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Group Choice as a Function of Group Size Differences and Assessment Time in Fish: The Influence of Species Vulnerability to Predation

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Abstract

The shoal-choice behaviour of two species of fish that differ in their vulnerability to predation was compared. Individuals of threespine stickleback, *Gasterosteus aculeatus*, and creek chub, *Semotilus atromaculatus*, were presented with a simultaneous choice of two equidistant stimulus shoals of conspecifics that differed in membership size (5 vs. 6 fish, 5 vs. 7, 5 vs. 8, 5 vs. 9 and 5 vs. 10). Test fish were allowed to view the stimulus shoals from a standard distance for either 10–20 or 120–150 s before being frightened with a stimulus from an overhead light and released to join either shoal. We observed which shoal (the smaller or the larger one) the test fish approached. Preference for the larger stimulus shoal generally increased with increasing shoal size difference and with the duration of the assessment period, and was more pronounced in chub (the more vulnerable of the two species). For the short assessment period, chub showed a significantly stronger preference for the larger stimulus shoal than sticklebacks, whereas there was no significant difference between species for the long assessment period. Furthermore, chub responded more readily to small differences in shoal size (of 1–3 fish) than sticklebacks, for both short and long assessment periods. The above results are consistent with the hypothesis that chub, as the more vulnerable of the two species (in terms of predation), should be able to identify the larger of two shoals more quickly and should be more sensitive to small differences in shoal size than sticklebacks.

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Introduction

Group size has an important influence on both the foraging success and predation risk of individuals in many social animal species (RUBENSTEIN 1978; PULLIAM & CARACO 1984; GODIN 1986; MANGEL 1990; PITCHER & PARRISH 1993; RANTA et al. 1994; KRAUSE & GODIN 1995). We should therefore expect that animals have evolved mechanisms for discriminating among groups on the basis of their group size. How well individuals from different species can discriminate among groups of different size and how strongly they respond to the perceived differences should depend on the ecological consequences (in terms of foraging and predation) of such group-size differences.

JEVONS (1871) was one of the first to point out the importance of assessment duration for discrimination tasks. For instance, psychophysical experiments have demon-

strated that, in humans, the accurate assessment of a particular number of objects is critically dependent on assessment duration (ATKINSON et al. 1976). Similar results have been reported for fish (TEGEDER & KRAUSE 1995).

In this study we compared the shoal-size choice of two fish species, the threespine stickleback, *Gasterosteus aculeatus*, and the creek chub, *Semotilus atromaculatus*, when under predation threat. Sticklebacks usually form tight shoals only in response to a predation threat and otherwise spend much of their time foraging solitarily, whereas (juvenile) chub are almost exclusively found in shoals (KRAUSE, unpubl. data). Due to their spines and bony lateral plates, sticklebacks are better protected against both avian and fish predators (ROBINSON 1989; REIMCHEN 1994), which presumably allows them to forage solitarily at relatively low risk, compared with the more vulnerable cyprinid species (ABRAHAMS 1994). First, we tested the prediction that individuals of both species, chub and sticklebacks, should increase their preference for the larger of two stimulus shoals with increasing size difference between the stimulus shoals. Second, we hypothesized that discrimination between shoals of different size would become more accurate with increasing assessment duration because fish will have more time to gather information on the shoals. Finally, we investigated species differences, predicting that chub should be more likely to respond to small shoal-size differences and to identify the larger of two shoals more quickly than sticklebacks owing to their (chub's) greater vulnerability to predators.

Materials and Methods

Threespine sticklebacks (mean \pm SD total length = 4.0 ± 0.2 cm) were collected with a beach seine in Morice Lake (near Sackville, NB, Canada) and creek chub (mean \pm SD total length = 3.8 ± 0.3 cm) originated from Stony Brook (near Princeton, NJ). Fish were kept in their respective countries in holding tanks at 15°C and fed *ad libitum* on TetraMinTM flakes & freeze-dried chironomids several times daily for about 2 mo before being used in the experiments.

