

Habitat-specific chemical cues influence association preferences and shoal cohesion in fish

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Abstract The structure of social animal groups can be dynamic, characterized by high rates of group fission and fusion. Despite this, group composition is often well ordered by factors such as species, body size and by numerous other phenotypic traits. Research in shoaling fishes has revealed that individuals refine group membership decisions still further and are capable of assimilating chemical cues pertaining to recent habitat and prey use by prospective group mates, preferring to associate with others whose recent resource use history closely matches their own. In this study, we firstly examined the dynamics of the formation and breakdown of these preferences, revealing that they can be acquired and replaced in a matter of just a few hours. Using such cues enables individuals to accurately assess the resource use of conspecifics, allowing them to indirectly sample the local environment while reducing the chances of acquiring outdated information that can precipitate maladaptive behaviors. Secondly, we found that shoals composed of individuals with shared recent habitat use history were more cohesive compared to those where the constituent individuals differed in recent habitat

use. Increased shoal cohesion may reduce predation risk, and could enhance the ability of individuals to detect and use social information.

Keywords Social organization · Social information · Familiarity · Recognition · Shoaling

Introduction

Group living is common in the animal kingdom, because sociality can benefit individuals by reducing predation risk costs and increasing the rate at which food resources are detected and exploited (Krause and Ruxton 2002). Group composition is not always stable, however, and can change through both fission and fusion processes, operating under a variety of dynamic environmental, predation, foraging, and sexual pressures (Raman 1997; Hoare et al. 2000; Croft et al. 2003). Consequently, individuals may have to make frequent decisions about which groups to join and which individuals to associate with. Group membership has adaptive implications, relating to for example, levels of intraspecific competition (Peuhkuri 1997), and oddity effects (Theodorakis 1989). The outcome of this is that social groups in nature tend to be highly sorted by general factors such as species, phenotype, and parasite load (Krause et al. 1996; Hoare et al. 2000), while individuals within these groups make fine-scale assessments based upon further, more subtle criteria.

In shoaling fishes, recognition of individual conspecifics has been posited as an important mechanism facilitating fine-scale shoal assortment, and numerous laboratory studies have revealed that fish of many species preferentially associate with individuals with which they have recently and repeatedly interacted (reviewed by Griffiths

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2003; Ward and Hart 2003; Griffiths and Ward 2006). This effect is termed familiarity, and familiar shoals have been shown to engage in lower levels of agonistic prey competition (Höjesjö et al. 1998; Utne-Palm and Hart 2000; Seppa et al. 2001; Webster and Hart 2006a; Webster and Hart 2007), to forage more efficiently (Swaney et al. 2001; Ward and Hart 2005), to transfer information and innovative behaviors more rapidly amongst members (Laland and Williams 1997; Lachlan et al. 1998), and to benefit from lower predation risk through greater shoal cohesion (Chivers et al. 1995). Evidence for familiarity as an important shoal structuring mechanism in nature remains equivocal, however. Shoal fidelity and stable shoaling preferences have been reported in some systems (see Klimley and Holloway 1999; Griffiths and Magurran 1997a; Ward et al. 2002), while others detected no evidence of persistent association patterns (see Helfman 1984; Hoare et al. 2000; Godin et al. 2003; Magurran and Queiroz 2003). This may be attributed to the fact that whilst these shoaling preferences are seen to arise over several days or weeks in the laboratory (Griffiths and Magurran 1997b; Croft et al. 2004a), the composition of free-ranging shoals often changes within seconds to hours in nature (Hoare et al. 2000; Croft et al. 2003). Furthermore, the cognitive demands of individual recognition limit the number of individual identities that can be learned (Griffiths and Magurran 1997a).

Recent research has identified a more parsimonious mechanism of recognition, one based upon self-referent matching of recent prey and habitat use that may be used over familiar recognition (Ward et al. 2004, 2005). Olsen et al. (2003) revealed that Arctic charr (*Salvelinus alpinus*) preferentially associated with conspecifics that had been fed upon the same type of artificial feed. Ward et al. (2004, 2005) revealed that three-spine stickleback, (*Gasterosteus aculeatus*) shoaled to a greater extent with individuals that had not only consumed the same prey as themselves, but also those that had spent time in the same habitat. Unlike preferences based upon learned recognition, these association preferences were evident after a single day and did not assume previous interaction between individuals. These preferences were based upon olfactory rather than visual cues, ones that could even be assimilated from closely related heterospecifics, and most significantly, fish were seen to preferentially shoal with unfamiliar conspecifics with a similar recent habitat use history over familiar fish that differed in this respect.

