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Repeatability of Boldness and Aggression in the Zebrafish and the Guppy

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Abstract- Recent studies suggest that personality traits that were previously thought to be plastic may be repeatable within individuals in a population. Repeatability measures how consistent personality traits are.In this study we tested whether boldness and aggression were repeatable in both sexes of three strains of zebrafish(London Wild Type (LWT), Tupfel Long fin (TL) and Nacre) and one population of guppies. Boldness and aggression were highly repeatable in both sexes of the three zebrafish strains, and boldness (not aggression) was repeatable in the population of guppies. The high repeatability estimates in the zebrafish trials suggested that the traits were potentially heritable.

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Repeatability of Boldness and Aggression in the Zebrafish and the Guppy

T. O. Ariyomo [α], T. Jegede [σ] & P. J. Watt [ρ]

Abstract- Recent studies suggest that personality traits that were previously thought to be plastic may be repeatable within individuals in a population. Repeatability measures how consistent personality traits are.In this study we tested whether boldness and aggression were repeatable in both sexes of three strains of zebrafish(London Wild Type (LWT), Tupfel Long fin (TL) and Nacre) and one population of guppies. Boldness and aggression were highly repeatable in both sexes of the three zebrafish strains, and boldness (not aggression) was repeatable in the population of guppies. The high repeatability estimates in the zebrafish trials suggested that the traits were potentially heritable.

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I. Introduction

Conventional ecological theory assumes that individuals should show behavioural plasticity in relation to the situations they encounter in their environment and the behavior be reversible (Sih et al. 2004a; Bell, 2007a; Edward & Jon, 2013; Tibblin et al., 2016). However, recent findings have shown that individuals show distinct behaviours that are consistent over time and across contexts and these behaviours are often referred to as personality traits, coping styles or temperaments (Koolhaas et al., 1999; Réale et al., 2007; Wolf &Weissing, 2012). Personality traits have been observed in many groups of animals and these traits have been shown to be linked to fitness because they can influence foraging, reproduction and survival (Dingemanse&Réale, 2005; Ariyomo & Watt, 2012). The implication of such consistency in behaviour over time is that it would impose a constraint on behavioural plasticity and prevent individuals from optimally adjusting their behaviour to the prevailing conditions in the environments they encounter (Dingemanse et al., 2002; Sih et al., 2003; Sih et al., 2004a, b; Bell, 2007b).

Two personality traits under focus in this study are boldness and aggression. Boldness is the propensity of an individual to take risks in an unfamiliar situation (Brown et al., 2007), while aggression is any sequence of behaviour that is deemed confrontational (Olivier & Young, 2002). Aggression can be used to gain access to food or mates, protect offspring or to establish dominance (Davies & Houston, 1981; Stamps, 1994; Larson et al., 2006; Spence & Smith, 2006; Spence et al., 2008; Paull et al., 2010; Nephew et al., 2010; Davis et al., 2011).

This study was aimed at determining whether boldness and aggression were repeatable in three strains of zebrafish, *Daniorerio*(London Wild Type (LWT), Tupfel Long fin (TL) and Nacre),and the guppy, *Poeciliareticulata*, two species that have been used extensively as comparative and experimental model species in biology.If individuals show consistency in behaviour and there is a wide range of variations among them, this would indicate that the variations in behaviour among individuals may have a genetic basis (Edward & Jon, 2013). Under normal conditions selection would act upon this that of variation. However, if there is inconsistency in the display of behaviour by individual within a population, then factors (such as hormonal changes) order than genetic factor may be responsible (Edward & Jon, 2013; Trillmich et al., 2015).

