© 2018. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2018) 221, jeb159723. doi:10.1242/jeb.159723

REVIEW

Hunting in archerfish – an ecological perspective on a remarkable combination of skills

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ABSTRACT

Archerfish are well known for using jets of water to dislodge distant aerial prey from twigs or leaves. This Review gives a brief overview of a number of skills that the fish need to secure prey with their shooting technique. Archerfish are opportunistic hunters and, even in the wild, shoot at artificial objects to determine whether these are rewarding. They can detect non-moving targets and use efficient search strategies with characteristics of human visual search. Their learning of how to engage targets can be remarkably efficient and can show impressive degrees of generalization, including learning from observation. In other cases, however, the fish seem unable to learn and it requires some understanding of the ecological and biophysical constraints to appreciate why. The act of shooting has turned out not to be of a simple all-or-none character. Rather, the fish adjust the volume of water fired according to target size and use fine adjustments in the timing of their mouth opening and closing manoeuvre to adjust the hydrodynamic stability of their jets to target distance. As soon as prey is dislodged and starts falling, the fish make rapid and yet sophisticated multi-dimensional decisions to secure their prey against many intraspecific and interspecific competitors. Although it is not known why and how archerfish evolved an ability to shoot in the first place, I suggest that the evolution of shooting has strongly pushed the co-evolution of diverse other skills that are needed to secure a catch.

KEY WORDS: Neuroethology, Behaviour, Predator, Animal cognition, Cognitive ecology

Introduction

Watching an archerfish take position and fire a precisely aimed jet of water at a tiny insect half a metre away is an experience that can quickly turn you on to these fish. Many aspects of their shooting behaviour are amenable to simple experimentation, and many rewarding questions remain wide open. By now, several skills have been discovered on various levels that are related to the natural hunting behaviour of archerfish. It thus seems timely to give a brief overview of these skills and to discuss how they might be related to the ecological constraints that the hunting fish face in their mangrove biotopes. Some of the findings could also be stimulating for work on other ballistically enabled taxa, such as spitting cobras, spitting spiders, velvet worms and others. Many problems almost equally apply to the many animals that throw themselves [e.g. dragonflies (Olberg, 2012; Gonzalez-Bellido et al., 2013), hoverflies (Collett and Land, 1978), robberflies (Wardill et al., 2017) or falcons (Kane and Zamani, 2014)] or their appendages [e.g. anurans (Ewert, 1997), chameleons (De Groot and van Leeuwen, 2004) or mantids (Rossel, 1983)] at prey. Thus, this Review may be of interest also to those studying non-spitting creatures. It should also be useful for researchers investigating which properties of brains might be crucial for allowing some species to use tools, imitate others or show insight into the tasks demanded of them (e.g. Sol et al., 2005; Emery, 2006; Huber et al., 2009; Morand-Ferron et al., 2016; Cauchoix et al., 2017; Powell et al., 2017; Street et al., 2017). Here, archerfish illustrate how difficult it is to devise standardized tests that could compare learning and ‘cognition’ across species. Such tests would require a detailed understanding of basic environmental constraints that can sometimes be far from obvious.

Although most of the archerfish’s prey appears to be aquatic (Smith, 1936; Simon and Mazlan, 2010), archerfish (*Toxotes* spp.) can capture aerial prey either by jumping at it (if prey is close) or by dislodging it with a powerful jet of water. Shooting is less costly than jumping and allows several shots to be produced in a row. However, retrieving fallen prey is costly and its outcome is not certain, because another group member might snatch the prey (e.g. Davis and Dill, 2012). In our experiments, success was always approximately equally distributed among the group members, with no specific advantage of the shooter (e.g. Rossel et al., 2002; Reinel and Schuster, 2018a). Jumping, per se, is more costly and can be used only at low target height, but it can secure prey with no further investment needed and at overall costs that are comparable to shooting plus subsequent retrieval (Shih et al., 2017). When jumping, the fish position themselves directly below their prey (e.g. Shih et al., 2017), but when shooting, they take more lateral positions (e.g. Timmermans, 2001; Rossel et al., 2002; Schuster et al., 2004). This is consistently seen in all studies, but the reason for this is unclear. What is clear is that it requires shooting archerfish to solve the ‘refraction problem’; because of their different speed in air and water, light rays that are reflected from an aerial target and enter the eye of the fish did not travel on straight paths. If the brain interprets them as having travelled straight, then the fish would perceive its target at a displaced position and aim incorrectly (e.g. see Dill, 1977; Sillar et al., 2016; or Katzir and Intrator, 1987, for the opposite problem faced by herons). Shooting from lateral positions creates an additional problem – the ejected jet of water will slightly bend as a result of gravity, and the effect of bending can be large enough that a correction is needed (Dill, 1977; S. Schuster and S. Rossel, unpublished). Archerfish use their jets not only to hunt aerial prey but also for exposing underwater prey hidden in the substrate (Dewenter et al., 2017). Many of the fascinating abilities of archerfish seem to only make sense in light of the constraints that the fish face in the wild. I therefore begin this Review with a first glimpse into the archerfish’s environment before entering into a more detailed discussion of some abilities of the fish.

A brief overview of major ecological constraints

Archerfish are widely distributed in mangrove areas of the Indo Pacific – from the north of Sri Lanka to Vanuatu (Smith, 1936,

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1945; Allen, 1978). Several interesting reports are available on the daily fluctuations of water levels in these habitats (e.g. Vongvisessomjai and Rojanakamthorn, 2000) or on the food archerfish actually consume (e.g. an extensive survey carried out in Malaysia: Simon and Mazlan, 2010), and it is comparatively easy to observe archerfish in the field in Thailand and to conduct experiments with them (Rischawy et al., 2015). If you have been impressed by archerfish in the laboratory, you will be more impressed after seeing the conditions with which the fish must cope in the wild (Fig. 1; see Movie 1). In the various habitats in which behavioural tests were run on archerfish in Thailand, the water was typically turbid and the fish needed to be close to the water surface to be able to spot potential prey. Wind and water currents cause ripples that contribute substantially to distorting the apparent location of prey as seen from underwater. But wind does not only cause ripples. It is often strong enough to displace the rising water jets fired by the archerfish and to change the path of falling prey and thus the point at which it can be caught. Water currents are typical and need to be compensated for when the shooting archerfish has taken position and is ready to release its jet. In this phase, it is crucial that fish remain stable (Gerullis and Schuster, 2014) (see Movie 1). Drift in strong currents also affects the fish later on their way toward the point of catch, much as it does in riverine fish that compete for falling figs (Krupczynski and Schuster, 2008). Recordings of successful shooting, jumping and prey retrieval in the wild suggest that the fish somehow manage to cope quite well with ripples on the water surface, wind and drift (see Movie 1).

