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Biology, behavior, and environmental enrichment for the captive African clawed frog (*Xenopus* spp)

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ABSTRACT

Xenopus are a hardy, long-lived, aquatic amphibian species which readily adapt to a captive environment. This characteristic makes *Xenopus* ideal for the laboratory, where they are used extensively in basic and biomedical research. Though husbandry practices for *Xenopus* have not been standardized, there is burgeoning evidence that environmental enrichment can limit fighting, cannibalism, and can optimize the general health, fecundity, and the welfare of captive *Xenopus*. Here we review the habitat, sensory biology, and the relevant features of normal *Xenopus* behavior and with those unique features in mind, propose strategies for effective environmental enrichment.

1. Introduction

Xenopus laevis (also called the African Clawed frog due to the sharp, black claws in the hind inner three toes) is an aquatic amphibian of the Order Anuran and the family Pipidae. *Xenopus* are a long-lived, aquatic amphibian commonly used in teaching classrooms and in research laboratories. From the early 1700s to the present, *Xenopus* have been studied as animal models of vertebrate development, anatomy, and physiology. In the 1940s, scientists discovered that injection of urine from a pregnant woman induced egg laying in *X. laevis*. This finding heralded the widespread use of *Xenopus* for human pregnancy testing in hospital laboratories, a practice that persisted through the 1970s. In the 1980s, research scientists developed the Frog Embryo Teratogenesis Assay *Xenopus* (the FETAX assay), which is now the current standardized test used to measure the toxicity of pollutants and other substances in the environment (Dumont et al., 1982). With over 41,000 research reports using *Xenopus* cited on Pubmed at the time of this publication, *Xenopus* has become a leading animal model in biomedical research, advancing important discoveries in cancer, developmental biology, and in cellular research (Green, 2009). To date, *X. laevis* has been the predominant laboratory species studied; however, *X. tropicalis* usage is on the rise, as this species is more amenable to genetic manipulation, is much smaller (i.e. requires less housing space) and reaches sexual maturity in just a few months (Green, 2009). In the not-too-distant future, the use of transgenic *X. tropicalis* in research may eclipse *X. laevis*.

As *X. laevis* are relatively "easy keepers" in the laboratory, with long life spans (15–20 years in captivity) and the ability to produce large, easily manipulable eggs year round, they can supply scientists with a steady stream of biological materials. Understanding *Xenopus* behavior in the wild is thus important to provide appropriate husbandry and enrichment for captive *Xenopus*. However, there is relatively little standardization or evidence based studies which define the optimal housing conditions for this species and thus a limited understanding about what kind of environmental enrichment, if any, would be effective. Here we review the natural habitat, the sensory biology, the normal behavior of *Xenopus*, and with those

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features in mind, review the enrichment strategies most commonly used in the laboratory environment.

2. Natural habitat

X. laevis are native to South Africa, but this highly adaptable species exhibits a vast tolerance to a wide range of habitats and is highly invasive. Through international commerce, pet trade, and unauthorized release (either intentional or well-meaning) of live *X. laevis*, this species can now be found outside of southern Africa: in Indonesia, Japan, Ascension Island, Italy, France, South Wales, United States, Great Britain, Portugal, Chile, and Germany (Faraone et al., 2008; Fouquet and Measey, 2006; Green, 2009; Lobos and Jaksic, 2005; Measey, 2001; Rebelo et al., 2010; Tinsley, 2010; Tinsley and McCoid, 1996). *X. tropicalis*, however, has stricter habitat requirements and is found predominantly in the warm tropical lowlands of West Africa where the canopy provides shade over the large bodies of water and the water temperature remains stable around 25 °C (Tinsley, 2010).

