

The effects of habitat- and diet-based cues on association preferences in three-spined sticklebacks

Ashley J. W. Ward,^a Paul J. B. Hart,^a and Jens Krause^b

^aDepartment of Biology, University of Leicester, Leicester LE1 7RH, UK, and

^bDepartment of Biology, University of Leeds, Leeds LS2 9JT, UK

A number of recent articles have investigated the potential of familiarity preferences to influence group membership in free-ranging animals. However, it is not clear to which extent individual recognition or a more general recognition of a group odor is responsible for familiarity preferences. First, we tested the sensory basis of the recognition of familiars in stickleback. When allowed to choose between a familiar and a nonfamiliar stimulus shoal on the basis of both visual and chemical communication, visual communication only, and chemical communication only, the preference of focal fish for familiars was shown to depend on the presence of chemical cues. We subsequently investigated the effects of recent habitat and diet on shoaling preferences in the three-spined stickleback (*Gasterosteus aculeatus*). Experimental fish were divided into four treatment groups consisting of two water treatments (saline and freshwater) and two diet treatments (*Daphnia* spp. and bloodworm). Focal fish subsequently showed significant association preferences for groups of nonfamiliar fish that had undergone the same water or diet treatment as themselves. These data indicate that individual recognition is not a prerequisite for the expression of association preferences. **Key words:** chemical cues, diet, habitat, three-spined stickleback. [*Behav Ecol* 15:925–929 (2004)]

Social animals are known to demonstrate self-referent smatching with regard to phenotype, preferentially associating with conspecifics (see Krause and Godin, 1994) and with size-matched individuals (Ward and Krause, 2001) in order to minimize phenotypic variation within the group and thereby individual predation risk. The selective forces promoting such phenotypic conformity in groups should in theory make it more difficult for group members to identify other individuals. Despite this, fish are known to be capable of such recognition (Dugatkin and Alfieri, 1991; Milinski et al., 1990). Furthermore, this ability enables fish to assort preferentially with related or familiar individuals (see Griffiths, 2003).

A number of recent studies have reported preferences for unrelated familiar individuals in a range of taxa (see Griffiths, 2003; Krause and Ruxton, 2002). Familiarity develops over a period of time; in both the guppy (*Poecilia reticulata*; Griffiths and Magurran, 1997) and the stickleback (Utne-Palm and Hart, 2000), it develops gradually over approximately 2 weeks. Once developed, it may persist for several weeks, even without reinforcement (Chivers et al., 1995). Associating with familiars can potentially provide individuals with important benefits, including enhanced group antipredator behavior (Chivers et al., 1995; see also Barber and Wright, 2001). Wisenden and Smith (1998) reported direct physiological effects relating to reduced per capita risk in familiar shoals of fathead minnows (*Pimephales promelas*). The “dear enemy” phenomenon of reduced aggression between familiar individuals acts to stabilize dominance hierarchies in trout (*Salmo trutta*; Höjesjö et al., 1998) and to mediate competitive interactions in three-spined stickleback, *Gasterosteus aculeatus* (Utne-Palm and Hart, 2000). In addition, familiarity has been shown to promote social learning in the guppy (Swaney et al. 2001).

The sensory mechanisms used in recognition and discrimination vary according to the context and between species. For example, research on kin recognition has highlighted the importance of odor cues associated with the major histocompatibility complex (MHC; Olsen et al., 2002). whereas evidence is more equivocal for the way familiar fish are recognized. Visual cues alone allow for the expression of a preference for familiars in guppies (Griffiths and Magurran, 1997) and rainbowfish (Brown, 2002). However, sticklebacks have been shown to be unable to distinguish familiar individuals in the absence of odor cues (VanHavre and Fitzgerald, 1988), and fathead minnows (Brown and Smith, 1994) and guppies (Griffiths SW, personal communication) are capable of discriminating familiar conspecifics on the basis of chemical cues alone. Where odor cues are important in the discrimination of, and preference for, familiars, the nature of those cues may be influenced by the manner in which an individual exploits its habitat. Moore et al. (1994) demonstrated that juvenile salmonids transmit and assess signals deriving from chemicals in the urine. Furthermore, Olsen et al. (2002) speculated that such signals may have many components, some of which may potentially be influenced by factors such as an individual’s diet.

