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Intra- and intersexual selection on male body size in the annual killifish *Austrolebias charrua*

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ABSTRACT

Since many traits are involved in both female mating decisions and male contest outcomes, female mate choice and male competition can act in concert to intensify sexual selection on male traits, or in opposition to weaken it. In the sexually dimorphic annual killifish, *Austrolebias charrua*, we evaluated the effect of male body size on female mate choice, male–male competition, and their interaction. We carried out an experiment with three consecutive stages: (i) female choice test between males of different size in a classic two-choice device, (ii) agonistic interactions between males used in the previous stage, and (iii) a second female choice test to evaluate preference consistency in females that either were allowed or were prevented from observing the male competition. Larger males were preferred by females and became socially dominant in agonistic interactions. Further, females were consistent in their choices, and this consistency was independent of whether they had observed or not the male contest. Our research shows that, in *A. charrua*, intrasexual competition and female mate choice act in concert with respect to male body size. The unique life-history of *Austrolebias* and the high repeatability of mate-choice assays make this system a promising candidate for studies of behavioural evolution.

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1. Introduction

Sexual selection results in differential reproductive success among individuals of the same sex (Darwin, 1871), and typically acts more strongly on males due to sex differences in search strategies and resource allocation among gametes (Kokko et al., 2006). Sexual selection can be subdivided into intrasexual selection (generally via male–male interference competition or sperm competition) and intersexual selection (usually via female mate choice). Although the evolution of certain male traits can be promoted exclusively by one of the two components of sexual selection, they often act simultaneously (in concert or in opposition) because many traits are involved in both female mating decisions and male contest outcomes (Andersson, 1994; Candolin, 2004; Moore and Moore, 1999; Qvarnström and Forsgren, 1998).

Empirical evidence suggests that sexual selection via intrasexual competition and sexual selection via mate choice could be in opposition for some traits (reviewed in Arnqvist and Rowe, 2005) and the net result will reflect the balance between these forces. In many cases, however, intra- and intersexual selection have complementary effects, promoting the expression of the same traits in males (Benson and Basolo, 2006; Gagliardi-Seeley and Itzkowitz, 2006; reviewed in Wong and Candolin, 2005). Any traits favoured by intrasexual selection will therefore also be favoured by intersexual selection. In some cases, there is direct experimental evidence that witnessing the outcome of male–male interaction influences subsequent mate choice (Candolin, 1999; Doutrelant and McGregor, 2000). Females will even incite competition among their pretenders to increase the chances of mating with the dominant male (e.g. Cox and LeBoeuf, 1977; Montgomerie and Thornhill, 1989).

The annual fishes *Austrolebias* (Rivulidae, Cypinodontiformes) comprise 39 species distributed across south-eastern South America (Costa, 2006; Loureiro et al., 2011). *Austrolebias* shares with other rivulids and aplocheilids a unique mode of embryonic development that involves deposition of desiccation-resistant eggs in the substrate of the temporary ponds they inhabit (Simpson, 1979). These ponds have water only in winter, and sometimes go entirely dry for a year due to cyclical droughts. Embryos under go up to three diapauses periods (Berois et al., 2012; Wourms, 1972), allowing them to delay development until environmental conditions are

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favourable for fry to emerge. Individuals then hatch, mature, reproduce, and die within the span of a very short season (4–6 months). Males and females engage in courtship interactions before fully or partially burying themselves in the substrate to deposit and fertilize eggs (Belote and Costa, 2002; García et al., 2008; Vaz-Ferreira et al., 1964).

Austrolebias charrua belongs to the "*A. adloffi*" species complex endemic to the lowlands of the Patos-Merin drainage system (Costa and Cheffe, 2001; García et al., 2009; Loureiro and García, 2008). Like other species in the complex, *A. charrua* is highly sexually dimorphic: males are larger and have a pattern of dark vertical bands upon a light background on its body flanks with unpaired fins strongly pigmented, while females are relatively cryptic (Costa, 2006; García et al., 2009).

In this study, we evaluated sexual selection on male body size in *A. charrua* via female mate choice, male competition, and their interaction. First, we used simultaneous choice tests to measure female preferences for body size. Second, we used male–male competition assays to measure the effect of size on contest outcomes. Finally, we directly measured the effect of male competition on females' mating preferences by allowing them to witness agonistic interactions and then allowing them to choose.

