

SHOAL CHOICE BEHAVIOUR IN FISH: THE RELATIONSHIP BETWEEN ASSESSMENT TIME AND ASSESSMENT QUALITY

by

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Summary

In this study, we investigated the role of assessment time in group size discrimination and in particular the trade-off between the time cost involved in gathering information and the potential benefits derived from the acquired information. In a first experiment, we presented individual chub, *Semotilus atromaculatus*, with a choice between 4 vs 4 and 8 vs 8 conspecific stimulus fish. After release we recorded the time taken by test fish to make a choice between the two stimulus shoals in the presence and absence of a fright stimulus. Test fish significantly reduced their response time in the presence of a fright stimulus and larger shoals (8 vs 8) were more quickly approached than smaller ones (4 vs 4). In a control experiment, chub were given a choice between an empty cylinder and a shoal (of 4 or 8 fish). By subtracting the response time in the control treatment from that in the choice treatment, we estimated the time test fish spent choosing between stimulus shoals to be 24-55% of the overall response time. These results indicate that choosing between different groups is associated with a significant time cost. In a second experiment, we presented test fish with stimulus shoals that differed in size: 4 vs 5, 4 vs 6, 4 vs 7 and 4 vs 8, to investigate how the response time of fish and their ability to distinguish between shoals of different size were affected by the magnitude of the shoal size difference and the presence and absence of a fright stimulus. The ability to discriminate between shoals of different size increased with increasing shoal size difference whereas response time decreased. Both response time and discrimination ability were significantly reduced in the presence of a fright stimulus. The latter suggests that the benefits derived from group size discrimination

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were increasingly outweighed by the time costs of making group size assessments in the presence of potential danger; *i.e.* making fast assessments became relatively more important than making correct ones.

Introduction

Most studies of group choice are focused on the outcome of choice behaviour in terms of foraging efficiency or predation risk (Rubenstein, 1978; Pulliam & Caraco, 1984; Godin, 1986; Krause & Godin, 1994; Ranta *et al.*, 1994). The role that assessment time plays (and the relationship between assessment time and assessment quality) has largely been neglected. How long it takes an animal to make a certain decision becomes particularly interesting when assessment time is costly. Therefore we should expect a trade-off between the time spent on an assessment (at the expense of other activities) and the potential benefits derived from the information obtained.

In the study reported here, we gave individual fish a choice between two different-sized shoals in the presence or absence of a fright stimulus. In the presence of a fright stimulus, assessment time should be more costly because the fish is alone during the assessment and therefore highly vulnerable to predators. However, a reduction in assessment time may be associated with an increased risk of choosing the smaller shoal and thus an increase in subsequent predation risk. Joining the larger of two groups becomes more important in the presence of potential danger (Hager & Helfman, 1991; Pitcher & Parrish, 1993; Tegeder & Krause, 1995). Whether or not fish reduce assessment time in this situation should therefore depend on how they trade off the costs of staying alone whilst choosing against the benefits of correctly identifying the larger shoal. This leads to the three questions: does choice behaviour involve a considerable time cost? If so, do fish reduce this time cost in the presence of a fright stimulus? And is this time cost reduced at the expense of the ability to discriminate between different group sizes?

For an investigation of the costs of assessment time due to choosing between two alternative options, it is essential to first show that an element of choice really introduces a cost in terms of time. Therefore, in a first experiment, we carried out a control treatment in which fish were presented with a choice between two shoals of the same size and subsequently with a single shoal of corresponding size. By subtracting the response time

in the control treatment from that in the choice treatment, we could then estimate how much time fish actually spent on 'choosing'. We should expect that overall response time also includes other components (besides choice time) such as reaction time, adjustment to the conditions in the test tank (acclimatisation to a novel environment *etc.*).

In a second experiment we investigated how difficult it is for a fish to detect a size difference between two groups as a function of the magnitude of that difference. We predicted that fish should take less time to make a decision between two shoals of different size and be more successful at identifying the larger shoal as shoal size difference increases.

Materials and methods

Creek chub, *Semotilus atromaculatus*, (mean \pm SD standard length = 4.7 ± 0.4 cm) originating from Stony Brook (near Princeton, USA) were kept in holding tanks at 15°C and fed *ad libitum* on TetraMinTM flakes and freeze-dried chironomids several times daily for about 1 month before being used in the experiments.