The mechanism of self-referent habitat use matching may therefore represent a general and inexpensive means of recognition, one that may be used alongside, or even in place of familiarity. To test this assertion, we need to further investigate its mechanisms. In this study, we firstly sought to determine the dynamics of the formation and breakdown

of these preferences. Ward et al. (2004, 2005) revealed that preferences are acquired within 24 h to a particular habitat or prey type. If this mechanism of recognition is adaptive, however, it must be easily and quickly reversible, to reflect changes in the habitat use of the individual that is receiving the cues and of the group members with which it is associating. We therefore predicted that habitat specific association preferences should build up and break down over a shorter time scale than 24 h, allowing for preferences to be rapidly adjusted. Secondly, we sought to determine the effect of recent habitat use upon shoal cohesion. We predicted that fish that share recent resource use history should benefit to a greater extent from using social information and that greater shoal cohesion should more easily facilitate this.

Materials and methods

Fish collection and housing

Several hundred juvenile threespine stickleback measuring 15 to 20 mm standard length were collected from Stonton Brook, Leicestershire, UK, in August and September 2005. They were divided into groups of approximately 50, and each was placed into a chemically and visually isolated holding tank, (40×25×25-cm water depth 20 cm, 1 cm deep fine sand substrate, flow through rate 0.1 l/min). The water temperature and light:dark regimes were held at 10°C and 12:12 h, respectively, for the duration of the experimental period. They were fed frozen Chironomid larvae once per day. Fish were held under these conditions for 8 weeks before the beginning of the study.

Part 1. How long do association preferences based upon habitat chemical cues take to break down and build up?

Previous studies have shown that fish preferentially associate with others with similar habitat experience to themselves (Ward et al. 2004, 2005). In this study, we investigated the short-term break down and build up of these preferences by quantifying the changing association preferences of focal fish that had been moved between habitat treatments in a laboratory study.

Habitat conditioning treatments

We used two habitat treatments, which we termed treatments A and B. Treatment A consisted of regular freshwater obtained from the recirculating laboratory supply and simulated areas of habitat free from decaying organic matter. Treatment B simulated a habitat unit with high concentrations of tannins, characteristic of areas where decaying vegetation matter accumulates, such as beneath riparian vegetation, along wind-exposed littoral zones of

still-water habitats, or in slow-flowing depositional habitats in stream channels. We replicated these habitat conditions by using 0.5 ml/l of a purpose designed solution (Blackwater Extract, Tetra GmbH, Herrenteich 78, 49324 Melle, Germany). Both of these habitat types occur along the channel of Stonton brook, giving our experimental design ecological relevance.

We performed four habitat time exposure experiments. Within each experiment, we performed 12 trials where the focal fish had been conditioned to habitat treatment A and 12 where it had been conditioned to habitat treatment B, giving a total of 24 trials per experiment. Focal fish were conditioned individually to their respective habitat treatment in visually and chemically isolated 12-l aquaria. These were not connected to the recirculating flow through system of the laboratory and were set in 10°C water baths to maintain constant temperatures. Stimulus fish were also held under these conditions, separate from the focal fish, at a density of six fish per tank. Fish were held in habitat conditioning tanks for a period of 48 h before trials began during which time they were not fed.

In the first habitat, exposure experiment focal fish were exposed to habitat treatment A or B and then given a binary choice test between shoaling with stimulus fish from habitat treatment A or B using the apparatus and procedure described below. In the second habitat, exposure experiment, the focal fish were exposed to either habitat treatment A or B for 48 h as above but were then switched to the opposite habitat and held there for 30 min before being given the binary choice association test. That is, focal fish conditioned for 48 h to treatment A, were then exposed to treatment B for 30 min before testing, and vice versa. In the third experiment focal fish were exposed to the opposite habitat for 120 min before being tested and in the fourth and final experiment for 240 min.

Within each trial, we used fish that had previously been housed together during the 8-week period before the beginning of the study. We did this to control for familiarity-based preferences (Griffiths 2003; Ward and Hart 2003; Griffiths and Ward 2006). We could not achieve this by simply segregating fish in the laboratory, because we had no data on their previous patterns of interaction in the field. Instead, we ensured that while patterns of familiarity were potentially high between individuals within trials, they were also homogenous.

