Assessment and assortment: how fishes use local and global cues to choose which school to go to

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Animals that live in groups are known preferentially to associate with phenotypically similar individuals. Despite this, groups of mixed phenotypic composition are the norm rather than the exception in several systems in the wild and this, combined with the large sizes of some animal groups, makes accurate global assessment by a choosing individual more difficult. In this study, we investigated the role of local and global information in mediating shoal-choice decisions in three-spined sticklebacks (*Gasterosteus aculeatus*) by manipulating the positions and phenotypes of stimulus fish in relation to a focal fish. Focal fish were able to assess globally mixed shoals composed of individuals of different body-length classes, preferring to associate with shoals where the majority phenotype matched their own. When local cues were manipulated this preference disappeared, although overall shoal composition remaining constant. Finally, if both stimulus shoals had the same overall composition but differed in their local cues, then the focus fish chose according to which local fish was of matching body length. These findings indicate that both local and global information play an important role in mediating assessment and shoal choice in fishes.

Keywords: shoaling; schooling; choice; assess; social

1. INTRODUCTION

Shoaling works most effectively as an anti-predator strategy when all individuals within a shoal are uniform in terms of their behaviour and appearance. Odd individuals within shoals suffer a disproportionate risk of predation because they are conspicuous (Landeau & Terborgh 1986). As such, there are strong selection pressures upon individuals to assort with individuals whose phenotypes match their own.

Considerable evidence exists to support the thesis that individuals of a shoaling species are capable of discriminating and showing a preference for shoals on the basis of phenotypic characteristics such as species (Ward *et al.* 2002), colour (McRobert & Bradner 1998) and body length (Ward & Krause 2001).

Despite this, free-ranging shoals are often more heterogeneous in character than may be predicted by laboratory-based studies (Krause *et al.* 2000). Often, however, there is a numerically dominant phenotype within such shoals (Krause *et al.* 1996) and there remain significant costs to individuals representing a minority phenotype within a shoal (Landeau & Terborgh 1986). The ability of fishes to assess the compositions of mixed shoals has been shown to be somewhat limited. Chub (*Leuciscus cephalus*) significantly avoided mixed species shoals only when conspecifics were in an extreme minority, despite high competition costs suffered by chub when associating with minnows, *Phoxinus phoxinus* (Ward *et al.* 2002). A further potential problem for a choosing fish is that the shoals it encounters may be composed of so many individuals that it is difficult to make an accurate assessment of all members owing to sensory overload (see Krakauer 1995). Given the potential complexity of accurately assessing entire shoals, fishes may adopt simple local assessments, perhaps being disproportionately influenced by proximal individuals.

In this paper, we test the hypothesis that local effects are more important than global effects in this context, and specifically that those shoal members nearest to a choosing individual exert a greater effect on shoal choice than the general composition of that shoal. We investigated (i) the effect of local cues; (ii) the effect of global cues; and (iii) and (iv) trade-offs between local and global information.

2. METHODS

(a) Fish and holding conditions

Three-spined sticklebacks were collected using hand-nets during September 2003 at Melton Brook, Leicestershire, UK (UK grid reference SK601 074). All fishes' lengths were measured and two size classes were identified: small (28 ± 2 mm) and large (40 ± 2 mm). Two groups of 60 large sticklebacks were each allocated to a 90 l holding aquarium and a single group of 60 small fish was allocated to a third 90 l holding aquarium. No communication, either visual or chemical, was possible between fish in the different holding aquariums. The fish were kept at a temperature of 11 °C with a light regime of 10 L : 14 D and were fed *ad libitum* with frozen bloodworm.

(b) Experimental procedure

The shoaling preferences of the fish were tested using an aquarium measuring 60 cm long $\times$ 15 cm wide $\times$ 30 cm deep filled to a water depth of 20 cm. The test aquarium was divided into five compartments along the longest axis using perforated transparent plastic, which allowed both visual and chemical communication between the compartments. A central compartment measuring 30 cm $\times$ 15 cm was flanked by two smaller side compartments at each side, each of which measured 7.5 cm $\times$ 15 cm. This produced two 'near' compartments that adjoined the central compartment and two 'far' compartments, each separated from the central compartment by a near compartment. Lines were drawn on the outside of the glass demarcating two 10 cm choice zones at either end of the central compartment. This distance represents two-and-a-half body lengths of the 40 mm focal fish, which falls within the range of inter-individual distances observed in free-ranging fish shoals (Pitcher & Parrish 1993).

The procedure, a straightforward binary choice, remained constant throughout. For each replicate, we introduced stimulus fish to the side compartments and allowed them to settle for 10 min. A focal fish was then introduced to the middle of the central compartment in a transparent, perforated plastic cylinder. The focal fish was given 5 min to settle before the cylinder was raised and the focal fish was allowed to swim freely throughout the central compartment for a period of 5 min. The amount of time spent by the focal fish in each of the two choice zones was recorded. Each focal fish was used only once throughout the study. Stimulus fish were changed for each replicate and drawn from a reservoir of 60 large and 60 small fish. Focal fish and stimulus fish were taken from different holding tanks to control for the influence of familiarity (Ward & Hart 2003).

