Shoaling decisions in female swordtails: how do fish gauge group size?

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Summary

Little is known about the mechanisms individuals might use to compare group sizes when making decisions about group membership. One possibility is that animals use ratio to determine differences in group sizes. Weber's Law states that the ease of any numerical comparison is based on the ratio between the stimuli compared; as the ratio becomes smaller the comparison becomes more difficult. We set out to test this prediction by offering female green swordtails, *Xiphophorus helleri*, dichotomous choices between different shoal sizes, varying both in ratios and absolute numbers of fish. Swordtails attended to the ratio of group size between stimulus shoals, rather than the numerical difference between shoals, when making shoaling decisions. Where group size ratio was 2:1, subjects showed a significant preference for the larger shoal, independent of the numerical difference between the shoals. When the ratio was 1.5:1, subjects showed no preference. The ratio between group sizes may, thus, be an important factor in shoaling decisions. More broadly, ratio could prove to be a widespread mechanism for animals to make numerical comparisons in group assessments.

Keywords: shoaling, swordtails, group choice, Weber's law.

Introduction

The ability to determine quantity is one of the most useful skills an organism can possess. Numerical quantities are salient to almost every aspect of an

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animal's life. For example, animals may need to determine concentrations of food patches, number of potential mates or competitors, or prevalence of predators. Establishing the relative quantities of objects or occurrences is termed 'relative numerosity' (Davis & Perusse, 1988). Relative numerosity is one of the most basic forms of number judgment and does not involve actual counting but, rather, the ability to have a general sense of 'more' versus 'less'. These types of judgments have been demonstrated in many species in the laboratory and in the field (ants: (Mallon & Franks, 2000); fish: (Tegeder & Krause, 1995); salamanders: (Uller et al., 2003); rats: (Capaldi & Miller, 1988); parrots: (Pepperberg, 1987); raccoons: (Davis, 1984); primates: (Hicks, 1956; Thomas et al., 1980; Woodruff & Premack, 1981; Matsuzawa, 1985; Rumbaugh et al., 1987; Hauser et al., 2000, 2003)). Judgments may be as straightforward as an animal being able to determine 'presence' or 'absence' of an object or event (Davis & Memmott, 1982; Davis & Perusse, 1988; Davis, 1993). However, the mechanisms underlying relative numerosity judgments are not well understood. This is true despite the fact that the ability to determine numerosity may have important implications in social behavior such as group choice.

One widespread form of social grouping is shoaling behavior in fish. In this regard, studies have identified group size as one of the most important variables guiding shoaling decisions (Pitcher & Parrish, 1993; Hoare et al., 2004). While fish generally prefer to join larger shoals, this is not always the case. Some fitness payoffs are density dependent and factors such as competition may mean that some individuals could prefer to join smaller groups (Metcalfe & Thompson, 1995; Hoare et al., 2004). Regardless, being able to discriminate between groups on the basis of size is likely to be important. How, then, do fish determine 'more' versus 'less' and how are they using that ability to make shoaling decisions?

Although shoaling has been the subject of considerable theoretical and empirical study (Pitcher & Parrish, 1993; Krause et al., 2000), research has largely focused on why it might be adaptive to join shoals of a particular composition rather than how these decisions about group membership are made (but see Hager & Helfman, 1991; Pritchard et al., 2001). Here we focus on how fish are able to determine numerical size differences in shoals. Fish could, for instance, be attending to the actual number of other individuals in a shoal or they could, instead, be making a relative comparison between shoals.

Previous work (Hager & Helfman, 1991) with fathead minnows, *Pimephales promelas*, has indicated that relative comparisons between shoals are more important than absolute ones. What kind of relative comparisons would fish use to determine shoal sizes? One solution may be that fish determine group size in a manner consistent with Weber's Law.

Weber's Law states that

$$\Delta I / I = K$$

where I is the stimulus and ΔI is the change in stimulus needed to produce a noticeable sensory response K (Sekuler & Blake, 1994). In the context of shoaling decisions based on group size, the stimulus is the number of fish in a shoal and the response would be a shoal choice by a focal fish. The difficulty of any numerical comparison between shoals should depend on the ratio between the numbers of fish in each. As the ratio (ΔI) becomes smaller, the comparison should become more difficult. For example, discriminating between a potential group of nine versus six shoaling partners (ratio of 3:2 or 1.5:1) may be as easy to compare as a group of eighteen versus twelve (ratio of 1.5:1) but more difficult to compare than when a choice is between a shoal of twelve versus six individuals (ratio of 2:1). Ratio appears to play an important role for many species in decision making processes such as memory (Bateson & Kacelnik, 1995), pattern discrimination (Fitzpatrick, 1997; Emmerton, 2001), object size and texture discrimination (Hille et al., 2001) and risk assessment (Sinn, 2003).

