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# Electrical signalling of dominance in a wild population of electric fish

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**Animals often use signals to communicate their dominance status and avoid the costs of combat. We investigated whether the frequency of the electric organ discharge (EOD) of the weakly electric fish, *Sternarchorhynchus* sp., signals the dominance status of individuals. We correlated EOD frequency with body size and found a strong positive relationship. We then performed a competition experiment in which we found that higher frequency individuals were dominant over lower frequency ones. Finally, we conducted an electrical playback experiment and found that subjects more readily approached and attacked the stimulus electrodes when they played low-frequency signals than high-frequency ones. We propose that EOD frequency communicates dominance status in this gymnotiform species.**

**Keywords:** communication; dominance; weakly electric fish; *Sternarchorhynchus*

## 1. INTRODUCTION

Aggressive encounters unfolding in combat can incur significant costs for animals. To minimize fighting costs, many species have evolved signalling systems in which the resource-holding potential (RHP; the probability of winning an aggressive contest) of competing individuals is recognizable via specific cues or signals, which allows individuals to gauge the status of conspecifics and not engage in combat with individuals of higher RHP [1]. Such signals have been found in many different animal taxa and sensory modalities (e.g. visual signal in bass [2]; acoustic signal in crickets [3]).

We hypothesized that Amazonian electric knifefish could use electrical signals to indicate their RHP. Weakly electric fish (African mormyriforms and South American gymnotiforms) orient and forage at night in murky tropical waters, using an active electric sense that combines an electric organ in the caudal part of the fish's body with an array of electroreceptors distributed over the fish skin (for reviews see [4]). This system also serves a communication function; various aspects of the electric organ discharge (EOD) of gymnotiforms have been implicated in courtship, aggressive displays, and individual, sex and species recognition [5–10].

In wave-type gymnotiforms, the EOD is a quasi-sinusoidal discharge whose frequency is extremely constant over time [11,12]. Individual fish differ in the frequency of their EOD (EODf; the number of discharges per second). Since laboratory studies have found a positive correlation between body size and EODf in *Apteronotus leptorhynchus* [13,14], and since anecdotal laboratory evidence from two breeding groups suggests that dominant male *A. leptorhynchus* have a higher EODf than subordinates [6], we hypothesized that EODf could signal RHP. We tested this hypothesis in a wild population of the wave-type gymnotiform *Sternarchorhynchus* sp. (Gymnotiformes: Apteronotidae; figure 1*a*) in Peru.

As we predicted, EODf and body size were positively correlated. To test whether EODf was linked to RHP, we performed a competition experiment with pairs of fish in a tank with a single refuge and predicted higher frequency fish to be more successful in controlling the refuge. To verify that the relevant information was carried by EODf and not by some other signal, we performed an electrical playback experiment and hypothesized that the fish would react more aggressively towards low frequencies than high frequencies.

## 2. MATERIAL AND METHODS

### (a) *Field site and subjects*

Fieldwork was conducted at the Panguana Biological Station in the Ucayali region of Peru (S 9°36′80.2″, W 74°56′07.9″) in July–August 2009. The station is located besides the Rio Llullapichis, a shallow clear-water stream (conductivity ≈ 170 $\mu$S cm$^{-1}$, pH ≈ 8.3) with *Sternarchorhynchus* sp. occurring in riffles with a gravel and cobble substrate. Using wire electrodes connected to a mini amplifier-speaker (Radioshack, Fort Worth, TX), we localized and captured fish that we transferred to the station and housed individually in Ziploc bags. After a fish was used in the behavioural experiments described below, we sacrificed it with an overdose of MS-222, measured its length and dissected its gonads. All fish were sexually undifferentiated (even very large individuals), presumably because we worked during the dry season. The specimens were deposited in the collection of the Museo de Historia Natural in Lima.

