

A novel apparatus for studying fish cognition in the wild

Catarina Vila-Pouca^{1,2}  | Hannah De Waele²  | Antoine Parsékian² | Simone Erroi² | Mariska De Rooij² | Emma Labohm² | Amy Deacon³  | Alexander Kotrschal² 

¹CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

²Behavioural Ecology Department, Wageningen University and Research, Wageningen, The Netherlands

³Department of Life Sciences, The University of the West Indies, St Augustine, Trinidad and Tobago

Correspondence

Catarina Vila-Pouca

Email: catarinavilapouca@gmail.com

Funding information

Koninklijke Nederlandse Akademie van Wetenschappen, Grant/Award Number: KNAWWF/705/202205 and KNAWWF/DA/973/Eco2013; Foundation Lucie Burgers for Comparative Behaviour Research, Arnhem, the Netherlands, Grant/Award Number: 2020 and 2021; Dr. J. L. Dobberke Foundation for Comparative Psychology, Grant/Award Number: 2229/202208; Association for the Study of Animal Behaviour, Grant/Award Number: ASAB 2020

Handling Editor: Natalie Cooper

Abstract

1. Fish show a huge variation of ecological, anatomical and behavioural traits, which makes them prime subjects for studying behaviour, cognition and their evolution. Lab-based studies allow a controlled examination of some of the mechanisms underpinning cognition and have yielded many insights into fish cognitive abilities. However, they may skew our understanding of fish cognition, as the artificial captive environment might affect cognitive and behavioural performance. Few fish cognition studies have been conducted in the field or with wild fish populations.
2. To address this, we introduce a novel cognitive apparatus designed for fish in their natural habitats. To demonstrate its efficacy, we conducted two tests using a social foraging task: one focused on learning and social foraging decisions in guppies (*Poecilia reticulata*) in tropical Trinidad, and another on learning in nine-spined sticklebacks (*Pungitius pungitius*) in the temperate Netherlands.
3. We obtained learning curves over sessions for both species, consistent with established laboratory assays. We also succeeded in analysing producer-scrounger dynamics; we found stable proportions of producer and scrounger individuals across populations, but low consistency of individual strategies over time.
4. Our results show that this low-cost, easy-to-adapt apparatus is effective for assessing a variety of cognitive abilities across different fish species. This study provides a starting point to test different aspects of fish cognition under natural conditions and can pave the way for examining in situ cognitive variation between species and populations exposed to different ecological conditions.

KEYWORDS

behaviour, field, learning, producer-scrounger, social foraging

Catarina Vila-Pouca and Hannah De Waele shared first-authorship.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2025 The Author(s). *Methods in Ecology and Evolution* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

1 | INTRODUCTION

Fish represent the most diverse group of vertebrates, showcasing an impressive array of ecological, anatomical and behavioural traits (Patton & Braithwaite, 2015). Additionally, the homology between the teleost brain and that of other vertebrates, the high and continuous neurogenic capacity of teleost brains, and the possibility of assaying wild-caught or captive populations thanks to the continued development of robust and replicable behavioural and cognitive tests over the last decades, has made fish a prime group for studying behaviour and cognition, as well as to examine potential ecological and evolutionary drivers of variation in cognitive performance (Salena et al., 2021; Vila Pouca & Brown, 2017). However, in contrast to other vertebrates, such as mammals or birds, studies on fish cognition are underrepresented and the bulk of existing research has been conducted in controlled, captive environments, focusing on either wild-caught or laboratory-raised individuals (Patton & Braithwaite, 2015; Salena et al., 2021). While these studies have revealed many valuable insights into the cognitive capacities of fishes, generalizing them to a wild and natural context is challenging. For instance, wild-caught fish, when removed from their natural environment, can show increased stress responses (Balcombe et al., 2004; Sneddon et al., 2016). Elevated stress hormones are known to impact learning ability (Barreto et al., 2006; Bebus et al., 2016) and can decrease an animal's motivation to participate in a cognitive test (Bowman, 2005). Also, captive-raised individuals run the risk of underperforming in ecologically relevant tasks compared with their wild counterparts due to a lack of experience (Patton & Braithwaite, 2015; Salena et al., 2021). Furthermore, captivity can profoundly impact behaviour and cognition both through plastic changes during an individual's lifespan and artificial selection across generations in a laboratory setting (Ebbesson & Braithwaite, 2012; Näslund, 2021; Salena et al., 2021). Relying predominantly on laboratory-based studies may thus skew our perception of fish cognition and behaviour in their natural habitats.

Studying animal cognition in natural settings offers a way to sidestep the potential pitfalls associated with laboratory-induced biases in testing animal cognition (Bshary & Triki, 2022; Pritchard et al., 2016; Rosati et al., 2022). Despite this, only a few fish cognition studies have been conducted in the field or with wild fish populations, as

evidenced by the recent review of Salena et al. (2021). Of 608 publications on fish cognition, the majority (69%) used captive-reared subjects rather than wild fish. Some studies used wild-caught individuals tested in laboratory experiments (22%), and very few studies used in situ experiments on wild individuals (9%). The main difficulty in testing wild individuals is to have a cognitive testing apparatus that can easily be used in situ, that is suitable for different species and that allows repeated testing of the same individuals over a long time period. One recent study has started to tackle this issue by developing a 'detour test' setup that examines inhibitory control in wild fish, showing it is possible to run repeated tests in fish in situ (Jungwirth et al., 2024). However, cognition encompasses several domains (e.g. self-control, learning from experience and memory), and even within domains there can be variation in the ecological relevance of each task for the populations or species of interest (e.g. spatial learning vs. numerical competence).

Here, we present a novel, low-budget interactive cognitive apparatus that can be easily adapted to test several cognitive abilities of wild fish in their natural habitat. We demonstrate its efficacy in three case studies (summarized in Table 1): two demonstrating its potential for examining learning and decision-making dynamics, which we conducted in guppies (*Poecilia reticulata*) in outdoor enclosures, and another demonstrating its flexibility to use in situ in the field with different species, which we conducted with nine-spined sticklebacks (*Pungitius pungitius*). We believe this study provides a starting point to test different aspects of cognition in fish, as well as other taxa, under natural conditions and can pave the way for examining in situ cognitive variation between species and populations exposed to different ecological factors.

