An investigation of the social behaviour of archerfish *Toxotes* spp.

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Abstract

Sociality has evolved multiple times in animals. Social living is a balance between the advantages and disadvantages of the increased presence of conspecifics. These costs and benefits are especially prevalent when foraging, as both the chance to discover resources and the rate at which they are depleted increase with group size. This holds true for archerfish *Toxotes* spp., a genus known for shooting down terrestrial prey using concentrated jets of water. This hunting method leaves the shooters open to theft, but whether and how their foraging behaviour and decision-making are affected by this threat is unclear. I investigated how group size affected aiming duration and shooting success, performed a pilot investigation into the use of video demonstrators for standardising social stimuli in such experiments, and tested whether archerfish socially learn target preferences when foraging in a group. I found evidence that archerfish decrease their aiming duration in the presence of more conspecifics. My results contradict previous research on kleptoparasitism in archerfish, mainly that the rate of kleptoparasitism is dependent on the behaviour of the shooter's neighbours rather than group size. I also showed that archerfish avoid videos of conspecifics, although the explanation for this remains elusive. I attempted to find out whether archerfish can learn socially but instead found no evidence of learning. As scientists, we must study the natural world and share our findings with the public who fund our work. Accordingly, I created a tabletop role-playing style game based on archerfish ecology to test whether it could educate the public about my research and found that most participants improved their knowledge of archerfish. This thesis not only helps to further elucidate the social behaviour of archerfish but also illustrates how an animal's ecology must be taken into consideration when conducting research and conveying the results to the public.

Candidate's declaration

I, Dagmar Jacqueline Der Weduwen, do hereby certify that this thesis, submitted for the degree of PhD, which is approximately 32,000 words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for any degree. I confirm that any appendices included in my thesis contain only material permitted by the 'Assessment of Postgraduate Research Students' policy.

I was admitted as a research student at the University of St Andrews in September 2019.

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Ethical Note

The experimental procedures used in this thesis were in accordance with the ethical standards of the University of St Andrews and methods were approved by the Animal Welfare and Ethics Review Body (AWERB) and University Teaching and Research Ethics Committee (UTREC). No procedures required U.K. Home Office licencing. No fish died or suffered ill health as a result of the experiments conducted as part of this thesis, and all individuals were rehomed to public aquaria at the conclusion of the research.

Declaration of Publications

The work described in Chapter 2 has been submitted for publication in Behavioral Ecology, having undergone two rounds of revisions at the time of submission of this thesis.

COVID-19 Impact Statement

As a result of the COVID-19 pandemic, the experiment described in Chapter 3 was delayed by three months. This delay contributed to the fish used in this experiment dying of natural causes before the planned second part of the experiment could be conducted.

Crime Impact Statement

In March 2023, a burglary in the Harold Mitchell Building resulted in the loss of the video data of the experiments described in Chapters 3 and 4. This video data has never been recovered, and the results described in the aforementioned chapters are based on the coded .csv data.

Contributions

The lab work described in Chapter 2 was conducted by Nicholas A. R. Jones at the University of Bayreuth, in collaboration with Stefan Schuster, who both assisted with editing the manuscript. Adele Dubosque assisted with video coding.

The video coding described in Chapter 3 was partially conducted by Arantzazu Pagonabaraga-Altisen and Annie Rowe.

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Chapter 1 – General introduction

Preamble

In this introductory chapter, I will lay out background information on social foraging in animals, as well as providing a review of research conducted on archerfish in the past five years. I will also explain the importance of public engagement to research, as although public engagement work is not traditionally a part of a PhD thesis on animal behaviour, I will argue that communicating research to the wider public is a critical component of any scientific career.

Background

Throughout the animal kingdom there exist a wide variety of social structures, ranging from solitary animals to bonded pairs, families to largely unrelated herds and shoals. Some animals live in obligately social groups, spending their entire lives around conspecifics, while others may be more facultatively social, grouping only at certain life stages or under certain circumstances (Ward and Webster, 2016). The different relationships within groups, and the different behaviours individuals within groups exhibit, provide a wealth of opportunities to answer numerous questions related to the ecology of group living.

Living in groups

Whether animals will evolve to live in groups is often decided by weighing the fitness costs and benefits of group living. Gregarious species are found everywhere, but the evolution of their sociality may vary greatly, as some species will derive different costs and benefits from group living than others (Krause and Ruxton, 2002; Ward and Webster, 2016).

One of the primary benefits of living in groups is the effect conspecifics in close proximity have on an individual's predation risk (Grand and Dill, 1999; Beauchamp, 2014). Hamilton (1971) suggested the "selfish herd" hypothesis, proposing gregariousness may evolve in part due to the dilution of predation risk amongst the herd. The reduced risk of predation is not merely caused by this risk dilution however, as predators may also experience faster satiation (Eckrich and Owens, 1995) and possibly a confusion effect, if predators are uncertain which individual in the group to target first (Olson et al., 2013). Density-dependant models of predation have so far found support for Hamilton's selfish herd hypothesis (Olson et al., 2016), thus it is likely individuals will group together, even if they are sessile (Lehtonen and Jaatinen, 2016).

Even in groups, many animals exhibit anti-predator responses like vigilance behaviour while foraging, but the amount of time spent on this behaviour decreases with increased group size, also known as the "many eyes effect" (Rieucau and Martin, 2008). A meta-analysis covering 97 species across 10 orders and 26 families found that there is a moderate negative effect of group size on vigilance, especially when time spent vigilant is measured as a percentage of total time (Beauchamp et al., 2021). Time spent vigilant for predators or competitors is not affected by the perceived risk of predation or competition, regardless of group size (Beauchamp, 2019). The reduction in time spent vigilant translates directly into an increased time spent foraging.

There are several other benefits conferred to foraging by gregariousness. Animals in groups tend to find and consume food faster than individuals (Clark and Mangel, 1986), and mean food intake rates can increase for groups at an optimal size. American white pelicans *Pelecanus erythrorhynchos* Gmelin, 1789 catch the most fish when they hunt in groups between two and six individuals, although strike frequency asymptotes at a group size of four individuals (Anderson, 1991). In birds in general, mean food intake rate increases with group size, although this is more likely if the food is seeds, not fish, invertebrates, or carcasses (Beauchamp, 1998).

Animals can learn about new foraging patches by individual discovery or by observing conspecifics, which is a facilitated by local enhancement, or the attraction to locations where others are seen (Stenberg and Persson, 2005; Thiebault et al., 2014). Animals are often attracted to areas where conspecifics are present as they are an indication of resource availability (Hake and Ekman, 1988; Anderson, 1991; Snijders et al., 2021). The number of individuals already present at a foraging patch can also play a role, as large aggregations are detectable from greater distances than smaller ones thus leading to a wider benefit for individuals in the area (Thiebault et al., 2014). However, the increased competition for resources has a number of drawbacks.

The presence of other individuals, and their foraging activity, affects prey availability. This means that, in general, individuals in groups larger than the optimal size experience decreased prey capture rates (Rita and Ranta, 1999) and increased rates of kleptoparasitism. The gains in search efficiency provided by group foraging do not always therefore counteract the smaller amount of food gained due to faster depletion of resource patches, although food intake variance can decrease due to local enhancement (Hake and Ekman, 1988). Group foraging is not inherently more beneficial than individual foraging, and in some cases confers no benefit at all (Stenberg and Persson, 2005). It may also increase energy expenditure to ensure foraging efficiency in the face of competition (Clark and Mangel, 1986). The increased resource competition faced by groups during foraging may also increase risk-taking behaviour. Multiple species have been reported to increase risk-taking behaviour with group size, regardless of predation risk (Grand and Dill, 1999; Johnsson, 2003; White and Warner, 2007). However, there are also species in which cooperative foraging is required for any resources to be obtained at all, such as meerkats *Suricata suricatta* (Schreber, 1776) (le Roux et al., 2009). Thus, there can be a trade-off between anti-predator benefits and foraging costs for animals living in groups, but sometimes foraging cannot occur without the presence of conspecifics.

A similar trade-off exists for gregarious species when it comes to parental care and fecundity. Alloparental care, or the care of offspring by individuals which are not their parents, provides a fitness benefit to both parents and offspring. In most cooperative breeders, alloparental care is provided by grown offspring or other close relatives (Griesser and Suzuki, 2016) although this is not always the case (Tučková et al., 2016). The reduced energetic output required from the parents to raise their offspring leads to increased fitness for the parents, and the increased provisioning to the offspring increases offspring fitness. In the communally nesting superb starling *Lamprotornis superbus* (Rüppel, 1845), adult females have a higher rate of survival in larger groups (Guindre-Parker and Rubenstein, 2020), while in the social spider *Stegodyphus dumicola* Pocock, 1898 late-instar juveniles, as well as whole colonies, survive better in larger colonies. Mean individual fitness across all life stages for this species is maximised in medium to large-sized colonies, although larger colonies do show reduced female fecundity and body size as well as decreased early juvenile survival (Bilde et al., 2007).

Reduced individual fitness is common in species which exhibit alloparental care, a type of care which can increase indirect fitness benefits. Pregnant dominant meerkat females regularly evict other females in order to discourage them from mating, as the evicted individuals experience significantly increased levels of stress hormones (Young et al., 2006; Maag et al., 2018). Gregarious species which do not perform alloparental can also experience reduced individual fitness, for example through misdirected parental care. Birds sometimes feed at different nests by mistake, or those which lose their own brood will on occasion begin feeding chicks at nearby nests, even chicks of different species (Griesser and Suzuki, 2016). Experience raising offspring can reduce the chances of misdirected parental care, as seen in the communally breeding Sinai spiny mouse *Acomus dimidiatus* (Cretzscmar, 1826), where more experienced mothers are less likely to nurse foreign offspring (Tučková et al., 2016).

Group living can confer benefits to energy conservation. The social spider *S. dumicola* loses less body mass during periods of desiccation when in groups (Vanthournout et al., 2016), while adult male superb starlings in larger groups have a higher rate of survival than males in smaller groups, in wet years (Guindre-Parker and Rubenstein, 2020). The energetic benefits of group living are numerous, including saving heat in cold periods, water during droughts, and saving energy during mass movement as with shoaling fish (Krause and Ruxton, 2002; Nadler et al., 2016).

Group living also affects parasite loads and the dynamics of transmissible diseases. Denser, larger groups are at increased risk of spreading pathogens, especially those in the early stages of their emergence, as there is little to no resilience against novel pathogens (Foley et al., 2011). It is therefore surprising that sometimes group living increases population resilience. Although gregariousness facilitates pathogen transmission, temporally stable groups can limit the pathogens from spreading to a wider area (Manlove et al., 2014). During epidemics, bighorn *Ovis canadensis* Shaw, 1804 lamb survival rate within a herd differs between sub-populations of ewes more than within the overall population, suggesting that pathogen transmission is localized (Manlove et al., 2014). Some gregarious species also practice parasite and pathogen avoidance, as seen in the European badger *Meles meles* (Linnaeus, 1758), where hotspots of infection are more common than consistent spread throughout populations, as infected individuals will stay away from uninfected individuals by reducing overall population density (Albery et al., 2020). However, parasite loads can affect group cohesion, as shown in the three-spined stickleback *Gasterosteus aculeatus* Linnaeus, 1758, which makes collective decisions regarding shoaling behaviour. Individuals infected with parasites are slower than healthy individuals, thus reducing group cohesion (Demandt et al., 2021).

The balance of costs and benefits provided by living in groups vary depending on group size, which can fluctuate throughout the group's lifetime. For example, banded killifish *Fundulus diaphanous* (Lesueur, 1817) exposed to food odour cues decrease their group size to increase individual foraging benefits, but group size increases when exposed to predator odour cues. When both cues are present, group size is at an intermediate, indicating that different contexts have different optimal population sizes (Hoare et al., 2004). Individuals must consider their performance in a group, as if there are high levels of competition for mates or other resources, dispersal or avoidance may be a more beneficial option (Ranta et al., 1993; Maag et al., 2018).

Different individuals may hold different roles within a group, as is often the case in groups which exhibit dominance hierarchies. Dominance is often determined by size or aggressive contests between group members (Mills et al., 2018; Wright et al., 2019), and more dominant individuals often control access to the best resources. Low-ranking individuals in groups can therefore benefit from solitary living or dispersal to new groups where they may hold a higher rank (Ranta et al., 1993). Individuals can also alter their role within a group in relation to their foraging behaviour, as at different group sizes, it may be more or less beneficial to forage or kleptoparasitise. Producer-scrounger dynamics, in which some individuals uncover resources and other individuals steal those resources, are typically studied in highly social species, although are also present in facultatively social groups, and this area deserves more research as in certain facultatively social species individuals appear to consistently take on either role (Evans et al., 2021). However, the dynamics of information ecology within any aggregation of animals can also have significant evolutionary effects.

Access to information

One of the key benefits to grouping animals is access to information about the distribution and quality of resources and appearance and intensity of threats. By responding to both signals and inadvertently-produced cues from group mates, animals can rapidly learn about their surroundings. Learning is a collection of complex ontogenetic processes that allow animals to gain, store, and use information about their environment (Galef and Laland, 2005). In many situations, an animal may be required to learn about a new stimulus or environment very rapidly, for example when first encountering predators, toxins, or harmful abiotic stressors (Galef and Laland, 2005). It has been shown that animals in multiple taxa can learn about such stimuli and environments through the process of social learning, in which an individual acquires new information or a new behaviour by interacting with other individuals or their products (Heyes, 1994).

Social learning provides a short-cut, allowing information to be gained more rapidly than it would be through an individual’s own experiences (Rendell et al., 2011). In order for a naïve individual to learn, they must seek the proximity of, or be exposed to, knowledgeable individuals who in turn must tolerate the naïve individual’s presence, or the naïve individual must be able to interact with the products of the knowledgeable individual’s behaviour. Therefore, it has long been thought that social learning may be present only in group living animals, although in mammals, social learning may not be thusly limited due to the extended parent-offspring relationship (Galef and Laland, 2005), and there is evidence of social learning in non-grouping fish (Webster et al., 2017). In fact, Kendal et al. (2018) argue that solitary species are still exposed to social information through interactions with mates, siblings, and neighbours. Therefore, there are enough reasons to investigate whether species commonly labelled as ‘asocial’ make use of social information.

There has been some debate about whether or not social and asocial learning actually uses separate neural learning mechanisms. Heyes (2012a) argues that social learning can be understood as the same type of associative mechanism that underpins asocial learning, but with different information input channels. From this perspective, social and asocial learning abilities would be expected to be evolutionarily related, and this does seem to be the case. Reader et al. (2011) showed, in a meta-analysis of published work on primate behaviour, that there was a strong positive correlation between asocial and social learning ability, even when controlling for confounding factors, thus indicating either that the same mechanisms may be used for both types of learning, or that there are two separate cognitive mechanisms that evolve together (Heyes, 2012a). Regardless of whether one or two mechanisms are responsible for social and asocial learning, what distinguishes social from asocial learning is that social learning requires another individual to play a role in providing the information to the learner (Heyes, 2012a).

There are several different processes that facilitate social learning, at varying levels of complexity (Brown and Laland, 2003). These processes range from the most basic, like ‘stimulus enhancement’, to complex processes like imitation. Stimulus enhancement occurs when a naïve observer’s attention is drawn to a specific location or stimulus by the behaviour or presence of another individual (Fritz et al., 2000; Brown and Laland, 2003). For example, in greylag geese *Anser anser* (Linnaeus, 1758), goslings that had been shown how to open a box by a human demonstrator explored the box more at that end, whereas naïve goslings explored the box more at other ends of the box (Fritz et al., 2000). Stimulus enhancement has also been shown in three-spine sticklebacks, where individuals were more likely to discover a new task faster if other group members had done so previously, but not more likely to solve it (Atton et al., 2012). Stimulus enhancement, and other simpler social learning processes have been found across the animal kingdom, unlike imitation (Ward and Webster, 2016).

Imitation can be defined as the process by which animals learn to make specific movements through the observation of others (Brown and Laland, 2003). The presence of imitation across the animal kingdom is widely debated, with some arguing that imitation requires complex cognitive abilities, and others instead claiming that imitation is not an overly sophisticated process, that is prevalent across the animal kingdom (Custance et al., 1995; Kis et al., 2015).

Few species have been proven to be capable of true imitation, and there is continued debate on the definition thereof. Some ethologists believe it to be either a uniquely human process, which is required for the development of cumulative culture (Mesoudi and Thornton, 2018), or otherwise unique to Hominidae (Rizzolatti and Craighero, 2004). However, van Bergen et al. (2004) argue that there is no empirical evidence to suggest differences in the types of social learning between primates and other mammals. They argue that the only psychological difference between primates and other animals are in the ability to imitate. However, there is no consensus on how capable apes are of imitation (van Bergen et al., 2004; Zentall, 2022). Perhaps more importantly, social learning in primates tends to be described as more complex due to their shared recent ancestry with humans. Instead, apes should be judged on the same basis as other animals (van Bergen et al., 2004; Heyes, 2012b; Bekkering, 2019).

Some of the first evidence of non-human animals learning through imitation comes from studies on human-reared chimpanzees *Pan troglodytes* (Blumenbach, 1775). Hayes and Hayes (1951), described how Viki, their home-raised chimpanzee, was capable of imitating pointless actions that were demonstrated to her, although only ten out of seventy actions were both novel and copied immediately, without her limbs being manipulated in the correct movement by the authors. A cage-raised chimpanzee, on the other hand, struggled to complete the tasks. Custance et al. (1995) further argued for the presence of imitation in chimpanzee learning processes, as they showed that, after an initial period where the subjects were taught several arbitrary gestures, the subjects were capable of imitating novel gestures. Contrarily, however, Tomasella et al. (1993) found that mother-reared chimpanzees fared less well in the imitation of actions than human-reared chimpanzees and human children, suggesting that being raised by humans improves imitative ability in apes. However, the chimpanzees used in this experiment varied widely in age, with the three human-reared chimpanzees aged between 4 years and 11 months and 10 years and 1 month, and the mother-reared chimpanzees aged between 3 years and 7 months and 21 years old. As these sample sizes are small, and one of the apes in the mother-reared group was more than a decade older than any of the human-reared chimpanzees, this may have impacted the results if the ability for apes to learn new actions declines with age, as it does in humans (Anguera et al., 2010).

Monkeys may also be capable of imitation. Common marmosets *Callithrix jacchus* (Linnaeus, 1758) were tasked with opening a wooden box to access food. Monkeys that had observed the box being opened (either by pushing or pulling) were likely to utilise the same method for opening the box, and also spent less time exploring the box itself than completely naïve monkeys before attempting to open it. However, the preference for the opening method which the observer monkeys had seen disappeared after five trials, thus indicating that the imitated behaviour may not have been fully assimilated into the foraging protocol (Bugnyar and Huber, 1997). A separate study showed that marmoset observers tasked to open a box after observing a demonstrator copied the demonstrator's movements. Only one out of the fourteen movements made by the observers was not also made by the demonstrator, suggesting that the marmosets learned the response topography, or the specific action by which the response was made, further suggesting that imitation is not solely found in humans (Voelkl and Huber, 2007).

Evidence also exists of imitation in birds, as Japanese quail *Coturnix japonica* Temminck & Schlegel, 1848 have been observed to imitate conspecifics in a bidirectional control procedure, where observer quail were exposed to demonstrators responding to a stimulus either to the left or the right. The observers showed correspondence to what they observed and responded in the same direction. This was not done if the demonstrator quail was absent (Akins et al., 2002). Richards et al. (2009) also showed that budgerigars *Melopsittacus undulatus* (Shaw, 1805) that observed the depression of a stopper by pecking were more likely to do it themselves, both immediately and after a 24-hour delay.

Cetaceans are also likely capable of imitation. Atlantic bottlenose dolphins *Tursiops truncatus* (Montagu, 1821) have been shown to imitate motor actions demonstrated by either dolphins or humans when blindfolded, relying on auditory cues and echolocation to determine what behaviour is being demonstrated (Jaakkola et al., 2013). Naïve orcas *Orcinus orca* (Linnaeus,

1758) rapidly learn to copy both familiar and novel actions when exposed to a trained demonstrator and learned to perform these actions on command (Abramson et al., 2013).

A bidirectional control test of bearded dragons *Pogona vitticeps* Ahl, 1927 showed that all experimental individuals opened a sliding door in the direction they had observed a demonstrator opening said door, where no naïve individual opened the sliding door (Kis et al., 2015). Furthermore, the method by which the door was opened by the demonstrator (by sliding the door open with its head) is not a natural behaviour for the reptiles but was copied by all the experimental subjects. This result does suggest that an imitative process occurred, as the novel action would not be expected to be either known or to spontaneously appear (Kis et al., 2015).