II. Material and Methods

All the fish used in these experiments came from stock maintained in the Department of Animal and Plant Sciences at the University of Sheffield. Fish were sexed and the females were separated from the males. Each fish was housed separately before the trials. 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. All fish were fed twice daily with brine shrimp and dry fish food. To ensure uniformity in hunger level, feeding took place after the experimental trials.Behavioural testing for boldness and aggression was similar to that described in Ariyomo and Watt (2012, 2013a, b, 2015) and Ariyomo et al., (2013).

a) Test of boldness

The open field test (Ariyomo & Watt, 2012; Ariyomo & Watt, 2013a, b; Ariyomo et al., 2013; Ariyomo & Watt, 2015; Burns, 2008; Walsh & Cummins, 1976) was used to determine boldness in the three strains of zebrafish (London Wild Type (LWT), Tupfel Long fin (TL) and Nacre) and in one population of guppies. A tank (48 cm x 23 cm x 26 cm) with a gridded base, marked into

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24 rectangles (8 cm x 5.5 cm; Fig. 1), was filled with three litres of dechlorinated water heated to 26°C. The tank was covered with green cardboard. A fish was placed into the tank and allowed 60 s to acclimatise. The number of lines crossed and how well the fish utilised the inner and outer portions of the tank in 180 s after the acclimatisation period were used as a measure of boldness. Fish that crossed the highest number of lines while effectively utilising the tank were deemed bold. Fish that crossed the least number of lines and did not utilise the tank were deemed shy. The time each fish spent freezing over a period of 180 s was also recorded. Freezing time was excluded from the analysis because the majority of the fish tested did not freeze.

Lighting during the experiments consisted of two 18 W daylight fluorescent tubes placed approximately 34 cm above the tank. 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 in this way. After each trial, the water in the test tank was replaced. Each fish was tested twice over two consecutive days. After these tests, the green cardboard was replaced with brown cardboard and each fish was retested (alternate form test) twice over two consecutive days.

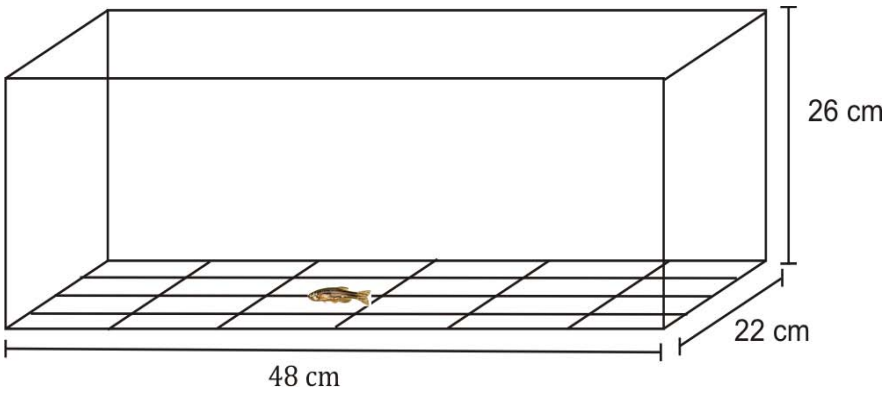

Fig.1: Diagrammatic representation of the open field test (Ariyomo & Watt, 2012; Ariyomo et al., 2013)

b) Test of aggression

The mirror test was used to test for aggression (Ariyomo & Watt, 2012; Ariyomo & Watt, 2013a, b; Ariyomo et al., 2013; Ariyomo & Watt, 2015; Gerlai et al.,2000; Moretz et al.,2007a, b). All individuals were tested on two consecutive days. A test tank (36 cm x 25 cm x 18 cmwas filled with six litres of water and a mirror (45 cm x 38 cm) was placed at the side of the tank at an angle of 22.5° (Fig. 2). Lighting was the same as that used in the open field test. The same batch of zebrafish and guppies that were used in the open field test were tested for aggression. Prior to the introduction of a fish into the test tank, the mirror was covered with dark Perspex and the fish was allowed to acclimatise for 60 s. After this period, the dark Perspex was removed and the behaviour of the fish was monitored for 300 s.

