



Agonistic sounds signal male quality in the Lusitanian toadfish



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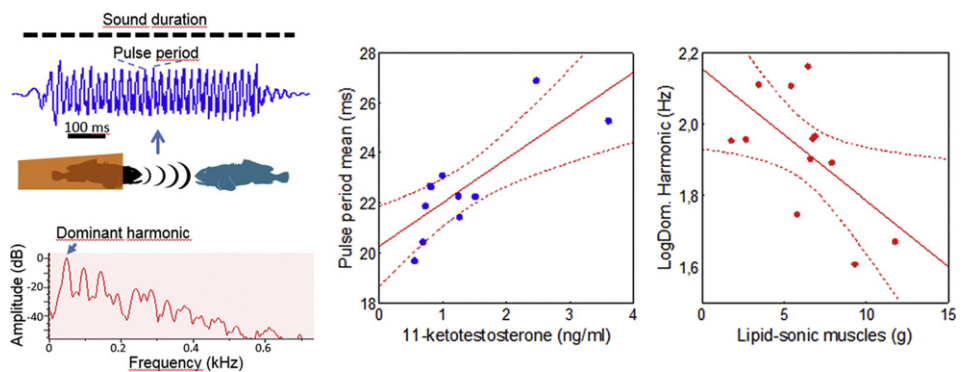
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HIGHLIGHTS

- Acoustic communication during agonistic behaviour is widespread in fishes.
- Breeding Lusitanian toadfish males defend nests from intruders with sounds.
- Low fundamental frequency (high mean pulse period) reflected high androgen levels.
- The dominant harmonic frequency decreased with sonic muscle lipid content.
- Spectral content of fish sounds signal male traits that are key to fight outcome.

GRAPHICAL ABSTRACT



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ABSTRACT

Acoustic communication during agonistic behaviour is widespread in fishes. Yet, compared to other taxa, little is known on the information content of fish agonistic calls and their effect on territorial defence. Lusitanian toadfish males (*Halobatrachus didactylus*) are highly territorial during the breeding season and use sounds (boatwhistles, BW) to defend nests from intruders. BW present most energy in either the fundamental frequency, set by the contraction rate of the sonic muscles attached to the swimbladder, or in the harmonics, which are multiples of the fundamental frequency. Here we investigated if temporal and spectral features of BW produced during territorial defence reflect aspects of male quality that may be important in resolving disputes. We found that higher mean pulse period (i.e. lower fundamental frequency) reflected higher levels of 11-ketotestosterone (11KT), the main teleost androgen which, in turn, was significantly related with male condition (relative body mass and glycogen content). BW dominant harmonic mean and variability decreased with sonic muscle lipid content. We found no association between BW duration and male quality. Taken together, these results suggest that the spectral content of fish agonistic sounds may signal male features that are key in fight outcome.

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1. Introduction

Animals' interactions, such as conflicts over limited resources, are mediated by the exchange of signals that provide information for adaptive decision making [1]. Territorial defence is often a key component of an individual's fitness and includes both signalling territorial ownership

and chasing away intruders. In this context, signals should provide species/sex-specific information to inform potential intruders of the owner's presence on site, and also provide information on fighting ability and motivation for territorial confrontations [1]. Hence, information content of territorial signals is expected to depend on whether a signal serves only for territorial ownership advertisement, to reveal the sender's quality and motivation, or both [1].

Multiple studies show that vocalizations can influence the resolution of contests as they reflect the sender's body size or condition (e.g. [2–4]). For example, low frequency vocalizations may give a reliable indication of a large body size and deter potential attackers [2] or, in the case of humans, influence the perception of leadership capacity [5]. In fish, the largest group of vertebrates exhibiting widespread evolution of sound production [6], acoustic signals are often produced during contests, including territorial defence [7]. In this taxon there is evidence for salient information content in the temporal pattern of sound pulses [6]. In addition, there is a strong selection pressure favouring complexity in the spectro-temporal content of vocal signals [8]. Surprisingly, little is known on whether temporal and spectral features of agonistic calls reflect the sender's quality and affect territorial defence (e.g. [7,9,10]). Importantly, while it has been shown that in some fishes larger individuals produce longer, louder and lower frequency agonistic sounds [11–14], few studies have provided an integrative view on how agonistic sounds reflect multiple aspects of male quality such as physical and physiologic features.

Fishes from the Batrachoididae family have become a key neuroethological model for studying acoustic communication in vertebrates because mate attraction and territorial defence in these fishes rely heavily on acoustic signalling [15–17]. While mating advertisement calls (boatwhistles and hums) produced by batrachoidid nest-holders have been also implied in signalling territorial ownership and in spacing out individuals [9,16,18], grunts are considered the main agonistic call [8, 15]. Within this family, Lusitanian toadfish (*Halobatrachus didactylus*) males mainly defend their nests with agonistic boatwhistles (BW) that are similar to mating advertisement BW except for presenting lower dominant frequencies and weaker amplitude modulation [16]. As BW have shown to be rather complex signals [8] they render the opportunity to assess the salience of relevant sound features for territorial defence in teleosts. Typically, BW are relatively long multiharmonic signals wherein the fundamental frequency is determined by the firing rate of the vocal-acoustic neural network that drives the contraction rate of the paired sonic muscles attached to the swimbladder [10].

