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Assortative interactions revealed by sorting of animal groups

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Animals living in groups can show substantial variation in social traits and this affects their social organization. However, as the specific mechanisms driving this organization are difficult to identify in already organized groups typically found in the wild, the contribution of interindividual variation to group level behaviour remains enigmatic. Here, we present results of an experiment to create and compare groups that vary in social organization, and study how individual behaviour varies between these groups. We iteratively sorted individuals between groups of guppies, *Poecilia reticulata*, by ranking the groups according to their directional alignment and then mixing similar groups. Over the rounds of sorting the consistency of the group rankings increased, producing groups that varied significantly in key social behaviours such as collective activity and group cohesion. The repeatability of the underlying individual behaviour was then estimated by comparing the experimental data to simulations. At the level of basic locomotion, individuals in more coordinated groups displayed stronger interactions with the centre of the group, and weaker interactions with their nearest neighbours. We propose that this provides the basis for a passive phenotypic assortment mechanism that may explain the structures of social networks in the wild.

Group living can reduce predation risk (Foster & Treherne, 1981; Hamilton, 1971; Magurran & Seghers, 1994; Seghers, 1974), improve reproductive opportunities (Krause & Ruxton, 2002; Silk, 2007) and provide access to social information about the location of food and shelter (Miller, Garnier, Hartnett, & Couzin, 2013; Pike & Laland, 2010; Sumpter, 2010; Sumpter & Pratt, 2009). However, groups of animals are typically not behaviourally uniform. Individuals of the same species commonly differ in repeatable interindividual behaviour, also known as behavioural phenotypes, for traits such as boldness, aggression and sociability (Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Wolf & Weissing, 2012).

How these traits affect social organization and therefore impact group behaviour is still not completely understood. Behavioural phenotypes can affect the function and organization of groups in at least three ways. First, properties of the group that emerge from many interindividual interactions can be affected by the presence or absence of different behavioural types in the group, that is, on its 'group phenotypic composition' (Farine, Montiglio, & Spiegel, 2015). For instance, more variation in boldness affects the shape of animal groups (Couzin, Krause, James, Ruxton, & Franks, 2002; Killen, Marras, Nadler, & Domenici, 2017) and their spatial distribution (Michelena, Jeanson, Deneubourg, & Sibbald, 2010). On longer timescales, the composition of behavioural types affects the survival of groups, and hence this may be subject to selection (Pruitt & Goodnight, 2014). Second, behaviour of the individuals within the group may also depend on the behavioural phenotypic composition of the group (Dingemanse & Araya-Ajoy, 2015; Webster & Ward, 2011). For example, conformity to the average group behaviour is widely observed (Herbert-Read et al., 2013; King, Williams, & Mettke-Hofmann, 2015), and the resulting similarity across group members can reduce risk of predation (Landeau & Terborgh, 1986). Certain behaviours may also be expressed to compensate for a lack of variation in a group, for instance by

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modulating aggression to reduce risk in conflict (Sih & Watters, 2005). Third, it has been shown that individuals can actively associate with other individuals depending on their phenotypes (Krause, Butlin, Peuhkuri, & Pritchard, 2000). For example, associating with dissimilar behavioural phenotypes may confer an advantage for competitive foragers (Metcalfe & Thomson, 1995).

These three mechanisms (which we refer to, respectively, as emergence, behavioural plasticity and active self-assortment) are functionally distinct but can all lead to animal groups being structured according to behaviour, which poses a challenge for inferring which mechanism applies. In addition, it is often difficult to analyse consistent differences between groups in the wild, such as when group membership is constantly changing. One fruitful mode of observational study has been social network analysis, in which the strength of social ties between pairs of individuals may be quantified by propensity to co-occur in the same groups (Aplin et al., 2013; Croft et al., 2005; Farine & Whitehead, 2015; Sundaresan, Fischhoff, Dushoff, & Rubenstein, 2007). These can be used to infer that, for example, individuals self-assort by shoaling tendency, as reflected in the structure of the network (Croft et al., 2005). However, using such methods, the role of interindividual influence on individual social behaviour still cannot be ruled out (Shalizi & Thomas, 2011). To determine the role of social context, laboratory methods may be used, such as analysing responses to specific phenotypic compositions (Dyer, Croft, Morrell, & Krause, 2009; Magnhagen & Staffan, 2005; Pike, Samanta, Lindström, & Royle, 2008).