2 | METHODS

2.1 | A foraging board for in situ cognition experiments

Our goal was to design a cognitive testing device that was simple to set up and that could be easily transported in the field and used across a range of habitats (e.g. streams, ponds and ocean) and species. We also wanted to ensure that a large number of species could easily engage with the testing set-up and that the produced

TABLE 1 Summary of experiments and analyses, with focal aims at the top.

	Proof-of-concept in controlled, field-like conditions	Proof-of-concept in field conditions	Example of additional applications
Test	1a	1b	2
Analysis	Group learning performance	Group learning performance	Individual producer-scrounger strategy use
Species	Guppy <i>Poecilia reticulata</i>	Nine-spined stickleback <i>Pungitius pungitius</i>	Guppy <i>Poecilia reticulata</i>
Experimental conditions	Wild-caught, outdoor enclosure	Wild, in situ	Wild-caught, outdoor enclosure

cognitive data can be added to and compared with the existing literature. Therefore, we decided to adapt one of the most widely used tasks of fish cognition in the laboratory, where fish are trained to dislodge plastic discs covering rewards on a perforated board (e.g. Lucon-Xiccato & Bisazza, 2014; Vila-Pouca et al., 2022). Building from this task, and with input from bird cognition studies in natural settings (Shaw et al., 2019), we decided to create a foraging board with pivoting discs. The foraging board is a solid opaque polyvinyl-chloride plastic (PVC) plate (30×30 cm). We chose to design it with 24 holes distributed equally along the edge of the board to be able to conduct a large number of trials with a single placement of the board, which we will refer to as a session (Figure 1a). Next to each hole, a 20-mm plastic disc (see below) is fixed to the board with a screw that allows pivoting of the disc. By adjusting the tightness of the screw, the disc can be loose and moveable (allowing the fish to expose the hole and retrieve a reward) or tight and impossible to move (preventing the fish from exposing the hole). As rewards, we successfully tested the use of pellets (TetraMin Mini Granules, Tetra, Spectrum Brands Inc), flakes (Guppy Mini Flakes, Tetra, Spectrum Brands Inc) and bloodworms (*Chironomus* sp. larvae), that we stuck

to the bottom of the holes in the foraging plate with a thin layer of Vaseline®.

2.2 | Stimuli for cognitive and behavioural tests

We chose a simple design where the fish interact directly with the stimuli by pushing it to retrieve the reward. Our stimuli were 20 mm plastic discs (www.spielmaterial.de) of varying colours (Figure 2a). Similar to laboratory assays, there is a motor learning component of our task, where fish learn to push each disc to dislodge it and expose the reward. For simple associative learning and motor task learning, a single colour can be used. For discrimination acquisition tasks, two (i.e. 12 trials/colour with each placement of the board) or three stimuli colours (i.e. 8 trials/colour) can be used. It is also possible to paint shapes/dots onto the discs with nail polish (Figure 2b) and in this way test discrimination acquisition with stimulus dimensions other than colours. Painting dots of varying number or size (Figure 2c) allows for numeracy tasks. And by simply reversing which discs are moveable and which are not, researchers can then test for

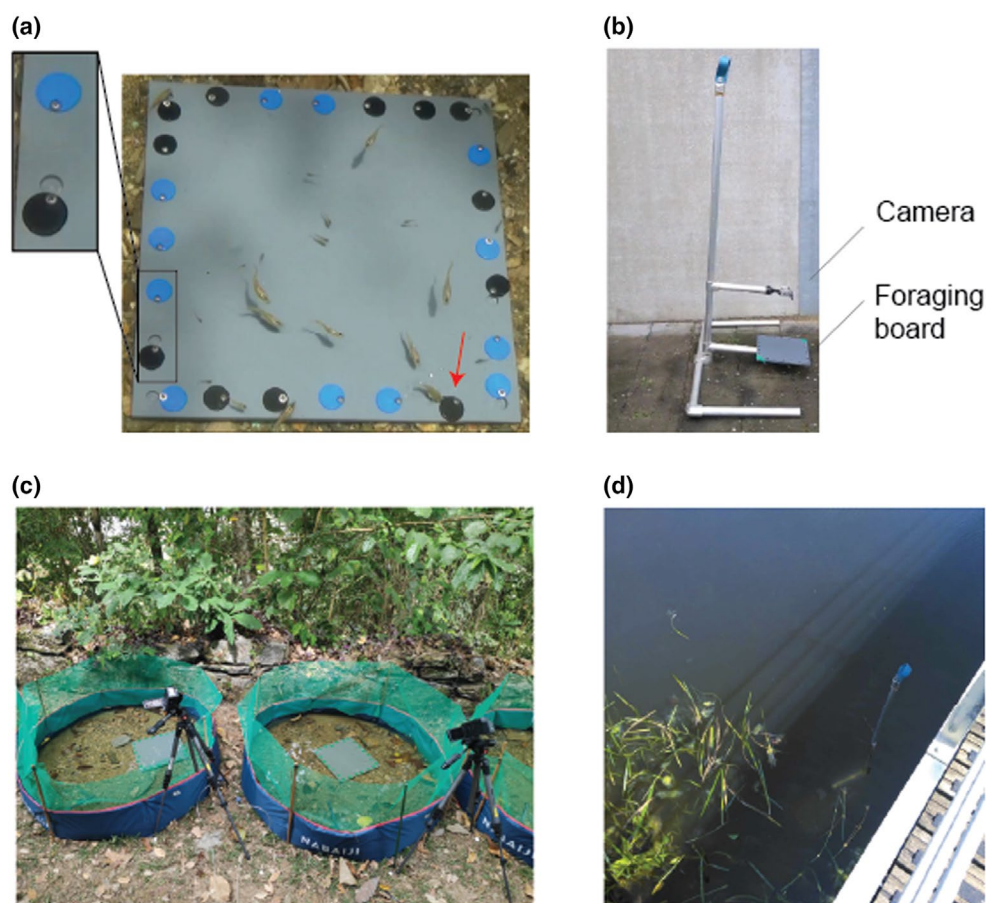


FIGURE 1 (a) Inset: Coloured discs attached to the board with a screw that allows them to pivot and expose the hole underneath. Main: Guppies interacting with the foraging board, with one individual pushing a black disc and solving the task (arrow). (b) Side photograph of the apparatus used to place the foraging board in Test 2. (c) In Test 1, the foraging board was placed directly on the bottom of outdoor enclosures to assay five subpopulations of wild-caught guppies. (d) In Test 2, the placement apparatus allowed us to present the foraging board coupled with a video camera to assay a wild population of nine-spined sticklebacks.