Archerfish do not seem to be territorial and may thus be unfamiliar with the specific aerial structures (Fig. 1A) in their hunting grounds. If they were territorial, this could potentially simplify many problems. It could, for instance, allow a comparison of actual and stored images to detect a fly that has landed while the fish was looking somewhere else. Knowing its proximity to specific landmarks – whose coordinates the fish has stored – would then provide the fish with the spatial information, including the prey's height above the water. Knowing height is essential for the fish to form the appropriate jet, to hit the target and to retrieve prey. However, simply storing data on target height would not be useful given the irregularity with which water levels fluctuate in archerfish habitats. Although tidal water movement is regular and could be corrected for, freshwater inflow from nearby rivers adds strong irregularities. Fig. 1B shows actual measurements of the height above the water surface of a spot at which archerfish actually fired. Interestingly, height not only varied quickly but also so irregularly

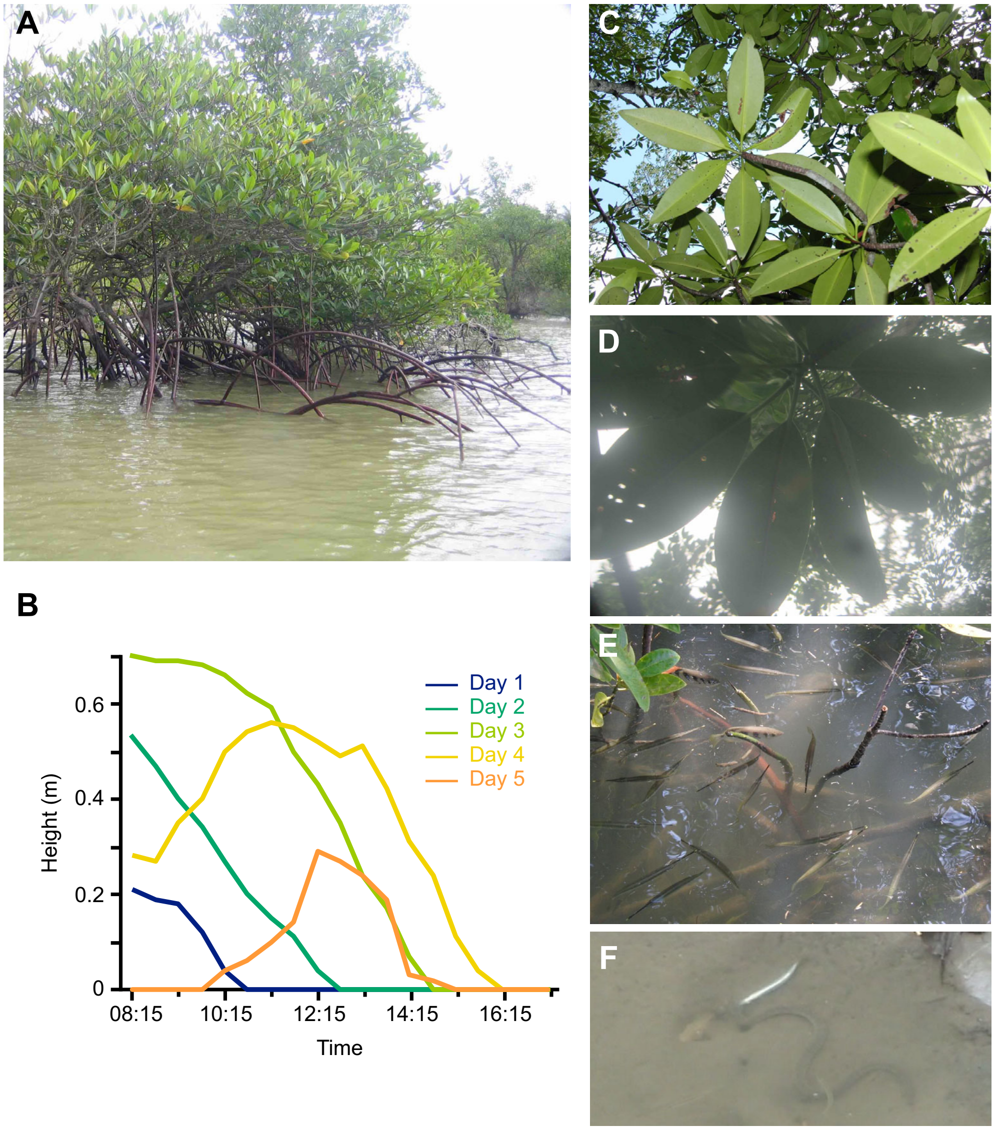

Fig. 1. Environmental constraints experienced by hunting archerfish. (A) A typical spot in Thailand at which hunting behaviour of archerfish could be studied. Note turbid water, ripples on the water surface and the rich diversity of aerial structures at which prey could be located. (B) Recordings of water height in the spot shown in A over five successive days illustrate how irregular the changes are in the accessibility of the location (height >0.1 m) and in the height of 'characteristic' twigs and leaves above the water level. (C) Example of a fly located on the lower side of a leaf. Can you spot it? (D) Example (underwater view) of a beetle located on the upper surface of a leaf. (E) Archerfish are consistently accompanied by numerous halfbeaks (most often *Zenarchopterus buffonis*) – surface-feeding fish that are more sensitive to water waves than archerfish, are active day and night, and compete to feed on archerfish aerial prey after it has been downed. (F) The mangrove fish are under threat of predation – here, a *Zenarchopterus* has been caught by a snake. Photo credits: (A,C–E) I. Rischawy and M. Blum; (F) J. Sonntag and A. Jakob.

that no simple correction could be applied to work out the actual height levels over a day and from one day to the next. Furthermore, at times the hunting area became inaccessible, with no easy way for the fish to know when the area would be accessible again. For instance, on the first day the area was accessible only in the morning, but 3 days later it was accessible only at noon, while just the day before it could be used almost for the full day. Findings such as these suggest that archerfish should be moving around to search for accessible good hunting areas. Unfortunately, no quantitative data are presently available to determine how far individual archerfish move or whether they have preferred locations. In the only case available, a marked individual could be observed over the course of 4 days. This fish regularly moved over at least 150 m along the coastline (the maximal distance that could be examined) and successfully fired at targets that we presented at various spots (S. Schuster, unpublished).

Spotting prey also appears to be challenging: substrates of potential prey show many detailed structures that could be mistaken for targets, leaves can move in the wind, prey can be located on the upper or on the lower side of a leaf, and the prey's illumination and contrast vary enormously from spot to spot (Fig. 1C,D). So, scrutiny is necessary to discriminate prey from unrewarding background objects. Because archerfish have been reported to down a large variety of animals from flies to small lizards (Smith, 1936), simple shape filters cannot be used to simplify the problem. Moreover, the few data available suggest a low abundance of stationary, not flying, aerial prey during daytime (Rischawy et al., 2015). This matches earlier reports on stomach content: in the vicinity of a shrimp farm the fish had mostly eaten shrimp, while fish caught in the vicinity of a village had mostly eaten corn (Smith, 1936), findings that could be reproduced on a 2005 trip (S. Schuster, unpublished). Also, in a more recent and detailed survey in various Malaysian estuaries, the majority of stomach content was aquatic food followed by roughly 25% of various prey (Simon and Mazlan, 2010), of which most should have been aerial (e.g. ants, spiders). Our own behavioural tests in the wild directly illustrated the readiness of the fish to explore anything novel as potential food: the fish readily shot at cameras, spherical pieces of bread, parts of equipment, objects printed on paper or the noses and eyes of experimenters. The fish also shot at objects that were placed on the top side of a leaf and that were detectable by their shadows. However, in the same spots where we readily elicited shooting and jumping behaviour, we only once recorded natural hunting behaviour. In this, a group of archerfish had taken position below a trail of *Oecophylla smaragdina* weaver ants, occasionally downing one. Prey abundance increases after nightfall, but at this time we were unable to elicit any hunting behaviours with the same targets that had worked for the same fish just shortly before, and the fish did not even respond to food thrown into the water. Also, LEDs flashing at various temporal patterns and wavelengths (that attracted the fish in the laboratory) never lured the fish to engage in any hunting. Interestingly, this contrasts markedly with the situation in the laboratory: here, archerfish can hunt during night-time and can shoot accurately at flies in the dark under conditions in which the dark-adapted human eye cannot see the target. It has been suggested that the absence of hunting after nightfall is due to the regular presence of many more surface-feeding fish – in Thailand often the halfbeak *Zenarchopterus buffonis* (Fig. 1E) – that are far better equipped with receptors to detect struggling prey on the water surface than are archerfish (Rischawy et al., 2015).

