Hormones and Behavior 58 (2010) 660–668

Contents lists available at ScienceDirect

Hormones and Behavior

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

Hormonal and behavioral correlates of morphological variation in an Amazonian electric fish (*Sternarchogiton nattereri*: Apteronotidae)

Cristina Cox Fernandes [a,b,*], G. Troy Smith [c], Jeffrey Podos [a], Adília Nogueira [b], Luis Inoue [d], Alberto Akama [e], Winnie W. Ho [c], José Alves-Gomes [b]

[a] Department of Biology, University of Massachusetts, Amherst MA, USA
[b] Coodenação de Pesquisa em Biologia Aquática, Laboratório de Fisiologia Comportametal e Evolução, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil
[c] Department of Biology, Indiana University, Bloomington IN, USA
[d] Embrapa, Manaus, Brazil
[e] Universidade Federal do Tocantins, Porto Nacional, Brazil

ARTICLE INFO

Article history:
Received 9 February 2010
Revised 21 May 2010
Accepted 6 June 2010
Available online 16 June 2010

Keywords:
Electric fish
Androgens
Testosterone
11-ketotestosterone
Sexual dimorphism
Electric organ discharge

ABSTRACT

The weakly electric fish from the main channel of the Amazon river, *Sternarchogiton nattereri*, offers a striking case of morphological variation. Females and most males are toothless, or present only few minute teeth on the mandible, whereas some males exhibit exaggerated, spike-like teeth that project externally from the snout and chin. Androgens are known to influence the expression of sexually dimorphic traits, and might be involved in tooth emergence. In this study we assess the relationship in *S. nattereri* between morphological variation, 11 ketotestosterone (11-KT) and testosterone (T). We also examine relationships of morphology and androgen levels with electric organ discharge (EOD) frequency, reproductive condition, and seasonality. Our main finding is that male morph categories differed significantly in plasma concentrations of 11-KT, with toothed males showing higher levels of 11-KT than toothless males. By contrast, we did not detect statistical differences in T levels among male morph categories. Reproductive condition, as measured by gonadosomatic indexes (GSI), differed across two sample years, increased as the season progressed, and was higher in toothed males than in non-toothed males. EOD frequency was higher in toothed males than in either toothless males or females. Taken together, our findings suggest that *S. nattereri* male sexual characters are regulated by 11-KT levels, and that both morphology and androgens interact with reproductive condition and EOD frequency in ways that vary within and across reproductive seasons.

Introduction

Androgens regulate secondary sex traits in many vertebrate taxa (e.g., vom Saal, 1983; Hews and Moore, 1995; Peters et al., 2000; Cox et al., 2009). Classical studies on the relationship between androgens and sexual traits often focused on behavioral differences between the sexes (e.g. Beach, 1945). Androgens, however, can also mediate intrasexual variation in traits, particularly in males. For example, exogenous testosterone treatment induces young male tree lizards (*Urosaurus ornatus*) to develop characteristics of territorial males, including territorial behavior and orange/blue coloration (Hews et al., 1994). Androgens presumably mediate secondary sexual traits through organizational and activational effects, thus providing animals with mechanisms by which they can adjust their phenotypes to varying environmental circumstances (Moore and Thompson, 1990).

In teleost fishes, androgens mediate the expression of a broad array of male secondary sex characters including swords in swordtails *Xiphophorus* (Baldwin and Goldin, 1939), nuptial coloration in male *Fundulus* (Lofts et al., 1966), sonic muscle mass in midshipman *Porichthys* (Brantley et al., 1993), head crest in peacock blennies *Salaria* (Oliveira et al., 2001; Saraiva et al., 2010), elongated spines of the dorsal fin in filefish *Monacanthus* (Gorbman et al., 1983), and indentation of the dorsal fin and electric organ discharge (EOD) in various species of mormyrids (Bass et al., 1986; Landsman and Moller, 1988; Herfeld and Moller, 1998). Accumulating evidence suggests a particularly central role in sexual trait development for two types of androgens, testosterone (T) and especially 11-ketotestosterone (11-KT, Kime, 1993).

The primary aim of our study is to describe relationships between 11-KT, T, and the expression of intrasexually dimorphic teeth in an Amazonian electric fish, *Sternarchogiton nattereri*. In this species, females and most males are toothless, or present only few minute teeth on the mandible. Some males, however, exhibit exaggerated, spike-like teeth that project externally from the snout and chin (Cox Fernandes et al., 2009; and Fig. 1). Male dentition projecting entirely outside the mouth is the only morphological trait that distinguishes

* Corresponding author. Department of Biology, University of Massachusetts, Amherst MA, USA.
E-mail address: cristina@bio.umass.edu (C. Cox Fernandes).

