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Grouping promotes risk-taking in unfamiliar settings

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ABSTRACT

Acting collectively in a group provides risk-reducing benefits. Yet individuals differ in how they take risks, with some being more willing than others to approach dangerous or unfamiliar settings. Therefore, individuals may need to adjust their behaviour when in groups, either as a result of perceiving greater safety or to coordinate collective responses, the latter of which may rely on within-group dynamics biased by group composition. In zebrafish we explored how these aspects of grouping affect risk-taking behaviour by comparing solitary to group conditions and testing the ability of group-member solitary responses to predict collective responses. We focused on approach-latency towards a novel object and an unusual food to test this, for shoals of five fish. There was no indication that collective latencies are predicted by how each fish responded when alone in terms of the extremes, the variance or the mean of group-member latency towards the unusual food and the novel-object. However, fish were overall faster and less variable in their approach when shoaling. This indicates lower risk aversion by individuals in groups, presumably as a result of group safety. An interesting consequence of the overall low risk-aversion in shoals is that more risk-aversive fish adjust their behaviour more than less risk averse fish.

1. Introduction

The benefits of being organised in groups have long been noted in many species (Scott, 1956). Threat detection and anti-predator functions are the most important examples, both of which depend on cooperation and synchronisation (Pitcher and Parrish, 1993). If information is successfully and rapidly distributed between group members then each member may spend less time on predator vigilance and more on feeding, while also improving efficiency when exploring areas for food (Magurran and Pitcher, 1983; Pitcher and Parrish, 1993; Laland and Williams, 1997). Further, the probability of an individual being attacked diminishes as group size increases because of dilution (Foster and Treherne, 1981) and the predator is less able to choose a specific target (Jeschke and Tollrian, 2007). Although these benefits should promote group formation, the tendency to group varies with local conditions (Magurran and Pitcher, 1983; Pitcher and Parrish, 1993). For example, killifish *Fundulus diaphanus* minimize competition by being individually spaced when sensing food odours and minimise risk by forming large aggregates when alarmed by cues from a dead conspecific. In more complex environments where both food and alarm cues are present, they average their response by forming smaller groups (Hoare et al., 2004). Therefore, group formation may depend on what is beneficial to individuals in each set of conditions.

Individuals of a range of species, however, exhibit consistent marked differences in their behavioural tendencies, including their willingness to take or avoid risk in unfamiliar or dangerous situations (Coleman and Wilson, 1998; Toms et al., 2010; Wolf and Weissing, 2012). Individual differences in risk-taking suggest different strategies: those taking less risk typically benefit from reduced mortality, whereas those taking more risk may benefit from more rewards and increased growth (Stamps, 2007). If individuals retain at least some aspects of their own risk-taking tendencies when they are in groups then group cohesion and unified responses may be disrupted (Ward et al., 2004; Webster et al., 2007; Magnhagen and Bunnefeld, 2009). Therefore, for the group to function, individuals should, at least partially, adjust their behavioural tendencies (Pitcher and Parrish, 1993; Jeschke and Tollrian, 2007; Miller and Gerlai, 2012; McDonald et al., 2016).

The benefits offered by organising into groups suggest that, in identical situations, being alone is more risky than being in a group (Magurran and Pitcher, 1983; Webster and Ward, 2011; Ward, 2012). Therefore, being in a group may facilitate less risk-aversive behaviour in all individuals. For example, individual fish become faster to approach food, more active and more explorative when in a group than when alone (Webster et al., 2007; Ward, 2012). This social facilitation of an increase in risk-taking behaviour is often attributed to the simple presence of others, and is arguably the result of the perceived safety

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offered by being organised in groups (Ryer and Olla, 1991; Guerin, 2009; Ward, 2012). Social facilitation of behavioural changes can be exhibited in both smaller and bigger groups, but the extent of the effect typically increases with group size (Ward et al., 2011; Ward, 2012) and may vary with individual tendencies, e.g. in risk-taking (Jolles et al., 2014).

Alternatively, changes to individual behaviour may simply be associated with the maintenance of group cohesion when responding collectively (Couzin and Krause, 2003). The collective responses of a group may arise from mechanisms of conformity, where individuals will progressively conform to the response of the majority or follow near-neighbours (Webster and Ward, 2011). However, majority responses may involve decisions made between individuals (Conradt and Roper, 2005; Sumpter et al., 2008; Couzin et al., 2011), which can be influenced by the nature of the individual differences between the animals comprising the group (Webster and Ward, 2011; Ioannou and Dall, 2016). On one hand, collective responses may reflect the mean behavioural tendency of individuals, but may also be limited by the extent to which differences between individuals affect the maintenance of group cohesion. For example, groups composed of bold fish are faster to approach food than if composed of shy fish (Dyer et al., 2009) and individual differences in feeding motivation can drive differences in grouping tendency, with hungrier fish being less likely to keep close to group mates (Ward et al., 2004). On the other hand, the majority may choose to follow a leader, such as a more reward-motivated or less risk-aversive individual (Krause et al., 1992; Krause et al., 2000; Ward et al., 2004). Consequently, collective (cohesive) responses would be largely determined by the behavioural response of leaders and the ability of followers to maintain short delays (Ioannou and Dall, 2016). Leadership can arise in larger and smaller groups (Couzin et al., 2005; Johnstone and Manica, 2011), but majority-decisions are generally facilitated in larger groups (Sumpter et al., 2008; Ward et al., 2008).