In a first experiment, individual test fish were presented with a binary choice between two equidistant conspecific stimulus shoals of the same membership size (see inset Fig. 1). Test fish were placed in an opaque plastic cylinder (7 cm in diameter) and stimulus fish in 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). The opaque plastic cylinder, which contained six test fish, had a v-shaped opening just below the water surface. The opening was not large enough to allow the test fish to leave by just swimming through it. They had to make a little jump during which they broke the water surface. This release mechanism ensured first of all that the test fish left one by one (and not all at the same time). Furthermore, fish had to explore the cylinder to search for the exit actively; thus we avoided using timid inactive fish (fish sometimes freeze when they are frightened) in the experiment. After leaving the cylinder, there was no way back into it (fish that left could not rejoin the others in the opaque cylinder). Due to the v-shaped form of the opening, fish faced directly between the two stimulus shoals on leaving the opaque cylinder which avoided any bias towards one of the two stimulus shoals. As soon as a test fish had left the opaque cylinder and made its choice between the stimulus shoals, it was replaced by a new test fish in the opaque cylinder to keep numbers constant at six. The fact that we always had six fish in the opaque cylinder and not just one helped to keep the test fish active because they are less timid in a group. Newly introduced test fish stayed close to the bottom of the cylinder and then gradually started exploring the cylinder moving upwards and leaving through the v-opening. This way fish left the cylinder at intervals of about 1 per minute (and we did not have problems with fish escaping from the cylinder in quick succession). The above procedure also ensured that all test fish eventually left the cylinder. Pilot studies showed that even the most timid test fish did not stay for longer than 10-12 min in the cylinder. After leaving the cylinder test fish stayed in the test tank until they had come within 5 cm (one body length) of either stimulus shoal. This is within typical inter-individual distances

observed in fish shoals (Pitcher, 1986) and confirms that the fish's approach was indeed aimed at joining one of the stimulus shoals (see also Tegeeder & Krause, 1995, for details).

On leaving the opaque cylinder, one group of test fish was left undisturbed to make their choice and the others were frightened with an overhead light flash. The light flash was created by switching off a light bulb (100 W) 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 (Krause & Tegeeder, 1994).

Test fish were presented with a choice of paired stimulus shoals: 4 vs 4 or 8 vs 8 fish in the choice treatment, or with just a single shoal of 4 or 8 fish vs an empty cylinder in the control treatment. We measured the time taken by a fish between leaving the opaque cylinder and orienting itself towards one of the stimulus shoals. Such orientation always resulted in an approach towards that shoal. By subtracting the response time in the control treatment (only one shoal vs an empty cylinder) from that in the choice treatment (presentation of two stimulus shoals), we were able to determine the time test fish spent choosing between the two stimulus shoals.

In summary, on release from its cylinder, a test fish was presented with three test conditions (each of which had two levels), shoal size (4 and 8), release stimulus (no flash and flash) and treatment (choice between two shoals and single shoal). Fifteen replicates were carried out for each combination of test conditions: $2 \times 2 \times 2 \times 15 = 120$ trials. Each test fish was used only once.

In a second experiment, the same release mechanism was used, but test fish were presented with different-sized stimulus shoals: 4 vs 5, 4 vs 6, 4 vs 7 and 4 vs 8. We measured the response time (and estimated choice time) of test fish in the presence and absence of a fright stimulus as above and additionally recorded which shoal (the smaller or the larger one) was approached. Twenty-four replicates were carried out for each combination of test conditions: $2 \times 4 \times 24 = 192$ trials.

In both experiment 1 and 2, stimulus fish were chosen randomly for each trial from a separate holding tank of about 30 fish. Several minutes before the beginning of a trial, the stimulus fish were introduced to the plastic cylinders. In experiment 2, the larger stimulus shoal was presented equally often on the right and left side (relative to the test fish) to control for side preferences. The behaviour of the test fish was recorded by a video camera from 1.5 m above the pool.

Data analysis

We used a generalised linear model (GLM) to test the influence of the explanatory variables on the two response variables, response time and the proportion of fish that approached the larger shoal. 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 and powerful than a multiple regression because of the distribution of the response variables: binomial for proportion of correct choices and positively skewed for the response time, modelled by a gamma distribution (Brown & Rothery, 1993).

