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Learning in fishes: from three-second memory to culture

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Learning plays a pivotal role in the behavioural development of all vertebrates, and fish are no exception. This collection of essays on learning in fishes is timely for at least two reasons. First, it is now over 10 years since the last substantive survey of the role of learning in fish behaviour (Kieffer and Colgan 1992) had been conducted, and the intervening period has witnessed a relative explosion of interest in this topic. James Kieffer and Patrick Colgan, in writing their comprehensive review, were able to draw on some 70 published papers on fish learning, a substantive advance on earlier reviews by Thorpe (1963) and Gleitman and Rozin (1971). In comparison, the articles in this special edition collectively refer to well over 500 such papers, the majority of them being published in the last few years. Both the sheer number of articles and the breadth of the research addressed leaves summarising what is now known about learning in fishes beyond the scope of a single paper, and a challenge that would tax all but the most wide-ranging of authors. Whether it be a concern with the genetic, neural, physiological, psychological, behavioural, ecological or evolutionary aspects of learning, researchers from a broad range of disciplines are, at long last, giving due recognition to the fact that learning plays a critical role in the development of fish behaviour.

Secondly, this escalation in interest coincides with a 'sea change' in conceptions of the psychological and cognitive abilities of fishes. Gone (or at least obsolete) is the image of fish as drudging and dim-witted pea brains, driven largely by 'instinct', with what little behavioural flexibility they possess being severely hampered by an infamous 'three-second memory'. Now, fish are regarded as steeped in social intelligence, pursuing Machiavellian strategies of manipulation, punishment and reconciliation (Bshary and Wurth 2001; Bshary *et al.* 2002), exhibiting stable cultural traditions (Helfman and Schultz 1984; Warner 1988, 1990) and co-operating to inspect predators and catch food (Milinski *et al.* 1990a,b; Dugatkin 1997). Fish not only recognise individual shoal mates, but they monitor the social prestige of others and track the relationships of the third-parties (McGregor 1993; Bshary *et al.* 2002; Griffiths 2003). They also use tools (Bshary *et al.* 2002), build complex nests and bowers (Paxton and Eschmeyer 1998) and can even exhibit impressive long-term memories (Brown 2001; Warburton 2003). Although it may seem extraordinary to those comfortably used to prejudging animal intelligence on the basis of brain volume, in some cognitive domains, fishes can even be favourably compared to nonhuman primates (Bshary *et al.* 2002; Laland and Hoppitt 2003). Also, apparent is the considerable variability in fish behaviour, both across the 27 000 known species and among the geographical variants of the same species (Magurran *et al.* 1995; Girvan and Braithwaite 1998; Odling-Smee and Braithwaite 2003). There are more fish species than all other vertebrates combined; they are the most ancient of the major extant vertebrate groups, and they exploit virtually every conceivable aquatic environment. There has been ample time for fish to evolve complex, plastic and diverse behaviour patterns that rival that of other vertebrates. These developments warrant a reappraisal of the behavioural flexibility of fishes, and highlight the need for a deeper understanding of the learning processes that underpin the newly recognised behavioural and social sophistication of this taxon.

In addition to this introduction, the special edition contains eight articles on different aspects of fish learning. The first, authored by Kevin Warburton, describes a number of experimental findings, from both psychological and behavioural ecology perspectives, which suggest that learning and memory play important roles in the foraging activities of fish. Warburton argues that, in terms of the basic learning mechanisms, 'the similarities across animal taxa are more striking than the differences' and, like other vertebrates, fishes use several distinct learning and memory systems as part of their foraging repertoire. Learning and associated improvements in prey search, capture and handling efficiency can lead to significant enhancements in fish foraging performance, frequently only after a few exposures. Warburton also describes how fish species vary in how long they remember foraging information, and that forgetting may, in some circumstances, be adaptive. The length of the memory window appears to be related to patterns of environmental variability. Warburton also details the use of fish in experiments that test the predictions of foraging theory. Fish can match exploitation rates to patch profitabilities, drawing on memories for general patch quality and on departure rules for leaving the current patch.

It has commonly been assumed that antipredator behaviour is less dependent on learning than many other aspects of fish behaviour because, as Kelley and Magurran point out in their article, the penalty for failure to recognise and avoid predators is death. Natural selection is expected to have fashioned appropriate unlearned responses among fishes commonly exposed to predators. However, Kelley and Magurran describe a growing body of experimental evidence, indicating that learning plays an important part in the development of antipredator behaviour in many species. Learning allows fish to make adaptive adjustments to their antipredator repertoire, building on unlearned predispositions to fine-tune their responses to local conditions. Kelley and Magurran stress that to prevent predation, an individual must be able to detect, recognise and assess predators, as well as avoid attack, and they provide evidence for learning being employed in each case, across an array of species. They also describe how early experience, such as exposure to predators or being chased by parents as fry, can facilitate the development of antipredator skills and highlight subtle interactions between the intensity of selection as a result of predation at different sites and the degree of enhancement in performance through experience.