Experimental tank

We tested association preferences using a standard binary choice experiment in an experimental tank (39 cm by 17 cm by 18 cm deep, water depth 15 cm). At each end of the tank along its longest axis was an 8-cm-wide stimulus chamber, separated from the central section of the tank by screens of

colorless perforated plastic (perforation diameter ca. 1 mm, 5 ± 1 perforations/cm²). This allowed the exchange of both visual and chemical cues. A 2-cm-deep substrate of 5 mm aquarium gravel was provided in the central section of the tank and in the two stimulus chambers. Three 10-cm lengths of artificial plastic vegetation were floated on the surface in each of the stimulus chambers. These served to keep the stimulus fish from becoming stressed by providing overhead cover. On the outside of the glass, we marked two association zones, indicated by vertical black lines, 2 cm from each of the stimulus chambers. This distance falls well within the range of interindividual distances seen in free-ranging shoals (Pitcher and Parrish 1993). The experimental tank contained freshwater obtained from the recirculating laboratory supply. Water from the recirculating laboratory supply was pumped into the center of each of the two stimulus chambers at a rate of 20 cm³ per minute, and allowed to drain out of an overflow outlet located at the waterline at the center of the rear wall of the tank. This water was collected in a separate reservoir and did not reenter the test tank. This served to carry chemical cues from stimulus fish from either compartment into the central section of the tank where the focal fish was housed. Two test tanks were set up and used alternately between trials.

Experimental procedure

Within each trial, the focal and stimulus fish were size matched by standard length to within <1 mm of each other. Three stimulus fish from habitat treatment A were added to one stimulus chamber, and three from habitat treatment B were added to the other. Each group of three stimulus fish was taken from within the same conditioning tank. Their positions were randomised between trials to control for tank-end bias. These were allowed to settle for 2 min. A single focal fish was then selected and was placed within a 7×7×22 cm tall holding unit constructed from the same perforated material as the stimulus compartment screens. The holding unit was situated in the center of the test tank. The focal fish was held with the holding unit for 1 min during which time, it could assimilate visual and chemical cues from the stimulus shoals. The holding unit was then removed and the focal fish released, beginning the trial. The trial duration was 2 min, and we recorded the first shoaling choice of the focal fish and the total amount of time it spent shoaling with either stimulus shoal. Focal fish from habitat treatments A and B were tested alternately.

After each trial, we added new stimulus shoals to the second test tank. While these were settling for 2 min, we changed the water in the first test tank to prevent habitat cues from accumulating between trials. When adding stimulus shoals and focal fish, we took care not to add water or debris from the treatment tanks. This ensured that

any habitat cues generated came from the stimulus fish only.

Statistical analyses

We investigated the first choice of the focal fish by comparing the number of trials in which they first shoaled with fish from the same habitat treatment as themselves against the number of trials in which they first shoaled with fish from the other habitat treatment, using a binary test with a null expected distribution of 50%. We compared shoaling preferences by subtracting the proportion of time spent by the test fish shoaling with fish from the same habitat, from the amount of time it spent shoaling with fish from the other habitat, and compared these values to a null expected value of zero using Wilcoxon signed rank tests. We did this for each of the four habitat exposure time experiments. Finally, we compared these values between the four habitat exposure time experiments using a one-way analysis of variance (ANOVA). All-time data were converted into proportions of total trial time, and arcsine transformed before analyses were carried out.

Part 2. Do habitat specific chemical cues influence shoal cohesion?

We sought to determine whether heterogeneity in recent habitat experience affected shoal cohesion. We ran an experiment with four treatments; one mixed shoal treatment, where each fish in the shoal had been conditioned within a different habitat, and three comparison treatments, in which all the fish in each shoal had been conditioned to the same habitat. Shoals contained four fish size matched to one another to within <1 mm, and we conducted 20 trials per treatment.

Mixed habitat experiment

We used four habitat conditions, one freshwater, using water taken from the recirculating flow through system of the laboratory, one of low and one of high concentration tannin conditions (0.25 and 0.75 ml/l of blackwater extract), and one with saline water (specific gravity 1.012, using Instant Ocean synthetic sea salt, Aquarium Systems, Sarrebourg Cedex, France). Threespine sticklebacks live in both freshwater and marine habitats and are commonly found in tidal estuaries, so the latter saline treatment is ecologically relevant.