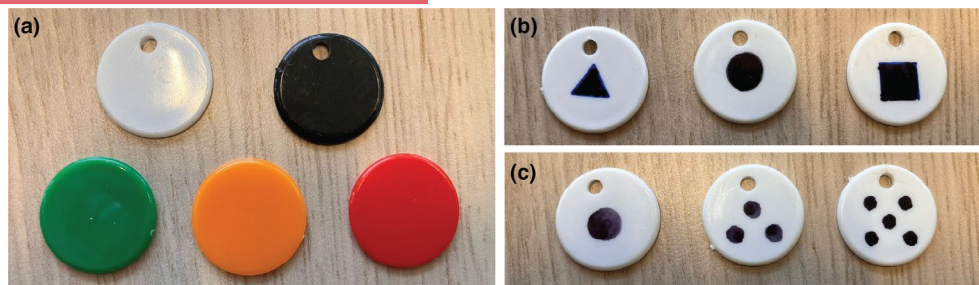


FIGURE 2 Examples of how the stimuli discs can be used to test different cognitive domains, by having discs of different colour (a), or displaying different shapes (b) or numbers (c).

reversal learning. If the board is placed in exactly the same position within the water, for example next to specific rock structures in a reef or a stream, or with landmarks, such as plastic plants attached to the board, it can also be used for simple spatial tasks. Additionally, if researchers can collect a few individuals from the study population and pre-train them in isolation with a specific stimulus (colour, shape, etc.), as commonly done in birds (Aplin & Morand-Ferron, 2017), our foraging board can be used to examine social learning and social information spread directly in wild populations. Finally, since our task involves a learnt motor skill and allows for interaction between several individuals during the trials, it can also be used by researchers interested in examining social foraging dynamics, such as producer–scrounger strategies.

2.3 | Apparatus for externally placing the foraging board

The foraging board can be placed directly by the experimenter at the bottom of a water body (Test 1a; Figure 1c) or be coupled with an apparatus that facilitates placement from a distance (Test 1b; Figure 1d), reducing disturbance of sediment and of the fish. The placement apparatus is composed of two main parts (Figure 1b, Figure S2): a stable base made to rest in situ throughout the whole experiment, and a sliding top part with one arm that holds the foraging board and another that holds a video camera (e.g. GoPro). Our apparatus had an aluminium base and a top part made with low-cost, standard PVC pipes and T-pipe junctions (see Appendix S1 and Video S1). The height of the board in the apparatus can be adjusted, allowing placement not only at the bottom of the water body but also along the water column (suitable to test species that forage at different water depths). The height and angle of the video camera can also be adjusted.

2.4 | Test 1a: Group learning of wild-caught guppies, tested in outdoor enclosures

To trial the foraging board in controlled yet field-like conditions, we examined associative learning performance of wild-caught Trinidadian guppies (*Poecilia reticulata*) in outdoor enclosures. In April 2022, we caught 70 adult female guppies in the Aripo river, Trinidad (see

Appendix S1 for details). We created five groups of 14 females (P1–5) and trained them to a blue vs. black discrimination task (P1, P2 and P4 trained on black; P3, P5 on blue) using the foraging board directly placed on the bottom of the enclosure. Group learning performance was examined for P1–3 by comparing the total number of pecks of all fish on the correct colour discs compared with incorrect colour discs across sessions. We scored pecks as any fish pushing/pecking the coloured disc or the screw that attached it to the board. Videos were scored by three researchers with very high inter-rater reliability ($ICC=0.903$, $p<0.001$, details in Appendix S1). As our goal was to examine learning performance at the group level, we did not score the identity of the fish for each peck for this analysis. Note that individual identification would be feasible for individual-level analyses.

2.5 | Test 1b: Group learning of wild nine-spined sticklebacks, tested in situ

To trial the foraging board in situ, we examined associative learning performance of wild nine-spined sticklebacks (*Pungitius pungitius*) from a freshwater wild population in a pond of the Wageningen University & Research campus, Netherlands (see Appendix S1 for details). In May 2023, a group of sticklebacks were trained to a blue/white discrimination task using the foraging board placed from outside the pond with the placement apparatus. Note that we did not restrict the access of animals to the testing apparatus and did not individually mark animals; from video footage, the maximum number of fish observed interacting with the board was 20 individuals. As in Test 1a, we assessed group learning performance by comparing the total number of pecks on the correct colour discs compared with incorrect colour discs across sessions, scored from videos of the trials by a single researcher (see Appendix S1 for details). As our goal was to examine learning performance at the group level, we did not score the identity of the fish for each peck for this analysis.

2.6 | Test 2: Individual producer–scrounger strategies of wild-caught guppies

To demonstrate that our apparatus can be used for a broader range of cognitive and social tasks, we also examined producer–scrounger

strategy use (Aplin & Morand-Ferron, 2017; Harten et al., 2018). These results give us insights into social cognition and decision-making strategies in the context of a foraging task that involves a learnt skill component, which to our knowledge has not yet been examined in wild fish.

Guppies were tagged with Visible Implant Elastomer tags (details in Appendix S1) to allow individual identification and examination of individual task proficiency. From the videos of Test 1a, we scored two behaviours (and associated fish identity): 'solve', when an individual successfully dislodged a correct coloured disc to reveal the reward; and 'scrounge', if a different individual poked into the rewarding hole within 5 s of a solve to profit from the exposed reward. Videos for Test 2 were all scored by a single researcher. We note that 'solves' are a specific motor skill that the fish learn to produce and that are limited by the number of correct colour discs in the foraging board, while pecking behaviour scored in Test 1 can occur multiple times with the same discs. To examine producer–scrounger strategy use, we compared the number of solves of each individual fish and how these changed over time, and compared individuals in their strategy use (proportion of solves over scrounges).

2.7 | Statistical analyses

All analyses were carried out in R v3.2.5 (R Core Team, 2022). Code is provided as Data S1.

