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Jones, Nick A.R.

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RESEARCH ARTICLE

Short-range hunters: exploring the function and constraints of water shooting in dwarf gouramis

Nick A. R. Jones[1,*], Barbara C. Klump[2], Teresa M. Abaurrea[3], Sophie Harrower[1,4], Clare Marr[1], Louise Scott[1], Luke Rendell[1] and Mike M. Webster[1]

ABSTRACT

Ballistic predation is a rare foraging adaptation: in fishes, most attention has focused on a single genus, the archerfish, known to manipulate water to shoot down prey above the water surface. However, several gourami species also exhibit apparently similar 'shooting' behaviour, spitting water up to 5 cm above the surface. In a series of experiments, we explored the shooting behaviour and aspects of its significance as a foraging ability in the dwarf gourami (*Trichogaster lalius*). We investigated sex differences in shooting abilities to determine whether gourami shooting is related to the sex-specific bubble nest manufacture where males mix air and water at the surface to form bubbles. We found that, actually, both sexes were equally able to shoot and could learn to shoot a novel target. In a second experiment, we presented untrained gouramis with opportunities to shoot at live prey and found they successfully shot down both fruit flies and crickets. Finally, we explored the effect of target height on shooting performance to establish potential constraints of shooting as a foraging ability. The frequency of attempted shots and success of hitting targets decreased with height, whereas latency to shoot increased. We also observed that repeatable individual differences account for variation in these measures of shooting performance. Together, our results provide evidence that gourami shooting has a foraging function analogous to that of archerfish. Gourami shooting may serve as an example of convergent evolution and provide opportunities for comparative studies into the, as yet unexplored, ecology and evolution of shooting in fishes.

KEY WORDS: Ballistic predation, Gourami, Shooting, *Trichogaster lalius*, Foraging adaptation

INTRODUCTION

Behavioural adaptations like tool use that afford access to otherwise unreachable foods sources can be an obvious advantage. A major benefit lies in the potential for the expansion of foraging niches and reduction of competition for food, especially when resources are sparse or unpredictable (Fellers and Fellers, 1976; Yamakoshi, 1998; Rutz et al., 2010; Spagnoletti et al., 2012; Krützen et al., 2014). For example, Galápagos woodpecker finches (*Cactospiza pallida*) use twig tools to extract otherwise inaccessible prey, burrowed within trees, to overcome food scarcity (Tebbich et al., 2002). Tool use and similar behavioural adaptations that expand foraging limits are relatively rare but not as taxon exclusive as once thought (Hansell and Ruxton, 2008; Seed and Byrne, 2010; Brown, 2011; Shumaker et al., 2011). Ballistic predation, where an object or body part is used as a projectile to capture prey (Sakes et al., 2016), is similarly rare, but occurs across a wide variety of taxa – such as salamanders from the genus *Hydromantes* (Deban and Richardson, 2011), mantis shrimp (Patek et al., 2004), slingshot and spitting spiders (Alexander and Bhamla, 2020; Suter and Stratton, 2013), *Loligo* squid species (Kier and Leeuwen, 1997) and humans (Wood et al., 2007; Roach et al., 2013). Ballistic predation can be used to expand the foraging limits and among non-human animals one of the more notable examples is the archerfish (*Toxotoes* spp.) with an impressive shooting ability that allows them to prey on terrestrial and aerial targets in addition to their aquatic prey (Elshoud and Koomen, 1985; Salini et al., 1990; Schuster, 2007). When shooting, archerfish form and direct a jet of water they use to down prey above up to 2 m above the water surface – affording them foraging opportunities inaccessible to most other fish species (Bekoff and Dorr, 1976; Dill, 1977). This ability is also considered tool use (Beck, 1980; Brown, 2011), as it fulfils criteria proposed by Shumaker et al. (2011), who considered a tool to be an object that must: (1) not be part of the animal itself; (2) be an unattached or manipulable attached environmental object; and (3) be manipulated to achieve some beneficial outcome. Archerfish are not the only fish that can 'shoot' jets of water. Many species are known to use hydraulic jetting – also referred to as water jetting – to produce underwater jets to dislodge prey from crevasses, or uncover prey burrowed within sandy substrates. Examples include triggerfish (Chen et al., 2001) and rays (Gregory et al., 1979; Sasko et al., 2006). Moreover, some species of gourami in the family Osphronemidae can manipulate water to produce aerial shots, albeit with much shorter shot distances than archerfish can achieve (Lüling, 1969; Vierke, 1969). Little research attention has been paid to shooting in gouramis and the mechanism and function of their aerial shooting is largely unknown.