Results

In the first experiment, choosing between the two stimulus shoals accounted for up to 55% of the response time (4 vs 4 fish: no flash: 55%, flash: 46%; 8 vs 8: no flash: 24%, flash: 26%). The remaining response time was probably due to the fish adjusting to the novel environment after leaving the test cylinder rather abruptly. Choice behaviour thus formed a significant part of the overall response time (see also Table 1 for treatment effect).

The presence of a fright stimulus led to a significant reduction in overall response time (Table 1). However, due to the large inter-individual variability (and smaller sample sizes), only one of the pairwise comparisons (4 vs 4 stimulus fish) showed a significant difference in response time (Fig. 1). The overall analysis showed only a weak, non-significant effect of shoal size on response time (Table 1).

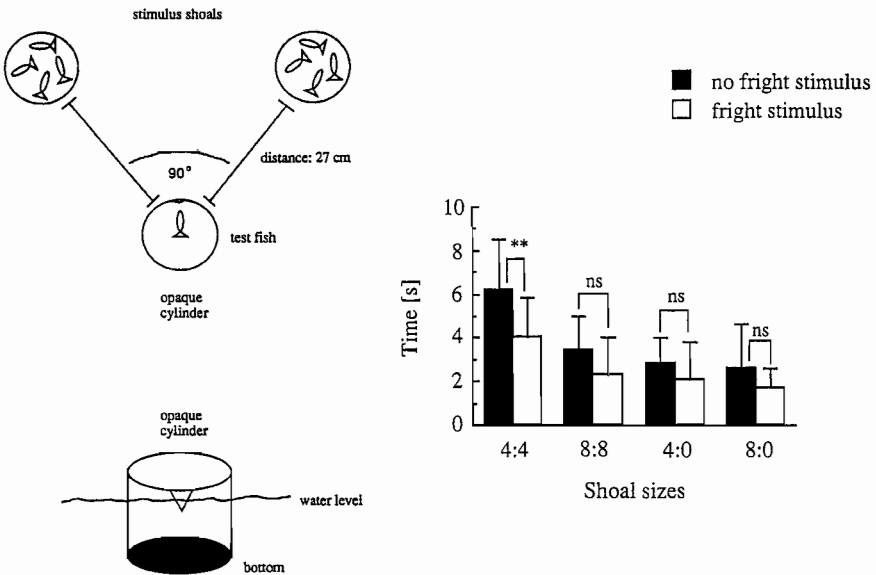


Fig. 1. Mean response time (+SD) of individual test fish that were either given a choice between two stimulus shoals of the same size (4 vs 4 or 8 vs 8) or presented with a single shoal vs an empty cylinder in the absence or presence of a fright stimulus. Significance was tested using independent *t*-tests and is indicated by asterisks: ** $p < 0.01$. The inset illustrates the experimental set-up. Test fish were kept in the opaque cylinder which they could leave through the v-shaped gap near the water surface. After leaving the cylinder, test fish were exposed to a choice between the two stimulus shoals which were placed at a distance of 27 cm.

TABLE 1. Results of generalised linear models relating the response time of test fish to treatment (choice between two stimulus shoals or presentation of single shoal), the presence or absence of a fright stimulus and shoal size (4 and 8 fish)

test term	df	deviance	p-value
(t) treatment	1	7.152	0.007
(fs) fright stimulus	1	4.598	0.032
(ss) shoal size	1	3.690	0.054
(fs) × (ss)	1	0.005	0.941
(fs) × (t)	1	0.021	0.886
(ss) × (t)	1	1.353	0.244

Statistical significance of each term was assessed while controlling for the influence of the other terms in question. The difference in residual deviances is distributed as χ^2 on the degrees of freedom (df) given.

TABLE 2. Results of fitting generalised linear models relating (a) the response time and (b) the proportion of test fish that approached the larger stimulus shoal to shoal size difference, both in the presence or absence of a fright stimulus

test term	df	deviance	p-value
<i>(a) response time</i>			
(ssd) shoal size difference	1	6.209	0.01
(fs) fright stimulus	1	4.247	0.03
(ssd) ²	1	0.014	0.90
(fs) × (ssd)	1	0.517	0.472
(fs) × (ssd) ²	1	0.009	0.92
<i>(b) performance</i>			
(ssd) shoal size difference	1	3.934	0.047
(fs) fright stimulus	1	9.546	0.002
(ssd) ²	1	0.343	0.557
(fs) × (ssd)	1	0.136	0.712
(fs) × (ssd) ²	1	0.159	0.689

Both linear and quadratic effects of shoal size difference were tested. We included the data on response time from experiment 1 (4 vs 4: shoal size difference equals zero) in the analysis. Statistical significance was assessed as in Table 1.