Frequent exchange of individuals between shoals (Krause et al., 2000) means that, in free ranging fish, decisions about who to associate with are often likely to be between individuals, or groups of individuals, that are unfamiliar. How then might individuals act adaptively? Decisions may be made on the basis of a behavioral context, for example whether they show predator inspection behavior (see Dugatkin and Alfieri, 1991; Milinski et al., 1990). In addition, European minnows (*Phoxinus phoxinus*) are known to be able to make decisions based on the competitive ability of potential shoalmates (Metcalf and Thomson, 1995). Where individuals are unable to make such complex assessments due to the absence of a behavioral context, other cues may be important. For example, recognition of a particular cue based on habitat

Address correspondence to A. J. Ward. E-mail: ajww2@le.ac.uk.

Received 10 October 2003; revised 8 January 2004; accepted 26 January 2004.

use may theoretically be as important as individual recognition in stimulating an association response.

In this article, we investigate the sensory modalities involved in the expression of a preference for familiars in three-spined sticklebacks. In addition, we examine whether individuals make association decisions based on conspecific cues relating to the local environment, or on recent foraging patterns and prey choice.

METHODS

Fish and holding conditions

Three-spined sticklebacks have been used extensively in work on individual recognition and familiarity (see Barber and Ruxton, 2000; Milinski et al., 1990; Ward et al., 2002). They are common throughout the temperate Northern hemisphere, occurring in both freshwater and coastal marine zones, and some populations are known to migrate between the two (Bell and Foster, 1994). They are generalist predators and take both benthic prey, such as insect larvae, and planktonic prey, such as copepods. The individuals used in this experiment were caught at Saffron Brook in Leicester, UK (52°36' N, 1°7' W) during October and November 2002.

Familiarity

We divided a total of 200 size-matched (40 ± 4 mm) fish equally between eight 30-l unfurnished aquaria. Water temperature was held constant at 12°C, the light regime was 12 h light and 12 h dark. We made no attempt to sex the fish, which were not in breeding condition. The fish were fed daily ad libitum with frozen bloodworms.

After 2 weeks, we measured shoal preference behavior by using a standard binary shoal choice procedure. The test tank measured 500 × 300 mm and 300 mm high, filled to a depth of 200 mm. The test tank was divided into three compartments by the addition of two sheets of PennPlax perforated plastic (perforation diameter was approximately 1 mm, 5 ± 1 perforations/cm²) 80 mm from either end of the tank along the longest axis. The use of clear perforated plastic allows olfactory, as well as visual, stimuli to be detected by a focal fish. A substrate of standard 5-mm aquarium gravel was added to a depth of 10 mm throughout both the test tank and the two compartments. We drew lines on the outside of the glass demarcating two 120-mm preference zones at either end of the central compartment. This distance represents three body lengths of a 40 ± 4 -mm focal fish, which falls within the range of interindividual distances observed in free-ranging shoals (Pitcher and Parrish, 1993).

We added two stimulus shoals of four fish each to the test tank, one shoal to each of the two outer compartments. Each stimulus shoal was taken from a different tank. The stimulus shoals were then given 10 min during which to acclimatize. After this period of acclimatization, a single focal fish was taken from the same tank as one of the stimulus shoals. In doing this, we could ensure that the focal fish was familiar with the individuals in one of the stimulus shoals and unfamiliar with the individuals in the other. We placed the focal fish in a centrally situated cylinder (diameter was 10 cm) in the middle compartment of the test tank. This cylinder was constructed from the same material as the barriers at either end of the tank, allowing both visual and chemical communication between the stimulus shoals and the focal fish. The focal fish remained inside this cylinder for a period of 5 min before being released. After release, the time spent by the focal fish within either of the preference zones was recorded for a further period of 5 min. After each experiment, both the

stimulus shoals and the focal fish were removed, new stimulus shoals were added and the process was repeated. The end of tank occupied by the familiar shoal was randomized between replicates. We carried out a total of 12 replicates.