For Tests 1a,b, we examined group learning performance over sessions with a binomial generalized linear model (GLM; *stats* package), with Choice (correct, incorrect) as response variable and Session number as predictor (plus subpopulation for Test 1a). We note that random effects should be added to these models if individual ID is scored for each peck, but this was not the case in our study. One should include a random intercept and/or slope if there is an expectation that: (i) individuals may differ in their naïve preference for one of the choice stimuli at the start of the experiment (e.g. differences in colour preference), resulting in different intercepts; and/or (ii) individuals may differ in their rate of learning, resulting in different slopes. We annotated our code to show how this can be done in R. In Test 1a, we also explored how group choice varied between the start and end of the experiment and within sessions, to detect 'warming-up' or satiation effects (Ajuwon et al., 2024). We ran a binomial GLM with session block (first five and last five), session period (beginning, end), and subpopulation and their interaction as potential predictors of choice. In Appendix S1, we detail how to calculate pairwise contrasts for interactions and how to interpret them.

For Test 2, we examined individual solving proficiency by calculating the number of solves per guppy relative to the total number of solves per session and by computing the cumulative number of solves per individual across sessions. To identify proficient task solvers, we fitted a *k-means* clustering algorithm (*stats* package) to the solving proficiency scores, partitioning individuals in two

clusters: proficient and non-proficient solvers. We provide details on clustering validation in Appendix S1. Moreover, three individual-level variables were considered as potential predictors of solving proficiency in a GLM (*stats* package): Latency to first solve, body size and subpopulation (P1-5). Latency to first solve was defined as the number of sessions from the beginning of the task until the individual performed its first solve. This measure is similar to that used in problem-solving studies (Aplin & Morand-Ferron, 2017), but here we have a group learning task so this score likely comprises a social component as well. All individual-level variables were uncorrelated to each other.

Additionally, we calculated a producer index (PI; Harten et al., 2018) for each individual over the entire experimental period, given by:

$$PI_i = (p_i - s_i) / (p_i + s_i),$$

where p_i is the number of solving (producing) events of fish i , and s_i is the number of scrounging events of fish i . The PI ranges between -1 and 1 . Producers are individuals with a positive PI (most behaviours are 'solves') and scroungers are individuals with a negative PI (most behaviours are 'scrounges'). This analysis was restricted to individuals that performed ≥ 12 behaviours over all sessions.

Finally, we examined potential individual-level determinants of strategy use, and if individuals showed temporal consistency in strategy use, details are given in Appendix S1.

2.8 | Ethics statement

All methods were carried out in accordance with published guidelines of the Association for the Study of Animal Behaviour. Experimental procedures were conducted under permits from the Fisheries Division of the Ministry of Agriculture, Land and Fisheries of the Republic of Trinidad and Tobago and from the Animal Welfare Body (Instantie voor Dierenwelzijn, IvD) at Wageningen University and Research (NAE_2034.W-015), Netherlands.

3 | RESULTS

3.1 | Test 1a: Group learning of wild-caught guppies

When examining group learning performance of three guppy subpopulations, we observed colour discrimination acquisition curves similar to published laboratory studies (Figure 3a). Guppies improved performance across sessions (est. = 0.097, $\chi^2 = 474$, $df = 1$, $p < 0.001$; Figure 3a), with differences in learning rate between subpopulations (session \times subpop.: $\chi^2 = 44.36$, $df = 2$, $p < 0.001$; Figure 3a).

When examining the proportion of correct choices between session blocks and within sessions, we found a difference between