It is important to note here that Weber's Law is concerned with the change in stimulus need to produce some sort of response. It does not, however, tell us the discrimination abilities of the subject. For example, fish may be able to determine smaller changes in stimuli and yet not alter their response until this change is sufficiently large.

Green swordtails, *Xiphophorus helleri*, are small, freshwater poeciliid fish from Central America. Like many species of fish, swordtails live in groups and associate with each other in small dynamic shoals, ranging from two to dozens of individuals (Wong & Rosenthal, 2005; pers. observ.). Swordtails have been studied extensively in behavior research and respond well in laboratory situations (Hamilton, 1979; Kazianis & Walter, 2002). Swordtails actively choose to shoal (Beaugrand et al., 1984; Franck et al., 2001), and a recent study on a naturally occurring swordtail hybrid, *X. birchmanni* × *X. malinche*, showed that fish preferred to join larger groups (Wong & Rosenthal, 2005). There is some argument that Weber's Law may be important

for fish in a non-shoaling context: in mate choice, females may make ratio judgments to compare the left and right side of a male for symmetry (Shettleworth, 1999; Merry & Morris, 2001). Swordtails are, therefore, a good candidate for testing the role of ratio in shoaling decisions.

We set up a series of dichotomous choice experiments to look at whether fish are using ratio or net difference to guide their shoaling decisions. If fish are attending to relative group size they should be sensitive to the ratio between prospective shoals. In contrast, if fish are attending to the actual number of individuals in a particular group their shoaling decisions should be based on the net difference between the shoals offered.

Material and methods

Test subjects

Female green swordtails were obtained from local commercial suppliers. These fish were captive-bred descendants of wild caught individuals. Females were used as both focal and stimulus fish in all experiments to avoid possible confounding effects of mate choice (Gabor, 1999; Krause et al., 2000; Wong & Rosenthal, 2005) or aggressive interactions (Beaugrand et al., 1984) that may occur by using mixed sex or all male shoals. All fish used in experiments were size-matched (mean $\pm$ SD standard length $=$ 31.2 ± 1.7 mm) to avoid shoal choice based on size differences (Pitcher & Parrish, 1993; Krause et al., 2000; Wong & Rosenthal, 2005). Fish were held in communal 140 L fish tanks and, thus, had extensive experience with one another. Aquaria were maintained at 25.8°C on a 12D:12L cycle. Fish were fed commercial fish food daily. All fish were fed immediately prior to any experiment to avoid food searching behavior, or shoal choice based on foraging competition (Pitcher & Parrish, 1993; Metcalfe & Thompson, 1995; Hensor et al., 2003; Hoare et al., 2004). Fish did not exhibit any obvious signs of stress before, after, or during experimentation. After all trials were completed fish were returned to lab stock tanks.

Test tanks

The dichotomous choice set up and tank design used to assess shoaling preferences were similar to those used in other studies (Krause et al., 1998;

Barber & Wright, 2001; Wong & Rosenthal, 2005). Briefly, experiments were carried out in a large rectangular opaque plastic holding tank (65 × 38 × 40 cm). Two smaller clear plastic containers (20 × 12 × 12 cm), housing the stimulus shoals were each placed at opposite ends of the holding tank. Test fish were placed in a clear plastic container (15 × 9 × 10 cm) in the center of the test tank during acclimation periods. Water was at a depth of 10 cm. No water exchanges occurred between containers. A 5 cm preference zone around the shoal containers, approximately 1.5 body lengths (Pitcher & Parrish, 1993), was marked on the walls of the test tank using a black marker. A fish was considered in the preference area when any part of its body crossed the line. The bottom of the test tank was covered with white gravel to enhance contrast for observation purposes.

Experimental protocol

Experiments were performed in April 2004 (four fish vs. zero fish, four fish vs. two fish, six fish vs. four fish, eight fish vs. four fish). Additional experiments to examine the effects of larger shoal sizes (eight fish vs. twelve fish, eight fish vs. sixteen fish) were performed in April 2005. Stimulus fish, chosen randomly from the available stock, were placed in the shoal containers and allowed to acclimatize for 5 min. Focal fish were then placed in the center container and allowed to acclimatize and view the shoal containers for 5 min. After acclimation, focal fish were released by carefully lifting the center container and monitored by a single observer for a 10-min period. Focal fish were scored once a minute for 10 min using an instantaneous sampling technique (Lehner, 1996). Scores were based on whether focal fish were with the larger shoal, the smaller shoal, or in the neutral middle area. No stimulus fish were subsequently used as focal fish (stimulus fish were kept separate from naïve fish) but focal fish may have been subsequently used as stimulus fish (used focal fish were placed with the stimulus fish and not returned to the focal fish tank). Between trials, stimulus fish were changed to randomize shoal presentation. To avoid a shoal bias, no shoal composition was ever repeated. The larger shoal was presented on alternating sides between trials to control for potential side biases.