To differentiate between the sensory modalities used in the recognition of familiars, we subsequently manipulated the barriers between the stimulus shoals and the focal fish. First, to exclude chemical communication and therefore test visual communication alone, we cut two pieces of acetate to size and placed one against each of the perforated barriers. Second, to exclude visual communication, the transparent perforated plastic barriers were replaced with opaque perforated plastic barriers. The experimental procedure was identical to that detailed earlier wherein the focal fish was given a choice of a shoal of familiar fish and a shoal of nonfamiliar fish. We carried out a total of 12 replicates for each. Each focal fish and each stimulus shoal were used only once per treatment to prevent pseudoreplication, and trial order was randomized.

Environment and diet cues

We divided a further 256 size-matched (40 ± 4 mm) fish equally between eight 30-l aquaria. The experimental fish were subject to a total of four treatments, with two aquaria being allocated for each treatment. Two of the aquaria contained fresh water (FW1 and FW2), and two aquaria contained slightly saline water at a specific gravity of 1.005 (approximately 20% of the salinity of seawater, which has a specific gravity of 1.023–1.027; SW1 and SW2); the occupants of all four tanks continued on a diet of frozen bloodworms. The four remaining aquaria contained freshwater, and we provisioned two of these ad libitum with live *Daphnia* spp. (D1 and D2) and the other two ad libitum with live bloodworms (B1 and B2). Prey were consumed immediately by the fish, precluding the development of behavioral differences in foraging between the treatments. Water temperature was held constant at 12°C with a light regime of 12 h light and 12 h dark. No visual or chemical communication was possible between the aquaria as each was an isolated unit. The conditioning phase lasted for 2 weeks.

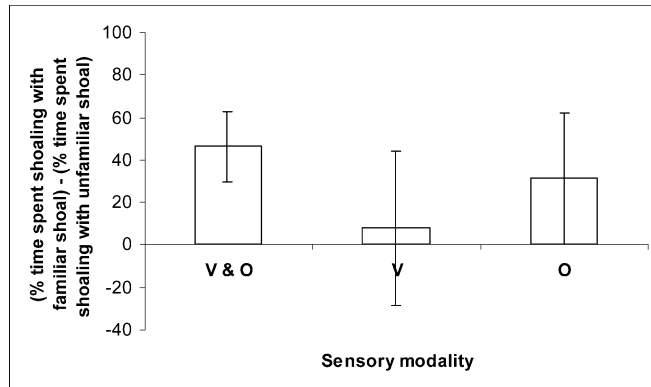
Focal fish were given a choice of two nonfamiliar stimulus shoals, one composed of fish that had undergone the same water or diet conditioning as the focal fish for 2 weeks and the other composed of the alternative. For example, focal fish that had been conditioned to a diet of *Daphnia* were given a choice between a stimulus shoal of nonfamiliar fish that had been conditioned on a diet of *Daphnia* and a shoal of nonfamiliar fish that had been conditioned on a diet of bloodworms. We followed the same basic binary shoal choice protocol as detailed above, using clear perforated barriers between the focal fish and the stimulus shoals.

Focal fish taken from FW1 were given a choice between a stimulus shoal taken from FW2 and a stimulus shoal taken from SW2; focal fish taken from SW1 were given a choice between a stimulus shoal taken from SW2 and a stimulus shoal taken from FW2. In the same manner, focal fish taken from D1 were given a choice between a stimulus shoal taken from D2 and a stimulus shoal taken from B2; focal fish taken from B1 were given a choice between a stimulus shoal taken from B2 and a stimulus shoal taken from D2.

