Journal of Experimental Marine Biology and Ecology 456 (2014) 65–69

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Reproductive success in the Lusitanian toadfish *Halobatrachus didactylus*: Influence of male and nest sizes

Rita Carriço [a,*], M. Clara P. Amorim [b], Paulo J. Fonseca [a]

[a] *Departamento de Biologia Animal, Centro de Biologia Ambiental, Faculdade de Ciências da Universidade de Lisboa, Bloco C2, Campo Grande, 1749-016 Lisbon, Portugal*
[b] *Unidade de Investigação em Eco-Etologia, I.S.P.A., Instituto Universitário, Rua Jardim do Tabaco 34, 1149-041 Lisbon, Portugal*

ARTICLE INFO

Article history:
Received 11 December 2013
Received in revised form 14 March 2014
Accepted 17 March 2014
Available online 13 April 2014

Keywords:
Batrachoididae
Breeding success
Male size
Nest area
Nest selection
Teleost fish

ABSTRACT

Male reproductive success often depends on male attributes and resource quality. Here, we examined male preference for nest size in the Lusitanian toadfish, a nest-guarding fish with parental care. We also investigated the combined effect of male length and nest size in male breeding success. Approximately 80 shelters with five different sizes were placed on an intertidal zone of the Tagus estuary. Nests were checked every fortnight at spring low tides for occupation, nest-holder length, and number of eggs. Males did not select for the larger nests despite their availability but showed size assortative nest choice. Only nest size was a significant predictor of clutch size in occupied nests and it explained 60% of the variability in the number of obtained eggs. Male length and the interaction of male length and nest size did not have a significant effect on male reproductive success. These results suggest that although nest size is key to male's reproductive success, the choice for nest size results from a trade-off between accrued costs of offspring care or risk of a nest take-over and possible benefits of increased fitness.

1. Introduction

Females are usually the choosy sex and select mates to maximise their breeding success (Andersson, 1994). Female choice can be driven by the quality of resources on offer, such as nuptial gifts and male territory quality (Grafen, 1990; Lehtonen et al., 2007), or by physical and behavioural male attributes associated with indirect benefits that increase the fitness of the offspring (Candolin and Voigt, 2001; Oliveira et al., 2000). In species with paternal care, such as in teleost fish where paternal care is common (Gross and Sargent, 1985), females are expected to choose both the quality of nests where they deposit the eggs and male quality traits that can affect their fitness (Lehtonen et al., 2007; Lindström, 1988). For example, some nests may be less prone to predation (Lindström and Ranta, 1992) or more likely to receive more care by the male (Pampoulie et al., 2004). For example, larger nests can contain more clutches and increased egg numbers are also predicted to increase a male's investment in his current reproduction (Gross and Sargent, 1985). Also, male traits such as size and condition are related to paternal ability and determinant for nest tenure and enhanced protection to the offspring (Lehtonen et al., 2007; Lindström, 1988).

On the other hand, males will compete for access to resources that are required for breeding (Andersson, 1994). In fish that reproduce in nests, the size of the nest can limit the number of clutches the male is able to receive and thus limit his reproductive success (DeMartini, 1988; Lindström, 1992). In this context, it should be expected that males compete for larger nest sites which can hold more eggs (Wong et al., 2008). However, even if it is an obvious constraint on own reproductive success males may not choose the best resource available because high quality resources may impose higher costs of defence, greater risks for losing nest ownership and higher maintenance costs including egg aeration and defence from egg predators (e.g. Björk and Kvarnemo, 2012; Kvarnemo, 1995). As a consequence, the best resource may not be the highest quality one but a compromise between resource value and the costs to maintain and secure it (Kvarnemo, 1995; Lindström and Pampoulie, 2005). For example, experimental studies on different populations of sand goby, *Pomatoschistus minutus*, have shown that in the Baltic sea males choose the largest nest site available (Wong et al., 2008), but in the west coast of Sweden male sand gobies choose nest sites according to their own body size (Kvarnemo, 1995), a finding that could be related with egg predator pressure, which is lower in the Baltic (Björk and Kvarnemo, 2012). Despite the implications in male fitness few studies have however addressed male preference for breeding resource quality (Wong et al., 2008).

In addition, because larger males with higher resource holding potential often win disputes over high-quality resources, a positive correlation is often found between resource and male quality (Candolin and Voigt, 2001; Marconato et al., 1989), since larger males or males in superior condition are capable of maintaining better territories, including nests (Alcock, 2000; Heg et al., 2000; Lindström, 1988). Consequently, it is difficult to disentangle which parameter determines female mate choice, and hence male breeding success, as females may

---

* Corresponding author.
E-mail address: ritcarrico@gmail.com (R. Carriço).

http://dx.doi.org/10.1016/j.jembe.2014.03.012

be choosing the best male (e.g. larger males) or the best territory (e.g. larger nests with better protection for the offspring). Several studies have focused on the influence of nest size or male size on the reproductive success of fish (Lehtonen et al., 2007) but less attention has been given to the joint effect of nest size and male quality, such as body size, on the reproductive success of fish with paternal care.