One of the biggest challenges in understanding imitation across species is in determining how the observer's motor system can match the sequence of muscle activations used to create the observed movement when it is only observed from a different perspective than which the individual views its own body and actions. This is known as the correspondence problem (Brass and Heyes, 2005). Currently, several different theories cover either generalist or specialist solutions. The most common specialist solution is the active intermodal matching model, which states that observed actions are mapped onto motor output using a "supramodal representation system" that encodes the visual information and matches it to a pattern of motor movements that can produce the same action (Brass and Heyes, 2005). The generalist theories instead suggest that imitation is a result of general learning and motor control mechanisms. They include the ideomotor theory, which suggests that actions are represented as 'images' of sensory feedback and these representations initiate and regulate motor control due to overlap between the sensory and motor representations. This theory in turn suggests that humans' ease in imitation is thus due to the general organisation of motor control, not a specialised, dedicated imitation mechanism. A second generalist theory, termed the associative sequence learning model, builds off the ideomotor theory and extends it further to include actions that cannot be observed by the imitator during imitation, such as facial movements. This model suggests that imitation is the product of associative learning, namely that if the same action is seen and executed simultaneously, the visual and motor representations of the same action are linked (Brass and Heyes, 2005).

There appears to currently be more support for the generalist theories than the specialist theories. A generalist solution to the correspondence problem would require a mechanism that is not solely restricted to situations where imitation is the intended outcome, whereas a specialist imitation mechanism would be expected to be active only when needed. There is evidence in humans of passive observation of action leading to the activation of brain regions associated with movement, including the dorsal pre-motor cortex, superior parietal lobule, and rostral mesial regions (Buccino et al., 2004), thus supporting a generalist solution to imitation. Furthermore, in humans, no brain regions have been found that are consistently active during imitation but not during passive observation (Brass and Heyes, 2005).

Imitation is still considered to be uniquely human by many people, although there is growing evidence that imitation is a form of learning present in many species (Zentall, 2022). It is well established that the origins of social learning lie early in the evolution of animals (Thonhauser et al., 2013), but if imitation also evolved early on, then animal models can be used to aid us in understanding our own abilities. Similarly, if imitation has evolved multiple times, it could shed light on the requirements for such behaviour to evolve. Understanding how cognition evolves in non-human animals can increase our understanding of how our own cognition evolved (MacLean et al., 2012). Cognition bridges the brain and behaviour (Byrne and Bates, 2006), and understanding how more simplistic brains process information and encode it to behaviour in which we also participate will provide a valuable understanding of our own psyche.

Why should we study group behaviour and social foraging in fish?

Fish are ideal for studies on social cognition, as they live in ecologically and socially complex environments (Vila Pouca and Brown 2017). In recent years, fish have become a model for studies on comparative cognition (Vila Pouca and Brown, 2017). Fish are as efficient at numerical discrimination as terrestrial vertebrates, and some studies even argue that fish may have two numerical processing systems, comparable with those of humans (Agrillo et al., 2014). Fish also spontaneously learn relative instead of absolute sizes (Schuster et al., 2004). Aspects of social cognition are also widespread among fish, with evidence existing for the presence of social learning (Thonhauser et al., 2013; Webster et al., 2017; Vila Pouca et al., 2020), individual recognition (Ward et al., 2007; White and Gowan, 2013), self-recognition (Thunken et al., 2009; Kohda et al., 2022), cooperation (Wismer et al., 2014), dominance hierarchies (David et al., 2007; Grosenick et al., 2007), and transitive inference (White and Gowan, 2013). When it comes to their spatial cognition, some fish species prioritise vertical over horizontal components of tasks, due to the importance of depth in their environment (Holbrook and Burt de Perera, 2009). This highlights the importance of the ecological cognition hypothesis, which claims that animals' learning and memory skills are shaped by selective pressures from their microhabitats (Real, 1993; Vila Pouca and Brown, 2017).

This idea that animals' cognitive abilities are linked to their ecology has seen increased support in recent years. A recent review on the link between cognitive performance and ecological specialization found that interspecific variation in cognitive abilities could be explained by differences in foraging adaptations (Henke-von der Malsburg et al., 2020). However, this review also showed that the majority of research investigating these links is conducted on birds and mammals, despite fish being equally suited for such research (Vila Pouca and Brown, 2017). Fish also can be cheaper to keep in captivity than mammals or birds, and their environment (the tanks) can be readily manipulated. Following this, one genus of fish appears particularly well-suited for studies on social foraging in a facultatively social organism.

A review of the behavioural ecology of archerfish *Toxotes* spp.

A significant number of developments have occurred since the last review of archerfish ecology was published by Schuster (2018). This review focussed on their hunting behaviour and the adaptations which facilitate it. Here I aim to provide an updated, comprehensive overview of the behavioural ecology of archerfish.

Although significant research has also been conducted on the neurology and visual abilities of archerfish, this review will not cover this research. For a review of archerfish neurology, see Karoubi et al. (2016). For a review on their visual abilities, see Newport and Schuster (2020).

Archerfish are tropical fish in the genus *Toxotes* Cuvier, 1816 (family Toxotidae),. It is generally accepted that there are seven species within this genus, though some argue there could be as many as ten (Kottelat and Hui, 2018). The first known scientific description of archerfish dates back to 1766, though research on this genus was limited until the 20th century (Gill, 1909). Archerfish are widespread, being found in littoral waters and rivers, in both brackish and freshwater depending on the species. They can be found from India to Polynesia, throughout all of Southern and South-Eastern Asia and as far south as Northern Australia.

Little is known of reproduction in this genus, although they are known to be broadcast spawners. Archerfish appear to be facultatively social, with limited social cohesion even at young ages (Timmermans and Maris, 2000).

Archerfish are best known for their ability to shoot down insects and other small prey using carefully aimed jets of water. This method of hunting is one of their primary ways of obtaining food (Timmermans, 2000), although they are also known to jump to reach prey (Shih et al., 2017), and do also hunt underwater (Simon and Mazlan, 2010). Jumping is similarly costly in terms of energy expenditure to the combination of shooting and C-starting, a rapid acceleration to reach the fallen prey, (Shih et al., 2017) but more consistently provides a food reward. However, the distances achieved by the archerfish shooting at prey vastly out-performs the jumping distance, thus shooting can easily be induced in a lab environment by placing the target at a sufficiently high distance from the water surface.

Archerfish are adapted to hunting terrestrial and aerial prey. While shooting down prey, their entire body remains below the surface, although it is not yet fully understood how the fish adjust their shots for the refraction of the water. Although initial reports suggested archerfish would position themselves directly below their prey to minimize the refraction (Luling, 1963), they instead orient themselves twice before shooting. The initial angle of the archerfish's body in relation to the water surface is used to estimate the true location of their prey, accounting for refraction and gravity's effect on the shot, with the final angle of the fish's body correlating with their prey's height (Dill, 1977).

Archerfish shots are generated when the archerfish presses its bony tongue against a groove into the top of its mouth, creating a narrow opening though which a thin stream of water is forced when the archerfish rapidly closes its gills (Luling, 1963). The water travels non-ballistically as the movement of the water is not solely affected by gravity, and the water at the front of the jet travels slower than the water at the back. This maximises the impact of the jet, as the water at the back pushes the water at the front further forward resulting in a large mass of water forming at the moment of impact (Burnette and Ashley-Ross, 2015). The speed of the waterjet is modulated by incremental changes in the opening of the fish's mouth, but the resultant force can be up to six times higher than the initial force generated by the muscles (Gerullis and Schuster, 2014). Archerfish use their fins to stabilize themselves while shooting, to prevent the shot from moving them backwards away from their falling prey (Gerullis et al., 2021).

Archerfish have co-opted an escape mechanism called a C-start, during which the trunk muscles on one side of the body contract rapidly, bending the fish to face a new direction, followed by a rapid straightening of the tail to propel the fish forward (Sillar et al., 2016), in order to reach their prey at the moment the prey impacts the water The prey's motion cues are enough for the archerfish to decide on the speed and angle of their C-start. If two prey simultaneously fall in different directions, the fish prefers the prey that will land closer, and the latency to move is not impacted (to a difference in prey-fish distance of 1cm) (Schlegel and Schuster, 2008). For an in-depth explanation of the neurology and mechanics of the C-start, see Sillar et al. (2016).

Archerfish also hunt by jumping to catch prey outside of the water. The fish will jump from directly below the prey, and the number of propulsive tail strokes and the fish's peak velocity correlate with the height at which the prey is located. The mechanical energy required to jump to catch prey appears to be similar to that required to spit (Shih et al., 2017). It is still unclear in what circumstances archerfish decide to jump versus shoot, but jumping does reduce the chances of kleptoparasitism.

The manner in which archerfish search for prey is very similar to human visual search abilities. Archerfish are the first reported non-primate to exhibit inhibition of return (Gabay et al., 2013), meaning that they appear to remember where they have searched, and have been shown to use inhibition of return in endogenous orienting tasks (Saban et al., 2017). Archerfish are also the first non-mammal to be reported to use "pop-out" in visual search, or the ability to detect targets against and despite complex backgrounds (Ben-Tov et al., 2015). They can detect their targets without motion clues or stored information about the background, and in all studies so far, their visual search abilities appear identical to those of humans (Rischawy and Schuster, 2013; Reichenthal et al., 2020).

Group Behaviour

Archerfish are facultatively social, meaning they exist both in groups and on their own. There have been few studies on archerfish in the wild, thus it is difficult to state how important sociality is in a natural environment. In a lab-based study, young archerfish were found to have little group cohesion and did not shoal (Timmermans and Maris, 2000). The lack of obligatory sociality may be explained by the likelihood of kleptoparasitism occurring when archerfish shoot down their prey. Archerfish in the wild have been reported to hunt only during the day, as they face competition from heterospecific fish like *Zenarchopterus* T. N. Gill, 1864, which possess water-wave detectors capable of sensing the vibrations of prey falling into the water, making them better equipped to find the downed prey in lower-light conditions. During the day, archerfish almost always caught their prey, thanks to their predictive C-start technique (Rischawy et al., 2015). However, archerfish also face regular competition by conspecifics. In captive conditions, the likelihood of the shooter catching the downed prey is dependent on group size, although this likelihood appears to plateau at a group size of five individuals (Dill and Davis, 2012).

Archerfish are known to alter their behaviour when under observation by conspecifics, possibly as a response to the risk of kleptoparasitism by conspecifics. When in the presence of a conspecific, even if that conspecific if in a different tank, archerfish take longer before shooting. They also make more corrective movements when targeting, and shoot from closer to the target (Jones et al., 2018). Archerfish appear to respond well to social attentional cues, responding faster to visual targets presented in a location that has previously been socially cued (Saban et al., 2017; Leadner et al., 2021), which could explain the increased latency to shoot.

Thus, archerfish may be facultatively social but aware of and wary of conspecifics due to the risk of competition for resources, as well as the likelihood that they cue competitors, or are cued, to prey presence.

In recent research, archerfish have even been found to respond to hunting robot "conspecifics" in a similar manner to real conspecifics (Brown et al., 2021a). Despite initial hesitation, live archerfish inspect robot archerfish even if the robot's "hunt" yields no reward. The earlier cues in the hunting sequence, such as the initial orientating movements made when taking aim, are possibly more important than the later cues (Brown et al., 2021b). Whether this holds true in live archerfish is yet unclear.

Research on archerfish has helped to develop new theories about human facial recognition. Archerfish have been found to be capable of recognizing up to forty-four different human faces (Newport et al., 2016). When shown two dimensional computer-generated faces, archerfish can recognise those faces they have learned to associate with food, even at novel angles. This suggests that rather than relying on strict image-matching, archerfish can generalize their recognition across multiple unlearned views, and that human faces are not a unique class of object as is thought by some evolutionary theorists (Newport et al., 2018). Archerfish are likely capable of recognising different human faces because they have good pattern and object recognition abilities, which is also evidenced in their ability to determine the true size of objects based on the object's position in comparison to their own (Schuster et al., 2004), but this new information regarding archerfish' ability to recognize humans has brought into question the theory that human facial recognition is a specially evolved or uniquely human trait (Newport et al., 2016).

Archerfish also appear to be capable of learning to distinguish between targets that provide differing amounts of rewards. In one study, archerfish were found to be able to distinguish between different colours and shapes to consistently choose those which provided a larger food reward (Karoubi et al., 2017), although another study failed to find similar results when presenting only different colour targets (Jones et al., 2020). Archerfish may also be capable of distinguishing between discrete categories of numbers, as a recent study found that archerfish were able to correctly identify larger or smaller groups of black dots, depending on whether they had been trained to shoot at larger or smaller groups of dots, in differing amounts to those presented during testing (Potrich et al., 2022).

One of the biggest developments in archerfish ecology are findings by Schuster et al. (2006) that archerfish can potentially learn to shoot down moving targets through observing a trained individual, a possible example of imitation. However, since then no new research has been published to indicate that archerfish are capable of learning socially, or to disprove those claims. The closest we have come in confirming social learning in archerfish is research by Leadner et al. (2021) which showed that archerfish respond faster to a target's appearance if its location has been cued by a conspecific. However, this is not evidence of social learning specifically, but merely evidence that archerfish pay attention to public information. Jones et al. (2021a) showed that archerfish' ability to learn to shoot novel cues varies between individuals, but not social context. This suggests that individual differences may play a significant role in archerfish shooting behaviour.

The individual behaviour and personalities of archerfish has received significant attention in recent years, especially in relation to their decision strategies. Archerfish exhibit consistent differences in their latency to shoot (Jones et al., 2018), and there is an inverse relationship between discrimination accuracy and this latency when the fish are presented with multiple, differentially rewarded targets (Jones et al., 2020). This is despite the fact that archerfish learn to avoid negative stimuli (Newport et al., 2013); some fish will always shoot faster at the first target they observe rather than observe all targets before deciding to shoot (Jones et al., 2020).

Individual archerfish also show natural preferences for specific colours and shapes (Karoubi et al., 2017) which could potentially be linked to preferences for specific prey types in the wild.

Finally, archerfish have, sadly, been subjected to the mirror test[1]. Archerfish were found not to demonstrate a preference for either a mirror or a video playback of an archerfish (Austin, 2020). This study was conducted on only three individuals and made assumptions regarding the social and self-directed behaviour of archerfish which have not yet been confirmed by other studies. More research is certainly required before conclusions can be drawn regarding whether archerfish possess a self-image.

Overall, significant progress has been made in recent years in the subject of archerfish behaviour, but many questions still remain unanswered. In this thesis, I aim to discover the answers to some of these questions, specifically on the subject of their social behaviour with a focus to determining how archerfish use use social information during their foraging.

Aims

Group foraging dynamics in a facultatively social organism

As archerfish appear to be facultatively social they provide a good model for researching the effects of group living on hunting behaviour. Archerfish face great competition from hetero- and conspecifics in the wild and could therefore be expected to exhibit behavioural adaptations to minimize the likelihood of kleptoparasitism when shooting for prey. I decided to test whether group size affected such shooting behaviour as latency to shoot (which has previously been

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[1] The mirror test is considered to be the standard for determining if animals are self-aware and is also used for tests of aggression and sociality. However, the mirror test should not be applied to all animals as it is often not an ecologically relevant task, and the responses shown to a mirror image cannot be interpreted identically for different species. See Cattelan S, Lucon-Xiccato T, Pilastro A, Griggio M, 2017. Is the mirror test a valid measure of fish sociability? Animal Behaviour 127:109-116. doi: 10.1016/j.anbehav.2017.03.009. for more information on the application of the mirror test in fish.

found to be affected by audience effects) and aiming duration, as well as to confirm whether previous findings on archerfish behaviour in groups was consistent across studies (Dill and Davis, 2012; Jones et al., 2018).

In chapter 2, I conducted a study on the effects of group size on shooting behaviour. This study built on the findings of Dill and Davis (2012), who found that the rates of kleptoparasitism in archerfish varied with group size. At a group size of three individuals, the likelihood of the shooter consuming the prey was approximately 50% higher than in groups of five or seven individuals. As kleptoparasitism rate appeared to plateau at a group size of five, I chose to compare groups of three and five individuals in a novel shooting task to compare the shooters' behaviour and how it may be affected by the perceived risk of kleptoparasitism.

Do archerfish learn novel foraging behaviour using social information?

One of the most ground-breaking studies on archerfish behaviour showed that archerfish are potentially capable of imitation. Naïve individuals, who had never before encountered a moving target, were able to consistently hit said target after observing a trained individual (Schuster et al., 2006). Imitation, or the act of learning a novel behaviour purely through observing another individual (Zentall, 2006; Fitch et al., 2010), is a controversial area of social learning research. Considered by some to be the most cognitively complex, there is an argument that only humans, and possibly other primates, are capable of exhibiting this form of social learning. Despite this, evidence has been found in a number of non-primate species including Japanese quail (Dorrance and Zentall, 2001; Akins et al., 2002), pigeons *Columba livia domestica* Gmelin, 1789 (Zentall et al., 1996), budgerigars (Richards et al., 2009), whales (Abramson et al., 2013; Jaakkola et al., 2013), bearded dragons (Kis et al., 2015), and bumblebees *Bombus terrestris* (Linnaeus, 1758) (Bridges et al., 2023), suggesting that imitation exists throughout the animal kingdom. If imitation were to be found to occur in fish, it could suggest that the cognitive mechanisms underlying imitation are much more widespread than is currently believed.

The original study which showed archerfish to potentially be capable of imitation was not conducted to test social learning in archerfish, and although some evidence suggests that archerfish could not learn to shoot down a moving target merely by observing the target (Schuster et al., 2006; Schuster, 2018), no further research since 2006 has found evidence of social learning occurring in this genus. A dedicated test or recreation of the original moving target experiment, using appropriate controls such as the use of a ghost demonstrator (Hopper, 2010), would be greatly beneficial. However, there are a number of challenges which exist due to the manner in which archerfish behave in groups which make testing social learning more difficult.

Archerfish alter their behaviour while under observation by conspecifics, specifically by increasing the time taken before shooting (Jones et al., 2018). This means that, when using a live demonstrator, training a naïve individual can take a significant amount of time. It is possible that some individuals are less affected by audience effects, as in the case of Schuster et al. (2006) where the demonstrator fell into said role ‘accidentally’, as it chased the other fish present away from the target, denying them the chance to shoot. It is unclear, however, if the demonstrator in this instance was affected by audience effects.

Video stimuli have been used reliably in behaviour experiments for a multitude of species (D'Eath, 1998; Bird and Emery, 2008; Woo and Rieucau, 2011; Hamalainen et al., 2020), including fish (Rowland et al., 1995; Doutrelant and McGregor, 2000; Polverino et al., 2013; Velkey et al., 2019). Archerfish have been shown to respond well to stationary images of conspecifics (Leadner et al., 2021) as well as to robotic models (Brown et al., 2021b), but whether they respond to videos of conspecifics is not yet known. The only study to date which has used video images was a version of the mirror test where the response to a mirrored screen was compared to that of video playback (Austin, 2020). This study was unable to conclude whether archerfish responded in a social or self-directed manner to either stimulus, thus the utility of video playback for archerfish research remains unclear.

Regardless, the social behaviour, and capacity for social learning, that archerfish exhibit remains largely unknown. Further research is required to determine whether any form of social learning, including imitation, occurs within this genus. Although the use of video demonstrators could potentially increase the rate of learning, or at least the rate at which individuals demonstrate the behaviour, we first need to know whether archerfish learn socially, and if so to what extent.

In chapter 3, I begin an investigation into the use of video models for archerfish research. I use video playback of an unfamiliar archerfish in comparison to video playback of an empty fish tank, and a control of a live empty fish tank, to establish whether archerfish investigate or avoid the video archerfish. Because archerfish eyes are quite complex, it is currently unclear if they would recognize the moving image of a conspecific as such, as monitors are calibrated to human sight (D'Eath et al., 1998). Due to archerfish's extensive visual capabilities (Ben-Simon et al., 2012), they may view the images as distorted instead. This chapter thus aims to discover whether archerfish respond in any manner to a video of a conspecific as a first step towards uncovering whether video demonstrators could be of use in future archerfish research.

