Report for the FSBI Small Research Grant award

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Title of Research:
A collaborative study between Edinburgh University and the University of British Columbia to compare spatial learning in benthic and limnetic stickleback species pairs

Summary of work undertaken and main findings:

A recent integration of psychological and biological approaches to animal learning has revealed that learned behaviours are often modified and fine-tuned in response to specific ecological conditions. Developmental and genetic control over the precise features of the learning process may reduce the potential costs of learning such as the energetic costs of information processing or the costs of making mistakes.
Here we compared spatial learning in two species of threespined stickleback that co-exist sympatrically in a number of lakes in British Columbia. The 'limnetic' species lives predominantly in the open water column, a relatively homogenous environment in terms of spatial complexity, and feeds mainly on pelagic prey. The stockier 'benthic' species lives predominantly in the more structured vegetated littoral region of the lakes feeding on invertebrates. 20 benthics and 20 limnetics collected from two lakes were trained in a T-maze to locate food and shoal mates using one of two cues, turn direction or plant landmarks. Probe trials revealed which spatial cue the fish were using. Although limnetics and benthics did not differ in the type of spatial information they used to solve the task (both species used turn and landmarks with no preference for either cue), benthics were significantly faster at learning the task. An additional experiment testing motivation revealed that this was not due to differences in benthics' and limnetics' motivation to reach the two types of reward. We conclude that the superior learning ability shown by benthics in this task is related to their experience of feeding and manoeuvring in a more structured habitat.

Detailed description of work:

BACKGROUND
Although learning has been at the centre of psychological research for over a century, we still know relatively little about how animals optimise and economise the use of learned behaviours within their natural environments. An integrative approach between psychology and ecology has begun to reveal that many learned behaviours are modified and fine-tuned in response to the precise details of the species environment (Garcia & Koelling, 1966). Invariably preferential attention is given to those cues that give the most relevant information. For example the quality and quantity of orientation information available to young birds affects the weighting of cues used later in life (Braithwaite & Guilford, 1995). In some cases learning ability itself is enhanced during periods when the animal most requires it. In the meadow

vole, superior spatial ability in males tracks a corresponding increase in male range size during the breeding season (Jacobs et al., 1990).

Here we investigate whether microhabitat differences select for differences in learning even within the same macrohabitat. Six lakes on three separate islands in the Strait of Georgia region of south-western British Columbia contain sympatric 'benthic' and 'limnetic' species of threespined stickleback, *Gasterosteus aculeatus*. Genetic, behavioural and ecological studies have shown that these morphs are reproductively isolated and exploit alternative trophic niches in sympatry (Schluter & McPhail 1992, McPhail 1994). The limnetic species lives predominantly in the open water column feeding mainly on plankton while the benthic species lives predominantly in the vegetated littoral zone feeding on invertebrates.

Although an array of differences in feeding morphologies and behaviours have already been identified in these species pairs, little is known about how the species differ in learning or in the kinds of information they use in orientation. This project compared cue preference in benthics and limnetics and their relative performance in learning a simple spatial task.

Methods - Experiment 1

Benthic and limnetic sub-adult sticklebacks were collected from Priest and Paxton Lakes both on Texada Island, British Columbia. Fish were housed in their holding tanks in pairs and identified from individual markings and size differences.

Pairs of fish were trained simultaneously to locate a double reward of food and shoal mates in two identical cross-shaped mazes constructed from 3-mm green plastic (see fig.1). Fish were first familiarised with the procedure by being transferred to the mazes in groups of 10, for five 4hour sessions. Fish were then trained individually to locate the rewarded end. The fish could learn to locate this end by learning the turn direction out of the start box or by using the plant landmarks as a guide. Each fish was transferred to the start box and left to settle for 5 minutes before the trap door was raised and the fish allowed to explore the arms of the maze. In trial 1-12 all doors remained raised allowing exploration of both arms. After trial 12, if a fish swam into the wrong arm the trap door in the opposite arm was lowered, preventing the fish from swimming back and accessing the food and shoal mates. Half the fish were trained to turn right and half were trained to turn left. Fish were given three trials a day with the position of the start box being switched for each trial.
Once the fish reached a criterion performance (9 correct trials out of 10), they were exposed to a probe trial in which the landmarks were switched to the opposite side from where they had been during training. This identified whether the fish were using turn direction or landmarks to solve the task. Each fish was given 3 probe trials being retrained to a criterion of 4 out of 5 correct trials after the first and second probe.

Main Results - experiment 1:

4 limnetics died leaving a total of 16 limnetics and 20 benthics. All 36 fish remaining reached criterion.

Results of the probe trials
There were no significant differences in cue preference shown by benthics and limnetics ($F_{1,33} = 0.22$, $p = 0.64$). Both species used both types of spatial information with no preference for either cue (see fig 2).

