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The role of social attraction and its link with boldness in the collective movements of three-spined sticklebacks

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Social animals must time and coordinate their behaviour to ensure the benefits of grouping, resulting in collective movements and the potential emergence of leaders and followers. However, individuals often differ consistently from one another in how they cope with their environment, a phenomenon known as animal personality, which may affect how individuals use coordination rules and requiring them to compromise. Here we tracked the movements of pairs of three-spined sticklebacks, *Gasterosteus aculeatus*, separated by a transparent partition that allowed them to observe and interact with one another in a context containing cover. Individuals differed consistently in their tendency to approach their partner's compartment during collective movements. The strength of this social attraction was positively correlated with the behavioural coordination between members of a pair but was negatively correlated with an individual's tendency to lead. Social attraction may form part of a broader behavioural syndrome as it was predicted by the boldness of an individual, measured in isolation prior to the observation of pairs, and by the boldness of the partner. We found that bolder fish, and those paired with bolder partners, tended to approach their partner's compartment less closely. These findings provide important insights into the mechanisms that govern the dynamics and functioning of social groups and the emergence and maintenance of consistent behavioural differences.

Social animals may benefit from grouping due to reduced predation risk, earlier predator detection and greater foraging success (Krause & Ruxton, 2002; Pitcher & Parrish, 1993). At the same time, grouping may entail costs in the form of increased competition and predator attraction (Krause & Ruxton, 2002). To ensure that individuals reap the full benefits of grouping, they must coordinate their behaviour with other group members (Conradt & Roper, 2009; Van Vugt, 2006), resulting in collective movements and decisions (Couzin et al., 2011; Miller, Garnier, Hartnett, & Couzin, 2013) and the possible emergence of leaders and followers (King, Johnson, & Van Vugt, 2009; Krause & Ruxton, 2002). Focus on the mechanisms that govern such collective behaviour may increase our understanding of the social organization and dynamics within and across groups, from aggregating insects to human societies (Conradt & List, 2009; King et al., 2009).

Group movements and decisions can often be explained by individuals following simple rules (Couzin & Krause, 2003; Couzin, Krause, Franks, & Levin, 2005; Sumpter, 2006). However, individuals often behave consistently different from one another, now mostly referred to as animal personality (Réale, Dingemanse, Kazem, & Wright, 2010; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004), with large potential consequences for the functioning and structure of social groups (Wolf & Krause, 2014). Particularly relevant in the context of collective behaviour is boldness, i.e. individual variation in the tendency to take risks. Bolder individuals may be more likely to lead, so as to maximize their foraging opportunities (Biro & Stamps, 2008; Jolles, Ostojić, & Clayton, 2013; Kurvers, Prins, et al., 2010), whereas shy individuals may be more likely to group (Bell & Sih, 2007) and respond to conspecifics (Croft et al., 2009; Harcourt, Biau, Johnstone, & Manica, 2010; Kurvers, van Oers, et al., 2010; Pike, Samanta, Lindström, & Royle, 2008; Trompf & Brown, 2014)

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for antipredator benefits (Krause & Ruxton, 2002). Although previous work has confirmed that bolder individuals are more likely to take the lead and shy individuals are more likely to follow (Harcourt, Ang, Sweetman, Johnstone, & Manica, 2009; Jolles et al., 2014; Kurvers et al., 2009; Nakayama, Harcourt, Johnstone, & Manica, 2012), the impact of boldness on social attraction during collective movement remains unclear.

Previous work that focused on the tendency for individuals to approach and interact with conspecifics, i.e. sociability, has revealed large ecological and evolutionary implications (Cote & Clobert, 2007; Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010; Réale et al., 2007). Also in the context of collective behaviour (Cote, Fogarty, & Sih, 2012; Dingemanse & Réale, 2005; Réale et al., 2007), sociable individuals have more and stronger social associations (Croft et al., 2009), have stronger grouping preferences (Cote et al., 2012), and play a key role in group exploration (Brown & Irving, 2014). However, studies typically measure the tendency of individuals to approach a static group of conspecifics or a larger over a smaller one (see Wright & Krause, 2006). Not only is this less relevant to the natural situation, where individuals can interact and respond to one another (see also Miller & Gerlai, 2007), but also the mechanistic role of sociability in coordination and leadership and the potential effects of social feedback remain unclear (Miller & Gerlai, 2008; Wilson, Krause, Dingemanse, & Krause, 2013). For example, sociability may be linked to the distance regulation between individuals (Krause, Hoare, Krause, Hemelrijk, & Rubenstein, 2000; Pitcher & Parrish, 1993), and thereby affect leading and following behaviour. Our aim in this study was to explore social attraction, i.e. the tendency for individuals to approach a partner, in the context of joint movement of pairs of stickleback fish. This allowed us to assess the impact of social attraction on collective behaviour and look at the role played by social feedback in a similar way to recent studies on boldness and leadership (Jolles et al., 2014; Nakayama, Stumpe, Manica, & Johnstone, 2013; Pettit, Perna, Biro, & Sumpter, 2013; Ward et al., 2013).