Several species of gouramis from the genera *Trichogaster* and *Trichopodus* are able to shoot water above the surface, a behaviour referred to as 'jetting' (Hall, 1966; Miller and Jearld, 1983) or 'spitting' (Vierke, 1969). We will use 'shooting' to refer to this behaviour here. Shooting in gouramis has been compared with that of archerfish historically (Lüling, 1969) and, like archerfish, their ability is considered an example of tool use (Brown, 2011). However, many questions remain regarding gourami shooting abilities and its function. Their shots reach limited height relative to

[1]Centre for Biological Diversity, School of Biology, University of St Andrews, St Andrews KY16 9TH, UK. [2]Cognitive and Cultural Ecology Research Group, Max Planck Institute of Animal Behavior, Am Obstberg 1, 78315 Radolfzell am Bodensee, Germany. [3]Helsinki Institute of Life Science HiLIFE, University of Helsinki, 00014 Helsinki, Finland. [4]School of Psychology and Neuroscience, University of St Andrews, St Andrews KY16 9JP, UK.

*Author for correspondence (narj@st-andrews.ac.uk)

N.A.R.J., 0000-0002-6031-7507; B.C.K., 0000-0003-3919-452X; T.M.A., 0000-0003-4304-9819

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archerfish (5 cm versus 2 m; Vierke, 1969) and while gouramis have been observed to shoot within a feeding context, this was normally with artificial foods (Lüling, 1969; Vierke, 1969; 1975; Miller and Jearld, 1983). There are also only anecdotal observations that gouramis shoot down live prey (Lüling, 1969; Vierke, 1973). Most observations of shooting were frequently incidental (Miller and Jearld, 1983) or limited to few fish – the same single male fish was used in two studies (Vierke, 1969 and Lüling, 1969). Similarly, there is little information on sex differences in shooting in gouramis: females have been recorded shooting, but only three female dwarf gouramis from a total of six tested (Vierke, 1973). The function (Tinbergen, 1963) or specifically, the current utility (*sensu* Bateson and Laland, 2013) and ecological importance of gourami shooting ability therefore remains unknown. A question that remains unaddressed is whether the shooting behaviour of this species is analogous to that of archerfish in being a behavioural adaptation or exaptation with a foraging function.

The shooting observed in gouramis may have functions other than foraging. First, gouramis as members of the Anabantoidei suborder, are facultative air-breathers and routinely suck in and exhale air directly from the surface as part of their air breathing system (Peters, 1978; Schuster, 1989; Graham, 1997). Second, they are bubble nesters, and males manipulate air and water at the surface as part of their nest building: all *Trichogaster* and most *Trichopodus* species construct 'bubble nests' where they blow bubbles to form rafts of mucus-lined bubbles where eggs are later placed and kept (Tate et al., 2017). Some species 'shoot' their bubbles and eggs into position on top of these nests; indeed, shooting or 'jetting' by a gourami was first described in the pearl gourami, *Trichopodus leerii*, in a spawning context (Hall, 1966). As males are the only sex that builds nests, shooting behaviour in gouramis may be sex-specific if shooting is related to bubble nest construction. As argued by Vierke (1969, 1973), shooting behaviour of gouramis may be a form of displacement behaviour, as an 'out-of-context' action expressed by organisms in stressful situations such as captivity (Anselme, 2008), rather than a foraging-specific behaviour.

Another aspect to consider with regards to the function of shooting is the effective range of shots and the willingness to make consecutive shooting attempts at a target. Gouramis exhibit much shorter shooting distances relative to archerfish, reaching only about 5 cm in vertical height (Vierke, 1969). However, the effect of height on shooting success has not been tested. We do not know whether the ability to hit targets is affected by height within their 5 cm range. Their limited range also raises the question of the ecological and dietary importance of shooting. Timmermans (2000) suggested that the persistence of shooting or 'endurance' – where repeated shots are made in an attempt to hit potential prey – is one indicator of the importance of shooting as a foraging behaviour and is easily testable in a laboratory context. Archerfish show such shooting endurance: they exhibit variable rates of hitting a target depending on target height (Dill, 1977; Timmermans, 2001) and will persist in shooting at a target until either making a successful hit (Timmermans, 2000; Schuster et al., 2004), or learn that a target is not rewarded (Newport et al., 2013). Do gouramis, like archerfish, focus on and make multiple attempts to shoot at targets, and does this endurance and success vary with target height?

In this study, we investigated the function of shooting behaviour in the dwarf gourami *Trichogaster lalius*, which is the gourami species with the most evidence for a shooting ability (Lüling, 1969; Vierke, 1969, 1973). We tested several hypotheses. First, we tested whether shooting behaviour varied with sex. Male gouramis manipulate water at the surface to create bubble nests, a behaviour that female gouramis do not exhibit. We reasoned that if shooting were related to nest-building behaviour then males may be more likely to shoot and learn to shoot novel targets more quickly. Second, we tested whether untrained fish would shoot at live prey. Vierke (1969) mentioned that the dwarf gourami he tested shot at live insect prey, but it is unclear whether the fish had been trained to shoot or not. We specifically aimed to test whether untrained fish would shoot at and feed on live insect prey presented above the water surface. Third, we explored potential constraints on their shooting by testing whether gouramis would show target 'endurance' by making repeated attempts to shoot targets, and the effects of target height on shooting performance, specifically latency to shoot and shot success (where shots hit the target). Our design allowed us to additionally investigate the individual repeatability of shooting latency across a range of target heights.