In chapter 4, I investigate whether archerfish exhibit group learning. Archerfish are known to use socially cued information to identify where a target may appear (Leadner et al., 2021), but whether this allows them to learn the differences between multiple targets is not yet known. There are currently conflicting reports on whether archerfish can learn to distinguish between targets that provide differential rewards, with several indicating that they can (Karoubi et al., 2017; Leibovich-Raveh et al., 2021) and another that indicates they cannot (Jones et al., 2020). Therefore, I decided to use two targets, one rewarded and one unrewarded, to test whether fish which are exposed to the targets in a group setting are more likely to learn to distinguish between the targets than fish in an individual setting.

The importance of public engagement

Scientific research plays a critically important role in modern society. Advances in technology, medicine, and engineering allow our society to thrive, while research on other subjects continues to illuminate the world around us. However, the majority of scientific research is published only behind paywalls, away from the eyes of the general public, whose taxes largely fund it. Those outside the institutions in which research takes place are unlikely to come into regular contact with said research unless it is reported in popular media.

Public engagement (PE) work is critical for informing the public about developments in science beyond what is reported in the headlines. It creates a dialogue between the researchers and their audience (Bauer and Jensen, 2011), allowing scientists to counteract false narratives purported by the media and increasing public trust in science (Leshner, 2003). Public engagement work is often supported by institutions, NGOs, and the government, primarily taking the form of public lectures and debates, interviews, and popular science publishing (Bauer and Jensen, 2011). Through these methods, researchers can directly impact policy, although since the advent of social media the public enthusiasm for “uncontrolled engagement” (not linked to larger institutions) has increased (Stilgoe et al., 2014). Science festivals, independent podcasts, blogs, and other less official forms of PE allow every scientist to potentially reach a novel audience.

Establishing a dialogue with the public is of critical importance in this day and age. The COVID-19 pandemic, and all the misinformation that continues to surround it, showed us how important direct communication from scientists can be in creating and maintaining a relationship of trust (Bromme et al., 2022; Intemann, 2023). That being said, there is a distinct skew in who participates in PE work. Senior researchers, and researchers who also teach, are more likely to engage in PE than early career researchers and researchers who do not teach, and certain disciplines, like astronomy, have a stronger history of PE work (Bauer and Jensen, 2011). Science communication and PE continues to take a paternalistic stance towards the public, something which serves only to alienate rather than inspire (Leshner, 2003).

I argue that, in today's age where a large proportion of the global population has access to the internet and social media, it is critical that PE work becomes a regular component of scientific research. If we continue to disseminate our findings only amongst our own institutions and colleagues, it matters little what we find. Scientific research is often conducted using the public's money but is published behind paywalls and presented at academic conferences which shun outsiders, often done using scientific language that the public struggles to understand. We are uniquely placed to utilize the advances in technology and the global network that exists online to bring our findings to the public, interacting directly with them through all forms of popular media, including audio, visual, and written content. If we make use of types of communication which are not traditionally used for PE work, we could reach brand new audiences that would otherwise not interact with our work.

In the fifth and final chapter of my thesis therefore, I explore how tabletop role-playing games can be used to educate and inform the public about archerfish ecology. These types of games, in which players take on fictional personas to collaboratively solve problems in a fictional setting, have been successfully used for cognitive and behavioural therapeutic purposes, primarily as a complementary tool for use alongside traditional psychotherapy (Arenas et al., 2022). They have also been used successfully in traditional education, most notably in New Zealand, to help teach a variety of subjects (Bolstad and McDowall, 2019), but little research on their use in a less organized setting has been conducted. I designed a game in which each player takes on the role of an archerfish, with the game mechanics and storylines grounded in archerfish ecology, and taught thirty-nine participants to play the game, testing their knowledge of archerfish both before and after to determine whether the game was an effective method of imparting information.

Chapter 2 - Archerfish foraging success varies with immediate competition level but not group size

Abstract

Group living can lead to kleptoparasitism, the theft of resources by competitors. Under such conditions, foragers may alter their behaviour to minimise competition. However, it is unclear how such behavioural changes impact foraging performance. Archerfish (*Toxotes* spp.) are a good model for investigating the behavioural responses to kleptoparasitism, as their hunting method (shooting waterjets at insects perched above the water) leaves them vulnerable to theft. They must hit the target prey with sufficient force to dislodge it; thus, the prey may land some distance away from the shooter. Kleptoparasitism rates increase with group size in archerfish, and individuals alter their behaviour around conspecifics. I investigated whether group size affected shooting success, using seven-spot archerfish *T. chatareus*. I considered a fish's shot to be successful if it knocked a fly, placed on a transparent platform above the tank, into the water. The probability of shooting success was modelled as a function of group size, aiming duration, nearest neighbour distance and position, and trial number. I found no effect of group size, aiming duration, or nearest neighbour distance or position on shooting success. Shooting success increased as trials progressed, likely due to the fish becoming more familiar with the task. I also found no change in the kleptoparasitism rate between group sizes. Instead, the likelihood of the shooter consuming the prey depended on the types of competition present at the time of shooting. I suggest that archerfish shooting behaviour can be influenced by the presence of conspecifics in ways not previously considered.

Introduction

The behaviour of many animals is shaped by their social environment. Group living is seen across the animal kingdom, as it brings a variety of benefits including protection for predators, faster food source discovery, and easier access to mates (Krause and Ruxton, 2002; Barnard, 2004; Ward and Webster, 2016). However, group living also incurs costs, the largest typically being competition for resources. With the exception of socially cooperative species, the larger the group the faster the resources deplete (Hake and Ekman, 1988; Thiebault et al., 2014), and the less food is available to each individual (Stenberg and Persson, 2005). The mechanisms of such competition are varied. Scramble competition is often present, as individuals will race to get as much of the available resource before the food source is depleted. Competition can also take the form of kleptoparasitism, the active stealing of a resource from a competitor (Broom and Ruxton, 2003), or aggressive contests, where individuals physically fight or intimidate competitors (Ryer and Olla, 1995).

The effects of competition can also play out in more subtle ways. To avoid the costs of attracting competitors and kleptoparasites, foragers may need to pay attention to the distribution of the rivals, which in itself may be costly. Furthermore, the individual who initially discovers a patch has the advantage to gain resources from that patch in the time between its initial discovery and the arrival of competitors (Giraldeau and Caraco 2000), while hunting foragers are attuned to cues from others and join those who are already foraging successfully (Webster et al., 2019). Those who have found food may thus be under pressure not to reveal that source to those around them and monitor conspecifics to determine whether they are at risk of being kleptoparasitised (Bugnyar and Heinrich, 2005). In this way, competitors can interfere with an individual’s foraging efforts even in the absence of overt aggression as individuals have to be aware of the presence and proximity of rivals (Cresswell, 1997). Kleptoparasitism can therefore have clear costs beyond loss of prey, being forced to spend less time with their prey, or increasing their foraging efforts to make up for the lost resources (Allen et al., 2021).

The risk of kleptoparasitism varies widely across and between species in response to several factors. Predators feeding on items requiring longer handling times tend to be at greater risk of having their food stolen (Steele and Hockey, 1995), and less experienced or younger foragers may be at greater risk of being kleptoparasitised (Ridley and Child, 2009). Juveniles may also show greater rates of kleptoparasitising than adults (Steele and Hockey, 1995), as food that has already been uncovered by another individual may be easier or less costly to access for less experienced foragers (Broom and Ruxton, 2003). Theft of resources that would normally be out of reach is quite commonly seen, for example, grey reef sharks *Carcharhinus amblyrhynchos* (Bleeker, 1856) kleptoparasitise whitetip reef sharks *Triaenodon obesus* (Rüppell, 1837), as the latter is capable of accessing prey in smaller crevices than the former (Labourgade et al., 2020). Such costs lead us to expect selection for behaviours that reduce the risk of kleptoparasitism.

Foraging individuals may minimise the risk of kleptoparasitism by altering their own behaviour. For example, the distance between individuals may be increased or group size decreased to reduce the chance of interference, or evasion tactics such as food caching deployed (Cresswell, 1997). Evasion methods may also be deployed during food caching itself, to prevent competitors from discovering the true caches (Bugnyar and Heinrich, 2005; Leaver et al., 2007). However, it is unclear how such behavioural tactics affect foraging success, which is important to understand the trade-offs involved at the individual level.

Archerfish are a good model for investigating the behavioural responses to the threat of kleptoparasitism. These fish prey on insects above the water's surface, which they shoot down by spitting a concentrated jet of water at the target (Gill, 1909). The shooter is left open to kleptoparasitism, although it does not as yet physically possess the prey, as another individual may reach the dislodged food item first (Rischawy et al., 2015). Archerfish evolution has co-opted an escape mechanism found in many fish, called a C-start, to quickly reach falling prey. The fish bends its body into a C-shape to rapidly change direction and accelerate towards the prey, using the prey's falling trajectory to calculate the speed required to reach the prey at the moment it impacts the water (Reinel and Schuster, 2014).

Kleptoparasitism is common in seven-spot archerfish *T. chatareus* (Hamilton, 1822), with loss rates for shooters reported in one lab-based study to be around 44% (Dill and Davis, 2012). This study also reported that the rate of kleptoparasitism increases with group size from three to five individuals but does not increase further in larger groups (Dill and Davis, 2012). Archerfish alter their shooting behaviour in the presence of a single conspecific, with fish taking longer to shoot overall, making more orientations while aiming, and being closer to the target when they do shoot (Jones et al., 2018). Whether archerfish alter their behaviour even more when under observation by more than one conspecific is not yet known but given the likelihood of kleptoparasitism is dependent on group size, it is possible that the changes made to shooting behaviour differs with group size. As we possess a baseline against which to measure the likelihood of kleptoparasitism in different-sized groups (Dill and Davis, 2012) and a baseline against which to measure changes in archerfish shooting behaviour while under observation (Jones et al., 2018), we can combine aspects of both these previous studies to investigate whether archerfish alter their behaviour based on the perceived threat of kleptoparasitism.

I used seven-spot archerfish to investigate whether changes in a shooter's behaviour in response to the threat of kleptoparasitism affect their foraging success. Because of the manner in which archerfish hunt, I was able to separate overall foraging success into two different stages: success in shooting the prey down into the water and success in consuming the prey. I will refer to these two components as "shooting success" and "intake success", respectively, throughout this chapter.

Here I set out to determine whether shooting success – the ability to knock a prey item off a platform and into the water – is affected by group size due to the potential changes in kleptoparasitism threat represented by the varying numbers of competitors. I expected shooting success to be greater in smaller groups, due to the decreased competition (Dill and Davis, 2012), and that this relationship may be influenced by aiming duration, assuming longer aiming times result in greater accuracy. I also expected nearest neighbour distance and position to affect aiming duration as individuals are sensitive to and adjust their aiming when a conspecific is visible (Jones et al., 2018), and therefore predicted that success would be greater when nearest neighbours were further away or facing away from the shooter.

I also investigated whether the shooter's intake success changed in relation to group size, and whether it was affected by the behaviour of their neighbours. I used two measures of kleptoparasitism threat, proximity to the shooter when it takes a shot (≤1 body length away), and other fish C-starting towards the predicted landing spot as the prey falls and analysed how each type affected prey consumption by the shooter. I predicted that the shooter's intake success would be higher in groups of three than in groups of five, and that intake success would be lowest if both types of competition were present.

Methods

Subjects and husbandry

Sixty seven-spot archerfish were used in the experiment. Fish ranged from 8-15cm in length. As archerfish are sexually monomorphic, I was unsure of the sex ratio of the groups used in this experiment. Groups of three or five were formed by size-matching fish, keeping fish in experimental groups within 1cm of each other in length, and each individual group was formed from the same stock tank to ensure familiarity and thereby reduce the likelihood of aggression. The fish had not been previously exposed to experimental conditions.

The study was designed and conducted by Dr Nicholas Jones in the fish laboratory in the Department of Animal Physiology at the University of Bayreuth, Germany. The fish were housed in seven identical sized (120 x 60 x 60cm) stock tanks in the same room. Temperature and water conditions were matched across all tanks. The water was brackish, maintained at a conductivity of 3.5 – 3.7 mS cm−1, and nitrates and nitrites were kept low. 30% water changes were conducted every two weeks. Each tank had a layer of gravel for enrichment and was equipped with two Eheim internal aquaball filters. The room temperature was maintained between 26 and 27°C with a light cycle of 12/12 hours light/dark. Water temperature was controlled primarily by room temperature, but each tank also contained a large submersible thermostat-controlled heater (450W). Fish were fed pellet food (Sera Cichlid Sticks) daily.

The behavioural trials run in this study were approved by the University of Bayreuth. The procedures used in this experiment were also in accordance with the ethical standards of the University of St Andrews. No fish died or suffered ill health during this study, and all individuals were retained in the laboratory for future use. None of the procedures used in this study required U.K. Home Office licensing. All tanks were enriched with plastic plants for cover and handling was kept to a minimum. When fish were moved between tanks, they were caught using two large hand nets to reduce the likelihood of extended capture periods. During this study I closely monitored each fish, specifically for signs of reduced feeding rate, responsiveness, stereotypic behaviour, and colour changes. I observed very few instances of these signs, and they were only temporary and only occurred in the period immediately after fish had been transferred between tanks.

Experimental Setup

Each group of three or five fish was placed in one of two identically set-up tanks of 150 x 150 x 50cm (Figure 2.1).

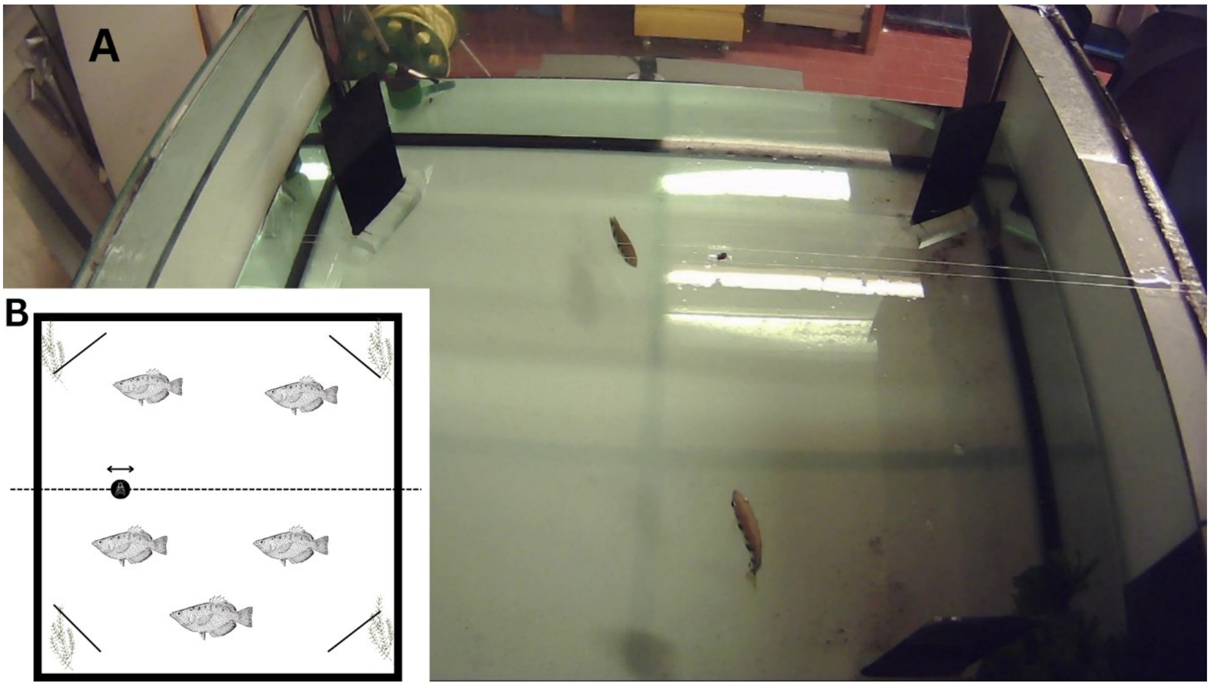

Figure 2.1 A) View of experimental tank with a fly presented above a group of three fish during a trial. B) Diagram showing the tank layout from above.

Each tank had a bare floor with a white base to ensure that the fish were visible for an overhead camera used to record each session. Environmental enrichment was provided in the form of four large plastic plants of equal dimensions (40cm high broad leafed bush replica with ceramic base) placed in two corners and four black opaque screens, one in each corner. Each tank also contained two Eheim internal aquaball filters and two large submersible heaters. Fish were moved into the experimental tanks between 16:30 and 17:00 and left to acclimate for approximately 40 (39.5 - 41) hours before testing sessions started. Each group experienced two experimental sessions per day starting at approximately 9:30 and 16:30 respectively.

A conveyor system was suspended over each tank to allow the food items to be moved into position above the tank while minimising disturbance. This conveyor was constructed out of a small transparent square plastic platform, thus allowing the fish to see the food, mounted onto two monofilament lines that allowed the platform to move along the conveyor. The platform was 25cm above water level such that the fish were more likely to shoot than jump at the food (Shih et al., 2017).

Ten groups of three and ten groups of five were tested during this experiment. A minimum of ten experimental sessions were conducted with each group. More sessions were conducted if the fish were unresponsive, defined as when a group made two shots or fewer in the whole session, during one or more of the initial sessions until ten sessions were conducted with at least 1 shot being made in at least eight out of ten trials per session. Each session consisted of multiple trials, normally ten trials (range 8 - 12 depending on conditions specified below). Each trial started when a thawed fly (frozen house fly, *Calliphora* sp Robineau-Desvoidy, 1830) was suspended above the tank on the conveyor platform. The fly would remain suspended until it was knocked off by an archerfish's shot, knocked off by a jumping archerfish (although this was a rare occurrence, at <0.1% of all trials), or fell off the platform due to manipulation of the conveyer by the experimenter (<0.5% of all trials). A trial ended when a fly had been knocked off the platform and a session ended after 10 trials in which the fly was knocked off by a shot. Additional trials were run if a previous trial had ended due to a fly falling without being shot. Each session was recorded using the overhead camera (ELP 5 Megapixel USB webcam recording 30fps) connected to a laptop running Debut Video Capture software.

Data Analysis

Although I was unable to contribute to the experimental design and data collection, I was primarily responsible for the data analysis. I used Solomon Coder software (https://solomon.andraspeter.com/) to view the videos at a speed of one frame every 0.2 seconds (thus viewing one in six frames). Each fish was identified by its markings and size in relation to the other fish present in the experimental tank and given a number. For every shooting event that occurred, I recorded the identity (number) of the shooter and nearest neighbour, whether the nearest neighbour was facing towards (the shooter within a 90° field of view of the nearest neighbour) or away from the shooter, and the distance (in body lengths) between the two fish. I also recorded the time (since the start of the trial) at which the shot occurred, whether the shot knocked the food off the platform, and the time the shooter took to aim at the food before shooting. Aiming behaviour was evident from the orientation of the archerfish, as they tilt backwards to line up the shot in the vertical plane (Dill, 1977), and aiming duration ended when the shot was released. After every successful shot, I identified what indices of kleptoparasitism threat were present. There were four options: at least one fish being within one body-length of the shooter, a fish other than the shooter C-starting towards the falling prey, both types of competition present, or no competition. I then identified which fish ate the prey, either the shooter, the nearest neighbour, another individual, or I noted that it was unclear which occurred sometimes when multiple fish reached the prey at the same time. I also made note of the group size and the trial number for each shot. Trial number was continuous across sessions within each group, and trial numbers above 157 were excluded as there was only one group which reached each of those high trial numbers, which resulted in this group having nearly double the amount of data as the other groups, thereby skewing the data. Fish used in trials of groups of three were sometimes reused in trials of groups of five, but new identity numbers were assigned within each group. Videos of three groups, one group of three and two groups of five, were deemed unreliable as the lighting conditions or camera angle made identification of the individual fish difficult, and thus 31 out of 200 (15.5%) videos were not coded or included in the analysis. The data was coded by two separate people, me included, and I calculated Krippendorf's alpha reliability coefficient to determine how consistent the coding was between us ($\alpha = 0.89$).

The unit of analysis was single shots by individual fish. I combined the data from each video and assigned group and session identity to each single shot, which was coded 0 if the shot failed to dislodge the prey and 1 if the shot did. Data points for which the nearest neighbour information was unavailable were removed from the dataset (7% of the total). Initial exploration determined that the nearest neighbour position and distance variables were confounded, as fish were more likely to be facing towards the shooter when they were closer. To prevent these confounding effects from unjustly influencing our analysis, nearest neighbour distance and position were grouped into one variable with four levels: ≤ one body length away and facing away from the shooter; ≤ one body length away and facing towards the shooter; ≥ two body lengths away and facing away from the shooter; and ≥ two body lengths away and facing towards the shooter. This allowed me to test whether orientation or distance were most influential in affecting shot success.

