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Neuroendocrine regulation of long-term pair maintenance in the monogamous zebra finch

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ABSTRACT

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Understanding affiliative behavior is critical to understanding social organisms. While affiliative behaviors are present across a wide range of taxa and contexts, much of what is known about the neuroendocrine regulation of affiliation comes from studies of pair-bond formation in prairie voles. This leaves at least three gaps in our current knowledge. First, little is known about long-term pair-bond maintenance. Second, few studies have examined non-mammalian systems, even though monogamy is much more common in birds than in mammals. Third, the influence of breeding condition on affiliation is largely unknown. The zebra finch (*Taeniopygia guttata*) is an excellent model system for examining the neuroendocrine regulation of affiliative behaviors, including the formation and maintenance of a long-term pair bond. Zebra finches form genetically monogamous pair bonds, which they actively maintain throughout the year. The genomic and neuroanatomical resources, combined with the wealth of knowledge on the ecology and ethology of wild zebra finches, give this model system unique advantages to study the neuroendocrine regulation of pair bonding. Here, we review the endocrinology of opportunistic breeding in zebra finches, the sex steroid profiles of breeding and non-breeding zebra finches (domesticated and wild), and the roles of sex steroids and other signaling molecules in pair-maintenance behaviors in the zebra finch and other monogamous species. Studies of zebra finches and other songbirds will be useful for broadly understanding the neuroendocrine regulation of affiliative behaviors, including pair bonding and monogamy.

Introduction

Studies of the neuroendocrine regulation of pair bonding in monogamous species deepen our understanding of the neuroscience of sociality and social bonding, an important issue for both basic science and human health (Insel, 1997; McGraw and Young, 2010). Research on the neuroendocrine bases of prosocial and affiliative behavior, including pair bonding, has largely investigated pair bonding in mammals, specifically within the first two weeks of pair-bond formation. Thus, little is known about the neuroendocrine regulation of pair-bond maintenance over the long term. Furthermore, less than 5% of mammals breed monogamously (Kleiman, 1977), while over 90% of birds breed monogamously (Lack, 1968; Black, 1996). Many avian species form life-long monogamous pair bonds and actively engage in pair-maintenance behaviors throughout the year. Some social behaviors, such as aggressive and reproductive behaviors, vary greatly across the seasons, but the extent to which pair-maintenance behaviors vary across seasons and breeding conditions is not clear.

Zebra finches (*Taeniopygia guttata*) are native to Australia, including the central deserts, where the environmental conditions are unpredictable and often severe (Morton, 2009; Zann, 1996). Zebra finches have many adaptations to these conditions, including the ability to breed opportunistically. The ability to form life-long monogamous pair bonds is also a likely adaptation (Adkins-Regan and Tomaszycki, 2007; Mariette and Griffith, 2012; Sánchez-Macouzet et al., 2014). Zebra finches are highly social and live in large groups; however, the extent to which a zebra finch depends on its partner is often underappreciated. The individuals within a large flock change greatly over time, and thus the most stable social relationship for a zebra finch is with its partner (Zann, 1996; Zann and Runciman, 1994). Zebra finches rarely engage in extra-pair courtship or copulations, and most pair bonds are socially as well as genetically monogamous (Birkhead et al., 1988; Griffith et al., 2010). Maintaining life-long pair bonds facilitates a rapid transition to breeding when environmental conditions are favorable for breeding in unpredictable desert habitats (Adkins-Regan and Tomaszycki, 2007). For such reasons, zebra finches are highly motivated to form and maintain a pair bond and are highly dependent on it (Remage-Healey et al.,

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2003; Perez et al., 2012). These characteristics make the zebra finch a valuable model system for examining the environmental and neuroendocrine regulation of long-term pair maintenance.

Zebra finches can be studied in the wild and are also relatively easily maintained and bred in captivity (Griffith and Buchanan, 2010). They have been used extensively to study the neuroendocrine mechanisms of social behaviors (Griffith and Buchanan, 2010), such as male song and courtship (Adkins-Regan, 1999; Riebel, 2009), female mate choice (Burley et al., 1996; Riebel, 2009), and sociality (Goodson et al., 2005, 2009a; Goodson and Kingsbury, 2011). A few studies have examined pair bonding in this species, but primarily pair-bond formation rather than pair-bond maintenance (examples: Goodson et al., 2004; Svec and Wade, 2009). Because pair bonds are life-long, individual zebra finches invest far more time in maintaining a pair bond than in forming a new pair bond. Only a very small number of studies have focused on the neuroendocrine regulation of long-term pair-maintenance behavior (Svec et al., 2009; Alger et al., 2011; Smiley et al., 2012; Prior et al., 2014), arguably the most important social behavior for a zebra finch.

Research exploring the neuroendocrine regulation of pair-maintenance behaviors in zebra finches is in its early stages, and long-term pair-maintenance behaviors need to be situated within social and reproductive contexts. Here, we will review the research on breeding-specific sex steroid profiles in zebra finches and how sex steroids might regulate long-term pair maintenance. We also highlight the value of using experimental water restriction as an efficient and effective way to manipulate the breeding condition of zebra finches in the laboratory.

