



The influence of habitat stability on landmark use during spatial learning in the three-spined stickleback

LUCY ODLING-SMEE & VICTORIA A. BRAITHWAITE

Institute of Cell, Animal and Population Biology, University of Edinburgh

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The capacity to learn enables animals to match their phenotypic response to a changing environment on the basis of experience but learning is likely to incur costs such as the cost of making mistakes or the energetic cost of processing information. Little is known about how animals optimize the use of learned behaviour within their natural environments such that potential costs are minimized. We investigated whether the use of local landmarks in learning orientation routes by the three-spined stickleback, *Gasterosteus aculeatus*, varied in response to the visual stability of their natural habitats. Sticklebacks collected from five fast-flowing rivers and five ponds were trained to locate a hidden reward in a T-maze. Locating the reward required the fish to learn a body-centred algorithmic behaviour (turn left or right) or to follow plant landmarks. Probe trials, in which these cues conflicted, revealed which spatial cue the fish was using. Pond fish appeared to rely more than river fish on visual landmarks, which is consistent with the suggestion that even within a species, learned behaviour is fine-tuned in response to local environmental conditions. Landmarks may be reliable indicators of location only in stable pond habitats. In rivers, turbulence and flow may continually disrupt the visual landscape such that river fish may benefit from learning orientation routes only if learning is constrained so that unreliable visual cues are ignored.

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Theoretical models that investigate the kinds of environmental unpredictability that should select for learning assume that there must be costs and limits to being plastic that constrain its evolution (Mangel 1990; Stephens 1991, 1993; Bergman & Feldman 1995). Proposed costs of learning include the cost of making mistakes, the energetic cost of processing information, delayed reproductive success, increased juvenile vulnerability and increased parental investment (Johnston 1982). However, little is known about how, or indeed whether, animals optimize the use of learned behaviour within their natural environments such that potential costs are minimized.

In some cases, plasticity of brain structures and neurological machinery may enable animals to reduce energetic expenditure when there is a reduced demand for information processing. For example, seasonal fluctuations in the rate of neurogenesis and hippocampal volume in black-capped chickadees, *Poecile atricapillus*, follow seasonal changes in foraging behaviour and space use (Barnea & Nottebohm 1994; Smulders 1995). Similarly, enhance-

ment and regression of spatial learning ability in various species of polygynous rodents appears to track seasonal shifts in the demand for this behaviour (Galea et al. 1994; Gaulin 1995). Interpretations of the adaptive function of seasonal changes in brain structures have been criticized for lacking experimental evidence (Bolhuis & Macphail 2001). However, it is likely that at least some animals are economical with their investment in neural tissue, building and maintaining neurological machinery only when the metabolic costs can be offset by the benefits of increased efficiency in acquiring food or mates.

More wide ranging are mechanisms that guide and direct learning and associated perceptual processes in response to specific ecological problems. Animals are often preprogrammed to pay attention to certain cues in preference to others. For example, when exposed to songs of multiple species, juveniles of a number of bird species preferentially learn conspecific song (Thorpe 1961; Marler & Tamura 1964; Immelmann 1969; Marler & Peters 1977, 1988). Furthermore, certain associations may be learned more readily than others (Garcia & Koelling 1966). Hummingbirds, *Archilochus alexandri*, can easily learn to discriminate colours but not objects of differing brightness (Goldsmith et al. 1981). Similarly, three species of hummingbirds (*A. alexandri*, *Eugenes ful-*

Correspondence: L. Odling-Smee, Division of Biological Sciences, Institute of Cell, Animal and Population Biology, University of Edinburgh, King's Buildings, West Mains Road, Edinburgh EH9 3JT, U.K. (email: Lucy.Odling-Smee@ed.ac.uk).

gens and *Lampornis clemenciae*) reinforced for visiting a flower location can more easily learn to choose a different location during subsequent foraging than learn to return to the same location (Cole et al. 1982). Differences in performance may be caused by differences in the ability of animals to learn and remember, or result from differences in associated processes such as perception or motivation. Therefore, where adaptive specializations that affect performance in learning tasks exist, they may directly involve learning and memory processes or sensory input systems. Either way, such predispositions may filter out uninformative or unreliable sources of information such that the risk of making mistakes, wasting time and processing redundant information is minimized.