Learning
Benthics took significantly fewer trials than limnetics to reach criterion ($F_{1,34} = 14$, $p = 0.001$). Benthics reached criterion in a mean of 16.1 trials (SE = 1.12) compared to a mean of 26.6 trials (SE = 3.49) for limnetics (See fig 3.). Limnetics also made significantly more errors after they had reached criterion than did benthics ($F_{1,34} = 15.64$, $p = 0.004$). See fig 4.

Methods - Experiment 2
Since limnetics are naturally pelagic feeders, they showed little interest in the bloodworm in the vaseline filled petri dishes feeding only 20-30% of the time on reaching the rewarded end. Benthics in contrast never entered the rewarded end without taking the food. It appeared that benthics were responding primarily to the food reward while limnetics were motivated primarily to reach the shoal mates. Differential motivation by benthics and limnetics to reach these two types of reward could have influenced their performance. A motivation test was designed to investigate whether this could have accounted for the differences in their rate of learning.

An additional 40 fish (20 limnetics and 20 benthics) were used for this experiment that were naïve to any experimental manipulation. The experimental tank was divided into 3 sections by clear perspex partitions (see fig 5.). A shoal of 5 fish was placed in one end division and a feeder containing copious amounts of bloodworm in the other end division. Individuals were released from a central start box in the middle larger section of the tank from where they were free to explore for 5 minutes. The time spent by the fish in the 'shoal zone', 'food zone' and 'release zone' was recorded.

Results - Experiment 2
Priest and Paxton benthics differed in the degree to which they preferred to shoal, Priest benthics showing a significantly stronger preference for shoaling over foraging compared to Paxton benthics. Both populations of limnetics showed an extremely strong preference for shoaling (see figs. 5 and 6).

Discussion
The results of the first experiment strongly imply that benthics are superior learners in this task. Given the strong motivation found in both populations of limnetics to find shoal mates found in experiment 2, this dramatic learning difference cannot be accounted for by differences in motivation to reach the rewarded end. I therefore conclude that at least in this task, benthics are superior learners to limnetics which seems likely to be a result of their experience in a more structure habitat in the vegetated littoral zone of lakes.
Without yet understanding the causal mechanism responsible for this difference we cannot conclude whether superior learning ability in the benthics is a genetically fixed product of natural selection or a plastic response to differential experience. However the finding that learned behaviours differ in sympatry even within the same

macrohabitat lends further support to evidence that learned behaviours are precisely tuned in response to environmental demand.

References

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Jacobs, L. F., Gaulin, S. J. C., Sherry, D. F. and Hoffman, G. E. (1990). Evolution of spatial cognition: sex specific patterns of spatial behaviour predict hippocampal size. *Proc. Natl. Acad. Sci. USA* **87**: 6349-6352.

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Schluter, D. & McPhail, J. D. 1992 Ecological character displacement and speciation in sticklebacks. *Am. Nat*. **140**: 85-108.

Breakdown of costs:

Funds awarded from FSBI: £973

Flight: £518.00
Insurance: £82.00
STA Admin charge: £15
Rent: CAN$ 726.05
Bus transport to UBC: CAN$ 171.50