Intraspecific competition (e.g. Rossel et al., 2002; Davis and Dill, 2012) also appears to be typical in the wild. Archerfish do not try to separate from others during hunting but typically shoot and move around in the company of other archerfish. It is presently unknown how stable archerfish groups are. Given the consistent finding that the shooter has no specific advantage in actually retrieving prey (e.g. Rossel et al., 2002; Reinel and Schuster, 2018a,b), it would be exciting to test whether groups tend to form between genetically related fish. No data are available on how the various manoeuvres of hunting archerfish increase their risk of being spotted by one of their many predators. During searching and shooting the fish are often easy to spot, and their rapid and powerful start toward the point of catch of their falling prey is almost impossible to overlook (see Movie 2). The number of fish-eating birds at the spots in which we ran experiments was always high, with many kingfishers and herons but also other fish-eating predators. Snakes have, on several occasions, been recorded with caught *Zenarchopterus* (Fig. 1F).

Finding and selecting prey

The apparent scarcity of prey, the difficulty of spotting it in the midst of small and variable structures, the variety of items potentially taken as prey and the vulnerability of the searching fish all suggest that it would be good to be efficient in spotting prey. In the laboratory, archerfish can be made to fire at almost any object. However, they also stop selecting objects if these are consistently unrewarding and instead turn to others that are rewarded. This can be used experimentally to make the fish fire at arbitrary targets, including silly ones that the fish would not be able to swallow (e.g. Schuster et al., 2004; Schuster, 2007; Rischawy and Schuster, 2013). Apparently, the fish are not irritated at all by a reward that is very different from the object at which they had fired (e.g. Schuster et al., 2004; Schlegel et al., 2006; Newport et al., 2016). They also do not expect a tight temporal relationship between their shooting effort and the reward. These features make archerfish a fantastic species for experimentation. Their eagerness to explore and discriminate arbitrary objects – regardless of whether they will ever encounter them in the wild – makes them perfectly suited for tests with stationary or moving patterns that have been designed cleverly and specifically for the scientific question at hand (Ben-Simon et al., 2012; Temple et al., 2013; Ben-Tov et al., 2015; Newport et al., 2016).

These experimental advantages have also been used to test how archerfish would perform in a hallmark paradigm of human visual search (e.g. Wolfe, 2010) that is sometimes seen as the doorway into human consciousness or into the design of our cortex (for an overview, see Nakayama and Martini, 2011). In matched tests – run on fish and humans – the fish had to face a task that prevented them from using motion cues or from memorizing the arrangement of background objects (Rischawy and Schuster, 2013) (Fig. 2). To make sure that background objects would not be ignored, all objects had previously acted as targets. In a prior training phase, the fish learned to categorize objects either as the (rewarded) 'target' or as unrewarding 'background' objects (Fig. 2A). In the experiments, both humans and archerfish were shown an assembly of the target plus a pre-assigned number of the background objects (Fig. 2B–D). In a 'simple task', all background objects were identical in shape (Fig. 2E), whereas in a 'complex task', discriminating the target from the background objects required more scrutiny because the latter ones now came in different shapes, contrasts and orientations (Fig. 2F). In both humans and fish, the median response times and the range of response times increased linearly with the number of background objects – such as if a fixed processing time per item was needed. This processing time per item increased similarly for fish and humans from the simple to the complex task. Most interestingly, the shapes of the response time distributions did not tell humans and archerfish apart and were similarly affected both by the number of

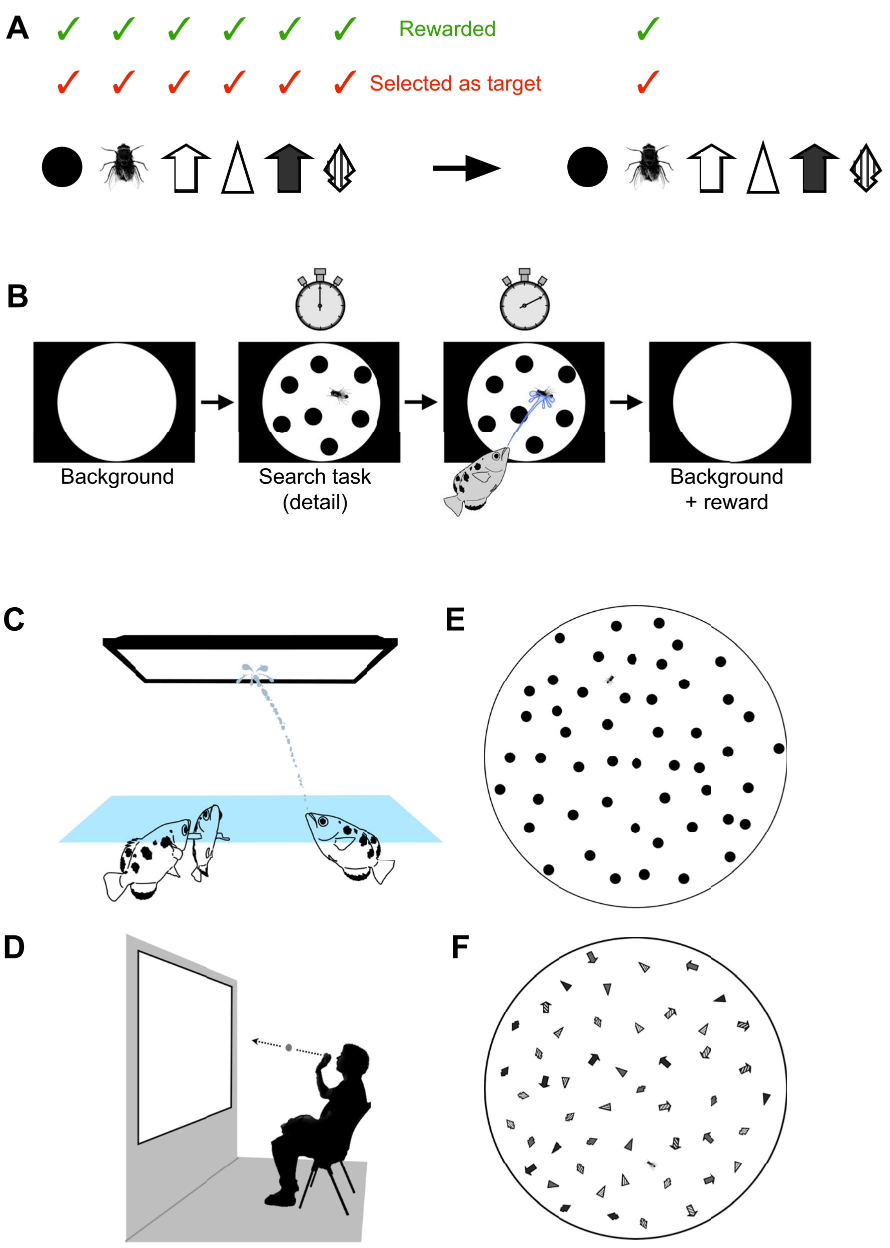

Fig. 2. Finding and selecting prey. (A) Pre-training to illustrate how archerfish quickly shift their preferences. Initially the experimental fish fired at all the objects that were later shown in search tasks. When only one of the objects was consistently rewarded, they fired only at this object and ignored all other objects. Hence, the fish learned to stably assign the objects into classes 'rewarding target' and 'unrewarding background' objects, and experiments in B were started after this was achieved. (B) To prevent the fish from using memory for a specific arrangement of background objects, experiments started with an empty screen on which a randomized assembly of background objects and the target was shown. The time was then recorded until the fish fired at the target. Because non-moving objects are shown on a flat screen, the task provides also no motion cues to discriminate target and background. This allows search trials to be performed similarly in fish (C) and humans (D). Search tasks could be 'simple', i.e. with only one type of background object (E) or 'complex', with background objects of various shapes (F) that also varied in contrast and orientation. B–F after Rischawy and Schuster (2013).