MATERIALS AND METHODS

Subjects

Fish used in the experiments were all captive bred adult *Trichogaster lalius* (Hamilton 1822), sourced from commercially bred fish via ornamental fish wholesalers (JMC aquatics, UK) and housed in a purpose-built warm-water fish laboratory in the Sir Harold Mitchell Building, University of St Andrews, UK. The fish we used were of unknown age but were sexually mature. Both stock and experimental tanks were maintained in the same room with the same conditions and water quality. The air temperature control system kept the water temperature of the tanks between 24.5 and 25°C. Lighting was maintained on a 12 h light:12 h dark cycle and the water pH level of all tanks was maintained at ∼8.1. Housing and experimental tanks were enriched with gravel, plastic plants and an internal filter (for details on additional enrichment provided in experimental tanks, see below). Fish were fed twice daily, after any experimental sessions, with a mixed diet of TetraMin flake food, small floating pellets (Tetra Pro cichlid disks), and freeze-dried bloodworm. Cut-off times for achieving performance criteria, and details on subjects that failed to achieve these, are listed below as per the STRANGE framework (Webster and Rutz, 2020). All individuals tested in our study were sourced from a single ornamental retailer and were likely from a single population.

All procedures performed were in accordance with the ethical standards of the University of St Andrews and methods used were approved by the University of St Andrews Animal Welfare and Ethics Committee (AWEC). No procedures required UK Home Office licensing. All individuals were retained in the laboratory for use in future experiments.

Overview of experiments

We conducted three separate experiments. In the first experiment, conducted between November 2017 and February 2018, we tested for sex differences in shooting ability and tendency to shoot. In the second experiment, conducted between September and November 2019, we tested whether untrained fish would shoot at and consume live prey when presented with the opportunity. The fish used in this experiment had not been exposed to live prey or trained to shoot previously. In experiment 3, conducted between October 2019 and February 2020 we explored the effect of height on shooting performance in gouramis. No individuals were used in more than one experiment.

Apparatus and experimental setup

A similar experimental set-up was used for all experiments. Subjects were housed individually in separate experimental tanks on a rack

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Fig. 1. Female dwarf gourami (*Trichogaster lalius*) making a shot at an artificial target. Targets were presented on a dowel 3 cm above the water surface as per the setup used in experiment 3.

with five tanks per row, each tank was 60×30×30 cm. Each tank was furnished with physical enrichment in the form of one plastic plant (30 cm tall artificial model of needle leaf java fern), a 1 cm layer of gravel with mixed grain size from 2 to 6 mm diameter (covering 100% of the surface area of the tank floor). Each tank also had a single bubble filter. Lighting was provided by a single LED strip running along the top of each rack, directly above the tanks, set at 12 h light:12 h dark cycle. Prior to testing, an opaque barrier was placed between neighbouring tanks to prevent visible contact between fish.

Targets were presented to the fish using one of two systems depending on the experiment. In experiment 1, we used a pulley system to present targets to the fish at the water surface and manipulate the target position and height above water level (see Fig. S1). A single black bead (5 mm in diameter) was used as the target for fish to learn to shoot at. This bead was suspended from the pulley above the water surface with clear monofilament fishing line.

In experiments 2 and 3, we used a vertical standing wooden dowel measuring 0.5 cm in diameter, glued into a small dish weighed down with gravel to present targets to the fish. For experiment 2, two of these dowels were use as supports for a horizontally positioned wooden beam (of the same thickness) upon which live prey were positioned. In experiment 3, a single dowel was used and artificial targets were placed on the dowel at specific pre-measured heights (Fig. 1 and Movie 1). Markings were placed on the dowel at each centimetre from 1 to 5 cm above the water surface and a dowel was left in each tank for the duration of the experiment to allow the fish to habituate to it. For shooting trials, an artificial target, a small ball of grey plasticine measuring 1 cm in diameter, was applied to the dowel at one of the height markings. The target was manually applied before the beginning and removed at the end of each trial to avoid habituation to the target outside of the trials. Once the plasticine target was applied, the experimenter would stand out of the fish's view during trials to avoid stressing or distracting the fish.

Experiment 1: sex differences in shooting behaviour

Here, 20 dwarf gouramis, ten of each sex, were trained to shoot jets of water at a black plastic bead for a food reward. Untested fish were randomly allocated to an individual experimental tank and allowed to acclimatise for 3 days before training began. Each fish was first trained to associate a plastic target (a single black bead 5 mm in diameter) with a food reward. During this phase, fish were given two training sessions per day where every time they bit or touched the bead with their snout a food reward was dropped into the water. Sessions ended after 15 min or if fish bit/touched the target and consumed the reward 10 times, whichever occurred first. A fish was considered to have learnt the association between target and food reward after it bit (made contact with the target using its mouth) ten times in each of three consecutive sessions. Fish were then trained to shoot the target by positioning it 2.5 cm above the surface of the water such that the fish had to shoot water to hit the target. The rest of the procedure was the same as that in the biting association training, with the same learning criterion with fish considered to have reached the learning criterion once they hit the target with water in each of ten trials across three consecutive sessions.

