



## Context-dependent group size preferences in large shoals of three-spined sticklebacks



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Grouping behaviour is widespread in animals. One important reason for grouping is the reduction of individual predation risk; the larger a group, the greater the protection for the individual. Fishes, in particular, have become a model taxon in experimental research to study proximate and ultimate causes of grouping. Accordingly, numerous studies have so far demonstrated that fishes prefer to shoal with larger groups. Thus far these studies have usually examined small groups, with up to 20 individuals. However, in nature groups are often much bigger (up to several hundreds of individuals), and theory predicts that benefits, for example due to dilution effects, decline exponentially with increasing group size. Furthermore, discrimination might be absent because of limited cognitive ability. Thus, it is essential to test whether the findings from small groups also apply to large groups. Here, we examined group size preferences in the three-spined stickleback, *Gasterosteus aculeatus*, a small fish that forms large shoals in nature. In five experiments, subadult sticklebacks were given the choice between two shoals differing in group size (numerical contrasts: 15 versus 60, 20 versus 60, 30 versus 60, 40 versus 60 and 50 versus 60). Test fish on average preferred the larger group; this preference was stronger in the beginning of the respective trial and decreased over time. Moreover, preferences for the larger shoal decreased with decreasing group size differences, implying context-dependent preferences. We found significant discrimination up to numerical contrasts of 40:60. Our results are in accordance with the findings of shoal size discrimination in small groups and with optimality hypotheses, but might also reflect the impact of cognitive constraints.

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Group living is widespread throughout the animal kingdom. Living in a group provides several benefits compared with solitary living (reviewed in Krause & Ruxton, 2002; Pitcher & Parrish, 1993). For example, groups find food faster (reviewed in Clark & Mangel, 1986) and are better protected against predators than single individuals (e.g. Magurran, 1990). These benefits are assumed to increase with increasing group size. For example, larger groups are more effective at detecting predators (the ‘many eyes effect’, reviewed in Roberts, 1996). Also, dilution effects and predator confusion effects are expected to be more effective the larger a group (Foster & Treherne, 1981; Krakauer, 1995). However, theory predicts that at a certain absolute group size the benefits of joining the larger of two groups are minimal (Pulliam, 1973; Roberts, 1996). Furthermore, group living also bears costs such as increased parasite transmission and competition over resources such as food or

mating partners (Krause & Ruxton, 2002). In addition, several studies have shown that larger groups are more conspicuous and are consequently attacked more often (e.g. spiders: Uetz & Hieber, 1994; mammals: Hebblewhite & Pletscher, 2002; fishes: Botham, Keerfoot, Louca, & Krause, 2005; but see Godin, 1986). Generally, the cost/benefit ratio of joining a larger group is expected to depend on current environmental conditions such as habitat structure or predation risk. Thus, natural selection is expected to favour individuals being able to detect the differences in group size accurately and to adjust their grouping behaviour according to ecological requirements.

Fishes have become a model group for studying ultimate and proximate factors of grouping (e.g. Bradner & McRobert, 2001; Hager & Helfman, 1991; Hoare, Couzin, Godin, & Krause, 2004; Pritchard, Lawrence, Butlin, & Krause, 2001; Weetman, Atkinson, & Chub, 1999). Several studies have demonstrated that fishes are able to distinguish between different group sizes and often prefer the larger group (e.g. Agrillo & Dadda, 2007; Barber, Downey, & Braithwaite, 1998; Gómez-Laplaza, 2012; Krause, 1993; Krause, Butlin, Peuhkuri, & Pritchard, 2000; Krause, Godin, & Rubenstein,

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1998; Krause, Loader, McDermott, & Ruxton, 1998; Stancher, Sovrano, Potrich, & Vallortigara, 2013; Tegeder & Krause, 1995). As a preference for large groups seems to be ubiquitous, group size discrimination experiments became a standard method to investigate the underlying mechanisms of quantity discrimination in fishes (Gómez-Laplaza, 2012). Thus far, group size preferences or quantity discrimination, respectively, have usually been examined using up to 20 individuals. Within this range, several studies showed that fishes are capable of distinguishing between different-sized groups (e.g. Agrillo, Dadda, & Bisazza, 2007; Gómez-Laplaza, 2012; Gómez-Laplaza & Gerlai, 2013; Hager & Helfman, 1991; Krause, Godin, et al., 1998; Piffer, Agrillo & Hyde, 2012; Ruhl & McRobert, 2005). Furthermore, species appear to differ in their ability to distinguish between different quantities (Agrillo, Miletto Petrazzini, Tagliapietra & Bisazza, 2012; Krause, Godin, et al., 1998; Krause, Loader, et al., 1998). This could (at least partly) be explained by different ecological conditions to which the respective species are exposed (Krause, Godin, et al., 1998), such as different predation risks, but it may also be caused by differences in methodological or experimental conditions (see Gómez-Laplaza & Gerlai, 2012; Henselek, Fischer, & Schloegl, 2012; Perdue, Talbot, Stone & Beran, 2012).