### (b) *Electrical recordings*

Subjects were transferred to a 30 × 30 × 20 cm tank filled with river water, and the fish's EOD was recorded via silver wire electrodes. The signal was amplified with a DAM 50 differential amplifier (World Precision Instruments, Sarasota, FL, USA) and digitized with a National Instruments (Austin, TX, USA) USB-6211 data-acquisition device at a sampling rate of 40 kHz. We extracted the EODf of each fish by performing a fast-Fourier transform using MATLAB (The Mathworks, Natick, MA, USA). We adjusted the EODf values to a standard temperature of 27°C using a Q10 of 1.62 [15].

### (c) *Dominance trials*

Because gymnotiform fish are nocturnal and hide in refuges during the day, we created a situation of competition for a limited resource by placing, during daytime, two fish in a cooler (80 × 65 × 70 cm) filled with river water and containing a single rock refuge in its centre. For each trial, we randomly selected two fish from the ones temporarily housed at the station (excluding fish smaller than 7 cm, for their lack of aggressiveness) and introduced them at the same time into the cooler, from opposite ends. We filmed the interaction for 20 min using a video-capture device (Pinnacle Systems, Mountain View, CA, USA). We quantified (i) the amount of time each fish spent inside the refuge and (ii) the number of attacks (head-butts) initiated by each fish. We determined a winner and a loser fish (winning being defined as spending more time in the refuge and initiating more attacks) and related the result to the subject's EODf (initially measured after fish capture and temperature-adjusted, as discussed above).

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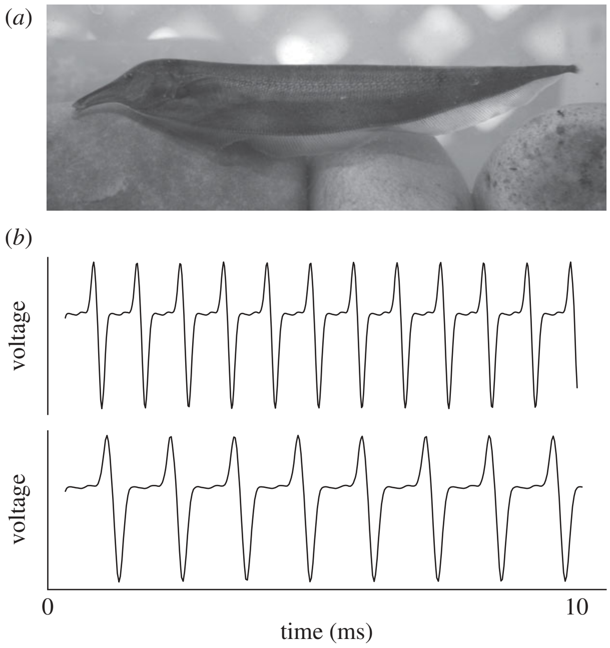

Figure 1. (*a*) *Sternarchorhynchus* sp. from Panguana (photo: Dr Angelika Meschede). (*b*) Voltage trace of two signals illustrating EODf differences between fish (top = 1236 Hz, bottom = 836 Hz).

### (d) ***Playback experiment***

We placed two stimulus electrodes in the middle of the cooler, spaced 12 cm apart (to mimic the presence of another fish), and drew a 16 × 16 cm square area around them (the playback area). A fish was introduced and presented with four 2 min-long stimuli separated by 4 min breaks. The stimuli consisted of a conspecific signal re-sampled (stretched or compressed in time) to create four stimuli of different frequencies corresponding to ±100 and ±50 Hz relative to the fish's own EODf (a Matlab script performed online measurement of the subject's EODf over the course of the experiment to account for possible changes in EODf owing to slight fluctuations in water temperature). All stimuli had the same amplitude and waveform; they differed only in frequency. Stimuli were presented in random order using the output channels of the National Instruments USB-6211 data-acquisition device in conjunction with a custom-made stimulus isolator. We filmed the fish behaviour and quantified the number of headbutts towards the electrodes as well as electrotaxis (the amount of time spent inside the playback area) during each stimulus. One-way repeated-measurement analysis of variances (ANOVAs) and paired *t*-tests were used to compare the responses to the four stimuli. All statistical tests were performed with the free statistical software R (www.r-project.org).