We carried out a total of 15 replicates for each of the four treatments. Focal fish and stimulus shoals were used only once throughout the experiment.

Controls

To prevent an accumulation of odor cues at either end of the test tank, the water in the test tanks was changed after each

**Figure 1**

Mean (percentage of time spent shoaling by focal fish with familiar fish) – (percentage of time spent shoaling by focal fish with unfamiliar fish). Error bars show 95% confidence intervals. O indicates olfactory; V, visual. Significant departures from zero are shown: * $p < .05$. Test results generated using one-sample t test, a levels adjusted according to Bonferroni method ($\alpha' = \alpha/k$). $n = 12$.

trial. In addition, the side of the test tank occupied by each stimulus shoal was switched between each trial. Neither focal fish nor stimulus fish were fed less than 15 h before the commencement of testing to avoid contamination of the test tank with uneaten or partially eaten food, which could act as a cue.

Fresh water was used in the test tanks. Fish that had been kept in slightly saline water were gradually acclimatized over the course of half an hour immediately before the experiments, and afterward were acclimatized back to the slightly saline (SG 1.005) conditions over the same period by gradual addition of fresh or saline water, respectively. None of these fish showed any signs of distress during this period, which is analogous to conditions experienced by this species in the changing saline environment of tidal rivers and estuaries.

Finally, we used care to prevent transfer of any tank water to the test tank when adding the stimulus shoals and the focal fish.

In undertaking these controls, we could be confident that any cues that did occur in the test tank arose directly from the fish themselves and not from any extraneous material introduced with the fish.

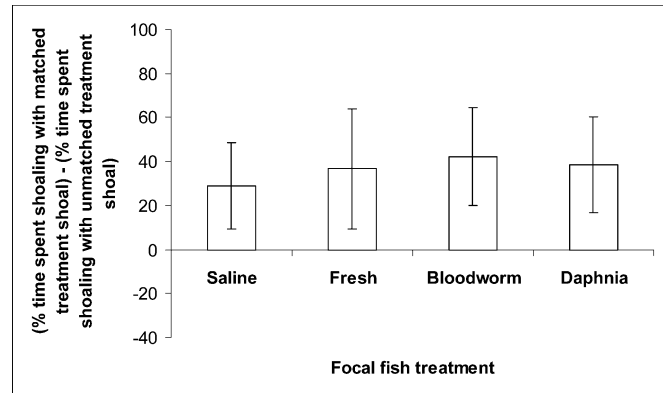
Data analysis

The data were normalized by using an arcsine transformation and were analyzed by using a one-sample t test comparing (proportion of time spent with shoal a) – (proportion of time spent with shoal b) against zero. α levels were adjusted according to the Bonferroni method ($\alpha' = \alpha/k$). All statistical tests were two-tailed.

RESULTS

Familiarity

The tendency of sticklebacks to associate with a stimulus shoal composed of familiar fish varied according to the available communication channels (ANOVA: $F_{2,33} = 3.8$, $p = .03$) (Figure 1). Stickleback preferentially associated with familiar fish when both visual and chemical cues were available (one-sample t test: $t = 3.4$, $n = 12$, $p = .02$) (Figure 1). When communication was restricted to one modality, focal fish showed no preference for familiar fish for which only visual cues

**Figure 2**

Mean (percentage of time spent shoaling by focal fish with shoal of unfamiliar fish that were subject to the same water or diet treatment) – (percentage of time spent shoaling by focal fish with shoal of unfamiliar fish that were subject to the alternative water or diet treatment). Error bars show 95% confidence intervals. Significant departures from zero at the 5% level are denoted by an asterisk. Test results generated by using one-sample t test, α levels adjusted according to Bonferroni method ($\alpha' = \alpha/k$). $n = 15$ for each treatment.

were available (one-sample t test: $t = 0.4$, $n = 12$, $p = .7$) (Figure 1) but did show a preference when chemical cues were available (one-sample t test: $t = 3$, $n = 12$, $p = .04$) (Figure 1).