I conducted statistical analysis in R, version 4.2.2. I constructed binomial family generalized linear mixed models using the *lme4* package (Bates et al., 2015) to fit the probability of a shot being successful as a function of group size. I included additional predictors in the model attempting to mitigate potential confounding effects of aiming duration, nearest neighbour distance and position, and trial number. Group size was a factor with levels ‘3’ and ‘5’ corresponding to the number of fish. Aiming duration was the total time in seconds that the shooter spent aiming at the target before shooting. This was indicated by the archerfish orienting itself at an angle near or below the food, its head facing upwards. I also included trial number (counted across all trials for that group). I had two opposing but plausible predictions for the effect of trial number on shooting success. Either the archerfish would become satiated throughout the experiment and shooting success would decrease with trial number, or the archerfish would become more familiar with, and focussed on, the food delivery mechanism, and shooting success would increase with trial number. Thus, experience during the experiment could potentially increase or decrease success, but in whichever case I wanted to incorporate that effect in my modelling. Group and session identity were included as intercept-only random effects since groups could have had different baseline success (because of differences in the individuals they contain) and sessions could be subject to temporary effects (e.g. varying noise levels on different days), with session ID nested within group ID. I tested models that did not include shooter identity as a random effect, and while there appeared to be an effect of nearest neighbour distance and position on shooting success in these models, this effect was attributed entirely to a single fish that favoured shooting when the nearest neighbour was more than two body lengths away and facing away. I therefore decided to include shooter identity as a random effect to control for the variation attributed to individual fish, nested within group ID. The final model was thus written in R / *lme4* syntax as glmer(Success ~ Group Size + Aiming Duration + NN Dis. Pos. + Trial Number + (1|GroupID : ShooterID) + (1|GroupID : SessionID), family = binomial).

On obtaining the estimates of the model testing my main experimental question, I constructed two additional models to explore other aspects of the data I had collected. Firstly, I wanted to examine whether group size affected shooting behaviour without influencing shooting success, as shooting is a costly behaviour and the shooter may change their behaviour in response to group size in such a way that it does not influence success alone but also, for example, the time spent aiming. I wanted to explore the idea that aiming duration might act as public information, predicting that if so, durations should be reduced in larger group sizes as the risk of detection is higher with more observers. The first model thus estimated the effects of group size and the nearest neighbour’s distance and position on aiming duration, assuming Gaussian errors after plotting the residuals: glmer(Aiming Duration ~ Group Size + NN Dis. Pos. + (1|GroupID : SessionID)). Group and session ID were included as random effects, with session ID nested within group ID, but shooter ID was removed as a random effect from this model as there was

<0.0005 variance attributed to it in a model that initially included it. Furthermore, I wanted to investigate whether the number of shots per trial changed with group size, as the act of shooting is also likely to act as public information, leading me to expect fewer shots per trial in larger groups. The second model therefore predicted the total number of shots in a trial as a function of group size and trial number while including group ID, session ID, and shooter ID as random effects, with session and shooter ID nested within group ID, and assuming Poisson errors for count data: glmer(Number of Shots ~ Group Size + Trial Number + (1|GroupID : ShooterID) + (1|GroupID : SessionID),family = poisson). The "Number of Shots" variable was scaled using the scale() function in R, as without scaling the model produced a very large eigenvalue.

To investigate the likelihood of the shooter consuming the prey (i.e. not being subject to kleptoparasitism), I constructed a separate model on a subset of the data. I removed all datapoints where shooting success was 0 and removed any datapoints where it was unclear which individual consumed the prey. The resulting dataset contained 1244 observations, representing 66% of the successful shooting events. I fitted a binomial model to a 1/0 response variable which took the value 1 when the shooter obtaining the prey and 0 otherwise. Model predictors were group size and the level of competition present (no competition, nearest neighbour within 1 body length of the shooter, other individual c-starting towards the prey, both types of competition present), with group identity as a random effect. Although I initially also included session identity and the identity of the coder as random effects, the variance assigned to these variables was <0.0005 and therefore they were removed from the model. The fitted model was therefore coded in R as glmer(Consumer ~ Group Size + Competition + (1|Group ID), family = binomial). As a follow-up, I conducted a post-hoc GLMM to determine whether the frequency of each competition level per session of ten shots varied with group size and competition level. The data followed a Poisson distribution, and the fitted model was therefore coded in R as glmer(Frequency ~ Group Size * Competition + (1| Group ID), family = poisson).

Predicted R^2 values were estimated for each model using the MuMIn package (Barton, 2009). All models were checked for collinearity by calculating the variance inflation factors using the performance package (Lüdecke et al., 2021), I found low collinearity between all variables in each model which did not contain interaction terms. Predicted mean probabilities and associated confidence intervals for shooting success and intake success were obtained for each model using the ggeffects package (Lüdecke, 2018). Figures were constructed using ggplot2 (Wickham, 2016).

Results

A total of 3082 shooting events were analysed, occurring across 175 sessions and 17 groups. A total of 70 shooters were recorded across all sessions. Shots tended to be successful (1870 successful vs. 1212 not successful), and there were more shots in the groups of 5 than in the groups of 3 (1842 shots vs. 1239 shots), although there was a similar mean number of shots per shooter in both groups (46 and 43 shots per fish in groups of 3 and 5, respectively).

Shooting success was not affected by group size in this experiment (Table 2.1A).

Table 2.1: Generalized linear mixed model results. Panel A shows the glmm results for the model testing the main experimental question ($R^2 = 0.460$), Panel B shows the glmm results for the first post-hoc analysis ($R^2 = 0.186$), and Panel C shows the glmm results for the second post-hoc analysis ($R^2 = 0.269$). Panel D shows the glmm results for the model testing the likelihood of the shooter consuming the prey ($R^2 = 0.400$), and Panel E shows the glmm results for the third post-hoc analysis ($R^2 = 0.277$). Significant ($p < 0.05$) estimates are shown in bold.

A: Shooting success modelled as a function of group size, aiming duration, nearest neighbour distance and position, and trial number (a priori hypothesis).

Fixed terms	**Coefficient ± SE**
Intercept	0.153 ± 0.388
Group Size = 5	0.466 ± 0.446
Aiming Duration	0.006 ± 0.065
Nearest Neighbour Distance and Position = 1BL, Facing Towards	0.015 ± 0.159
Nearest Neighbour Distance and Position = 2+BL, Facing Away	-0.295 ± 0.187
Nearest Neighbour Distance and Position = 2+BL, Facing Towards	-0.148 ± 0.191
Trial Number	**0.005 ± 0.002**
Random terms	**Variance ± SD**
Group identity : Shooter identity	2.594 ± 1.612
Group identity : Session identity	0.259 ± 0.509
B: Aiming duration modelled as a function of group size and nearest neighbour distance and position (post-hoc hypothesis).	
Fixed terms	**Coefficient ± SE**
Intercept	**0.574 ± 0.049**
Group Size = 5	**-0.347 ± 0.043**
Nearest Neighbour Distance and Position = 1BL, Facing Towards	0.019 ± 0.044
Nearest Neighbour Distance and Position = 2+BL, Facing Away	0.082 ± 0.050
Nearest Neighbour Distance and Position = 2+BL, Facing Towards	-0.028 ± 0.053
Random terms	**Variance ± SD**
Group identity : Session identity	0.040 ± 0.199
Residual	0.535 ± 0.731
C: Total number of shots per trial modelled as a function of group size and trial number (post-hoc hypothesis).	
Fixed terms	**Coefficient ± SE**
Intercept	0.258 ± 0.156
Group Size = 5	0.065 ± 0.249
Trial Number	**-0.001 ± 0.0007**
Random terms	**Variance ± SD**

Group identity : Shooter identity	0.440 ± 0.664
Group identity : Session identity	0.065 ± 0.256
Residual	0.680 ± 0.825
D: Likelihood of the shooter consuming the prey modelled as a function of group size and competition (a priori hypothesis).	
Fixed terms	**Coefficient ± SE**
Intercept	**3.861 ± 0.511**
Group Size = 5	-0.103 ±0.354
Competition = 1 body-length away	**-1.961 ± 0.641**
Competition = C-start	**-2.868 ± 0.469**
Competition = both	**-3.457 ± 0.468**
Random terms	**Variance ± SD**
Group ID	0.405 ± 0.637
E: Frequency of competition levels per session modelled as a function of group size and competition level (post-hoc hypothesis)	
Fixed terms	**Coefficient ± SE**
Intercept	**0.962 ± 0.097**
Group size = 5	0.161 ± 0.151
Competition = 1 body-length away	-0.412 ± 0.211
Competition = C-start	0.185 ± 0.107
Competition = both	0.073 ± 0.111
Group size = 5 : Competition = 1 body-length away	-0.446 ± 0.315
Group size = 5 : Competition = C-start	**-0.343 ± 0.168**
Group size = 5 : Competition = both	**0.418 ± 0.161**
Random terms	**Coefficient ± SE**
ID	0.021 ± 0.144

When including random effects for group, session, and shooter identity, there was no statistically significant change in shooting success between groups of three or five. The success of archerfish shooting did improve within sessions, increasing in later trials (Table 2.1, Figure 2.2).

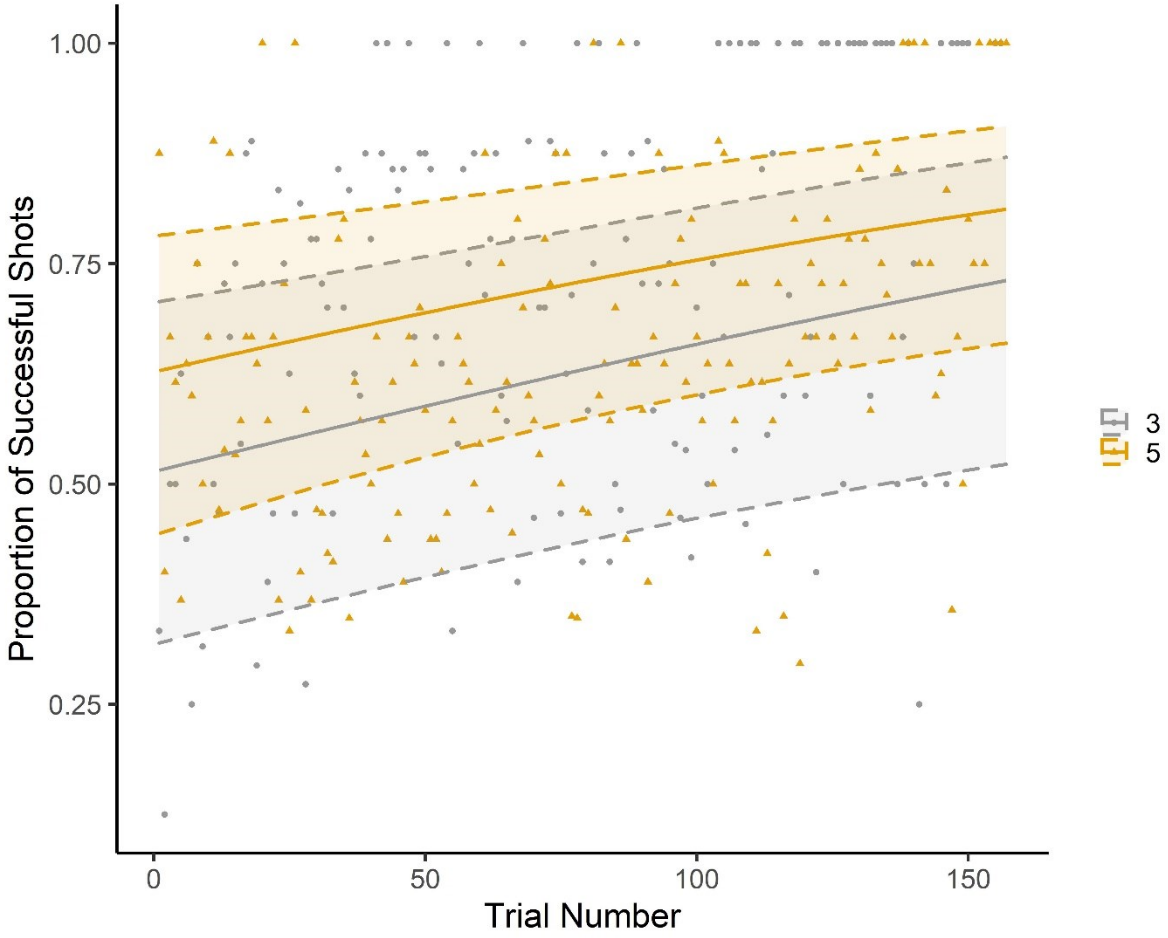

Figure 2.2: Proportion of successful shots per group per trial. The proportion of successful shots increases at later trials for groups of both sizes. The points represent the raw data (grey circles for groups of three and yellow triangles for groups of five). Shaded regions show the 95% confidence intervals.

There were also no statistically significant effects of aiming duration and nearest neighbour distance and position on the success of archerfish shooting, and effect estimates were very small. Although there are multiple data points indicating low success when nearest neighbours are more than two body lengths away and facing away, these points come from a single fish that shot very frequently, and we thus could detect no overall average effect of nearest neighbour distance and position on shooting success (Figure 2.3).

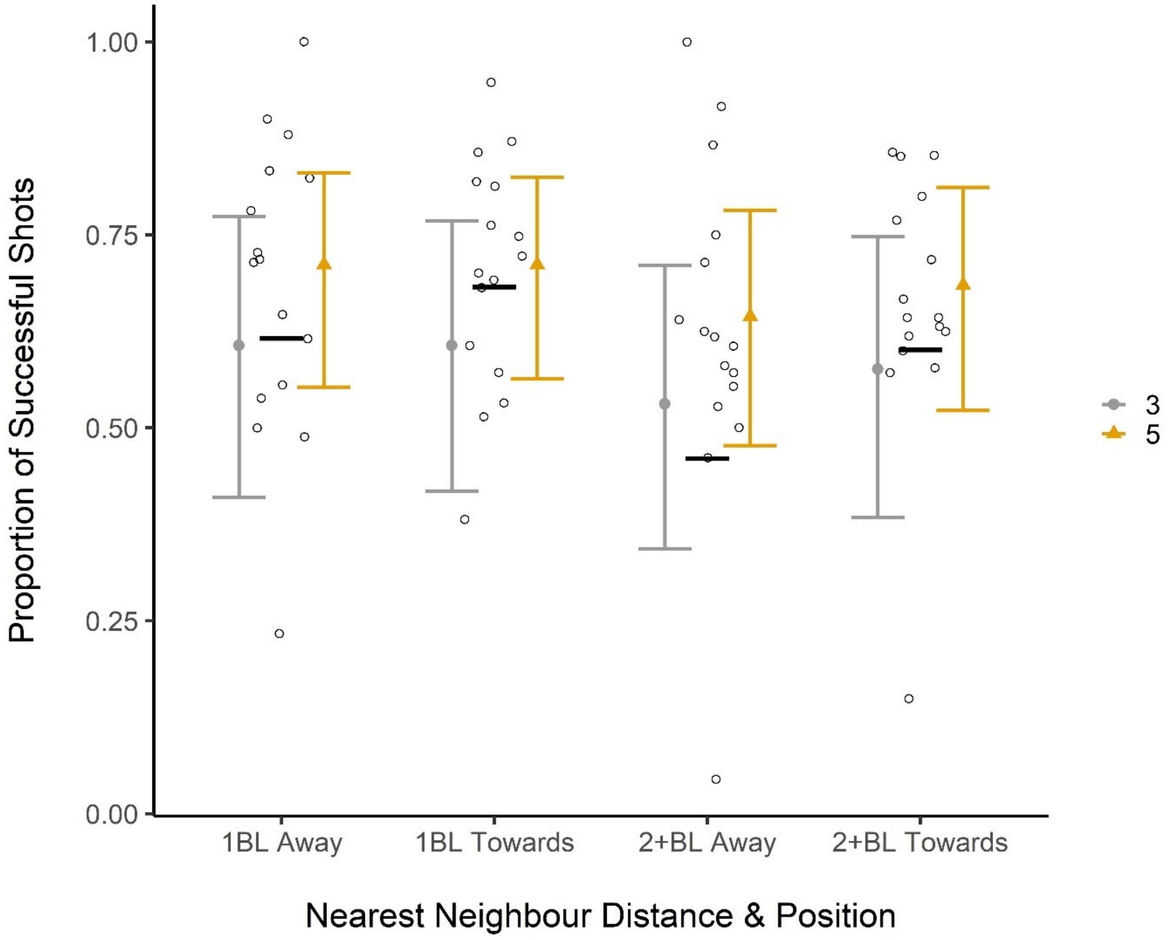

Figure 2.3: Proportion of successful shots per group size per nearest neighbour distance and position. "BL" stands for "body length" and "Away" and "Toward" refers to which way the nearest neighbour was facing in relation to the shooter. There is no difference in the shooting success with changes in the nearest neighbour's distance and position. The black bars indicate mean proportions across all groups.

As I did not find the expected effects of group size and aiming duration on shooting success, I fitted two post-hoc exploratory models to look for evidence of any possible underlying effect of group size on shooting behaviour. When I included group and session identity as random effects, aiming duration was predicted to decrease with group size (Table 2.1B, Figure 2.4A).

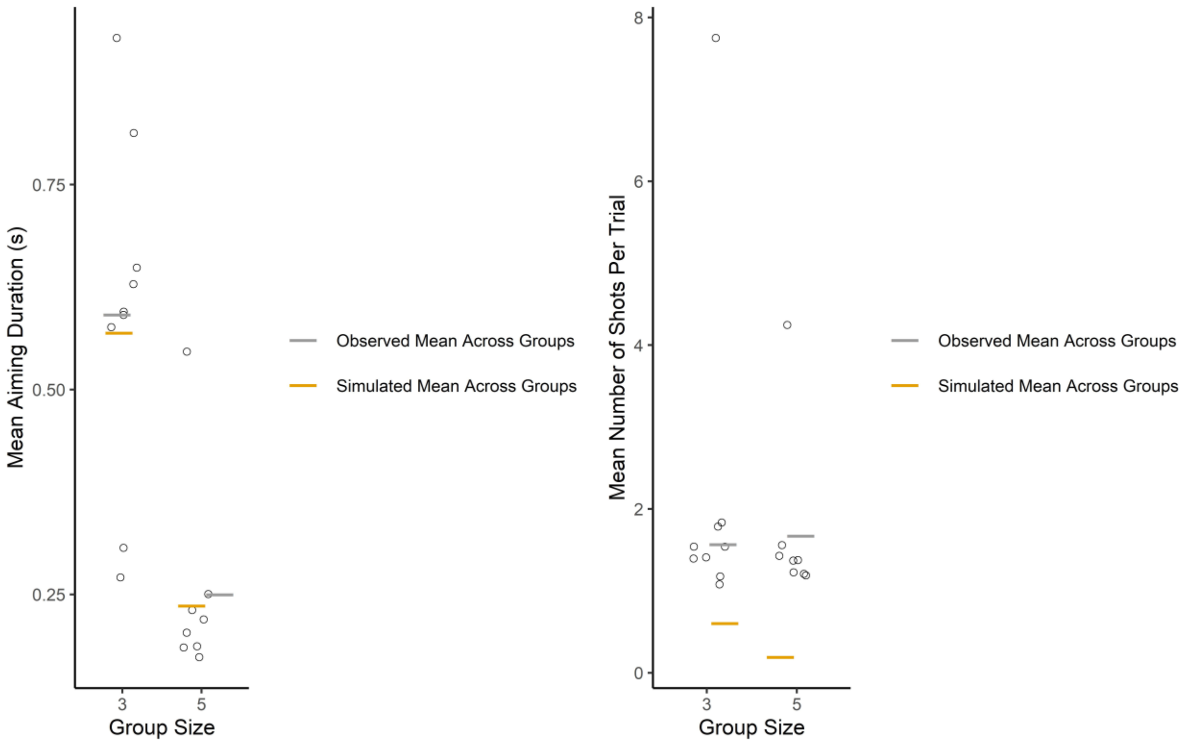

Figure 2.4: A) Mean aiming duration in seconds in relation to group size. Open circles represent group means; bars represent means across all groups. Mean aiming duration is 0.39 seconds longer in groups of three than in groups of five. This relationship remains the same even when the large outlier in group size 3 is excluded. **B) Mean number of shots per trial in relation to group size.** Open circles represent group means; bars represent means across all groups. There are no significant differences in the mean number of shots per trial for different group sizes.