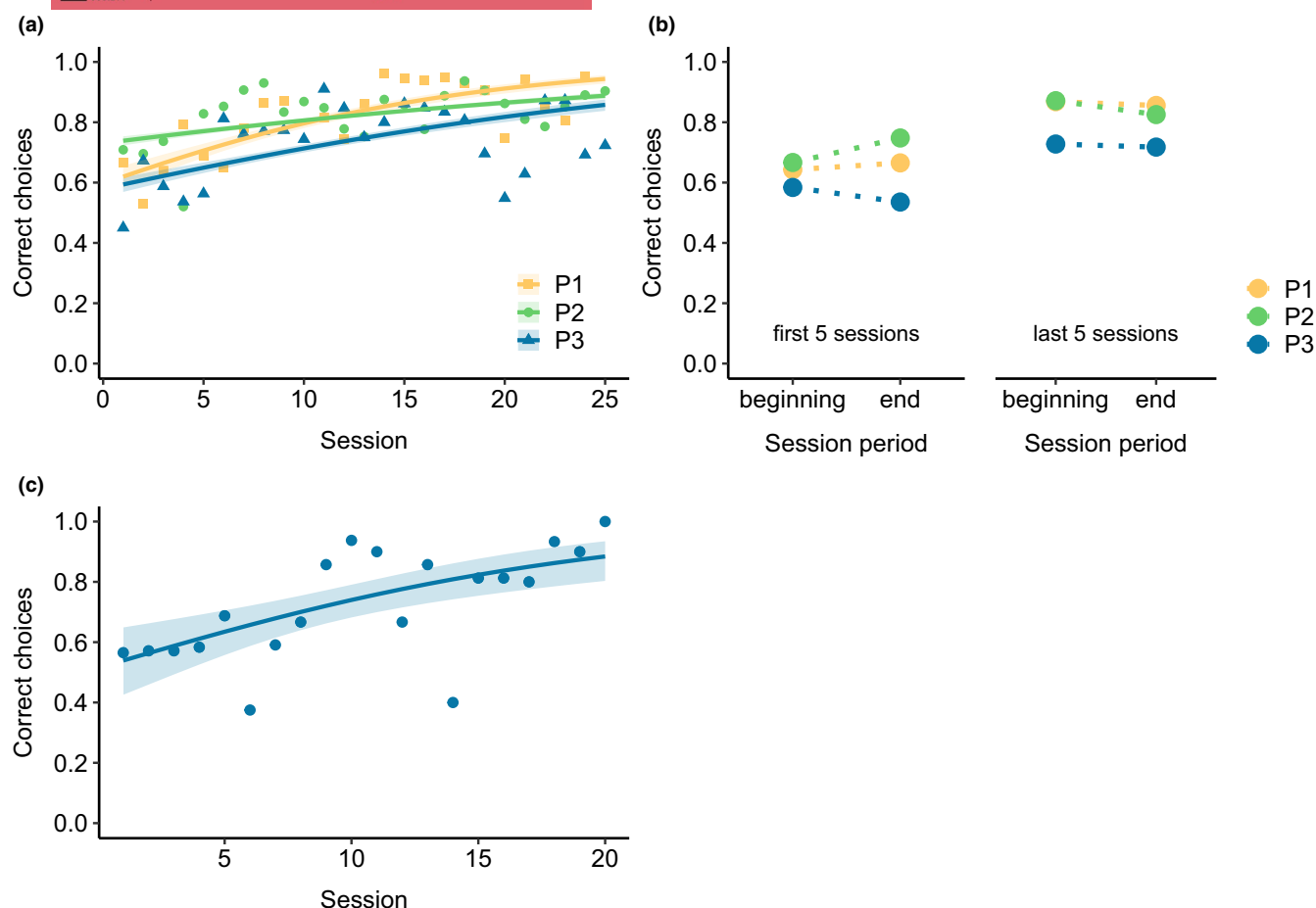


FIGURE 3 Learning performance of (a) three guppy (P1–3) and (c) one stickleback populations trained with the foraging board in Test 1 (lines show model predictions with 95% CI; points show mean success per session). (b) Proportion of correct choices of three guppy populations (P1–3) during the first five (left) and last five (right) sessions.

the three subpopulations (session period \times session block \times subpop.: $\chi^2 = 22.81$, $df = 2$, $p < 0.01$; Figure 3c). From pairwise contrasts (full table given in Appendix S1), we found that P2 and P3 differed at the beginning period of the first block of five sessions, while P1 was intermediate and not statistically different from the two. In terms of learning within the block of first five sessions, only P2 showed a significant (positive) slope between the beginning and end of the block. Furthermore, P2 also showed a significant (negative) slope within the block of last five sessions, suggesting a satiation effect at the end of experiment (Ajuwon et al., 2024; Figure 3c). As expected, we also find that all three subpopulations show higher success at the end of the last block compared with the end of the first block, indicative of learning. We find no differences between subpopulations at the end of the last block.

3.2 | Test 1b: Group learning of wild nine-spined sticklebacks

Wild sticklebacks readily engaged with our task setup and showed a positive slope in the colour discrimination acquisition curve. Sticklebacks increasingly chose the correct colour more often and

improved performance across sessions (est. = 0.099, $\chi^2 = 16.9$, $df = 1$, $p < 0.001$; Figure 3b).

3.3 | Test 2: Producer–scrounger strategies of wild-caught guppies

A total of 65 out of the 70 guppies (P1 = 12, P2 = 14, P3 = 12, P4 = 14, P5 = 13) engaged with the foraging board over the course of the experiment and performed a varying number of solving events (Figure 4). Of these 65, nine guppies had solving proficiency scores greater than 0.2, that is, each of them alone solved more than 20% of all solves in their subpopulation and were categorized as proficient solvers. Seven guppies never solved the task (proficiency score of zero). Proficient solvers and non-solvers occurred at similar proportions across subpopulations (Figure 4a). Additionally, the cumulative number of solves increased steadily per session for the proficient individuals (Figure 4b), indicating that they were consistent in their solving performance across sessions.

When examining individual-level determinants of solving proficiency, we found a trend for a positive impact of latency to first

solve, albeit non-significant ($\chi^2=3.76$, $df=1$, $p=0.052$) and no effect of either body size ($\chi^2=0.34$, $df=1$, $p=0.56$) or subpopulation ($\chi^2=0.06$, $df=4$, $p=0.99$) on solving proficiency scores.

Of the 65 guppies that engaged with the learning apparatus over the course of the experiment, 51 individuals (P1=9, P2=10, P3=11, P4=10, P5=11) performed ≥ 12 behaviours over the 25 sessions. Of these 51 guppies, we find that only nine are producers (positive

PI; Figure 5). All producers except G68 are also the individuals who were the most proficient in solving the task, that is, that contributed more than 20% of all solves in their subpopulation (Figure 5, blue bars), and all scroungers except G42 were non-proficient solvers (Figure 5, grey bars). Taken together, these results indicate the existence of two alternative behavioural strategies: a producer strategy, that consists of being proficient and consistently solving the task