We used chub and sticklebacks of similar body size to avoid the potential confounding effects of body size on behaviour and vulnerability to predation. However, matching species for body size meant that adult sticklebacks and juvenile chub were used which could potentially introduce an ontogenetic effect as a confounding factor. This problem was addressed in pilot trials which showed that a predation threat causes an increase in shoaling tendency in both fish species (chub: Wilcoxon matched-pairs test, $n = 10$, $T = 0$, $p < 0.01$; sticklebacks: $n = 10$, $T = 0$, $p < 0.01$; see KRAUSE & GODIN 1994 for details of the experimental procedure), thus confirming that shoaling behaviour is linked to an antipredator response irrespective of age (see also KRAUSE & TEGEDER 1994). We also know from field observations that both species are preyed upon by kingfishers, herons and probably also predatory fish (such as trout), suggesting that shoaling is an adaptation to predation pressure (KRAUSE, unpubl. data). Individual test fish were presented with a binary choice between two equidistant, but differently sized conspecific stimulus shoals (see inset Fig. 1). Fish in the paired stimulus shoals were matched for body length. Test fish and stimulus shoals were placed inside clear plastic cylinders (7 cm in diameter) to control their respective positions within the test tank ($1 \times 1 \times 0.3$ m, $L \times W \times H$, water depth 5 cm; see KRAUSE & TEGEDER 1994 for details of the experimental set-up). The test fish was frightened with an overhead light flash upon release from its plastic cylinder (which was remotely lifted by a few cm using a pulley system). To avoid any potential bias, the test fish was released only when it was facing directly between the two stimulus shoals. The light flash was created by switching off a light bulb above the test tank for about 0.5 s and then switching it on again. This simulated the shadow of an avian predator passing overhead but did not provide any directional cues which could have biased the behaviour of the test fish.

Test fish were presented with the following choices of paired stimulus shoals: 5 vs. 6 fish, 5 vs. 7, 5 vs. 8, 5 vs. 9 and 5 vs. 10. Individual test fish were allowed to view the stimulus shoals for either 10–20 s or 120–150 s before release (test fish faced towards one of the stimulus shoals or between them during the assessment period; see inset Fig. 1). The same test procedure was used for both fish species. Ten replicates were carried out for each