Shooter identity was not included as a random effect in this model as the proportion of variation attributed was negligible (<0.0005). In a second exploratory model, I found no effect of group size or trial number on the scaled number of shots taken during a trial (Table 2.1C, Figure 2.4 B) when including the group, session, and shooter identity as random effects.

Finally, I found that there was a reduced likelihood of the shooter consuming the prey when competition was present, but this varied depending on the type of competition present (Table 2.1D, Figure 2.5 A). When both another individual was within one body-length of the shooter and another individual C-started towards the shooter, the probability of the shooter consuming the food decreased by approximately 40%. I also found that there was an increased frequency of competitors C-starting towards the prey from one body-length away in groups of 5, and an increased frequency of competitors C-starting towards the prey from more than one body-length away in groups of 3 (Table 2.1E, Figure 2.5B).

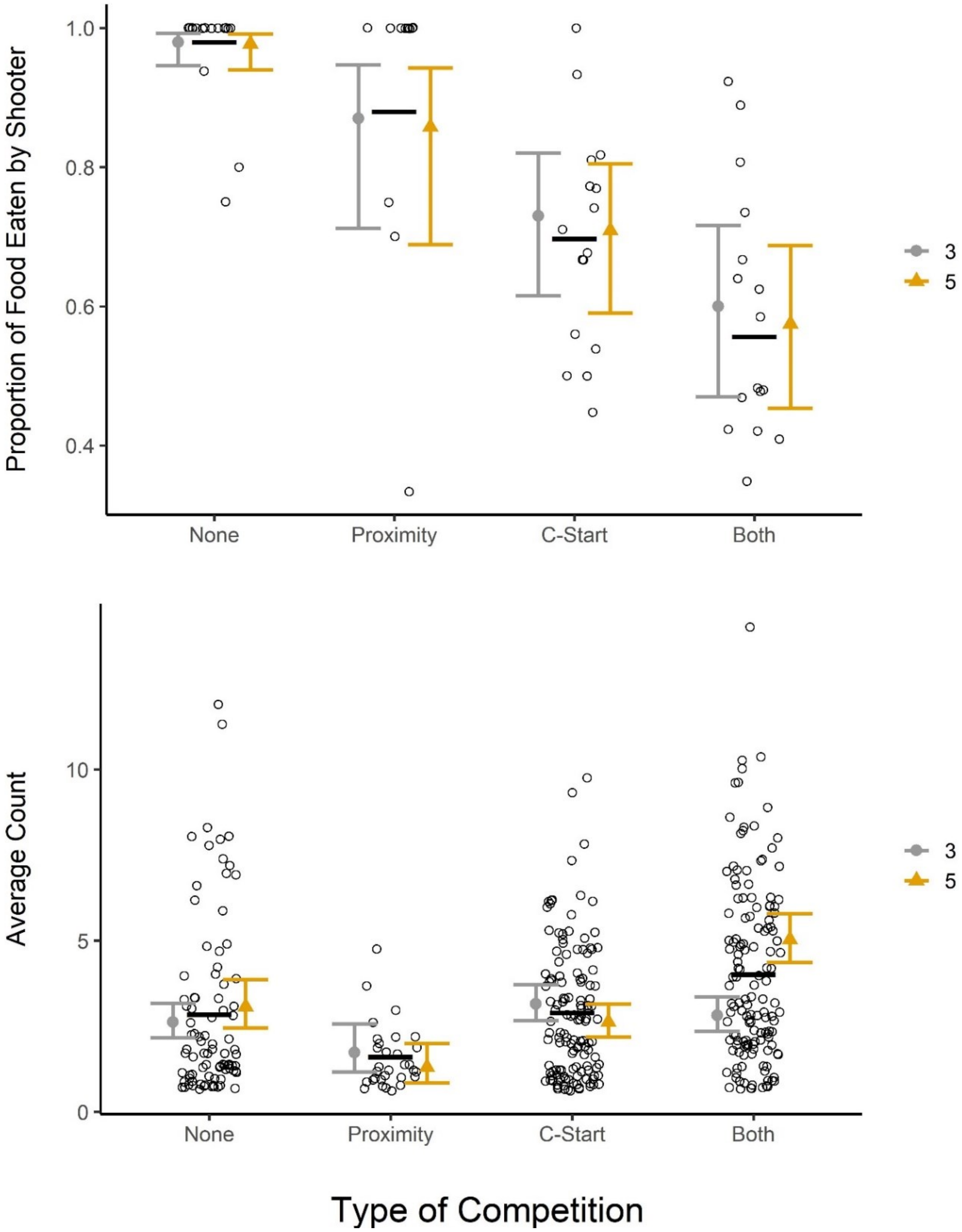

Figure 2.5: A) Mean proportion of prey eaten by the shooter in relation to type of competition present. The black bars indicate mean proportions across all groups. The types of competition are “none” (no competition

occurred), “proximity” (nearest neighbour within 1 body-length of the shooter), “C-start” (when another individual C-starts towards the prey), or “both” when both types of competition are present. There are no significant differences in the proportion of food eaten by the shooter for different group sizes. **B) Average count per session of each competition type per group size.** The black bars indicate mean proportions across all groups. C-starting when more than one body-length away is more common in groups of 3, and C-starting when within one body-length is more common in groups of five.s

Discussion

Foraging success was not affected by group size in this experiment. Shooting success was not affected by aiming duration, or the behaviour of the nearest neighbour, but the probability of successful shots increased with experience and exposure to the targets. I suggest that, as each session progressed, the fish became more familiar with the food delivery mechanism, thus leading to increased shooting success. The platform needed to be hit from the right angle and with the right amount of force to dislodge the food, so the task required some skill. Practice may have been required for the fish to adjust their shots to the right speed and angle, as they are known to improve their shooting abilities over time when faced with a new task or delivery mechanism (Schuster et al., 2006). However, despite my findings, I cannot rule out that speed-accuracy trade-offs may exist when greater precision is required (Jones et al., 2020). The target height in this experiment was relatively low given the typical shooting range for archerfish (Luling, 1963), and if a higher target were to be presented, it is possible that aiming duration may impact shooting success.

In the wild, the presence of conspecifics is often a good indicator of the presence of food or other beneficial resources. Therefore, individuals often tend to investigate areas where conspecifics are present (Anderson, 1991; Midford et al., 2000). A study in juvenile walleye pollock *Gadus chalcogrammus* Pallas, 1814 determined that this type of local enhancement was only present when food was provided in clumps, and not when food was dispersed (Ryer and Olla, 1995). This same study also found that when food was dispersed, some fish aggressively defended areas of their tank to prevent conspecifics from obtaining resources. I observed that some dominant shooters would monopolise the area near the target and chase away encroaching individuals. It is possible, therefore, that I did not observe group size affecting shooting success in regard to the perceived threat of kleptoparasitism, because the other individuals were excluded by an aggressive dominant fish, i.e., that dominant shooters could reduce the risk of kleptoparasitism by the threat of aggression. It is conceivable that individual differences between shooters masked any changes made in shooting behaviour in relation to group size. I should also note that movements of the fish in our experimental tanks are likely to be constricted compared to natural conditions, although I cannot say if or how this may have influenced our results, as there is little research published on archerfish in the wild.

I was surprised not to find an effect of either group size or nearest neighbour distance and position on shooting success, however this may be explained by my results on the shooter's intake success depending on group size and competition. Dill and Davis (2012) established that the risk of kleptoparasitism to the shooter increases with group size from three fish to five fish, thus I had expected to see changes in the shooters' behaviour to minimise the possibility that the food would be stolen. I further expected these changes in shooting behaviour to influence the success rate, as we had predicted a reduced aiming duration in larger groups and, intuitively, that less time spent aiming would negatively impact shooting success. My post-hoc analyses do suggest that group size does affect the time shooters spend aiming, but, counter-intuitively, that this reduction in aiming duration in larger groups does not in turn influence shooting success. I also found no effect of group size on the shooter's intake success, in contrast to the findings of Dill and Davis (2012). Their study determined that the rate of intraspecific kleptoparasitism increases with group size from three to five individuals but does not increase further at even greater group sizes. In contrast, I found that the risk of kleptoparasitism was mediated by the level of perceived kleptoparasitism threat present. Although there was a reduced likelihood of the shooter eating the food if another individual was within one body-length at the time of shooting, the likelihood was not as low as when an individual more than one body-length away C-started towards the prey (88% vs 70%). Although this level of competition was more likely to occur in groups of three, there was no difference in the likelihood of the shooter consuming the prey between groups overall. Therefore, the mere presence of a conspecific close to the shooter is not necessarily a large enough threat to alter the shooter's behaviour, and in this experiment the fish were close enough together even in smaller groups that there was no difference in kleptoparasitism risk with group size. It is possible that my findings differed from those of Dill and Davis (2012) as my model included the different types of competition present, which is itself affected by group size. Although I did not find increased levels of kleptoparasitism at increased group size, competition is more likely, and I found that kleptoparasitism rates differ with different types of competition. Therefore, it is possible that the competition types present is the underlying cause of Dill and Davis (2012) findings.

If archerfish success in shooting down a target is not linked to the time spent aiming, why would fish in smaller groups increase their aiming duration? The difference in aiming duration may seem small, but archerfish hunting sequences happen incredibly fast; previous findings report decision making during hunting to occur on the scale of milliseconds (Schlegel and Schuster, 2008). Thus, for an archerfish, 0.39 of a second could be a serious delay. Although I considered that it is possible that the angle from which the target is shot may impact the shooter's likelihood to reach the downed food, our findings in this study appear to not support this theory. It is still possible that increased aiming duration makes it more likely for conspecifics to notice the behaviour and become aware of the prey item, however I must consider other theories as to why aiming duration is longer in smaller groups. One possibility is that, given shooting water is conspicuous outside of the water (Schuster, 2018), the increased aiming duration is an anti-predator response. In smaller groups, risk of predation is greater therefore increased time in the aiming position may allow the shooter to scan for predators for longer. Further research is required, including examining how likely the shooter is to get the reward as a function of its own position relative to the target, to determine whether the changes in aiming duration are an anti-predator response, a counter-kleptoparasitism response, or a combination of the two.

Overall, I found little evidence of adjustments in archerfish behaviour in response to perceived kleptoparasitism risk with increasing groups sizes. My results, however, suggest some evidence that archerfish shooting accuracy increases as trials progressed. I found no evidence that archerfish aiming duration affects shooting success, but some limited evidence that aiming duration does decrease with group size. I also found that the shooter’s intake success depends on the level of perceived kleptoparasitism threat, but not group size. My findings suggest that the interaction between effects like public information use and kleptoparasitism defence are perhaps more complex than we initially thought.

Chapter 3 - An investigation into the use of video models in social learning research: Archerfish actively avoid videos of conspecifics

Abstract

Artificial stimuli like videos are commonly used to investigate animal behaviour, as they allow the experimenter greater control over the experimental conditions. The use of videos allows demonstrator individuals to be recorded without their natural behaviour being affected by the observers, but also comes with several drawbacks. Video screens are calibrated to human vision, thus moving images may appear distorted, pixelated, or two-dimensional to animals with higher visual acuity than humans. There is great potential for the use of video demonstrators for tests on social learning in archerfish, as the demonstrators are known to alter their behaviour when under observation by conspecifics, but it is unclear if archerfish can recognize conspecifics on videos. I tested how ten seven-spot archerfish responded to a video of an unfamiliar conspecific in comparison to a video of an empty fish tank and a real empty fish tank. There was no difference in the amount of time spent near or looking towards any of the stimuli, but the focal fish did spend more time further away from the video fish. This suggests the observers may have recognized the video stimulus as a conspecific and exhibited an avoidance response, or they may have moved further away to minimize pixelation of the video fish. I discuss the need for additional research comparing archerfish social responses to live conspecifics to video stimuli, as well as the potential for using robot conspecifics instead.

Introduction

For decades, animal behaviour research has made use of artificial stimuli to investigate the behavioural responses of animals. Examples of artificial stimuli include cardboard models like Tinbergen's gull heads (Tinbergen and Perdeck, 1951) to advanced robotic conspecifics (Brown et al., 2021a), virtual reality (Chouinard-Thuly et al., 2017), and 3D models (Woo and

Rieucau, 2011; Chouinard-Thuly et al., 2017). Although live stimuli are most likely to mimic situations in nature, there are many benefits to using artificial stimuli instead. The use of artificial stimuli allows for a greater control over the stimulus itself, for example by making it easier to alter colour, shape, or even the behaviour (D'Eath, 1998). In experiments where a specific behaviour is required to be shown by a demonstrator, artificial stimuli like videos allow those behaviours to be shown without the demonstrator adjusting their behaviour in response to the observer's actions (Rohwer, 1985), or the stimulus can be manipulated to show new outcomes (Cook and Mineka, 1989). Furthermore, live stimuli could induce stress responses in study animals if the stimuli used represent prey or predator threat, thus using artificial stimuli may be more ethical in certain studies, from an animal welfare perspective.

Video stimuli are commonly used in mate choice and grouping studies and have begun to be used in tests of social cognition (Balshine-Earn and Lotem, 1998; Polverino et al., 2013; Velkey et al., 2019). For example, fairy cichlids, *Neolamprologus brichardi* (Poll, 1974), have been shown to treat images of unfamiliar and familiar fish in similar ways as they do live fish (Balshine-Earn and Lotem, 1998). Although live stimuli are still often preferred over video models (Velkey et al., 2019), there are occasions when videos may be more appropriate, such as in studies where a consistent behaviour must be shown, or in studies where manipulation of a live stimulus is difficult or unethical (Webster et al., 2019).

There are several caveats that must be considered when using video models for behavioural experiments, as video systems are designed for human use (Oliveira et al., 2000). This is especially important for an animal like the archerfish, whose eyes have evolved to exist at the junction between land and water, anda are thus different from human eyes (Ben-Simon et al., 2012; Ben-Tov et al., 2018). For example, the rods and cones are distributed non-randomly in the archerfish retina to facilitate better contrast detection, with the cones tuned to recognize different shades of brown, which are prevalent in mangrove habitats (Temple et al., 2010). How the different distribution of cones tuned to different colours affects the ability to discriminate between colours when viewed from different angles remains unclear, but we cannot rule out that archerfish may see colours differently than humans. Furthermore, the refresh rate of the video screen must be high, with a critical flicker fusion frequency (the frequency at which an intermittent light stimulus is perceived as a continuous image) above 95Hz, as otherwise some animals may not perceive a continuous image (Kunzler, 2001). Depth perception will also differ between a video and a live model, thus animals on video images should appear life-sized and the background should be kept plain. Furthermore, the use of natural light conditions is preferrable because prolonged exposure to artificial light can alter visual perception (Oliveira et al., 2000). Lastly, as many teleosts can perceive wavelengths of light which are beyond the human visual spectrum of 400-710nm, primarily in the ultraviolet spectrum of 300-400nm (Losey et al., 2005), and the number of cone classes can vary between species (Neumeyer, 1992), colours may not be perceived correctly when shown on a video screen. Thus, animals may sometimes fail to respond to video images. However, sometimes, the shape or motions of an individual or a behaviour may provide the observer with enough cues for a response (D'Eath et al., 1998).

Like in all studies on animal behaviour, an important part of using artificial stimuli like videos is correctly interpreting the results. The spontaneous occurrence of natural behaviour in response to being shown a video stimulus is often interpreted as the animal recognizing the video for the real thing, but there are many reasons why that natural behaviour might occur (D'Eath, 1998). For example, an animal may exhibit a fear response when being shown footage of a predator or a threatening conspecific, but it might equally be showing neophobia to the movement of the stimulus without specifically recognizing it as a predator or conspecific, or reacting to the light stimulus of the screen (Ryan and Lea, 1994). To help interpreting spontaneous responses to the video stimulus, D'Eath (1998) suggested using a blank video or a video of irrelevant objects as a control before commencing the experiment proper. This would allow for a comparison between the response to the stimulus to a baseline response to, for example, the novelty of the video screen.

The use of video stimuli can be especially useful in social learning research, as it allows for a demonstrator to show a behaviour without the demonstrator's own behaviour being altered by the presence of the observer, as the video recording of the demonstrator can be made in the absence of observers. Research by Jones et al. (2018) has shown that archerfish can be hesitant to shoot down prey if they are under observation by conspecifics; this can make training naïve individuals with live demonstrators difficult and time-consuming. If archerfish recognise conspecifics on video, video demonstrators could be used to train naïve demonstrators, potentially reducing the amount of time needed to train the naïve individuals. The demonstrators can then also be very easily removed (by turning off the video screen) to reduce the likelihood of audience effects affecting the observer during testing, while also minimizing effects on animal welfare from constant moving of fish between tanks. The use of video may increase the rate of learning in archerfish and provide an adequate method of ensuring that the training between different individuals remains consistent.

This chapter addresses the question: do archerfish respond to video recordings of conspecifics differently than to videos of an empty fish tank, or an actual empty fish tank. These treatments were designed to allow me to determine, firstly, if the archerfish responded to the moving image of a conspecific as opposed to the video screen itself, and secondly, if the archerfish responded to a control stimulus presented without screen display artefacts. This second control stimulus was used because archerfish prefer dimly lit areas, and the screens themselves may have been distressing to the fish. By providing a non-video stimulus, we hoped to determine if the fish objected to the presence of the monitors. I considered a "response" to the stimulus to include either swimming on the side of the tank closest to said stimulus, looking towards the stimulus, or marked avoidance of said stimulus.

I did not, in this study, test how archerfish responded to the video fish compared with a real archerfish as I wished to determine if the fish responded to the video in the absence of real conspecifics. A follow-up study had been planned to compare video stimuli to real fish, but due to the deaths of the fish used in the first experiment I was unable to complete the second study. There was also a matter of consistency amongst the potential live demonstrators, as moving the demonstrators between tanks to alternate sides would have been distressing and potentially altered their behaviour, thus potentially influencing the actions of the focal fish.

For this study, I predicted that, if the archerfish recognize the video fish as a conspecific, they would spend more time near the screen showing the video or more time looking towards the video compared to the empty fish tank or the video of the empty fish tank. There is also the possibility that, if they recognise the video fish as a conspecific, they will move further away from the screen to avoid potential conflict. That response could, however, also be interpreted as a fear response to an unknown 2D stimuli. If they do not recognize the video of an archerfish as a conspecific, and are not afraid of the stimulus, we expected the archerfish to spend their time randomly between the two screens. If the fish, which we know from observation to be cautious around bright lights, dislike the screens, or moving images on them, we expected the fish to spend more time near the empty fish tank.

Methods

Subjects

I tested 10 seven-spot archerfish from animals housed at the University of St Andrews. All fish were wild-caught as juveniles from a fresh-water population, sourced from an accredited ornamental fish supplier. The ages of the fish were therefore unknown, nor were their sexes known as archerfish are sexually monomorphic. All fish were approximately 8-10cm long. The fish had been kept in the lab for at least three years prior to the start of this experiment and had previously been used in behavioural experiments (Jones et al., 2018; Jones, 2020; Jones et al., 2020; Jones et al., 2021b) but had never been exposed to video footage of any kind. The stock tanks (183 x 46 x 35cm L x W x H) were kept between 25 and 26°C using a central heater that warms the whole room, under a 12:12 h light:dark cycle, and contained a layer of gravel substrate and multiple plastic plants and tubing to provide enrichment and cover. Water quality (pH, NO^{-}_2, NO^{-}_3, NH_3) was measured every two weeks and maintained using large canister filters and regular water changes. Fish were fed four Tetra brand cichlid sticks every day around noon.

Experimental Design

Two video stimuli were prepared using a JVC GC-PX100 camera, at a framerate of 30fps. A tank measuring 56 x 56 x 41cm L x W x H was prepared with a thin layer of gravel, an aquarium filter (Eheim Aquaball 130), and a plastic plant placed in front of the filter to provide shelter and enrichment. It was filled with approximately 97 L^3 of freshwater. One archerfish which was unfamiliar to the subject fish used in this experiment (that is, had never been housed in the same tank) was recorded for one hour as it swam around this tank. It was not fed during this time or disturbed in any other way. The fish was then removed from the tank and the empty tank was recorded for another hour. This resulted in two hour-long videos of the same tank, one featuring an archerfish and one not. I chose to film only a single individual in the preparation of the video stimuli as personal observations by myself and other researchers seem to indicate that archerfish exhibit a dominance hierarchy of some kind. The exact nature of this hierarchy is unclear, but to prevent any effects thereof on the observers I chose to use a single fish as a video model.