objects in the visual scene and by task complexity (Rischawy and Schuster, 2013). Differences in the shapes, for instance larger skewness of the distributions, and also a more profound influence of the increase in task complexity, would have been expected if the memory for previously scanned objects was not as efficiently allocated in the fish brain as it is in the human search mechanism (e.g. Wolfe et al., 2010). It needs to be stressed that the inferred 'scan times' were 4.3–5.4 times faster in humans (Rischawy and Schuster, 2013), but the hallmark characteristics, used to 'constrain cortical architectures', failed to discriminate fish from humans. Clearly, archerfish could be using other mechanisms, but it is clear that they can scan stationary visual scenes efficiently in the absence of motion cues and without prior knowledge of the configuration of background objects.

Shaping the jets

A number of earlier reports on archerfish have described rather low hit rates (e.g. Lüling, 1958, 1963; Dill, 1977; Timmermans, 2001) at target distances that are well below the ∼2 m range recorded in the wild. It has also been reported that the fish would need to broaden their jets to score hits (Lüling, 1958). These results indicate the level of variation among individual fish, but do not characterize general performance limits of the fish. Sufficiently trained and motivated archerfish can readily and consistently achieve 100% hit rates of targets at 65 cm distance (e.g. Reinel and Schuster, 2018a), can fire sharp water jets (e.g. Schuster et al., 2004, 2006; Schlegel et al., 2006; Gerullis and Schuster, 2014), and can even be cooperative enough to fire and to hit from positions they would not use spontaneously (e.g. Timmermans, 2001; Timmermans and Souren, 2004; Schuster et al., 2004). These aspects are particularly handy for studies on how archerfish adjust their water jets.

If prey is scarce, a larger hunting range would clearly be an advantage. This would require the jet to still be forceful enough to overcome the adhesive forces of prey, regardless of how far it had travelled (Schlegel et al., 2006; Vailati et al., 2012; Gerullis and Schuster, 2014; Burnette and Ashley-Ross, 2015). At large distances, the last bit of water should not arrive much later than the jet tip; this would only make the target wet but would not have the power to knock it off its substrate. To exert strong force, a concentration of water at the jet tip would be ideal. It would seem that simple physics can easily solve this problem (Vailati et al., 2012). Consider a vessel under pressure. When water is allowed to flow out by opening a valve, the first drop will necessarily be slower (because it starts from rest) than the later ones. This could mean that water released later can actually catch up with the front of the jet, thus causing the desired focusing of the water. Measurements showed that such focusing would account for the characteristics of jets aimed at 10 cm distance. Moreover, the forces estimated (Vailati et al., 2012) coincided with earlier measurements of the force transfer on targets at 30 cm distance (Schlegel et al., 2006). If the drop simply stayed together within the full hunting range from 20 cm to ∼2 m, then this would solve all problems: the drop would form automatically after approximately 10 cm of travel, and then forcefully strike anything in its path. Direct measurements on trained fish (Fig. 3A) showed that this simple view is wrong. Water masses up at the jet tip not after a fixed distance of travel, but earlier for close targets and later for distant targets so that it occurs just immediately before impact (Fig. 3B). Furthermore, the fish also adjust the lifetime of their jets to how far they have to travel – with more stable jets used for more distant targets (Fig. 3C) (Gerullis and Schuster, 2014). Interestingly, neither active movement of the fish nor the addition of various amounts of slime or other chemicals to modulate viscosity and/or surface tension were involved. Rather, the fish simply fire water, keep the position of their mouth and the orientation of their body stable, and open and close their mouths in a characteristic pattern that they vary systematically with target height (Fig. 3D). Accordingly, the mouth acts like an ‘active nozzle’ with a time-dependent cross-section. It opens slowly and continuously, but starts slowly closing before the jet is even formed. To engage targets at greater heights, the durations of the opening and closing phases are increased. However, not all aspects of the manoeuvre are equally adjusted. Many exciting and perhaps technically useful discoveries remain to be made, and important aspects, such as the coupling between jet stability and its focusing characteristics, are not understood.

Like many other fish, archerfish also use water jets to search for prey buried in the substratum. Hydrodynamically, such underwater jets should ‘ideally’ be different from aerial jets: no cohesion is required, and larger forces and lifetimes would be produced by generating vortices (e.g. Hanke and Bleckmann, 2004). Nevertheless, the archerfish’s aquatic jets seem to involve the same basic opening-and-closing manoeuvre as used for aerial jet production (Dewenter et al., 2017). Moreover, the freedom of varying the mouth opening–closing manoeuvre is also employed in underwater jet production: a longer duration manoeuvre is used to uncover prey that is hidden in fine mangrove mud, but a faster one is used to lift up prey that is buried in coarse-grained sand (Dewenter et al., 2017). The apparent coupling between the production of the aerial and underwater jets and the use of adaptive variations in both contexts is interesting. It could mean that improving the manoeuvre in one context also improves it in the other, which could have speeded up its evolution.

