

Quantification acuity in spontaneous shoaling decisions of three-spined sticklebacks

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Abstract The ability to discriminate between different quantities is widespread throughout the animal kingdom, and the underlying mechanisms of quantity discrimination are currently intensely discussed. In contrast, questions elucidating the limits of quantity estimation received rather little attention so far. Here, we examined fine-tuned quantity estimation in the three-spined stickleback (*Gasterosteus aculeatus*) in a natural context, i.e. during shoaling decisions. Wild-caught focal fish were given the spontaneous choice between two shoals which differed in group size by 1 fish (0 vs. 1, 1 vs. 2, 2 vs. 3, 3 vs. 4, 4 vs. 5, 5 vs. 6 and 6 vs. 7), based on visual assessment. The results show that sticklebacks generally prefer to shoal with the larger group. They discriminated numerical contrasts up to 6 versus 7, equalling a numerical ratio of 0.86. Preference patterns followed Weber's law, i.e. decreased with increasing numerical ratio. This pattern was found across all numerical conditions as well as within the small number range (ranging from 1 vs. 2 to 3 vs. 4). The results suggest that wild-caught three-spined sticklebacks are spontaneously able (i.e. without prior learning) to detect subtle differences in shoal sizes. Further, they confirm findings of

previous studies highlighting the contribution of the analogue magnitude system to quantity estimation in fishes.

Keywords Counting · Fishes · *Gasterosteus aculeatus* · Numerical abilities · Shoaling · Weber's law

Introduction

The ability to assess different quantities is common throughout the animal kingdom (Cantlon and Brannon 2007). It has been described, for example, in primates (Beran 2001, 2007; Call 2000; Shumaker et al. 2001; Vonk 2003) and other species of mammals (e.g. Baker et al. 2011; Irie-Sugimoto et al. 2009; Kilian et al. 2003; Pisa and Agrillo 2009; Vonk and Beran 2012; Ward and Smuts 2007; West and Young 2002), birds (Garland et al. 2012; Pepperberg 2006; Rugani et al. 2010, 2013), amphibians (Uller et al. 2003; Stancher et al. 2015), fishes (Agrillo et al. 2012a; Gómez-Laplaza and Gerlai 2011) and invertebrates (Evans et al. 2007; Reznikova and Ryabko 2011). The ability to differentiate between different quantities allows individuals to optimally adjust their behaviour and hence to increase their survival or reproduction prospects, for instance by avoiding places with a higher number of predators or by preferring habitats with more food or fewer competitors (see Shettleworth 2009).

It is often assumed that animals (including humans) use similar, ancestral mechanisms for number quantification (Agrillo et al. 2012b; Feigenson et al. 2004; Reznikova and Ryabko 2011). Small quantities (≤ 4) are thought to be processed by a process termed “subitizing” (Kaufman et al. 1949). Here, each item is individually recognized by an “object file system” (OFS). The OFS represents a fast and precise mechanism, which is, however, limited up to four

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entities, probably because of limited capacities of the short-term memory (Feigenson et al. 2004). Quantities above 4 are thought being processed by an “analogue magnitude system” (AMS), based on ratios (Feigenson et al. 2004). While the AMS is also fast, it is less precise. Furthermore, accuracy is predicted to decrease as the numerical ratio approaches 1, a phenomenon termed Weber’s law (Gómez-Laplaza and Gerlai 2011; Krause et al. 1998; Weber 1905). In accordance, many animals show highly precise discrimination abilities when dealing with numbers smaller than 4, while their discrimination ability is less precise when quantities are higher (e.g. Agrillo et al. 2007, 2010; Hauser et al. 2003; but see Garland et al. 2012). However, the concept of two distinct discrimination mechanisms has recently been challenged by studies suggesting that the AMS might also be responsible for the estimation of quantities in the subitizing range (e.g. Gallistel and Gelman 1992; Rugani et al. 2013; Stancher et al. 2013; see also Agrillo et al. 2014 and references therein).