Here we used a novel method in a laboratory setting to maximize the variation in shoaling tendency between groups of guppies, *Poecilia reticulata*, which resembles the variation between self-assorted groups in the wild. By creating groups with consistent differences in individual behaviour, we could investigate the traits underlying the properties of shoals, and hence obtain insights into how specific group behaviours may evolve under selection (Ioannou, Guttal, & Couzin, 2012). Guppies are a model species in the study of antipredator shoaling behaviour (van der Bijl, Thyselius, Kotrschal, & Kolm, 2015; Dugatkin & Godin, 1992; Farr, 1975; Herbert-Read et al., 2017), known for fission–fusion dynamics and self-assortment according to sociability (Croft et al., 2005). We investigated the differences between these sorted groups' shoaling behaviours, to identify possible mechanisms for self-assortment. We divided three independent collections of 128 guppies each into 16 groups of eight. We subjected each of these groups repeatedly to open field assays to quantify their directional 'alignment', that is, the degree to which the eight guppies moved in the same direction. This measurement combines cohesiveness, crucial in the 'selfish herd' response to predation (Hamilton, 1971), and coordination, which facilitates information transfer (Rosenthal, Twomey, Hartnett, Wu, & Couzin, 2015; Strandburg-Peshkin et al., 2013). In subsequent iterations, we manipulated the membership of the groups based on the results of the previous round (i.e. we switched individuals between groups that showed similar social scores). If variation in group alignment was primarily driven by behavioural phenotype, we predicted that groups would keep consistent rankings between rounds. We further predicted that with an increasing number of iterations, this consistency would increase as the traits became sorted according to phenotype, and, hence, within-individual variation would become relatively less important. By fitting our experimental results to a simulated model of the sorting process, we estimated the trait repeatability *R*. Finding *R* from purely group level data may seem counterintuitive, but maximum-likelihood fitting is possible as the sorting dynamics depend heavily on the underlying variation between individuals (Szorkovszky et al., 2017). We then analysed differences between the sorted groups at three scales: the group level, the level of subgroups (local aggregations) and the level of basic locomotion and interactions. Using these data, we then investigated how variation at all levels may provide a mechanism for self-assortment as seen in the wild.

METHODS

Sorting

The laboratory population of guppies used for this study originated from a downstream population of the Quare river in Trinidad, which is subject to high predation levels. The original collection was made in 1998 (Pélabon et al., 2014) and the laboratory population has since been kept in several large (>500-litre) tanks of >500 individuals each to avoid inbreeding. Our current experiments were performed with a subset of this original collection at the Stockholm University aquatic facilities. The laboratory was maintained at 26 °C with a 12:12 h light:dark schedule. Fish were fed a diet of flake food and freshly hatched brine shrimp 6 days per week.

On the first day of filming, mature, unmarked female guppies were allocated to 16 groups of eight fish such that all conspecifics within each group were unfamiliar to each other. Each group was

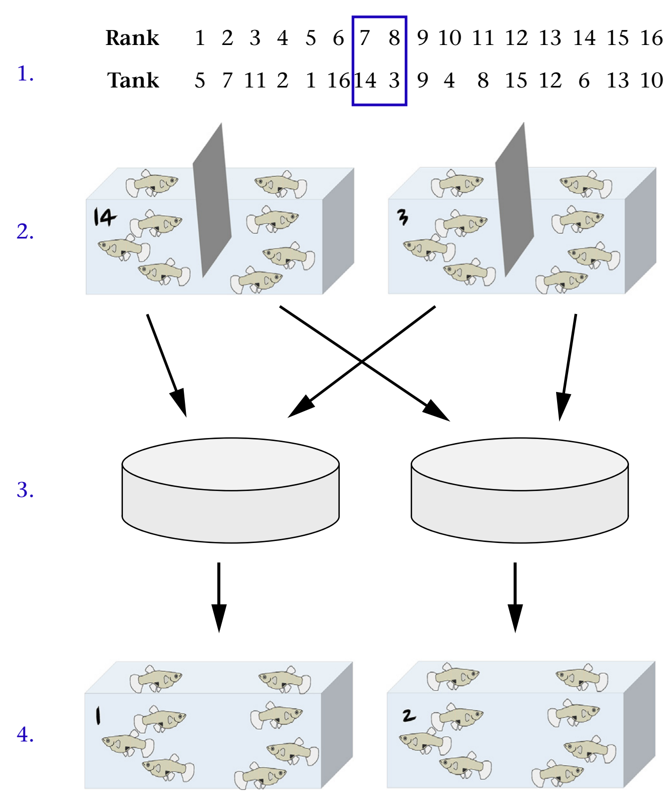

Figure 1. Mixing the first pair of groups in a sorting round. The groups were initially paired according to the previous round's rankings. (1) A random adjacent pair of groups was chosen. (2) Each group was separated into groups of four, and the groups were mixed. (3) The new groups were filmed in two arenas. (4) The new groups were put into tanks, renumbered in order of filming. Steps 1–4 were repeated until all 16 groups had been mixed and filmed. The videos were then tracked and ranked according to the global alignment.