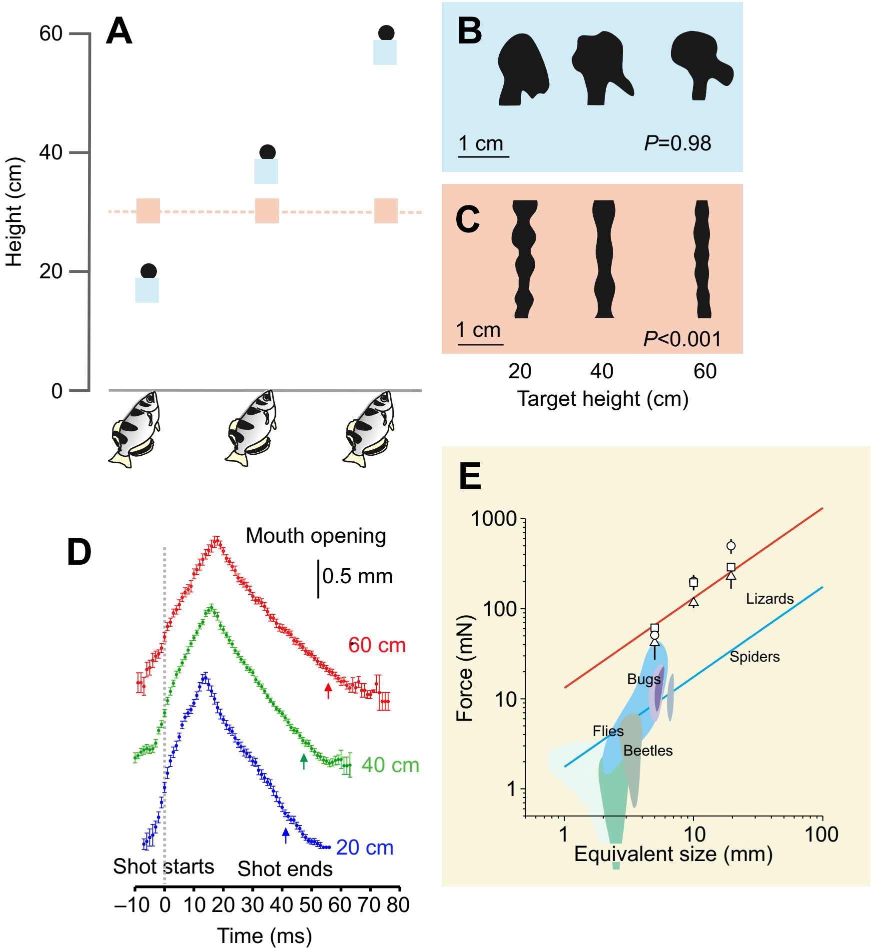

Fig. 3. Shaping the jets. (A) Fish were trained to shoot from a specified spot at a target at 20, 40 or 60 cm height so that jet formation and the ‘part-way’ (red points) and pre-impact (blue points) structure of jets could be monitored. (B) Immediately before impact, the tips of jets that had travelled over different distances could not be discriminated. (C) However, ‘part-way’ (after travelling to 30 cm height) the jets were different, showing lesser Rayleigh instabilities (fluctuations at the boundary) when they still had further travel ahead. For targets at 20 cm height this required sampling the (infrequent) failures in which the jet did not interact with the target. (D) Timing control of the archerfish’s ‘active nozzle’: time course of changes in mouth opening for the three height levels shows how the time course is adapted to target height. Graphs report means±s.e.m. for n=16, 30 and 17 jets at heights of 20, 40 and 60 cm, respectively, and are displaced vertically for clarity. Absolute maximal mouth opening was the same at all target height levels. (E) Maximum force transfer to targets of different size (means±s.e.m.; total of 192 shots from three different fish; indicated by different open symbols) with regression line (red). Blue line shows the universal scaling of maximum adhesive forces of prey, coloured areas indicate actual measurements. Archerfish adjust their force transfer so as to follow the general increase of adhesive force with size of their various prey (flies, beetles, bugs, spiders, lizards). A–D after Gerullis and Schuster (2014); E after Schlegel et al. (2006).

In most 'spitting' animals, the desired effect is guaranteed as soon as enough fluid elements with the venomous substance or glue reach the target (e.g. Berthé et al., 2013; Concha et al., 2015; Gilbert and Rayor, 1985; Nentwig, 1985; Rifflet et al., 2011; Westhoff et al., 2005, 2010). Archerfish, in contrast, have to exert sufficient force to dislodge their prey. How do the fish 'know' what force to apply? It turns out that archerfish do adjust the power of their shots, and transfer forces between 40 and 500 mN, depending on prey size (Schlegel et al., 2006). However, it was quite puzzling at first that these 'clever' fish seemed to be unable to adjust power based on past experience. For instance, they would not lower it when a reward was consistently obtainable with much less power (Schlegel et al., 2006; S. Schuster, unpublished). In this particular context, the fish do not seem to learn anything, regardless of how useful this would appear from the experimenter's point of view. Instead, the fish seem to stick to a simple 'rule of thumb'. Interestingly, it turns out that this rule automatically captures the way attachment forces of all sorts of prey vary with size. For surprised prey (that has no time to claw onto its substrate), the attachment force scales linearly with size, regardless of the very different structure of the attachment pads used by animals as diverse as flies and lizards (Arzt et al., 2003). Measurements of forces transferred to spherical objects suggest that archerfish copy this relationship by increasing the force of their jets linearly with target size but applying approximately 10 times the attachment force of an average object of the given size (Fig. 3E) (Schlegel et al., 2006). By making the fish fire at dots printed on cotton, monitoring the amount of water absorbed and simultaneously recording the initial speed of the shots, Schlegel et al. (2006) showed that the fish adjust force in the least costly way, not by increasing speed but by increasing the amount of water fired. Because the interaction time of the jet with its target was size independent, increasing momentum transfer requires an increase of the momentum ('mass times speed') of the shot. Increasing it by increasing the mass of water fired requires only a doubling of energetic investment (one half of the mass times speed squared), whereas achieving the same by doubling speed would cause fourfold costs (Schlegel et al., 2006).

Learning efficiently: generalization and learning from observing

With few prey items and many competitors around, it seems plausible that there was strong selection pressure to speed up any learning that increased the chances of an archerfish getting food. One study asked how the fish learn the absolute size of a target (Schuster et al., 2004), which they need to know in order to adjust the volume of water fired. Unlike most animals that judge the absolute size of objects, archerfish have to watch them through the water–air interface. This introduces strong effects not only on apparent target position but also on the apparent size of an object. Accounting for these distortions requires very detailed judgement of the fish's own spatial position relative to the target (Fig. 4A) (Schuster et al., 2004).

Experiments were performed on fish that initially only had relative size preferences, i.e. they preferred larger targets if these were more distant (Schuster et al., 2004). To study how the fish would learn to select objects based on their absolute size, individual disks were printed on paper and one disk at a time was presented at one of four height levels. If the disk was of the correct size, firing at it was rewarded. In the tests, an assembly of eight disks was shown, and the one at which the fish fired was noted, but no reward was given, to prevent the fish from receiving feedback that would allow it to directly compare the sizes of the various disks (Fig. 4B). Several different copies of the disks were used, both in the training and in the tests, to prevent the fish from recognizing them from details other than size. In light of the variations in the positions that the shooters were in relative to the disks, the tests confirmed that archerfish were able to learn to account for the strong viewpoint-dependent aspects (Fig. 4A) and to gauge absolute size despite the strong viewpoint dependency.

Another experiment (Schuster et al., 2004) checked whether the fish had selected the correct disk based on stored 'templates' of the retinal image of the rewarded target at the various viewpoints experienced during training. Two fish were re-trained to a novel target size but the re-training was conducted only at the two lowest height levels. Again, only single disks were shown. If the fish learned during the re-training that a new absolute size is generally being rewarded, then they should select the novel size also at the height levels in which no re-training had occurred. However, if they have used stored templates, then they should choose the old size. The findings showed that the fish were not using hypothetical templates but had learned something general about absolute size, which enabled them to select the correct disk at the new (un-trained) height levels (Fig. 4C).

Archerfish also have interesting ways of learning how to engage moving prey (Schuster et al., 2006). In a series of experiments, adult fish were used that were excellent at shooting at stationary prey but consistently failed to hit even slowly moving targets. These fish were then trained to be more and more efficient in hitting moving targets. Several aspects of this study point to remarkable features of how the fish learn this task. First, at low target height, the fish came up with two different strategies to hit the moving targets (and receive a reward): they either used a 'leading strategy' in which they aimed in front of the moving target, or a 'rotate and fire' strategy in which they tracked the target and released their water when approximately level with the moving target. In the latter strategy, used only for low target height, tracking would then lend the amount of speed to the water that was needed to make the water automatically follow its target. Second, after having exclusively been trained to horizontal motion, tests were performed with an additional vertical component of speed – large enough that the fish would make an error if they ignored this component and used only horizontal motion. The fish were readily able to hit these targets (Fig. 4D). These findings suggested that the fish had learned a more general solution than would seem to have been sufficient in the training. Third, the most intriguing observation was that the fish could somehow learn the task either by extensive practice or by watching a fish learning and performing the task over an extensive period (Fig. 4E). Because observing fish were distant from the practising fish, this ability must somehow include (or elegantly circumvent) taking the angles and speed as seen by the practising fish. Presently, it is unclear what information the observing fish were using and whether they were looking more at the moving target or at the shooting fish. It does not seem likely, however, that they can learn from only watching the moving target: a group that could only watch moving targets was not successful when tested later (Schuster et al., 2006). Learning from others is probably of great importance in archerfish and will be an exciting field to explore further; perhaps the first steps will require much simpler settings that are inspired by what would actually be useful for the fish in the wild.

