

Male 11-ketotestosterone levels change as a result of being watched in Siamese fighting fish, *Betta splendens*

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Abstract

This study investigated the effects of nesting status and the presence of an audience on 11-ketotestosterone (11KT) levels in male Siamese fighting fish, *Betta splendens*. Prior studies have demonstrated that both nesting status, an indicator of territory-holding power and reproductive state, and the sex of a conspecific audience lead to differences in male behavior during aggressive encounters. Since behavioral changes have already been demonstrated, we chose to investigate whether 11KT levels were also influenced by nesting status and audience presence as 11KT both stimulates, and is stimulated by, reproductive and aggressive behaviors in male teleosts. Male 11KT levels were measured from water samples taken from containers holding fish both before and after interaction. Males interacted under three treatment conditions: no audience, female audience, and male audience. Within these treatments were two nest paradigms: both males had nests or neither male had a nest. 11KT levels varied depending on nesting status and audience type. In general, 11KT levels were lower in interacting males when a female audience was present or when males had nests. Overall, 11KT showed increases or decreases as aggression increased or decreased, as shown by already established behavioral findings [see Dzieweczynski T.L., Green T.M., Earley R.L., Rowland W.J., 2005. Audience effect is context dependent in Siamese fighting fish, *Betta splendens*. Behav. Ecol. 16, 1025–1030; Doutrelant, C., McGregor, P.K., Oliveira, R.F., 2001. Effect of an audience on intrasexual communication in male Siamese fighting fish (*Betta splendens*). Behav. Ecol. 12, 283–286]. Our results suggest that 11KT levels are influenced by reproductive status, as indicated by nest ownership, and audience presence and are most likely modulated by territorial behavior and social environment.
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1. Introduction

While androgens are typically thought of as controlling seasonal changes in male reproductive behavior, studies in recent years have demonstrated that androgen levels can be influenced by interactions with conspecifics. Social interactions have been found to influence reproduction through a number of ways including regulating ovulation (Cheng, 1986; Stern and McClintock, 1998) and producing dramatic transformations such as sex changes (wrasse (*Thalassoma*

duperrey) Larson et al., 2003; clownfish Buston, 2003). Sexual maturation may be suppressed in the presence of dominant individuals in a number of social species including an African cichlid fish, *Haplochromis burtoni* (e.g., Davis and Fernald, 1990; Sapolsky, 1993). As a consequence, dominant members of a hierarchy experience greater reproductive success than subordinate animals (e.g., primates, Ellis, 1995; dwarf mongeese, Creel et al., 2002; African cichlid fish (*Haplochromis burtoni*), Hofmann et al., 1999). In all vertebrates, final regulation of androgen levels occurs in the hypothalamic–pituitary–gonadal (HPG) axis, beginning with the GnRH neurons, which are directly influenced by aggressive interactions (e.g., Francis et al., 1993). This indicates that some form of reciprocal relationship likely exists

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between androgens and behavior and may provide a way for individuals to adjust to changes in their social environment (see Oliveira et al., 2002 for review in teleosts).

According to the challenge hypothesis (Wingfield et al., 1990), interactions between males should stimulate the production of androgens within these males; in turn, the amount of androgen stimulation should be a product of the stability of a male's social environment. Under this hypothesis, we would expect males of higher social status to have greater androgen levels because dominant/territorial males must be more aggressive in order to maintain their territories. We would also expect these levels to be highest during periods of social instability, such as initial territory formation or the establishment of a dominance hierarchy (e.g. Cardwell and Liley, 1991; Pankhurst and Barnett, 1993). In contrast, when the social environment is relatively stable, levels of aggression will drop and androgen levels will no longer be closely associated with aggression levels. Finally, androgen levels should be negatively correlated with the degree of paternal care; this is supported by the finding that males in the parental phase of a breeding cycle tend to decrease their androgen levels (e.g. Townsend and Moger, 1987). These predictions would suggest that manipulating the reproductive context (i.e., presence or absence of a nest) during an interaction between males may impact the androgen levels of male Siamese fighting fish.