Environmental and diet cues

Water treatment

Focal fish taken from the saline water treatment showed a significant preference for a shoal of nonfamiliar fish taken from the saline water treatment over a stimulus shoal of nonfamiliar fish taken from the freshwater treatment (one-sample t test: $t = 3.15$, $n = 15$, $p = .007$) (Figure 2). Similarly, focal fish taken from the freshwater treatment showed a significant preference for a shoal of nonfamiliar fish taken from the freshwater treatment over a stimulus shoal of nonfamiliar fish taken from the saline water treatment (one-sample t test: $t = 2.88$, $n = 15$, $p = .012$) (Figure 2).

Diet treatment

Focal fish taken from the *Daphnia* diet treatment showed a significant preference for a shoal of nonfamiliar fish taken from the *Daphnia* diet treatment over a stimulus shoal of nonfamiliar fish taken from the bloodworm treatment (one-sample t test: $t = 4.09$, $n = 15$, $p = .001$) (Figure 2). Finally, focal fish taken from the bloodworm diet treatment significantly preferred a shoal of nonfamiliar fish taken from the bloodworm treatment over a stimulus shoal of nonfamiliar fish taken from the *Daphnia* diet treatment (one-sample t test: $t = 3.8$, $n = 15$, $p = .002$) (Figure 2).

DISCUSSION

Three-spined stickleback showed significant preferences for stimulus shoals composed of nonfamiliar fish that had been subject to the same water or diet treatment as themselves for a 2-week period. This preference was exhibited for both kinds of water treatment, fresh and saline, and for both diet treatments, bloodworm and *Daphnia*. They showed a preference for stimulus shoals composed of familiar fish over a shoal of the same size composed of nonfamiliar fish when both visual and chemical communication, and when chemical

communication alone, was possible but not when only visual communication was possible.

For all four tested treatments, focal fish preferentially associated with conspecifics that had been subject to the same environment or diet treatment. The use of cues produced by individuals' habitat exploitation in order to determine an association preference may be adaptive as it may allow a choosing individual to assort with conspecifics that exploit the habitat in a similar way to themselves and may therefore be adaptive in terms of acquiring information on the habitat. Cues based on diet and habitat may be expressed in individuals from the same local area who are likely to have information that is relevant to a choosing fish. Outsiders that enter the area with a new and unfamiliar smell are, in contrast, less likely to have information that is relevant at the local level to that fish. Furthermore, fish from similar habitats may potentially have similar experiences and, as a result, behave in a more similar and predictable fashion than do those from dissimilar habitats. This could be beneficial in terms of minimizing behavioral oddity between individuals in groups.

Alternatively, however, it may be argued that in order to minimize competition costs, fish should actively avoid conspecifics that exploit the habitat in the same manner as themselves. In this case, the observed preferences may be explicable in terms of the acquisition of foraging preferences—learnt recognition and preference for a familiar recent food source. On the other hand, the focal fish may simply form an association between familiar olfactory cues and its experience of good foraging conditions over the previous 2 weeks.

It is difficult to assess the potential importance of these results to fish in a free-ranging context. Because three-spined sticklebacks are opportunistic omnivores, it seems unlikely that wild fish would have a diet consisting exclusively of one prey item. Nonetheless, it may be possible that the diets of fish living in populations occupying different areas of the same habitat may vary sufficiently as a result of different prey habitat preferences to produce the effect described here. In addition, the effect is not limited to sticklebacks: diet is known to affect odor cues produced not only by other fish species (Arctic charr, *Salvelinus alpinus*; Olsen et al., 2003) but also by rodents (Brown et al., 1996; Schellink et al., 1997). Similarly, although water chemistry can fluctuate significantly over short spatial and temporal ranges, particularly in estuarine habitats, it is difficult to predict how this might interact with association preferences. Environmental cues such as these may also be important in mediating other areas, such as mate choice. Ziuganov (1995) reported that reproductive isolation evolves rapidly (less than eight generations) between marine and freshwater lateral plate morphs of three-spined sticklebacks when experimentally separated. Clearly, further work is required in the field to elucidate.