In the Lusitanian toadfish (*Halobatrachus didactylus*), breeding males defend nests in estuarine shallow waters and call in a chorus to attract females to mate with (Amorim and Vasconcelos, 2008; Jordão et al., 2012). Parental males continue calling until the nest ceiling is fully covered with multiple clutches (Dos Santos et al., 2000) suggesting that nest size is an important factor to male's reproductive success as it is in other Batrachoididae (DeMartini, 1988). Males care for the offspring until the juveniles are free swimming (c. three weeks per clutch depending on temperature), which involves fanning the eggs and nest defence from conspecific territorial or sneaker males and from egg predators such as crabs (Modesto and Canário, 2003; Ramos et al., 2012). A recent study has shown that acoustic behaviour is key to mate selection in the Lusitanian toadfish since males with higher vocal activity received more eggs in their nests (Vasconcelos et al., 2012). This study generated however unclear results in relation to the effect of male size on male reproductive success as male vocal activity was related with male size but males with eggs in the nest did not differ in size from males without eggs (Vasconcelos et al., 2012). In addition, the influence of nest size and of the interaction of nest and male sizes on male reproductive success also remains unknown. Our aim was to examine male preference for nest size. We further aimed to unravel whether male and nest sizes may contribute to mate choice and hence to male reproductive success in this highly vocal fish species with paternal care. We conducted a field study in which we assessed the occupation of different-sized artificial nests by Lusitanian toadfish males throughout the breeding season as well as the presence and number of eggs in the nest. We hypothesise that males will choose the larger nests to maximise spawning substrate area when intrasexual competition is low, i.e. when there is a surplus of adequate nests available. We also hypothesise that mate choice will be influenced by both nest and male quality as larger nests with more clutches will allow for a dilution effect in case of predation or cannibalism and male size is likely associated with the ability to defend the nest from invaders and with parental skills.

2. Materials and methods

This study was conducted in an intertidal area of the Tagus estuary (Portugal, Montijo, Air-Force Base 6; 38° 42′N, 8° 58′W), from May to July 2010, during the breeding season of *H. didactylus*. We placed 87 artificial nests of different sizes ca. 1.5 m apart in the lower limit of the intertidal area. Water level varied between 0 m and 2.8 m, and the nests were only exposed to air during spring low tides, i.e. approximately every fortnight. Lusitanian toadfish males are known to occupy intertidal nests at the peak of the breeding season when competition for nesting sites is high (Amorim et al., 2010). We used five different nest sizes with different internal areas (i.e. surface available for depositing eggs): size 1 (length: 44.5 cm × width: 19.5 cm × height: 9 cm; internal area: 0.123 m^2); size 2 (54.5 cm × 20.5 cm × 14.5 cm; 0.163 m^2); size 3 (53.5 cm × 25.5 cm × 17.5 cm; 0.183 m^2); size 4 (53.5 cm × 30 cm × 19 cm; 0.261 m^2); and size 5 (54 cm × 30 cm × 18 cm; 0.313 m^2) (Fig. 1). Size 1 nests were ceramic tiles open in both sides and all the others were hemicylinder concrete structures closed at one end. Nests 3 and 5 had a similar shape to nests 2 and 4, respectively, except for a wider section at the closed-end which increased internal size and egg-laying surface. Although size 1 nests were from a different material than the remaining ones we think that this did not have any effect of the experiment outcome as Lusitanian toadfish have been found to nest under rocks, ceramic tiles, concrete structures or any other substrate suitable to receive eggs and that can be used as a nesting site. It should be emphasized that these artificial nests were spontaneously occupied by males and, therefore, males were not only subject to natural intrasexual competition but also to female mate choice if they had nested under rocks or other structures found in the natural environment of the estuary. Moreover, all nests were large enough to house a male and up to several females.

Every two weeks, when the tides were low enough to access the nesting area, we checked every nest for male occupation, size of male occupants (total and standard length) and the presence of eggs. After sampling, males tended to abandon the nests as a result of handling. We have also observed that males often abandon their nest when nests start being exposed to air in spring low tides since it is very common to find unoccupied nests covered with eggs, and unguarded eggs tend to be predated very fast. Hence, new occupants were most likely found in each sampling event. This was consistent with the fact that eggs were always in early development stages showing that they were recently laid by females visiting the nest-holders and were therefore from that sampling fortnight. The average number of nests sampled at each fortnight was 72 nests (range: 45–87). We examined a total of 359 nests in 5 consecutive sampling periods from May to July. The availability of each nest size varied throughout the study as some nests were removed (and later replaced) to be used in a parallel experiment but this variability was taken into account in the statistics analyses (see below). The proportion (%) of each nest size throughout the study was (mean ± SD): size 1 (26.6 ± 6.9), size 2 (14.8 ± 8.5), size 3 (13.4 ± 6.1), size 4 (27.3 ± 5.6), and size 5 (36.5 ± 3.0).

A photograph was taken whenever there were eggs attached to the ceiling of the nest. We used the software Image J (Wayne Rasband, NIH, USA) to estimate the number of eggs in each image as follows: first the total area occupied by the eggs was measured. Then, the egg density, i.e. number of eggs per unit area, of three representative sub-areas was evaluated. Finally, the total number of eggs was estimated as the product of the average egg density by the total area occupied by the eggs. The error of this method was estimated below 8% by comparing the results obtained in 8 pictures with the respective manual counts.

The estuary water temperature was recorded every 15 min by a data logger (Iotech, USB-501-LT) sealed in a jar and placed in one of the nests. Water temperature during the study period averaged 23 °C ranging from 19.5 °C to 28 °C.

Fig. 1. Nest sizes 1 (A), 4 (B) and 5 (C). Nests 2 and 3 are identical to nests 4 and 5, respectively.