Fish groups are traditionally referred to as *schools* or *shoals*, with discriminations between the two relying on aspects of sociability and function; shoaling may refer generally to fish groups or those formed for social reasons, conversely schooling specifically refers to directed movement (Pitcher and Parrish, 1993). However, as Delcourt and Poncin (2012) point out, groups can be better characterised by precise metrics such as polarity (i.e. the level in which fish orient towards the same direction) and cohesion (i.e. the level in which fish stay close together). In zebrafish, larger shoals are less polarised and this could, arguably, be linked to the risk-reduction offered by more individuals staying together (Miller and Gerlai, 2012). However, cohesion and polarisation generally fluctuate, which may affect information transfer during zebrafish collective responses (Miller and Gerlai, 2011). To elucidate what drives collective response in zebrafish shoals, we first examine effects of social facilitation by comparing shoaling and solitary risk-taking in *Danio rerio*. We then examine the ability of shoal-member solitary response in predicting collective response, as a process of inter-member interactions. We aimed to identify any changes in behaviour due to social conditions and whether the solitary behaviour of shoal members determines their collective response.

The approach latency of individuals and shoals was used to indicate levels of risk-taking in two contexts, novel-object exploration and feeding on unusual food (Toms et al., 2010). First, we compared the individual response in a solitary condition (slowest solitary fish) to the individual response during shoaling (slowest shoal member). Based on the literature, we expected greater risk-taking by fish during shoaling, as compared to being alone (Webster et al., 2007; Ward, 2012). Second, the predictive power of shoal-member solitary behaviour was tested by examining whether collective latencies (i.e. until last fish, given cohesion was maintained) were: slower for shoals with members that have on average slower solitary responses (effect of general composition; Dyer et al., 2009), slower for shoals with members more dissimilar in their solitary response (degree of conformity; Ward et al., 2004), faster for shoals whose fastest member was particularly fast when alone (leadership by most reward-driven; Krause et al., 1992) and slower for shoals whose slowest member was particularly slow when alone (delay by most risk-aversive; Ioannou and Dall, 2016).

2. Methods

2.1. Animals and husbandry

Male *D. rerio* zebrafish were acquired from a local supplier and first kept individually (n = 50) in 15 L tanks (30 cm × 25 cm × 20 cm) and then as shoals of five (n = 10) in 25 L tanks (42 cm × 30 cm × 20 cm). Given strain variations in the supplier's stock were unknown, we used only males that show no strain preferences during shoaling (Snekser et al., 2010), which also removed the chance of mating during group-living and controlled for sex-related differences in risk-taking. The different tank sizes used gave reasonable space for the individuals and shoals. During individual housing, neighbouring tanks on either side (two individuals) were kept visible to control effects from social isolation. Housing tanks were enriched with shelter (plastic pipes), plants and soft sediment. The water in the tanks was filtered, regularly tested, kept at 25 ± 1 °C and maintained between 6.8–7.6 pH. Photoperiods were kept at 12 h light and 12 h dark (07.00–19.00) and food was provided daily (TetraMin® tropical flakes).

2.2. Behavioural tests

Fish were left to acclimatise to individual housing for a week and then tested individually in their solitary housing tanks. A week following individual (solitary) testing, all fish were randomly arranged in sets of five and housed together for a further week. This provided time for individuals to experience group living before being tested for their collective response as a shoal, carried out in the housing tanks of shoals. Both individual and shoal testing was repeated in two contexts: when exploring/inspecting a novel object and when feeding on unusual food-items (not previously offered to them in the laboratory). When tested individually, fish were given brine shrimp at the feeding test and 48 h later presented with a ~10 cm long plastic soldier figurine for the novel-object test. When tested in shoals, fish were given bloodworm at the feeding test and 48 h later presented with a ~12 cm long plastic dinosaur toy for the novel-object test. The location and time (11.00–12.00) items were presented were kept constant, but a change in food and objects maintained novelty and controlled for episodic-like memorisation of familiar items (Hamilton et al., 2016). Objects were lowered at an uncovered part of the tank by a pulley system to the bottom of the tank, at which point recording started. Food was released with a pipette from the top-edge of the front-facing tank-wall and recording started after release in the water. The experimenter remained hidden behind opaque sheets surrounding the tanks during tests. Individuals and shoals were given 300 s to approach the object or food and if no approach was noted within this period, latency was recorded as 300 s. Latency to approach the food was measured until starting to feed and latency to approach the novel object was measured until fish were within a distance of ~1.5 body lengths from the object, estimated through a digital grid from recordings (Kinovea© version 8; J. Charmant & Co.). In keeping with other studies (Magnhagen and Bunnefeld, 2009; McDonald et al., 2016), all fish had the same order of testing, both for social-conditions and context. Further, all shoals received the same items in either social condition. The order of testing and of previously experiencing particular items could have effects on latency. Importantly, however, it ensures that any carry-over effects from experience of previous items and from temporal order would be identical for all fish and therefore not contribute to inter-individual and inter-shoal variance (Wilson et al., 2012).

In order to validate responses as being collective we examined cohesion (ability to stay together) by identifying dispersal events and significant reductions in estimations of nearest-neighbour distances