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ORIGINAL PAPER

Disentangling the effects of group size and density on shoaling decisions of three-spined sticklebacks (*Gasterosteus aculeatus*)

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Abstract Many animals live in groups most of their life. One function of this behaviour is an increased predator protection whereas larger groups provide better protection than smaller ones. A causal explanation is that due to a higher number of shoal members the individual risk of being predated will decrease ("dilution effect"). Additionally, shoaling leads to increased predator confusion. This "confusion effect" can be strengthened by an increased group density, which often correlates with group size. Many studies found that individuals prefer the larger of two groups. However, whether this preference is due to a larger group size or because of an increased density of the larger group remained unclear. To disentangle these factors we gave three-spined sticklebacks (*Gasterosteus aculeatus*) the choice between shoals of (1) different group size and density, (2) different group size, but equal density and (3) equal group sizes, but different densities. As expected, test fish preferred the larger and denser shoal over the smaller, less dense one. This preference was lost when shoal size differed but density was kept constant. When shoal size was equal but density differed, test fish preferred the less dense shoal. However, this was only the case when test fish chose between two relatively dense shoals. On the other hand, when overall density was low, test fish did not discriminate between shoals of different densities. This result may be explained in terms of predator avoidance. The results show that shoaling preferences might not always be influenced by a higher number of group members but also by the density and cohesiveness of the respective groups.

Keywords Fish · Safety in numbers · Schooling · Selfish herd · Grouping · Predation · Confusion effect

Introduction

Group living has evolved in many species throughout the animal kingdom. The benefits of living in a group are multifarious (reviewed in Pitcher and Parrish 1993; Krause and Ruxton 2002). During foraging, for example, groups find food faster than single individuals (reviewed in Clark and Mangel 1986) while in group-spawning species the individuals find mating partners in the group (e.g. Wedekind 1996). Maybe the most important factor leading to group living is the avoidance of predation (e.g. Brock and Riffenburgh 1960; Magurran 1990). Here, group size has been known to be of importance for over 70 years (Welty 1934; Pitcher and Parrish 1993; Krause and Ruxton 2002). For example, larger groups are more effective at detecting predators ("many eyes effect") (reviewed in Roberts 1996). Furthermore, risk dilution leads to a higher survival of the individual ("dilution effect"). If a predator is only able to catch one prey at a time, then the larger the group the lower the chance that a particular individual will be attacked (Pitcher and Parrish 1993). An example for this phenomenon is provided by Foster and Treherne (1981), who found that ocean skaters' (*Halobates robustus*) chance to survive a fish's attack increased with group size because of risk

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dilution. However, the dilution theory assumes that all members of the group face the same risk of being attacked (Krause and Ruxton 2002), which is often not the case in nature (e.g. Hamilton 1971; Bumann et al. 1997). Furthermore, several studies have shown that larger groups are more conspicuous and are consequently attacked more often (e.g. spiders: Uetz and Hieber 1994; mammals: Hebblewhite and Pletscher 2002; fish: Botham et al. 2005; but see Godin 1986), still, for a single individual the risk to be the victim in the group might be reduced (Krause and Godin 1995). However, this only holds true if groups are not encountered proportionally to their size ("encounter-dilution effect", Turner and Pitcher 1986; Mooring and Hart 1992).

An additional causal explanation for an individual's preference to join a larger group is that through an increase in group size, predator confusion increases as well (Krakauer 1995; Ruxton et al. 2007). This "confusion effect" is expected to be strengthened by an increased group density (Krakauer 1995), which often correlates with group size. Indeed, it has frequently been observed that fish shoals under predation threat become more compact (e.g. Seghers 1974; Magurran and Pitcher 1987; Domenici et al. 2000). However, empirical studies showing an increase of confusion when group density rises are scarce thus far (Ruxton et al. 2007). In contrast, a recent theoretical study found no evidence of enhanced confusion in denser groups (Tosh et al. 2006). This finding is in accordance with two empirical studies. In Ruxton et al. (2007) confusion of humans "predating" on a highly artificial prey shown on a computer screen did not increase with higher prey density. Likewise, density of *Daphnia magna* did not seem to impair predation success of three-spined sticklebacks (*Gasterosteus aculeatus*) (Ioannou et al. 2008). Hence, it might be possible that compaction of fish shoals did not evolve as a result of predator confusion but because single group members hide behind each other. These "selfish herd effects" (Hamilton 1971) influence the aggregation behaviour of fish (Krause 1993c; Krause 1993a) as well as fiddler crabs (*Uca pugilator*) (Viscido and Wethey 2002), but have also been criticised on various theoretical grounds (see Morrell and James 2008 for details).

