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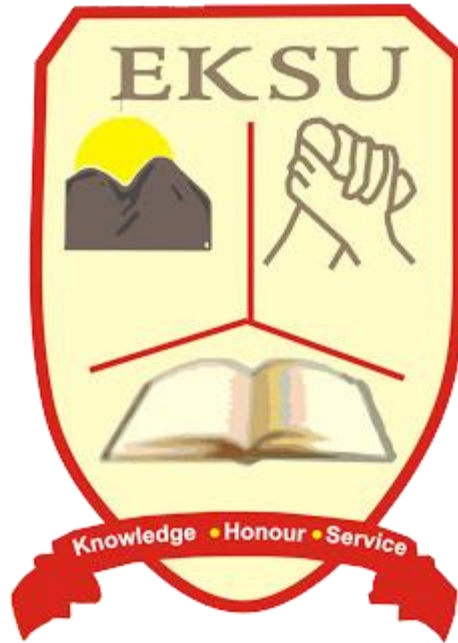
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Boldness-aggression Syndromes in the zebrafish and the guppies

T. O. Ariyomo¹, T. Jegede² and P. J. Watt³

¹Department of Fisheries and Aquaculture, Federal University, Oye-Ekiti, Ekiti State, Nigeria.

²Department Fisheries and Aquaculture Management, Ekiti State University, Ado-Ekiti, Ekiti State, Nigeria.

³Department of Animal and Plant Sciences, University of Sheffield, Western Bank, S10 2TN, UK.

Email: temitopejegede@yahoo.com

Abstract

Correlations between unrelated personality traits in different contexts often referred to as behavioural syndromes, have been found to exist among individuals. Behavioural syndromes have been documented in a wide variety of taxa and may arise due to correlated behaviours having a similar underlying genetic basis, so that they have become coupled (genetic constraint), or when one hormone acts on several traits (hormonal constraints) or if adaptations to existing selection pressure act simultaneously on multiple traits (adaptive constraints). We examined if there were correlations between boldness and aggression, which would be an indication of a behavioural syndrome in three strains of zebrafish and the guppy. There was some evidence of a boldness and aggression syndrome in only females of two of the zebrafish strains and in the male guppies. Given the limited correlation of these traits within the populations studied, this syndrome was probably due to adaptations to prevailing selection pressures rather than due to genetic constraints.

Keywords: behavioural syndromes, zebrafish, guppies, boldness, aggression.

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Introduction

Behavioural syndromes occur when consistent but unrelated personality traits, such as boldness and aggression, become correlated across contexts (Bell & Stamps, 2004; Bell, 2005). This means that organisms do not express the traits independently of each other but together, such that, in a bold-aggression syndrome, a bold individual would also be aggressive too, and so it may be impossible for behavioural traits to develop separately (Bell, 2005; Brydges *et al.*, 2008). In the rodent *Dipodomys merriami*, Dochtermann & Jenkins (2007) found that boldness and aggression were significantly correlated and bold and aggressive individuals were A number of possible mechanisms have been suggested, which include genetic constraints, where

often less flexible in their responses to changing environmental situations. This inflexibility is consistent with other studies (Koolhaas *et al.*, 1997, 1999). The activity-boldness behavioural syndrome in the damselfly, *Lestes congener*, is carried over from the larval stage into the adult, such that, an active larva may survive but an active adult may fall prey to a predator (Brodin, 2009). However, despite being a taxonomically widespread phenomenon (reviewed in Sih *et al.*, 2004a, b; Bell, 2007), the mechanisms sustaining the occurrence of these syndromes are unclear.

a single gene controls the unrelated traits (Deng *et al.*, 1994; Dingemans *et al.*, 2007), hormonal

constraints, when the same hormones act on several traits (Koolhaas *et al.*, 1999; Veenema *et al.*, 2003) and adaptive constraints, or if adaptations to existing selection pressure act simultaneously on multiple traits (Bell, 2005; Bell & Sih, 2007). The consequence of behavioural syndromes in a population, apart from being maladaptive in specific context, is that it may constrain the ability of such a population to respond to selection. In this study, we explored the possibility of a boldness-aggression syndrome in three strains of zebrafish and the guppies which are species that are widely used in behavioural and experimental studies.

