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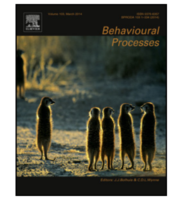

Interactions between aggression, boldness and shoaling within a brood of convict cichlids (*Amatitlania nigrofasciatus*)

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ABSTRACT

A behavioral syndrome is considered present when individuals consistently express correlated behaviors across two or more axes of behavior. These axes of behavior are shy–bold, exploration-avoidance, activity, aggression, and sociability. In this study we examined aggression, boldness and sociability (shoaling) within a juvenile convict cichlid brood (*Amatitlania nigrofasciatus*). Because young convict cichlids are social, we used methodologies commonly used by ethologists studying social fishes. We did not detect an aggression–boldness behavioral syndrome, but we did find that the aggression, boldness, and possibly the exploration behavioral axes play significant roles in shaping the observed variation in individual convict cichlid behavior. While juvenile convict cichlids did express a shoaling preference, this social preference was likely convoluted by aggressive interactions, despite the small size and young age of the fish. There is a need for the development of behavioral assays that allow for more reliable measurement of behavioral axes in juvenile neo-tropical cichlids.

1. Introduction

Individuals are thought to behave along five different behavioral axes or continuums (reviewed by Réale et al., 2007; Conrad et al., 2011): aggression, sociability, activity, shyness–boldness (boldness), and exploration–avoidance (exploration). Assigning an observed behavior to an axis of behavior is not straight-forward because the context in which the behavior is measured can influence expression. Conceptually, aggression is probably the easiest axis of behavior to recognize. Aggressive behavior may be observed as engagement in hostile or intimidating behavior such as the initiation of an attack. Behaviors in the sociability axis may be represented by interactions that imply affinity for a conspecific. The activity axis of behavior is measured as some general measure of movement independent of the other axes.

The remaining behavioral axes, boldness and exploration, are more difficult to measure and classify (Réale et al., 2007; Norton and Bally-Cuif, 2012). Boldness is described as the way in which an individual reacts to an unfamiliar situation that may be perceived as threatening. In turn, exploration refers to the way an individual reacts to something novel. The difficulty lies in determining if an individual finds something novel to be threatening or not. In order to mitigate the difficulty in differentiating between how a treatment is perceived by the individual under consideration (as being threatening or novel), Réale et al. (2007) propose that behaviors measured in response to a novel environment fall under the exploration–avoidance axis while behaviors measured in response to something else being novel (food, objects, etc.) occur along the shy–bold axis of behavior. Another approach to dealing with the boldness and exploration axes is to combine them into a proactive-reaction (proactive) axis (reviewed by Kotrschal et al., 2014). This approach has had success (Tudorache et al., 2013; Kotrschal et al., 2014), but that success comes at the cost of ignoring the differences between responses to novel versus threatening situations (Rodriquez-Prieto et al., 2011) and the potential for conflating aggression with boldness and exploration (Sih et al., 2004a)

Sih et al. (2004a) define behavioral syndromes as occurring when individuals within a population express correlated behaviors across different contexts. This definition has been further refined to differentiate between two broadly different sets of contexts; correlations between and within behavioral axes. Behavioral correlations occurring within a behavioral axis are evidence of 'personality', while correlations occurring between behavioral axes are evidence of a 'behavioral syndrome' (Jandt et al., 2014).

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$$\frac{(Time_{shoal}/Volume_{shoal}) - (Time_{center}/Volume_{center}) - (Time_{empty}/Volume_{empty})}{(Time_{shoal}/Volume_{shoal}) + (Time_{center}/Volume_{center}) + (Time_{empty}/Volume_{empty})}$$

Fig. 1. Equation for the strength of shoaling (SoS) variable. This equation was used to assess possible behavioral influences on the shoaling measurement. Regression scores for each behavioral component were extracted and compared to the calculated SoS variable.

The evolutionary maintenance of a behavioral syndrome may be explained by two different hypotheses: the constraint and the adaptive hypotheses (Bell, 2005). The constraint hypothesis states that behavioral syndromes result from the inability of two behaviors to evolve independently because the behaviors are controlled by the same hormones or the same genes. The adaptive hypothesis argues that behavioral syndromes exist because correlations between certain behaviors confer advantages. A common example of a behavioral syndrome is the aggression–boldness syndrome, where aggressive individuals are also bold. If a fish is bold enough to enter a new territory, it would be advantageous for this individual to be aggressive enough to fend off competitors. Thus a positive correlation would be observed between boldness and aggression and the syndrome may be reinforced by natural selection.