The neurophysiological basis for the "confusion effect" might be an overloading of the predator's visual analysis channel (Broadbent 1965; Pitcher and Parrish 1993). Because visual predators rely on complex movement and trajectory analysis (Guthrie 1980), it is difficult for them to overcome channel confusion (Pitcher and Parrish 1993). Recent neural network models of the "confusion effect" make the prediction that accuracy is reduced due to the poor neural mapping of targeted prey induced by the large number of potential targets (see Ioannou et al. 2008 for a summary). While theoretical work on the neural background of the "confusion effect" is still under-represented in the literature (but see for example Krakauer 1995; Tosh et al. 2006; Tosh and Ruxton 2006), there exists multiple experimental evidence for this phenomenon. Schradin (2000), for example, found that both leopard geckos (*Eublepharis macularius*) and common marmosets (*Callithrix jacchus*) took longer to catch one out of several prey compared to one single prey. Milinski (1990) showed that humans also suffer from an inability to hit a target as group size and distraction increased. Similar results were found in hunting three-spined sticklebacks (Milinski 1977; Ohguchi 1978; Milinski 1979).

Several theoretical studies (e.g. Turner and Pitcher 1986) show that individuals would be safer in larger groups. Furthermore, a whole range of empirical studies find that individuals under predation risk, when given the choice between two groups, prefer the larger one (see Krause and Ruxton 2002 for an overview). Most examples for this preference come from fish (e.g. Hager and Helfman 1991; Weetman et al. 1999; Bradner and McRobert 2001; Pritchard et al. 2001; Hoare et al. 2004). Barber and Wright (2001), for example, showed that European minnows (*Phoxinus phoxinus*) preferred the larger of two groups and that this effect might outweigh preferences for familiar fish. Banded killifish (*Fundulus diaphanus*) scared by a predator chose the larger of two shoals, but only if members of both stimulus shoals were of the same size class (Krause and Godin 1994). However, in most of the experimental studies an increase in group size came along with an increase in shoal density. Little is known whether test fish preferred the larger shoal because of the higher number of group members or because of an increase in density and thus a higher potential for predator confusion.

Three-spined sticklebacks form loose shoals outside their breeding season (Wootton 1976). These shoals tighten when fish are attacked by a predator (Krause et al. 1998). Shoal choice is influenced by several factors, e.g. standard length (Hoare et al. 2000; Barber 2003) and nutritional state (Krause 1993b; Barber et al. 1995; Frommen et al. 2007). Several studies have also demonstrated a preference for larger shoals (e.g. Krause 1993b; Tegeder and Krause 1995; Barber et al. 1998; Krause et al. 1998; Krause et al. 2000), while little is known about the influence of shoal density.

To disentangle the effects of group size and group density on shoaling preferences of three-spined sticklebacks, we conducted four different experiments. In the control experiment, we gave single test fish the opportunity to shoal either with a group of 12 fish or a group of eight fish placed into two equal-sized compartments at the opposite sides of the test aquarium (Fig. 1). Because stimulus compartments were of equal-size fish density was 50% higher in the larger shoal. In the 'equal-density experiment', the difference in number of shoal members was the same as in the control experiment, but by reducing the size of the compartment of the smaller shoal density was kept constant. In the ‘equal-size/high-density experiment’ both shoals were composed of ten stimulus fish, but density was increased in one group by 50%. Because ten fish in a small compartment represented the highest density of all experiments, we conducted a fourth experiment controlling for general effects of high density (‘equal-size/low-density experiment’). Here, both shoals were composed of eight stimulus fish, while density was increased in one group by 50%. This resulted in two shoals whose density was comparable to the control experiment.