The ability of fish to discriminate and preferentially associate with nonfamiliar conspecifics on the basis of a shared recent history of environmental exploitation may suggest one possible mechanism by which familiarity (as it is generally understood) may arise. Such proximate cues avoid the potentially high memory cost of individual recognition. It is possible that familiarity may arise through a variety of different mechanisms, including recognition of subtle behavioral, physiological, and morphological cues. Although no effects were directly observed, it is conceivable that the different conditioning environments used in the present study may have resulted in slight alterations in any or all of the above cues.

Our findings suggest the possibility that the results of some previous studies, previously explicable solely in terms of a preference for familiars, may have an additional explanation. Clearly, attention should be paid to potential tank effects and husbandry in future laboratory studies to avoid this

potentially confounding factor. Notwithstanding this, however, a preference for familiars in the present study was expressed in the absence of variability in recent environmental and diet history. The possibility exists, therefore, that recognition of familiars and a recognition of cues based on these factors may augment one another and help to maintain assorted shoals, especially given that shoals of familiar fish are likely to exploit the environment in similar ways simply as a result of the high degree of spatial and temporal proximity of individuals in the same shoal.

The finding that chemical communication, either in the presence or in the absence of visual stimuli, was necessary to elicit an association preference with familiar fish seems to suggest that the recognition mechanism operated by sticklebacks in this context was based on chemical cues (Brown and Smith, 1994). This, however, does not necessarily preclude the possibility that sticklebacks are able to use both chemical and visual means of recognition according to the circumstances; indeed, evidence suggests that they are capable of individual recognition (Milinski et al., 1990; Ward et al., 2002). The importance of vision as a sensory modality in sticklebacks is highlighted by the large size of the visual cortex as a proportion of the overall brain. Indeed, the results presented here were clearest and least variable when both modalities were available. It seems likely, therefore, that both are important in discrimination. Environmental characteristics, such as habitat complexity or turbidity, and densities of fish, both conspecifics and predators, may determine the costs-to-benefits ratios of the respective recognition systems and therefore the contexts in which they may be used.

This work also raises a number of other potentially interesting questions. For example, do the observed association preferences between nonfamiliars based on these cues translate into an increased likelihood of cooperation. What other cues, in addition to water and diet, may generate the preference behavior? How do these preferences interact with familiarity responses? Do association preferences derive only from positive experiences in terms of interactions or feeding regimes?

We thank Iain Barber, Cullum Brown, and two anonymous referees whose comments greatly improved the manuscript. This work was funded by the National Environmental Research Council of the United Kingdom.

REFERENCES

- Barber I, Ruxton GD, 2000. The importance of stable schooling: do familiar sticklebacks stick together? *Proc R Soc Lond B* 267: 151–155.
- Barber I, Wright HA, 2001. How strong are familiarity preferences in shoaling fish? *Anim Behav* 61:975–979.
- Bell MA, Foster SA, 1994. Introduction to the evolutionary biology of the threespine stickleback. In: *The evolutionary biology of the threespine stickleback* (Bell MA, Foster SA, eds). Oxford: Oxford Science Publications.
- Brown C, 2002. Do female rainbow fish (*Melanotaenia* spp.) prefer to shoal with individuals under predation pressure? *J Ethol* 20:89–94.
- Brown RE, Schellink HM, West AM, 1996. The influence of dietary and genetic cues on the ability of rats to discriminate between the urinary odors of MHC-congenic mice. *Physiol Behav* 60:365–372.
- Brown GE, Smith RJF, 1994. Fathead minnows use chemical cues to discriminate natural shoalmates from unfamiliar conspecifics. *J Chem Ecol* 20:3051–3061.
- Chivers DP, Brown GE, Smith, RJF, 1995. Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*): implications for antipredator behavior. *Can J Zool* 73:955–960.
- Dugatkin LA, Alfieri M, 1991. Guppies and the tit-for-tat strategy: preference based on past interaction. *Behav Ecol Sociobiol* 28: 243–246.