Fishes are a frequently used model group for studying proximate and ultimate factors of quantity discrimination (Agrillo et al. 2012a; Gómez-Laplaza 2012; Stancher et al. 2013). A standard way to measure numerical abilities in fishes takes advantage of the innate preference of many fish species to shoal with the larger of two groups in order to reduce predation risk (Bradner and McRobert 2001; Hager and Helfman 1991; Hoare et al. 2004; Krause and Godin 1994). Recent research is focussing especially on the general underlying mechanisms of quantity discrimination (Agrillo et al. 2014; Frommen et al. 2009; Gómez-Laplaza and Gerlai 2011, 2013; Piffer et al. 2013). Generally, most fishes are able to discriminate amounts of 0 versus 1, 1 versus 2 and 2 versus 3 (see Gómez-Laplaza 2012 for a review). However, different fish species seem to differ in discrimination accuracy. For instance guppies, *Poecilia reticulata*, discriminate between 3 versus 4 (Piffer et al. 2012), whereas redbtail splitfin fish, *Xenotoca eiseni*, failed (Stancher et al. 2013). When discriminating numbers above 4, ratios up to 0.5, e.g. 3 versus 6 or 5 versus 10 are differentiated by angelfish, *Pterophyllum scalare* (Gómez-Laplaza 2012), guppies (Piffer et al. 2013) and zebrafish, *Danio rerio* (Ruhl and McRobert 2005). Mosquitofish, *Gambusia affinis* (Agrillo et al. 2007), and three-spined sticklebacks, *Gasterosteus aculeatus*, are also shown to discriminate ratios of 0.66 (e.g. 8 vs. 12 or 40 vs. 60, see Frommen et al. 2009; Thünken et al. 2014). Even more subtle discrimination is described in fathead minnows, *Pimephales promelas* (Hager and Helfman 1991), which differentiated 18 versus 23, which equals a ratio of 0.78. However, although accuracy is a crucial component of quantity estimation, this issue was seldom pursued in detail. Knowledge about variation in accuracy may contribute to a comprehensive understanding of quantity estimation and the underlying mechanism in animals.

Thus, the present study aimed to contribute to filling this gap of knowledge, by investigating fine-tuned group size discrimination in three-spined sticklebacks.

The three-spined stickleback, *G. aculeatus*, is a small fish widely distributed across the Northern Hemisphere. Non-reproductive three-spined sticklebacks form shoals with group sizes ranging from a few to several hundred individuals (Peuhkuri 1998; Poulin 1999; Wootton 1984). Shoaling as an anti-predator response (Magurran 1990) has been intensively studied in this species (Doucette et al. 2004; Godin and Crossman 1994; Krause et al. 1998), and safety is generally expected to increase with increasing group size (Cresswell and Quinn 2011). Accordingly, three-spined sticklebacks preferred to shoal with the larger of two relatively small groups at different numerical contrasts, e.g. 3 versus 20, 3 versus 5 (Krause 1993), 5 versus 10, 5 versus 9 (Krause et al. 1998), 8 versus 12 (Frommen et al. 2009) or 3 versus 6 (Fischer and Frommen 2013). Moreover, the results from small groups appear to be transferable to large shoals as sticklebacks preferred groups consisting of 60 fish over groups of 15, 20 and 40 fish (Thünken et al. 2014).

In the present study, we examined whether three-spined sticklebacks show fine-tuned discrimination accuracy between shoal sizes differing in only 1 fish within (≤ 4) and beyond (> 4) the subitizing range. Fish were offered the choice between seven different numerical contrasts ranging from 0 versus 1 to 6 versus 7. This includes ratios ranging from 0.5 to 0.86. Furthermore, we aimed to elucidate whether the strength of the preference for the larger group changes according to the numerical ratio. The OFS hypothesis predicts that quantities ≤ 4 are discriminated independent of ratio, whereas the AMS hypothesis predicts that discrimination is in general ratio-related.

Materials and methods

Shoal choice trials took place during three-spined sticklebacks’ non-reproductive season in the years 2007, 2008 and 2010 at the Institute for Evolutionary Biology and Ecology, University of Bonn. In each year discrimination between the following group sizes was tested in random order to avoid sequence effects: 0 versus 1 ($N = 30$), 1 versus 2 ($N = 35$), 2 versus 3 ($N = 35$), 3 versus 4 ($N = 35$), 4 versus 5 ($N = 35$), 5 versus 6 ($N = 35$) and 6 versus 7 ($N = 35$) [from now on termed numerical contrast (NC) 1–7]. This equals ratios of 0.5, 0.67, 0.75, 0.8, 0.83 and 0.86 (1 vs. 2–6 vs. 7).