A set of three tanks identical to the one used in preparing the video stimuli were set up side by side. The tanks were spaced so that a 27-inch (69 cm) ASUS MG278Q gaming monitor could be easily placed on either side of the central tank. The monitors have a 2560 x 1440 resolution and 144 Hz refresh rate, high enough that the fish should see a continuous image (Kunzler, 2001). The height of the monitors was able to be adjusted so that it matched the height of the fish tanks. A laptop was plugged in using an HDMI connection to play the video stimuli. This set-up meant that the focal fish may have realized the video fish were not in the same tank, but previous research has established that, even if an observer is not in the same tank, archerfish change their behaviour when under observation by a conspecific (Jones et al., 2018). Each tank was filled with fresh dechlorinated water to identical levels, approximately 10cm below the lip of the tank. The tanks also contained similar levels of pebbles on the floor of the tank, water filters, and one plastic plant each. The middle tank was the "experimental tank". It was separated from the other tanks, or monitors, by opaque black sheeting. An aquarium light was placed behind the tanks, with similar, white, opaque sheeting dimming the light slightly. The light was kept switched off until before the experimental sessions began.

One archerfish was randomly chosen from the stock population and placed in the experimental tank. The fish was allowed to acclimatise for at least three days, until its behaviour had returned to a baseline assessed by response to the experimenter (not hiding). Plastic, transparent tank covers were placed on top of the tank to prevent the archerfish from escaping by jumping. A tripod with an attached webcam was placed above the experimental tank so that the entire tank was in view.

Each archerfish used in this experiment underwent a total of four trials, consisting of two separate treatments (Figure 3.1). In the first treatment, a monitor was placed on one side of the experimental tank. The opaque sheeting was removed from the sides of the experimental tank, and the archerfish was recorded using the webcam above for approximately one hour while the monitor played a video of a different archerfish swimming in a tank identical to the tanks set up on either side of the experimental tank. On the other side, an empty fish tank identical to the one in the video stimulus was shown. This treatment was repeated twice, switching on which side the monitor was placed.

The second treatment was like the first, except that monitors were placed on both sides of the experimental tank. The same video of an archerfish was shown on one monitor, while the other monitor showed a video of the same tank, but with the archerfish removed. This treatment was also repeated twice, switching on which side the monitor was placed. The order in which each treatment was presented was chosen randomly using a number generator.

The videos of the archerfish in the experimental tank were blind coded by three separate people, including myself, using the Solomon Coder software (https://solomon.andraspeter.com/). The experimental tank was divided into three sections (Figure 3.1) and the location of the archerfish was continuously recorded every 0.2 seconds (thus every 6 frames). Their orientation (facing left, right, or neither) and their behaviour (swimming or stationary) were also recorded.

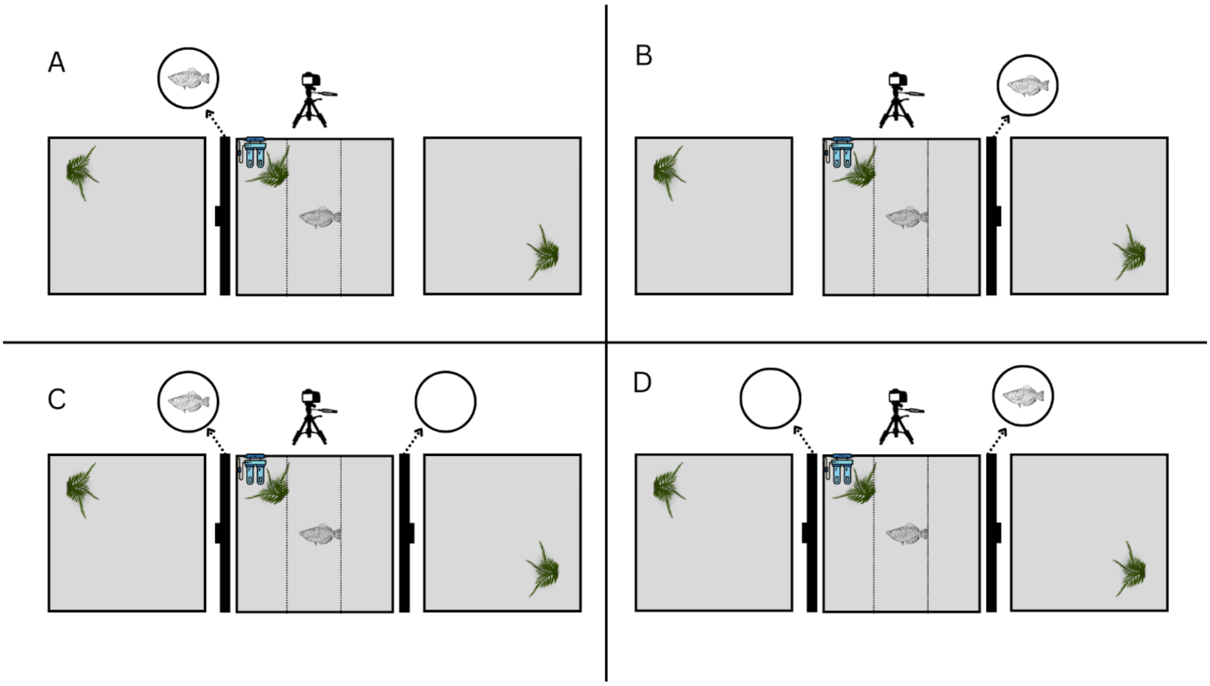

Figure 3.1: Experimental Set-up. Top-down view of all four trial set-ups. The blue icon in the central tank indicates the location of the filter in the tank. The circles indicate whether the screen was showing a video of an empty fish tank or of a fish. The dashed lines indicate how the tank was visually divided (roughly into thirds) when the videos were coded.

Analysis

Analysis was conducted in R version 4.2.2. I used the package "irr" to compare the results from the different coders and found an inter-rater reliability score (Gisev et al., 2013) of 0.95-0.99 indicating strong repeatability of the measurements. I calculated the mean time the fish spent near the video fish per treatment and the mean time the fish spent looking towards the video fish. I then used the lme4 and lmerTest packages to fit a linear mixed effects model where the dependent variable was the log mean time in seconds the focal fish spent near the video fish. The independent variable was the treatment, which was a factor with two levels, "Empty Tank" and "Video Tank", which were the two controls used. I predicted that, if the focal fish recognized the video fish as a conspecific, they would either spend more time near, or more time away from the video fish than it would to either of the control stimuli. I included fish identity as a random effect because there was the possibility that individuals may respond differently to the video fish due to known personality differences in archerfish (Jones et al., 2018) or unknown dominance hierarchies. I also fitted a linear model with normal error relating the log amount of time in seconds the fish spent looking towards the video fish to treatment. Here I predicted that, if the focal fish was more interested in the video fish stimulus than either control, it would spend more time looking towards that stimulus. I did not include fish identity as a random effect as testing with models including it showed that the proportion of variance attributable to this effect was less than 0.001.

I also conducted paired signs tests using the rstatix package to determine if the median time the fish spent near or away from the video fish differed across all treatments. I also used a Friedman test to compare whether there was any difference in the time the focal fish spent looking towards the video fish, away from the video fish towards the other stimulus, or towards one of the blacked-out sides of the fish tank. I applied a Bonferroni correction to the Friedman test to adjust the *p* values for multiple hypothesis testing using Conover's test from the *PMCMRplus* package.

Results

I found no relationship between the treatments and the amount of time fish spent near the video fish (Table 3.1 A). I also found no relationship between the treatments and the amount of time fish spent watching the video fish (Table 3.1 B). This means the fish did not change the amount of time they spent near, or observing, the video fish regardless of the other stimuli available.

Table 3.1: Results for GLMM comparing the time the focal fish spent near the video fish in relation to treatment and the GLM comparing the time the focal fish spent looking towards the video fish in relation to treatment.

A: Results of model comparing the time the focal fish spent near the video fish in relation to treatment.	
Fixed terms	Coefficient ± SE
Intercept	6.238 ± 0.432
Treatment	0.753 ± 0.479
Random terms	Variance ± SD
Fish Identity	0.715 ± 0.846
Residual	1.147 ± 1.071
B: Results of model comparing the time the focal fish spent looking towards the video fish in relation to treatment.	

Intercept	1098.54 ± 134.39
Treatment	70.29 ± 190.06

However, I did find that fish did not equally distribute how much time they spent near and away from the video fish (paired sign test, p = 0.003). The focal fish spent more time away from the video fish than closer to the video fish (Figure 3.2 A). In contrast, although initial results seemed to indicate that there was a difference in the time the fish spent looking towards the video fish, looking towards the other stimulus, and towards the blacked-out sides of the tank (Friedman test, $X^2 = 6.1$, d.f. = 2, p = 0.047), a post-hoc Conover test with Bonferroni correction showed that there was no difference between the three groups (adjusted $\alpha = 0.016$, p values for each pairwise comparison ranged from 0.099-1.000) (Figure 3.2 B). The focal fish's behaviour was not affected by the treatment (Figure 3.3 A and Figure 3.3 B).

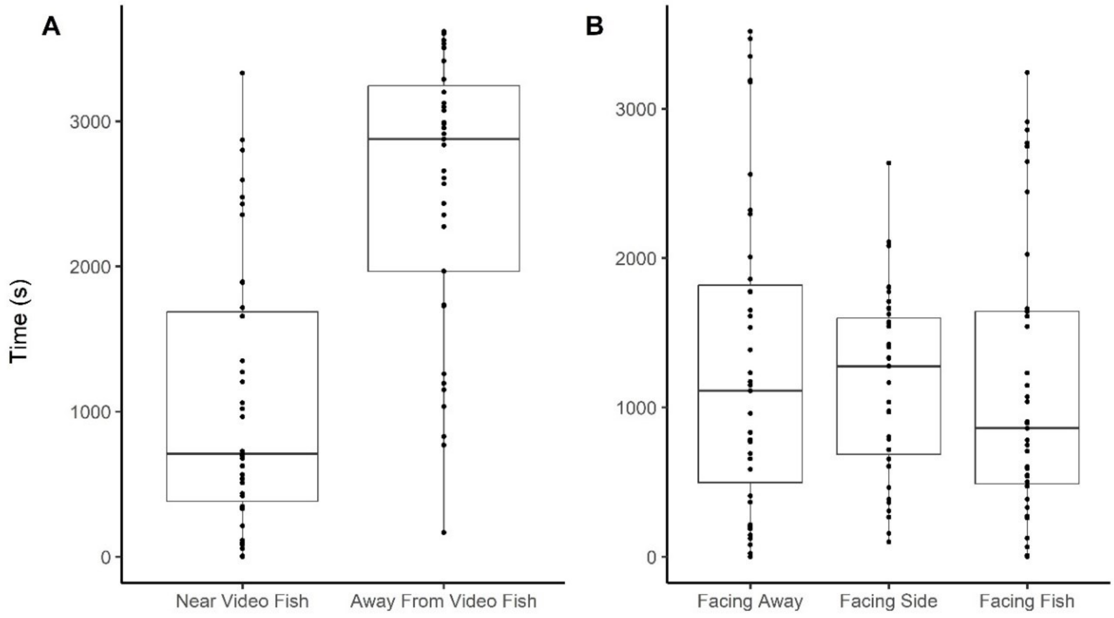

Figure 3.2: A) Time spent in proximity of the video fish versus away from the video fish. B) Time spent facing each direction in relation to the video fish.

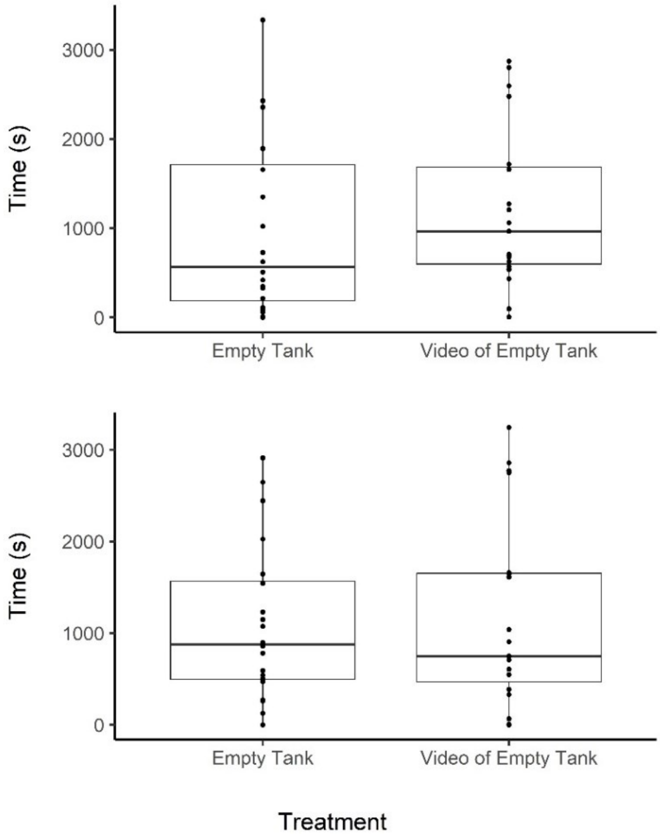

Figure 3.3: A) Time spent near the video fish depending on treatment. B) Time spent looking towards the video fish depending on treatment.

Discussion

Archerfish spent less time in the section of the tank closest to the video of an archerfish and did not differ in the time they spent looking towards any of the stimuli or the blacked-out sides of the tank in the different experimental treatments. This behaviour was consistent regardless of the other stimulus present on the opposite side to the video of an archerfish. These results suggest that the focal fish did not show an increased interest in the video model, although this does not mean that it did not recognise it as a conspecific.

There are multiple reasons why the focal fish may have spent increased time away from the video model compared to the video of an empty fish tank or the live empty fish tank. It is possible that the focal fish recognised the video of an archerfish as a conspecific and moved away from it to minimize the chance of an aggressive encounter. It is also possible that the focal fish did not recognize the video as a conspecific and instead moved away from the video as it was an unfamiliar 2D stimulus. Lastly, it is possible that the archerfish moved further away from the video of the fish because it would give them a clearer image of the moving object on the screen. Images on monitors are created by having a trio of pixels interact with one another to create the illusion of colour. Each of the three main colours (red, green, and blue) is located adjacent to one another, but are processed by human eyes as if the colours are originating from a single point. This means that animals which have a higher visual acuity than humans may perceive video and static images as pixelated, especially when viewed up close (D'Eath, 1998). The archerfish may thus have moved further away from the video fish to better identify the image on screen. Future research on fish which uses visual stimuli should take into consideration the anatomy and neurology of the species' eyes, rather than relying on generalizations and assumptions based on (unrelated) model species.

The experiment described in this chapter cannot answer the question whether archerfish recognize a video of an archerfish as a conspecific, as I did not compare the response the focal fish had to the videos with a response to a live conspecific. However, the response to the video fish may still provide valuable information on how archerfish treat such stimuli. Research in other species have found a variety of responses to videos and static images of conspecifics. The cooperatively breeding cichlid *N. brichardi* was found to respond similarly to videos of conspecifics and videos of an empty fish tank in regard to courtship and aggressive behaviours, as well as spending similar amount of time near the monitor showing the video stimuli (Balshine-Earn and Lotem, 1998). By contrast, the focal fish in that experiment reacted aggressively towards live conspecifics in a neighbouring tank and spent more time near live conspecifics than either video stimulus. As the live conspecifics were unable to interact with the focal fish due to the use of a one-way mirror, it suggests that *N. brichardi* is able to visually recognize the live conspecifics as such but is unable to do so with the videos of conspecifics.

Similar results have been found in zebrafish *Danio rerio* (F. Hamilton, 1822), which when given the choice between shoaling near live conspecifics and a video of conspecifics, spent more time near the live stimuli (Velkey et al., 2019). This same study found that zebrafish also spent more time near motorized plastic models of conspecifics than videos of conspecifics, although this could be an effect of the plastic objects being a novel object, not necessarily recognized as conspecifics. My experiment provides a basis for comparing archerfish responses to live conspecifics and other artificial stimuli in similar manners as have been done in the above studies.

One caveat of my study is the fact that I only used one video per stimulus. Therefore, the stimuli (except the live empty fish tanks, of which there were two) are technically “simple pseudoreplicates” (Kroodsma et al., 2001). As only one type of each video stimulus was used, I cannot rule out that the responses exhibited by the focal fish were a result of that specific video, rather than the overall category of stimulus. This could have been prevented if I had used more than one unfamiliar fish for the stimuli, although this would have introduced potential other problems. There was only one fish which was kept fully separate in a different part of the lab from all other individuals, thus any other “unfamiliar” fish would have still been visible to all the focal fish (albeit in a different tank) and would have shared a tank with three or four of the focal fish, thus requiring even more stimuli videos. Given the sample sizes available to me, this would have decreased the power of the experiment.

In future research, it is worth considering the use of live-streamed footage of a stimulus instead of recorded videos. By transmitting the live behaviour of, for example, conspecifics, each trial will have a unique stimulus; this not only helps to prevent pseudoreplication but also introduces additional elements of randomness to each stimulus. The conspecifics would have to be monitored as well as the focal individuals, so that the focal individual’s responses may be mapped to specific behaviours exhibited by the stimulus. A live-streaming set-up similar to that used by Balshine-Earn and Lotem (1998) could be appropriate for many studies investigating social behaviour, fear responses, and mate choice where the stimulus must be kept separate from the observers.

If archerfish do not respond to video stimuli, there is the possibility that social learning and other social behaviours can be studied through the use of a robotic conspecific. Brown et al. (2021a) have created a robot archerfish which moves in similar manners to real archerfish and have begun investigating the response of live archerfish to the presence of the robot. So far, there is evidence that archerfish will approach the robot when it mimics the archerfish hunting position, and when it shoots at prey, even if no food reward is provided after shooting (Brown et al., 2021b). The archerfish used in this study appeared to acclimate towards the robot over time, initially only moving towards it after it shot at prey, but eventually moving towards it at the initiation of the hunting sequence. Archerfish hunting positioning is a conspicuous behaviour, as the fish tilt their body so that their mouth is just below the surface of the water, a position they do not take in other circumstances. However, it is currently unclear if the response of the archerfish to the robot's hunting sequence mimics that of the archerfish towards a hunting conspecific.

Future research into how archerfish respond to artificial conspecifics should take into consideration how the fish respond to live conspecifics. In fact, although the purpose of this study was to take a first step towards investigating if archerfish can learn by observing a video of a conspecific, there is still little evidence that archerfish can learn socially at all. Although a study by Schuster et al. (2006) claimed that naïve archerfish learned to shoot down moving targets solely by observing a trained conspecific, this study was not set-up to test for social learning, and could not rule out that the naïve fish learned by watching the targets, rather than the demonstrator. The only clear evidence so far that archerfish can use social cues to influence their hunting behaviour is a recent study by Leadner et al. (2021) which showed that archerfish respond more rapidly to a presented target if its location is first cued by a static image of an archerfish looking in the target's direction. It is not surprising that archerfish, despite being considered only facultatively social, would use social cues while hunting as they are known to adjust their own behaviour while under observation by a conspecific (Jones et al., 2018), possibly as a response to the threat of kleptoparasitism (Dill and Davis, 2012). However, this does not necessarily mean that archerfish can use social cues to learn to shoot at novel objects.

Although the use of video models may be beneficial to future research investigating whether archerfish can learn socially, as well as studies on other aspects of social cues, it first needs to be determined if archerfish respond similarly to a live conspecific as they would to a video of a conspecific. Given my findings in this study, it would appear that video models do not hold an archerfish's attention more than a video of an empty fish tank, or even a black barrier, and potentially elicit an adverse response as the fish moved further away from the video of a fish than they did with any other cues. The reason for this needs to be further investigated, as it would be difficult to distinguish between a response to a strange unknown stimulus and the fish moving further away to view a less-pixelated image.

Chapter 4 - No evidence of collective learning in archerfish in an operant conditioning experiment.

Abstract

Animals learn in a variety of ways. Learning from others, or social learning, provides a shortcut for rapid information acquisition by removing the need for individuals to interact with new stimuli through trial-and-error. Group-living animals can also benefit from collective learning, by which the group's success increases at a novel task due to information gained through individual improvement, better coordination, or development of complementary actions between group members. Archerfish are facultatively social perciform fish most known for their ability to shoot down terrestrial prey using condensed waterjets. There is evidence to suggest they are able to learn to shoot new targets by observing conspecifics. I decided to test whether archerfish learn to shoot a novel target faster in a group or individually. I found no evidence of either collective or individual learning, which contradicts previous findings on archerfish learning. The lack of learning could be due to a variety of reasons, primarily the experimental design which did not allow for the targets to be a sufficient distance from the water surface, thereby potentially reducing the likelihood the fish would shoot, and the use of a previously unstudied species of archerfish. More research is required into the behaviour of archerfish, specifically considering group dynamics and species-specific differences.

