



Reproductive success in the Lusitanian toadfish: Influence of calling activity, male quality and experimental design



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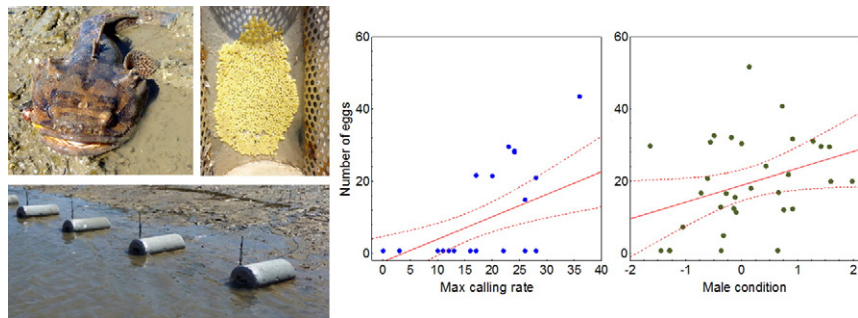
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HIGHLIGHTS

- Vocalizing is needed for successful mating in Lusitanian toadfish.
- Both male vocal activity and condition impacted male breeding outcome.
- Relative effect of these male traits may depend on mate choice costs.

GRAPHICAL ABSTRACT



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ABSTRACT

Acoustic signals are sexual ornaments with an established role on mate choice in several taxa, but not in fish. Recent studies have suggested that fish vocal activity may signal male quality and influence male's reproductive success but experimental evidence is lacking. Here we made two experiments to test the hypothesis that vocal activity is essential for male breeding success in a highly vocal fish, the Lusitanian toadfish. We first compared the reproduction success between muted and vocal males. In a second experiment we related male reproduction success with acoustic activity and male quality, including biometric, condition and physiological features. As a proxy for reproductive success we tallied both total number and number of sired eggs, which were correlated. Muting experiments showed that successful mating was dependent on vocalizing. In addition, the number of eggs was positively associated with the male's maximum calling rate. In the second experiment male's reproductive success was positively associated with male condition and negatively related with circulating androgen levels and relative gonad mass, but was not associated with vocal activity. Differences in results may be related with nest design which could have influenced mate choice costs and intra-sexual competition. In the muting experiment nests had a small opening that restrained the large nest-holder but allowed smaller fish, such as females, to pass while in the second experiment fish could move freely. These experiments suggest that a combination of factors, including vocal activity, influence reproductive success in this highly vocal species.

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1. Introduction

Mating signals are well-known for their positive influence on mating success [7]. Advertisement signals, such as bird, anuran and insect songs or calls, are usually long ranging and convey information on species and sex identity, sexual motivation and location [12,23]. In several species these signals are also involved in competitive mate-attraction and courtship. Thus, not only they include stereotyped elements to provide unambiguous information on species identity but also contain dynamic features related to mate quality and motivation relevant for mate assessment [9,22]. Display rate and display performance quality are highly dynamic and provide a basis for mate choice in several taxa [23,45]. Mate preference for vigorous displays is widespread as it often reflects male condition or health [16], and is associated with both direct (e.g. higher egg fertilization rates, [52]) and indirect benefits (e.g. higher rate of offspring survival, [24]) for females.

Acoustic signals are sexual selected traits with an established role on female mating decisions in several taxa, including birds, anurans and insects [12,23]. It is becoming accepted that fish mating sounds act also as sexual ornaments subject to sexual selection as in other taxa [6]. However, there is limited evidence of which acoustic features are under mate choice in teleost fish [4,31,32,35,50]. Recent studies have pointed that calling rate may be salient to male's reproductive success in fish with parental care [5,40,49]. In one-choice laboratory experiments painted goby males that exhibited high calling rates were more likely to mate than less vocal males [5]. In damselfish, calling rate was positively correlated with male mating success measured by the number of clutches per breeding cycle [40]. In the Lusitanian toadfish maximum calling rate and the percentage of time spent calling (calling effort) were the best predictors of the number of eggs found in a male's nest [49]. In these three studies silent fish did not succeed in mating suggesting that acoustic activity is key to male reproductive success. However, both in the painted goby and in the Lusitanian toadfish vocal males could fail to obtain clutches suggesting that other factors may be at play during mating decisions. In some species, such as in nest-holding fish, females may enter the male's nest lured by its acoustic signals and only there assess other male traits (e.g. chemical cues) that will also contribute to spawning decisions.