Experiment 2: shooting at live prey

Female dwarf gouramis that had not previously been given any opportunities to shoot were presented with live prey; all naive fish that were available at the time were tested. We used females as experiment 1 showed they were as capable as males at shooting and females are easier to maintain than males, which show high intra-specific aggression, especially to other males. Each fish was given one session per day with one of two types of live prey presented to them at the beginning of the trial by releasing the prey onto the horizontal dowel. Prey were either *Drosophila pseudoobscura* averaging 2 mm in length or juvenile 'black' crickets (*Gryllus bimaculatis*), averaging 4 mm in length. In each session, five of a particular prey species were released onto slim wooden dowels (3 mm width), which were positioned 2 cm above the water surface. A close-fitting Perspex lid was placed on top of the tank to prevent any of the prey from escaping. Each session was recorded with a USB 5 megapixel camera. Any un-eaten prey was removed at the end of a session, which lasted 15 min, and at this time numbers of prey eaten were confirmed by counting the numbers that remained. The two prey types used were chosen from several types of live food commercially available for pets. We used a pilot study, to select the species that had lower mobility compared with the other species, meaning they were less likely to jump into the water of their own accord.

Experiment 3: endurance and effect of height

In this experiment, 10 female fish were exposed to shooting opportunities at different heights. Each fish was first trained to shoot at a particular target (a 1 cm ball of grey plasticine), those fish that passed training were given equal numbers (N=100) of opportunities to shoot at a target that could be fixed to one of the five specific heights for each trial (N=20 trials per height per fish). Fish were trained and then tested in two batches of five.

Fish were first trained to shoot the plasticine target. Each fish was given 9 days of training over 2 weeks. For each of the first 4 days, the target was placed on the dowel just above (0.1 cm) the water surface for them to associate the cue with a food reward. Fish were rewarded

by the experimenter with a dried bloodworm if they shot at, or bit/touched the target with their mouth. Fish were trained twice a day, in random order, and the trial ended when the fish had either been rewarded 10 times or 30 min had passed. The target was then raised to 3 cm above the water surface for the remaining 5 days of training. Fish were rewarded for shots that successfully hit the target, but also for attempting to hit the target, to encourage shooting. A fish was considered to have met the training criterion once it had performed at least one shot in each of three consecutive trials, shots were counted regardless of whether they hit the target. After reaching the training criterion fish were moved to the experimental phase detailed below. Any fish that had not met the training criterion by the end of day 9 did not participate further in the experiment; 2 of the initial 10 fish failed to meet the criterion.

After the training stage was complete, experimental trials were carried out. Each of the remaining 8 fish was subjected to a session of trials twice a day, with 10 trials per session. For each trial the target was placed at one of five different heights from 1 cm up to 5 cm above the water surface. A random sequence generator was used to designate the order in which fish were presented with targets at specific heights. A trial lasted 5 min or ended when the fish had shot and been rewarded. There was no break between the 10 trials. After a reward was eaten, the target was immediately moved to the next height level and the clock was reset. We recorded the number of shots, whether they hit the target, latency to attempt a first shot and latency to make a successful shot (that hit the target) for each trial. Overall, each fish was given 20 trials at each height level from a total of 100 trials per fish over 5 days. See Fig. 1 for photograph sequence of gourami shooting at a target at 3 cm height.

Statistical analyses

All analyses were conducted using R base package (https://www.r-project.org/). The lme4 package (https://CRAN.R-project.org/package=lme4; Bates et al., 2015) was used to fit the multi-level models and post hoc pairwise comparisons were conducted using the emmeans package (https://CRAN.R-project.org/package=emmeans) where appropriate.

Experiment 1: sex differences

To compare the proportions of male and female fish that shot, we used Fisher's exact test. To examine potential sex differences in learning to shoot a novel target, we fitted a generalized linear mixed model (GLMM), with the number of sessions required to reach the learning criterion as the response variable, and a Poisson family link function to account for the distribution of the count data. The fixed effect was sex and we included individual identity as a random term, given the large inter-individual differences we observed in time to train the fish. For the fixed effect of sex, we ran a likelihood ratio test (LRT), comparing the models with and without sex included as a factor, to calculate its significance.

Experiment 2: shooting at live prey

As we merely wanted to confirm whether fish shot down and ate prey, this experiment was observational only.

Experiment 3: effect of height on shooting performance

We examined the effects of height on three variables: (1) the numbers of shots attempted per trial, (2) the latency to make a shot attempt after the target was revealed and (3) the numbers of successful shots made per trial (where success was recorded when a shot hit the target). To do this we fitted a GLMM, for each response variable with height as the fixed factor. We used a Poisson family link function for all three models. Fish identity, day of testing, session number and trial number were initially included as random factors to account for changing satiation affecting shooting motivation and related effects on performance between days and within sessions. Session number and day were removed as random terms from the final models fitted as they each accounted for less than 0.01 of variance within the full models.