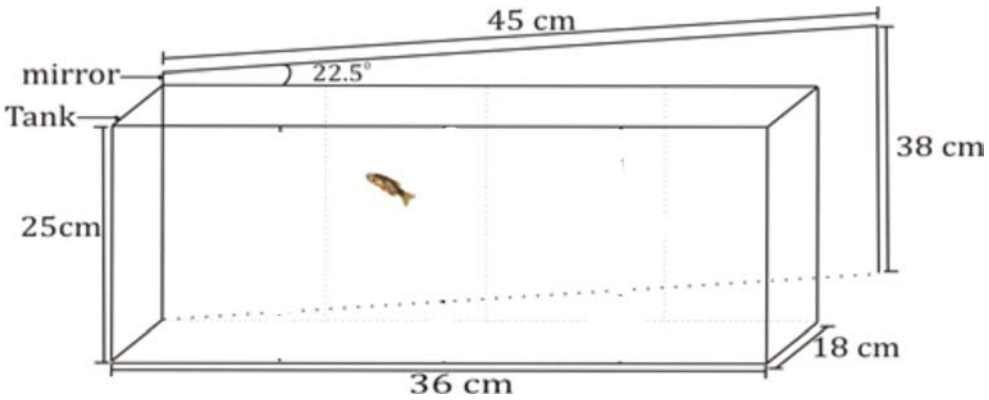

Fig.2: Diagrammatic representation of the mirror test (Ariyomo & Watt, 2012; Ariyomo et al., 2013 adapted from Gerlai et al.,2000).

The number of bites, displays and fast bouts of swimming the fish made towards its mirror image were counted and recorded. The total number of aggressive interactions was used as a measure of aggression.

III. Data Analysis

The variance components of boldness and aggression were estimated using a one-way analysis of variance (ANOVA). Repeatability *(r)*was calculatedas an intraclass correlation coefficient (Sokal&Rohlf, I981), using $r = S^2_A / (S^2 + S^2_A)$. Where S^2_A is the among-group variance component and S^2 is the within-group variance component, calculated from the mean squares in the ANOVA and given as $S^2_A = (MS_A - MS_W)/n_o$ and $S^2 = MS_W$. Where MS_A is the between-individual mean square, MS_W within-individual mean square and n_o is a coefficient related to the samplesize per group in the analysis of variance (Lessels&Boag, 1987). The standard error for repeatability based on F ratios was calculated according to Becker (1992).

IV. Results

a) Repeatability of boldness in the zebrafish

Boldness was repeatable in both males and females of all the strains of zebrafish in both the first test and the alternate form of the test. Repeatability estimates for boldness ($r \pm$ SE) ranged from 0.34 ± 0.27 to 0.88 ± 0.03 (Tables 1, 2 and 3 for details).

Table 1: Repeatability of the number of lines crossed (boldness) by the female and the male Nacre zebrafish strain, their F ratio, degrees of freedom (df) and their corresponding p values.

Source of Variation	F ratio (df)	r ± SE	P
Number of lines crossed			
Open field first test			
All individuals (irrespective of sex)	15.74 (49,50)	0.88 ± 0.03	<0.001
Females	12.14 (24,25)	0.85 ± 0.06	<0.001
Males	6.577 (24,25)	0.74 ± 0.09	<0.001
Alternate form test			
All individuals (irrespective of sex)	5.10 (49,50)	0.67 ± 0.08	<0.001
Females	12.14 (24,25)	0.85 ± 0.06	<0.001
Males	3.62 (24,25)	0.40 ± 0.17	>0.001
Across tests			
All individuals (irrespective of sex)	13.31(49,150)	0.75 ± 0.03	<0.001
Females	9.57(24,75)	0.68 ± 0.05	<0.001
Males	5.96(24,75)	0.55 ± 0.06	<0.001

Table 2: Repeatability of the number of lines crossed (boldness) by the female and the male LWT zebrafish strain, their F ratio, degrees of freedom (df) and their corresponding *p* values.