Competition and fast-start decisions

The presence of numerous other surface-feeding fish that readily feed on downed archerfish prey, that are active day and night and that are superbly equipped with water-wave sensors means that the majority of archerfish prey should be lost to these competitors.

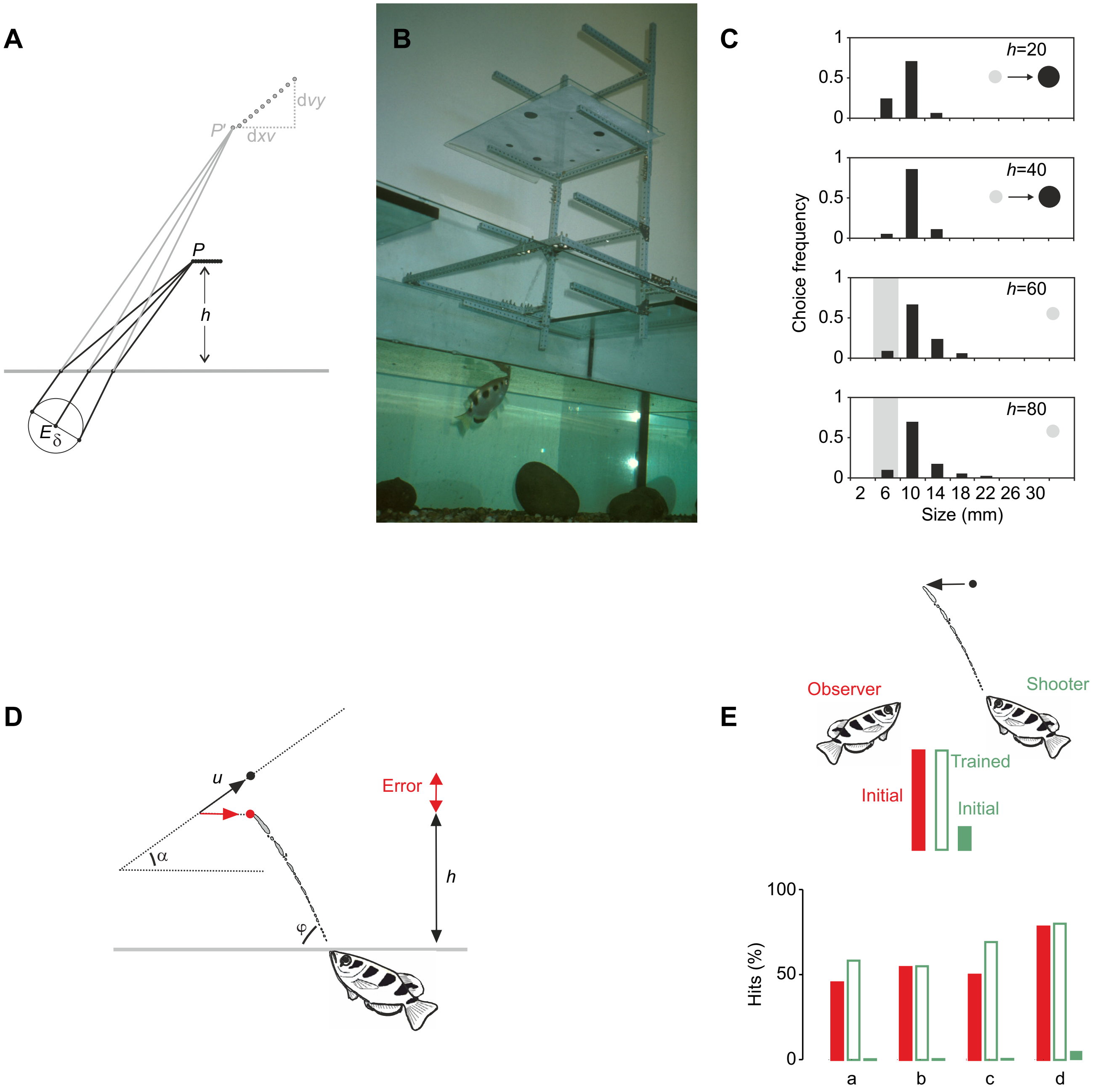

Fig. 4. Speeding up learning. (A) Archerfish have to account for the refraction of light to recognize absolute size from different viewpoints. Illustration of how the virtual image of a target disk can be computed. *E*, center of pupil; δ, pupil diameter; *h*, height. *P* and *P*′ denote a real point of the aerial disk and its corresponding virtual point. d*xv* and d*vy* indicate inferred horizontal and vertical extension, respectively, of the virtual disk. (B) A test of how archerfish learn the absolute size of aerial targets. The fish had to choose a disk with appropriate diameter from an assembly of eight disks. Note the simplicity of the setup, with targets simply printed on paper (and secured by a glass plate), presented at pre-assigned height levels and rewarded with food thrown in by hand. (C) Example of a critical test to show that the fish learned to recognize absolute size. After learning to select a disk of 6 mm diameter at each of four height levels (*h*=20, 40, 60 or 80 cm) the fish was retrained to select a novel target size (10 mm). However, the re-training occurred only at the two lower height levels and not at the two higher ones. Nevertheless, the fish also chose the new target size in unrewarded tests made at the un-trained height levels. (D) Generalization was also evident in tests in which fish had been trained to shoot at horizontally moving targets at height *h*. In tests in which vertical motion was added (angle α, speed *u*) the fish did not make the errors that would be expected if they had simply ignored the vertical speed component and fired as appropriate for the horizontal component (red, requiring shooting angle φ). (E) Experiment that suggests fish can learn from observation how to efficiently shoot at a horizontally moving target. The filled green column indicates the low success rate in an initial series of tests on a fish that learned by practising. The unfilled green column indicates the success rate this fish had reached after extensive training. The filled red column shows the initial success rate of observer fish in their first series of tests. Groups of columns show the hit rates of four different observer fish (a–d) in their first encounter with various tasks for which the model fish they had been watching had needed extensive training. A–C after Schuster et al. (2004); D,E after Schuster et al. (2006).

However, in the field, over 98% of ballistically falling prey went to one of the archerfish and not to any of the more numerous halfbeaks (*Zenarchopterus buffonis*; Rischawy et al., 2015). This impressive success rate is attributable to another interesting aspect of archerfish hunting, their predictive C-start (Fig. 5A,D) (Rossel et al., 2002; Wöhl and Schuster, 2007). As soon as prey starts falling, the fish

