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Habitat stability and predation pressure influence learning and memory in populations of three-spined sticklebacks

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Learning and memory enable animals to adjust their behaviour in variable environments. Not all habitats vary to the same extent, and thus different environments can affect learning and memory in different ways. Habitat stability is one of numerous environmental variables proposed to influence what animals learn, but it is unlikely to act alone. To investigate how multiple variables affect learning and memory behaviour, we compared spatial learning and memory in three-spined sticklebacks from four ponds (stable habitat) and four rivers (unstable habitat) of varying predation pressure. Contrary to initial predictions, river fish had longer memory duration (>1 week) than pond fish (<1 week). Learning rate was affected by an interaction between habitat stability and predation pressure, with low-predation river populations learning faster than high-predation river populations. These results show that learning and memory can be affected in different ways by contrasting ecological factors and that multiple ecological factors can interact to shape learning and memory, thus emphasizing the importance of considering multiple ecological variables when investigating behaviour.

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Learning and memory allow animals to adjust their behaviour to adapt to changeable environments and thus cope with a degree of unpredictability (Shettleworth 1998). In such environments, animals that use learning and memory to hone their behaviour will have advantages over other more behaviourally fixed individuals. For example, parasitoid wasps that select host substrate based on experience can parasitize a larger number of host eggs and produce more offspring than those forced to select at random (Dukas & Duan 2000). However, in environments where there is little or no change we find that animals sometimes show reduced or even no learning and memory skills (Potting et al. 1997). This suggests that there are costs associated with learning and memory; for example, it is speculated that there is a physical cost to producing and maintaining the required neurological machinery and there is the cost of making mistakes (e.g. Dukas 1999; Laughlin 2001). There are numerous theoretical models that consider the costs and benefits of learning

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and memory (e.g. Papaj & Prokopy 1989; Dukas 1999). Several of these models predict circumstances under which the benefits of learning and memory are greater than the costs and a key factor affecting this appears to be the degree of environmental variability (e.g. Stephens 1991; Kerr & Feldman 2003). Surprisingly, there are only a few direct demonstrations of the costs associated with learning. In Drosophila melanogaster, populations selectively bred for enhanced learning ability had decreased productivity and the competitive ability of larvae was reduced (Mery & Kawecki 2003, 2004).

Environments inhabited by different populations are likely to differ from one another in many aspects. As such, we might expect learning and memory processes to be fine tuned within a population to suit specific environmental requirements that the animals encounter. A few avian studies have investigated this, both between and within species (e.g. Brodin 2005; Sherry 2006). For example, Pravosudov & Clayton (2002) found that a population of blackcapped chickadees inhabiting a less favourable habitat had a better learning and memory capacity for cache storage and recovery and a larger hippocampus (a structure known to be important in spatial memory) than a conspecific population living in a more favourable environment. This

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suggests that the benefits outweigh the costs of investing in enhanced learning and memory ability in the harsher terrain. Learning behaviour in fish also appears to be fine tuned to the local environment. Populations of the tropical poeciliid Brachyraphis episcopi originating from lowpredation sites solved a spatial task almost twice as fast as those from high-predation locations (Brown & Braithwaite 2004). Similarly, pond and river three-spined sticklebacks pay attention to different cues when learning the location of a food reward in a maze: pond fish prefer to use visual landmarks, whereas river fish prefer to use the turn direction of their own body (Girvan & Braithwaite 1998; Braithwaite & Girvan 2003). The stability of a landmark is known to affect its use as a spatial cue; the more unreliable the landmark, the less likely an animal will use it as a guide to a goal (Biegler & Morris 1996). Ponds are thought to be more spatially stable environments; rivers, however, are subject to flow and flooding, so cues that might be used as landmarks in a pond will be less reliable in a river.

Although numerous studies have investigated learning, less attention has been directed at memory. Learning and memory are linked; there is little point to learning if the information cannot be recalled and remembered. However, the processes are distinct, and there are differences between them. Learning is essentially the acquisition of memory, whereas memory has other composites, such as retention and the potential for interference. Research directed at quantifying memory duration, how rates of forgetting progress or what factors cause variation in forgetting rates is far less common than studies investigating the acquisition of information (Shettleworth 1998).