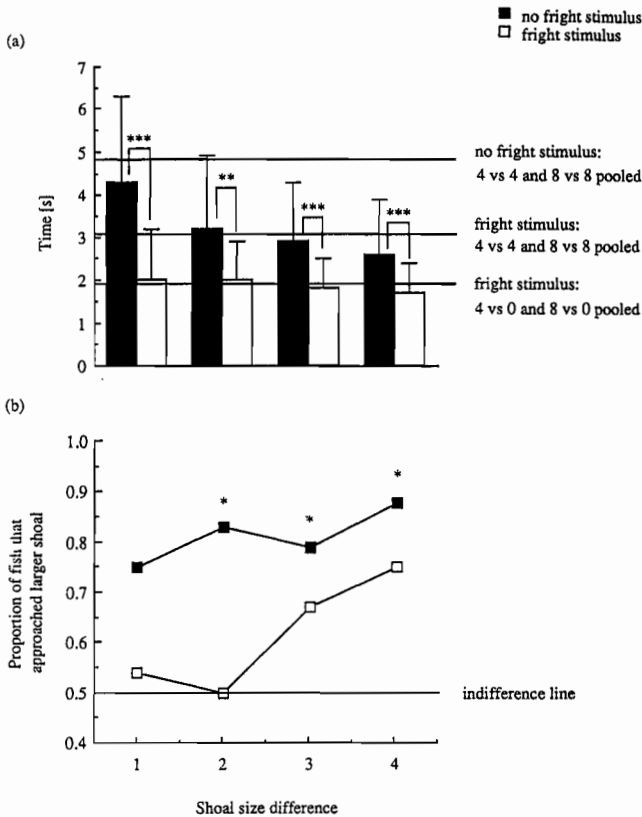


Fig. 2. (a) Mean response time (+SD) of individual test fish that were given a choice between two different-sized stimulus shoals. Membership size difference between paired stimulus shoals increased from 1 to 4. Significance was tested using independent t -tests and is indicated by asterisks: ** $p < 0.01$; *** $p < 0.001$. Horizontal lines indicate the mean response times for experiment 1. (b) Proportion of test fish that approached the larger of two stimulus shoals. Shoal choice was investigated in the presence and absence of a fright stimulus. Significance was tested at the 5% level using a χ^2 -test (adjusted for multiple testing using the Bonferroni method) and is indicated by an asterisk.

When two shoals of different size were presented, shoal size discrimination increased significantly with increasing shoal size difference whereas response time significantly decreased (Table 2, Fig. 2). Shoal size difference was included as a linear variate in the analysis (see Methods) and higher order terms did not provide a significant improvement of the assumption of linearity (Table 2). The presence of a fright stimulus was associated with a reduction in both response time and a fish's ability to

TABLE 3. *Accumulated analysis of deviance relating the proportion of fish that approached the larger stimulus shoal to shoal size difference (including quadratic effects) and response time*

	df	deviance	mean deviance	significance
<i>no fright stimulus</i>				
(ssd) shoal size difference	1	0.8798	0.8798	NS
(ssd) ²	1	0.0034	0.0034	NS
response time	1	0.2957	0.2957	NS
residual	92	91.4760	0.9943	
total	95	92.6549	0.9753	
<i>fright stimulus</i>				
(ssd) shoal size difference	1	3.207	3.207	NS
(ssd) ²	1	0.499	0.499	NS
response time	1	0.738	0.738	NS
residual	92	123.554	1.343	
total	95	127.998	1.370	

The response time term explores a potential relationship between the two response variables, response time and performance. Significance of each term was assessed while controlling for the influence of the other terms in question. The mean deviances give approximate χ^2 -values.

correctly identify the larger of the two stimulus shoals (Table 2, Fig. 2). Table 3 shows that after controlling for the effect of the fright stimulus on response time, there was no significant residual effect of response time on discrimination performance.

Discussion

Our data show clearly that choosing between two groups (of the same or different membership size) was associated with a considerable time cost that comprised up to 55% of the overall response time. Furthermore, response time was significantly reduced in the presence of a fright stimulus. The fact that choice behaviour is associated with a high time cost (and that fish reduced this cost when under predation threat) was an important prerequisite for the second part of our study in which we looked at how the duration of assessment time influenced the ability of test fish to discriminate between two stimulus shoals of different size.