Ecologists have studied behavioral syndromes in a variety of taxa, including fishes (Sih et al., 2004b; Conrad et al., 2011). These studies tend to focus on small shoaling fishes such as Poeciliids and Cyprinids due to their ease of housing and handling, but behavioral syndromes have also been investigated in other social species, including group-living cichlids (Hamilton and Ligocki, 2012; Riebli et al., 2012). While a behavioral syndrome may be important for fishes that shoal or live in groups as fry through adulthood, their entire lives, it might also be important for fishes that shoal only for part of their lives. Recent research indicates that the development of behavior may be plastic, influenced by the local environment and the context in which fish develop (Hesse and Thunken, 2014; Martins and Bhat, 2014), in turn affecting the presence or absence of a behavioral syndrome (Martins and Bhat, 2014). In other words, the experience of being raised in a social group could have a lasting effect on the behavior of an individual (Mateo, 2004), but the impact of that experience may decay with age (Mateo, 2010).

Neotropical cichlids fit this paradigm. They are largely biparental brooders that defend and tend to their young for weeks (Keenleyside, 1991), during which time the juveniles travel in a shoal composed of their siblings and likely receive benefits associated with being part of a shoal (e.g., reduction of predation risk) as a result (Wisenden, 1995). As the juveniles mature they transition from living as a shoal under the protection of their parents to exist as free-roaming territorial/aggressive individuals. In other words, juvenile Neotropical cichlids may transition from a behavioral state where positive social interactions are reinforced along the sociability axis of behavior to a state where a variety of positive and/or negative social interactions may be reinforced.

Convict cichlids (*Amatitlania* sp.) may be ideal for investigating the influence of early-life sociability on behavior later in life because they are commonly used for evaluating the effectiveness of the biparental care mating system (Wisenden, 1995; Snekser and Itzkowitz, 2014). Despite a large body of literature, only one study (to our knowledge) has attempted to investigate early social-history on future behavioral expression in convict cichlids. In that study, Lee-Jenkins and Godin (2013) used juvenile convict cichlids (*Amatitlania siquia*) to investigate the influence of relatedness and familiarity on shoaling preferences, determining that developmental stage (length) had an influence on social behavior.

Convict cichlids also provide an opportunity to investigate behavioral syndromes at multiple scales. That is, expressed behavior may vary within broods, between broods, within local populations, and between populations. At least one study has found scale-related differences in a behavioral syndrome (Chapman et al., 2011), but to our knowledge, this possibility has not been assessed in fishes. Using standard techniques for small social fishes, our study has two simple goals: (1) to determine whether immature convict cichlids from the same brood shoal and, (2) to determine whether an aggression–boldness behavioral syndrome exists within a single brood of immature convict cichlids.

Fig. 2. Bar graph of juvenile convict cichlid (*Amatitlania nigrofasciata*) preference for time spent shoaling versus not shoaling in a standard three-chambered shoaling assay. Error bars represent ± standard error (paired *t*-test; $t = 2.972$; $p = 0.007825$).

2. Methods

2.1. Study subject history

The convict cichlid chosen for this study was *A. nigrofasciatus* (Schmitter-Soto, 2007). A monogamous pair from a local importer (Seven Star Tropical Fish, Philadelphia, PA) were allowed to mate and raise their brood in a 284 L tank decorated with gravel and a few plants. This tank was kept under normal laboratory conditions (26.5–28.5 °C under a 12:12 light/dark cycle), did not contain any other fish, but other fish were visible in adjacent tanks. Once the fry were no longer demonstrating an obvious tendency to shoal unless threatened, they were randomly split into two groups. "Focal" fishes were housed in a large group of their siblings while a second group of "stimulus" siblings were housed in a different tank. These groups were held for an additional month in order to allow the fish to continue developing and to give time for familiarity to wane. The fish were aged 3–4 months when their behavioral preferences were measured and had a mean total length (nose to caudal fin) of 34 (±8.4) mm. At this age and size it is possible for a convict cichlid to be mature, but this is very unlikely (Ishikawa and Tachihara, 2010).

2.2. Animal care and housing

About 50 focal fishes were housed in a 76 L aquarium from 26.5 to 28.5 °C under a 12:12 light/dark cycle. The stimulus fish were housed in a smaller group of about 5 individuals in an 18.9 L tank under similar conditions. All fishes were fed flake food daily, always in the morning hours, including on days when testing was scheduled. Testing occurred between 09:00 AM EST and 17:00 PM EST from October 2013 to November 2013 in order to reduce circadian effects (Paciorek and McRobert, 2012). Focal fish were not returned