Traditionally, forgetting was considered a failing of memory, but over the past two decades we have moved towards the idea that the ability to forget may be advantageous (Kraemer & Golding 1997). For example, forgetting the locations of previously rich but now poor feeding sites will benefit individuals. As such, forgetting is increasingly considered an adaptive trait rather than a flaw associated with failed memory processes (Kraemer & Golding 1997). For example, foraging nine-spined sticklebacks, Pungitius pungitius, use recently acquired private information about food patch profitability when choosing where to feed, but their tendency to use this information decreases over time and instead they begin to rely more on what other fish are doing, so-called public information (van Bergen et al. 2004). This may demonstrate flexible memory use depending on the perceived reliability of available information and shows how forgetting can be adaptive in certain circumstances. However, an alternative explanation for this observation is that after 7 days a fish may have forgotten its own experience and so must rely on publicly acquired information.

To explain population differences in behaviour, typically only one ecological variable is considered at a time. However, habitats are likely to differ in many aspects, and variables may interact when shaping behaviour. Hence, studying them in isolation can be misleading. To date, few studies have investigated the influence of multiple ecological variables on learning and memory and how these variables might interact. Thus, we investigated how learning and memory varies across a range of different conspecific populations and examined how these processes are affected by two environmental variables already found to affect learning behaviour: habitat stability (threespined sticklebacks: Braithwaite & Girvan 1998; Odling-Smee & Braithwaite 2003) and predation pressure (*B. episcopi*: Brown & Braithwaite 2004). We used a simple spatial task to investigate individual learning and memory ability in annual populations of pond and river fish sampled from sites with different levels of predation pressure. We hypothesized that fish from less spatially stable river habitats would update their foraging information sooner and hence be less likely to return to a previously rewarded patch than pond fish. We also hypothesized that fish from low-predation sites would learn the task faster than fish from high-predation sites.

METHODS

Subjects and Housing

Three-spined sticklebacks were collected from four ponds and four rivers in central and southern Scotland, U.K. (ponds: Beecraig Pond (3°47'W, 55°57'N), Craiglockhart Pond (3°14'W, 55°55'N), North Belton Pond (2°35'W, 55°59'N) and Balmaha Pond (4°31.5'W, 56°05'N); rivers: Water of Leith (3°14'W, 55°57'N), River Biel (2°35'W, 55°59'N), River Endrick (4°24'W, 56°02'N) and River Esk (3°10′W, 55°51′N)). A 1-year survey of these sites revealed that they did not differ significantly in many factors that may be expected to influence the potential value of visual stimuli, for example turbidity and vegetation structure. Coupled with the results of Odling-Smee & Braithwaite (2003) who found differences in spatial learning in pond and river three-spined sticklebacks, we believe that this provides good evidence that ponds are more spatially stable habitats than rivers. Fish were collected in November 2004 and 2005 with minnow traps and large nets. We found similar densities of fish in traps in all habitats, indicating similar school sizes. A total of 66 fish were tested (10 from River Biel and eight from each of the other seven sites). Populations were housed separately in holding tanks (76 cm $long \times 30$ cm wide $\times 38$ cm high) furnished with plastic plants, gravel substrate, biofilters and refuges and fed on a diet of frozen bloodworm. Laboratory temperature was maintained on a day:night cycle at 14:9.5°C and a light:dark cycle of 10:14 h for the duration of the experiment. Fish were collected outside of their breeding season and, as males and females are morphologically identical at this time, populations were assumed to be mixed sex. Outside of the breeding season male and female sticklebacks do not differ in their behaviour (Bell & Foster 1994). All populations were of a similar mean body length (ANOVA: $F_{7.57} = 1.4$, P = 0.2, mean \pm SE = 3.7 \pm 0.6 cm).

Quantifying Predation Pressure

Field observations

Field observations of predation pressure were made in the summer of 2006. A 50-m stretch of each river or the entirety of each pond was electrofished. All captured fish were allowed to recover fully in buckets before being replaced, and no adverse effects were observed on the resident wildlife. The number, relative size and species of captured piscivorous fish were recorded.

Morphometric measurements

We used 52 preserved and 79 fresh-caught specimens (immediately euthanized in MS222) to compare the morphology of fish from the eight populations. The data from preserved and fresh-caught specimens were compared to ensure that the preservation process had not affected morphology (there was no effect, see Results).