Seasonal changes in sex steroid regulation of social behavior

For many vertebrate species, breeding is limited to specific and predictable times during the year, when environmental conditions are favorable for raising offspring (e.g., warmer temperature, greater food availability) (Wingfield and Kenagy, 1991). For species with short gestation or incubation durations, the breeding season occurs in spring, when photoperiod is increasing. Photoperiod is often the main environmental cue that initiates the physiological cascade in preparation for reproduction in seasonally-breeding vertebrates (Fig. 1; Wingfield and Kenagy, 1991). Photostimulation causes the upregulation of hypothalamic-pituitary-gonadal (HPG) axis activity, starting with the secretion of gonadotropin-releasing hormone (GnRH) from the hypothalamus to the pituitary, where it causes the secretion of luteinizing hormone (LH) and follicle stimulating hormone (FSH) into the systemic circulation (Fig. 1). These hormones act on the gonads, stimulating the production of sex steroid hormones (e.g., testosterone (T) and estradiol (E2)) and the development of gametes, respectively.

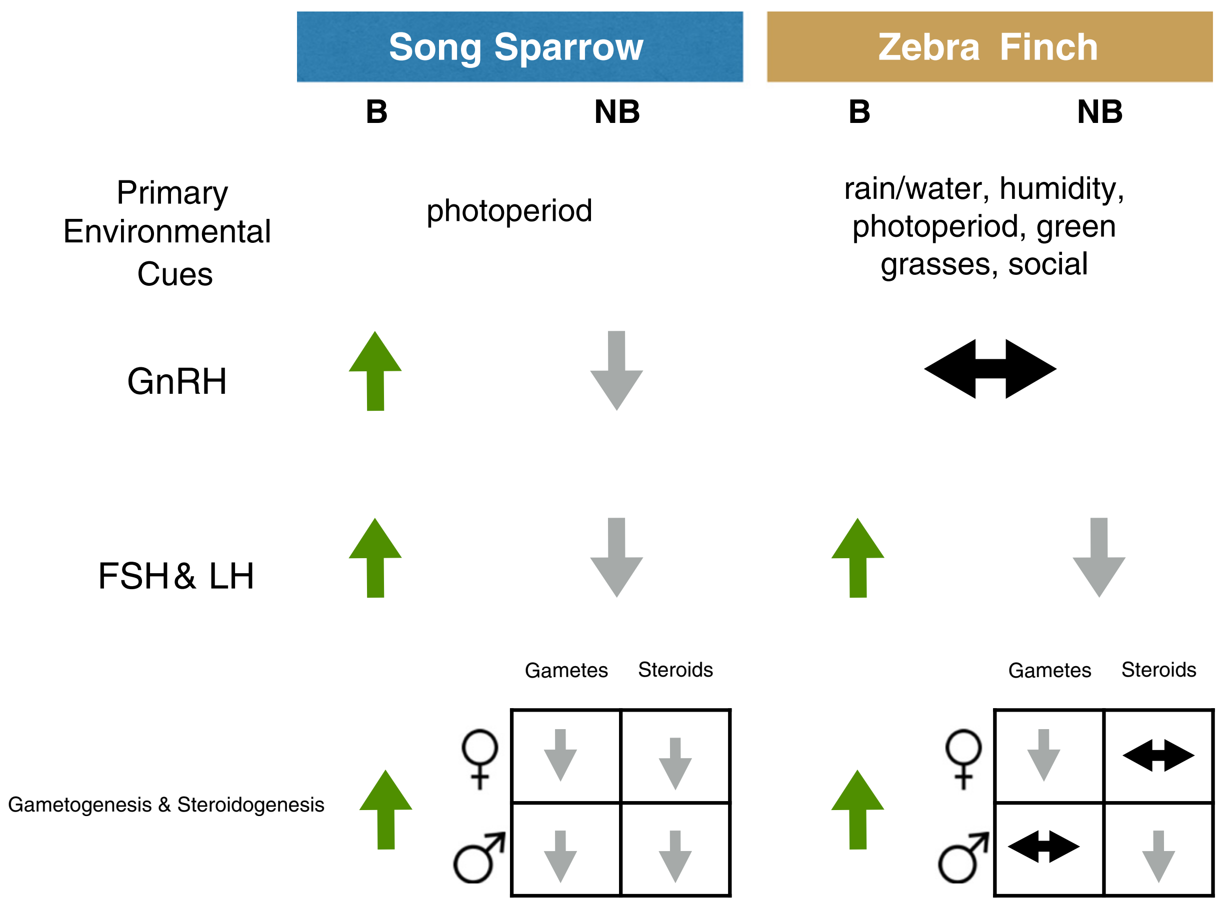

Fig. 1. HPG axis in a seasonally-breeding songbird (song sparrow) and an opportunistically-breeding songbird (zebra finch). In many seasonally-breeding songbirds, such as the song sparrow, the HPG axis is up-regulated in response to increased photoperiod during the breeding (B) season in the spring. Conversely, the HPG axis is down-regulated during the non-breeding (NB) season, including fully regressed gonads and basal circulating sex steroid levels (Bentley et al., 1997, 1998). In contrast, in opportunistically-breeding songbirds, such as the zebra finch, there is not a strict dichotomy in reproductive state. Zebra finches integrate several environmental cues to make decisions about when to initiate and terminate breeding attempts (Waas et al., 2005; Perfito, 2010). Following the cessation of breeding, zebra finches partially down-regulate the HPG axis. Hypothalamic GnRH and GnIH neurons are largely unaffected by breeding condition (Perfito et al., 2006, 2011). Circulating LH levels are decreased during non-breeding periods (Perfito, 2010; Perfito et al., 2006, 2007, 2011). Male zebra finches may partial regress their testes during non-breeding periods, but gametogenesis in the testes appears to be largely maintained during non-breeding periods (Perfito, 2010). There is a greater suppression of female gametogenesis during non-breeding periods (Prior et al., 2013). In males, systemic T levels are reduced in non-breeding periods, but there is no change in systemic E2 levels in males or females (Prior et al., 2013). Unless otherwise specified, the arrows in this figure represent general patterns for both males and females.