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# Association patterns and shoal fidelity in the three-spined stickleback

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We investigated pairwise association patterns and shoal fidelity in free-ranging, individual three-spine sticklebacks (*Gasterosteus aculeatus*) by capturing entire shoals of sticklebacks and tagging each shoal member with a unique individual mark before releasing the shoal at the point of capture. We recaptured tagged fishes in the study area on five subsequent days, noting their identity, their location and the individuals with which they were associated. Stable partner associations between fishes were observed which might provide the basis for shoal fidelity via social networks. These results suggest the potential for the kinds of inter-individual association patterns assumed by models of predator inspection and 'tit-for-tat' behaviours in free-ranging fishes.

**Keywords:** reciprocal altruism; familiarity; school

## 1. INTRODUCTION

Theoretical studies and empirical work suggest that individuals should associate with others of similar phenotype to reduce the costs of competition for resources (Ranta *et al.* 1993) and the risk of predation (Landeau & Terborgh 1986; Theodorakis 1989). This view is supported by field studies that have shown the grouping patterns of free-ranging animals to be non-random (Krause *et al.* 1996; Peuhkuri 1997; Conradt & Roper 2000). In several species of shoaling fishes, there is strong evidence for individuals to be assorted by body length, species and parasite load (Krause *et al.* 1996). The mechanisms underlying this assortment are likely to be based on active choice of shoal mates and differential habitat choice (Krause *et al.* 2000). Freshwater fish shoals have been observed to encounter each other frequently (e.g. one encounter per minute per shoal in banded killifish, *Fundulus diaphanus*) with many opportunities for individuals to swap between shoals (Seghers 1982; Krause *et al.* 2000). In addition, shoals tend to break up at twilight, reforming after reassortment at dawn (Helfman 1993). Opportunities for exchange between groups are therefore unlikely to be a constraint.

Laboratory experiments have shown that several species of freshwater fishes have the capacity for individual recognition (Dugatkin 1997) and kin recognition (Krause & Ruxton 2002). However, it remains unclear to what extent these discrimination abilities play a role for the structuring of shoals in the wild. Individual recognition is an important prerequisite for the evolution of reciprocity between unrelated individuals and has been discussed extensively in the context of predator inspection behaviour and 'tit-for-tat' interactions. For reciprocity to be established, individuals need to have repeated interactions, and to remember the identity of the individual they interacted with, as well as the outcome of the interaction (Dugatkin 1997). Kin recognition has been shown to be based, at least partly, on the major histocompatibility complex in several vertebrate species (Olsen *et al.* 1998), but it is unclear which cues are involved in individual recognition in fishes.

Field studies investigating the association patterns of individuals in shoals have taken two different approaches. One is to give fishes within shoals the same marks and different marks between shoals; the other is to mark fishes individually. The latter method allows the experimenter to extract more information but also involves substantially more work and is difficult to practise with small species and juveniles (because of their fragility). Hoare *et al.* (2000) collected 10 shoals and gave 788 banded killifish (*F. diaphanus*) shoal-based marks but did not detect any significant trend for shoal fidelity when resampling started one day later. In a pioneering study, Helfman (1984) individually marked 102 yellow perch (*Perca flavescens*) and followed their association patterns over several months but did not find any preference in shoal mates in this species. A more recent study by Klimley & Holloway (1999) is, to our knowledge, the only one to provide some support for shoal fidelity in the wild. They tagged 38 yellowfin tuna (*Thunnus albacares*) with coded ultrasonic beacons and reported that certain fishes arrived at the same time in specific sites, indicating that tuna have partner preferences.