Introduction

Learning is a collection of complex processes that allow animals to gain, store, and use information about their environment (Galef and Laland, 2005). In many situations, an animal may be required to learn about a new stimulus or environment very rapidly, for example when first encountering predators, toxins, or harmful abiotic stressors (Galef and Laland, 2005). Social learning allows animals to avoid some of the costs of learning through direct experience or trial and error. In these circumstances, it has been demonstrated that animals can learn about such stimuli and environments through the process of social learning, in which an individual acquires new information or a new behaviour by interacting with other individuals or their products (Heyes, 1994).

Social learning provides a learning short-cut, allowing information to be gained more rapidly than it would be through an individual's own experiences (Rendell et al., 2011). For a naïve individual to learn, they must seek the proximity of, or be exposed to, knowledgeable individuals who in turn must tolerate the naïve individual's presence. Although social species are more likely to regularly encounter conspecifics from which they can learn, non-social species are also capable of social learning (Webster et al., 2017; Webster, 2023). Kendal et al. (2018) argue that solitary species are still exposed to social information through interactions with mates, siblings, and neighbours.

There has been some debate about whether social and asocial learning occur through separate mechanisms (Heyes, 2012a). In fact, social and asocial learning most likely do make use of at least parts of the same mechanisms, for if they did not, then social and asocial learning abilities would be expected to be unrelated. This is not consistent with empirical evidence. In a comprehensive survey of published work on primate behaviour Reader et al. (2011) showed a strong positive correlation between asocial and social learning ability, even when controlling for confounding factors, thus indicating either that the same mechanisms may be used for both types of learning or that there are two separate cognitive mechanisms but they evolved together (Heyes, 2012a). Regardless of whether one or two mechanisms are responsible for social and asocial learning, what distinguishes social from asocial learning is that social learning requires another individual to play a role that results in information becoming available to the learner (Heyes, 2012a).

Animals which live in groups can also exhibit a type of learning called "collective learning". Collective learning occurs when group performance at a task consistently changes when the task is repeated, such as during group foraging, navigation, predator defence, and breeding (Collet et al., 2023). Although collective learning is expected to improve performance at a task, if the information being relied upon is incorrect the group may instead decrease at their performance (Collet et al., 2023). There are multiple ways in which group performance could improve. Individuals could improve at the task thereby improving their contributions to the group behaviour, as seen in homing pigeons learning a new route (Sasaki et al., 2022) or zebrafish navigation around a maze (McAroe et al., 2017). To determine if this type of learning occurs, the individuals must be tested after the group learning phase to determine if they have improved at the task individually. Social learning may facilitate individual improvement, for example by exposing naïve individuals to new stimuli or behaviours (Collet et al., 2023). It is also possible that social facilitation, or the improvement of individual performance due to the presence of others, in a group context could reduce neophobia or vigilance behaviour, thus improving individual performance. Another explanation is that a leader emerges in the group, in which case group performance could increase faster than individual performance as the leader dominates the group's decision-making process (Rands et al., 2008; Harcourt et al., 2009; Pettit et al., 2015; Nakayama et al., 2016; Collet et al., 2023).

A second mechanism proposed by Collet et al. (2023) to explain collective learning is that individuals could learn about other group members and improve their responses to each other. Individual behaviour can be a response to the behaviour of neighbours and conspecifics; this mechanism would require the individuals to learn about as well as from others. It does not require individual improvement at a task, but merely requires coordination between the members of a group (Collet et al., 2023). This type of collective learning is seen in common bottlenose dolphins, specifically those which hunt using mud rings. One dolphin will beat its tail against the substrate, stirring up dust clouds, in a circular pattern to trap shoals of fish. The herd of dolphins then catches the fish when they attempt to escape the mud circle, or dive in to catch fish within the circle. Increased coordination between the dolphins, such as learning how the instigator will move to create the mud circle, would increase group performance. To determine if individuals learn collectively by learning about other group members, group composition can be manipulated during the collective learning phase (Collet et al., 2023).

The final method by which collective learning could occur is that individuals could alter their response specifically to complement the response of other group members. This is also known as the "many-wrongs" hypothesis (Sasaki et al., 2022). If individuals incorporate group members' individual experiences, it eliminates error by averaging over imperfect estimates, thereby more likely to lead to increased group performance, despite no individual learning about the task occurring (Collet et al., 2023).

There are some methodological challenges to determining which type of collective learning occurs, such as the need to manipulate group composition or individually test group members. This means lab-based studies are beneficial for research into collective learning for they allow for more controlled environments and group compositions. Collective learning has been shown in a number of fish species (Lachlan et al., 1998; Kareklas et al., 2018; Vega-Trejo et al., 2020; Roy et al., 2022). One genus which has not yet been proven to learn collectively is archerfish, although there is the potential for them to do so. Although we know that archerfish improve their performance at novel tasks over time (Jones et al., 2021b), but we do not yet know how archerfish learn about novel prey in the wild. Collective learning is one possibility.

Archerfish are not gregarious and exhibit little group cohesion (Timmermans and Maris, 2000), despite often being found near conspecifics in the wild (Gill, 1909; Schuster, 2018). Although much is known about their hunting methods, one question that remains is whether their hunting method is an innate ability or if it is learned, and if it is the latter by which mechanism learning occurs. There is evidence that archerfish improve at shooting tasks over time when learning to shoot novel targets (Schuster et al., 2004; Schuster et al., 2006; Newport et al., 2013; Jones et al., 2021b), as well as limited evidence of social learning (Schuster et al., 2006; Leadner et al., 2021). In a study by Schuster et al. (2006) archerfish which were able to observe a conspecific learn to down a moving target (a behaviour which does not occur in the wild) were able to hit the target with a similar level of accuracy as the trained individual. However, this study was not designed to test social learning and thus it is possible that the learning occurred because the fish observed the target rather than the conspecific. A more recent study by Leadner et al. (2021) did find evidence that archerfish are more likely to shoot down a target if its location is first primed by an image of an archerfish pointing in the correct direction. This could be explained by the mechanism of stimulus enhancement, a form of social learning by which an individual's behaviour draws other animals' attention to a location or stimulus and the observers subsequently learn something (van Bergen et al., 2004).

There is thus some evidence that archerfish are capable of learning socially, but whether they are capable of collective learning is still unknown. Archerfish are facultatively social, meaning they can be found both with conspecifics and on their own, and are known to pay attention to nearby conspecifics (Schuster et al., 2006; Dill and Davis, 2012; Brown et al., 2021b; Leadner et al., 2021) and change their behaviour while hunting when under observation by conspecifics (Jones et al., 2018). There is thus the potential that archerfish can learn socially and collectively, both mechanisms which could begin to explain the findings of Schuster et al. (2006). In this chapter, I set out to determine if archerfish are capable of collective and social learning in a move towards investigating the mechanisms underlying the aforementioned study. Studies on archerfish are generally conducted on one of two species, *T. chatareus* and *T. jaculatrix* (Pallas, 1767), who appear to exhibit similar social behaviour. Due to supply issues outside of my control, the majority of the fish I had access to were *T. blythii* (Boulenger, 1892). Anecdotal evidence suggests this species also exhibits similar social behaviour to the more well-known species.

In this study, I investigated whether archerfish exhibit group learning by determining if they could learn a task (to shoot at a rewarded target when given a choice of two targets) more rapidly in a group environment than individually (Figure 4.1, 1A-1B AND 2A-2B), and whether the individuals which had been exposed to the group condition learned which target was the rewarded target (Figure 4.1, 1C), as a test to see whether improved group performance also translated to increased individual performance. I predicted that, if archerfish are capable of group learning, the fish in the group treatment would learn to shoot at the correct target faster than the fish in the individual treatment. If archerfish group learning was caused by social learning, I expected the fish from the group treatment to continue shooting at the learned target even when removed from the group as the individuals within the group would have observed their shooting conspecifics to learn the difference between the targets. If archerfish do not exhibit group learning, I expected the fish in the group and individual treatments not to differ in their rate of learning. If the fish in the individual treatment learned the correct target faster than the fish in the group treatment, it would suggest that archerfish learning is hampered by the presence of other individuals, which is possible given that they are not obligately social and are known to alter their behaviour when under observation by conspecifics (Jones et al., 2018).

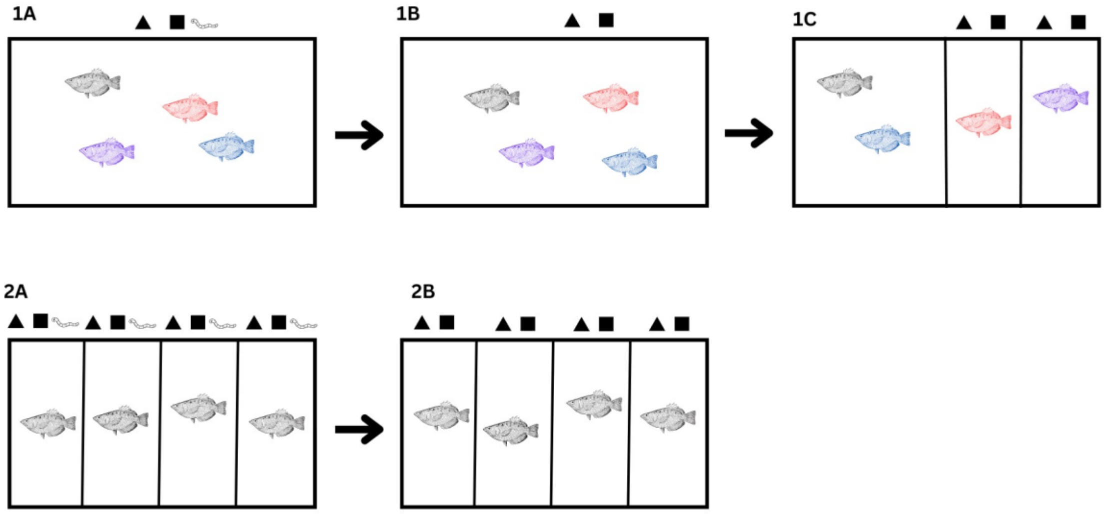

Figure 4.1: Final experimental set-up. Group treatment is shown at the top (1A-C), while individual treatment is shown at the bottom (2A-2B). Fish were exposed to condition A (maggot shown) for 4 trials, to condition B (only shapes shown) for 14 trials, and, in the group treatment, condition C (shapes shown to the two lowest-shooting individuals, removed from the group) for 4 trials. If fish learn which target is the rewarded target faster in a group environment, I expected the fish in 1B to shoot at the rewarded target more consistently than the fish in 2B. If the fish which were low shooters in the group treatment still learned which target was rewarded, I expected these fish to shoot at the rewarded target when removed from the group treatment (1C).

Methods

Animal Husbandry

Seventeen archerfish (four *Toxotes jaculatrix* and thirteen *T. blythii*) were used in this experiment. They were housed in the Harold Mitchell Building at the University of St Andrews in four separate stock tanks, in three groups of four and one group of five. The tanks measured 183 x 46 x 34cm L x W x H and were kept between 25 and 26°C using a central heater that warmed the whole room and a 12:12 h light:dark cycle. Each tank contained a layer of gravel substrate and multiple plastic plants and tubing to provide enrichment and cover (Jones et al., 2021c). The tanks were blacked out using black cardboard and plastic sheeting on all but one long side to reduce stress and distraction from the surrounding environment. Water quality (pH,

NO^-_2, NO^-_3, NH_3) was measured every two weeks and maintained using large canister filters and regular water changes. Fish were fed 0.1g of Cichlid Gold "mini" fish food pellets per fish every day around the same time.

Initial Experimental Design

The initial experimental design aimed to test whether archerfish could learn to distinguish between a rewarded and unrewarded target solely by watching another individual practice. To test this, I set up a fish tank measuring 142 x 61 x 61 cm L x W x H, dividing it into two sections of unequal length (the smaller section being 39.5cm and the larger section being 102.5cm in length) using a see-through Perspex barrier that could be slid into place and secured using clips suction-cupped to the sides of the tank. The Perspex barrier had 50 mm diameter holes drilled into it at regular intervals to allow water to flow between the two sections of the tank. One fish was randomly selected from a stock tank and placed in the smaller section of the experimental tank. Three other fish from the same stock tank were placed in the larger section. This was to ensure that the fish used in each group were familiar with one another, which is known to improve social learning in a number of species (Swaney et al., 2001; Velkey et al., 2019).

The lone fish (hereafter described as the "demonstrator") was given two training sessions per day. During each session, it was initially presented with two different targets. The targets were made from black plastic sheeting, approximately $25mm^2$. One was shaped like a triangle, and the other was shaped like a square. Similar targets have previously been used by Newport et al. (2013) to study whether archerfish can discriminate between up to four different shapes, and all fish used in that experiment learned to hit the correct target consistently (75% or more correct shots across two consecutive sessions) within two to five sessions. The targets were attached to lollypop sticks which were secured to the glass strut bridging the sides of the fish tank, so that the targets were loose and able to be moved – this allowed the me to distinguish when the targets had been hit, as they would show movement after getting shot. One of the targets was randomly assigned the “rewarded” condition using a random number generator at the start of each group.

Each session consisted of one hour, or until the demonstrator shot water that struck near the rewarded target ten times. However, after fifty sessions, the demonstrator had only spat during one session, a total number of five shots, one on the rewarded target, one on the unrewarded target, and three not on target at all. At this point, I decided it was necessary to change the experimental design to encourage the demonstrator to spit more frequently.

The second attempted design replaced the targets with an electronic target. A tablet (Amazon Fire HD 10) showing a moving gif image of an insect was presented to the demonstrator by placing the tablet on the glass strut over the tank. The movement of the gif and the natural appearance of the prey was meant to increase the likelihood that the demonstrator would spit at the target. The demonstrator underwent fifteen trials under this new protocol, before it was aborted. The fish did not spit at any time during these fifteen trials, and the protocol was aborted as the building was repeatedly shaken during building works over several days, which induced a stress response including behavioural changes, specifically the fish stopped eating consistently, C-started away from anyone or anything approaching the tank, rapid breathing when under observation, and hiding, for nearly two weeks.

When the fish had returned to their normal behaviour again, I once again changed the protocol to find a target which the fish would consistently spit at. I also changed out the demonstrator, replacing it with one of the three fish which had previously been observing from the larger section of the experimental fish tank. Having observed from some of the stock tanks that the fish would spit at shiny or reflective objects, I showed the new demonstrator multiple possible targets, including metallic tape in different colours (gold, silver, and bronze) and craft jewel studs (red, blue, and green). I presented these two sets of targets for four sessions each, but the demonstrator did not spit. I observed that the demonstrator appeared distressed at being unable to reach the other fish in the tank due to the see-through barrier, and decided to test whether the fish would spit in a group instead.

I removed the barrier and presented the whole group of four fish with a Cichlid gold "mini" pellet, placed on the central glass strut of the tank. I allowed one hour or forty shots per session. The fish began spitting from session one and continued to do so for the first five sessions. Only one of the fish spat, but it stopped spitting after five sessions and did not spit again until session 14. At no point did it spit on-target; it merely spat at the strut at first, and eventually began spitting at me.

Due to this first group failing to reach criteria with any of the targets, I decided to change out the group. I replaced the fish in the experimental tank with four individuals from a different stock tank. I changed the number of shots allowed per session to twenty, to prevent fish becoming satiated. In forty-three sessions, only one fish spat in one session, and then only three times.

It was at this point I decided to test whether the fish in the stock tanks would shoot. It was possible that the fish were distressed in the experimental fish tank, due to differences in lighting, habituation time, or other, unknown properties of the fish tank. Using the same protocol, presenting a maggot *Calliphora vomitoria* (Linnaeus, 1758), I discovered that the *T. jaculatrix* would spit consistently. They reached criteria (at least 80% correct shots) within four sessions, or two days.

I adjusted the methodology to build upon research by Jones et al. (2020) which established that archerfish were incapable of distinguishing between different-sized pellet food rewards. From personal observations, I predicted that archerfish may distinguish between different food rewards when presented with a choice of live prey and pellet food. I thus assigned maggot rewards, approximately 1-2cm in length, to one shape, and pellet rewards to the other. I first presented the shapes alongside the rewards, placing the pellet and the maggot under transparent bottle lids (to prevent the maggot escaping). I conducted four trials with the rewards shown over a period of two days, allowing 10 shots or 1 hour, and providing the reward associated with the target the fish spat at. I then removed the rewards and conducted a further 10 trials, continuing to reward each target with their respective rewards. Targets were randomly alternated in location. However, after the 10 trials completed, it became clear that the fish showed a distinct preference for whichever target was placed on the left and did not appear to learn the difference between the two targets.

Final Experimental Design

The final changes to the experimental design were as follows. I decided to test whether archerfish could learn a simpler task, distinguishing between a rewarded and an unrewarded target, and if their learning was impacted by their social environment (group and individual). Three of the stock tanks (two containing four *T. blythii* each and one containing five *T. jaculatrix*) were selected for the group treatment (for a total of thirteen fish), whereas the final tank was used for the individual treatment (for a total of four fish). The two black targets were randomly assigned the "rewarded" and "unrewarded" condition using a random number generator at the start of each group's sessions. A transparent plastic tank cover with a 3cm diameter hole cut in it was placed on top of each tank, approximately 10cm above the water surface. In the group treatment, fish were shown the two targets as well as a maggot by placing the targets and maggot on a transparent tank cover, placed under a transparent lid so that it did not escape. The maggot was placed next to the "rewarded" target. Fish were allowed to spit at the targets 10 times and were given a maggot any time they spat at the "rewarded" target. Trials were terminated after 1 hour if the fish had not spat 10 times. Each group was exposed to the maggot alongside the shapes for four trials, where a trial was one hour or ten shots, over a period of two days, once in the morning and once in the afternoon.

After these four trials, the maggot was removed and only the shapes were shown. Trials continued for one week (14 trials) or until the fish hit the “rewarded” target 80% of the time in ¾ trials across two days. At this point, black Perspex barriers were placed in the tank to separate out the two fish which had spat the least across the training trials. These two fish were tested individually for four trials across two days after receiving a 24-hour acclimatization period. The lowest shooters were chosen in order to test if being in a group suppressed shooting in the subordinates, and whether, given the chance to shoot, the lowest shooters in the group would choose the correct target.

The fish assigned to the individual treatment were exposed to the training conditions (2 days where the maggot was shown, 7 days without maggot) individually to compare how the individuals learned compared to the groups (Figure 4.1 2A-2B). They were separated using the same black Perspex barriers as used in the group treatment and given a similar 24-hour acclimatization period.

Analysis

To determine whether there was a difference between the likelihood of shooting at the rewarded target between the three treatments (group, individual after group exposure, or individual without group exposure), I constructed a binomial linear mixed effects model using the lme4 package. I calculated the total number of shots within each trial and from there transformed the number of shots at the rewarded target into a probability of shooting at the correct (rewarded) target. The final model related the probability of shooting the correct target (response) to treatment (group, individual, or individual after group exposure), target type (maggot shown with shapes or only shapes shown, with both shown as the baseline), and trial number, with group identity and time of day (morning and afternoon) as random effects. Each trial-specific estimate of the probability of shooting was weighted by the total number of shots in that trial. If treatment was estimated as significantly different from 0 then I considered collective learning to have occurred.

A second model was constructed to determine whether fish were more likely to shoot in groups or on their own. This model also tested if the fish which shot the least in the group treatment were more likely to shoot when removed from the group, to see whether they had learned about the targets or where disinclined to shoot in a group context due to the presence of other individuals. I constructed a binomial linear mixed effects model to relate the likelihood of the fish shooting (regardless of which target they shot at) to the treatment (group, individual, and individual after group exposure) and the trial number, including the group identity as a random effect. If treatment was significantly different from 0 then I considered that social learning may have occurred. All analyses were conducted in R version 4.2.2.