Material and methods

Experimental subjects

Three-spined sticklebacks used in the experiments were caught using minnow traps from a pond near Euskirchen, Germany (50°38′ N/6°47′ E) (Modarressie et al. 2006) and brought to the Institute for Evolutionary Biology and Ecology, Bonn, Germany. About 600 individuals were kept in outside stock tanks (volume 700 litres) with constant tap water supply (flow rate of 3 l/min) and air ventilation. Fish were fed daily on frozen *Chironomus* larvae.

Prior to the experiments, 120 haphazardly chosen fish were transferred to the laboratory where they were kept in two aquaria (80×40×40 cm, L×W×H) located in an air-conditioned room under standardised winter light regime (day length, 8L:16D, temperature 17±1 °C). During the experiments these fish functioned as test fish, while the remaining fish in the outside tanks provided the stimulus shoals. Water in the aquarium was cleaned and aerated through an internal filter and was partly replaced regularly. Light was provided by a fluorescent lamp (36 W) placed above the aquarium. Test fish were fed once daily to excess with *Chironomus* larvae.

In the experiment, only fish showing no signs of reproductive activity were used. Each test fish was used only once, while stimulus fish were used several times. However, stimulus fish were never used twice a day or in the same combination.

Experimental design

The test aquarium measuring 80×40×40 cm was filled with 1-day-old tap water up to a water level of 15 cm. It was divided into two stimulus compartments (16.5×40×19 cm) on the right and left hand side and a test fish compartment in the middle (47×40×19 cm) (Fig. 1). The compartments were separated by transparent Plexiglas allowing visual contact only. In the test fish compartment, a choice zone measuring 5 cm was indicated by a black line drawn onto the bottom of the tank in front of each stimulus compartment. The size of both stimulus compartments could be reduced by adding two removable transparent Plexiglas partitions (Fig. 1). The reduced stimulus compartment’s size amounted to two-thirds of the unreduced compartment. Consequently, a shoal of equal group size was 50% denser in the reduced compartment than a shoal in the unreduced compartment. To avoid preference for one side, the position of the size-reduced compartment alternated between the trials. To prevent any interaction of the fish with their environment a black curtain was stretched around the test tank. Two small spy-holes for observation were cut out at the height of the water level. During the experiments, the only source of light was a fluorescent lamp (36 W), which was centred lengthwise above the aquarium. For each trial stimulus fish were randomly caught from the outside tank and matched by visual judgement. All fish were fed shortly prior to the experiments to avoid confounding effects of different hunger levels (e.g. Frommen et al. 2007).

In the control experiment (different shoal size and different shoal density), no removable Plexiglas partitions were added and 12 and eight individuals were placed into the stimulus compartments, respectively. Consequently, the larger shoal composed of 12 individuals exceeded the smaller shoal of eight individuals by 50% in group size. Thus, there were two stimulus shoals with a different number of individuals also differing in shoal density.

In the ‘equal-density experiment’ (different shoal size, but equal shoal density), eight fish were released into the 33% size-reduced stimulus compartment and 12 fish into the bigger compartment. Thus, there were two stimulus

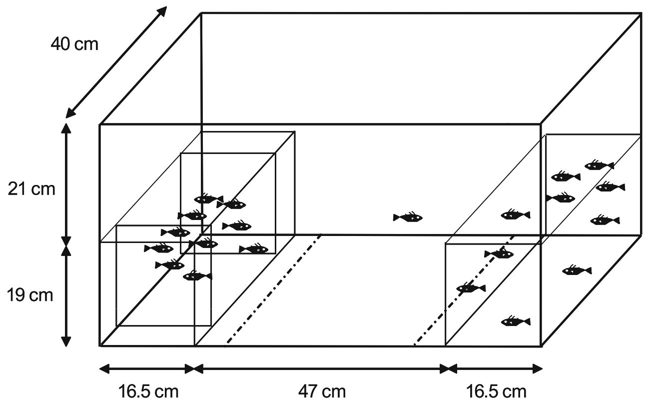

Fig. 1 The aquarium used to measure shoaling preferences. A stimulus shoal was placed into the left and the right stimulus compartment. Stimulus compartments could be size-reduced by 33% using clear sheets of Plexiglas, here shown for the left compartment. The water level was 15 cm. In front of each compartment a choice zone measuring 5 cm was drawn onto the bottom of the tank. Stimulus shoals differed both in size and density (experiment 1), in shoal size only (experiment 2) or in shoal density only (experiments 3 and 4)

shoals with a different number of individuals but with the same density.