We investigated the degree to which individuals form stable pairwise associations, and the extent to which fishes from the same shoal stay together. Due to the fact that pairwise interactions between animals have been highlighted in the context of reciprocity (Milinski *et al.* 1990), we decided to make pairs the unit of analysis in our study. To do this, we captured entire shoals of sticklebacks,

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marked them individually with a unique microtag on the anterior dorsal spine, and released them again at their point of capture. We measured each marked fish to avoid the confounding effects of size sorting. Furthermore, we collected our shoals within a small area to allow the fishes to have frequent interactions with each other. The latter is important to avoid the potentially confounding effects of site fidelity (Krause *et al.* 2000). A recent laboratory study by Barber & Ruxton (2000) showed that sticklebacks prefer to associate with familiar individuals but the evidence for a preference of kin is ambiguous. Van Havre & FitzGerald (1988) reported that stickleback fry preferentially associated with siblings rather than non-siblings in choice experiments. However, a carefully designed study by Steck *et al.* (1999) found no preference of stickleback fry for the odour of siblings. Similarly, an analysis of the shoal composition of free-ranging sticklebacks did not reveal any strong evidence in favour of kin associations in this species (Peuhkuri & Seppä 1998). Based on the work by Barber & Ruxton (2000), we predicted that fishes are more likely to be found repeatedly in association with particular individuals and that the shoal mate choice of sticklebacks would be different from random. This prediction was tested by comparing the shoal composition of recaptured shoals with that produced by a simulation model, which assumed random interactions between fishes.

## 2. METHODS

The study site was a 90 m straight stretch of the main inflow channel to Morice Lake (near Sackville, New Brunswick, Canada) (45°55′ N, 64°21′ W). The channel ranged from 8 to 10 m in width along the stretch studied. The water in the channel was clear, slow flowing (1.5 m $\text{min}^{-1}$) and shallow (1.2 m at the deepest part). The substrate was fine sand and mud. Aquatic plants occurred in a 0.5 m band along each bank; the central channel was free of vegetation. A number of species of fishes were present at the site including banded killifish (*F. diaphanus*), four-spined stickleback (*Apeltes quadracus*), white suckers (*Catostomus commersoni*), yellow perch (*P. flavescens*) and trout (*Salmo trutta*).

### (a) *Procedure*

Shoals of three-spine stickleback were collected using a beach seine (3 m long, mesh size 2.5 mm × 2.5 mm) during September 2001. Shoals were located visually and only those shoals caught in their entirety were used in the analysis. Sticklebacks are slow swimmers and captures are generally successful at the first attempt (see Krause *et al.* (1996) for details of the capture technique). The exact point of capture of each shoal was recorded as the distance from shore and the distance along the channel. The standard length was measured and recorded for each fish caught and a tag fixed to the anterior dorsal spine. Tags were 2 mm sections of Tygon laboratory tubing with an internal diameter of 0.9 mm. Each tag bore a unique code allowing fishes to be individually identified. We captured several fish shoals in this way and released each of them at their point of capture immediately after all fishes (in all shoals) had been marked. When tagged fishes were recaptured, the individual tag code was recorded along with the codes of other marked fishes in the shoal and the location of the capture of the shoal. Captures and recaptures took place between 0900 and 1600, and the water temperature was 14.4 °C; 1.1 °C (median; range). No evidence was seen of reproductive behaviour characterized by enhanced male coloration and territoriality during the study.

In our first mark–recapture experiment, we captured five shoals and marked a total of 67 fishes, and in the second experiment, we captured and marked four shoals containing 53 fishes (table 1). Recapturing was carried out daily for the next 5 days. Recapture success of marked individuals varied between days partly because of variable weather conditions. Strong winds and occasional rains made it difficult to detect fishes on certain days. In both experiments, we collected the shoals from within an area of 15 m in the channel to maximize the chances that the fish shoals would encounter each other frequently and thereby give individuals the option to stay in their shoal or switch between shoals. Shoals were frequently observed to meet within the experimental area, a process that often involved exchange of shoal members (A. J. W. Ward, personal observation). This is important because shoal fidelity could otherwise simply be a by-product of site fidelity.