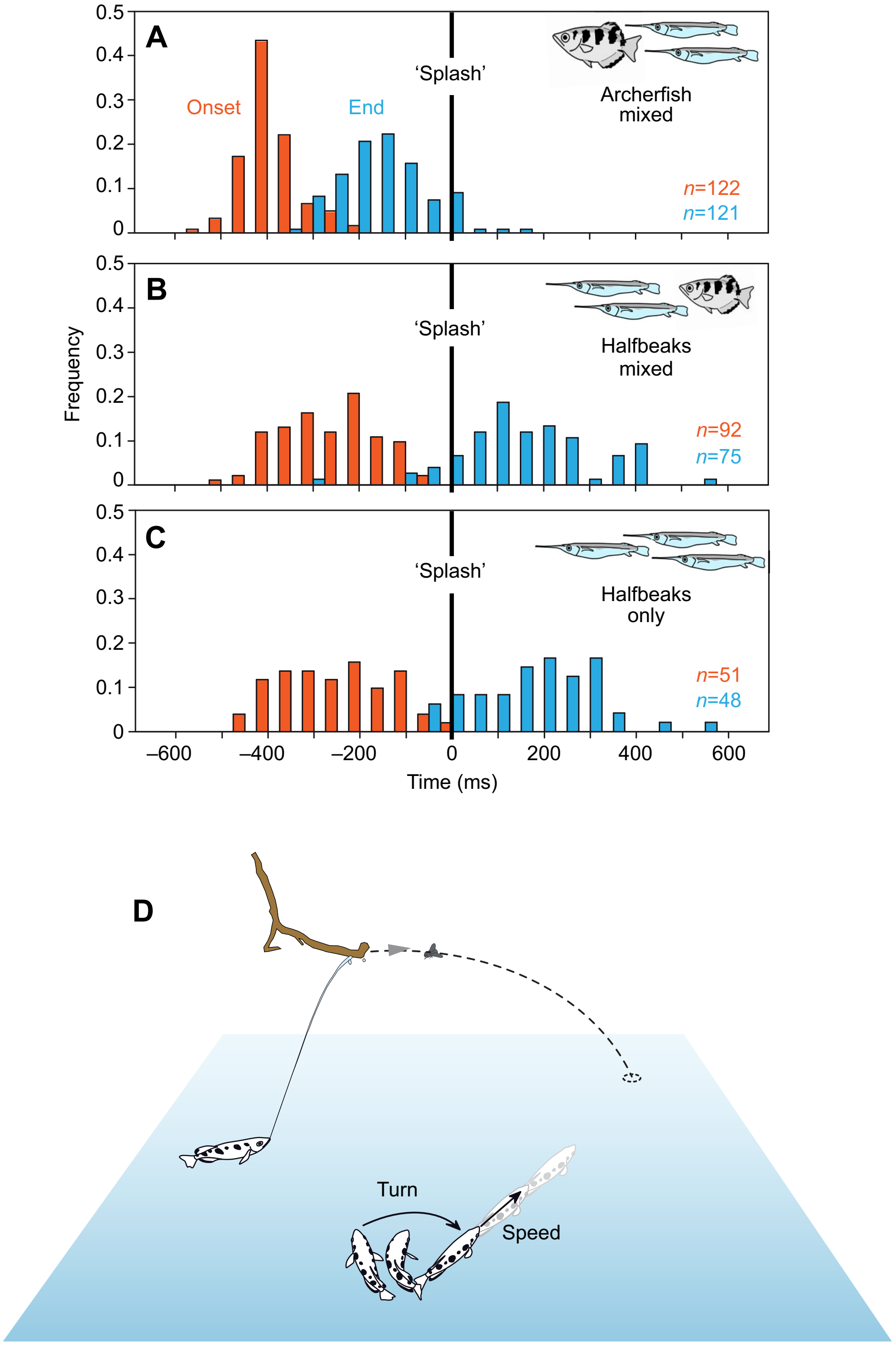

Fig. 5. Securing prey. (A) In the wild, archerfish are the first to respond to ballistically falling prey, even if they have not themselves set the prey into motion. Time before splashing impact when archerfish initiated (onset; red) and finished (end; blue) their predictive starts after prey motion was started from an initial height of 1 m. Almost all archerfish responded, and in 98% of the experiments the prey went to an archerfish. In the experiments, prey was initially invisible and was launched by the experimenter, not by an archerfish shot, to travel on a ballistic trajectory toward the water surface. (B) The responses of the halfbeaks in the same scenes. Interestingly, ∼25% of the halfbeaks responded to visual pre-impact cues by initiating a turn. Note that most of the turns were not finished at the moment of prey impact. (C) Halfbeaks also show pre-impact responses in absence of archerfish, showing that the starts in B were not responses to starting archerfish. (D) Illustration of key aspects of the archerfish predictive C-starts. A prey object, initially located on an overhead perch such as a branch, is dislodged by a shot and sent onto a ballistic path to the water surface. Responding fish now monitor the initial motion to select an appropriate C-start. This start turns the fish so that it is aligned to the later point of impact but also releases the fish at a speed that – when maintained – would make the fish arrive most economically and at precisely the right time. A–C redrawn from Rischawy et al. (2015); D redrawn from Krupczynski and Schuster (2013).

determine its horizontal and vertical speed, direction and height, and use this information to select an appropriate C-start (e.g. Schlegel and Schuster, 2008; Reinel and Schuster, 2016, 2018a,b). Such C-starts are typically employed by fish to rapidly escape danger (e.g. Sillar et al., 2016). They are called C-starts because the fish's body first bends into the shape of a letter 'C'. Subsequent straightening – with fins erected – allows the fish to accelerate and then to take off. The predictive C-starts are kinematically equivalent to the equally powerful archerfish escape C-starts (Wöhl and Schuster, 2007) but are precisely adjusted according to the initial movement of falling prey. Immediately at the end of the C-start, i.e. when the fish first is straight again, it is already aligned towards the point where prey is later going to land. The C-start (and not later fin strokes; Reinel and Schuster, 2014) also releases the fish at a speed that is adjusted to both distance and time remaining until impact, such that the fish would arrive very shortly after its prey and in the most energy-saving manner, i.e. with constant speed throughout (Wöhl and Schuster, 2006). The precision of selecting the most appropriate start is buffered against changes in contrast (Schlegel and Schuster, 2008) or in temperature (Krupczynski and Schuster, 2013). The rapid decisions – in which direction and at what speed to start – show many intriguing properties (e.g. Schuster, 2012). One of the most surprising characteristics is that the fish do not seem to use information that they would potentially have available in a natural situation: the shooter knows the height, size and location of its target, can perhaps manage to guide the direction in which prey will be dislodged, and knows when and where prey will start falling. And yet, this information is not used and is not even helpful for the start decisions. The decisions are made equally well when information is only available after the prey starts moving (Schlegel and Schuster, 2008; Reinel and Schuster, 2016, 2018a,b). This finding simplifies experimentation and makes the predictive starts a great behaviour in which to study 'high-speed' decision-making. The starts are not simple reflexes: they are selected according to the time and position of the later landing point of ballistically falling prey and are accurate from all possible viewpoints and orientations of the responding fish (e.g. see Reinel and Schuster, 2018a,b). When the members of an archerfish group were separated so that each was alone when downing prey, they no longer showed predictive C-starts. The C-starts, however, came back when the individuals were put together again (Schlegel and Schuster, 2008; Schuster, 2010).

In principle, just noting that prey starts to fall would already be much better than waiting for its impact on the water surface. So, why did archerfish do more and evolve their sophisticated predictive C-starts? A clue might be that their *Zenarchopterus* competitors – even with no archerfish around – do not simply wait for the impact of falling prey items. Rather, they can also respond to visual cues of falling potential prey (Fig. 5B,C). This was shown in the absence of archerfish (so that their responses could not trigger the starts) and without actual impact, so that the usual mechanosensory cues were also not available. Nevertheless, the responding halfbeaks were still oriented to where the prey would have landed. So, outcompeting the halfbeaks requires much more than simply being alerted by the onset of falling motion of prey. The evolution of the predictive C-starts seems to be the solution needed to outperform *Zenarchopterus* halfbeaks and perhaps other surface-feeding fish.