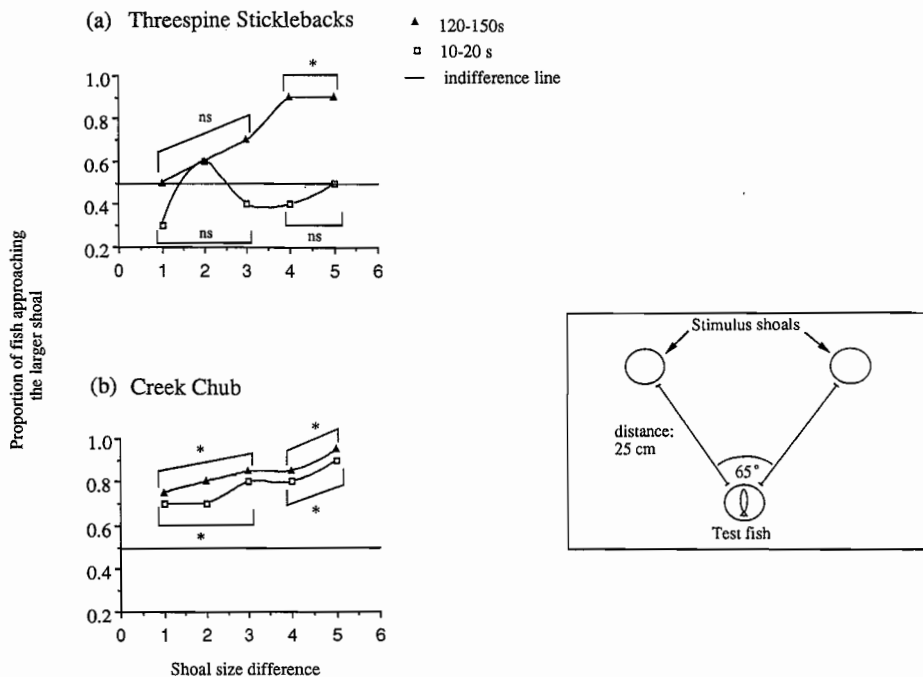


Fig. 1: Proportion of test fish (out of 10 individuals; but out of 20 fish for long assessment time in chub) that approached the larger of two conspecific stimulus shoals. Membership-size difference between paired stimulus shoals varies from 1 to 5 fish. Test fish were given either 10–20 s or 120–150 s to assess the size of the stimulus shoals. The responses of threespine sticklebacks (a) and creek chub (b) are shown. We pooled the first three shoal-size differences (1–3) and the last two (4 and 5) for each species and assessment period to test whether the larger stimulus shoal was preferred using a χ^2 -test (adjusted for multiple testing using the Bonferroni method). Significance at the 5% level is indicated by an asterisk. Data were classed into two groups (small and large differences in shoal size indicated by brackets) because the sample sizes were too small for testing of single data points. The inset illustrates the positioning of the stimulus shoals and the test fish at the onset of an experimental trial

combination of shoal size difference, assessment duration and species (with the exception of 20 trials for the long assessment period in chub). Each test fish was used only once. Stimulus fish were randomly taken from a separate tank of about 50 fish for each species separately. A trial was defined as completed whenever the test fish approached to within 4 cm (=body length) of either stimulus shoal. This distance falls within the typical inter-individual distances observed in fish shoals (PITCHER & PARRISH 1993).

Shoal choice was measured as the proportion of the test fish ($n/10$ or $n/20$) that approached the larger of the paired stimulus shoals. We used a generalized linear model (GLM) to test the influence of the explanatory variables, namely species identity (a factor with two levels, stickleback and chub), assessment duration (two levels, 10–20 s and 120–150 s) and shoal size difference (a linear variate, 1, 2 ... 5), on the response variable (the aforementioned proportion). A GLM tests for the effect of an explanatory variable by comparing the difference between the residual deviances of two fitted models — one including the variable in question and the other identical but excluding it — with χ^2 on degrees of freedom equal to the difference in the number of parameters in the model (BROWN & ROTHERY 1993). A GLM is more appropriate than a multiple regression (on arcsin squareroot transformed data) because of the binomial distribution of the response variable.

Results

The overall analysis shows that species identity, assessment duration and shoal size difference all had a significant effect on shoal-size choice of the test fish (Table 1). No significant interactions between the above effects were found (Table 1). For assessment duration, we observed the reverse trend. Preference for the larger shoal increased significantly with increasing assessment duration in sticklebacks but not in chub (Table 2a). Despite the fact that there is a strong effect of assessment duration in sticklebacks but not in chub (Table 2a), there is no significant interaction term between species and assessment duration in the overall analysis (Table 1). This may seem peculiar at first. However, although the effect of assessment duration is highly significant in one species but not in the other,

Table 1: Results of generalized linear models relating the proportion of test fish that approached the larger stimulus shoal to shoal-size difference, assessment duration and species identity. Statistical significance of each term was assessed while controlling for the influence of other terms in question. The difference in residual deviances is distributed as chi-squared on the degrees of freedom (df) given

Test term	df	χ^2	p-value
(1) Shoal size difference	1	8.331	<0.01
(2) Assessment duration	1	7.500	<0.01
(3) Species	1	14.159	<0.001
(1) * (2)	1	1.608	0.205
(2) * (3)	1	1.518	0.218
(1) * (3)	1	0.004	0.952

Table 2: Results of generalized linear models testing for the influence of (a) assessment duration and shoal-size difference on the proportion of fish that approached the larger stimulus shoal for each species separately, and of (b) species identity and shoal size difference on the above proportion for each assessment period (short assessment: 10–20 s, long assessment: 120–150 s) (see Fig. 1 for comparison). Significance was determined as in Table 1

	Test term	df	χ^2	p-value	
(a)	Creek chub	Shoal size difference	1	4.53	0.033
		Assessment duration	1	0.82	0.365
	Threespine stickleback	Shoal size difference	1	3.49	0.061
		Assessment duration	1	8.49	0.004
(b)	Short assessment	Species	1	12.47	0.001
		Shoal size difference	1	1.18	0.277
	Long assessment	Species	1	3.08	0.079
		Shoal size difference	1	8.78	0.003

the difference between the two effects is not significantly different from zero. The same is true for the test of shoal size difference between the two species, but the apparent discrepancy between the overall analysis (Table 1) and that of the subsets (Table 2a) is less strong.