To measure how widely the fishes dispersed in the area, we marked a total of 321 individuals over a 90 m stretch of the channel. The position where each individual first occurred was recorded and compared with the positions where recaptures of the same individuals occurred over a one-week period. This was taken as a measure of the activity radius of fishes as a function of time. In addition, we estimated the population using a basic mark–recapture procedure comparing the number of marked individuals as a proportion of the total number caught.

To provide a control to assess the effects of tagging on the fishes, and the persistence of the tag, a group of 20 sticklebacks collected at the site were tagged and observed in the laboratory over a five-day period.

### (b) *Data analysis*

We performed two different tests of association preferences; one that examined whether fishes had a tendency to be repeatedly found with particular individuals and a second, which tested whether individuals were more likely to be found with members of their original shoal than with other conspecifics. Both tests were carried out by constructing a simulation model which used a random resampling technique to allocate marked fishes to observed recaptured daily shoal sizes. This operation was repeated 1000 times to provide expected frequency distributions, which were then ranked. *p*-Values were obtained by comparing the frequency distribution of expected values with our observed values (see Crowley (1992) for details of the resampling method). The simulation model made no assumptions about prior associations as it assumed the nocturnal disintegration of shoal structures, followed by reforming and reassortment of shoals at dawn (see Helfman 1993). Reassortment of shoals by exchange of members was also observed diurnally (A. J. W. Ward, personal observation).

In our first test, we looked for consistent partner preferences by determining how many pairs of fishes were found together on three or more recapture days.

In our second test, we examined which pairs of fishes were shoal mates in the original shoals (that were first marked) and determined the number of these pairs (of marked fishes) that were found together again on any given day of recapture (table 1). The observed number of re-occurring pairs was compared for each day, and for each of the two shoal samples. We only analysed recaptures that contained more than 10 marked fishes because smaller numbers would not provide sufficient test

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Table 1. Two sets of shoals (5 and 4, respectively) were captured within a 15 m stretch of a channel in Morice Lake. (The fishes in these shoals were individually marked but remained with their shoal members during the marking procedure and were released at their point of capture. Subsequently, shoals were captured in the channel over an area of 15 m and the number and identity of recaptured individuals were recorded. The number of re-occurring pairs (from the original captures) is given.)

| | shoal sample 1 | | | shoal sample 2 | | |
|---|---|---|---|---|---|---|
| | fish no. | (shoal no.) | pairs | | | pairs |
| original captures | 67 | (5) | | 53 | (4) | |
| recaptures: | | | | | | |
| day 1 | 25 | (6) | 44 | 7 | (3) | 3 |
| day 2 | 14 | (5) | 8 | 10 | (4) | 15 |
| day 3 | 12 | (5) | 5 | 23 | (6) | 37 |
| day 4 | 9 | (3) | 6 | 14 | (6) | 14 |
| day 5 | 6 | (2) | 4 | 4 | (2) | 1 |

power. The above test was carried out for each of the two shoal samples (in the mark–recapture experiments mentioned above) and each of the recapture days separately.

## 3. RESULTS

In the laboratory fish-marking control, none of the 20 fishes had died or had lost their tags after a period of 5 days, corresponding to the period of the field recaptures. Fishes were observed to behave normally following the tagging process, both in the laboratory and in the field, where they were seen to move off as a shoal after release.

Our data indicate that fishes moved 9.9 ± 4.7 m (mean ± s.d.) during the first 24 hours after the tagging process. Standard mark–recapture procedures provided us with a three-spined stickleback population estimate for the entire 90 m stretch of 1264 fishes; we estimated the population of the 15 m recapture area to be 365 fishes.

The mean ± s.d. of the standard body length of fishes that we marked was 41 ± 6 mm. Work by Ward & Krause (2001) showed that minnows (of 40 mm body length) significantly discriminated against conspecifics if they were 25% smaller or larger than them. Therefore, we assumed that the body length differences observed in our stickleback samples did produce sufficient grounds for a strong discrimination among individuals on the basis of body length differences.