Fish were conditioned to their respective habitat treatment individually in visually and chemically isolated 12-l aquaria. These were not connected to the recirculating flow through system of the laboratory and were set in 10°C water baths to maintain constant temperatures. Fish were held under these conditions for 48 h before being tested, using the procedure described below.

Comparison treatments

These were carried out as above except that within each treatment all fish were conditioned to the same habitat conditions. We ran one freshwater set, in which all of the 12-l-conditioning aquaria contained water obtained from the recirculating laboratory supply and one saline set (specific gravity 1.012). We only ran one tannin set, using a concentration of 0.5 ml/l blackwater extract, intermediate between the two used in the mixed habitat treatment described above. As above fish were conditioned individually, we performed 20 trials per treatment.

Experimental tank and procedure

We used an experimental tank (60×45×15 cm deep, water depth of 8 cm) surrounded on all sides by 60 cm tall nontransparent screening. A remote controlled 3.2-mega-pixel digital camera attached to a tripod was placed centrally above the tank at a height of 80 cm.

Experimental shoals of four fish each were formed. Fish had been conditioned individually for the previous 48 h. We formed the shoals from fish that had been housed together in the laboratory immediately before this to control for familiarity effects, as described in part 1. In the mixed habitat experience treatment, we selected one fish from each of the four habitat conditions to form a shoal of heterogeneous recent habitat experience. In the three comparison treatments, all fish had been held individually but under the same habitat conditions.

The members of the experimental shoal were placed together in a 12-l-aquarium and allowed to settle for 5 min. They were then netted out and placed together in the center of the experimental tank, where they were allowed to settle for a further 5 min. As before, care was taken to ensure that tank water or debris were not transferred to the test tank. After this, we took one digital photograph of the shoal every minute for a further 5 min, giving a total of five images per shoal. We used the digital measuring program TPSdig32 (Rohlf 2005) to analyze the images. For each image, we measured the nearest neighbor distance for each individual. Measurements were made of the smallest distance between the bodies of the nearest neighbors. We also measured the standard length of each individual, with all of these measurements made in pixels. Each nearest neighbor distance was then divided by the mean standard length of the shoal, giving a measurement of interindividual spacing that was standardized into body lengths. We made measurements in two dimensions, as the 8-cm water depth restricted the potential for shoals to form in three dimensions. For each experimental shoal, we calculated the mean nearest neighbor distance based upon the five images taken during the experiment, giving a total of 20

measurements each for the mixed habitat treatment, and for each of the three comparison treatments.

Statistical analysis

We compared nearest neighbor distances for each of the four treatments using a one-way ANOVA and Tukey post-hoc analyses.

Results

Part 1. How long do association preferences based upon habitat chemical cues take to break down and build up?

When test fish were taken from their respective habitat treatment tank and tested immediately, they showed a significant preference for shoaling with stimulus fish from the same habitat treatment as themselves, both in terms of their first choice (binomial test, null expected distribution 50%: $p < 0.001$) and time spent shoaling with either stimulus shoal (Wilcoxon signed rank test: $n = 24$, $Z = -2.996$, $p = 0.003$). When fish were transferred to the opposite habitat treatment for either 30 or 120 min before being tested, they showed no preference for either stimulus shoal, either in terms of their first choice (binomial test, null expected distribution 50%: $p = 1$; and $p = 0.307$, 30 and 120 min, respectively), or in terms of time spent shoaling (Wilcoxon signed rank test: $n = 24$, $Z = -1.443$, $p = 0.148$; and $n = 24$, $Z = -0.543$, $p = 0.587$, 30 and 120 min, respectively). When fish were transferred to the opposite habitat treatment for 240 min before being tested, they showed an association preference for fish from the new habitat. This was not seen in terms of first choice (binomial test, null expected distribution 50%: $p = 0.063$), but it was clear in terms of time allocation (Wilcoxon signed rank test: $n = 24$, $Z = -2.557$, $p = 0.010$).

Focal fish that had been conditioned to the blackwater or the freshwater treatments did not differ in their tendency to shoal with stimulus fish from the same habitats as themselves (one-way ANOVA: $F_{(2, 22)} = 0.17$, $p = 0.68$; $F_{(2, 22)} = 0.14$, $p = 0.71$; $F_{(2, 22)} = 0.37$, $p = 0.54$; $F_{(2, 22)} = 0.21$, $p = 0.65$ for the 0, 30, 120 and 240 min treatments, respectively).