Kelley and Magurran's article is complemented by Grant Brown's paper, summarising how fishes use chemical alarm cues to learn about danger. Brown describes how a diverse range of prey fishes are known to utilise such chemical cues, which, when detected by conspecifics and some heterospecifics, elicit a variety of overt and covert responses. Many fishes do not show recognition of potential predators without appropriate experience, but commonly acquire this knowledge through the learned association of alarm cues emitted by other fishes with the visual or chemical cues of the predator. Such cues also allow some fishes to identify risky habitats. Brown also details how fishes use chemical cues to acquire information during predator inspection, for instance, the presence of alarm cues in the faeces of predators can label the predator as dangerous. Moreover, taxonomically distant species that share common habitats and predation threats have been found to learn to respond to each other's alarm cues with appropriate antipredator responses.

In the next article, Lucy Odling-Smee and Victoria Braithwaite point out that for many species of fish, biologically important locations and resources are widely separated in space. Food is often distributed among distant sites that vary in profitability. Other regions of the environment may be associated with predators or receptive mates, while some fish return to their natal area for reproduction. Orientation thus represents a fundamental challenge for many fishes. Odling-Smee and Braithwaite suggest that, on the basis of experience, the capacity to learn in fishes allows them to match their orientation strategy to the environment. Odling-Smee and Braithwaite cite research demonstrating that fish are capable of flexible orientation strategies involving learning and memory, and argue that this flexibility is constrained or modified by evolved mechanisms that guide learning and associated perceptual processes. In the last section, they investigate homing in salmon, paying particular attention to the final return by reproductive adults to freshwater streams, a behaviour primarily governed by olfactory memory of their home stream.

The emphasis on spatial cognition is continued in the article of Cristina Broglio, Fernando Rodríguez and Cosme Salas on the neural basis of fish learning. Broglio *et al.* describe the findings of naturalistic and laboratory studies on the spatial behaviour of fishes, and the neural circuitry underpinning this behaviour. They report evidence that the spatial behaviour of fishes is based on learning and cognitive processes dependant on particular brain circuits that are probably homologous to those identified in mammals and birds. For example, the fish hippocampal pallium is essential for processing and encoding complex spatial information to form map-like representations of the environment. In contrast, body-centred orientation strategies or emotional learning are subserved by different cerebral structures, such as the optic tectum, the cerebellum or the amygdalar pallium. Broglio *et al.* interpret these results as demonstrating a striking similarity of cognitive and neural processing in fish and land vertebrates, and suggest that these vertebrate groups share an ancient basic pattern of brain and behaviour organisation.

The following article, by Siân Griffiths, dwells on learned recognition in fishes, and notes the now widespread evidence that fishes can discriminate among conspecifics and recognise kin. However, Griffiths also points out that fishes discriminate between conspecifics on the basis of previous experience, i.e., they recognise familiar conspecifics. There is now considerable evidence to show that individuals in many fish species learn to recognise and discriminate between shoal mates or neighbouring territory holders. Griffiths argues that these learned recognition abilities have important implications for our understanding of the population structure, and their recognition may help to develop research frameworks for conservation and management of fish stocks.

The familiarity of actual or potential shoal mates is one factor mentioned by Dan Hoare and Jens Krause as affecting the decisions fishes make about joining shoals, and the resultant spread of learned information. Hoare and Krause's article focuses on how social organisation and shoal structure affect information transmission through fish shoals. Their paper describes how shoals are typically nonrandom aggregations, with individuals assorting according to species, size, sex, parasites, familiarity and experience. Hoare and Krause go on to discuss the implications of this structuring for the transfer of learned information, and suggest that, to understand the ramifications of social organisation, it is necessary to know how often shoals meet and exchange members. Moreover, through their impact on the structure and stability of shoals, ecological differences between habitats may affect the flow of learned information through populations. Hoare and Krause describe how knowledge of the mechanisms of shoaling behaviour, and in particular, of fission–fusion rates, could be used to make predictions regarding the information transfer in fish populations, which can be tested through experimentation or theoretical analyses. Most models in the past have assumed that fish exchange randomly between shoals, but, in the light of recent findings of self-sorting behaviour in fish, this seems too simplistic.