## 3. RESULTS

We collected a total of 45 *Sternarchorhynchus* of varying sizes (range = 3.7–22.9 cm; mean ± s.d. = 10.97 ± 3.74 cm) and EODf (range = 836–1236 Hz; mean ± s.d. = 1019 ± 82 Hz; figure 1*b*). EODf correlated positively with body size ($r^2 = 0.6866$, $t_{45} = 9.7059$, $p < 0.001$; figure 2*a*).

Fish readily fought for access to the rock refuge in the competition experiment. In all cases ($n = 11$), one fish was clearly dominant over the other and the dominance status of the subjects could be attributed unambiguously. Irrespective of the frequency difference between the two subjects, all trials unfolded in the same sequence. First, one of the fish (the dominant one) chased the other fish for a few seconds, after which the dominant fish would occupy the refuge for the remainder of the experiment while the subordinate fish hid in a corner of the tank. In all but one trial, the dominant fish was the one with the higher EODf (figure 2*b*). However, because dominant fish were also bigger than their opponents (electronic supplementary material, table S1), their victory could simply be due to their greater size (which correlates with EODf).

To verify that fish do pay attention to EODf (and not just body size) when assessing an opponent's RHP, we performed playback experiments with stimuli varying only in frequency. Electrotaxis was clearly influenced by the difference in frequency between the fish and the stimulus ($F_{4,44} = 3.3108$, $p = 0.0186$); subjects showed greater electrotaxis towards stimuli lower in frequency than their own EODf (figure 2*c*). Since fish varied greatly in their electrotaxis as well as their headbutt rates, we present in figure 2*c* relative data rather than the absolute data that were used in the ANOVA. Headbutt production was more variable than electrotaxis; only seven out of 12 fish performed any headbutts at all (possibly because of sexual/maturational effects that we were unable to assess). Although the across-stimulus pattern is similar for headbutts and electrotaxis, the ANOVA for headbutts was not significant ($F_{4,44} = 1.2227$, $p = 0.3149$; figure 2*c*).

## 4. DISCUSSION

Our study is the first to report a correlation between body size and EODf in a wild population of apteronotid gymnotiforms. We also found that bigger, higher EODf individuals have a greater RHP (in that case, the capacity to chase away another fish to keep a refuge) and that fish react distinctly to different EODfs, showing more aggressivity towards lower frequencies. Taken together, these results suggest that EODf could signal RHP in *Sternarchorhynchus* sp. We suggest that these fish assess the EODf of conspecifics as a proxy for body size and RHP, and that in a competition context, a fish will attack another one only if the opponent's EODf is smaller than his own.

Other studies of dominance in gymnotiforms have linked RHP with electrical cues but the dominance signals appeared to be frequency or amplitude modulations of the EOD rather than EODf itself [16,17]. The EOD probably serves a RHP signalling function in many gymnotiform species but the specifics of what aspects of the EOD carry the relevant information is likely to vary across taxa.

Previous studies have looked at the relationship between EODf and body size (in *A. leptorhynchus*) but results have proven contradictory [9,13,14,17]. This discrepancy probably arises from the lack of competition and predation in laboratory tanks; low-quality individuals survive and feed as much as high-quality individuals, which should relax the relationship between individual quality and body size and therefore between body size and any indicator of individual quality (i.e. EODf). Our study of a natural population confirms that a correlation between body size and EODf exists in the field, at least for *Sternarchorhynchus* sp., and it suggests an important role of EODf in signalling dominance.

