



Recent social conditions affect boldness repeatability in individual sticklebacks



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Animal personalities are ubiquitous across the animal kingdom and have been shown both to influence individual behaviour in the social context and to be affected by it. However, little attention has been paid to possible carryover effects of social conditions on personality expression, especially when individuals are alone. Here we investigated how the recent social context affected the boldness and repeatability of three-spined sticklebacks, *Gasterosteus aculeatus*, during individual assays. We housed fish either solitarily, solitarily part of the time or socially in groups of four, and subjected them twice to a risk-taking task. The social conditions had a large effect on boldness repeatability, with fish housed solitarily before the trials showing much higher behavioural repeatability than fish housed socially, for which repeatability was not significant. Social conditions also had a temporal effect on the boldness of the fish, with only fish housed solitarily taking more risks during the first than the second trial. These results show that recent social conditions can thus affect the short-term repeatability of behaviour and obfuscate the expression of personality even in later contexts when individuals are alone. This finding highlights the need to consider social housing conditions when designing personality studies and emphasizes the important link between animal personality and the social context by showing the potential role of social carryover effects.

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It is now well known that animal personalities are omnipresent in the animal kingdom (Réale, Dingemanse, Kazem, & Wright, 2010; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004). These consistent individual differences in behaviour play a fundamental role in the social organization of animals (Aplin et al., 2013; Croft et al., 2009; Pike, Samanta, Lindström, & Royle, 2008; Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Webster & Ward, 2011) and have considerable impact on a range of evolutionary and ecological processes (Réale et al., 2010, 2007; Sih et al., 2012; Smith & Blumstein, 2008; Wolf & Weissing, 2012). However, while the number of studies that document the existence of animal personalities continues to grow (Réale et al., 2007; Sih et al., 2012), there is still a lack of knowledge about the stability of personality traits and the factors that may affect it (Bell & Stamps, 2004; Dingemanse, Kazem, Réale, & Wright, 2010; Laskowski & Pruitt, 2014).

The social environment is one of the major modulating factors of individual behaviour (Van den Bos, Jolles, & Homberg, 2013;

Webster & Ward, 2011), and may both restrict and enhance individuals' behavioural responses (Webster & Ward, 2011). For example, individual fish are more active and exploratory in a social group (Gómez-Laplaza & Morgan, 1986; Jolles et al., 2014; Webster, Ward, & Hart, 2007), but more persistent in their attention when alone (Gómez-Laplaza & Morgan, 1986). Personality differences affect individual behaviour in a social context, such as risk-taking behaviour (Jolles et al., 2014; Magnhagen & Bunnefeld, 2009), leadership (Harcourt, Ang, Sweetman, Johnstone, & Manica, 2009; Jolles et al., 2014; Kurvers et al., 2009), producer-scrounger dynamics (Dyer, Croft, Morrell, & Krause, 2009; Jolles, Ostojic, & Clayton, 2013; Kurvers et al., 2010) and the social organization of individuals (Aplin et al., 2013; Croft et al., 2009; Pike et al., 2008). However, the behaviour and personality of individuals are also strongly affected by the social context (Webster & Ward, 2011), and individuals often behave rather plastically across social contexts (David, Cézilly, & Giraldeau, 2011; Morand-Ferron, Wu, & Giraldeau, 2011; Van Oers, Klunder, & Drent, 2005; Webster et al., 2007). Individuals thereby modulate their behaviour based on that of others (Herbert-Read et al., 2012; Reeb, 2000; Webster & Ward, 2011), such as that related to the composition of the group (Magnhagen & Staffan, 2005) and the sex (Piyapong et al., 2010;

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Schuett & Dall, 2009) and personality (Jolles et al., 2015; Magnhagen & Bunnefeld, 2009; Van Oers et al., 2005) of their group mates. For example, although in three-spined sticklebacks, *Gasterosteus aculeatus*, risk-taking behaviour and leadership of individuals in a social context are positively linked to their propensity to take risks when alone ('boldness'), this effect can be strongly enhanced or reduced by the personality of their current (Harcourt et al., 2009; Jolles et al., 2015) and previous group mates (Jolles et al., 2014). Consequently, in a social group, the behavioural variance among individuals tends to be reduced (Gómez-Laplaza & Morgan, 1986; Herbert-Read et al., 2012; Magnhagen & Bunnefeld, 2009) and the personalities of individuals, quantified in individual assays, only expressed to a certain extent (Castanheira, Herrera, Costas, Conceição, & Martins, 2013; Magnhagen & Bunnefeld, 2009; Webster et al., 2007). However, in relatively stable social environments individuals are more likely to repeat certain behaviours by positive feedback from experience and optimal behaviour via repeated interactions (Harcourt et al., 2009; Laskowski & Pruitt, 2014; Nakayama, Stumpe, Manica, & Johnstone, 2013). These interactions may increase the behavioural variability among individuals (Laskowski & Pruitt, 2014) and the behavioural repeatability of individuals (Laskowski & Bell, 2013; Wolf, Van Doorn, & Weissing, 2011).