In both sets of shoals, we found pairwise associations that re-occurred on three or more days at a frequency greater than expected by chance (resampling test, 1000 simulations, $p = 0.005$ and $p = 0.017$, respectively) (see tables 1 and 2).

In the first set of shoals, we found significant shoal fidelity on recapture days 1 and 2 (resampling test, 1000 simulations, $p < 0.001$ and $p = 0.023$, respectively), but not on day 3 ($p = 0.059$). In the second set of shoals, we found significant shoal fidelity on recapture days 4 and 5 ($p = 0.011$ and $p = 0.002$, respectively). On all other days, numbers of recaptured fishes were too small for testing. The problem with small sample sizes in this context is that even when the maximum number of pairs from the original shoals is observed in a recapture, the observation is often not significant because of the generally small number of possible combinations of fishes in a small sample, resulting in low test power.

It could be argued that fish shoal composition does not become random all at once and that, even in the absence of any active partner choice or shoal fidelity in fishes, one might expect to see a gradual decline in shoal integrity with time. Therefore, our comparisons of shoal composition with a random model might seem artificial. In our above analysis, we compared shoal composition with a random model for two reasons. First, we observed that our stickleback shoals dispersed overnight in the shallow waters, which results in a complete breakdown of shoal composition (i.e. fishes are found as singletons spread out over the channel bottom) and a reassembly every morning (J. Krause, personal observation). Second, fish density was high at *ca.* 1.6 fishes m$^{-2}$. This density corresponds closely to what we found in killifish in the same lake. At this density, we observed encounters between killifish shoals every 1.1 min for a given shoal resulting in several hundred encounters in a single day per shoal. Given the small sizes of our stickleback shoals (mean ± s.d. = 14 fishes ± 11) on the original capture day, this means that shoal composition should approximate randomness during a single daylight period (*ca.* 12 hour period) even before shoals disperse at night unless fishes show some active tendency to stay with shoal mates. Therefore, the assumption of randomness of shoal composition as our null model after a 24 hour period has a biological basis.

Finally, even if shoal encounters were much less frequent (i.e. only once or twice per day) we should see a gradual decline in the number of pairs of fishes that are still together from the original capture day. To investigate this we plotted the ratio of observed pairs (the number of pairs of fishes that were observed on the original capture day and that still occurred together on a given resampling day) to the maximum number of pairs given by 1000 random simulations of the dataset (i.e. the fishes from the original capture day that occurred on a given resampling day were randomly distributed across the resampled shoals, and the maximum number of re-occuring pairs was recorded). We used the maximum number of pairs predicted by a random simulation and not the absolute maximum number of possible pairs because the latter would be confounded by sample size: the larger the number of resampled fishes, the smaller the probability that the configuration leading to the absolute maximum number of pairs would be observed. For the first shoal sample, there

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Table 2. Pairs of fishes that were captured three times or more.

| shoal sample 1 | day | shoal sample 2 | day |
|---|---|---|---|
| 109 & 106 | 1, 2, 5 | 225 & 229 | 1, 4, 5 |
| 109 & 90 | 1, 2, 4, 5 | 225 & 214 | 1, 4, 5 |
| 106 & 90 | 1, 2, 5 | 214 & 229 | 1, 4, 5 |
| 102 & 104 | 1, 2, 5 | 228 & 229 | 1, 3, 5 |