Understanding how learning is used in its natural context in a cost-effective way is likely to require a deeper understanding of the nature and degree to which perceptual processes or learning and memory biases guide and enable learned behaviour. We investigated whether different habitat conditions shape learned behaviour in populations within a species, asking specifically whether habitat stability influences the use of visual cues in orientation in the three-spined stickleback, *Gasterosteus aculeatus*. Several studies imply that habitat stability can influence the use of visual cues in spatial learning (Taube & Burton 1995; Biegler & Morris 1996a, b). For example, food-storing bird species differ from nonstoring species in responding preferentially to spatial position over local visual cues (Brodbeck 1994; Clayton & Krebs 1994). One explanation is that local visual cues are more prone to change between storage and retrieval of food than is spatial location. However, many factors differ between species that could potentially explain differences in their use of local visual cues. These confounding factors are typically reduced in intraspecific comparisons (Papaj & Prokopy 1989; Carlier & Lefebvre 1996). The three-spined stickleback comprises thousands of phenotypically diverse populations inhabiting a range of aquatic habitats (Bell & Foster 1994), making it ideal for a comparative analysis of perceptual and learning processes.

In habitats such as rivers and streams, disturbance of the visual landscape by flow and currents is likely to render local visual landmarks unreliable indicators of location for use in orienting to feeding patches or nests. We predicted that fish from unstable river habitats should rely on visual cues less than fish inhabiting visually stable habitats such as ponds. In support of this prediction, Girvan & Braithwaite (1998) showed that sticklebacks collected from two ponds learned an orientation task faster if landmarks were present than when they were absent, but this trend was not observed in fish collected from two rivers. Although intuitively compelling, it is difficult to rule out the role of alternative variables when only a few populations are compared. Girvan & Braithwaite also suggested that adaptation to differences in water clarity might account for variation in the use of visual cues observed between the two river populations. Our aim here was to clarify this ambiguity and investigate whether the relation between habitat stability and the use of visual cues persists in a comparison of 10 populations.

We tested fish from five fast-flowing rivers and five ponds to reduce the possibility of variables other than stability, such as predation level or water clarity, covarying in a nonrandom manner with pond and river habitats.

Pond and river fish were trained to learn a simple orientation task whereby they had to locate a goal arm in a T-maze, a procedure that has often been used to analyse learning and memory (Olton 1979; Rodriguez et al. 1994). Fish could locate the goal arm either by using an algorithmic behaviour (turn left or right) or by tracking the position of plant landmarks. We used probe trials, in which the cues conflicted, to investigate the types of spatial information used and to assess whether pond and river fish differed in their propensity to use landmarks.

METHODS

Subjects

We collected three-spined sticklebacks from 10 sites in southern and central Scotland, U.K. The rivers were River Kelvin (NS 54 70), River Garry (NN 90 63), River Avon (NS 97 78), River Almond (NS 96 76) and Water of Leith (NT 23 73). These were 4–10 m wide and 0.5–2.5 m deep. All were in spate at the time of sampling. The ponds were Balmaha pond (NS 42 91), Inverleith pond (NT 24 75), Cuilc pond (NN 93 58), Queens Park pond (NS 57 62) and Beecraig pond (NS 99 74). They were 10–100 m in diameter and 0.5–2 m deep. All fish were collected in September 2000 outside their reproductive season, with 3-mm-mesh dip nets and standard minnow traps.

We used 40 fish (four fish from each site). All fish were allowed to acclimate in the laboratory for 4 weeks, on a diet of defrosted frozen bloodworm (chironomid spp.). They were kept in groups of four in holding aquaria (46 × 30 cm and 30 cm high). Each aquarium was furnished with a plastic plant and terracotta refuge. The temperature was maintained at 12°C and overhead lighting was provided by 40-W fluorescent tubes, operating on a 12:12 h light:dark cycle. In the fourth week of the settling period, fish were individually tagged with coloured plastic rings (Girvan & Braithwaite 1998). These rings were dabbed with Superglue before being slipped over the second dorsal spine or the pelvic spine of the fish. Tagging did not affect the health of the fish and did not appear to affect their behaviour. At the end of the experiment, all fish were killed with the anaesthetic MS 222, for use in a morphological analysis.