Source of Variation	F ratio (df)	r ± SE	*P*
Number of lines crossed			
Open field first test			
All individuals (irrespective of sex)	5.02 (49,50)	0.67 ± 0.08	<0.001
Females	6.30 (24,25)	0.73 ± 0.09	<0.001
Males	2.21 (24,25)	0.38 ± 0.17	0.027
Alternate form test			
All individuals (irrespective of sex)	6.64(49,50)	0.74 ± 0.06	<0.001
Females	14.11 (24,25)	0.85 ± 0.06	<0.001
Males	2.03 (24,25)	0.34 ± 0.27	0.043
Across tests			
All individuals (irrespective of sex)	11.89(49,150)	0.73 ± 0.03	<0.001
Female	15.54 (24,75)	0.78 ± 0.03	<0.001
Male	4.47(24,75)	0.48 ± 0.06	<0.001

Table 3: Repeatability of the number of lines crossed (boldness) by the female and the male TL zebrafish strain, their F ratio, degrees of freedom (df) and their corresponding *p* values.

Source of Variation	F ratio (df)	r ± SE	*P*
Number of lines crossed			
Open field first test			
All individuals (irrespective of sex)	5.75(49,50)	0.70 ± 0.07	<0.001
Females	2.56 (24,25)	0.44 ± 0.16	0.011
Males	10.30 (24,25)	0.82 ± 0.07	<0.001
Alternate form test			
All individuals (irrespective of sex)	8.08(49,50)	0.78 ± 0.56	<0.001
Females	21.32 (24,25)	0.91 ± 0.04	<0.001
Males	4.58 (24,25)	0.64 ± 0.12	>0.001
Across tests			
All individuals (irrespective of sex)	8.27(49,150)	0.64 ± 0.03	<0.001
Females	5.90(24,75)	0.55 ± 0.06	<0.001
Males	10.11(24,75)	0.69 ± 0.04	<0.001

b) Repeatability of aggression in the zerbrafish

Aggression was repeatable in both sexes in all strains tested and ranged from 0.60 ± 0.13 to 0.88 ± 0.03 (see Tables 4, 5 and 6 in the appendix for details).

Table 4: Repeatability of the mean number of aggressive interactions made towards the mirror image by the Nacre zebrafish strain, their F ratio, degrees of freedom (df) and their corresponding *p* values.

Source of Variation	F ratio (df)	r ± SE	*P*
Aggressive interactions in Nacre strain			
All individuals (irrespective of sex)	6.69(49,50)	0.76 ± 0.06	<0.001
Females	4.02 (24,25)	0.60 ± 0.13	<0.001
Males	4.49 (24,25)	0.79 ± 0.08	<0.001

Table 5: Repeatability of the mean number of aggressive interactions made towards the mirror image by the LWT zebrafish strain, their F ratio, degrees of freedom (df) and their corresponding *p* values.

Source of Variation	F ratio (df)	r ± SE	*P*
Aggressive interactions in LWT strain			
All individuals (irrespective of sex)	16.06 (49,50)	0.88 ± 0.03	<0.001
Females	13.95 (24,25)	0.87 ± 0.05	<0.001
Males	19.19 (24,25)	0.79 ± 0.08	<0.001

Table 6: Repeatability of the mean number of aggressive interactions made towards the mirror image by the TL zebrafish strain, their F ratio, degrees of freedom (df) and their corresponding *p* values.

Source of Variation	F ratio (df)	r ± SE	*P*
Aggressive interactions in TL strain			
All individuals (irrespective of sex)	5.35(49,50)	0.69 ± 0.07	<0.001
Females	5.72 (24,25)	0.70 ± 0.10	<0.001
Males	5.17 (24,25)	0.68 ± 0.11	<0.001

c) Repeatability of boldness in the guppy

Boldness was repeatable in male guppies in both the first test ($r \pm SE = 0.47 \pm 0.16$, $p < 0.001$) and the alternate form of the test ($r \pm SE = 0.52 \pm 0.15$, $p = 0.037$). In the female guppies, boldness was not repeatable in the first test but was repeatable in the alternate form of the test (-0.26 ± 0.19, $p = 0.902$ and 0.66 ± 0.11, $p < 0.001$ respectively: Table 8).

Table 8: Repeatability of number of lines crossed by the female and the male guppies, their F ratio, degrees of freedom (df) and their corresponding *p* values.