Finally, the amount of time that the test fish spent shoaling with stimulus fish from the same habitat to which it was originally conditioned was lower in treatments where the test fish had spent more time in the opposite habitat treatment (one-way ANOVA: $F_{(3, 92)} = 9.419$, $p < 0.001$, Tukey post-hoc test, 0 min in opposite habitat vs 120 min in opposite habitat $p < 0.001$; 0 min in opposite habitat vs 240 min in opposite habitat $p < 0.001$, Fig. 1).

Part 2. Do habitat chemical cues affect shoal cohesion?

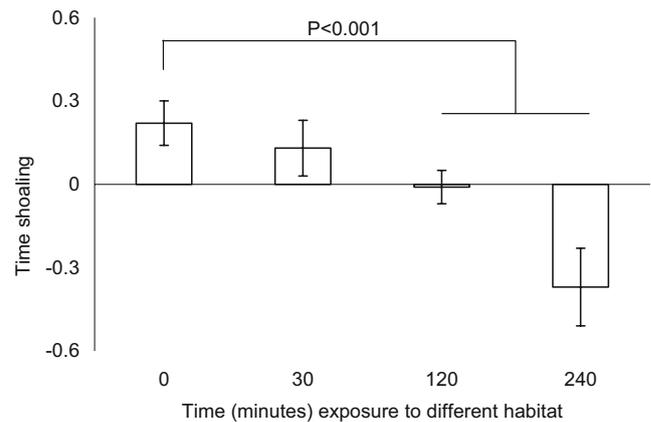


Fig. 1 Association preferences (proportion of trial time shoaling with fish from the same habitat minus proportion of trial time shoaling with fish from the different habitat \pm S.E.)

Shoal cohesion was lower in the treatment where shoals were composed of fish from different habitat types compared to treatments where shoals were composed of fish from the same habitat type (one-way ANOVA: $F_{(3, 76)} = 16.578$, $p < 0.001$, Tukey post-hoc test, $p < 0.001$ in all cases, Fig. 2).

Discussion

This study shows that the association preferences of threespine sticklebacks for conspecifics that have recently occupied the same habitat as themselves alter on a time scale of hours to reflect changes in the choosing individual's own habitat use. Furthermore, we reveal that individuals from the same habitat form more cohesive shoals than do those with differing habitat use history.

Associating with others that are using the same resources likely infers both benefits and costs. Social foragers benefit from higher rates of prey detection than do solitary foragers, and by shoaling with others that are exploiting similar units of habitat, a forager may benefit by assimilating and acting upon social cues pertaining to the location and means of access to specific resources that a solitary individual may not otherwise detect. Viewed in this context, association preferences mediated by habitat-use specific cues may represent a form of social or informational parasitism. Whether such habitat cues allow receivers to indirectly gauge resource quality, that is, whether they constitute a form of public information (Valone and Templeton 2002) is unknown and is worthy of further investigation. A likely cost of actively grouping with others that are exploiting similar resources is increased competition. This may be manifest in various forms, ranging from exploitative competition, whereby the presence of additional individuals causes the resource to be depleted more

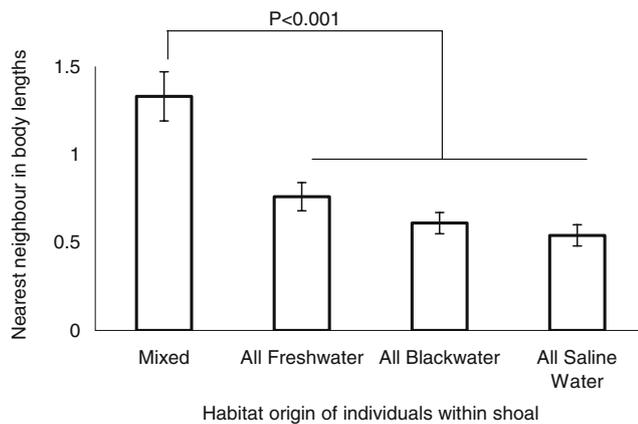


Fig. 2 Shoals composed of fish from the same habitat were more cohesive than shoals composed of fish from different habitats (mean nearest neighbor distance \pm S.E.)

rapidly, to contest competition, where individuals actively and aggressively compete over a resource (Ward et al. 2006). These, and other costs and benefits must be balanced against each other by individuals when making decisions on whether to join a group, and may in nature be subject to trade-offs dictated by the intensity of prevailing local environmental and social pressures.