Repeatability of shooting behaviour and success

Repeatability of latency to shoot across the different target heights was estimated using the rptR package in R (https://CRAN.R-project.org/package=rptR; Stoffel et al., 2017), which builds on the mixed-model functions and uses parametric bootstrapping to provide reliable estimates for repeatability '*R*' and the uncertainty (confidence intervals) of these estimates. When using the model, we fitted for latency to make a first shot, as above, with the rpt function from the rptR package to obtain measures of repeatability for each fish.

To examine the effect of individual latency to shoot on overall success we fitted a generalized linear model (GLM) to the mean number of successful shots from all trials for each fish, with individual mean latency as the independent variables. Similarly, we estimated the mean number of shots attempted (including both shots that hit and missed) per trial for each fish by fitting a generalized linear model (GLM) with mean success rate and numbers of a shots as the independent variables.

RESULTS

Experiment 1: sex differences

Both males and females shot (Fig. 2A), and there was no significant difference in the proportion of fish that shot across sexes (Fisher's exact test: P=0.591, odds ratio=2.847). Similarly, when being trained to shoot novel objects, there was no effect of sex on time to reach the learning criterion (LRT on 'Sex' predictor:χ^2_1=1.83, P=0.176; Fig. 2B).

Experiment 2: live prey

When naive untrained female fish were given opportunities to shoot live prey, 4 out of 5 individuals had shot at the prey by the third trial, although the fifth individual never attempted a shot (Table 1).

Experiment 3: endurance and effects of height on shooting performance

Target height had an important effect on shooting performance. Gouramis exhibited shooting 'endurance' and would repeat shots, up to a recorded maximum of 10 times, before hitting the target and being rewarded. Height was an important factor, (LRT:χ^2_4=48.984, P<0.001; Fig. 3A), and the frequency of attempted shots decreased with height. However, while there were significantly fewer shots attempted at targets set at both 4 and 5 cm (P<0.001) than 1 cm targets, *post hoc* comparisons showed there were no difference between frequency of attempted shots made at targets set at 1, 2 or 3 cm.

Height also affected both latency to shoot and shooting success (shot that hits the target). Latency to make a first shot in a trial, was influenced by height (LRT:χ^2_4=1420.8, P<0.001; Fig. 3B). Latencies to shoot increased significantly at targets presented at heights of 3 cm and above. *Post hoc* contrasts for targets set at 3, 4 and 5 cm above the water surface were significantly different from those set at 1 cm, (emmean contrasts, all P<0.001). The ability to hit the target also varied with target height and the numbers of shots that successfully hit the target decreased with height

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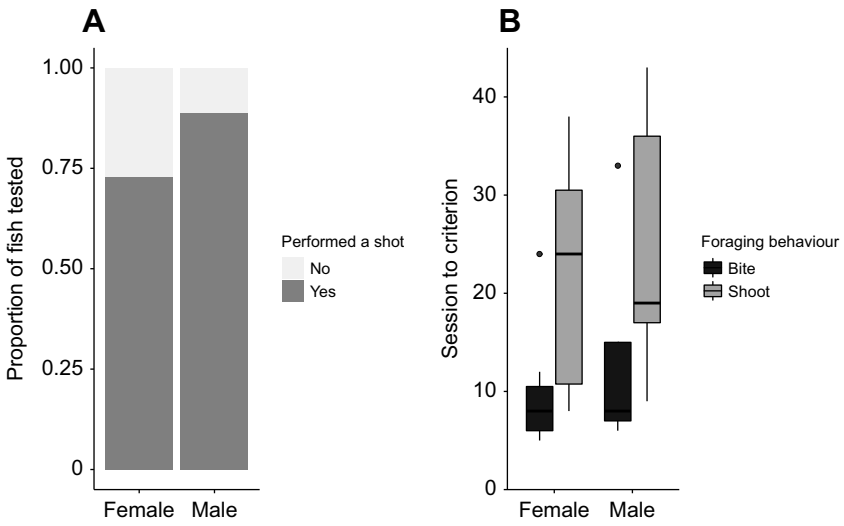

Fig. 2. Shooting in dwarf gouramis across sexes. (A) Both sexes shoot, and similar proportions of individuals shot at least once during experimental testing; P=0.591, Fisher's exact test. (B) Males and females learn to shoot novel targets at similar rates (P=0.176, LR) first associating artificial targets with reward, by learning to bite targets presented at the water surface and then by learning to shoot targets raised above the surface. N=20 (10 males and 10 females) for both A and B. The box plots show the median, 25th and 75th percentiles, and the whiskers extend to the data point that is no more than 1.5 times the length of the box as per the Tukey method (ggplot2). Points represent values outside these limits.

(LRT:χ^2_4=28.642, P<0.001). Mean success, as a proportion of shots attempted, dropped at each level of height from emmean 0.956±0.137 at 1 cm to emmean 0.555±0.145 at 5 cm (means±s.e.). Success at heights 4 and 5 cm were not significantly different from each other (lsmean: $z_{0.168}$=0.093 P≤0.374).