Measurements and analysis of defensive armour traits based on Vamosi & Schluter (2004) comprised eight external traits measured on the left side of each fish: body length, body depth, gape width, first and second dorsal spine length, pelvic spine length, pelvic girdle length and lateral plate number. The first three traits were used to correct for body size. To count plate number, fish were stained with alazarin dye using the following protocol: fish were transferred from 70% ethanol into 50% ethanol, 3.5% NaCl for 24 h. They were then moved into 25% ethanol, 3.5% NaCl for a further 24 h and then into 100% ethanol, 3.5% NaCl for 24 h. Finally, fish were placed into alazarin solution (0.04 g/litre) for 24 h. They were then transferred into 100% ethanol, 3.5% NaCl solution to rinse off excess dye for 24 h. They were then placed directly into 70% ethanol and stored until needed.

Learning and Memory Assay

During the experiment, fish were individually housed in tanks measuring 35 cm long \times 20 cm wide \times 24.5 cm high with a water depth of 15 cm, 1 cm of gravel substrate, and an individual biofilter. Housing fish individually in this way eliminates the need for transport between trials, which the fish find stressful (N. M. Brydges, P. Boulcott & V. A. Braithwaite, unpublished data). Tanks were placed next to one another in a row, so, although they were physically separated, fish had visual contact with neighbours to reduce isolation stress in this naturally shoaling species. Tanks were divided into a home chamber and two 'foraging patches' using plastic dividers (see Fig. 1). The patches were accessible at all times (except when a patch was being baited) via doors cut into the dividing wall (measuring 4.5 cm high \times 2.5 cm wide). Each door was surrounded by coloured white or yellow polyvinyl chloride to provide a conspicuous visual cue for each patch. Half of each population had a yellow door on the left and a white door on the right and vice versa for the other half. This controlled for the possibility that associations may be more readily formed with certain colours. A small, weighted plastic cup (3 cm diameter) filled with Vaseline was placed in each foraging patch.

During a trial, between-tank plastic partitions were placed down both sides of the tank so that a fish could not watch and learn the task from its neighbour. At the start of a trial, a plastic barrier was also placed in front of the doors and the plastic cups were removed from both



Figure 1. Schematic view of a tank used to house fish individually during the experiments.

patches to ensure that fish were not following which compartment the feeder was placed into but were using spatial memory to locate the food rewards. Three bloodworms were placed into one of these plastic cups. Sticklebacks cannot locate these worms by smell (Girvan & Braithwaite 1998), and the development of the olfactory epithelium compared to the development of the retina suggests that they are predominantly visual predators (Honkanen & Ekstrom 1992). Furthermore, filters in the tanks and regular cleaning prevented the build-up of any potential olfactory cues in rewarded compartments. Cups were then placed back into the compartments, with the left cup always followed by the right, and a curtain was placed in front of the tank to ensure minimum disturbance to the fish during a trial. Fish were given 2 min to settle and then the barrier was gently removed remotely via a piece of string looped over a plastic rod suspended above the tank. Fish were observed over the top of the tank, with the observer standing 1 m away from the tank and remaining motionless. Pilot trials showed that fish did not alter their behaviour in response to the presence of an observer if the observer remained perfectly still during the observations. The door entered first (right or left) and the latency to move into the food patch and begin feeding were recorded. If this was an incorrect choice the fish was observed until either it entered the correct side or 15 min had elapsed. The experiment was divided into three phases.

Phase one: acquisition

Fish were given two trials a day, with the food in the same patch each time, until they selected the correct patch first in 9/10 trials, indicating they had learned the task, or until 45 trials had elapsed, at which point it was assumed the fish was incapable of learning the task.

Phase two: acquisition

When criterion performance was reached in phase one, fish were fed in the opposite patch until they reached the same criterion level of 9/10 correct choices.

Phase three: return to previously rewarded patch

During this phase, the plastic dividers that created the foraging patches were removed from the tank. Half of

each population was left for 7 days, the other half was left for 21 days. Fish were fed six bloodworms a day via a pipette at the front centre of their tanks for the duration of this phase. After the appropriate interval the apparatus was reinserted into the tank, and a trial was performed to determine whether the fish returned to the last rewarded side (phase two rewarded side).

As a maximum of 18 fish could be tested at any one time, experiments were conducted in four blocks, using two fish from each population per replicate, except in the second replicate where four fish were used from River Biel. All fish were humanely euthanized using overanaesthesia with MS222 at the end of the experiment. To minimize spreading infections between fish we do not release fish back into the wild after they have been maintained in the laboratory.