If the effect of the social context is so strong, could it be that it still affects the subsequent expression of personality (and thus its repeatability) when individuals are alone? This carryover effect may be likely, as the prior social context has already been shown to affect behaviour in later social contexts in terms of an individual's shoaling decisions (Gómez-Laplaza, 2009), risk-taking behaviour (Frost, Winrow-Giffen, Ashley, & Sneddon, 2007; Jolles et al., 2014) and leadership (Jolles et al., 2014). Furthermore, it takes time for individuals to adjust between (social) environments, resulting in habituation (decline in behaviour) and/or acclimatization (change in behaviour) responses (Biro, 2012; Budaev, 1997; Gómez-Laplaza & Morgan, 2000; Martin & Réale, 2008), such as individuals becoming less active over solitary test trials (Martin & Réale, 2008) and showing more stable behavioural patterns after longer social isolation (Biro, 2012). Behavioural repeatability may be further compromised at the group level by the large variability in the way individuals are affected by prior social experiences (Jolles et al., 2014), and the speed (Rodríguez-Prieto, Martín, & Fernández-Juricic, 2011) and extent to which they adjust to environmental change (Dingemans & Wolf, 2013). For example, shy individuals are less affected by previous social experiences than bold individuals (Jolles et al., 2014) and show higher behavioural plasticity between social contexts, in three-spined sticklebacks, perch, *Esox lucius*, and zebra finches, *Taeniopygia guttata* (Jolles et al., 2014; Magnhagen & Bunnefeld, 2009; Magnhagen & Staffan, 2005; Schuett & Dall, 2009; Webster et al., 2007).

Here we investigated to what extent recent social conditions affect the boldness and repeatability of individual three-spined sticklebacks that were either solitarily housed, solitarily housed part of the time or socially housed in small groups of four prior to two trials of a boldness test (see Table 1). As only fish in the solitary treatment had time to habituate and acclimatize to being alone, we

hypothesized that these fish would show the most risk-taking behaviour due to lower stress of isolation. We also hypothesized that solitary fish would show the highest repeatability in their behaviour as they had more time for social modulation effects to fade and individual variability in acclimatization responses to stabilize. Fish that were housed solitarily only part of the time were predicted to show intermediate levels of repeatability. We assessed behavioural repeatability by three of the most used indices to get a full picture of personality expression following Bell, Hankison, and Laskowski (2009): agreement repeatability, the extent to which individual differences in trait scores are maintained over time relative to the change of the group (Biro & Stamps, 2015), consistency repeatability, which measures the agreement in relative measurements between individuals (Nakagawa & Schielzeth, 2010), and raw rank order consistency. The three-spined stickleback is an excellent model system to investigate these questions on personality and social dynamics (see e.g. Bell & Sih, 2007; Bell & Stamps, 2004; Harcourt et al., 2009; Jolles et al., 2014, 2015; Laskowski & Bell, 2014; Pike et al., 2008; Ward, Holbrook, Krause, & Hart, 2005; Webster et al., 2007; Webster, Ward, & Hart, 2009), as it is a social species, with a strong tendency to shoal most of the year (Huntingford & Coyle, 2010; Ostlund-Nilsson, Mayer, & Huntingford, 2010), and is also physically and behaviourally robust, and can thus be kept both solitarily and in groups in a laboratory environment (Huntingford & Ruiz-Gomez, 2009).

METHODS

Subjects and Housing

We collected three-spined sticklebacks using a sweep net from a tributary of the river Cam, near Cambridge, U.K., and housed them in an environmentally controlled laboratory for at least 4 months before the start of experiments. Ambient temperature was maintained at 14 °C and the photoperiod at 12:12 h light:dark. Fish were kept socially (ca. 200 fish) in a large glass holding aquarium (120 × 60 cm and 60 cm high) with artificial plants, aeration and under-gravel filtration, and fed frozen bloodworms (chironomid larvae) ad libitum once daily. During the experimental period, fish were housed in custom holding tanks (60 × 30 cm and 40 cm high) lined with gravel and divided lengthwise into six compartments (30 × 12 cm and 15 cm depth) by opaque acrylic partitions. Of each tank, five compartments were used to house fish and contained an artificial plant; the remaining compartment contained an under-gravel filter. The partitions prevented fish from seeing conspecifics in adjacent compartments and minimized the transfer of olfactory cues. All fish were of similar length (41 ± 0.7 mm) and age (ca. 12 months) and were taken from a single population to minimize population-specific effects that may influence personality (Bell, 2005). The temperature and photoperiod regime in the laboratory resemble early spring/late autumn conditions, and prevented the fish from coming into breeding condition (Borg, Bornestaf, & Hellqvist, 2004; Ostlund-Nilsson et al., 2010). Therefore the sex of the fish was not determined. Fish had not been used in any previous experiments.

Boldness Test

To investigate an individual's propensity to take risks ('boldness'), we subjected them individually to one of eight identical white acrylic tanks (70 × 15 cm and 30 cm high) that contained gravel sloping from a deep area (14 cm depth) to an increasingly shallow 'exposed' area (4 cm depth at the other side). The deep area was covered by semitransparent green acrylic that protruded 10 cm from the back of the tank to provide shelter ('cover'). We defined

Table 1
Overview of the experimental schedule

Treatment	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6		
Solitary	Social	Social	<i>Alone</i>	<i>Alone</i>	T1	<i>Alone</i>	T2	End
Partial solitary	Social	Social	Social	Social	T1	<i>Alone</i>	T2	End
Social	Social	Social	Social	Social	T1	Social	T2	End

Periods when individuals were alone are shown in italics. Boldness test trials were conducted at the start of days 5 (T1) and 6 (T2).

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