Individual differences

Latency to shoot was significantly impacted by fish identity when comparing the model with and without fish identity as a random factor (LRT:χ^2_1=4437.5, P<0.001), and latency was repeatable within individuals across heights, albeit at a low level (Fig. 4; Table 2), following Wolak et al. (2012). These inter-individual differences in latency had consequences on shooting success. Individual mean latency significantly affected shooting success: slower fish had lower success at hitting the target (GLM:χ^2_1=9.334, P=0.002; Fig. 5A), with the fitted model estimates suggesting success dropped by 0.009±0.003 (mean±s.e.) for each second increase in latency to shoot. This increased success by 'fast' fish may be driven by the fact that fast fish tended to attempt more shots and success in a trial increased with the number of shots made (GLM:χ^2_1=16.724, P<0.001; Fig. 5B).

DISCUSSION

We found no sex differences in tendency to shoot, or time taken to learn to shoot at a novel object in our experiments. In conjunction with observations of three female dwarf gouramis shooting (Vierke, 1975), our results rule out the hypothesis that their shooting ability is a sex-specific exaptation from bubble nesting. We also show that female gouramis will use shooting to forage for live prey: untrained females rapidly learnt to shoot live prey when presented with opportunities to do so. We have also shown that gouramis are persistent and exhibit shooting 'endurance', making multiple repeated shots at a target until successfully hitting it, providing some evidence of the functional relevance of ballistic predation, as tested and shown for archerfish by Timmermans (2000). Together, our results suggest that the shooting behaviour of dwarf gouramis has a foraging function or at least current utility.

With regards to shooting performance, our results confirm that while gouramis are able to hit targets up to 5 cm high as per earlier studies (Lüling, 1969; Vierke, 1973), their success rates begin to drop at prey heights above 3 cm, and there is reduced tendency to shoot at targets over 4 cm high. Given this limited effective hunting range, it remains unclear how important shooting is as a foraging adaptation. The height limitations of shooting must be considered in conjunction with ecological aspects and dietary importance of shooting, and unfortunately there is limited detail of the foraging behaviour and environmental characteristics of gouramis in the wild. There is little published information regarding the preferred habitat of dwarf gouramis, but references from Fishbase (Froese and Pauly, 2000) suggest that they inhabit highly vegetated areas (Menon, 1999). The density and height of vegetation close to the surface of the water may lend themselves to short range shots being sufficient for hunting prey. It is worth noting that across ballistic foragers in the animal kingdom also tend to have limited range (Sakes et al., 2016). Other fish known to successfully prey on aerial and terrestrial prey have short effective ranges too: redside dace (*Clinostomus elongatus*) use short-range jumps of <10 cm to capture flying insects, which can constitute over 80% of their diet (Daniels and Wisniewski, 1994). Despite their comparative shooting prowess and much longer shot range, questions around the dietary importance of shooting also remain unaddressed in archerfish. Gut content analysis suggests that the archerfish diet may consist primarily of aquatic prey (Salini et al., 1990; Simon and Mazlan, 2010) and some archerfish are apparently morphologically unable to shoot (Elshoud and Koomen, 1985; Timmermans and Vossen, 2000).

Table 1. Shooting at live prey without training by individual female fish presented with two types of live prey over consecutive single trial sessions

Session	1	2	3	4	5	6	7	8
Prey type	Fly	Fly	Fly	Fly	Cricket	Cricket	Cricket	Cricket
Fish 1	No	No	Yes	Yes	Yes	Yes	Yes	Yes
Fish 2	No	No	Yes	Yes	Yes	Yes	No	Yes
Fish 3	No	No	No	No	No	No	No	No
Fish 4	No	No	Yes	No	Yes	No	Yes	Yes
Fish 5	No	No	Yes	No	Yes	No	Yes	Yes

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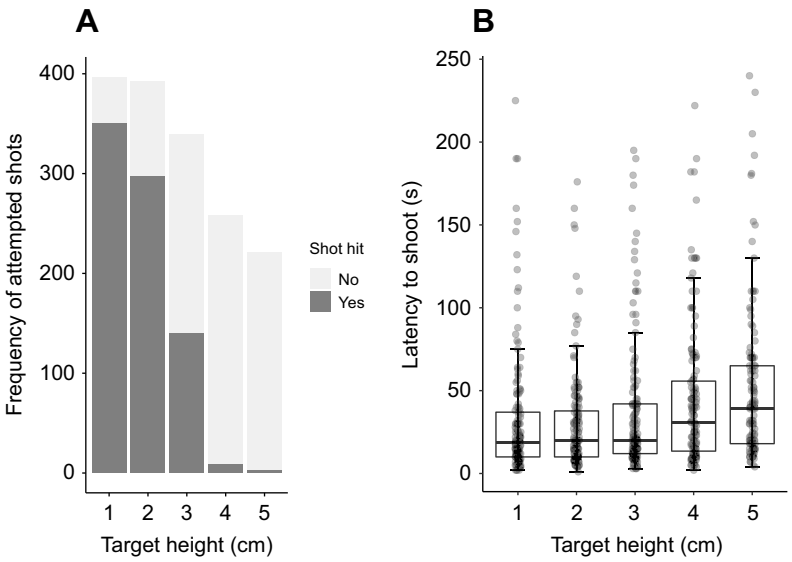