Because the predictive C-starts are essential for securing prey, archerfish should leave the field to their competitors when their predictive starts are compromised in the dark. In the laboratory, archerfish stop producing predictive starts at low light levels but are perfectly able to accurately hit aerial targets at much lower light levels. In the dark, after scoring successful hits, it takes the archerfish many seconds to find their prey, whereas *Zenarchopterus* needs only approximately 180 ms (Rischawy et al., 2015). So, archerfish would have almost no chance of making a catch in the dark. However, in spots with no halfbeak competitors around, archerfish should be perfectly able to hunt in the dark. In the habitats sampled in Thailand, this was never the case, and archerfish hunting was limited to daytime – with all the problems that entails.

Counting cognitive skills

In a highly influential review, Bshary, Wickler and Fricke examined skills that were at that time discussed in the literature on primate cognition, and for each skill identified a species of fish that performs similarly (Bshary et al., 2002). Their analysis suggested that fish brains can, in principle, solve tasks that we find impressive in primates and that could be labelled 'cognitive'. Previously, Marler (1996) had compiled similar arguments for birds. By now, similar compilations are available in many taxa, including archerfish victims (insects: e.g. Giurfa, 2013; Perry et al., 2017; spiders: Japyassú and Laland, 2017) and even single cells (e.g. see Lyon, 2015). These attempts may help to bring some order to the observations and to eventually link them to the brains (or networks) used. An interesting aspect was also noted by Bshary et al. (2002), who emphasized that they had to use different species of fish for each of the many 'cognitive' skills of a chimpanzee. Archerfish combine many of the skills (e.g. 'foraging skills', 'tool use', 'deception', 'social learning', 'memory', 'living in groups', according to Bshary et al., 2002) that were discussed and thus would be a remarkable addition to their original array of species. Counting how many 'hallmark skills' an animal can combine could be more helpful than looking for a unique skill, and could be the variable that may better correlate with aspects of its brain. Unfortunately, it should be apparent from the examples provided in this Review that actually comparing skill counts is difficult. For instance, if one knew nothing about the scaling of adhesive forces (Arzt et al., 2003), one would have to consider archerfish as incapable of learning, given that they cannot even learn to lower their shooting powers (Schlegel et al., 2006), a task of apparently 'obvious' ecological value. Also, running standardized tests on archerfish seemed to imply that they are not capable of 'higher' forms of learning (e.g. Newport et al., 2014, 2015). However, when tested for abilities that they seem to directly need in their hunting, they clearly show impressive capabilities (e.g. Schuster et al., 2004, 2006). These examples may suffice to suggest that simply throwing species into a 'cognition contest' with tasks that do not fully take into account the environmental constraints of the various species will not be useful.

Speculations on the evolution of shooting and its consequences

The forces transferred by archerfish shots and their adjustment with distance prompts comparison with human throwing, which is often seen as an important step in human brain evolution (e.g. Calvin, 1983; Bingham, 1999; Schoenemann, 2006; Wood et al., 2007). It has been argued (Calvin, 1983) that doubling the range at which a powerful hit can be scored from 4 to 8 m narrows the timing precision eightfold and – if precision is achieved by averaging statistically independent neuronal units – the eightfold reduction of temporal variability requires a 64-fold (8^2) increase of neuronal units. In archerfish, it has turned out that adjusting the jets to target distance also requires precise adjustments of timing (Gerullis and Schuster, 2014), and so it is tempting to speculate that shooting could have acted similarly in the evolution of archerfish. However, if Calvin's argument was correct, then it should also extend to other more precisely adjusted manoeuvres. For instance, the predictive starts of archerfish could similarly be seen as the fish throwing their body in the direction of the future landing point, and precision is needed to get the initial angles and timing right. It would be interesting to see whether Calvin's reasoning applies to the many animals that similarly throw themselves at prey or strike at prey – or to those that impress (or annoy) us with their precisely timed and rapid manoeuvres. Each of these could potentially, in Calvin's view, require large numbers of neurons and could, if these neurons were employed for other tasks, have been boosting the evolution of the brain of its bearer. However, increased precision could potentially be achieved in other ways than by increasing the actual number of neurons, and this would seem to be much more fitting for small animals or for networks (as the ones driving the archerfish predictive start) that have to operate at top speed.

It is quite remarkable that among the ∼35,000 species of fish – a group that successfully inhabits almost all aquatic habitats on Earth – the only other 'spitters' are some anabantoid fish that spit water over small ranges (only 2–3 cm; Vierke, 1973). Ejecting fluids that act across a distance, however, is clearly not unique to archerfish. Various forms of spitting slime, glue and venom in various patterns and at different distances are found in many taxa, and many of these abilities might be far more adjustable than initially thought. Spitting cobras use the same mechanism they use for injecting prey to spit venom at the face or eyes of a predator that is over 2 m away, can adapt the area over which they distribute their jets and can even track moving targets (Young et al., 2004; Westhoff et al., 2010; Berthé et al., 2013; Triep et al., 2013). Velvet worms (*Onychophora*) can immobilize prey by squirting a jet of slime at it. This jet is not straight but has a remarkable shape that is produced by rapid oscillations of the oral papillae (Concha et al., 2015). *Crematogaster* ants paralyze termites from a safe distance (Rifflet et al., 2011) and spitting spiders pin their prey by ejecting glue from their chelicerae (e.g. Gilbert and Rayor, 1985; Nentwig, 1985). It should be noted that in all cases the effect requires enough venom or glue to reach the target, but not to transfer strong forces. This is quite different from hunting with stones and spears or from archerfish shooting. In terms of underwater jets, which are widespread among aquatic animals (e.g. Brown, 2012; Mann and Patterson, 2013; Marshall et al., 2014), archerfish do not excel in any way, and the record in terms of power is held by snapping shrimp, whose claws can produce velocity fields with an associated 10^5 Pa pressure drop that can cause serious damage (Versluis et al., 2000; Hess et al., 2013).

This Review cannot, unfortunately, present a solution to the most intriguing question about archerfish: why is this the only group of fish that has evolved powerful shooting? Perhaps a good starting point to explore initial difficulties in the evolution of shooting would be to explore how shooting could have arisen from variations of suction feeding mechanisms that are employed by most teleost fish. Detailed analyses of the complexity of such manoeuvres have been attained (e.g. Lauder, 1980; Higham et al., 2006; Day et al., 2015), and biorobotic models (e.g. Kenaley and Lauder, 2016) could be employed to test the functional effects of any modifications that may have been useful for evolving shooting. However, the question of why shooting was 'needed' at all, given that most of the archerfish's diet appears to be aquatic, is not so easy to approach. Perhaps strong seasonal or local fluctuations occur in the availability of aquatic versus aerial prey or perhaps aerial prey provides important nutritional components. Once invented, however, using shooting to actually secure prey must have 'shaken' the world of these fish and should have boosted the evolution of other behavioural innovations that were needed to face environmental variability and strong intraspecific but also interspecific competition, as well as allowing individuals to profit from other group members always being around.

Acknowledgements

It is a pleasure to thank the reviewers as well as David Hatton and Charlotte Rutledge for many helpful and stimulating remarks. I also thank Pamela Adam, Daniel Buckel, Maria Eder, Jochen Eisenhut, Julian Eysenbach, Angelika Jacob, Philipp Malz, Nadja Reyer, Janina Sonntag, Stefanie Stutzer, Sabine Sulimma and Angela Walenta for their help in the field, and Caroline Reinel, Peggy Gerullis, Wolfram Schulze, Ingo Rischawy, Michael Blum, Alexander Hecker and Philipp Krupczynski for their help and advice.

Competing interests

The author declares no competing or financial interests.

Funding

This work was supported by the Deutsche Forschungsgemeinschaft (Schu1470/1, 3, 6–11).

Supplementary information

Supplementary information available online at http://jeb.biologists.org/lookup/doi/10.1242/jeb.159723.supplemental

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