

# *Hormonal Regulation of Motor Output in Amphibians: *Xenopus laevis* Vocalizations as a Model System*

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## I. INTRODUCTION

Sexually differentiated motor patterns are common to many vertebrate reproductive systems. Their occurrence is due to the action of gonadal steroids during development and in adult life. Understanding how sex-specific motor programs are generated requires uncovering the mechanisms for motor program production and for hormonal regulation of the sensory, neural, and muscular elements that produce these behaviors. The complexity of most vertebrate systems poses a steep challenge. However, the vocal behaviors of the South African clawed frog, *Xenopus laevis*, have proved to be a highly useful model system in addressing these issues. These frogs are native to Southern Africa and are entirely aquatic. Their vocal repertoire is rich and sex-specific, but the mechanisms of vocal production are relatively simple. Steroid hormones regulate the sexual differentiation of vocal elements and are required for vocal displays in adulthood. These features permit us to dissect the cellular and molecular mechanisms used in sexually differentiated motor control and to place these elements within the behavioral context of the animal's natural habitat.

## II. VOCAL REPERTOIRE

*Xenopus laevis* is an anuran (frogs and toads), a member of a large genus of approximately 29 species; all *Xenopus* are aquatic throughout their life span. This latter feature is secondary; *Xenopus* is believed to be derived from an ancestral terrestrial anuran because it retains many common features (Trueb, 1996). The preferred habitat for *Xenopus laevis* is murky ponds filled with decaying vegetable matter. Frogs call at night and this characteristic, together with lack of visibility in the ponds, probably accounts for the very complex vocal repertoire used in social communication.

*X. laevis* uses eight distinct vocalizations in social interactions (Fig. 1). Five of these are exclusive to males, one is shared and, one is exclusive to females. The basic vocal unit is a click, a brief burst of sound with a relatively wide range of component frequencies. Male clicks are generally distinguishable from female clicks by having the majority of sound energy at approximately 2 kHz; for females clicks, most sound energy is at approximately 1 kHz. An exception is the click in growling (Fig. 1C), a male-specific vocal behavior, at approximately 1 kHz.