Apparatus

Two four-arm mazes were constructed from 3-mm green plastic, each arm being 30 cm long, 12 cm wide and 20 cm high (Fig. 1). The mazes were lined with white coral gravel and submerged into aerated and filtered water to a depth of 15 cm within a rectangular pool (1.7 × 1.2 m and 0.3 m high). Grooves, into which a removable screen 15 cm wide and 20 cm high could be slid, enabled any one of the arms to be shut off, producing a T-maze. A trap door (12 × 20 cm) placed 15 cm from

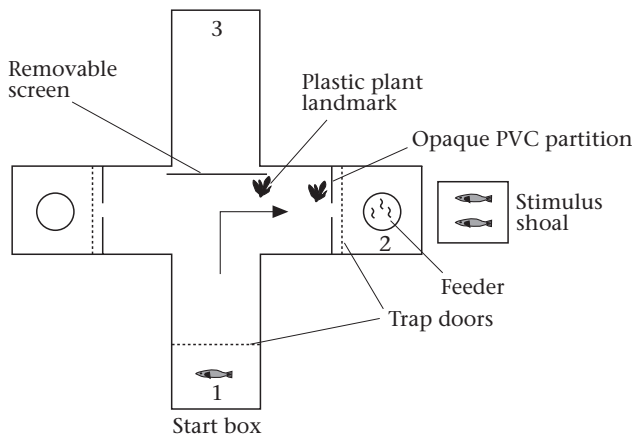


Figure 1. Diagram of the spatial task. The arrow indicates the correct route a right-trained fish had to take to obtain food and shoalmates. Numbers indicate the sequence of start box positions for a run of three consecutive trials starting at position 1.

the central stem of the T-maze was used to close the start box for each trial. This was attached to nylon filament and controlled remotely by a hand-operated pulley system. We provided food rewards by securing bloodworms into Vaseline-filled petri dishes (3 cm in diameter and 1.5 cm deep), which were placed 5 cm from the ends of each arm. The worms were sunk into a cavity in the Vaseline such that the fish were not able to see the food until they were a few centimetres away. Two opaque PVC partitions (12 × 20 cm) were positioned in the maze 15 cm from the ends of each arm. Mid-way and at the bottom of each partition was a small hole (4 cm high and 2 cm wide) through which the fish could swim to reach the end of the arm. Trap doors (12 × 20 cm) held in grooves just behind the PVC partitions could be raised and lowered remotely. If a fish swam into the wrong arm, we could lower the trap door in the opposite arm, preventing the fish from swimming back and reaching the food. We could therefore restrict rewards to fish whose first choice was correct. The end walls of each arm were made of transparent Perspex. A transparent bottle housing two randomly selected, nonexperimental sticklebacks could be placed alongside the Perspex to simulate the presence of a shoal. The shoal was visible to the fish only after it had passed through the hole in the PVC partition, and was designed to reduce stress caused by training sticklebacks in isolation. The fish therefore received a double reward (food and shoalmates) when it reached the goal. Ambiguity as to whether fish responded to the food reward or to the shoalmates does not matter because the experiment investigated how fish learned the route to the rewarded end, regardless of what motivated them. Two plastic plant landmarks were also placed in the maze, one directly next to the hole leading to the food reward and the other in the correct arm just in front of the removable barrier, visible from the exit of the start box (Fig. 1). A Vantage CCD camera with a Computer 2.6-mm wide-angle lens 1 m above the centre of the pool allowed us to view the fish on a black and white monitor next to the pool. Trials could be recorded on a VCR connected to the

monitor. The entire apparatus was surrounded by white curtains to avoid disturbance from the observer and to minimize the availability of global extramaze cues.