Experimental fish

Annually, about 500 individuals were caught prior to the experimental trials from a pond near the institute using

minnow traps. Fish were kept under natural light conditions in a large outdoor tank (750 l) with constant water flow (flow rate 3 l min^{-1}). In total, 240 focal fish were used; each focal fish was used only once to avoid pseudoreplication. The remaining fish served to create the stimulus shoals. Stimulus fish were used several times, but never on the same day or in the same shoal combination. Prior to testing, focal and stimulus fish were randomly selected from the outdoor tank and kept separately from each other in group tanks (L 60 cm \times W 30 cm \times H 30 cm) in the laboratory under standardized conditions (day length: 8 h light, 16 h dark; room temperature $17 \pm 1 \text{ }^\circ\text{C}$). All fish had an acclimation time of at least 24 h in the laboratory before they participated in a trial. All individuals were daily fed *in excess* in the morning with defrosted mosquito larvae (*Chironomus* spp.) to avoid confounding effects caused by different hunger levels (e.g. Frommen et al. 2007; Krause 1993).

Experimental set-up

The experimental tank (80 cm \times 40 cm \times 45 cm, water height 15.5 cm) was divided by transparent Plexiglas partitions into two stimulus compartments (15 cm \times 40 cm \times 45 cm) on the right- and left-hand side and a focal compartment in the middle (50 cm \times 40 cm \times 45 cm). The partitions were glued to the tank wall. Thus, diffusion of chemical cues between compartments was not possible and quantities had to be visually estimated (cf. Frommen et al. 2009; Thünken et al. 2014). The middle of the experimental tank as well as 12 cm preference zones in front of each stimulus compartment were indicated by black lines drawn on the side walls and the bottom. To avoid disturbance from outside, a black curtain was stretched around the experimental tank. The set-up was illuminated by a fluorescent tube (36 W), which was centred lengthwise directly above the aquarium. The trials were recorded from the front using a webcam (Creative WebCam Live!) connected to a laptop behind the curtain.

For each trial, fish were randomly caught from their respective holding tanks using a hand net. After transferring stimulus shoals into their compartments, the focal fish was placed into a transparent Plexiglas cylinder (diameter 10 cm \times H 35 cm) in the centre of the experimental tank. To control for potential side effects, the side on which the larger shoal was presented was alternated. After an acclimation time of 2 min, the focal fish was released by carefully lifting the cylinder from behind the curtain using a pulley system. The behaviour of the focal fish was recorded for 10 min as soon as it had crossed the middle line for the first time. After each trial, the body mass and standard length of all experimental fish were measured and the body condition was calculated as a function of body

mass and standard length [$(100 \times \text{body mass})/\text{standard length}^3$], following Bolger and Connolly (1989). Stimulus fish were released in the outdoor tanks, while focal fish were kept in a separated tank. Between trials, the experimental tank was emptied and cleaned to remove chemical traces. Afterwards, the tank was refilled with water which was put in an empty 200 l tank at least 12 h before testing to adjust the temperature and to remove gases.

Data analysis

Videos were analysed by one person (MM) blindly with respect to group size differences between the stimulus shoals. The time the focal fish spent in the association zones in front of the stimulus shoals was quantified over a period of 10 min using the time stamp shown in the video. For analyses, the proportion of time (%) the focal fish spent in each association zone (relative to total time in both zones) was calculated. Statistics were performed with the R. 2.9.1 statistical software package (R-Development-Core-Team 2009). As data were normally distributed according to Shapiro–Wilk tests, linear mixed-effect models (LMEs) were fitted. Tests of statistical significance were based on likelihood ratio tests (LRT), which follow a χ^2 -distribution. These routines use maximum likelihood parameter estimation. In all fitted models non-significant factors were removed in order of statistical relevance. Thus, reported *P* values of models refer to the increase in deviance when the respective variable had been removed.