We repeatedly observed three-spined sticklebacks, *Gasterosteus aculeatus*, in a context in which they could rest under cover or explore an open, potentially risky environment. We first assessed the boldness of all fish by recording their behaviour in isolation, after which we subjected them to the same environment again but this time allowing observation of a conspecific through a transparent partition. By tracking the movements of both fish in and out of cover and determining their tendency to approach their partner's compartment, we aimed to determine (1) whether individuals are consistent in the strength of social attraction they exhibit, in an ecologically relevant setting, (2) what link may exist between the tendency for social attraction and boldness, (3) whether social attraction is influenced by the personality of a partner as well as that of the focal individual and (4) how social attraction varies during collective movements (when both fish are out of cover) compared to when fish are out alone, either during the initiation and return of such movements or during solitary trips. This approach of subjecting fish to a dynamic social context in which they can move with conspecifics as well as rest under cover provides a unique opportunity to describe important new aspects of sociability and risk-taking behaviour and their role in the mechanisms underlying collective behaviour.

METHODS

Overview

Ninety-six fish were tested repeatedly in a task in which they could either rest under cover or explore an open, potentially risky environment (risk-taking task). Two such task compartments were positioned adjacent to one another and separated by either an opaque or a transparent partition (see Fig. 1). First, we tested fish individually in the compartments separated by an opaque partition to investigate their propensity to explore a risky area when alone ('isolation stage'). Second, we tested fish in the risk-taking task again but now with the compartments separated by a transparent partition, thus allowing fish to see each other and interact ('pairing stage'). By testing fish twice in each stage we were able to get individual consistency scores of risk-taking behaviour when alone (boldness) and their tendency to approach the partner's compartment when together (social attraction). Third, we tested an additional 16 fish using the same procedure as above, but with a transparent instead of an opaque partition and an empty adjacent compartment during the isolation stage. This allowed us to ensure differences in behaviour between the two stages were not simply due to the transparency of the partition.

Subjects and Housing

We collected three-spined sticklebacks during the summers of 2010–2012 using a sweep net from a small branch of the River Cam (Cambridge, U.K.). Fish were taken from a single population to minimize population-specific genetic effects that may influence personality (Bell, 2005). After collection, fish were immediately housed in a temperature-controlled laboratory (14 ± 1 °C) with constant light regime (lights on from 0900 to 1900 hours), and kept in large, glass social-housing tanks (120×60 cm and 60 cm high) with artificial plants, aeration and under-gravel filtration. During this period before experiments, fish were fed frozen bloodworms (chironomid larvae) ad libitum once daily. As the temperature and photoperiod regime in the laboratory prevented the fish from becoming sexually mature (Borg, Bornestaf, & Hellqvist, 2004), we did not sex the fish.

We performed our experiments with four batches of fish ($N = 96$ total), which were about 6 months old at the time of testing. After an acclimatization period of at least 1 month, for each batch we randomly selected fish from the social-housing tanks controlling for size (mean ± SE: 44 ± 1 mm from tip of snout to caudal peduncle). Fish were subsequently housed in custom holding tanks (60×30 cm and 40 cm high) lined with gravel and divided lengthwise into six compartments (30×12 cm; 15 cm deep). Five of the compartments contained an artificial plant; the remaining compartment contained an under-gravel filter and was not used to house fish. Fish were randomly allocated to compartments. To minimize potential stress effects that may be caused by isolation, the compartments were divided by perforated transparent Perspex partitions, thus allowing fish to receive chemical and visual cues from conspecifics. After the experiments, fish were kept in the laboratory and used for additional behavioural experiments. Animal care and experimental procedures were approved by the Animal Users Management Committee of the University of Cambridge under a nonregulated procedures regime because of the nonintrusive and observational nature of our work.

Experimental Set-up

To investigate fish's willingness to take risks as well as their tendency to approach conspecifics during collective behaviour, we used a tank set-up as previously used in our laboratory for similar experiments (Harcourt et al., 2009; Jolles et al. 2014; Nakayama et al. 2012). In short, experiments were carried out in four identical experimental tanks (70×30 cm and 30 cm high), each divided by either an opaque or a transparent Perspex partition to create two long compartments (15 cm wide). Each compartment was lined with gravel in a slope ranging from a deep area (14 cm deep) that