2. Methods

2.1. Collection and maintenance

Adult *A. charrua* were collected with a hand net from temporary ponds located in Rocha Department, Uruguay (Fig. 1), at the beginning of the reproductive season (August 2009). Test fishes were kept in the laboratory for at least 10 days under constant temperature (19 °C) and natural photoperiod conditions, and were fed daily with live *Tubifex* sp. Males were kept in individual tanks (20 cm × 9 cm × 15 cm, length × width × height) while females were kept in communal tanks (40 cm × 13 cm × 15 cm) in groups of up to 5 individuals. Aquariums were visually isolated from each other and their water was replaced weekly. Collection and experimental procedures were approved by the ethical committee of the Universidad de la República, Uruguay (Comisión de Ética en el uso de animales, Facultad de Ciencias, UdelaR, approval date 10-03-2009). Fish were returned to the same aquarium after experiments were completed, and retained as breeding stock.

2.2. Experimental aquarium

The experimental device consisted of aquariums (45 cm × 28 cm × 20 cm) divided lengthwise by a transparent glass into two compartments of equal size. For female preference trials, one of these compartments was halved by a black opaque glass (Fig. 2). Dividers were removable but were lined with silicone to prevent flow of olfactory cues between compartments. In order to resemble the natural substrate in-habited by annual fishes, the bottom of the aquarium was completely covered with a 2 cm deep layer of peat moss. To reduce any external disturbance and provide uniform background, black screens were placed covering both side walls and the rear wall of the aquarium. All experiments were performed between 8:00 and 14:00 local time.

2.3. Mating preferences

To determine whether females respond differently to males of different sizes, at day 1 the preference of 30 females was examined using 30 different pairs of males varying in their body size by 8.2 ± 0.5 mm (Table S1). Each individual was used only once. To avoid biased results due to female preferences for a sector of the aquarium, for each test, the focal female was placed in the choice

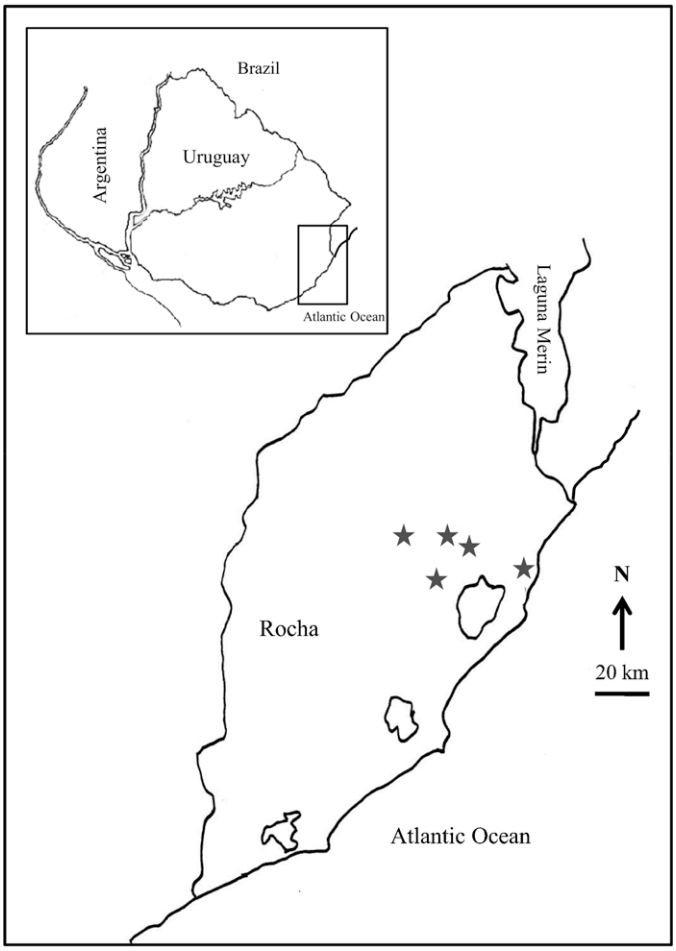

Fig. 1. Distribution of *A. charrua* and collection sites. The ponds are indicated by black stars.

compartment and both males were placed randomly one the right and the other one in the left compartment. The experimental design prevented males from seeing each other and therefore any effect of competition between them (Fig. 2a). During the first hour of acclimation to the experimental aquarium, a black screen visually isolated the female from the males. Later, the screen was removed and two 15 min periods separated by a 1 h interval video records were obtained. After the choice test, the screen was placed back again between the compartments of the female and both males, and individuals were visually isolated the rest of the day.

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2.4. Agonistic interaction

At day 2, the partition between the two males was removed, allowing them to interact freely. Preliminary observations were conducted of male–male encounters, to identify agonistic behavioural units, to establish contest resolution criteria and to determine the winner of the contest. Males exhibited two types of aggressive behaviour: attacks and fins display with body undulations (Table 1). The contest outcome was indicated by morphological and behavioural differences between the contenders. The subordinate male was characterized by colour loss, optional disappearance of vertical stripes and the folding of the dorsal fin, resembling a female. Also, the loser retreated to the periphery of aquarium and remained inactive most of the time, avoiding the other male. In contrast, the dominant fish had the dorsal

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