Figures

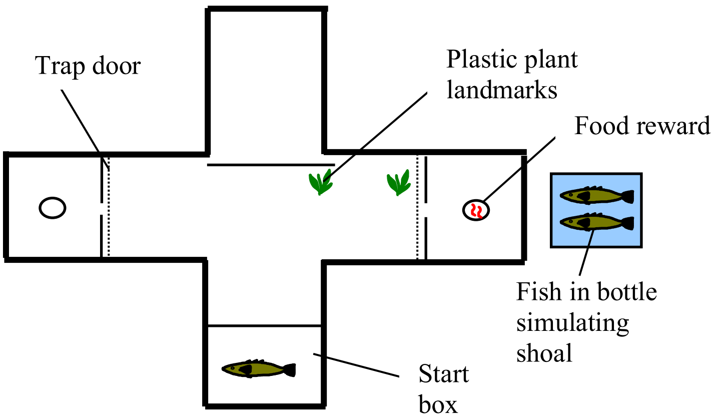

Figure 1 – experimental protocol

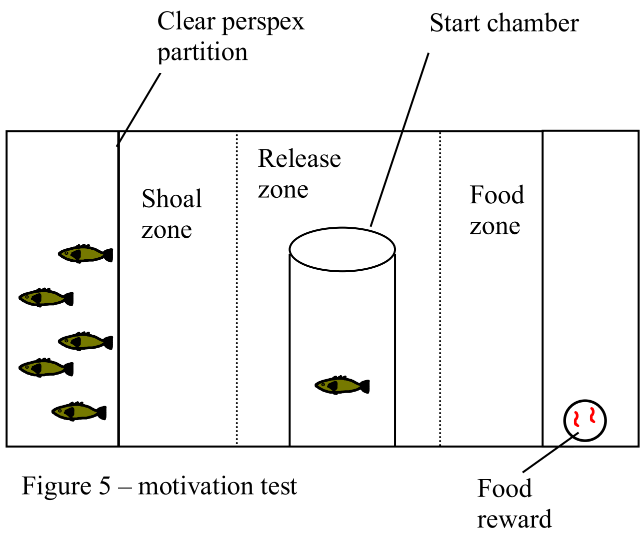

Figure 5 – motivation test

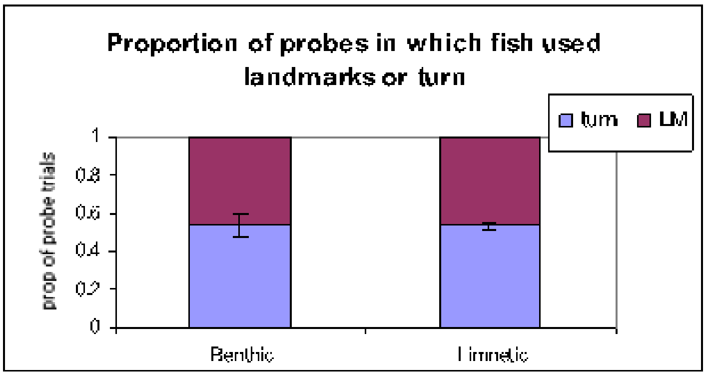

Figure 2 – cue preference

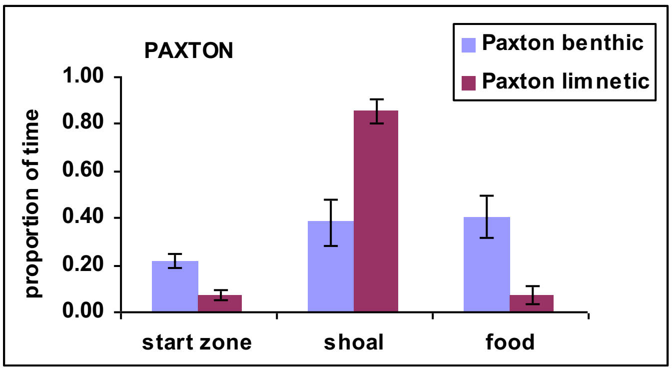

Figure 6 – Paxton motivation results

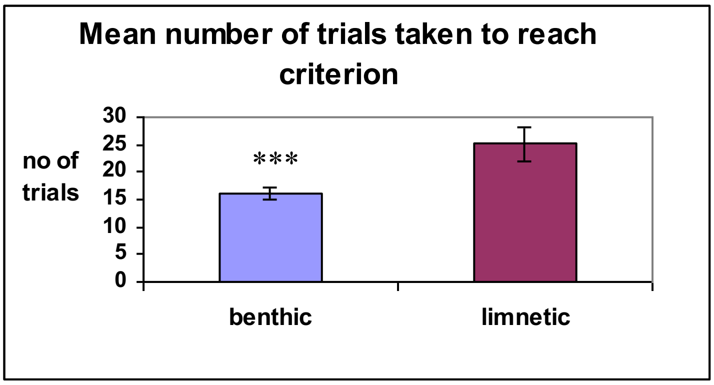

Figure 3 – rate of learning

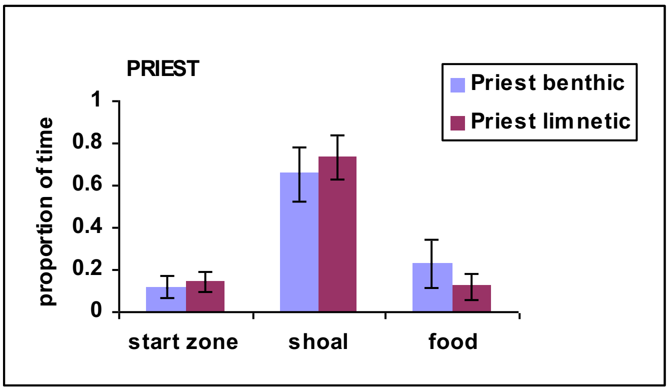

Figure 7 – Priest motivation results

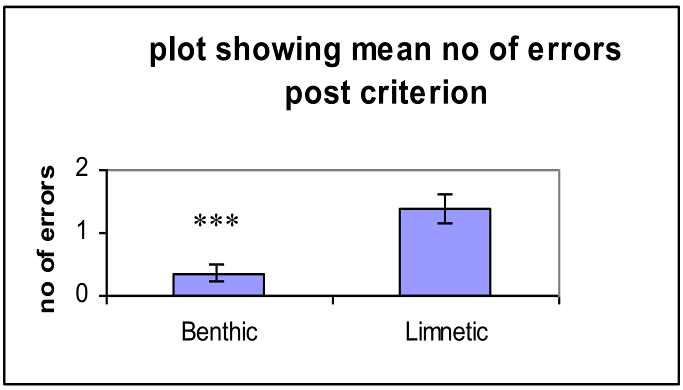

Figure 4 – errors post criterion