In the wild, fish shoals are often very large, comprising dozens or more individuals (Krause & Ruxton, 2002). Thus, under natural conditions fish may have the option to choose between groups much larger than 20 individuals. The knowledge gained from small group experiments cannot necessarily be transferred to larger groups, because the benefits of choosing a larger group might be different when all available shoals are relatively large. For example, benefits might decline exponentially (Cresswell & Quinn, 2011 and references therein). Furthermore, owing to cognitive constraints quantity discrimination might be affected when the total number is large (Agrillo, Piffer, & Bisazza, 2010). However, little is known about group size preferences in groups exceeding 20 individuals. A recent study on trained western mosquitofish, *Gambusia affinis*, showed that these fish can discriminate between large sets at a ratio of 1:2, in this case between 100 and 200 artificial objects (Agrillo et al., 2010), whereas a comparative study reported that none of five investigated fish species discriminated numerical contrasts of 25 versus 50 (Agrillo et al., 2012).

In the present study, we investigated spontaneous group size discrimination in the three-spined stickleback, *Gasterosteus aculeatus*. The three-spined stickleback is a small fish widely distributed across the northern hemisphere. Outside the breeding season, it forms shoals with group sizes ranging from a few individuals to several hundred fish (Peuhkuri, 1998; Poulin, 1999; Wootton, 1984). Sticklebacks have evolved several morphological features, such as spines for protection against predators (e.g. Frommen et al., 2011). Living in shoals is assumed to reduce individual predation risk further (Magurran, 1990). Shoaling in sticklebacks has been intensively studied (e.g. reviewed in Frommen, Mehli, Brendler, & Bakker, 2007). When given the choice, sticklebacks prefer to shoal with the larger of two groups at different numerical contrasts: for example, 3 versus 20, 3 versus 5 (Krause, 1993), 5 versus 10, 5 versus 9 (Krause, Godin, et al., 1998), 8 versus 12 (Frommen, Hiermes, & Bakker, 2009) or 3 versus 6 (Fischer & Frommen, 2013). In the present study the first aim was to test whether sticklebacks discriminate between two shoals differing in group size when both are relatively large, using numerical ratios similar to those used in previous 'small group' studies. Therefore, we conducted five experiments with numerical contrasts ranging from 15:60 to 50:60. The second aim was to test whether the strength of the preference for the large group changes according to the benefits that are assumed to decrease with decreasing group size differences. Finally, we tested whether

preferences change over time, because habituation effects might influence shoaling preferences.

## METHODS

### Experimental Subjects

Sticklebacks used in the experiments were subadult (aged between 3 and 4 months), F1 offspring originating from wild-caught fish. Parental fish were purchased in April 2010 from a commercial fisherman who had the permission to catch sticklebacks during their spring migration on the island of Texel, the Netherlands. Here, fish can pass the dyke from the sea to freshwater habitats via an artificial passage, where they can be easily caught by netting (Kemper, 1995).

The fish were transported in three large plastic tanks (75 × 50 cm and 40 cm high, with approximately 150 fish per tank, half filled with sea water and tap water and aerated by battery-run membrane pumps) in an air-conditioned vehicle (at approximately 17 °C air temperature) within 5 h to the Institute for Evolutionary Biology and Ecology in Bonn, Germany. There they were kept together for 1 week in a large outdoor tank (750 litres), with air ventilation and a constant supply of tap water at a flow rate of 3 litres/min. They were fed with defrosted red mosquito larvae (*Chironomus* spp.). Then they were transferred under similar conditions to those already described within 12 h to the Konrad Lorenz Institute for Ethology, Vienna, Austria, where they were kept in a large outdoor tank (750 litres, air ventilation, regular water exchange).

No permits were required for the export and import of the fish. During both periods of transport the condition of the fish was frequently monitored. No fish died during the transport, and afterwards they showed normal shoaling behaviour. Fifty pairs of these fish were bred under standardized laboratory conditions (see Frommen et al., 2013 for details). Resulting offspring were kept in four large outdoor tanks (750 litres, approximately 250 fish per tank) with air ventilation and regular water exchange. All fish were fed daily in excess with defrosted mosquito larvae.

Before the experiments, 120 F1 fish were haphazardly caught using a hand net and were transferred to the laboratory using a water-filled bucket (10 litres). Here, they were equally distributed among three tanks (130 × 65 cm and 50 cm high) located in an air-conditioned room under standardized winter light regime (8:16 h light:dark cycle, temperature 18 ± 1 °C). Light was provided by a fluorescent lamp (36 W) placed above the tanks. Each tank was equipped with an internal filter to clean and aerate the water and with five clay pots for shelter. The tank water was partially replaced by fresh water once a week; water nitrite concentration was regularly checked. The fish were checked daily for health (e.g. the constitution of the fish was estimated during feeding). During the experiments these fish functioned as stock for test fish, while the fish in the outdoor tanks provided the stimulus shoals.

### Experimental Design and Procedure

The test aquarium measured 130 × 65 cm and 50 cm high and was filled with 1-day-old tap water up to a water level of 30 cm. It was divided into two stimulus compartments (32.5 × 65 cm and 50 cm high) on the right- and left-hand sides with a test compartment in the middle (65 × 65 cm and 50 cm high). The compartments were separated by glass plates, allowing visual contact only (cf. Frommen et al., 2009; Fischer & Frommen, 2013). The set-up was illuminated by a fluorescent tube (36 W), which was centred lengthwise above the aquarium. Experiments were videotaped from the side using a webcam (LifeCam Cinema, Microsoft) mounted on a tripod in front of the experimental tank.

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