In this study we tested the hypothesis that calling activity is essential for male Lusitanian toadfish breeding success with two field experiments. In the first experiment we compared the reproduction success between muted and vocal males using two controls, sham-operated and intact males. This experiment followed the design of Vasconcelos et al. [49] where all males were restrained in their nests with a mesh that presented an opening allowing the females to enter and spawn but that prevented the larger subject males from escaping. In a second experiment we assumed a more natural setup where males could move freely in the breeding area and we related male reproduction success with several measures of male quality including biometric, condition and physiological features. We tallied both the total number of obtained eggs and the number of sired eggs as a proxy for male reproductive success.

2. Methods

2.1. Study model

Similar to other species of the family Batrachoididae the Lusitanian toadfish has two fixed male reproductive phenotypes that differ in a suite of morphological and neuroendocrine traits [30,34]. Larger type I males nest under rocks or in crevices in shallow water, are territorial, vocalize to attract mates and provide parental care to the eggs in the nest. In contrast, smaller type II males are not territorial and sneak fertilizations [34]. Females are smaller than type I males and lay only a few hundreds of large eggs in a single batch per breeding season [34].

2.2. Study site

Experiments took place during the Lusitanian toadfish breeding season (May to July 2012 and 2013) in an intertidal area of the Tagus estuary (Air Force Base no. 6, Montijo, Portugal; 38°42'N, 8°58'W).

2.3. Muting experiments

We deployed 16 artificial concrete hemicylindrical nests, capped at one end, in one row parallel to the shoreline (Fig. 1a). Nests were kept evenly spaced (every 2 m). These nests were usually submersed and only exposed to air at spring low tides, approximately every fortnight. Subject males were collected from similar nests deployed nearby and readily occupied by territorial (type I) males. Each fortnight 16 males were randomly assigned to treatment groups (muted, sham-operated and intact) and restrained in the concrete nests in the estuary. Males were restrained by covering the nest entrance with a stainless steel mesh with an opening large enough to allow small prey (e.g. crabs) or females to enter and spawn but that prevented the larger subject males from escaping (Fig. 1b). Males subjected to surgery (muted and sham) were anaesthetized in a 0.01% ethyl p-aminobenzoate (benzocaine; ALFA AESAR, Germany) salt water bath for a few minutes. Muting was achieved by cutting a small portion of the swimbladder wall and deflating it (Fig. 1c). The abdominal opening was then closed with a couple of stitches and fish were allowed to recover from anaesthesia. This procedure prevented audible sound production but did not affect the activation of the sonic muscles. To control for possible effects of the surgery (apart from the ability to vocalize) sham males were similarly operated but the swimbladder was left intact. After recovery from the surgery these males were still able to vocalize normally (see [15]). A removable plastic sheet lined the internal nest surface easily allowing photographing any eggs laid by females at the end of the recording period (in the subsequent spring tide). Egg sheets were labelled and transferred to the lab for further development needed for paternity assessment (see below). Males were measured to the nearest mm for total length (TL) and to the nearest g for total body mass (M).

We used a total of 11 muted, 11 sham and 9 intact males. Males averaged 41.1 cm (range, 35.7–49.0 cm) in TL and 1267 g (910–1885 g) in M. Males from different groups did not differ in TL (ANOVA, $F_{2,27} = 0.49$, $p > 0.05$) or M ($F_{2,27} = 0.09$, $p > 0.05$).

2.4. Open-nest experiments

In a second experiment (2013) we deployed in the same location 27 artificial concrete nests every 2 m in two rows, also internally lined with a removable plastic sheet. Nests were similar to the ones used in the previous experiment except from the absence of the restraining mesh at the opening of the nest. Subject males occupied spontaneously the nests during the submersion period and could move freely throughout recordings. Every fortnight, when nests were exposed, they were inspected for occupation and the presence of egg clutches. Plastic sheets with eggs were photographed, labelled and transferred to the lab for further development needed for paternity assessment (see below). Subject males were removed from the nests, anaesthetised in a salt water bath with tricaine methane sulphonate (MS222; PHARMAQ, Norway) buffered (1:1) with sodium bicarbonate, and a blood sample was collected from the caudal vein for steroid quantification (see below). Following blood sampling fish were immediately sacrificed with an excessive dosage of MS222 and dissected. Samples of body muscle (epaxial muscle fibres), sonic muscle and liver were taken and were immediately placed in ice and in dry ice until stored in the lab at $-20\text{ }^{\circ}\text{C}$ and $-80\text{ }^{\circ}\text{C}$ for subsequent quantification of lipid and glycogen content, respectively. Fish were measured to the nearest mm for TL and to the nearest g for M. The mass of the gonads (M_G), the liver (M_L), and the sonic muscles (M_{SM}) were weighed to the nearest mg, while the eviscerated body mass was tallied to the nearest g (M_E). A total of 33

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