This mechanism of recognition could operate in nature because individuals within populations frequently differ in their spatial and temporal use of habitat and prey resources. These patterns of variation may be discrete, as in the case of trophic polymorphism (Bolnick et al. 2003), commonly manifest in fishes as division between benthic and pelagic resource specialization (e.g., Robinson et al. 1993; Mittelbach et al. 1999; Proulx and Magnan 2004). Ecomorphs specializing upon resources in one habitat type are thought to trade away foraging efficiency in others (Svanbäck and Eklöv 2003, 2004), however little is known about how individuals move between these habitat units, and at what rates they encounter and interact with other habitat specialists. It is conceivable that encounters between habitat specialists may occur regularly, particularly along the frontiers and transitional zones between different habitat types. In this study, the ability to recognize and discriminate between resource-use specific cues could allow individuals to assess potential shoal mates, enabling them to ally patterns of resource use and to avoid associating with groups that are exploiting different prey, something that may put them at a competitive disadvantage.

Related to this, generalist foragers often specialize upon resources within foraging sessions, for example, by adopting search images when hunting for cryptic or concealed prey (Reid and Shettleworth 1992; Morgan and Brown 1996). Such behavior can lead to individuals disproportionately concentrating foraging effort upon certain prey types (Quevedo and Olsson 2006) or subunits of the habitat

(Webster and Hart 2004, 2006b), although resource use may vary between foraging sessions over the course of a day. In this study, we saw that the ability to detect differences between the habitat use of conspecifics after just 4 h, a much shorter time period than the 24 h previously reported by Ward et al. (2005). The ability to detect short-term changes in the nature of the habitat specific cues accrued and released by different groups of foragers allows individuals to recognize and discriminate between potential shoal mates and to accurately match their own resource use patterns accordingly.

It was also seen that shoals composed of individuals with shared recent habitat history were more cohesive than those from different habitat types, with the observed interindividual distances falling well within those determined by Pitcher and Parish (1993) to constitute active shoaling, even in the mixed habitat cue treatment. Assuming that a function of shoaling with groups engaged in similar resource use patterns is to increase foraging efficiency via informational parasitism, then such foragers may form more cohesive groups to better observe and assimilate social information cues. Such cues are likely to be visual in mode, revealing the successful discovery or capture of prey, and allowing the observer to join the finder in exploiting the patch, or to engage in kleptoparasitic behavior. Maintaining close proximity to others may be especially necessary in structurally complex habitats where fields of vision are otherwise restricted. Where individuals differ in resource use, they may form looser aggregations because differences in individual search image use render social information less valuable, or because heterogeneity in prey detection and handling efficiency puts some individuals at a foraging disadvantage, increasing the costs of competition.

Associating with others of shared habitat use history may infer a second advantage, in that it may reduce predation risk by reducing olfactory oddity. Many predators, both terrestrial and aquatic, use prey odor cues when hunting, and prey species may evolve behavioral counter measures to minimize their risk of detection or capture by predators that use such cues (e.g., Roberts et al. 2001; Reneerkens et al. 2005; Pastro and Banks 2006). In this context, grouping with other fish that are producing similar habitat specific chemical cues may seem counterintuitive, because doing so potentially presents a larger or more concentrated stimulus to searching predators. However, it may be that by doing so, a group of fish present a common olfactory profile, something that may reduce per capita predation risk at close quarters through the reduction in the oddity effect. They may further off-set this disadvantage by forming more cohesive shoals as we observed in experiment 2.

Association preferences and enhanced shoal cohesion amongst phenotypically similar fishes of a number of

species are behaviors that have previously been ascribed to familiar recognition (Griffiths 2003; Ward and Hart 2003; Griffiths and Ward 2006). This study, alongside those of Ward et al. (2004, 2005) promotes self-referent matching of habitats cues as an alternative mechanism, one that assumes no prolonged prior interaction between individuals and one that does not require the capacity to learn and recall individual identities. Although individual recognition is certainly used by fishes, for example, when selecting predator inspection partners (Milinski 1990), the opportunity to engage in the required period of prolonged interaction needed for it to arise may not always be available in natural systems. Self-referent matching of habitat cues, however, is an inexpensive mechanism, allowing association preferences to be rapidly over-ridden and replaced, reflecting short term changes in resource use; we suggest that its use should be widespread in nature.