NC 1 (0 vs. 1) served as a control to ensure that focal fish generally preferred to shoal. It was thus analysed separately as it differed from the remaining NCs 2–7 (1 vs. 2–6 vs. 7) due the fact that focal fish had not the choice between two shoals as one stimulus compartment contained no fish. For the NCs 2–7, combined data were analysed first. Proportion of time in the two association zones served as the dependent variable. Shoal size (small/large) was entered as explanatory variable and focal fish ID as a random factor (to control for the paired experimental set-up). “Tank side” was always entered as a fixed factor to control for potential side preferences unrelated to shoal size. Average standard length and body condition of stimulus shoal fish as well as relative body size and condition of the focal fish in relation to the stimulus fish were added as covariates in the statistical analyses. Neither the mean body size (LME, LRT, $\chi^2 = 1.334$, *df* = 1, *P* = 0.248), body condition of the stimulus shoal (LME, LRT, $\chi^2 = 3.426$, *df* = 1, *P* = 0.064), nor the relative body size or condition of the focal fish in relation to the stimulus fish (LME, LRT, $\chi^2 = 0.054$, *df* = 1, *P* = 0.817 and $\chi^2 = 0.067$, *df* = 1, *P* = 0.795, respectively) significantly affected shoal choice and were thus not included in the further analyses. Additionally, to examine whether

preference for the larger shoal changed according to the numerical ratio, the interaction between “shoal size” (small/large) and “ratio” was examined. This was done for the NCs 2–7 and for the NCs 2–4 (1 vs. 2, 2 vs. 3 and 3 vs. 4) and the NCs 5–7 (4 vs. 5, 5 vs. 6 and 6 vs. 7) separately, to test ratio dependence within and beyond the subitizing number range. Furthermore, all NCs were analysed separately using similar LMEs as described above to examine potential discrimination thresholds.

Results

Three-spined sticklebacks spent significantly more time near the compartment containing a conspecific than near the empty compartment (NC 1, 0 vs. 1; LME, LRT, $\chi^2 = 150.806$, $df = 1$, $P < 0.001$; Fig. 1). Across the other six contrasts, fish spent significantly more time near the larger of the two offered shoals (NCs 2–7; LME, LRT, $\chi^2 = 54.582$, $df = 1$, $P < 0.001$; Fig. 1). Analysing these six contrasts separately revealed significant preferences for the larger group in all numerical combinations except in NC 4 (3 vs. 4), where no significant preference could be detected for any shoal size (see Fig. 1; Table 1).

Across NCs 2–7, preference for the larger group decreased with increasing numerical ratio (group size \times ratio, LME, LRT, $\chi^2 = 7.547$, $df = 1$, $P = 0.006$; Fig. 2). This relationship was also significant when only including the contrasts within the subitizing number range

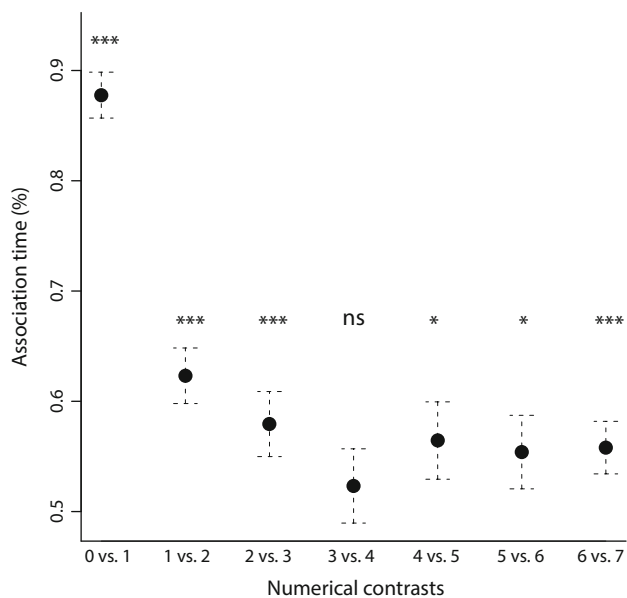


Fig. 1 Mean proportion \pm SE of time spent near the larger group across the seven different numerical contrasts tested in this study. P values refer to deviation from chance expectation level of 0.5. *** $P < 0.001$; * $P < 0.05$; ns $P > 0.05$

(NCs 2–4, 1 vs. 2, 2 vs. 3 and 3 vs. 4; LME, LRT, $\chi^2 = 11.094$, $df = 1$, $P < 0.001$, Fig. 2), but not beyond that range (NCs 5–7, 4 vs. 5, 5 vs. 6 and 6 vs. 7; LME, LRT, $\chi^2 = 0.102$, $df = 1$, $P = 0.749$).