Procedure

Pretraining

The purpose of pretraining was to familiarize fish with the apparatus and procedure. During pretraining no landmarks were present and the trap doors were raised, allowing fish free access through both holes in the PVC partitions and to both ends of the T-maze. Petri dishes containing large amounts of bloodworm were placed in both arms of the maze but we did not use the simulated shoal, as fish were not yet in isolation. Both mazes were used simultaneously and fish were pretrained in groups of 10. Each group had five 24-h periods in a maze alternated with 24 h in their home tanks. Ten fish, one from each site, were transferred in a clear plastic cup from their holding tanks to a start box. For each session, the maze and start box were randomly selected with the constraint that no maze or start box was used more than twice in a row. An opaque cover was placed over the start box to minimize disturbance. After 5 min, the door was raised remotely and the fish were given free access to both arms of the T-maze. Feeding took place only in the maze. After five pretraining sessions, the fish swam out of the start box and found food in the ends of the T-maze in less than 1 min. Fish were food deprived for 2 days between pretraining and training, a procedure that has no ill-effects on the fish, which can survive at this temperature without food for several days (Bell & Foster 1994).

Training

Fish were given three trials a day, once every 2 days, and we randomized the order in which the fish were trained for each day. In each trial two petri dishes were placed in the maze, only one of which contained a food reward (three bloodworms). The simulated shoal in the bottle was placed at the end of the rewarded arm. We trained half the fish from each site to turn right and half to turn left to control for any directional bias. The plastic plant landmarks were positioned in the right arm or left arm accordingly. Experiments have shown that neither pond nor river fish can track the rewarded end by responding to olfactory or uncontrolled visual cues within the maze (L. Odling-Smee, unpublished data). Each fish was introduced into a start box and left for 5 min with the opaque cover in position. For each three-trial session, the maze and start box were randomly selected with the constraint that no maze or start box was used more than twice in a row. After 5 min, the door was raised and we recorded the time taken for the fish to leave the start box and to enter an arm, and which arm the fish chose first. We judged arm entry to have occurred when the base of the caudal fin had passed through the hole. Each trial was terminated after the fish had fed, or after 10 min. Fish were left for 3 min after feeding, then if they had left the rewarded end we encouraged them to swim back there. The trap door was then lowered, and the

apparatus manipulated such that the previously rewarded end became the start box for the next trial. In this way, fish rotated around the arms of the maze: anticlockwise (for right-turners) and clockwise (for left-turners). This allowed us to train individuals in blocks of three trials, with minimum handling between trials.

In the first 12 trials, we raised the trap doors in the arms of the T-maze allowing fish access to both ends. For the remainder of the experiment, after the fish entered a hole in the partition at one end, the trap door raised above the entrance to the opposite end was lowered. Fish were then rewarded only on making a correct first choice. The learning criterion was established as nine correct trials out of 10. Fish were trained until they had reached criterion or for a maximum of 45 trials. When the fish reached criterion, we conducted additional postcriterion sessions interspersed by probe trials. A minimum of four correct trials out of a run of five had to be achieved between any two probe trials. We recorded on VCR the final training trial before the first probe trial.

Probe trials

We used probe trials to determine the fish's spatial strategy. During probe trials, food and shoals were placed at both arms of the maze to avoid punishing the fish for selecting one or other of the available cues. In each probe trial, the plant landmarks were repositioned to the opposite side from where they had been during training. For fish trained to turn right, the landmarks were now positioned in the left arm of the maze and vice versa for fish trained to turn left. We allowed fish to enter an arm and feed before we removed them from the maze. We recorded a turn response if, regardless of the position of the landmarks, the fish turned in the same direction as it had done during training. A landmark response was recorded when the fish selected the arm presenting the plastic plant landmarks. All fish received three probe trials interspersed between at least five training trials. All probe trials were recorded on VCR.

VCR Recordings

We scored two behaviours indicating 'hesitancy' or 'confusion' from video recordings of the three probe trials and of the last training trial before the first probe test. A 'pause' was scored if a fish remained stationary for a minimum of 3 s. A 'reversal' was scored if a fish, having swum in one direction, made a 180° turn and swam in the opposite direction. Behaviours were scored immediately after the fish left the start box and before it entered the end of an arm. During video analysis, fish were identified on the monitor from codes, which gave no information as to whether they were pond or river fish.

Statistical Analysis

Where appropriate, data were log transformed to meet required assumptions of homogeneity of variance and normality of residuals. Success of the transformation was confirmed with the Kolmogorov-Smirnov test.