Data Analysis

Predation pressure

A principal components analysis (PCA) was run on body size traits to obtain a single 'body size' variable (PC1). All traits contributed equally and significantly to PC1: body length (component coefficient = 0.62), body depth (0.59) and gape width (0.51). PC1 accounted for 78% of the variance among individuals. To correct for body size variation among individuals, each armour trait was then regressed against PC1 for all individuals from all populations. The remaining variation (residuals) was saved for each trait. Number of plates was uncorrelated with size and thus was not adjusted.

A PCA was then performed on the regressed values for first and second dorsal spine length, pelvic spine length and pelvic girdle length to give an overall 'armour' variable. This resulted in a clustering of fish with long spines and pelvic girdles at one end and fish with short spines and pelvic girdles at the other. PC1 accounted for 64% of the variation in the data. Length of the first dorsal spine had the highest loading coefficient (0.58), followed by the pelvic spine (0.57), the second dorsal spine (0.56) and finally the pelvic girdle (0.16). PC1 (overall armour variable) was analysed using an analysis of variance (ANOVA), with old versus new samples and population as factors. Nonsignificant terms were removed to leave the minimal model.

As plate number data were not normally distributed, and could not be transformed to normality, a Kruskal– Wallis test was used to analyse the effect of population on plate number.

Populations were also categorized as high or low predation based on the field data. All three categories (spine measurements, plate number and field data) were considered when devising the final predation category for each population.

Learning and memory assay

One fish from North Belton was excluded from the analysis as it did not reach the criterion level of performance even after 45 trials. The number of trials taken to reach criteria in phases one and two (Box–Cox transformed) were analysed using two-way ANOVA. Maximal models, including habitat type (river or pond), predation pressure, habitat type*predation pressure interaction, length, replicate and tank number as explanatory variables, were initially used. Nonsignificant terms were removed to create minimal models. χ^2 tests were used to determine whether pond and river fish and high- and low-predation fish could remember the task after 7 and 21 days.

RESULTS

Quantifying Predation Pressure

There was no effect of old versus new samples $(F_{1,116} = 0.0006, P = 0.98)$ on PC1 (overall armour variable), so this term was removed from the model. There was a significant main effect of population on PC1 (overall armour variable; ANOVA: $F_{7,124} = 6.1$, P < 0.0001). A post hoc Tukey test revealed that fish from River Esk, Water of Leith, Craiglockhart Pond and River Biel had significantly more armour than fish from North Belton Pond, River Endrick and Balmaha Pond. Consequently, River Esk, Water of Leith, Craiglockhart Pond and River Biel were classified as high predation, and North Belton Pond, River Endrick and Balmaha Pond were classified as low predation. Beecraig Pond was in the middle of the predation level characterization but had a negative score that was closer to the low-predation sites and thus was classified as low predation (see Table 1).

There was a significant effect of population on plate number (Kruskal–Wallis test: $H_7 = 24.4$, P = 0.001). A post hoc comparison of means (Games–Howell; Zar 1996) revealed that North Belton Pond fish were significantly more plated than all other fish populations except for River Biel fish and these fish were significantly more plated than Craiglockhart Pond and Balmaha Pond fish. There were no differences between any of the other fish populations. Thus, North Belton Pond and River Biel fish were classified as high predation, and all other sites were classified as low predation. When North Belton and River Biel fish were removed from the analysis, there appeared to be a significant effect of population on plate number (Kruskal–Wallis test: $H_7 = 16.4$, P = 0.006), but

Table 1. Categorization of field sites as either high (H) or low (L) predation in three predation categories and the overall category

Site	Morphometric data (PCA)	Plate number	Field data	Overall
Beecraig Pond	L	L	н	L
Craiglockhart	Н	L	Н	Н
Pond				
North Belton Pond	L	н	L	L
Balmaha Pond	L	L	L	L
Water of Leith	Н	L	Н	Н
River Biel	Н	Н	Н	Н
River Endrick	L	L	L	L
River Esk	Н	L	L	L

PCA: principal components analysis.

controlling for multiple comparisons (Games–Howell post hoc test) revealed that there were no significant differences in plate number in the remaining populations.

Based on field observations, River Esk, River Endrick, North Belton Pond and Balmaha Pond were classified as low predation because few small piscivores were caught at these sites. Beecraig Pond, Water of Leith, Craiglockhart Pond and River Biel were classified as high predation because many large piscivores were caught at these sites (Table 2).

Taking the average of all three predation categories therefore classified River Esk, Beecraigs Pond, North Belton Pond, River Endrick and Balmaha Pond as lowpredation sites and Water of Leith, Craiglockhart Pond and River Biel as high-predation sites (Table 1).