Materials and methods

All the zebrafish strains (London Wild Type (LWT), Tupfel Long fin (TL) and Nacre) and the guppies used in this study came from laboratory-maintained stock at the University of Sheffield. Prior to behavioural testing which was similar to that described in Ariyomo and Watt (2012, 2013a, b, 2015) and Ariyomo *et al.*, (2013), zebrafish were housed in 10 litre tanks (30 cm x 15 cm x 24 cm) in a recirculatory system kept at 26 ± 1 C, whereas the guppies were placed in aerated tanks (18 cm x 11.5 cm x 11.8 cm) and the water changed daily, under a 12:12 h light/dark photoperiod with a 40 min dusk and dawn period. The fish were fed twice daily with dry fish food and brine shrimp.

Behavioural testing

Twenty-five males and 25 females of each of the zebrafish strains (LWT, TL and Nacre) and 25 male and 25 female guppies were tested for boldness and aggression. Behavioural testing was similar to that described in Ariyomo and Watt (2012, 2013a, b, 2015) and Ariyomo *et al.*, (2013). The open field test which has been previously shown to be the most valid measure of boldness (Burns 2008; Ariyomo & Watt, 2012, 2013a & b, 2015; Ariyomo *et al.*, 2013) was used to test for boldness in this study. The number of lines crossed and the degree to which a fish utilized the open field was used as a measure of boldness (Burns 2008; Ariyomo & Watt 2012, 2015; Ariyomo *et al.*, 2013). Fish were placed in a novel tank (48 cm X 26 cm X 22 cm), with the base marked into 24

rectangles (each 8 cm X 5.5 cm) and filled with 3 L of dechlorinated water heated to 26 C (Ariyomo *et al.*, 2013). Fish that effectively utilized the inner and outer rectangles on the base of the tank and crossed more lines were deemed bold, while the shy ones were those that crossed the fewest lines and did not utilize the inner and outer rectangles on the base of the tank; (Ariyomo *et al.*, 2013). Two 18 W daylight fluorescent tubes were placed about 34 cm above the tank to provide light during the experiments. Fish tested for boldness in the open field assays were then tested for aggressiveness using the mirror test (Gerlai *et al.* 2000; Moretz *et al.* 2007a, b; Ariyomo and Watt 2012; Ariyomo *et al.*, 2013). The number of aggressive interactions made by an individual towards its mirror image was recorded. Fish with the greatest number of aggressive interactions were considered aggressive while those with few aggressive interactions were considered non aggressive.

Statistical analysis

The relationship between boldness and aggression in the males and females of the three strains of zebrafish and the guppies was analysed using the non-parametric Spearman's rank correlation (ρ). Statistical analyses were conducted using R statistical software, version 2.12.2 (R Development Core Team 2011).

Results

Behavioural syndromes in strains of the zebrafish

There was a positive correlation between boldness and aggression in LWT females (Spearman correlation: $\rho = 0.52$, $p = 0.008$; Fig. 1a) and in TL females (Spearman correlation: $\rho = 0.50$, $p = 0.017$; Fig. 1b), but not for any males or females of the other strains (Table 1).

Behavioural syndromes in the guppy

There was a positive correlation between boldness and aggression in the male guppies (Spearman correlation: $\rho = 0.50$, $p = 0.012$; Fig. 2a) but not for the females (Spearman correlation: $\rho = 0.14$, $p = 0.504$; Fig. 2b)

Table 1: Correlation between boldness and aggression in strains of zebrafish

Strain/sex	rho value	<i>p</i> value
Nacre female	0.13	0.525
Nacre male	0.13	0.329
LWT male	0.03	0.877
TL male	0.19	0.372