- Griffiths SW, 2003. Learned recognition of conspecifics by fishes. *Fish Fisheries* 4:256–268.
- Griffiths SW, Magurran, AE, 1997. Familiarity in schooling fish: how long does it take to acquire? *Anim Behav* 53:945–949.
- Höjesjö J, Johnsson JI, Petersson E, Järvi T, 1998. The importance of being familiar: individual recognition and social behaviour in sea trout. *Behav Ecol* 9:445–451.
- Krause J, Godin J-GJ, 1994. Shoal choice in the banded killifish: effects of predation risk, fish size, species composition and size of shoals. *Ethology* 98:128.
- Krause J, Hoare DJ, Croft D, Lawrence J, Ward A, Ruxton GD, Godin J-GJ, James R, 2000. Fish shoal composition: mechanisms and constraints. *Proc R Soc Lond B* 267:2011–2017.
- Krause J, Ruxton GD, 2002. *Living in groups*. Oxford: Oxford University Press.
- Metcalf NB, Thomson BC, 1995. Fish recognize and prefer to shoal with poor competitors. *Proc R Soc Lond B* 259:207–210.
- Milinski M, Pflüger D, Kulling D, Kettler R, 1990. Do sticklebacks cooperate repeatedly in reciprocal pairs? *Behav Ecol Sociobiol* 27: 17–21.
- Moore A, Ives MJ, Kell LT, 1994. The role of urine in sibling recognition in Atlantic salmon, *Salmo salar* parr. *Proc R Soc Lond B* 255:173–180.
- Olsen KH, Grahn M, Lohm J, 2002. Influence of MHC on sibling discrimination in Arctic charr, *Salvelinus alpinus* (L.). *J Chem Ecol* 28:783–795.
- Olsen KH, Grahn 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.
- Pitcher TJ, Parrish JK, 1993. Functions of shoaling behaviour in teleosts. In: *Behaviour of teleost fishes* (Pitcher TJ, ed). London: Chapman & Hall; 363–439.
- Schellink HM, Slotnick BM, Brown RE, 1997. Odors of individuality originating from the major histocompatibility complex are masked by diet cues in the urine of rats. *Anim Learn Behav* 25:193–199.
- Swaney W, Kendal J, Capon H, Brown C, Laland, K.N, 2001. Familiarity facilitates social learning of foraging behaviour in the guppy. *Anim Behav* 62:591–598.
- Utne-Palm AC, Hart PJB, 2000. The effects of familiarity on competitive interactions between threespined sticklebacks. *Oikos* 91:225–232.
- VanHavre N, FitzGerald G, 1988. Shoaling and kin recognition in the threespine stickleback (*Gasterosteus aculeatus*). *Biol Behav* 13: 190–201.
- Ward AJW, Botham MS, Hoare DJ, James R, Broom M, Godin J-GJ, Krause J, 2002. Association patterns and shoal fidelity in the threespined stickleback. *Proc R Soc Lond B* 269:2451–2455.
- Ward AJW, Krause J, 2001. Body length assortative shoaling in the European minnow, *Phoxinus phoxinus*. *Anim Behav* 62:617–621.
- Wisenden BD, Smith RJF, 1998. A re-evaluation of the effect of shoalmate familiarity on the proliferation of alarm substance cells in ostariophysan fishes. *J Fish Biol* 53:841–846.
- Ziuganov VV, 1995. Reproductive isolation among lateral plate phenotypes (low, partial, complete) of the threespine stickleback, *Gasterosteus aculeatus*, from the White Sea basin and the Kamchatka Peninsula, Russia. *Behaviour* 132:1173–1181.