In the ‘equal-size experiments’ (equal shoal size, but different shoal density), ten (high-density experiment) or eight (low-density experiment) fish were put into the smaller as well as the bigger stimulus compartment. Thus, there were two stimulus shoals with an equal number of individuals but with different density of the shoal members.

After introducing the stimulus fish they were allowed to acclimate for 5 min. Stimulus shoals spaced out evenly in their respective stimulus compartments. Meanwhile, the test fish was haphazardly caught out of the test fish aquarium. After the acclimatisation period, the test fish was placed into a transparent, perforated Plexiglas cylinder ($10\times7\times17$ cm) in the centre of the test fish compartment. The cylinder could be lifted by a string from outside the curtain. As soon as the test fish had tried to approach both stimulus shoals (indicated by nudging the plastic cylinder on both sides), but after 2 min maximally, the cylinder was lifted up and the trial began. An observer recorded the time the test fish spent within the choice zones over a period of 5 min. Time measurement started and ended as soon as the test fish had entered or left the choice zone with more than half its body length. In addition, the side the test fish approached first was noted.

For the ‘control experiment’ 25, for the ‘equal-density experiment’ 31, for the ‘equal-size/high-density experiment’ 30 and for the ‘equal-size/low-density experiment’ 25 replicates were carried out. After each replicate, the test aquarium was rinsed and the water was renewed. Standard length (SL) and body mass were measured for test and stimulus fish and the condition factor (CF) was calculated as $100\times\text{body mass (g)}/\text{SL (cm)}^3$ (Bolger and Connolly 1989). The standard length of the test fish ranged between 3.5 and 6.0 cm (mean±SD, 4.82±0.5), the condition factor between 0.94 and 1.63 (mean±SD, 1.28±0.16). Due to an error, body measurements in the control experiment were conducted only in 24 trials. For the stimulus shoals the mean SL and CF were calculated. Furthermore, as some studies found that fish preferred the more similar of two shoals compared to their own body measures (e.g. Hoare et al. 2000; Barber 2003), the SL and CF of the test fish relative to the average of each shoal were calculated by dividing the SL and CF of the test fish by the mean values of the respective shoal. Body measures of the stimulus shoals did not differ significantly in all experiments (Table 1), except for mean and relative CF of the stimulus shoals in the ‘equal-density experiment’ (Table 1). However, these differences did not significantly influence test fish’s choice (see “Results”). After the experiments, stimulus fish were released into a further outside stock tank similar to the one described above to assure that fish were not used in experiments twice daily.

Statistical analysis

To analyse differences in time test fish spent near the respective stimulus shoals a preference index was used, which was calculated by subtracting the time the test fish spent near the smaller or less dense shoal from the time it spent near the larger or denser one. Data were analysed with linear models, comparing the preference index to zero. Parametric statistics were used as variables were normally distributed according to Kolmogorov–Smirnov tests with Lilliefors correction. Time values obtained in the ‘equal-size/high-density’ experiment were square-transformed before calculating the preference index to reach normal distribution. The preference indices served as dependent variables. To control for shoal differences, the absolute and relative differences in mean standard length (Δ SL/Δ rel. SL) and condition factor (Δ CF/Δ rel. CF) of the stimulus shoals were included as covariates in the model. Non-significant factors were removed from the analysis. *p* values are two-tailed throughout. Analyses were performed using SPSS (Version 11.0) and the R 2.6.1 statistical package.

Results

In the ‘control experiment’, test fish spent significantly more time near the larger shoal (Table 2, Fig. 2). Out of the 25 test fish, 16 spent more time near the larger shoal (χ^2-test, $\chi_1^2=1.96$, $p=0.162$). The first approach of the test fish did not differ significantly between the shoal containing 12 ($N=14$) or eight ($N=11$) individuals (χ^2-test, $\chi_1^2=0.36$, $p=0.549$). Variation between shoals in mean SL and CF and these measures relative to the test fish’s SL and CF did not have any significant effect on shoaling preferences (Table 2).

