

# Neuroendocrine control of spawning in amphibians and its practical applications



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## ABSTRACT

Across vertebrates, ovulation and sperm release are primarily triggered by the timed surge of luteinizing hormone (LH). These key reproductive events are governed by the action of several brain neuropeptides, pituitary hormones and gonadal steroids which operate to synchronize physiology with behaviour. In amphibians, it has long been recognized that the neuropeptide gonadotropin-releasing hormone (GnRH) has stimulatory effects to induce spawning. Extensive work in teleosts reveals an inhibitory role of dopamine in the GnRH-regulated release of LH. Preliminary evidence suggests that this may be a conserved function in amphibians. Emerging studies are proposing a growing list of modulators beyond GnRH that are involved in the control of spawning including prolactin, kisspeptins, pituitary adenylate cyclase-activating polypeptide, gonadotropin-inhibitory hormone and endocannabinoids. Based on these physiological data, spawning induction methods have been developed to test on selective amphibian species. However, several limitations remain to be investigated to strengthen the evidence for future applications. The current state of knowledge regarding the neuroendocrine control of spawning in amphibians will be reviewed in detail, the elements of which will have wide implications towards the captive breeding of endangered amphibian species for conservation.

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## 1. Introduction

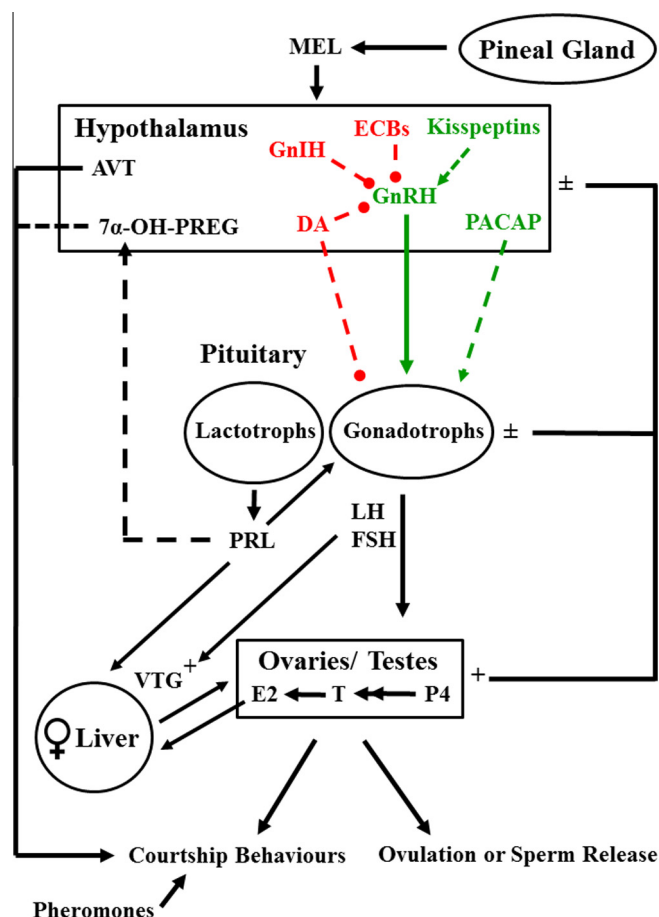
With an immense diversity spanning across three phylogenetic orders, amphibians exhibit a wide range of remarkable courtship rituals and reproductive strategies. This vertebrate class includes frogs and toads (Anura) that fertilize externally with a few exceptions, salamanders and newts (Caudata/Urodela) that primarily deposit spermatophores for females, and caecilians (Gymnophiona) where fertilization is strictly internal (Duellman and Trueb, 1986). Although the majority of amphibians lay and fertilize their eggs in moist environments where larval tadpoles progress through metamorphosis, there exists newly discovered cases of adaptive radiation (Duellman and Trueb, 1986; Haddad and Prado, 2005; Hödl, 1990). For instance, frogs in the family *Eleutherodactylidae* reproduce through direct development where eggs hatch as miniature adults, completely bypassing the tadpole stage (Hödl, 1990). In other species, egg incubation and development may take place in the male vocal sacs (*Rhinoderma darwinii*), female stomachs (*Rheobatrachus silus*) or be implanted in dorsal brood pouches (*Gastrotheca*). These reproductive events are driven

by unique seasonal cycles and social stimuli that cue brain activity and courtship behaviours. Timing of successful reproduction is therefore complex, requiring a delicate coordination between several physiological, behavioural as well as environmental signals that are dependent on underlying interactions between the endocrine and nervous systems. This is especially relevant for spawning, i.e., optimally timed release of gametes for fertilization.