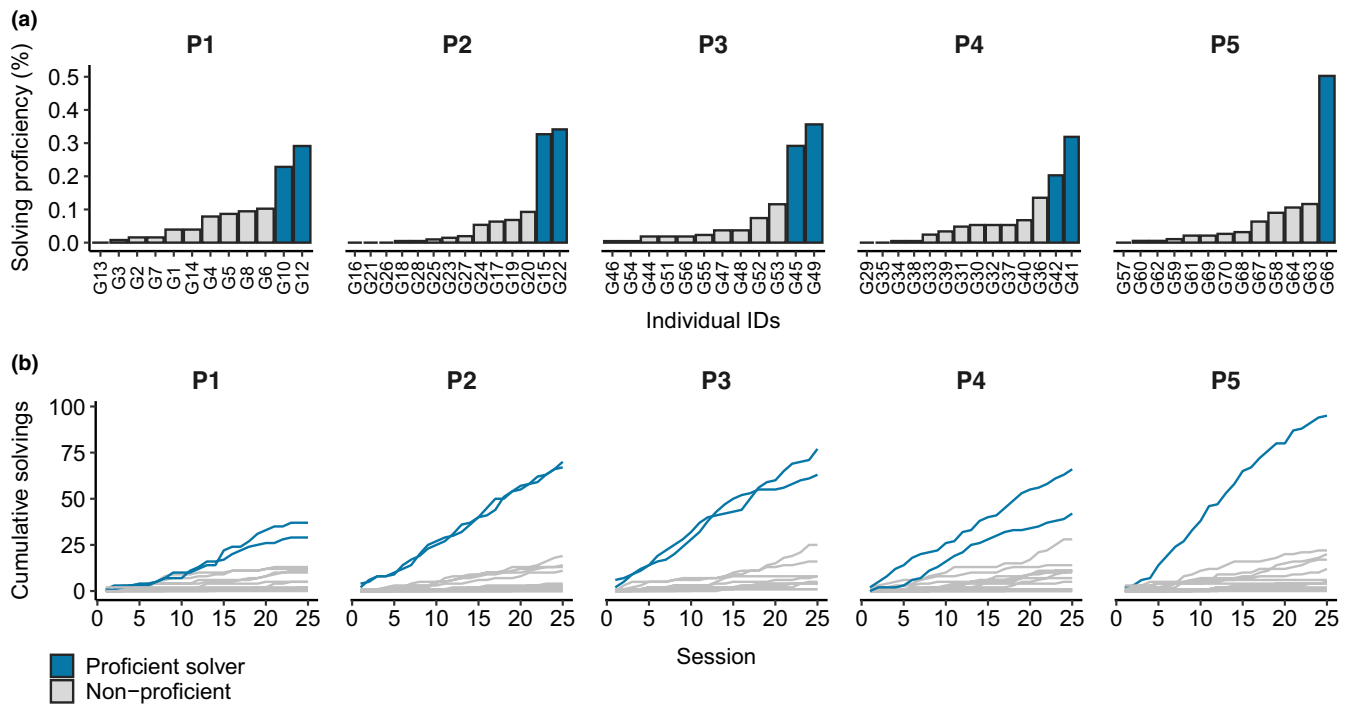


FIGURE 4 (a) Individual guppies (G1–G70) showed variation in solving proficiency scores (number of solves relative to all solves per session), with some individuals solving more than 20% of all solves in their subpopulation (proficient solvers, dark bars). (b) The cumulative number of solves increased consistently over sessions for the proficient solvers (blue lines) compared with non-proficient guppies (grey lines).

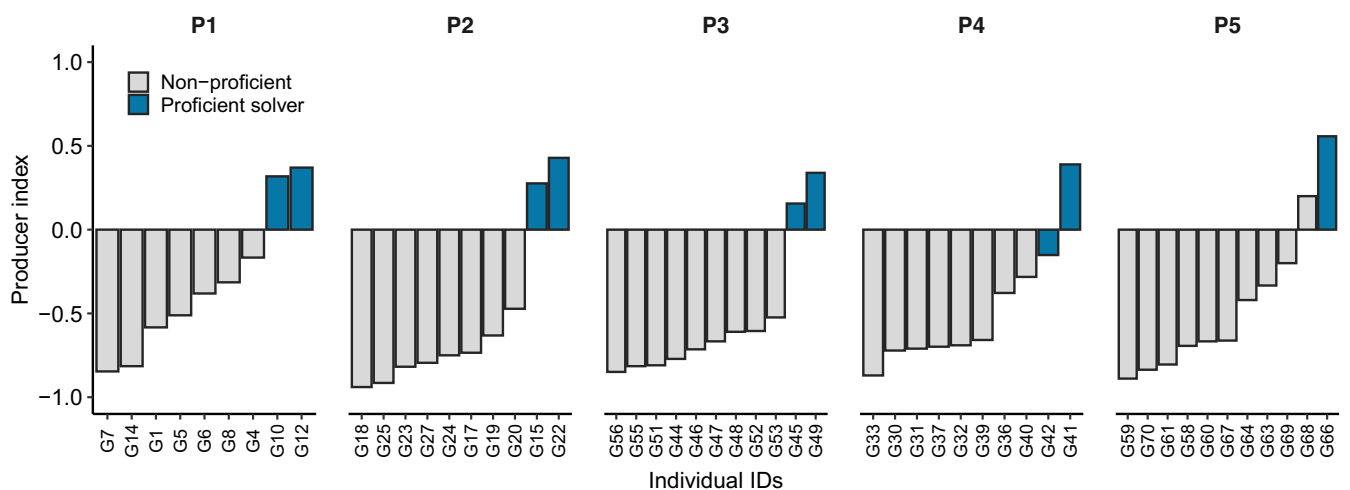


FIGURE 5 Wild-caught guppies showed variation in producer index (PI) which correlated well with solving proficiency scores (blue and grey bars), indicating individual guppies (G1–G70) within each subpopulation use one of the two alternative producer–scrounger behavioural strategies.

and almost never scrounging; and a scrounging strategy, that consists almost entirely on profiting from the solves of others. These strategies occurred at a similar frequency across subpopulations (proportion of scroungers $P1=0.78$, $P2=0.80$, $P3=0.82$, $P4=0.90$, $P5=0.82$).

4 | DISCUSSION

Despite a growing research interest in fish cognition, and in fish cognitive ecology in particular (Bshary & Triki, 2022; Patton & Braithwaite, 2015; Salena et al., 2021), the majority of studies to date (69%) use captive-bred rather than wild fish and rely heavily (91%) on lab-based experiments (Salena et al., 2021). In this paper, we present a new apparatus that can be used to measure fish cognition in situ in the field, allowing us to examine perception, several learning domains, decision-making and memory of wild fish directly in their natural environment. By providing a flexible and accessible tool to take fish cognition testing into the wild, we hope to advance research on the ecological and evolutionary drivers of variation in behaviour and cognition.

Our testing of the cognitive apparatus using wild-caught guppies in outdoor enclosures and wild nine-spined sticklebacks in situ shows that our foraging board was successfully used to obtain group-level learning curves in a colour association task. Importantly, the apparatus allows for multiple trials to be undertaken within a session without intervention of the experimenter, which reduces disturbance of fish in the wild, and can be adapted to simultaneously present more than two stimuli. It is therefore a valuable tool to efficiently assay multiple species or populations in their natural environment. While we only describe results on associative learning using two colours as stimuli in the case studies presented here, other behavioural and cognitive tasks can be easily implemented with this apparatus, which can then be linked to ecological factors, such as predation risk (Brown & Braithwaite, 2005; Kotrschal et al., 2017), or to fitness-related traits of individuals in the wild (Shaw et al., 2019; Szabo et al., 2022). Additionally, since the foraging board apparatus builds on a laboratory task widely used to assay associative learning in fish, including guppies, mollies and cichlids (Fischer et al., 2021; Lucon-Xiccato & Bisazza, 2014; Reyes-Contreras & Taborsky, 2022; Vila-Pouca et al., 2022) and also in other taxa, such as birds (Guillette et al., 2015; Shaw et al., 2019), it also allows a comparative approach between laboratory versus wild cognitive testing across species and taxa. The original design of our apparatus can be easily modified, for example by changing the size of the holes or the opening mechanism of the discs, thus making it adaptable to a wide range of fish of different sizes and ecology, and potentially even other taxa, such as reptiles (Szabo et al., 2022).