Here we relate spectral and temporal features of the agonistic BW with Lusitanian toadfish male quality, including biometric, condition, and physiological features. We predict that BW acoustic features convey information on male quality including energetic reserves and hormonal status which influence the outcome of contest behaviour [19].

2. Methods

2.1. Subject males and maintenance

The Lusitanian toadfish, like other batrachoidids, has two fixed male reproductive phenotypes that differ in a suite of morphological and neuroendocrine traits [10,20]. Type I males nest under rocks or in crevices, are territorial, vocalize to attract mates and provide parental care to the eggs in the nest. In contrast, Type II males are not territorial and sneak fertilizations [20].

We captured territorial males that spontaneously occupied artificial concrete shelters placed in the lower intertidal of the Tagus River estuary (Military Air Force Base 6, Montijo, Portugal; 38° 42'N; 8° 58'W). Fish use these shelters as nests during the breeding season that spans from May to July in Portugal (e.g. [17]). We used plastic round swimming-pools (2.5 m diameter, 0.5 m water depth) as stock and experimental tanks. Tanks were placed on the sand just above the high tide shoreline, near the collection area and under a shadow net cover

held 170 cm high to prevent excessive solar radiation and water heating. Water temperature varied in all tanks from 18 to 26 °C (mean = 21.4 °C), within the range of the estuary water temperature variation during the same period. Tank water was renewed every 2–3 days, by pumping directly from the estuary. A natural light cycle was maintained as tanks were outdoors.

2.2. Territorial experiments

We carried out territorial intrusion experiments following Vasconcelos et al. [16]. Briefly, 24 h before trials two subject males were placed in an experimental tank provided with two roof tiles (internal dimensions 44 cm × 18 cm × 10 cm) placed 50 cm apart and 20 cm away from the tank's border. In each 1 h trial, two intruder males were placed sequentially in the experimental tank, one at the start of the trial and the second 30 min after, both remaining in the tank until the end of the trial (Supplementary material, Video 1). This experimental design resembles the natural chorusing aggregations, where territorial males nest close together [21] and may sequentially attract competitor males [17]. Visual and acoustic behaviours were monitored during trials and noted in detail on paper. Fish were marked with small cuts between the fin rays to ensure their identity. Marking did not cause any measurable change in the fish behaviour. Fish were never used in more than one trial.

We placed one hydrophone (High Tech 94 SSO, High Tech Inc., Gulfport, MS, USA; frequency response: 30 Hz to 6 kHz ± 1 dB; voltage sensitivity: –165 dB re. 1 V/μPa) in front of each nest, at about 10 cm from its entrance and from the tank bottom, attached to a wooden rod kept over the tank. Simultaneous two channel recordings were made with a USB audio capture device (Edirol UA-25, Roland, Osaka, Japan; 16 bit, 44.1 kHz acquisition rate per channel) connected to a laptop and down-sampled to 6 kHz by Adobe Audition 3.0 (Adobe Systems, San José, CA, USA). Recorded sounds could be attributed to a particular territorial male (henceforth named nest-holder) due to the close proximity of each hydrophone to one nest. Also, in the course of similar experiments (e.g. [16]) we have observed that only nest-holders produce sounds. In one exception (unpublished data), the intruder entered the nest and also made BW but these could clearly be distinguished from the nest-holder's sounds due to spectral differences.

At the end of the 19 trials, residents ($n = 38$) and intruders ($n = 34$) that engaged in social interactions were measured to the nearest mm for total length (TL) and to the nearest g for total body mass (M). Note that in four trials one of the intruders did not interact with nest-holders. Residents measured mean ± sd (range) 42.0 ± 3.0 (37.5–49.5) cm in TL and intruders 36.9 ± 2.7 (30.0–42.0) cm in TL. Residents produced on average 4.7 ± 5.9 (range: 0–22, mode = 1) BW during trials.

For this study we only considered resident males that made at least 4 BW ($n = 14$; note that one male only had 2 BW suitable for analysis). These nest-holders made an average of 10.4 ± 6.4 (4–22) BW during a 1 h trial. All resident males not used for sound analysis and the intruders were returned to the estuary after trials. Territorial males that made fewer than 4 BW did not differ in TL from more vocal males (t test, $p > 0.05$). They likely made fewer sounds because they experienced fewer interactions with intruders than the males that were more vocal ($t = 3.34$, d.f. = 36, $p < 0.01$, mean no. of interactions = 4.9 vs. 2.8 for more vocal vs. less vocal fish).

The 14 males used to relate sounds with male quality averaged 41.9 ± 1.8 (39.3–46.0) cm in TL and 1221 ± 199 (970–1600) g in M. Immediately after the end of trials, these males were sacrificed with an excessive dosage of MS222 (tricaine methane sulphonate; Pharmaq, Norway) buffered (1:1) with sodium bicarbonate. Blood samples were collected from the caudal vein in heparinized syringes within 4 min from first handling of the fish. Plasma samples were subsequently separated by centrifugation (6000 rpm for 5 min) on site and stored on ice until taken to the lab, where they were stored at –20 °C until steroid quantification. Following blood sampling, males were immediately

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