In addition, manipulating the audience type should also affect androgen levels. Audience, or bystander effects, on behavior are well-documented (e.g., Cheney and Seyfarth, 1985; Evans and Marler, 1992; Mennill and Ratcliffe, 2004). They are often sex-specific and can cause both individuals that are being watched and those watching the interaction, known as eavesdroppers, to modify their behavior (e.g., chickens, Evans and Marler, 1994; lions, Grinnell and McComb, 2001; stickleback, Dzieweczynski and Rowland, 2004; Bettas, Doutrelant et al., 2001; Oliveira et al., 1998). Many of the studies on bystander effects have demonstrated that male–male interactions are affected by the presence of an audience in Siamese fighting fish, *Betta splendens* (e.g., Doutrelant et al., 2001; Matos and McGregor, 2002; McGregor et al., 2001). Whether or not a male has a nest also influences the costs and benefits of being aggressive in the presence of an audience. For example, males that have invested energy into producing a nest are less likely to fight in the presence of a male audience, perhaps because the risk of losing a territory to a potential usurper is too great (Dzieweczynski et al., 2005). It would seem logical that hormone levels would change as a result of these behavioral changes. While it has been demonstrated that watching fights leads to elevated hormone levels in a male eavesdropper cichlid fish (Oliveira et al., 2001), we are unaware of any studies in Siamese fighting fish that investigate how hormonal levels amongst interacting males might be affected by being watched.

Siamese fighting fish males are known for their coloration, long fins, and highly conspicuous and stereotypical displays. Males direct aggressive behaviors such as bites,

gill flares, and tail beats at other males when fighting (Simpson, 1968) and use many of these same behaviors when they are interacting with females. However, the frequency and intensity of the display elements may differ (Simpson, 1968). Given these findings, one would expect that the type of individuals (i.e., bystanders) that are near a given male would affect his behavior. Males compete for territories and, once they have obtained a territory, build a nest of mucous-coated air bubbles on the water surface. This nest will serve to entice females as well as provide a home for eggs and newly hatched fry (Simpson, 1968). Building a nest and establishing a territory is presumably energetically costly and nesting status influences male behavior in aggressive interactions (Dzieweczynski et al., 2005).

Because we previously demonstrated (Dzieweczynski et al., 2005) behavioral differences when audience and reproductive context were varied in Siamese fighting fish, we were interested in investigating whether hormonal changes accompanied these behavioral changes. We chose to assay 11-ketotestosterone (11KT), a principle fish androgen, because other studies have found that 11KT is an influencer of, and is influenced by, aggressive interactions in fish (e.g., Fostier et al., 1983; Hay and Pankhurst, 2005; Liley and Stacey, 1983; Oliveira et al., 1996). Circulating plasma levels of 11KT are also higher in males while testosterone levels are generally similar between males and females, indicating that 11KT is likely important in modifying male behavior (Borg, 1994). If androgens are produced in response to social interactions, we would expect that hormone levels would change after an interaction. In addition, changing the context of an interaction by altering the sex of an audience and male nesting status should influence male androgen levels after an interaction. We predicted that hormone levels would be higher in males after interacting than before. We also predicted that males with nests would have lower 11KT levels than those without nests, and that males interacting in the presence of an audience would have elevated 11KT levels compared to males interacting without an audience.

2. Materials and methods

2.1. Animals

Siamese fighting fish subjects were obtained from a commercial distributor in Indianapolis, Indiana in May 2003. Males were measured for standard length (distance between the mouth and the base of the tail) and weighed (g) before being placed into 500 ml opaque containers to prevent exposure to other males prior to testing. Subjects were maintained at 24.4 °C and a 16L/8D photoperiod throughout the testing period. Subjects were fed Tetra BettaMin once a day.

2.2. Experimental design

For a behavioral trial, males were allowed to interact for 20 min under varying nesting conditions (neither, one or both males had nests) and audience paradigms (female, male, or no audience) for a total of nine combined treatments (Dzieweczynski et al., 2005). All fish were tested in separate tanks that abutted one another (see Fig. 1). These tanks were separated by opaque partitions prior to testing. None of the individuals used in this study, regardless of whether they served as a subject or audience fish, were

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