0018-506X/$ – see front matter © 2010 Elsevier Inc. All rights reserved.
doi:10.1016/j.yhbeh.2010.06.006

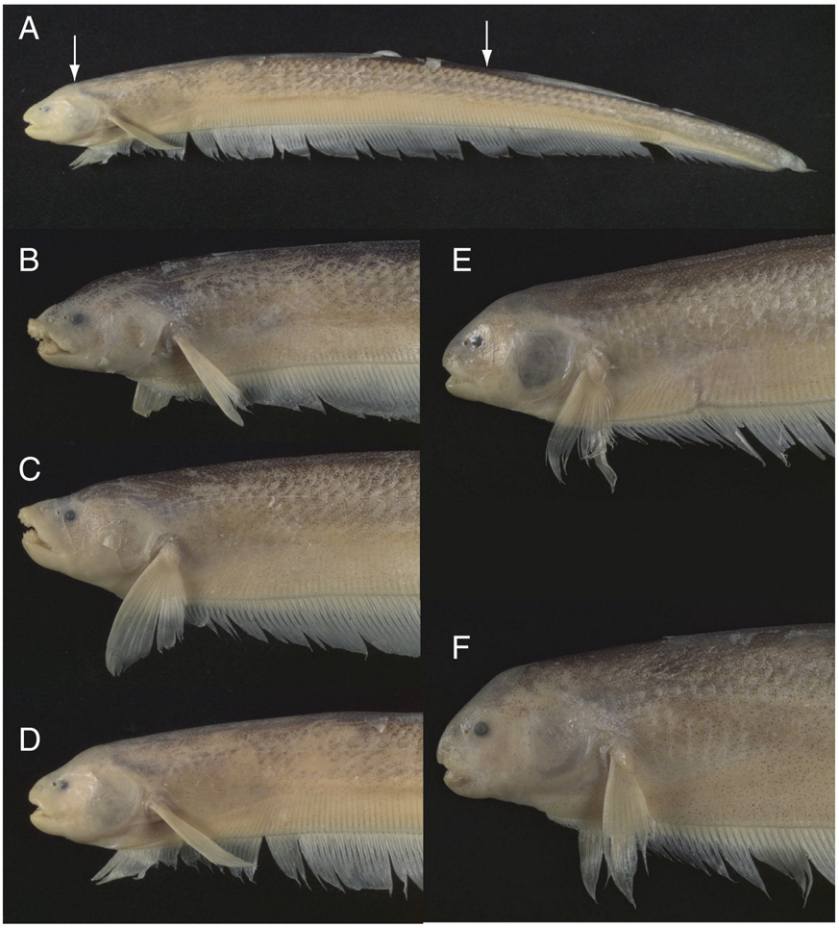

Fig. 1. Representative specimens of *Sternarchogiton nattereri*. A. Full body view showing the supraoccipital bone (front arrow) and the base of the dorsal filament (rear arrow). The distance between these two points, ST, provided a measure of body size not influenced by head or tail morphology. Note the regenerated tail. B and C. Category I fishes, with prominent external teeth. Scars and scratches are visible on the nape. D. Category II fish, with incipient teeth (visible only via x-ray). E. Category III fish, no teeth on the premaxilla. F. Female.

these male morphs. Indeed, morphological sexual dimorphism in this species is so extreme that toothed males had been previously classified as a different genus and species (*Oedemognathus exodon*, Myers, 1936, see Cox Fernandes et al., 2002 for a similarly pronounced example of sexual dimorphism).

Organizational and activational effects of androgens on tooth development were first identified in salamanders, in studies involving testicular transplants and castration. Noble and Pope (1929) found that the typical dentition of male *Desmognathus fuscus* (large distinctive premaxillary monocuspid teeth) was expressed in adult females who received testicular transplants, and that castration caused male dentition to develop with a more typically female pattern (short premaxillary bicuspids). More recent work in salamanders has shown that androgen levels influence tooth size and form (Ehmcke et al., 2003). In fishes, to the best of our knowledge only one prior study has examined the effects of androgens on tooth formation. Female medakas (*Oryzias latipes*) given exogenous methyl testosterone were found to develop enlarged distal teeth typically found only in adult males (Takeuchi, 1967). As a sexually dimorphic trait, enlarged distal teeth seem likely to be used by male fishes as weapons, in intrasexual competition for mates (Emlen, 2008). In our study species, scars and scratches are often found on the heads and napes of toothed males, but never on toothless males or females (Cox Fernandes et al., 2009). These marks likely result from direct fights, or perhaps from aggressive social interactions during courtship. Toothless males, on the other hand, more likely use other kinds of non-aggressive behavioral tactics to access females. A broad literature indicates that multiple reproductive tactics in fishes are mediated by androgens (e.g., Taborsky, 1997; Oliveira et al., 2001; Saraiva et al., 2010).

Secondary aims of our work are to describe specific relationships of male morph and androgens with electrical communication signals, reproductive condition, and seasonality. Like other electric fishes of the family Apteronotidae, *S. nattereri* produces weak, wave-type electric organ discharges (EODs), which are used for electrolocation and communication. In some apteronotid species, EOD frequency has been shown to vary with sex and/or social status, both of which are regulated in part by androgens (Hagedorn and Heiligenberg, 1985; Dunlap et al., 1998; Dunlap and Oliveri, 2002; Kolodziejski et al., 2005; Tallarovic and Zakon, 2005). Exogenous application of androgenic hormones has been found to raise EOD frequency in some species of electric fishes, and to lower EOD frequency in other species (Dunlap et al., 1997; Zakon and Dunlap, 1999). The relationship between androgens and EOD frequency in *S. nattereri* is presently unknown.

In natural populations of electric fishes, little is known about the seasonality of reproduction, hormones, and the development of secondary sexual traits. Reproductive condition in most tropical freshwater fishes varies in synchrony with flood pulses of rainy seasons. Environmental conditions that may trigger seasonal changes in reproductive physiology include food availability, water conductivity, water speed, turbulence, and oxygen concentration levels (Schwassmann, 1978; Junk, 1984; Fernandes, 1997). Manipulation of some environmental factors, such as conductivity, water level and simulated rain, have been shown in several gymnotiform species to influence gonadal recrudescence and regression (Kirschbaum, 1979). In central Amazonia, fish typically reproduce for several months,