Learning and Memory

Phase one: acquisition

Length, replicate and tank number had no effect on number of trials to learn phase one and so were removed to leave the minimal model. There was no effect of habitat type ($F_{1,61} = 0.6$, P = 0.43), but there was an almost significant effect of predation pressure ($F_{1,61} = 3.6$, P = 0.06) and a significant interaction between habitat type and predation pressure on the number of trials to learn phase one (ANOVA: $F_{1,61} = 6.7$, P = 0.01). A post hoc Tukey test revealed that this interaction occurred because low-predation river fish learned significantly faster than high-predation river fish (Fig. 2a).

Phase two: acquisition

There was no effect of length ($F_{1,59} = 0.09$, P = 0.76), replicate ($F_{1,59} = 0.63$, P = 0.43), habitat type ($F_{1,59} = 0.48$, P = 0.49) or predation pressure ($F_{1,59} = 0.18$, P = 0.7) on the number of trials taken to learn phase two. However, the interaction between habitat type and predation pressure showed a trend in the same direction as learning in phase one, but this was not significant ($F_{1,59} = 3.2$, P = 0.08; Fig. 2b).

Phase three: return to previously rewarded patch

The ability of pond versus river and high-predation versus low-predation fish to return to the food patch that

Table 2. Type of predators cauging at each sig	Table 2.	Type of	predators	caught at	each site
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Site	Predator species	High/low predation
Beecraig Pond	Trout, perch	High
Craiglockhart Pond	Perch	High
North Belton Pond	None	Low
Balmaha Pond	None	Low
Water of Leith	Large trout, eels, bullhead, Lamprey, rainbow trout, salmon, sea trout, stone loach	High
River Biel	Large brown trout, eels	High
River Endrick	Small trout	Low
River Esk	Small trout	Low



Figure 2. Mean number of trials to reach criterion performance (correct patch selection in 9/10 trials) in pond and river fish from habitats of differing predation pressure in (a) phase one and (b) phase two. Bars connected by an asterisk are significantly different from one another (P < 0.05). Error bars represent 1 SE.

had most recently been rewarded in their last training phase was compared after 7 and 21 days. After 7 days, river $(\chi^2_{1.16} = 13.2, P < 0.01)$ but not pond $(\chi^2_{1.15} = 2.25,$ P > 0.05) fish performed significantly above chance levels, indicating that river fish remembered the task (Fig. 3a). Additionally, although not significant, there was a tendency for river fish to perform better than pond fish after 7 days (Contingency table analysis: $\chi^2 = 3.57$, P = 0.059). After 21 days, neither river ($\chi^2_{1,16} = 0.53$, P > 0.05) nor pond ($\chi^2_{1,14} = 0.5$, P > 0.05) fish performed above chance levels (Fig. 3b). This indicates that river fish have a memory for this task that lasts at least 7 but not longer than 21 days, whereas pond fish have a memory of less than 7 but at least 1 day as they remembered the task from day to day during the acquisition phase. After 7 days, high-predation $(\chi^2_{1.14} = 5.4, P < 0.05)$ and low-predation $(\chi^2_{1.18} = 4.3, P < 0.05)$ P < 0.05) fish performed significantly above chance levels, indicating that they remembered the task (Fig. 3c). After 21 days, neither high-predation ($\chi^2_{1,12} = 0.04$, P > 0.05) nor low-predation ($\chi^2_{1,19} = 3.2$, P > 0.05) fish performed



Figure 3. Proportion of pond and river fish returning to the last rewarded patch after (a) 7 days and (b) 21 days and proportion of high- and low-predation fish returning to the last rewarded patch after (c) 7 days and (d) 21 days.

above chance levels (Fig. 3d). This indicates that both high- and low-predation fish could remember the task after 7 days but neither could remember after 21 days, showing that predation pressure does not influence memory retention of this foraging task.

DISCUSSION

Memory Retention

River three-spined sticklebacks were less likely to update their foraging information than ponds fish. River fish returned to a previously rewarded foraging patch after 7 days but did not show a preference to return to it after 21 days. This result suggests that fish originating from habitats of contrasting spatial stability differ in the way they update their long-term memory. Surprisingly, pond fish showed no tendency to return to the foraging patch after only 7 days of the memory retention test. Contrary to our original habitat stability hypothesis, which predicted that fish originating from more spatially stable pond environments would be less likely to update their memory and hence have a longer memory duration than those from less stable rivers, we found the reverse to be true.