Source of Variation	F ratio (df)	r ± SE	*P*
Number of lines crossed			
Openfield first test			
All individuals (irrespective of sex)	1.67 (49,50)	0.14 ± 0.14	0.037
Females	0.59 (24,25)	-0.26 ± 0.19	0.902
Males	2.76 (24,25)	0.47 ± 0.16	<0.001
Alternate form test			
All individuals (irrespective of sex)	5.10 (49,50)	0.67 ± 0.08	<0.001
Females	4.9 (24,25)	0.66 ± 0.11	<0.001
Males	3.18 (24,25)	0.52 ± 0.15	>0.001
Across tests			
All individuals (irrespective of sex)	4 .08(49,150)	0.44 ± 0.05	<0.001
Females	1.95(24,75)	0.19 ± 0.08	0.018
Males	4.03(24,75)	0.43 ± 0.07	<0.001

d) Repeatability of aggression in the guppy

Aggression was not repeatable for either sexes (female: $r \pm SE$: 0.13 ± 0.20, $p = 0.263$ and male:$r \pm SE$: 0.14 ± 0.20, $p = 0.247$: Table 9).

Table 9: Repeatability of aggression in the guppies, their F ratio, degrees of freedom (df) and their corresponding *p* values.

Source of Variation	F ratio (df)	r ± SE	*P*
Aggressive interactions in the guppies			
All individuals (irrespective of sex)	1.43 (49,50)	0.18 ± 0.14	0.107
Females	1.29 (24,25)	0.13 ± 0.20	0.263
Males	1.32 (24,25)	0.14 ± 0.20	0.247

V. Discussion

Boldness and aggression were highly repeatable in both males and females of all three strains of zebrafish regardless of when the test was conducted and the colour of the test tank. This consistency in the behavioural pattern suggests that multiple measures of these personality traits may not be necessary (Dohm,2002; Falconer & Mackay 1996; Bell et al., 2009). Boldness and aggression varied among individuals within the strains but the variations were consistent, indicating that the observed variation may be genetic (Falconer & Mackay, 1996). Alternatively, high repeatability estimates reported here could have been due to the short interval between the test and retest period (Bell et al., 2009). It has been found that repeatability estimates can decrease as the time between testing increases, possibly because of changes in developmental stage or age leading to differences in the traits (Bell et al., 2009; Norin&Malte, 2011). The implication of such consistency in behaviour over time is that it would impose a constraint on behavioural plasticity and prevent individuals from optimally adjusting their behaviour to the prevailing conditions in the environments they encounter (Dingemanse et al., 2002; Sih et al. 2003; Sih et al., 2004a, b; Bell, 2007b).

Boldness was repeatable in the males guppies in the first open field test and in the alternate form of the test. However, boldness was not repeatable in the first test for the female guppies, but it was repeatable in the alternate form of the test. The fact that male guppies expressed more consistent behaviour in the open field

than females has been shown previously (Griffiths &Magurran, 1998), and it is possible that behavioural variation seen in the females is linked to their ovarian cycle (Warren & Callaghan, 1975). Variation in the optimal behavioural strategies of the males and females may also account for differences in the repeatability (Bell et al., 2009) such that males may take more risks while females are more interested in foraging (Brown & Warburton, 1997; Magurran&Macías Garcia, 2000).

Aggression was not repeatable in both the male and the female guppies. The implication is that the animals did not respond to the mirror in the same way during the trials, which may be due to the fact that guppies are not overly aggressive (Kodric-Brown, 1992).Moreover, behavioural variation in female guppies has been linked to their ovarian cycle (Warren & Callaghan, 1975), but it is not known why aggression in the males was not consistent.

In conclusion, overall, boldness was repeatable in the three strains of zebrafish and to some extent in the guppies, while aggression was repeatable in the three strains of zebrafish but not in the guppies. Bell et al. (2009) argued that differences in repeatability of behaviour between male and females may occur but the degree to which this occurs may depend on the behaviour tested, the test interval, the age and the species tested. The high repeatability in the zebrafish trials suggested that the traits were potentially heritable (Ariyomo et al., 2013).

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