Discussion

Three-spined sticklebacks distinguished between different-sized shoals differing in 1 fish and preferred the larger shoal. In particular, they were able to discriminate a shoal consisting of 6 fish from a shoal consisting of 7 fish, which correspond to a numerical ratio of 0.86. Such a large ratio has to our knowledge not been shown to be discriminated by any other fish species. Within this number range, previous studies on quantity discrimination revealed discrimination abilities in other fish species as well. Still, angelfish *P. scalare* (Gómez-Laplaza 2012), zebrafish *D. rerio* and Siamese fighting fish *Betta splendens* (Agrillo et al. 2012a) or redtail splitfin *X. eiseni* (Stancher et al. 2013) did not differentiate ratios larger than 0.66 (e.g. 2 vs. 3, 5 vs. 9, 8 vs. 12). Mosquitofish *G. affinis* and guppies *P. reticulata* discriminated ratios of 0.75 only in the subitizing number range (up to four entities), but failed to do so when quantities were bigger than 4, e.g. 9 versus 12 (Agrillo et al. 2014, 2010). However, it has to be mentioned that different studies were based on different methodological approaches (e.g. trained or spontaneous response, abstract objects or live conspecifics as stimuli) and samples sizes. Using behavioural experiments, cognitive abilities can only be

Table 1 Performance of three-spined sticklebacks in quantity discrimination trials

Numerical contrast	Explanatory variable	χ^2	P
0 versus 1	Tank side	0.278	0.598
	Shoal size	150.806	<0.001
1 versus 2	Tank side	8.051	0.005
	Shoal size	39.960	<0.001
2 versus 3	Tank side	8.645	0.003
	Shoal size	15.664	<0.001
3 versus 4	Tank side	0.248	0.618
	Shoal size	0.973	0.324
4 versus 5	Tank side	2.785	0.095
	Shoal size	6.617	0.010
5 versus 6	Tank side	4.377	0.036
	Shoal size	5.780	0.016
6 versus 7	Tank side	5.343	0.021
	Shoal size	11.650	<0.001

Results of linear mixed-effect models examining the effect of shoal size (large vs. small) and tank side on shoaling preferences across different numerical contrasts [significant effects ($P < 0.05$) are marked bold]

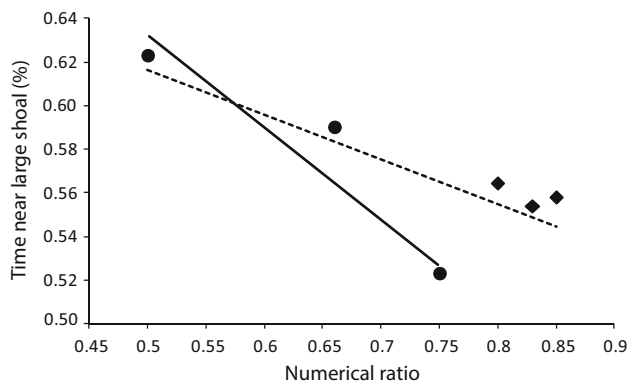


Fig. 2 Mean time spent near the larger shoal in relation to the numerical ratio. *Circles* represent contrasts within the subitizing range (NCs 2–4), and *squares* contrasts above the subitizing range (NCs 5–7). *Lines* represent least-square regression lines [*dashed line* across all (NCs 2–7); *continuous line* within subitizing range (NCs 2–4)]

measured indirectly, by examining whether and to which extent animals do discriminate or not. As a consequence, lack of discrimination does not necessarily mean lack of possessing the cognitive abilities to solve a task, as for example, motivation to show a given behaviour might be absent. Therefore, examinations of species differences should optimally control for potential variation in motivational states, which might be particularly pronounced in wild-caught fishes.

In other taxa than fishes, even higher accuracy than in the current study has been shown. Besides adult humans and other primates, which possess highly advanced numerical abilities enabling them to correctly estimate 0.9 ratios (Halberda and Feigenson 2008; Hanus and Call 2007), also North Island robins *Petroica longipes* differentiated between 7 versus 8 food items, i.e. a 0.875 ratio (Garland et al. 2012). In contrast, bottlenose dolphins *Tursiops truncatus* differentiate numerical contrasts up to 6 versus 7, but were not able to differentiate between 7 versus 8 (Jaakkola et al. 2005). In our study, the most difficult numerical contrast, i.e. 6 versus 7 was mastered by sticklebacks. Thus, the aim of future experiments should be to clarify the limits of fine-tuned accuracy in this species.

