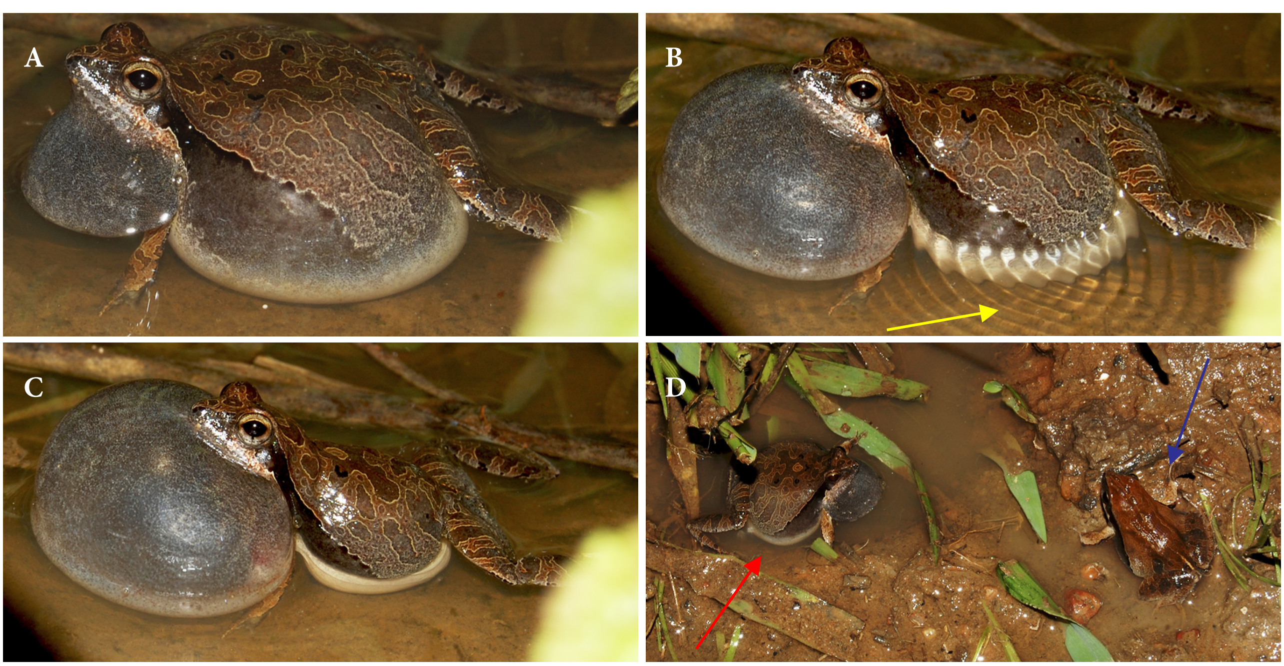

Figure 1. (A) *Physalaemus albonotatus* male from the Pantanal of Poconé-MT with his abdominal cavity inflated. (B) Male contracting the abdominal musculature and pushing air through the larynx into the vocal sac; the yellow arrow points to the water waves produced during the contraction of the abdominal musculature; (C) Male with fully inflated vocal sac during sound production; (D) Territorial interaction between two males: Resident male (red arrow) vocalizing towards an invading male (blue arrow).

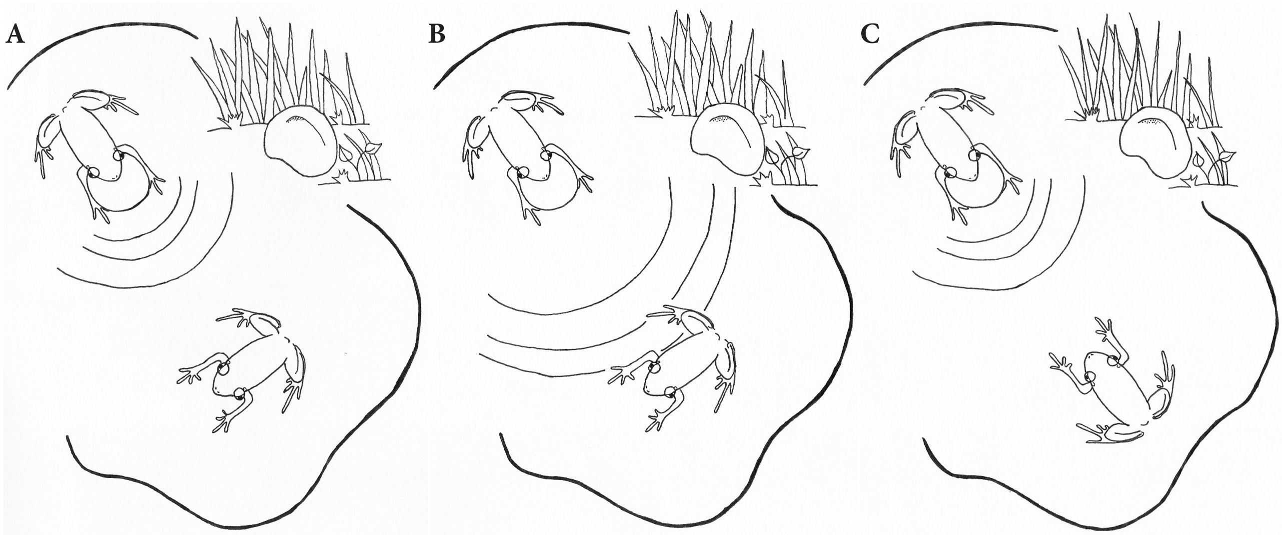

Figure 2. Water-wave communication in *Pseudopaludicola mystacalis*. (A) Water waves are formed without sound production; (B) waves arriving at the recipient; (C) The recipient of the waves immediately changed his body orientation towards the wave-producing individual.

We suppose that the behaviour of producing seismic signals described here represents a potential mode of communication that may be important for terrestrial animals that communicate on the water surface. Such signals can be efficient in "noisy" environments like those charged with acoustic communication from large choruses of reproductive frogs. Seismic signals at the water surface may represent another advantage in that they avoid attracting distant predators that are guided by sound (Narins 1990, Hartmann et al. 2005). However, on the water surface, the emission of waves by male frogs could increase the chance of localisation by aquatic predators (see Haddad & Bastos 1997). Nevertheless, the evolution of this ability seems to be a result of the balance between effective mate attraction, territory establishment, and predation rate on the water surface.

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