Furthermore, we also show the potential for using this apparatus to explore social cognition and decision-making strategies, such as producer–scrounger dynamics (Aplin & Morand-Ferron, 2017; Harten et al., 2018), in the context of a foraging task that involves a learnt skill component. In our additional case study with guppies that

were individually marked (Test 2), we found that individuals tended to alternate between producer and scrounger tactics across sessions, and only few individuals were consistently proficient solvers. All our subpopulations displayed a similar frequency of scroungers (approx. 80% of the individuals in each subpopulation) whereby both tactics obtain the same payoff, which is consistent with predictions from producer–scrounger games (Mottley & Giraldeau, 2000; Phillips et al., 2018). These analyses require that individuals can be uniquely identified; depending on the target species, this can be achieved through classic methods of marking individuals (e.g. elastomer tags, passive-integrated transponder tags) if it is possible to capture and tag all individuals in the study locations. On the other hand, current advances in software to identify and track unmarked individuals (Lauer et al., 2022; Walter & Couzin, 2021) will also allow automated data collection on unmanipulated, unmarked wild animals, especially when species show individual marking patterns (Phillips et al., 2024). One apparent caveat of the approach presented here may be the lack of access control for con- or heterospecifics. To ensure such control in areas with many opportunistically feeding species (e.g. coral reefs), the apparatus would need to be caged, enabling access only to the individuals of interest, similar to set-ups testing learning and memory in wild birds, that need to exclude squirrels (Aplin et al., 2015).

While most guppies in each subpopulation interacted with our apparatus and pecked at the discs (Test 1a), we determined in Test 2 that only a few fish were proficient in dislodging the discs. These results may arise from individual differences in learning speed and/or behavioural traits and social interactions during the experiment, namely exploratory tendency, boldness or aggression (Aplin & Morand-Ferron, 2017; Harten et al., 2018). It is also possible that social interactions, such as dominance or aggressive displays led to the lack of stability we found in producer–scrounger strategy use over time. These are important aspects that may need to be considered when testing groups of individuals that interact voluntarily with the experimental task, especially if we aim to compare experimental groups or laboratory and field studies.

This study provides a flexible and accessible tool for cognitive ecologists, behavioural ecologists and comparative psychologists to take fish cognition testing into the wild. We hope to advance research on the ecological and evolutionary drivers of variation in behaviour and cognition, as well as contributing to research on comparative cognition and animal welfare.

AUTHOR CONTRIBUTIONS

Catarina Vila-Pouca, Hannah De Waele, Antoine Parsékian, Amy Deacon and Alexander Kotrschal conceived the foraging board, placement apparatus and designed the case studies. Catarina Vila-Pouca, Hannah De Waele, Amy Deacon and Alexander Kotrschal obtained the research permits. Catarina Vila-Pouca, Hannah De Waele, Antoine Parsékian, Simone Erroi, Mariska De Rooij and Emma Labohm collected the data. Catarina Vila-Pouca and Antoine Parsékian analysed the data. Catarina Vila-Pouca, Hannah De Waele and Antoine Parsékian wrote a first version of the manuscript. All

authors contributed to improve the manuscript and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank Mr. Rupert Radix and the staff at the William Beebe Research Station, as well as the staff at the Guppy Project's research station in Temple Village, for the assistance provided during our stay in Trinidad. Thanks also to Mr. Eric Karruppannan and his team at the Technical Development Studio, WUR, for assistance with building the foraging board and placement apparatus. We further thank L. Snijders, J. Krause and A. Valentim for discussions on anaesthesia and VIE tagging methods.

FUNDING INFORMATION

This work was funded by ASAB (ASAB 2020 Research Grant to C.V.P.), KNAW (KNAWWF/DA/973/Eco2013 to C.V.P.; KNAWWF/705/202205 to H.D.W.), Foundation Lucie Burgers for Comparative Behaviour Research, Arnhem, the Netherlands (2020 to C.V.P. and 2021 to H.D.W.) and Dr. J. L. Dobberke Foundation for Comparative Psychology (2229/202208 to A.K.).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.70002>.

DATA AVAILABILITY STATEMENT

Data and code for analyses are available via <https://doi.org/10.6084/m9.figshare.25316365.v1> (Vila-Pouca, 2025).