The challenges for future research are numerous. Firstly, it is important that we further investigate the relative contribution of habitat cues vs familiar recognition in determining shoal structuring and association preferences. It would be of particular interest to determine whether some of the behaviors previously thought to be based upon familiar recognition can be described by this more parsimonious mechanism. Secondly, it would be useful to identify the habitat and diet derived volatile compounds that form the basis of these cues, the means by which fish accrue and release them, and the sensory receptors that allow the fish to receive and process them. Finally, there is a need to better understand the function of association preferences based upon self-referent matching of these cues, the fitness benefits derived from doing so, and the trade-offs associated with using them.

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References

- Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: Incidence and implications of individual specialization. *Am Nat* 161:1–28
- Chivers DP, Brown GE, Smith RJF (1995) Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*)—implications for antipredator behaviour. *Can J Zool* 73:955–960
- Croft DP, Arrowsmith BJ, Bielby J, Skinner K, White E, Couzin ID, Magurran AE, Ramnarine I, Krause J (2003) Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia reticulata*. *Oikos* 100:429–438
- Croft DP, Arrowsmith BJ, Webster M, Krause J (2004a) Intra-sexual preferences for familiar fish in male guppies. *J Fish Biol* 64: 279–283
- Godin J-GJ, Alfieri MS, Hoare DJ, Sadowski JA (2003) Conspecific familiarity and shoaling preferences in a wild guppy population. *Can J Zool* 81:1899–1904
- Griffiths SW (2003) Learned recognition of conspecifics by fishes. *Fish Fish* 4:256–268
- Griffiths SW, Magurran AE (1997a) Schooling preferences for familiar fish vary with group size in a wild guppy population. *Proc R Soc Lond, B Biol Sci* 264:547–551
- Griffiths SW, Magurran AE (1997b) Familiarity in schooling fish: how long does it take to acquire? *Anim Behav* 53:945–949
- Griffiths SW, Ward AJW (2006) Learned Recognition of Conspecifics. In: Brown C, Laland K, Krause J (Eds.) *Fish learning and behaviour*. Blackwell, Oxford
- Helfman GS (1984) School fidelity in fishes—the Yellow Perch pattern. *Anim Behav* 32:663–672
- Hoare DJ, Ruxton GD, Godin J-GJ, Krause J (2000) The social organisation of free-ranging fish shoals. *Oikos* 89:546–554
- Höjesjö J, Johnsson JI, Petersson E, Jarvi T (1998) The importance of being familiar: individual recognition and social behavior in sea trout (*Salmo trutta*). *Behav Ecol* 9:445–451
- Klimley AP, Holloway CF (1999) School fidelity and homing synchronicity of yellow fin tuna, *Thunnus albacares*. *Mar Biol* 133:307–317
- Krause J, Godin J-GJ, Brown G (1996) Phenotypic variability within and between fish shoals. *Ecology* 77:1586–1591
- Krause J, Ruxton GD (2002) *Living in groups*. Oxford University Press, Oxford
- Lachlan RF, Crooks L, Laland K (1998) Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Anim Behav* 56:181–190
- Laland KN, Williams K (1997). Shoaling generates social learning of foraging information in guppies. *Anim Behav* 53:1161–1169
- Magurran AE, Queiroz HL (2003) Partner choice in piranha shoals. *Behaviour* 140:289–299
- Milinski M (1990) On cooperation in sticklebacks. *Anim Behav* 40:1190–1191
- Mittelbach GC, Osenberg CW, Wainwright PC (1999) Variation in feeding morphology between pumpkinseed populations: Phenotypic plasticity or evolution? *Evol Ecol Res* 1:111–128
- Morgan RA, Brown JS (1996) Using giving-up densities to detect search images. *Am Nat* 148:1059–1074
- Olsen KH, Grahm M, Lohm J (2003) The influence of dominance and diet on individual odours in MHC identical juvenile Arctic charr siblings. *J Fish Biol* 63:855–862
- Pastor LA, Banks PB (2006) Foraging responses of wild house mice to accumulations of conspecific odor as a predation risk. *Behav Ecol Sociobiol* 60:101–107
- Peuhkuri N (1997) Size-assortative shoaling in fish: the effect of oddity on foraging behaviour. *Anim Behav* 54:271–278
- Pitcher TJ, Parrish JK (1993) Functions of shoaling behaviour in teleosts. In: Pitcher TJ (Ed.) *Behaviour of Teleost fishes*. Chapman & Hall, London, pp 363–439
- Proulx R, Magnan P (2004) Contribution of phenotypic plasticity and heredity to the trophic polymorphism of lacustrine brook charr (*Salvelinus fontinalis* M.). *Evol Ecol Res* 6:503–522
- Quevedo M, Olsson J (2006) The effect of small-scale resource origin on trophic position estimates in Eurasian perch. *J Fish Biol* 69:141–151
- Raman TRS (1997) Factors influencing seasonal and monthly changes in the group size of chital or axis deer in southern India. *J Biosci* 22:203–218
- Reid PJ, Shettleworth SJ (1992) Detection of cryptic prey—search image or search rate. *J Exp Psychol, Anim Behav Processes* 18:273–286