In the ‘equal-density experiment’, test fish did not spend significantly more time with the larger or the smaller shoal (Table 2, Fig. 2). Out of the 31 test fish, 14 spent more time near the larger shoal (χ^2-test, $\chi_1^2=0.29$, $p=0.59$). The first approach of the test fish did not differ significantly between the shoal containing 12 ($N=14$) or eight ($N=17$) individuals (χ^2-test, $\chi_1^2=0.29$, $p=0.59$). Test fish preferred to associate with the shoal with the smaller mean SL (Table 2), while differences in relative SL or mean and relative shoal CF did not have a significant influence (Table 2).

In the ‘equal-size/high-density experiment’ test fish spent significantly more time near the less dense shoal (Table 2, Fig. 2). Out of the 30 test fish, 22 spent more time near the less dense shoal (χ^2-test, $\chi_1^2=6.533$, $p=0.011$). In accordance with this result the first approach of the test fish differed significantly in favour of the less dense shoal ($N_{\text{less dense}}=22$, $N_{\text{denser}}=8$, χ^2-test, $\chi_1^2=6.533$, $p=0.011$). Furthermore, test fish preferred the shoal with the higher and

Table 1 Results of paired *t*-tests comparing the stimulus shoals' mean standard length (SL) and mean condition (CF) factor as well as stimulus shoals' mean SL and mean CF in relation to the test fish's SL (rel. SL) and CF (rel. CF)

Body measures	**Experiments**							
	Control		Equal-density		Equal-size/high-density		Equal-size/low-density	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Mean SL	−1.243	0.226	−0.494	0.625	0.844	0.405	<0.01	>0.99
Mean CF	−1.154	0.260	−6.278	**<0.001**	−0.211	0.826	−0.168	0.868
rel. SL	1.239	0.228	0.404	0.689	−0.737	0.467	0.115	0.910
rel. CF	0.762	0.454	6.080	**<0.001**	0.245	0.808	0.318	0.753

Body measures did not differ significantly in all experiments, except for mean and relative CF of the stimulus shoals in the 'equal density experiment'. However, these differences did not significantly influence test fish's choice (see "Results"). Significant influences are printed in bold

more similar mean SL (Table 2). Variation in mean and relative CF did not have a significant effect.

In the 'equal-size/low-density experiment', test fish did not spend significantly more time with one of the two shoals (Table 2, Fig. 2). Out of the 25 test fish, 15 spent more time near the less dense shoal (χ^2-test, $\chi_1^2=1.0$, $p=0.317$). The first approach of the test fish did not differ significantly between the two shoals (χ^2-test, $N_{\text{less dense}}=11$, $N_{\text{denser}}=14$, $\chi_1^2=0.36$, $p=0.549$). Variation between the stimulus shoals' mean and relative SL did not significantly influence the test fish's choice (Table 2), while the test fish preferred the better as well as the less similar conditioned stimulus shoal (Table 2).

The time test fish spent in proximity to both shoals combined differed significantly between the four experiments (ANOVA, $F_{3,107}=7.471$, $p<0.001$, Fig. 3). Test fish in the 'equal-size/high-density experiment' spent significantly more time shoaling than test fish in the 'control experiment' and in the 'equal-size/low-density experiment' (Scheffé-test, $p=0.005$ and 0.001, respectively, Fig. 3).

Discussion

Group size is a well-known factor influencing group preferences (reviewed in Krause and Ruxton 2002), mainly because larger groups are known to provide an increased protection against predators (Magurran 1990). This might be because of an increased vigilance of group members, the dilution of risk or a higher confusion of the predator (Pitcher and Parrish 1993; Krause and Ruxton 2002). However, although many studies find preferences for the larger of two groups under predation risk, little is known whether these preferences are mediated by group size or group density.