The transfer of learned information between individuals is reliant on social learning processes. The term 'social learning' refers to cases in which individuals acquire new behaviour or information about their environment via observation of, or interaction with, other animals. It is widely believed that social learning allows individuals to acquire adaptive behaviour quickly and efficiently from more knowledgeable others, for instance, without having to incur the costs of exploration or the risks of learning about predators. In the final article, Culum Brown and Kevin Laland document the strong experimental evidence that many species of fish exhibit social learning and traditional behaviour across a broad array of contexts. Brown and Laland report evidence that laboratory and natural fish populations learn from knowledgeable conspecifics to orientate in their environment, generating long-standing 'cultural traditions' for particular pathways to feeding, schooling, resting or mating sites. They also describe experimental evidence that fishes learn to recognise and respond to natural and artificial predators, learn what to eat and where to find it, who to mate with and who not to pick a fight with, by attending to the behaviour of conspecifics. Brown and Laland conclude by noting that the widespread use of social learning by fishes is likely to have important implications for conservation and fisheries, for instance, by allowing hatchery-reared fish to be trained *en masse* to recognise predators and prey.

Two themes emerge from this collection of articles. The first is that the learning abilities of fishes are comparable to land vertebrates, and whether one considers the neural circuitry, psychological processes or behavioural strategies, fish learning appears to rely on processes strikingly similar to that of other vertebrates. The second is that fish provide a flexible and pragmatic biological model system for studying learning and information transmission processes, and in many respects, can be regarded as ideal subjects for research into learning and memory. These observations lead us to the view that interest in the topic of learning in fish is likely to continue to grow for the foreseeable future.

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References

Brown, C. (2001) Familiarity with the test environment improves escape responses in the crimson spotted rainbowfish, *Melanotaenia duboulayi*. *Animal Cognition* **4**, 109–113.

Bshary, R., Wickler, W. and Fricke, H. (2002) Fish cognition: a primate eye's view. *Animal Cognition* **5**, 1–13.

Bshary, R. and Wurth, M. (2001) Cleaner fish *Labroides dimidiatus* manipulate client reef fish by providing tactile stimulation. *Proceedings of the Royal Society of London Series B* **268**, 1495–1501.

Dugatkin, L.A. (1997) *Cooperation Among Animals*. Oxford University Press, New York.

Girvan, J.R. and Braithwaite, V.A. (1998) Population differences in spatial learning in three-spined sticklebacks. *Proceedings of the Royal Society of London B* **265**, 913–919.

Gleitman, H. and Rozin, P. (1971) Learning and memory. In: *Fish Physiology*, Vol. 6. (eds W.S. Hoar and D.J. Randall) Academic Press, New York, pp. 191–278.

Griffiths, S.W. (2003) Learned recognition of conspecifics by fishes. *Fish and Fisheries* **4**, 256–268.

Helfman, G.S. and Schultz, E.T. (1984) Social tradition of behavioural traditions in a coral reef fish. *Animal Behaviour* **32**, 379–384.

Kieffer, J.D. and Colgan, P.W. (1992) The role of learning in fish behaviour. *Reviews in Fish Biology and Fisheries* **2**, 125–143.

Laland, K.N. and Hoppitt, W. (2003) Do animals have culture? *Special Edition of Evolutionary Anthropology on 'Cultural Evolution'* (in press).

Magurran, A.E., Seghers, B.H., Shaw, P.W. and Carvalho, G.R. (1995) The behavioral diversity and evolution of guppy, *Poecilia reticulata*, populations in Trinidad. *Advances in the Study of Behavior* **24**, 155–202.

McGregor, P.K. (1993) Signaling in territorial systems – a context for individual identification, ranging and eavesdropping. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **340**, 237–244.

Milinski, M., Kulling, D. and Kettler, R. (1990a) Tit for tat: sticklebacks, *Gasterosteus aculeatus*, 'trusting' a cooperative partner. *Behavioural Ecology* **1**, 7–11.

Milinski, M., Pfluger, D., Kulling, D. and Kettler, R. (1990b) Do sticklebacks cooperate repeatedly in reciprocal pairs? *Behavioral Ecology and Sociobiology* **27**, 17–21.

Odling-Smee, L. and Braithwaite, V.A. (2003) The influence of habitat stability on landmark use during spatial learning in the threespine stickleback. *Animal Behaviour* **65**, 701–707.

Paxton, J.R. and Eschmeyer, W.N. (1998) *Encyclopedia of Fishes*, 2nd edn. Academic Press, New York.

Thorpe, W.H. (1963) *Learning and Instinct in Animals*. Methuen, London.

Warburton, K. (2003) Learning of foraging skills by fish. *Fish and Fisheries* **4**, 203–215.

Warner, R.R. (1988) Traditionality of mating-site preferences in a coral reef fish. *Nature* **335**, 719–721.

Warner, R.R. (1990) Resource assessment versus traditionality in mating site determination. *American Naturalist* **135**, 205–217.