Fig. 3. Target height affects propensity to shoot, shot success and latency to shoot. (A) Counts of shots across all trials and all fish that either hit (success) or missed the target as a function of target height. (B) Latency to shoot as a function of target height, showing increased latency with heights above 3 cm; $P<0.001$, LRT. The points in B represent the latency of all shots, with overlaid box plots that show the median (white/black line), 25th and 75th percentiles (lower and upper boundary of the box), and whiskers extend to the data point that is no more than 1.5 times the length of the box as per the Tukey method (ggplot2). N=800 shots, 20 trials per height per 8 fish.

The results of this study open multiple avenues for further research. Our live prey experiment was descriptive only and limited to a small sample size. The gouramis seemed to more readily shoot the crickets than the flies, raising the question as to whether gouramis show preferences for certain prey types, sizes or activity that might be relevant to their ecology. However, our observations of potential prey preference may be due to order effects, as flies were presented before crickets and hence dedicated experiments with larger sample size and a randomised prey presentation are necessary. It is worth noting that archerfish are highly responsive to moving targets and motion is a highly salient visual features that guides their attention (Schuster et al., 2006; Ben-Tov et al., 2015; Reichenthal et al., 2019). We would predict that movement may be important in eliciting gouramis to make shots, and this may be related to prey type. Another question we have not addressed is whether there is a relationship between their air-breathing and the ability to shoot. Many species within the gourami sub-order build bubble nests and all of them breathe air, but there is limited evidence of shooting in other species, besides reports from the closest relatives to the dwarf gourami *Trichogaster chuna* and *Trichogaster fasciata* and one other species from a separate genus, *Trichogaster trichopterus* (Vierke, 1973, 1975). Testing for the ability to shoot from a broader selection of fishes from this sub-order and other air-breathing fishes (Graham, 1997) will also help us to understand the phylogeny of shooting in this group and whether the behaviour is limited to specific environmental conditions.

Whether or not gourami shooting is linked to their air-breathing, their shooting is very likely derived from hydraulic jetting, which is a relatively common element in foraging tactics of aquatic predators, including fish (Marshall et al., 2008; Kane and Marshall, 2009). Hydraulic jetting is itself a specific form of suction feeding, a basal biomechanical mechanism for prey capture in fish. Most fish use some form of suction feeding – where fishes generate a flow of water though a rapid expansion of the buccal cavity – to capture prey, and the form and strength of the flow is dictated by biomechanical factors (Higham et al., 2006; Muller et al., 1985). Identifying the behavioural and mechanical components involved and how those components are functionally integrated to enable shooting in gouramis may help to place shooting phylogenetically within continuum of prey capture behaviours in fishes (Kane et al., 2019).

There is also scope for more directly comparative studies with archerfish. At the biomechanical and neurological level, the adaptations that enable archerfish to use shooting as an effective foraging behaviour are relatively well studied (Schuster, 2018). Archerfish use coordinated fin movements to hold position while shooting (Gerullis et al., 2021), and they use the 'predictive C-start', an adaptation of the teleost general reflex escape response, which they use to reach prey they have shot down before competitors

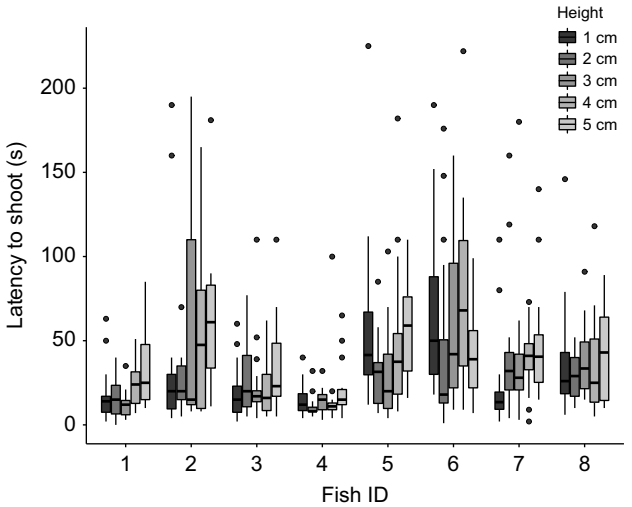

Fig. 4. Repeatable inter-individual differences in shooting ability and consequences on performance. Boxplots of latency to shoot data at different heights for each fish, across all heights, for each fish (N=20 trials per fish per height). The box plots show the median (black line), 25th and 75th percentiles (lower and upper boundary of the box), and the whiskers extend to the data point that is no more than 1.5 times the length of the box as per the Tukey method (ggplot2). Points represent values outside these limits.