ORCID

Catarina Vila-Pouca  <https://orcid.org/0000-0001-6956-5198>

Hannah De Waele  <https://orcid.org/0000-0002-8513-634X>

Amy Deacon  <https://orcid.org/0000-0002-7739-2925>

Alexander Kotrschal  <https://orcid.org/0000-0003-3473-1402>

REFERENCES

- Ajuwon, V., Cruz, B. F., & Carriço, P., Champalimaud Research Scientific Hardware Platform, Kacelnik, A., & Monteiro, T. (2024). GoFish: A low-cost, open-source platform for closed-loop behavioural experiments on fish. *Behavior Research Methods*, 56(1), 318–329.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518(7540), 538–541.
- Aplin, L. M., & Morand-Ferron, J. (2017). Stable producer–scrounger dynamics in wild birds: Sociability and learning speed covary with scrounging behaviour. *Proceedings of the Royal Society B: Biological Sciences*, 284(1852), 20162872.
- Balcombe, J. P., Barnard, N. D., & Sandusky, C. (2004). Laboratory routines cause animal stress. *Journal of the American Association for Laboratory Animal Science*, 43(6), 42–51.
- Barreto, R. E., Volpato, G. L., & Pottinger, T. G. (2006). The effect of elevated blood cortisol levels on the extinction of a conditioned stress response in rainbow trout. *Hormones and Behavior*, 50(3), 484–488.
- Bebus, S. E., Small, T. W., Jones, B. C., Elderbrock, E. K., & Schoech, S. J. (2016). Associative learning is inversely related to reversal learning and varies with nestling corticosterone exposure. *Animal Behaviour*, 111, 251–260.
- Bowman, R. E. (2005). Stress-induced changes in spatial memory are sexually differentiated and vary across the lifespan. *Journal of Neuroendocrinology*, 17(8), 526–535.
- Brown, C., & Braithwaite, V. A. (2005). Effects of predation pressure on the cognitive ability of the poeciliid *Brachyraphis episcopi*. *Behavioral Ecology*, 16(2), 482–487.
- Bshary, R., & Triki, Z. (2022). Fish ecology and cognition: Insights from studies on wild and wild-caught teleost fishes. *Current Opinion in Behavioral Sciences*, 46, 101174.
- Ebbesson, L. O. E., & Braithwaite, V. A. (2012). Environmental effects on fish neural plasticity and cognition. *Journal of Fish Biology*, 81(7), 2151–2174.
- Fischer, S., Balshine, S., Hadolt, M. C., & Schaedelin, F. C. (2021). Siblings matter: Family heterogeneity improves associative learning later in life. *Ethology*, 127(10), 897–907.
- Guillette, L. M., Hahn, A. H., Hoeschele, M., Przyslopski, A.-M., & Sturdy, C. B. (2015). Individual differences in learning speed, performance accuracy and exploratory behaviour in black-capped chickadees. *Animal Cognition*, 18, 165–178.
- Harten, L., Matalon, Y., Galli, N., Navon, H., Dor, R., & Yovel, Y. (2018). Persistent producer–scrounger relationships in bats. *Science Advances*, 4(2), e1603293.
- Jungwirth, A., Horsfield, A., Nührenberg, P., & Fischer, S. (2024). Estimating cognitive ability in the wild: Validation of a detour test paradigm using a cichlid fish (*Neolamprologus pulcher*). *Fishes*, 9(2), 50.
- Kotrschal, A., Deacon, A. E., Magurran, A. E., & Kolm, N. (2017). Predation pressure shapes brain anatomy in the wild. *Evolutionary Ecology*, 31, 619–633.
- Lauer, J., Zhou, M., Ye, S., Menegas, W., Schneider, S., Nath, T., Rahman, M. M., Di Santo, V., Soberanes, D., & Feng, G. (2022). Multi-animal pose estimation, identification and tracking with DeepLabCut. *Nature Methods*, 19(4), 496–504.
- Lucon-Xiccato, T., & Bisazza, A. (2014). Discrimination reversal learning reveals greater female behavioural flexibility in guppies. *Biology Letters*, 10(6), 20140206.
- Mottley, K., & Giraldeau, L.-A. (2000). Experimental evidence that group foragers can converge on predicted producer–scrounger equilibria. *Animal Behaviour*, 60(3), 341–350.
- Näslund, J. (2021). Reared to become wild-like: Addressing behavioral and cognitive deficits in cultured aquatic animals destined for stocking into natural environments—A critical review. *Bulletin of Marine Science*, 97(4), 489–538.
- Patton, B. W., & Braithwaite, V. A. (2015). Changing tides: Ecological and historical perspectives on fish cognition. *Wiley Interdisciplinary Reviews: Cognitive Science*, 6(2), 159–176.
- Phillips, E. W., Bottacini, D., Schoonhoven, A. N., Kamstra, Y. J., De Waele, H., Jimenez, C., Hadjioannou, L., & Kotrschal, A. (2024). Limited effects of culling on the behavior of invasive lionfish (*Pterois miles*) in the Mediterranean. *Journal of Fish Biology*, 104(5), 1401–1410. <https://doi.org/10.1111/jfb.15686>
- Phillips, J. A., Peacock, S. J., Bateman, A., Bartlett, M., Lewis, M. A., & Krkošek, M. (2018). An asymmetric producer–scrounger game: Body size and the social foraging behavior of coho salmon. *Theoretical Ecology*, 11, 417–431.
- Pritchard, D. J., Hurly, T. A., Tello-Ramos, M. C., & Healy, S. D. (2016). Why study cognition in the wild (and how to test it)? *Journal of the Experimental Analysis of Behavior*, 105(1), 41–55.

- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Reyes-Contreras, M., & Taborsky, B. (2022). Stress axis programming generates long-term effects on cognitive abilities in a cooperative breeder. *Proceedings of the Royal Society B: Biological Sciences*, 289(1975), 9.
- Rosati, A. G., Machanda, Z. P., & Slocombe, K. E. (2022). Cognition in the wild: Understanding animal thought in its natural context. *Current Opinion in Behavioral Sciences*, 47, 101210.
- Salena, M. G., Turko, A. J., Singh, A., Pathak, A., Hughes, E., Brown, C., & Balshine, S. (2021). Understanding fish cognition: A review and appraisal of current practices. *Animal Cognition*, 24, 395–406.
- Shaw, R. C., MacKinlay, R. D., Clayton, N. S., & Burns, K. C. (2019). Memory performance influences male reproductive success in a wild bird. *Current Biology*, 29(9), 1498–1502.e3.
- Sneddon, L. U., Wolfenden, D. C., & Thomson, J. S. (2016). Stress management and welfare. *Fish Physiology*, 35, 463–539.
- Szabo, B., Valencia-Aguilar, A., Damas-Moreira, I., & Ringler, E. (2022). Wild cognition—linking form and function of cognitive abilities within a natural context. *Current Opinion in Behavioral Sciences*, 44, 101115.
- Vila Pouca, C., & Brown, C. (2017). Contemporary topics in fish cognition and behaviour. *Current Opinion in Behavioral Sciences*, 16, 46–52.
- Vila-Pouca, C. (2025). Data, code, and supp video for 'A novel apparatus for studying fish cognition in the wild'. *Figshare*. <https://doi.org/10.6084/m9.figshare.25316365.v1>
- Vila-Pouca, C., Vedder, S., & Kotrschal, A. (2022). Hybridization may promote variation in cognitive phenotypes in experimental guppy hybrids. *The American Naturalist*, 13, 607–619.
- Walter, T., & Couzin, I. D. (2021). TRex, a fast multi-animal tracking system with markerless identification, and 2D estimation of posture and visual fields. *eLife*, 10, e64000.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Code.

Appendix S1: A novel apparatus for studying fish cognition in the wild.

Video S1: Video demonstrating the assembly of the cognitive testing apparatus and its application possibilities with different species and in different bodies of water, such as a pond or a shallow stream.

How to cite this article: Vila-Pouca, C., De Waele, H., Parsékian, A., Erroi, S., De Rooij, M., Labohm, E., Deacon, A., & Kotrschal, A. (2025). A novel apparatus for studying fish cognition in the wild. *Methods in Ecology and Evolution*, 00, 1–10. <https://doi.org/10.1111/2041-210X.70002>