In the present study preferences for the larger group decreased with increasing numerical ratio, i.e. it follows Weber's law. This finding is in accordance with a recently published study, which examined quantity discrimination in large stickleback groups (see Thünken et al. 2014). Interestingly, this relationship was also present within the subitizing range (i.e. NCs 2–4). This is in contrast to the OFS hypothesis, which predicts that small number discrimination is not affected by ratio effects. Thus, the AMS might also contribute to quantity discrimination in sticklebacks in the subitizing range. However, further experiments including further numerical contrasts in the small

number range (e.g. 1 vs. 3, 1 vs. 4, 2 vs. 4) are needed to corroborate this conclusion. Also, it would be interesting to know whether the decreased acuity at higher ratios is due to inter-individual differences, i.e. poorer discrimination of certain individuals or due to general effects.

The question whether quantity discrimination is based on numerical abilities or continuous attributes such as density, cumulative surface area or overall space occupied by a group is currently disputed by using sophisticated experimental approaches (see Agrillo et al. 2009; Frommen et al. 2009; Gómez-Laplaza and Gerlai 2013; Piffer et al. 2013). In our case, the larger group might occupy more space or might show a higher density. Thus, instead of using any numerical system, preferences for the larger shoal as shown in the present study might in fact be explained by preferences for the denser shoal. However, it was not the aim of our study to examine the underlying proximate causes of quantity discrimination but to investigate fine-tuned quantification accuracy in a functionally realistic context.

Under natural conditions, sticklebacks' preference for the larger shoal is assumed to be adaptive because individual predation risk is supposed to decrease with increasing shoal size, for instance, due to dilution effects (Foster and Treherne 1981). This benefit of choosing the bigger group should be largest when groups are small, while it is thought to be less important to choose between two rather large groups (Pulliam 1973; Roberts 1996). Accordingly, in the present study the strongest preference and motivation to shoal with the larger group was found in the experimental condition with the largest relative group size differences (1 vs. 2), i.e. at the smallest ratio. Furthermore, sticklebacks strongly avoided swimming solitary, as indicated by the result of NC 1 (0 vs. 1). However, even at the smallest relative size differences tested (6 vs. 7), sticklebacks' preference should be adaptive because individuals may reduce their predation risk by joining the larger group. Under natural conditions shoal sizes of many other fish species are similar to that tested in the present study (e.g. Agrillo et al. 2007; Hain and Neff 2007). Thus, from a functional perspective, one would expect similar discrimination abilities in other fish species.

While stickleback's preferences for the larger shoal clearly indicated pronounced quantity discrimination abilities, there was an overall great variation in individual shoaling decisions. This variation can be explained by the fact that shoaling decisions in fishes are influenced by a range of factors, including, for example, nutritional state (Reebs and Saulnier 1997), personality type (Cote et al. 2012), body size (Ward and Currie 2013) or reproductive state (Frommen et al. 2012). While we aimed at correcting for some of these factors by including body measures and tank side biases in our analyses and testing fish outside the

breeding season, others are more difficult to control for. Furthermore, variation in shoaling preference might also be explained by intrinsic differences in individuals' discrimination ability, both within and across species; for example, it might depend on developmental stage. For instance, 6-month-old human children are able to discriminate a ratio of 0.50 (8 vs. 16) but not 0.66 (8 vs. 12), whereas 9-month-olds are able to discriminate a ratio of 0.66 but not 0.80 (8 vs. 10, Lipton and Spelke 2003). Similar patterns have been shown in guppies; juveniles discriminate 0.25 and 0.5 ratios but not—in contrast to adults—0.66 ratios (Miletto Petrazzini et al. 2014). Finally, discrimination might be impaired when the total set size is very big as several fish species failed to differentiate between 25 versus 50 objects (0.5 ratio) (Agrillo et al. 2012a). Nevertheless, three-spined sticklebacks still discriminated between shoal sizes of 40 versus 60 (a ratio 0.66) (Thünken et al. 2014).

To conclude, the present study showed fine-tuned quantity discrimination accuracy in three-spined sticklebacks. Fish discriminated numerical contrasts of 6 versus 7, equalling a ratio of 0.86. Such a highly accurate discrimination has to our knowledge never been observed for another fish species. In addition, we found that preference for the large group decreased with increasing numerical ratio which is in accordance with Weber's law and probably reflects cognitive limitation.

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Ethical standard The experiments comply with the current laws of the country in which they were performed.

Conflict of interest The authors declare that they have no competing interests.

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