



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

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 black-capped 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 low-predation 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 components, 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

conspicuous populations and examined how these processes are affected by two environmental variables already found to affect learning behaviour: habitat stability (three-spined 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 × 30 cm wide × 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 ± SE = 3.7 ± 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

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