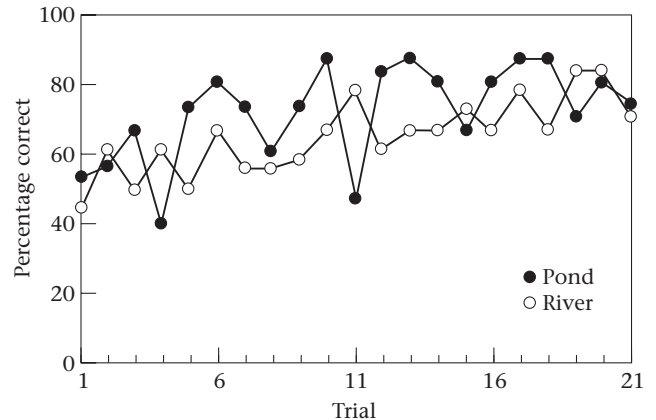


Figure 2. Percentage of correct choices of pond and river fish during the first 21 trials of training.

Parametric tests were used throughout, except for the results of the probe trials, which were analysed with the G test.

RESULTS

There were no significant differences between the counterbalanced right-trained and left-trained conditions within groups in any phase of the experiment (all $P_s > 0.1$); we therefore collapsed these data when calculating the group averages.

Acquisition

Figure 2 shows the percentages of pond and river fish performing the task correctly during the first 21 trials of training. The scores of seven individuals that did not reach criterion in 45 trials were excluded from the analysis. The final sizes of the groups were 15 pond fish and 18 river fish ($N=33$). To compare performance between pond and river fish, we carried out a one-way analysis of variance (ANOVA) with the number of trials taken to reach criterion as the dependent variable. Pond and river fish did not differ significantly in the number of trials they took to reach criterion ($F_{1,31}=0.42$, $P=0.52$; pond: $\bar{X} \pm SE=22.5 \pm 2.94$ trials; river: 25.1 ± 2.59 trials). There were too few fish from each site to look at the effect of population within a full model including habitat type and population as factors. However, a one-way ANOVA on the collapsed data revealed no significant effect of population on the number of trials taken to reach criterion (ANOVA: $F_{9,23}=0.98$, $P=0.5$).

Postcriterion Performance

Throughout the postcriterion trials during which probe trials were interspersed, pond and river fish maintained a high and steady level of accuracy (pond: $\bar{X} \pm SE=85.8 \pm 0.03\%$ correct; river: $94.9 \pm 0.02\%$ correct). However, performance of the pond fish appeared to be significantly more disrupted by the probe trials than that of river fish. A one-way ANOVA with the number of postcriterion

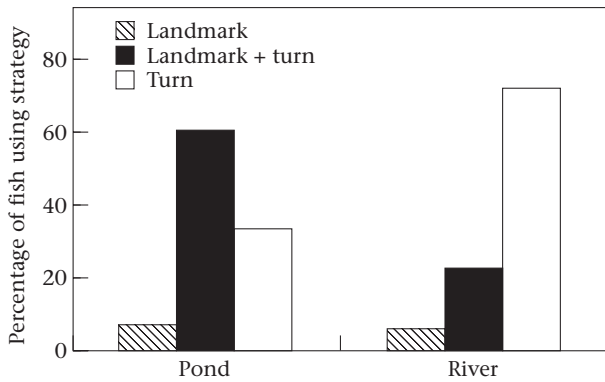


Figure 3. Percentage of pond and river fish using each of three strategies: landmarks across all three probe trials (Landmark), both landmarks and turn (Landmark+Turn) or turn across all three probe trials (Turn).

errors as the dependent variable revealed a significant difference between pond and river fish ($F_{1,31}=6.35$, $P=0.02$), with pond fish making significantly more errors (pond: $\bar{X} \pm SE=1.35 \pm 0.35$ errors; river: 0.57 ± 0.19 errors)

Probe Trials

A G test compared the distribution of fish using three possible strategies (landmarks only, turn only or a combination of landmarks and turn across the three probe trials) to a random expectation assuming no preference for either cue. Pond and river fish appeared to differ in the strategies they used to solve the spatial task (Fig. 3). Although pond fish used turn across all three probe trials (33%) more often than they used landmarks across all three probes (7%), overall, pond fish showed no significant preference for using turn direction over landmarks (G test: $G_2=2.18$, $P>0.20$). Sixty per cent of pond fish used a combination of turn and landmarks across the three probe trials. In contrast, river fish showed a significant preference for using turn direction over landmarks (G test: $G_2=16.46$, $P<0.001$). Seventy-two per cent of river fish consistently used turn across all three probe trials, 22% used turn and landmarks and 6% consistently used landmarks.