The results of the 'control experiment' showed that sticklebacks from the used population preferred the shoal composed of 12 individuals over the one composed of eight individuals when density differed as well. This is in accordance with several other studies using sticklebacks as a model system showing that they prefer the larger of two shoals (e.g. Krause 1993b; Tegeder and Krause 1995;

Table 2 Results of the linear models analysing different factors influencing test fish's shoal choice

Factors	**Experiments**											
	Control			Equal-density			Equal-size/high-density			Equal-size/low-density		
	df	*t*	*p*	df	*t*	*p*	df	*t*	*p*	df	*t*	*p*
Δ SL	23	−1.015	0.321	29	−2.554	**0.016**	27	−2.215	**0.035**	20	0.379	0.709
Δ CF	20	0.689	0.499	27	−1.339	0.192	26	0.806	0.427	22	−2.203	**0.038**
Δ rel. SL	22	−1.087	0.289	26	−0.428	0.672	27	−2.273	**0.031**	21	0.327	0.747
Δ rel. CF	21	0.731	0.474	28	−0.369	0.715	25	0.144	0.887	22	−2.258	**0.034**
Shoal differences	24	2.299	**0.031**	29	−0.172	0.865	27	2.457	**0.021**	22	0.509	0.616

In the control experiment (12 vs. 8, different densities) as well as in the 'equal-size/high-density experiment' (10 vs. 10), test fish's choice was explained by differences in shoal size and/or density. In the 'equal-size/high-density experiment' this was also the case for differences in standard lengths between shoals (mean and relative SL at the group level). In the 'equal-density experiment' (12 vs. 8, equal density), differences in mean SL at the group level was the only factor significantly influencing test fish's choice, while in the 'equal-size/low-density' differences in condition factor (mean and relative CF) played a crucial role. Significant influences are printed in bold

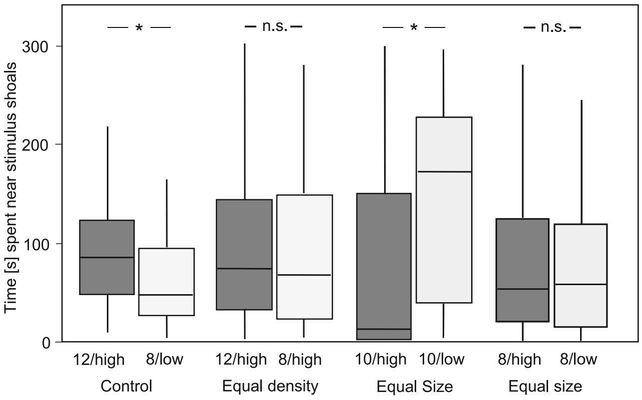

Fig. 2 Time in seconds test fish spent near the stimulus shoals in the ‘control experiment’, the ‘equal-density experiment’ and the two ‘equal-size experiments’. Given are medians, quartiles and ranges of the untransformed data. From these data preference indices were calculated (see ‘Statistical analyses’ for details). On the *x*-axis the number of shoal members as well as shoal density is provided. Each test lasted 300 s. *Statistics above the bars* represent the results of the respective model. *n.s.* non-significant, *asterisk* $p<0.05$. See text for statistics

Barber et al. 1998; Krause et al. 1998; Krause et al. 2000). In contrast, in the ‘equal-density experiment’, in which group size was the same as in the ‘control experiment’, while the size of the stimulus compartment containing the smaller shoal was reduced so that shoal density was equal, test fish spent a comparable amount of time near the larger and the smaller groups. There might be two reasons for this result. First, it is possible that fish do not ‘count’ individuals in a shoal but roughly estimate group size using group density as an indicator (Agrillo et al. 2007). Indeed, there are several studies in birds, non-human primates as well as human babies showing that there are two mechanisms to discriminate among different numerosities, one for counting small numbers (less than four) precisely and the second for quantifying large numbers approximately (reviewed in Feigenson et al. 2004; Agrillo et al. 2007). Here, test fish might use non-numerical cues like surface area, contour length or group density. These mechanisms have recently been shown to work in fish, too (Agrillo et al. 2007). Consequently, when density is the cue sticklebacks use to assess large numbers and both shoals are equal compact, test fish might simply not be able to estimate which one is composed of more individuals. Second, it is possible that sticklebacks in the control experiment chose the larger shoal not because of risk dilution or higher vigilance of larger shoals but because of an increase in predator confusion. When confusion is mainly induced by shoal density, which might in nature correlate with an increased group size, the shoals with equal densities might be of equal attractiveness to the test fish.