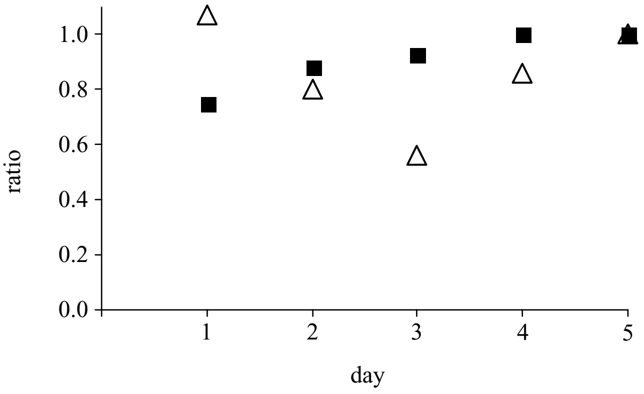

Figure 1. Shoal fidelity as a function of time. The ratio of observed pairs (the number of pairs of fishes that were observed on the orginal capture day and that occurred together on a given resampling day) to a maximum number of pairs provided by 1000 random simulations of the dataset (i.e. the fishes from the original capture day that occurred on a given resampling day were randomly distributed across the resampled shoals and the maximum number of re-occurring pairs was recorded) as a function of recapture day. Shoal 1 (triangles), shoal 2 (squares).

was no significant relationship between sampling day and the ratio of observed number of pairs to maximum number of pairs (Spearman correlation, $n = 5$, $r_s = -0.1$, $p = 0.87$). For the second shoal sample we found a significant positive relationship, indicating an increase in the ratio of observed-to-maximum-number pairs (Spearman correlation, $n = 5$, $r_s = 0.97$, $p = 0.05$) (see figure 1).

## 4. DISCUSSION

We believe this is the first study to show non-random patterns of association between pairs of free-ranging fishes and to show shoal fidelity in free-ranging three-spined stickleback.

Our observation that pairs of free-ranging three-spined sticklebacks formed persistent associations over a number of days is novel and corroborates earlier findings that individual sticklebacks prefer to associate in pairs with particular partners under laboratory conditions (Milinski 1987). Our results cannot be explained simply by stickleback site fidelity or body-length assortative shoaling. Furthermore, the probability of finding such pairwise associations was not a function of time, indicating that they may be stable.

Theory predicts that individuals trapped in an iterative Prisoner's Dilemma are more likely to evolve cooperative behaviour patterns (Dugatkin 1997). Such repeated interactions are more likely to occur where pairwise associations are stable. The stability and persistence of pairwise interactions found here satisfies the most basic prerequisite for the development of reciprocity. One key area of research into reciprocity in pairs of sticklebacks has been in predator inspection behaviour (e.g. Milinski *et al.* 1997).

Recapture data showed non-random patterns of association between subsets of individuals, which we termed shoal fidelity. One mechanism that is likely to contribute towards this is the preference of individuals to shoal with familiar individuals. This phenomenon has been investigated in a number of recent laboratory studies, both on stickleback (Barber & Ruxton 2000) and on a number of other fish species, for instance guppies (*Poecilia reticulata*; Griffiths & Magurran 1999) and minnows (*Phoxinus phoxinus*; Griffiths 1997). Grouping with familiar individuals is adaptive for a number of reasons, including enhanced anti-predator behaviour (Chivers *et al.* 1995) and improved foraging, possibly as a result of lower competition (Höjesjö *et al.* 1998).

An interesting facet of the data is the patterns of subsets formed by individuals. These appear to demonstrate some characteristics of 'small-world' networks (Watts & Strogatz 1998) of regular lattices, and random graphs, in that small associating groups, or clusters of fishes are linked, by one or more members, to other clusters. In a similar fashion to the familiar 'six degrees of separation' concept (Guare 1990), individuals had a range of links to close shoaling partners, plus a smaller number of connections to more distant points. The existence of such networks, already postulated in models of social networks in animals (e.g. Abramson & Kuperman 2001), disease propagation (Zekri & Clerc 2001) and neural networks (Achacoso & Yamamoto 1992), in free-ranging fishes raises the possibility of enhanced proliferation of information throughout a local population.

One potential alternative explanation for the patterns observed in this study would be coinciding activity cycles between repeatedly caught pairs (Conradt & Roper 2000). However, as repeatedly associating partners were always captured together at different locations within the study site on different recapture days, it seems unlikely that this mechanism can satisfactorily explain the data.

This study has provided the natural context for repeated cooperative interactions in freshwater fishes. A combined field and laboratory approach has the potential to reveal the extent and importance of such behaviour in nature.

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