The presentation of a fright stimulus led to a reduction in response time that was associated with a significant decrease in shoal size discrimination. This suggests that the benefits derived from successful shoal size discrimination were increasingly outweighed by the costs of long assessment times. These results are consistent with studies on the fast-start behaviour of various animal species (Eaton & Emberley, 1991; Will, 1991). Following a fright stimulus an individual performs a short-term evasion of a potential predator. It is characteristic of fast-starts that the promptness of the response (in form of evasion behaviour) is maximised at the expense of sensory input (information gathered about the environment) which is why this behaviour was previously believed to be a reflex and the direction of the fast start to be unaffected by the position of the predator. The latter has shown to be incorrect but recent evidence has confirmed that the nervous system no longer uses sensory information to compute the trajectory of the escape response once the animal is on its way (Eaton & Emberley, 1991).

The results presented in this paper raise the question of whether there is a clearly-defined threshold assessment time below which fish (chub) are incapable of clearly distinguishing between two shoals of different size (see also Tegeder & Krause, 1995). This threshold seems to be dependent on the magnitude of the shoal size difference. The larger the shoal size difference, the less time is needed for discrimination. An average assessment time of over 4 s was not enough for the test fish to discriminate between 4 vs 5 (no fright stimulus) fish whereas even 2.6 s were sufficient to detect a difference between 4 vs 8 (see Fig. 2).

The time needed for group size assessments should be seen in the context of the time that is available to individuals under predator attack. In other words the amount of time that elapses between the prey detecting an approaching predator and the predator's attack should define the assessment time available to an animal under these circumstances. Very little is known about this important factor which may provide an interesting area for future research. Note that chub showed very little variation in response time (1.7-2.0 s) in experiment 2 when under predator threat which suggests that they try to minimise the time needed to join a shoal. Experimental work on sticklebacks has shown that time minimisation plays a very important role in shoal choice behaviour under predator threat (Krause & Tegeder, 1994; Tegeder & Krause, 1995). Test fish were observed to prefer the

smaller of two stimulus shoals if approach time was considerably shorter. Based on this observation Tegeder & Krause (1995) developed a model which assumes a multiplicative relationship between shoal size and shoal distance; *i.e.* fish were willing to swim approximately twice as far for a shoal twice as large.

The results of this paper are consistent with other studies that identified assessment time as an important factor for decision-making processes (Jevons, 1871; Atkinson *et al.*, 1976; Tegeder & Krause, 1995; Krause *et al.*, in press). Jevons (1871) and Atkinson *et al.* (1976) reported a temporal and numerical threshold for the assessment of object numbers in human observers. Similar observations were made by Tegeder & Krause (1995) on fish. Sticklebacks, *Gasterosteus aculeatus*, did not discriminate between shoal sizes larger than 4 individuals if assessment time decreased from 120 to about 30 s (see also Krause *et al.*, in press). Contrary to that the ability of chub, *S. atromaculatus*, to discriminate shoal sizes was unaffected (by the above change in assessment time) suggesting that the greater vulnerability of chub to predators has led to the evolution of faster and more accurate assessment mechanisms in this species (Krause *et al.*, in press). In the present study, the presentation of a fright stimulus was associated with a considerable reduction in assessment time which is likely responsible for the decrease in discrimination performance. However, a fright stimulus might also induce higher vigilance behaviour and make the fish search for a potential predator (or for shelter) as well as trying to discriminate between the size of the stimulus shoals. Therefore it need not be the reduction in assessment time alone that is responsible for a change in discrimination ability. In this context it is interesting that changes in response time other than those mediated by the presence or absence of a fright stimulus did not have a significance influence on shoal size discrimination ability (see Table 3).

The way we assessed the time fish spent on making a choice between two shoals is based on the assumption that fish faced with only one shoal are not attempting to assess the presence of another yet undetected shoal. This implies that fish should generally take less time to assess shoal size when only one shoal is present (instead of two) which is strongly supported by our data. Therefore we believe that our method of measuring choice

time is a realistic measure of the time costs involved in the decision-making process.

The high density of fish and fish shoals in the littoral zone of many lakes and streams suggests that individual fish are frequently faced with the kind of choice situations they were exposed to in this study (Krause *et al.*, 1996a, b). More observations are needed, however, to provide accurate data on the assessment times that are available to fish under natural conditions to make their decision which group to join.

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