- Reneerkens J, Piersma T, Damste JSS (2005) Switch to diester preen waxes may reduce avian nest predation by mammalian predators using olfactory cues. *J Exp Biol* 208:4199–4202
- Roberts SC, Gosling LM, Thornton EA, McClung J (2001) Scent-marking by male mice under the risk of predation. *Behav Ecol* 12:698–705
- Robinson BW, Wilson DS, Margosian AS, Lotito PT (1993) Ecological and morphological-differentiation of pumpkinseed sunfish in lakes without bluegill sunfish. *Evol Ecol* 7:451–464
- Rohlf FJ (2005) Freeware at <http://life.bio.sunysb.edu/morph/>
- Seppa T, Laurila A, Peuhkuri N, Piironen J, Lower N (2001). Early familiarity has fitness consequences for Arctic char (*Salvelinus alpinus*) juveniles. *Can J Fish Aquat Sci* 58:1380–1385
- Svanbäck R, Eklöv P (2003) Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? *Oikos* 102:273–284
- Svanbäck R, Eklöv P (2004) Morphology in perch affects habitat specific feeding efficiency. *Funct Ecol* 18:503–510
- Swaney W, Kendal J, Capon H, Brown C, Laland KN (2001) Familiarity facilitates social learning of foraging behaviour in the guppy. *Anim Behav* 62:591–598
- Theodorakis CW (1989) Size segregation and the effects of oddity on predation risk in minnow schools. *Anim Behav* 38:496–502
- Utne-Palm AC, Hart PJB (2000) The effects of familiarity on competitive interactions between threespined sticklebacks. *Oikos* 91:225–232
- Valone TJ, Templeton JJ (2002) Public information for the assessment of quality: a widespread social phenomenon. *Philos Trans R Soc Lond, B Biol Sci* 357:1549–1557
- Ward AJW, Botham MS, Hoare D, James R, Broom M, Godin J-GJ, Krause J (2002) Association patterns and shoal fidelity in the three-spined stickleback. *Proc R Soc Lond, B Biol Sci* 269: 2451–2455
- Ward AJW, Hart PJB (2003) The effects of kin and familiarity on interactions between fish. *Fish Fish* 4:348–358
- Ward AJW, Hart PJB. (2005) Foraging benefits of shoaling with familiars may be exploited by outsiders. *Anim Behav* 69: 329–335
- Ward AJW, Hart PJB, Krause J (2004) The effects of habitat- and diet-based cues on association preferences in three-spined sticklebacks. *Behav Ecol* 15:925–929
- Ward AJW, Holbrook RI, Krause J, Hart PJB (2005) Social recognition in sticklebacks: the role of direct experience and habitat cues. *Behav Ecol Sociobiol* 57:575–583
- Ward AJW, Webster MM, Hart PJB (2006) Intraspecific food competition in fishes. *Fish Fish* 7:1–31
- Webster MM, Hart PJB (2004) Substrate discrimination and preference in foraging fish. *Anim Behav* 68:1071–1077
- Webster MM, Hart PJB (2006a) Kleptoparasitic prey competition in shoaling fish: effects of familiarity and prey distribution. *Behav Ecol* 17:959–964
- Webster MM, Hart PJB (2006b) Subhabitat selection by foraging threespine stickleback (*Gasterosteus aculeatus*): previous experience and social conformity. *Behav Ecol Sociobiol* 60: 77–86
- Webster MM Hart PJB (2007). Prior association mediates kleptoparasitic prey competition in shoals of threespine stickleback. *Anim Behav* (in press)