Table 2. Repeatability '*R*' estimates for the fish identity and height variables from the fitted model for latency to shoot.

Variable	Repeatability	s.e.	Lower CI	Upper CI
Fish ID	0.116	0.055	0.025	0.210
Height	0.0383	0.015	0.038	0.096

Estimates were obtained with 1000 bootstraps.

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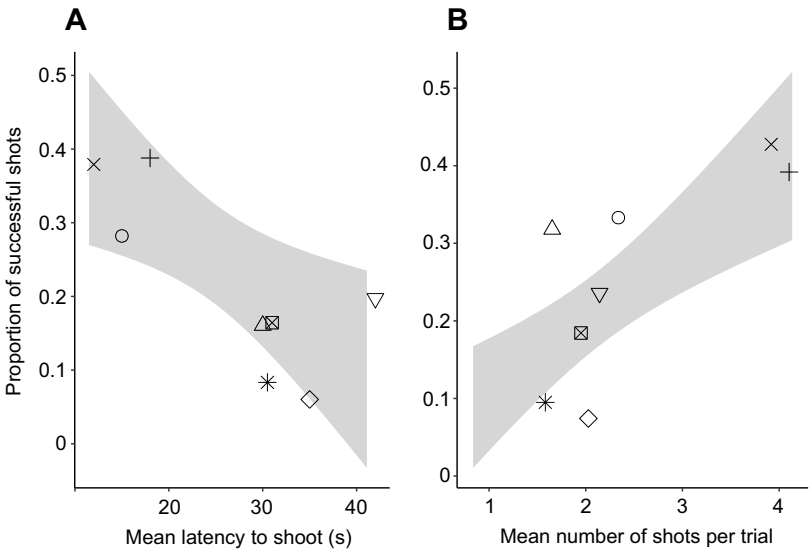

Fig. 5. Inter-individual differences in shooting behaviour have consequences on performance. Proportion of success (shots that hit the target) relative to (A) mean latency to shoot and (B) mean frequency of shots made at the target (*N*=8 fish with 100 shots each). The points denote the mean success for each individual fish (represented by a specific shape) plotted against their individual mean latency or mean frequencies to shoot. The grey band is the estimated 95% prediction interval from simulated data given the fitted model.

(Reinel and Schuster, 2018; Rischawy et al., 2015; Rossel et al., 2002; Wöhl and Schuster, 2007). We did not explore the biomechanics of gourami shooting behaviour or explicitly test for whether they perform some form of predictive C-start; however, we observed no indication of either of these abilities during our experiments. An important point to raise here is that the gouramis in this study were sourced from the ornamental trade and are likely several generations removed from the wild. This could also have resulted in anatomical and phylogenetical constraints. If this behaviour evolved more recently in the gouramis than in the archerfish, then the mouth parts may be less specialised for this task. For a proper comparison with archerfish investigations of wild caught gouramis will be required.

We have also shown that gouramis display repeatable inter-individual differences in latency to shoot, with related consequences on shooting performance and success. This is increasingly expected as such inter-individual differences in behaviour can play an important role in the ecology and evolution of foraging behaviours across species (Dall et al., 2012; Toscano et al., 2016; Metcalfe et al., 2016; Troxell-Smith and Mella, 2017; Snijders et al., 2018; Grecian et al., 2019; Hansen et al., 2020). Such repeatable inter-individual differences in latency to shoot have been observed in archerfish, (Jones et al., 2018) with analogous differences in latency to attack in other predatory fish (Szopa-Comley et al., 2020). These individual differences can be particularly important where targeting specific individual prey can increase the intensity of competition (Ward et al., 2006), as is the case in archerfish (Rischawy et al., 2015) and may be the case in gourami shooting. Our results suggest that gouramis that are quicker to shoot are more likely to make successful shot and show higher endurance. This may be driven by physiological state whereby more food-motivated individuals perform better (Metcalfe et al., 2016) or they are more energetically capable of producing greater numbers or shots with longer range. Further work into the trade-offs between latencies to shoot and the consequences for individual fish may be productive.

Shooting behaviour in the gourami's more famous cousin, the archerfish, has captured the attention of sensory and cognitive ecologists and neurobiologists. Archerfish research has provided insights into visual search, discrimination, and high speed decision making – all of which are required by archerfish when searching, targeting and shooting for prey while accounting for refraction and other environmental and social variables (Schlegel and Schuster, 2008; Ben-Simon et al., 2012; Newport et al., 2013; Saban et al., 2017; Ben-Tov et al., 2018; Newport and Schuster, 2020). Our study aims to establish gouramis as a new model system that may ultimately provide opportunities for comparative studies into the exploration of convergent evolution of the extreme and charismatic foraging ability of shooting in fishes.

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Competing interests
The authors declare no competing or financial interests.

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Data availability
The data used in the analysis of the experiments presented in this paper are available from the OSF (Open Science Framework): doi:10.17605/OSF.IO/KBVH5

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