Xenopus depend on water for all stages of their life cycle. They flourish in standing bodies of brackish water: lakes, dams, swamps, ditches, and wells (Tinsley et al., 1996). They are commonly found in stagnant, turbid water where fertilized eggs can develop undisturbed and visual detection of growing and adult frogs by predators is more difficult. However, they can also be found in river beds and along drainage ditches where water is flowing (Tinsley et al., 1996) and clearly, they have adapted to alternate aquatic environments. *Xenopus* are considered ectotherms, meaning they cannot increase their metabolism to increase their body temperature. Typically, they prefer warmer water temperatures between 17 and 24 °C, with a slightly alkaline water pH: between 7.4 and 7.5. However, as a testament to their adaptability, thriving *X. laevis* populations have been documented in the wild in water with a pH ranging from 5 to 9 and in water temperatures ranging from 10 to 30 °C (Green, 2009; Tinsley et al., 1996; Tinsley and McCoid, 1996; Wu and Gerhart, 1991). If conditions in the environment become unfavorable (freezing cold or prolonged drought), *Xenopus* will burrow in the mud (estivate), remaining dormant for up to a year or longer, until conditions are more favorable (Green, 2009; Tinsley et al., 1996). They can survive for short periods outside of the water and groups of adults and individuals have been observed moving over land in the wild in search of water (Lobos and Garin, 2002; Tinsley and McCoid, 1996).

3. Sensory biology: the lateral line system, visual, olfactory and auditory systems

Xenopus have a well developed lateral line system that is used to detect wave stimuli and electrical fields created by prey and predators in the water, as well as to orientate themselves in the environment (Claas and Dean, 2006; Elepfandt, 1996a; Green, 2009). The lateral line, made of rows of hair cell-like receptors, appears as vertical 'stitches' on the body (Fig. 1; Green, 2009). The lateral line system functions as a mechanoreceptor and electroreceptor which is important for orientation and for detection of water vibrations and electrical fields indicative of prey and predators. *Xenopus*' eyes are on the top of the head. The dorsal positioning and ocular anatomy suggests the importance of sight in detection of predators and prey in air and overhead (Tinsley et al., 1996), rather than through water. They do not appear to be able to see out or in the water more than a short distance away. Under experimental conditions, no individuals were observed catching prey more than one body's length from the surface of the water (Measey, 1998). The olfactory system also aids in the detection of prey, even at great distances (Elepfandt, 1996a). *Xenopus* feeding behaviors (for details see Section 4.1) can be stimulated by the olfactory system's detection of the amino acids, histidine, methionine, isoleucine, and phenylalanine (essential amino acids) and by the gustatory (taste) system (Elepfandt, 1996a). In any event, the lateral line system, the visual and the olfactory systems make *Xenopus* highly proficient hunters. They are, in fact, considered a predator species.

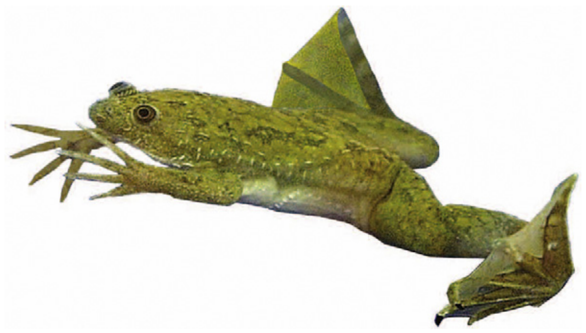

Fig. 1. Lateral lines. Lateral lines appear as vertical "stitches" running along the sides of the body and around the eyes and head.

The hearing range of *X. laevis* spans from 200 to 3900 Hz (Elepfandt, 1996b). Human optimal hearing range is between 2000 and 5000 Hz (Costanzo, 2002), suggesting that *Xenopus* hear at a lower relative optimal frequency. *Xenopus* emit and hear sound underwater only, and thus the anatomy of the *Xenopus* ear is adapted to underwater sound propagation. Anatomically, the structure of the ear in *Xenopus* is analogous to that seen in other aquatic species (Elepfandt, 1996b). Their "ears" lack pinna, are buried beneath soft tissue, and have a cartilaginous tympanic membrane, which is more sensitive for detecting sound in water than air (Elepfandt, 1996b). The auditory system of *Xenopus* appears to be important primarily for communication of dominance and fertility (Tobias et al., 2004). Both males and females call to each other, especially during the spring mating season, with males preferring to vocalize from deeper depths where sound transmission is better (Elepfandt, 1996b).

4. *Xenopus* behavior: feeding, breeding, and response to threats

4.1. Feeding

Adult *Xenopus* have a varied diet, depending on the season and availability. Insects, vertebrates, fish, amphibians,