Stimulus presentation

First we wanted to validate that green swordtails would, indeed, shoal in the lab. In order to do this, focal fish were given a choice between four fish and

no fish (control). We then conducted trials with shoals of varying ratios and net differences (four fish vs. two fish, six fish vs. four fish, eight fish vs. four fish, eight fish vs. twelve fish, eight fish vs. sixteen fish).

Statistical analysis

For each treatment, each minute scored within a preference zone was categorized as either with the larger shoal denoted as a $+1$, the neutral middle area denoted as a 0, or as being with the smaller shoal denoted as a -1. A fish was considered in a zone if its entire body was in that zone's area; zones were denoted by lines on the tank wall. These values were then added to give a net preference score. Therefore, we had a possible range of responses from 10 (scored every time with the larger shoal) to -10 (scored every time with the smaller shoal). We used a Student's t-test for a mean of zero to analyze our control (four fish vs. zero fish). If no preference was shown we would expect a mean of zero while a positive mean would indicate a preference for the larger shoal and a negative mean would indicate a preference for the smaller shoal. We then ran a one-way ANOVA on the experimental trials and used post-hoc pair wise comparisons to evaluate responses to difference and ratio with a Bonferroni-corrected α of 0.0125 indicating significance. Trials where fish did not choose either shoal (remaining only in the neutral zone) during the test period, a total of five instances out of 226 trials, were removed from analysis. Statistical analysis was performed using the SAS program.

Results

When presented with shoals of four fish and no fish, test fish showed a significant preference to shoal with four fish with a mean preference score of 5.725 ($t_{39} = 7.61$, $p < 0.0001$) we used this experiment as a control indicating that fish did indeed shoal in our lab. ANOVA results showed a significant difference between treatments. We were most interested in whether or not there was a difference in response based on either ratio or net difference. Figure 1 shows the net preference for the larger shoal for each of the individual treatments grouped by net difference. We expected that if net difference was an important factor in shoal choice we would have seen increasing preference for the larger shoal with increasing net differences. In order to determine this we used contrasts to make four comparisons of the
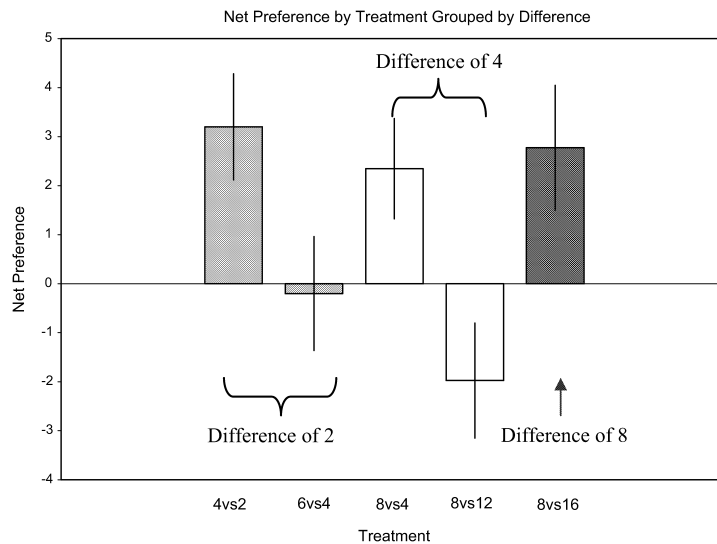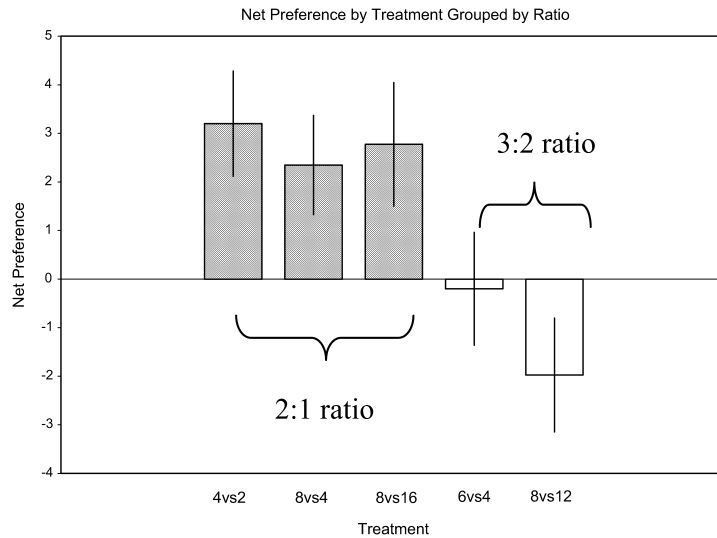
Figure 1. Net preference (number of times observed with larger shoal − number of times observed with smaller shoal; mean ± SE) of subjects between treatments grouped by difference. Positive numbers indicate a preference for the larger shoal; negative numbers indicate a preference for the smaller shoal. Light gray bars indicate treatments with a difference of 2. White bars indicate treatments with a difference of 4. Dark gray bars indicate a difference of 8. No significant effect of net difference on preference was found ($p = 0.53$).