Pauses and Reversals

For each fish, we compared the mean number of pauses or reversals made across the three probe trials (probe score) with the number of pauses or reversals made in the final training trial before the probe tests began (criterion score). Pond fish paused significantly more often during the probe trials than at criterion (paired t test: $t_{14}=-3.75$, $P=0.002$; Fig. 4). This difference was not observed in river fish (paired t test: $t_{17}=-0.44$, $P=0.66$). A two-way ANOVA with the probe score as the dependent variable revealed that pond fish paused significantly more often than river fish ($F_{1,30}=12.47$, $P<0.001$). Fish using a mixed strategy (i.e. landmarks and turn) to solve the task did not pause significantly more often than fish using a consistent strategy of either turn only or landmarks only

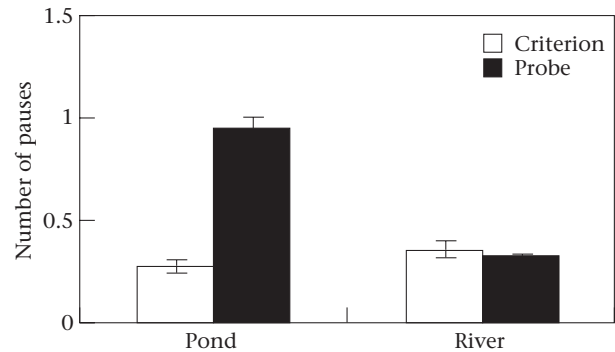


Figure 4. Mean \pm SE number of pauses made by pond and river fish at criterion and during probe trials.

($F_{1,30}=2.49$, $P=0.13$). This suggests that pond fish paused significantly more often than river fish, regardless of which spatial strategy they used.

Neither pond fish nor river fish showed more reversals across probe trials than at criterion (paired t test: pond: $t_{14}=-0.99$, $P=0.34$; river: $t_{17}=-1.54$, $P=0.14$). Pond fish showed no more reversals than river fish during probe trials ($F_{1,30}=0.03$, $P=0.87$). There was no effect of spatial strategy on the number of reversals made during probe trials ($F_{1,30}=0.82$, $P=0.37$).

DISCUSSION

Our results suggest that populations exposed to different environmental conditions differ in the types of information they use to solve a spatial task. Although pond and river fish learned a spatial task at similar rates, several lines of evidence suggest that they used different strategies. First, during probe trials, pond fish showed no significant preference for either cue, and river fish preferentially relied on turn direction. Second, in the training trials after the first probe trial, pond fish made more mistakes than river fish. Disrupting the relation between the cues in the probe trials might be expected to cause confusion if fish paid attention to both types of cue and to the relation between the cues. Differences in swimming behaviour also suggest that pond fish were more disoriented by the repositioning of plant landmarks in the probe trials. Pond fish paused more often during the probe trials than river fish and, unlike river fish, more often during the probe trials than at criterion. These results are consistent with the hypothesis that populations experiencing stable habitats rely more on local landmarks as positional cues than fish living in unstable habitats, where local landmarks are likely to be unreliable.

The differences observed between pond and river fish may be specific to the use of local visual cues and may not extend to the use of all available visual information. River fish may be unable to learn to use local landmarks as goal-directing beacons but they may be capable of locating a goal by referring to a spatial array of visual cues (Hughes & Blight 1999) or by using global cues external to the maze. Experiments have shown that neither pond

nor river fish can track the rewarded end by responding to olfactory or uncontrolled visual cues within the maze (L. Odling-Smee, unpublished data). However, we cannot eliminate the possibility that fish might have been using global features outside the maze. Learning the movements around the arms of the maze might have been aided by tracking global features such as differences in light level or the camera lens. We think this explanation is unlikely for two reasons. First, enclosing the entire apparatus within a uniform white tent-like structure meant that few global cues were available. Other experiments testing spatial learning in fish effectively eliminated the use of extramaze cues by using similar curtains or screens (Warburton 1990; Rodríguez et al. 1994). In addition, both the maze and the start box for each three-trial session was randomized such that the fish were presented with a different array of global cues each day. However, large-scale features of rivers, such as overhanging trees or the spatial arrangement of a river bend, may present a stable and reliable source of visual information which can be effectively used in orientation. Experiments are needed to test whether the differences observed between pond and river fish in their use of local visual cues extend to their use of spatial arrays of landmarks and extramaze global cues.