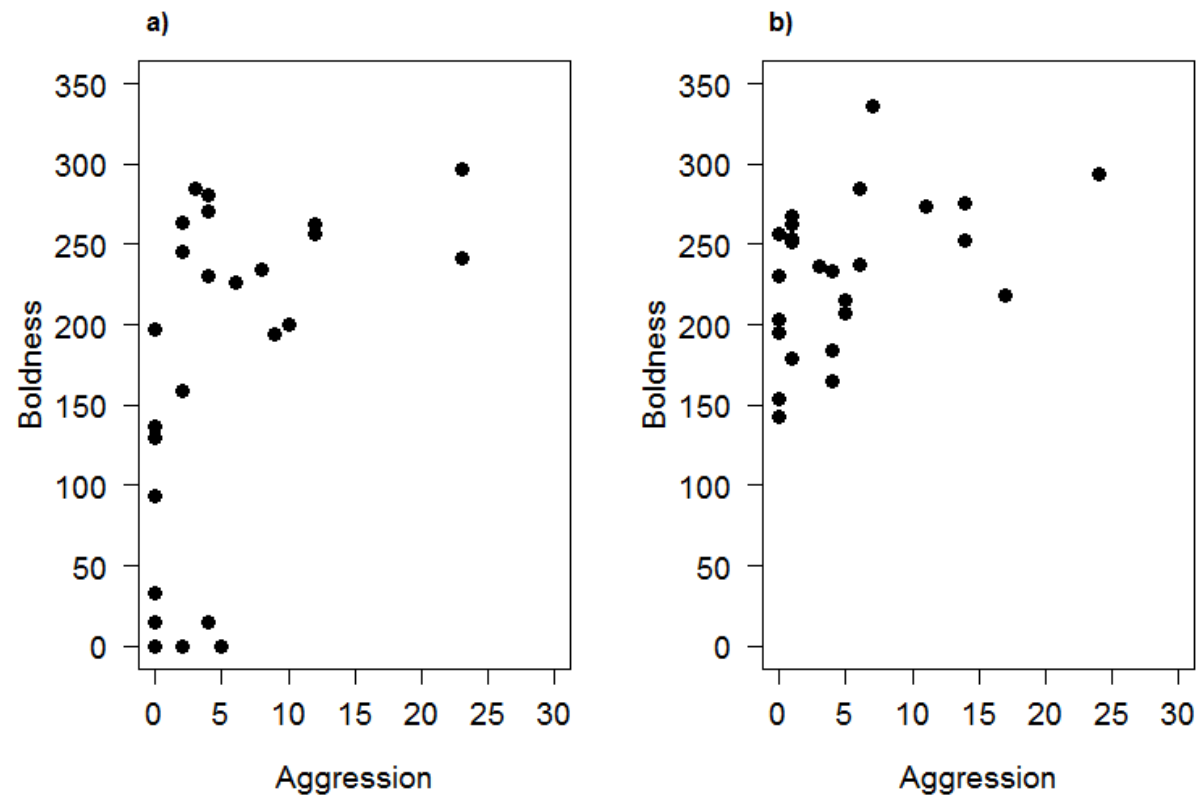


Fig. 1: Correlation between boldness and aggression in females of (a) LWT and (b) TL strains of zebrafish.