data, namely we contrasted the 2:1 to 3:2 ratios, net difference of 2 to net difference of 4, net difference of 2 to net difference of 8, and net difference of 4 to net difference of 8. However, no pattern between net difference and preference was seen in any of the comparisons; comparison of net differences 2 and 4 ($F_{4,181} = 1.47$, $N = 186$, $p = 0.227$), comparison of net differences 2 and 8 ($F_{3,181} = 0.74$, $p = 0.392$), and comparison of net differences 4 and 8 ($F_{2,181} = 3.41$, $N = 186$, $p = 0.0666$). We did, however, see a highly significant response to ratio using a Bonferroni-corrected α of 0.0125 ($F_{1,181} = 13.73$, $N = 186$, $p < 0.0003$) with ratios of 2:1 having a positive net preference and ratios of 3:2 having a negative net preference (Figure 2).

Discussion

As predicted, female green swordtails preferred to shoal in larger groups. This result is consistent with those found in other taxa (Pitcher & Parrish,

Net Preference by Treatment Grouped by Ratio

Figure 2. Net preference (number of times observed with larger shoal − number of times observed with smaller shoal; mean ± SE) of subjects between treatments grouped by ratio. Positive numbers indicate a preference for the larger shoal; negative numbers indicate a preference for the smaller shoal. Gray bars indicate treatments with a ratio of 2:1. White bars indicate treatments with a ratio of 3:2. There was a significant effect of ratio on preference ($p < 0.001$).

1993), including other swordtails (Wong & Rosenthal, 2005). Researchers have long considered the benefits of shoaling in larger groups, yet the mechanisms underlying numerical comparisons have remained obscure. How were females able to determine group size? Focal fish attended to the ratio of group size between stimulus shoals rather than to the numerical difference between shoals. Subjects offered shoals differing by a factor of 2:1 significantly preferred the larger shoals, independent of differences in the number of fish. Shoals with a 1.5:1 ratio over the smaller shoal, however, were not preferred. Our results, therefore, indicate that female swordtails are attending to the ratio between shoal sizes, rather than absolute numerical differences, to compare among shoals.

It is important to stress here that ratio sensitivity may not necessarily involve any complex cognitive mechanisms and could, instead, be based on spontaneous and rather rudimentary abilities to distinguish between 'more' or 'larger' and 'less' or 'smaller'. As ratios become smaller, Weber's Law predicts that comparisons should become more difficult. There is, thus, likely to be a threshold ratio where two groups cease to be distinguished as 'larger'

and 'smaller' and simply become 'same' or 'equal'. Does a 2:1 ratio approach the limit of numerical discrimination between groups in species which, like swordtails, form relatively small shoals? This question has not, as far as we are aware, been explicitly investigated. However, studies examining shoaling decisions in other contexts suggest that there may, indeed, be comparable limits in discrimination between shoal sizes in other species. For example, during an experiment on body color segregation, Bradner & McRobert (2001) offered mollies, *Poecilia latipinna*, a choice between shoals of different sizes. They found that mollies preferred larger shoals when given a choice of six fish and three fish which corresponds to a ratio of 2:1. They did not, however, find a preference for larger shoals when given the choice between four versus three fish, and five versus three fish which correspond to ratios lower than 2:1. In an experiment on familiarity preferences of shoal mates, Binoy & Thomas (2004) found that climbing perch, *Anabas testudineus*, preferred larger shoals when given a choice of shoals with ratios of 4:1 and 1.9:1 but did not prefer larger shoals at smaller ratios. In a similar experiment, Barber & Wright (2001) noted that European minnows, *Phoxinus phoxinus*, preferred larger shoals when shoal size ratios were 4:1 and 1.9:1 but not when ratios were smaller.