This differs from the results obtained by Mackney & Hughes (1995), who found that sticklebacks originating from more temporally stable habitats with respect to prey availability had a longer memory duration for prey handling skills than fish from more changeable environments. In a more temporally stable habitat, longer memory duration for particular prey handling would be advantageous. Fish from more variable (spatially and environmentally changeable) marine environments are likely to encounter a greater diversity of prey over time and so

are likely to have a less predictable diet, favouring shorter memory duration and an ability to learn how to exploit the prey type that is most locally available. Our results indicate that spatial memory duration is affected in a different way to that of memory for prey handling.

Memory is thought to be divided into discrete systems or cognitive modules, each with separate underlying neurology and physiology (e.g. Klein et al. 2002; Squire 2004). Different memory systems may be adapted in different ways to the environment and have different rules of operation (Sherry & Schacter 1987; Shettleworth 1998). Hence, the factors that shape memory for prey handling skills may not be the same as those that shape memory for spatial locations. Compared to Mackney & Hughes (1995), our data would seem to support this hypothesis.

In terms of spatial memory, some factor other than spatial stability may be driving differences between river and pond fish populations. In a river habitat, fish have a greater chance of being relocated to new areas due either to the flow of the river or to exploration. In this situation, having a good and extensive spatial memory will be beneficial because it will allow fish to relocate shelter or feeding sites rapidly if they return to areas visited in the recent past. However, for pond fish living in a more enclosed environment, the same spatial memory capacity may not be as important; if food is plentiful then it may not be necessary for fish to remember the positions of specific food patches.

Learning Phases

In contrast to memory retention, there were no clear pond/river differences in the ability of fish to learn phases one and two of the spatial foraging task. This corroborates earlier observations of spatial learning in pond and river sticklebacks (Odling-Smee & Braithwaite 2003). However, adding predation pressure into the model reveals that learning was affected by an interaction between habitat type and predation pressure. Low-predation river fish learned phase one significantly faster than high-predation river fish, but this was not seen within pond populations. There is a similar nonsignificant trend apparent for learning in phase two. This result mirrors observations in tropical rivers where predation pressure varies between different populations of *B. episcopi* and where populations from low-predation sites learned a spatial foraging task almost twice as fast as those from high-predation sites (Brown & Braithwaite 2004).

A potential explanation for these observed differences in learning rate is divided attention. Animals continually receive information about their environment and must filter this information to focus on those aspects most important to survival (Dukas 2002). The ability of an animal to successfully perform a given task can be affected by the amount of attention simultaneously being focused on other activities (see Dukas 2002 for a review on limited attention). For example, guppies engaged in more complex foraging tasks are more vulnerable to predation and are preferred targets for predators (Krause & Godin 1995), presumably because their attention is divided between foraging and predator vigilance. Similarly, fish selectively bred to have a lateralized brain had a foraging advantage over nonlateralized fish when a predator was present, which was attributed to lateralized fish being better able to process multiple sources of information, processing each task with one brain hemisphere (Dadda & Bisazza 2006).

In our system, high-predation river fish have several activities to divide their attention: they must be vigilant for predators and monitor their spatial location to avoid becoming moved to unfavourable areas by water currents or exploration. This leaves less attention for locating profitable feeding sites and may explain why high-predation river sticklebacks take longer to learn the spatial foraging task presented here. It can also partly explain why the trend is nonsignificant by phase two: having been in the maze for several days they may have learned that it is a safe, predator-free environment. Fish are also more familiar with the task by phase two, which may increase their learning rate. Low-predation river fish do not have to expend the same amount of attention on predator detection, enabling them to devote more attention to other tasks, such as locating feeding sites, translating to faster learning rate in the present experiment. In contrast to this, in pond environments, fish do not have so many tasks to divide their attention. They will not be relocated to unfavourable areas by current or exploration, and they have stable local landmark cues to aid navigation. Thus, high-predation pond fish do not learn more slowly than low-predation pond fish because they do not have so many variables to monitor, allowing them to learn this relatively simple spatial task at equal rates.

In conclusion, the learning and memory ability of three-spined sticklebacks differs between populations. It appears that differences in habitat stability create differences in long-term memory in pond and river fish populations, whereas an interaction between habitat stability and predation pressure influences learning rate. This shows that, although they are linked, learning and memory are distinct and are not necessarily shaped in the same way by the same ecological factors. It also highlights the complex nature of natural habitats and shows how multiple ecological factors can interact to fine tune behaviour.

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