By including 10 populations in this analysis, we aimed to reduce the possibility that an ecological factor other than habitat stability could covary in a consistent way with the pond–river dichotomy. We selected a river and pond site from each geographical area within a 10-mile radius, to remove geographical location as a confounding variable. Three of the five ponds were highly eutrophic or sediment rich, with visibility being considerably less in these ponds than in any of the five rivers. It is therefore unlikely that differences in water clarity could explain why pond fish use local visual cues more than river fish. Limited evidence suggests that exposure to different levels of predation can influence the use of visual cues in the three-spined stickleback (Huntingford & Wright 1989). We cannot speculate on this possibility since the predation risk associated with each of the 10 sites is not known.

So far, habitat stability remains the most compelling ecological factor that can account for differences in the use of local visual cues by pond and river fish. In turbulent and fast-flowing rivers, local features within microhabitats are likely to be subject to continual change. Equally likely are displacements of the fish themselves to new locations within the river system and to unfamiliar arrays of local landmarks. Learning to orient back to feeding or nest sites could prove costly if fish extract information from unreliable sources such as moving or unfamiliar landmarks. In addition to making more mistakes, fish using landmarks in unstable habitats may waste exploration time if there is a delay between a change in the environment and a shift in behavioural response. For example, in goldfish, *Carassius auratus*, previously relevant landmarks have been shown to inhibit attentional shifts to new patch-related stimuli after a change in the spatial relation between food and landmarks (Warburton 1990).

Differences in the use of landmarks by pond and river fish may be genetic, the result of differential experience, or both. Human-mediated movements of stickleback populations combined with the close proximity of sites (<40 miles apart) make genetic isolation unlikely, although stickleback populations have been found to be genetically divergent among lakes and rivers separated by similar distances (Reusch et al. 2001). Therefore, river fish might have been selected to use mechanisms other than visual cues for orienting. Alternatively, cue preference may be flexible with fish learning to respond differently to landmarks in different habitat conditions. Within rivers, habitat stability may vary between microhabitats with certain regions cut off from the main channel remaining relatively stable. Equally likely is seasonal variation in stability, with turbulence and flow rate being considerably reduced in dry summer months. It may therefore pay fish to update continually their assessment of cue reliability. If cue preference is itself flexible and learned, we might predict population differences to disappear soon after the fish are placed in a stable laboratory environment. However, our subjects had been housed in tanks containing rocks and plants in fixed positions for 2–3 months by the time they were tested in the probe trials. Despite this, the possibility remains that the differences we observed between pond and river fish were less than those we would have observed had we tested them immediately on bringing them into the laboratory. A further possibility is that cue preference is fixed during a restricted plastic period in development. Early experience of a more stable habitat may result in greater reliance on visual landmarks later in life.

Equally open to speculation is whether genetic or environmental influences, or both, act directly on the ability to learn and remember or on associated sensory input systems. River fish may differ from pond fish in their ability to perceive visual landmarks or to learn associations based on this type of information. If learning and memory processes are involved, populations may differ in the storage or retrieval of memory, or both, or by a difference in the way they respond to their memories. Based on the current data, we cannot differentiate between these possibilities.

In conclusion, local visual landmarks may provide reliable indicators of location for three-spined sticklebacks inhabiting ponds but not rivers. River fish appear largely to ignore landmark information when learning an orientation task. Potential costs of learning, such as the cost of making mistakes, may be significantly reduced by genetic or developmental programs that guide perceptual and learning processes even at the population level. Understanding how animals maximize the benefits of being behaviourally plastic while minimizing the potential costs will demand a closer look at the interplay between learning, genetics and development.

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