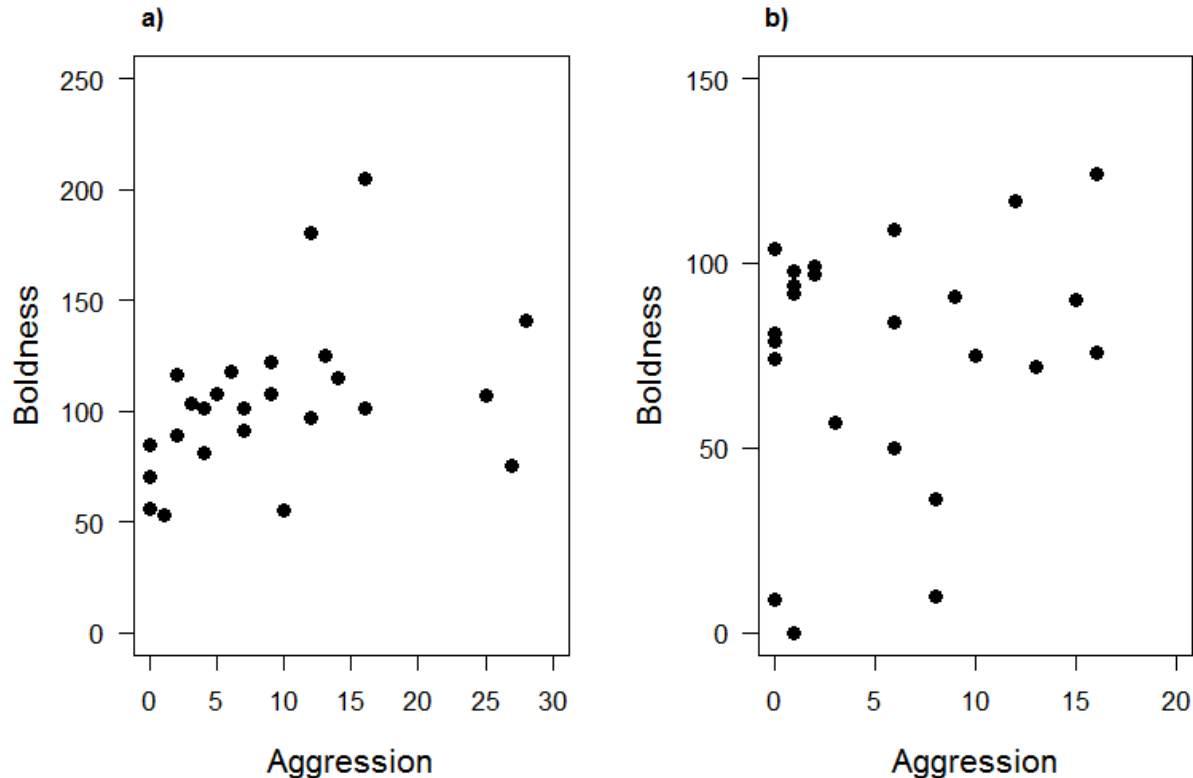


Fig. 2: Correlation between boldness and aggression in (a) the male and (b) the female guppies

Discussion

Evidence of a behavioural syndrome in females of two strains was noticed. It has been suggested that behavioural syndromes are more likely to be present in populations with high predation levels rather than in populations with little or no predation, such as in the populations tested in this study (Bell & Stamps, 2004; Bell, 2005; Dingemanse *et al.*, 2007, 2010). This is because directional selection by predators might act on multiple traits of a phenotype simultaneously, resulting in a strong correlation between such traits and hence the behavioural syndrome. It may be more advantageous for individuals to show behavioural plasticity across multiple contexts (Sih *et al.*, 2004a) because there are costs associated with rigidity, for example, an overly aggressive individual might be aggressive in situations where care is needed, such as towards offspring (Johnson & Sih, 2005) or mates (Wingfield *et al.*, 1990).

There was no evidence of a boldness-aggression behavioural syndrome in the female guppies but there was in the males. It is not clear why there

were differences between the sexes. The males were more risk prone and curious than the females and so it could be that the behaviours expressed by the males reflected their adaptive responses to what was optimal in the two contexts (Dingemanse *et al.*, 2007) hence the strong positive correlation found between both traits. The notion of behavioural syndromes opposes the adaptive hypothesis (Wilson, 1998), which suggests that personality traits are context specific and involve organisms adjusting to the prevailing conditions in their environment (Wilson, 1998). For example, pumpkinseed sunfish, *Lepomis gibbosus*, were consistent with respect to individual variation when exposed to a non-threatening stimulus and also to a predator. However, there was no correlation between these variations across both situations (Coleman & Wilson 1998). Similarly, male Iberian rock lizards, *Lacerta monticola*, that were bold when exposed to high risk predatory attacks, were not particularly bold when faced with low risk predatory attacks (Lopez *et al.*, 2005). These studies indicate that organisms show adaptive

individual differences to the prevailing selection pressures in their environment in order to maximise fitness (Wilson, 1998; Dingemanse *et al.*, 2007). An important ecological implication of behavioural syndromes is that they involve tradeoffs that may reduce behavioural plasticity and they may be maladaptive in specific contexts (Sih *et al.*, 2004a, b). Furthermore, correlated traits are forced to evolve together and this may constrain the ability of populations, where behavioural syndromes persist,

to respond to selection (Dochtermann & Jenkins, 2007).

Overall, there was some evidence of a boldness and aggression syndrome in females of two of the zebrafish strains and in the male guppies, but, given the limited correlation of these traits within the populations studied, this syndrome was probably due to adaptations to prevailing selection pressures rather than due to genetic constraints (Dingemanse *et al.*, 2007).

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