The neuroendocrine control of ovulation and sperm release in amphibians is poorly understood and is largely limited to anurans (Fig. 1). There is a notable lack in progress in this field compared to other vertebrate models. Indeed, this subject has not been reviewed in any detail since the late 1980s (Moore, 1987). At that time, scientists were only beginning to explore the roles of luteinizing hormone (LH) and follicle-stimulating hormone (FSH) in amphibians. Major breakthroughs have confirmed that amphibians share basic aspects of the hypothalamo-pituitary-gonadal (HPG) axis with other vertebrates such as neuropeptides, pituitary hormones and gonadal steroids. While it has long been assumed that the hypothalamic decapeptide gonadotropin-releasing hormone (GnRH) is the principal stimulatory system driving the LH surge, and subsequently ovulation and sperm release in amphibians (Daniels and Licht, 1980; McCreery and Licht, 1983a), that is far from being proven. There are new players emerging from

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The global decline and disappearance of many amphibians around the world has persisted to become an imminent crisis with now an estimated 32.4% of species that are categorized as threatened (IUCN). This is suspected to be driven primarily by disease, habitat loss and pollution (Bishop et al., 2012; Houlihan et al., 2000; Wake and Vredenburg, 2008). Consequently, there is now an urgent need to develop new amphibian reproductive technologies to establish captive colonies followed by reintroduction into suitable habitats. Hormone induction represents a powerful tool

This review will focus on the principal neuroendocrine mechanisms that are known to govern the control of spawning in amphibians. Major breakthroughs throughout the past years will be outlined as will the major gaps in our knowledge of the neuroendocrine control of amphibian reproduction. It is hoped that this review will provide a background for future research on hormone manipulations and captive breeding techniques for amphibian conservation in the face of rapid population declines.

The hypothalamo-pituitary complex in amphibians is composed of several identifiable regions that share structural similarities with fish, reptiles and mammals (Ball, 1981). Mapping out this neuroanatomical organization is key to understanding how the brain exerts control over the pituitary to translate neuronal inputs into hormone signals. The preoptic area of the hypothalamus is located in the ventral diencephalon and is key to the regulation of reproduction. Attached to the hypothalamus through an infundibular stalk is the pituitary gland that consists of the neurohypophysis (posterior) and adenohypophysis (anterior). The amphibian neurohypophyseal peptides arginine vasotocin (AVT) and mesotocin are respectively the homologs of mammalian vasopressin and oxytocin that are released into systemic circulation. In amphibians, the adenohypophysis is controlled by hypothalamic neuropeptides and catecholamines released into and transported by the median eminence. It is specifically the cells of the *pars distalis* of the pituitary that biosynthesize and secrete hormones that are involved in growth, reproduction and stress response among many other functions (Ball, 1981; Moore, 1987). The particular group of pituitary hormones that are directly involved in gametogenesis, steroidogenesis and spawning are termed the gonadotropins.

Two distinct forms of gonadotropins were initially isolated from the pituitaries of bullfrogs (*Lithobates catesbeianus*) and Northern leopard frogs (*Lithobates pipiens*) that closely resembled mammalian LH and FSH (Farmer et al., 1977; Licht and Papkoff, 1974; Papkoff et al., 1976). The basic structure of these glycoproteins is a heterodimer consisting of a common alpha subunit and a unique beta subunit that confers specificity of action as in other tetrapods. These gonadotropins are biosynthesized by gonadotrophs and are stored in secretory vesicles either separately or together in the *pars distalis* (Gracia-Navarro and Licht, 1987). Both LH and FSH receptors have been partially characterized in bullfrog testes (Yamanouchi and Ishii, 1990) and liver (Kubokawa and Ishii, 1987), in addition to newt (*Cynops pyrrhogaster*) testes (Kubokawa and Ishii, 1980). Early data on the biological actions of amphibian LH and FSH are somewhat confusing, likely related to the lack of specificity of bioassays. Consequently, the development of radioimmunoassays with specific antisera against LH and FSH was a valuable tool towards assessing these separate gonadotropic functions (Daniels et al., 1977). Critically, progress on the roles of LH and FSH has been severely hampered by a limited availability of purified amphibian LH and FSH. Nevertheless, the gonadal steroidogenic functions of LH and FSH are conserved across the vertebrate classes, with notable differences in teleosts

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