We did four separate treatments (see table 1). Large focal fish were given a choice between two groups of five fish, each of which differed in terms of their composition and/or their positioning relative to the focal fish.

Table 1. A focus fish was presented with a choice of two groups of five fish that differed in terms of their composition and/or their positioning relative to the focal fish.
(S, small; L, large.)

shoal A		shoal B		%A-%B			
far	near	near	far	mean $\pm$ s.d.	<i>t</i>	<i>n</i>	<i>p</i>
LLLL	L		LLLLL	1.1 $\pm$ 26.8	0.08	15	0.939
SLLLL			LSSSS	47.7 $\pm$ 22.2	4.16	15	0.001
LLLL	S	L	SSSS	12.3 $\pm$ 26.0	0.92	15	0.374
SLLL	L	S	SLLL	55.0 $\pm$ 20.0	5.32	15	0.000

- (i) Five large fish in the far compartment versus four large fish in the far compartment and one large fish in the near compartment. This treatment tests whether there is an effect of proximity in the absence of differences in overall shoal composition.
- (ii) Four large fish and one small fish in the far compartment versus four small fish and one large fish in the far compartment. This treatment tests whether the focal fish can discriminate between the overall composition of shoals where the proportion of matching fish differed.
- (iii) Four large fish in the far compartment and one small fish in the near compartment versus four small fish in the far compartment and one large fish in the near compartment. This treatment was the same as treatment (ii) except that the local information (i.e. fish in the near compartment) was manipulated, providing a trade-off between local cues and overall shoal composition.
- (iv) Three large fish and one small fish in the far compartment and one small fish in the near compartment versus two large fish and two small fish in the far compartment and one large fish in the near compartment. The overall shoal composition is the same for both stimulus shoals but the local cues differ.

(c) Data analysis

Test statistics were generated by subtracting the time spent with shoal B from the time spent with shoal A and comparing this with a null model of nil or no difference, using a one-sample *t*-test. α -Levels were adjusted according to the Bonferroni method [$\alpha' = \alpha/k$].

3. RESULTS

In the absence of differences in shoal composition, proximity of a shoal member alone had no effect on shoal choice. Fish were able to assess the overall composition of shoals and preferred the shoal where the majority of members were phenotypically matched to themselves. No preference for either stimulus shoal was observed when local cues and overall shoal composition were traded off against each other (i.e. one stimulus had a larger proportion of fish matching the body length of the focal fish whereas the other had a matching local fish). If the overall composition of shoals was the same but the local cues differed, then focal fish were found to prefer the stimulus shoal containing a matching local fish (see table 1).

The proximity of a matched individual caused a significant change in shoaling preference between treatment (ii) and treatment (iii), although the overall shoal composition remaining constant between the two treatments (independent samples *t*-test: $t_{15,15} = 2.23$, $p = 0.034$).

4. DISCUSSION

Choosing fish were able to use both local and global information to assess shoals, but local information was more important in mediating decisions about which shoal to join. Where a fish is confronted with a large shoal composed of numerous individuals, accurate assessment may

be difficult or even impossible. In such cases, general association preferences may be based on simple local association rules, for example, by individuals being attracted towards the nearest matching individual, rather than assessing the composition of an entire shoal. The individuals on the periphery of a shoal therefore provide relatively more information to a choosing fish than centrally positioned shoal members.

Fish in the present study showed themselves to be capable of making global assessments of mixed shoals and acting adaptively on the basis of that assessment by joining a shoal the majority of whose members were matched in phenotype. If, however, the nearest individual in a shoal matched the focal fish, the composition of the shoal as a whole was less influential on the decision. When given a choice between two identical shoals, focal fish based association decisions on the phenotype of the nearest fish in each shoal. Studies have shown that individuals occupying peripheral positions may not be representative of the overall phenotypic composition of the shoal. For example, minnows parasitized by the cestode, *Ligula intestinalis*, occupy peripheral shoal positions (Barber & Huntingford 1996), as do banded killifish (*Fundulus diaphanus*) when parasitized by the trematode, *Crassiphiala bulboglossa* (Ward *et al.* 2002). In shoals of red-bellied piranhas (*Pygocentrus nattereri*), smaller individuals occupy peripheral positions (Magurran & Queiroz 2003). By limiting the assessment to nearby individuals, a choosing fish potentially avoids the costs of more lengthy assessment, such as increased conspicuousness while outside a shoal: it may be better to be in a sub-optimal shoal than in no shoal at all (Landeau & Terborgh 1986). This may be especially relevant in systems where encounters between shoals are frequent, giving fishes opportunities to re-assort (Hoare *et al.* 2000). Furthermore, choices based on local cues may themselves produce patterns of assortment leading to localized groupings of individuals with the same phenotype within a single, larger group (Pitcher *et al.* 1985). If predators also face the same constraints on their ability to assess the global picture (see Krakauer 1995), such localized groupings may retain some of the functional benefits of entirely homogeneous shoals.

This paper reports the abilities of prey species to use local and global information in shoal assessment. Because the cost-benefit ratio of accurate assessment and assortment into shoals by prey species is determined by the interactions of the perceptual abilities of predators and prey, it would be extremely interesting to extend this research by comparing these abilities in an ecological context.

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