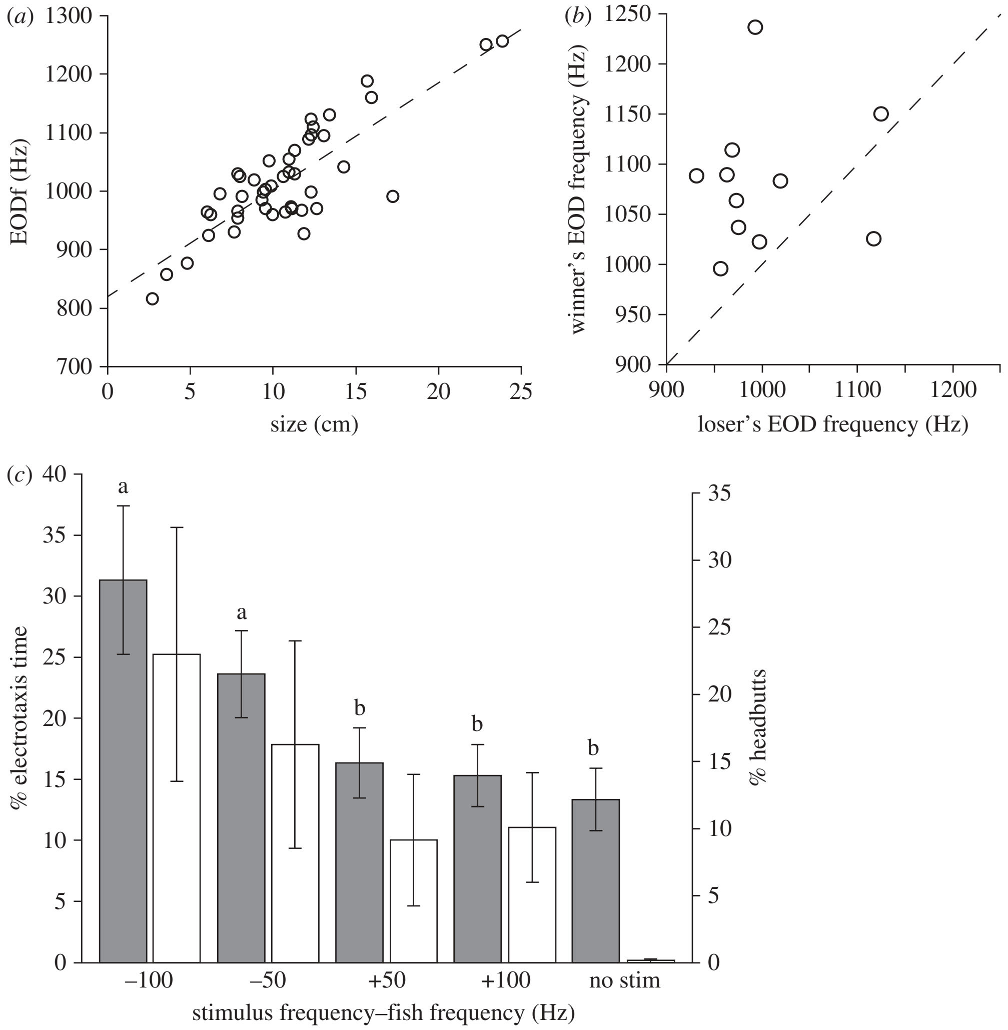

Figure 2. (*a*) Correlation between fish size and EODf. (*b*) Results of the 11 competition trials showing the EODf of the dominant and subordinate fish; the dotted line indicates equal EODf for the two fish. (*c*) Results of the playback experiment showing relative electrotaxis (time spent in playback area during that stimulus/total amount of time spent in playback area during the entire experiment × 100, grey bars) and headbutting (number of headbutts initiated during that stimulus/total number of headbutts performed during the entire experiment × 100, white bars) in response to stimuli of different frequencies. Error bar = s.e.m. Small letters above bars indicate significant differences between groups at $p < 0.05$ (one-sided post hoc *t*-tests).

All animal manipulations were approved by the animal care committee of McGill University and the Peruvian Ministerio de la Producción.

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