Although we found a resolution limit approaching 2:1, anecdotal evidence suggests that different species may be more or less sensitive to ratio. Krause et al. (1998) noted in their experiment on shoal choice under predation risk that creek chub, *Semotilus atromaculatus*, discriminated between shoals of six and five fish (1.2:1) while threespine sticklebacks, *Gasterosteus aculeatus*, did not. It is interesting to note that chubs are presumably at a greater predation risk than armored stickleback (Krause et al., 1998; Mathis & Chivers, 2003) and, therefore, finer resolutions of ratio may be advantageous. For some species there may not be a substantive difference between shoals varying by small amounts. Fine discrimination would only be beneficial for individuals that derived a fitness advantage from the addition of one or two individuals to a shoal. Discrimination of shoal size may also be an incidental consequence of the ability to make numerical judgments in other contexts, like foraging.

Again it is important to point out that shoaling decisions need not reflect the perceptual or cognitive limits of discrimination abilities. For example, species may be able to discriminate between smaller ratios (e.g., 1.5:1) but these ratios may not produce a response; discriminating between such ratios

may not be as beneficial as discriminating between larger ratios (Morgan & Godin, 1985; Landeau & Terborgh, 1986). Therefore, discrimination at lower ratios may not be apparent even though the species involved are capable of it. Regardless, our results indicate that certain ratio limits, as opposed to numerical differences, may be important in shoaling decisions. The extent to which ratio comparisons influence shoal choice in the wild is unknown.

Due to the practical limitations of laboratory conditions, we only looked at shoals of relatively small sizes; in nature, fish shoals may reach sizes of hundreds or more. At some point, even with very large ratios, fish may cease to discriminate between shoals once the upper limit of their ability to distinguish shoal traits is reached. This may happen, for example, in open ocean environments where shoals of species, such as herring, may be hundreds of meters long. In this situation, individuals may not be able to evaluate a shoal in its entirety. Furthermore, increases in the benefits of shoaling with a larger group may taper off as shoals reach certain critical sizes. Once this size is reached it may not be any more advantageous for a fish to join a larger group and, thus, discriminate between groups. For example, Landeau & Terborgh (1986) showed that successful attacks by largemouth bass, *Micropterus salmoides*, on silvery minnows, *Hybognathus nuchalis*, were significantly decreased as shoal size increased. This decrease in successful attacks was attributed to the 'confusion effect'. Their results indicated that once a minnow shoal reached a size of fifteen individuals successful attacks approached zero. In this case (assuming no other benefits besides predator evasion) fish may only need to discriminate between shoals of fifteen or less and not between shoals of fifteen or more as no further predator advantage is gained. Morgan & Godin (1985) also found that antipredator benefits increased at a decelerating rate as shoal size increased in the banded killifish, *Fundulus diaphanus*. The time taken to assess groups is costly and, therefore, trade-offs may be made between speed of comparison and correctness of comparison (Krause et al., 1997, 1998). Perceptual constraints, cost and decreasing returns, thus, suggest that animals should cease to discriminate among groups once they have reached a 'large enough' size.

Group living is a flexible strategy in that individuals can choose to join or leave a group based on the costs and benefits of association. Factors that favor grouping (such as protection from predators) should vie with factors that discourage grouping (such as competition). The decision to join or leave a group

should reflect tradeoffs among these factors. We used only female sword-tails in our experiments. Experiments have indicated sex biases in shoaling behavior in other species. For example, male guppies, *Poecilia reticulata*, have been found to switch between and leave shoals more often than females (Croft et al., 2003). This presumably, is because males are more willing to trade off the protective advantages of shoaling for increased mating opportunities (Magurran & Seghers, 1994). Because we did not test male swordtails and because of possibly different shoaling motivations we cannot be sure that they also use ratio in making shoaling assessments or even have the capacity to make ratio judgments.

Our data suggest that swordtails use ratio to determine size differences in potential shoals. Pritchard et al. (2001) have shown that zebrafish, *Danio rerio*, attend to the overall activity of a shoal, and that small, active shoals are preferred over larger, less active ones. They suggested that activity might, thus, serve as a means of determining shoal size. Weber's law and the ratio of activity between shoals may be an important means of determining activity differences. The same underlying mechanisms may, therefore, be used to make numerical comparisons in a variety of contexts.

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