The results of the ‘equal-size/high-density experiment’, in which both stimulus shoals were composed of ten fish but differed in compactness, were in contrast to the findings of the control experiment. The prediction of this experiment was that test fish would prefer the denser group when density leads to an increase in predator protection (Krakauer 1995). Contrary, our results showed that when both shoals differed only in density and density was overall high test fish spent significantly more time near the less dense group. This finding might be explained by three recent studies (Tosh et al. 2006; Ruxton et al. 2007; Ioannou et al. 2008), which all found that an increase in density does not lead to greater predator confusion. Furthermore, fish density in the smaller compartment was the highest of all treatments. As shoals often tighten when attacked by a predator, high density might signal higher predation risk. A recent theoretical study by Peacor (2003) suggested that individuals assess the risk of predation using the density of conspecifics and adjust their phenotype (e.g. behaviour) accordingly. Although Peacor’s model deals with long-term modifications of morphology, its theoretical baseline is also applicable for short-term reactions like behavioural preferences. Furthermore, in European minnows it has been shown that single individuals change their behaviour after observing a groups’ response to an approaching predator without seeing the predator itself (Magurran and Higham 1988). Thus, it is plausible that, when lower group density implies a lower threat of predation, test fish in the ‘equal-size/high-density experiment’ might simply have chosen the less dense and thus safer shoal. This assumption is in concordance with results of the ‘equal-size/low-density experiment’. Here, test fish did not show a preference for either of the two shoals, irrespective of density. However, density in both shoals was low and thus might not have provided information about possible predation risks. Finally, the finding that test fish in the ‘equal-size/high-density

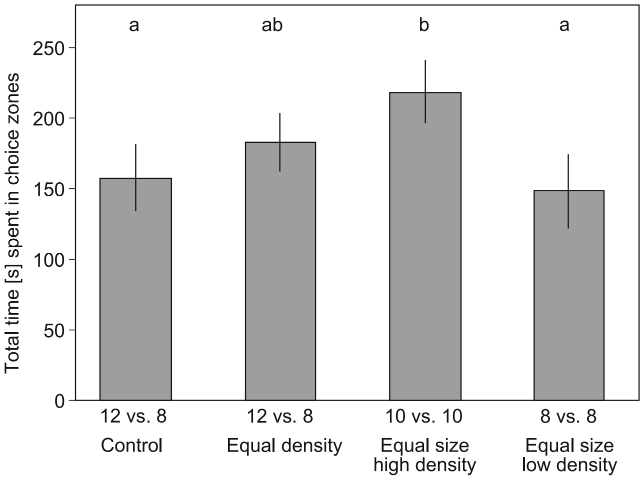

Fig. 3 Total time in seconds test fish spent in close proximity to both stimulus shoals combined. Given are mean values±two SE. Different *letters above the bars* indicate significant differences between the respective experiments. See text for statistics

experiment' spent significantly more time shoaling than in the control experiment and 'equal-size/low-density experiment' might indicate that they were more anxious about an assumed predator. On the other hand if density plays the crucial role in sticklebacks' shoaling decisions and shoals with higher density are generally less attractive one would also have expected a preference for the smaller and thus less dense shoal in the 'control experiment', which was not the case. Thus, the results might suggest some kind of non-linearity in group size and density effects on sticklebacks' shoaling preferences.

In addition to shoal size and density, body measures like standard length (Hoare et al. 2000; Barber 2003) or condition factor (Krause 1993b; Barber et al. 1995; Frommen et al. 2007) are well-known to mediate shoaling preferences of sticklebacks. Such patterns were also to be found in the present study, although their directions were somewhat controversial between the respective experiments. However, the body measures that influence the test fish's choice did not differ significantly between the respective stimulus shoals. Consequently, they cannot explain the influence of different shoal sizes and densities on shoaling preferences of the three-spined sticklebacks used in this study.

The results of this study indicate that shoal size and shoal density might play different roles in sticklebacks' shoaling decisions depending on the situation, leaving space for future work to elucidate this question in more detail.

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ERRATUM

Disentangling the effects of group size and density on shoaling decisions of three-spined sticklebacks (*Gasterosteus aculeatus*)

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