Chub had a significantly stronger preference for the larger stimulus shoal than sticklebacks when assessment duration was short, but not when it was long (Table 2b). Furthermore, chub showed a significant preference for the larger stimulus shoals even when shoal-size differences were small (for both short and long assessment periods), whereas the sticklebacks did not (Fig. 1).

Discussion

In this study, we observed species differences in shoal-choice behaviour. Chub more readily responded to small shoal-size differences, and strongly preferred the larger stimulus shoal even when assessment time was short, compared with sticklebacks (Fig. 1, Table 2). This difference in behaviour between the two species is consistent with our prediction that the more vulnerable species should respond more sensitively to differences in the membership size of conspecific shoals. A similar result, linking morphological adaptations against predators to behavioural differences, was obtained by MCLEAN & GODIN (1989) and GODIN & VALDRON CLARK (1997) (review, SIH 1987). Comparing three different fish species with differing amounts of body armour, MCLEAN & GODIN found that the most armoured species, the threespine stickleback, was the least likely to flee in response to a fright stimulus and exhibited the shortest flight initiation distance. In contrast, the non-armoured killifish, *Fundulus diaphanus*, showed the strongest antipredator responses. Similarly, ABRAHAMS & HEALEY (1993) reported that the least vulnerable of four species of Pacific salmon, *Oncorhynchus* spp., exhibited the weakest antipredator responses. ABRAHAMS (1994) showed that in the presence of a predatory yellow perch, *Perca flavescens*, the feeding rate of non-armoured fathead minnows, *Pimephales promelas*, decreased whereas that of armoured brook sticklebacks, *Culaea inconstans*, was unaffected. Morphological adaptations against predation therefore allow sticklebacks to continue feeding unabated in the presence of predators. However, in the absence of predators, minnows had higher feeding rates than sticklebacks, suggesting that armour has considerable costs in terms of competitive ability.

However, the difference in discrimination ability between chub and sticklebacks could potentially also be related to factors other than differences in vulnerability. Morphological differences (such as body shape and colour contrast) between the two species may account for the ability of chub to assess shoal-size differences more accurately, for instance. This is difficult to test experimentally because a stickleback that is presented with two shoals of chub may find it easier to discriminate shoal-size differences but may not necessarily respond in the same way as it does to shoal-size differences between conspecific shoals. This could be because shoaling with con- and heterospecifics is associated with different costs and benefits, which is reflected by the preference of many fish species to shoal with conspecifics (KRAUSE & GODIN 1994).

Another potential alternative explanation of differences in discrimination ability could be that chub and sticklebacks are subject to different predation pressures in their

respective habitats. This means that the behavioural differences observed in this study could be accounted for on the basis of differences in predation intensity between habitats rather than differential vulnerability between species. We observed that both habitats were regularly visited by predatory birds (kingfishers and grey herons) and contained a number of piscivorous fish species. However, we did not carry out any measurements to quantify the intensity of predation.

Sticklebacks were found in the littoral zone of a lake and responded to disturbances by forming tight shoals that performed evasive manoeuvres. Chub occurred in small pools of a stream where they aggregated in large shoals in response to potential predators. Thus both species occupied similar regions in their habitat and exhibited similar antipredator behaviours despite the fact that they originated from different habitats (stream and lake, respectively). This makes it unlikely that the behavioural differences reported in this study can be accounted for by different habitat preferences or different antipredator strategies.

Note that, for long assessment periods, chub significantly discriminated between shoals of 5 and 6 fish (i.e. shoal size difference of 1) whereas sticklebacks did not (Fig. 1). In this case, the longer assessment duration had no influence on the choice behaviour of sticklebacks (Fig. 1). And it remains questionable whether sticklebacks perceived a difference in shoal size but failed to respond to it, because the benefits of associating with the larger shoal might be negligible for them when shoal size difference is that small. This highlights a general problem with this kind of study. We cannot be certain about the smallest difference in shoal membership size that fish can detect. We can only measure the smallest difference that they respond to, that is, the smallest shoal size difference that is ecologically relevant to an individual of a particular species.

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