Results

Archerfish were more likely to shoot at the correct target if a maggot was presented alongside the black shape, regardless of whether the fish was in a group, on its own, or on its own after being exposed to a group treatment (Table 4.1 A, Figure 4.2). The fish did not improve over time, but instead their likelihood of shooting at the rewarded target dropped off sharply once the targets were shown without the maggot present (Figure 4.3). Shooting was more likely to occur in groups than when fish were kept individually, regardless of whether the individuals had been exposed to the group treatment (Table 4.1 B, Figure 4.4). Only half of the fish which were exposed to the individual treatment alone shot at the targets, resulting in only 9 out of the 72 individual trials containing shooting events. The fish that were exposed to the individual treatment after the group treatment also shot much less than the average shooting rate for the groups, with only a third of the fish shooting and only 3 trials out of 24 containing shooting events.

Table 4.1: General linear mixed model results. Panel A shows the glmm results for the model comparing the probability of shooting the correct target compared to treatment, target, and trial number. Panel B shows the results for the model comparing the probability of any fish shooting dependent on treatment and trial number. Significant results are emboldened.

A: Probability of shooting the correct target modelled as a function of treatment, target, and trial number.	
Fixed terms	**Coefficient ± SE**
Intercept = Group & Maggot and shapes shown	2.283 ± 0.349
Treatment = Individual after group exposure	-1.022 ± 0.586
Treatment = Individual without group exposure	0.349 ± 0.578
Target = Only shapes shown	**-2.487 ± 0.351**
Trial Number	-0.024 ± 0.025
Random terms	**Variance ± SD**
Group Identity	4.919e-02 ± 0.222
Time of Day	1.842e-08 ± 0.000
B: Probability of shooting modelled as a function of treatment and trial number.	
Fixed terms	**Coefficient ± SE**
Intercept = Group	**6.056 ± 1.765**
Treatment = Individual after group exposure	**-8.010 ± 1.770**
Treatment = Individual without group exposure	**-7.590 ± 1.936**
Trial Number	-0.182 ± 0.0994
Random terms	**Variance ± SD**
Group Identity	1.962 ± 1.401

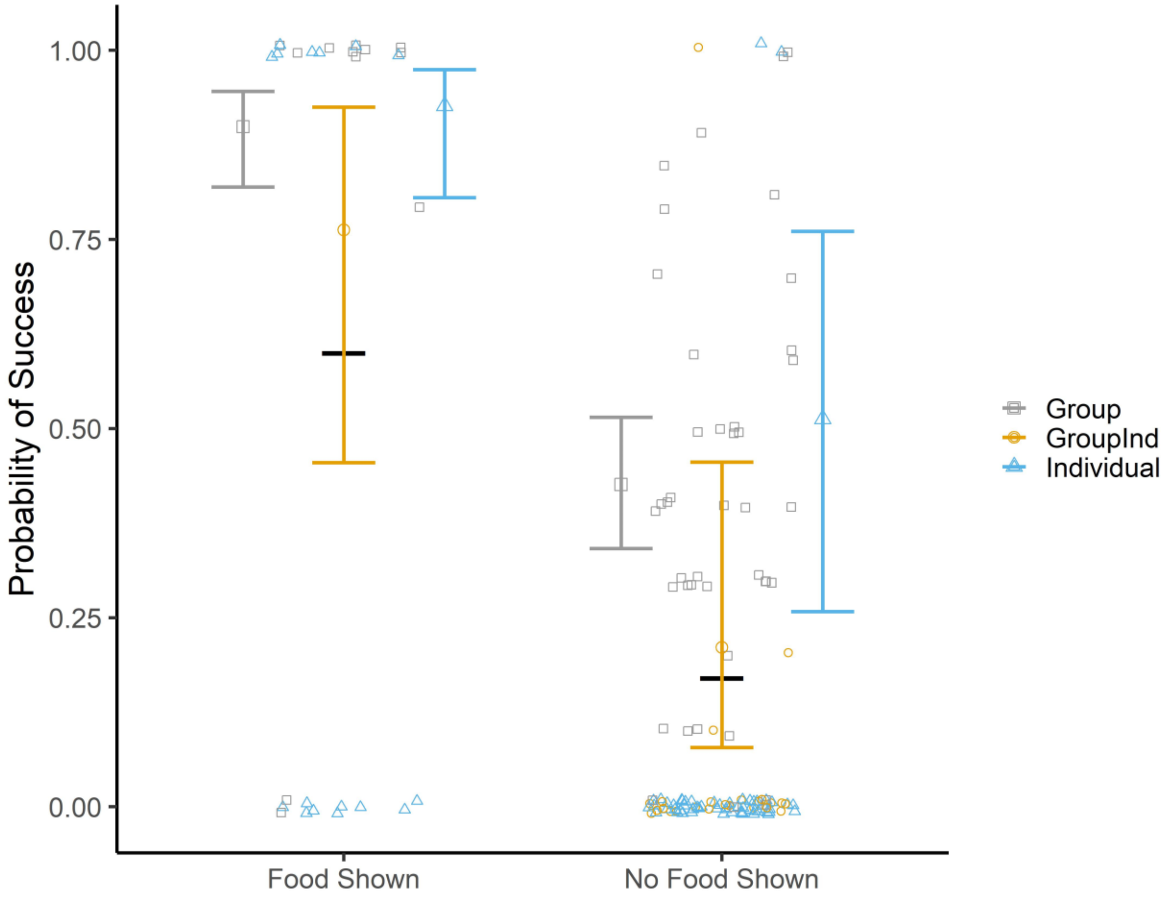

Figure 4.2: Probability of shooting the correct target when food is shown vs. not shown. The coloured points and error bars are the predicted probabilities for each treatment. The points indicate the raw data per trial, and the black bars indicate the actual mean probability across all treatments.

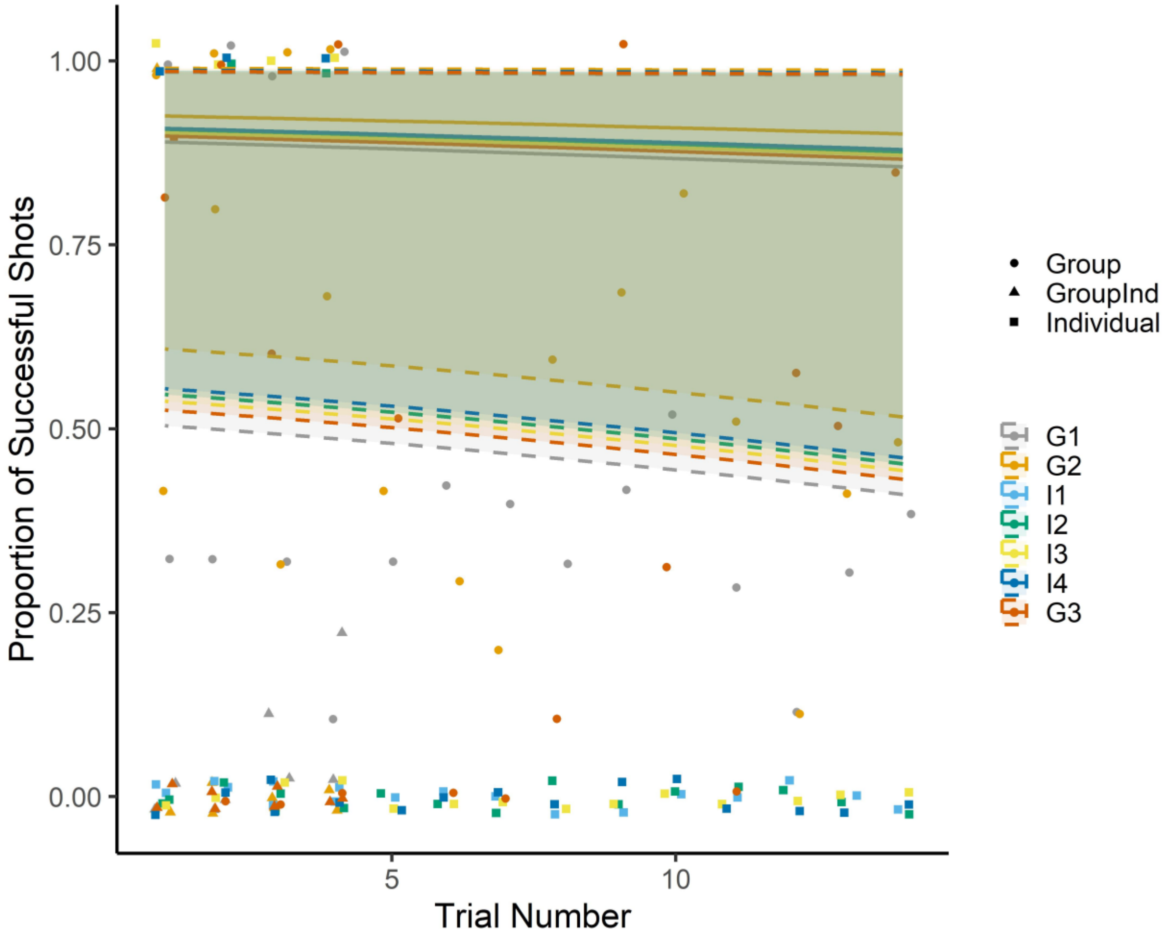

Figure 4.3: Proportion of shots at the rewarded target over time. During the first four trials for the "Group" and "Individual" treatments, the maggot was shown alongside the targets. The colour of the points designates the different groups. DW1, DW2, and DW4 were the group treatments, while DW3 A1-A4 were the individual treatments. The shape of the points indicates the treatment ("Group", "Individual after group exposure", and "Individual"), the solid lines indicate the predicted learning trajectories with the 95% CI indicated by the dashed lines.

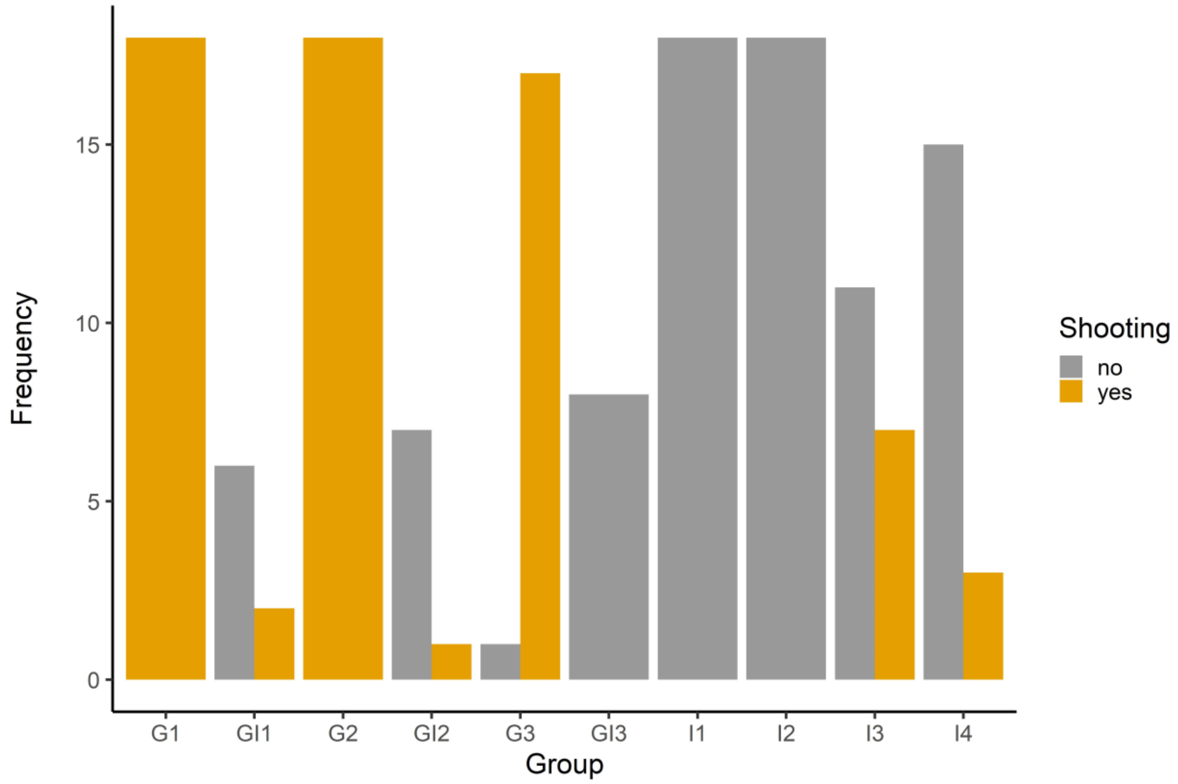

Figure 4.4: Probability of shooting depending on treatment. GI indicates the data for those individuals which were first exposed to the group treatments. The probability of shooting was nearly 100% in groups, but much more variable when only a single fish was present.

Discussion

I found no evidence that archerfish learn either collectively or socially. In fact, there is no evidence that the archerfish were able to learn to distinguish between the two targets, which was surprising as previous studies have used similar targets and established archerfish were able to distinguish between the rewarded and unrewarded targets (Newport et al., 2013; Jones et al., 2020). I did find that shooting was more likely to occur when the fish were kept in groups, and that fish which shot very little or not at all in groups did not change their behaviour when removed from the group, indicating they were not socially excluded from shooting but instead low shooters in general. Lastly, I found that fish were more likely to shoot towards the correct target when a maggot was shown adjacent to it, despite the fish not being fed live prey for more than a year before the start of this experiment.

There are several reasons why shooting was more likely in the group treatment, which I will discuss here. Firstly, it should be noted that there were more individuals in the group treatment than in the individual treatments, thereby potentially increasing the chance that any fish would shoot at one of the targets. In each group treatment, each of the in-total thirteen fish shot at least once, whereas in the individual without group exposure treatments, only two out of the four fish shot. In the individual after group exposure treatment, two out of the six individuals shot.

The fish chosen from each group for the individual treatments after group exposure were the fish which shot the least within each group, so the reduced likelihood of shooting for this treatment could be explained by the existence of a producer-scrounger dynamic in archerfish communities, the existence of a dominance hierarchy, or possibly both. Archerfish are known to experience high rates of both intra- and inter-specific kleptoparasitism in the wild (Dill and Davis, 2012; Rischawy et al., 2015). Kleptoparasitism may be a valid tactic depending on group size. Intraspecific kleptoparasitism rates are known to increase with group size up to 5 individuals, with an average probability of a fish other than the shooter consuming the food at 44.1% (Dill and Davis, 2012). In a group of four individuals, I would expect two fish to attempt to steal the prey based on previous work done in this genus (Dill and Davis, 2012). Producer-scrounger tactics are quite common in group-living animals (Evans et al., 2021; Reichert et al., 2021), as is kleptoparasitism (Steele and Hockey, 1995; Hamilton and Dill, 2003; Webster and Hart, 2006; Labourgade et al., 2020; Allen et al., 2021). Therefore, it is certainly possible that some archerfish may rely on stealing food shot down by other individuals rather than expending the not insignificant energetic costs to shoot prey down themselves (Milburn and Alexander, 1976; Schlegel et al., 2006). If archerfish exhibit a producer-scrounger dynamic, this could influence future research into archerfish behaviour. If some individuals choose never to shoot, taking on the scrounger role permanently, those individuals will be difficult to train to shoot at specific targets. It is also possible the balance of producers and scroungers within a group will affect anti-kleptoparasitism behaviour in the shooters. Given the possibility that archerfish may have dominance hierarchies, as suggested by a previous study which found that archerfish in a group trade off the shooting role over time (Jones, 2020), the producer-scrounger model should perhaps be updated to include the possibility of dominance effects. This is not addressed here so remains an interesting topic for future research.

It was surprising that the archerfish did not learn to distinguish between the targets. In a previous study using a similar task and training method, archerfish learned to distinguish between four different shapes in 2-5 sessions (Newport et al., 2013). It is unclear why the archerfish in my experiment failed to learn the difference between the two targets, but it appears unlikely that these individuals would have learned the difference without an extended, intensive further training period. Given that the fish had been kept in captivity for more than a year and had been fed daily without requiring the fish to shoot first, it might be that if the experimenter also primarily conducts routine husbandry feeding this may confuse reward expectations in the fish (Newport et al., 2016; Newport et al., 2018). Instead, they may have formed a connection between the act of spitting itself and the food reward. One way to counteract this possibility in future studies is to prevent the fish from seeing the experimenter. However, this would have been difficult to achieve given the set-up for this experiment. It may have been possible had the fish responded well to the initial experimental tank but given the changes in the set-up required to encourage the fish to shoot at all it was not possible to hide my presence from the fish.

As the majority of the fish I used were *T. blythii*, it is possible that my results were due to the mistaken assumption that this species behaves similarly to the more well-studied *T. chatareus* and *T. jaculatrix*. The stress I observed in the *T. blythii* during the initial experimental design when separating individuals from their groups could indicate the *T. blythii* are more social than other archerfish species. They may also exhibit different capacities for learning, although this requires further study. *T. blythii* have a narrower geographic range than *T. chatareus* and *T. jaculatrix*, although all three species ranges do overlap. Whether the difference in species distribution and ecology affects their behaviour is unclear, but future studies should reconsider whether all species of archerfish are interchangeable.

Another weakness of this study was the distance between the surface of the water and the targets. Due to the experiment being conducted in the stock tanks, there was limited height above the tanks where the targets could be placed. The energetic expenditure of shooting and C-starting to collect the prey is more than the energetic expenditure of jumping (Shih et al., 2017), thus at lower heights where jumping to capture prey is possible it provides a more consistent energetic payoff than shooting. The archerfish did jump at the targets, but were not rewarded for jumping and, when jumping, smacked into the tank cover. Therefore, they may have been dissuaded from jumping, but not motivated enough to shoot when they were on their own, especially as they were used to being fed after the experiment if they did not shoot.

Archerfish are known to possess a strong prey image (Rischawy and Schuster, 2013), so it is not surprising that they were more likely to shoot at the correct target when the maggot was placed next to it. In the wild, archerfish typically hunt in a visually complex environment and are required to distinguish between small, stationary prey against a background of overhanging foliage (Temple et al., 2010). Archerfish eyes are not only well-adapted to work at the interface of air and water, with their rods and cones tuned differentially across their retina (Temple et al., 2010), but their method of searching for prey is identical to that of humans (Rischawy and Schuster, 2013). Archerfish visual processing time is similar to humans and increases in a similar manner with background complexity (Rischawy and Schuster, 2013), and archerfish are also known to experience “pop-out” in visual search, where the target stands out from the background (Ben-Tov et al., 2015). I therefore expected that the archerfish would respond to the presence of the maggot placed next to the rewarded target, but they did not learn the connection between the maggot and the adjacent shape. It is possible that, due to how archerfish search for prey, discounting the background in their search, they took the adjacent shapes as background objects and therefore did not learn to associate the prey with the focal objects. Archerfish visual abilities may be similar to those of humans, but their interpretation of background and surrounding objects could differ. This is a potentially interesting area for future research, to determine the extent to which associations between objects can be made by these fish.

Overall, I found no evidence of learning in archerfish in the context of a rewarded-unrewarded choice experiment, either individual or collective. Despite previous evidence that archerfish may be able to learn socially, I found no evidence thereof and would suggest that a recreation of Schuster et al. (2006)'s study would be greatly beneficial to determining whether social learning occurs in this genus. Shooting was more likely to occur in a group context, possibly due to the development of a producer-scrounger dynamic. Further investigation into the group dynamics of archerfish would be beneficial, as there may be a trade-off between these roles depending on group size.

Chapter 5 - An investigation into the use of tabletop role-playing games for science communication.

Abstract

Engaging the public with scientific research is critically important for maintaining public trust in science. Different types of public engagement (PE) provide different benefits, but all PE requires an element of learning on behalf of the participants. Learning-by-doing is an effective method of teaching as it allows the learner to engage and create memories of their experiences, which can be more effective than rote memorization. Tabletop role-playing games (TRPGs) could be particularly well-suited to PE for this reason; they require participants to take on roles within a story and directly influence the outcomes. In this study, I investigated the potential for using TRPGs for PE by designing a game based on archerfish ecology. I tested thirty-nine adult participants' knowledge of archerfish ecology before and after playing this game using a ten-question multiple choice quiz, as well as gathering qualitative feedback using a Likert scale questionnaire. All but one participant improved their knowledge of archerfish after playing the game, the median number of correct questions improving from four to eight, before and after the game respectively. Each participant indicated enjoyment and felt like they learned new information by playing the game. These findings suggest that TRPGs can be very effective for PE with a wide range of audiences, although future research should investigate whether the use of TRPGs provides benefits which other forms of PE do not.

Introduction

The dissemination of science to a wider audience beyond the institutions in which our research and discussion occurs is currently of critical importance. This was proven during the recent COVID-19 pandemic, when scientists were not only important in influencing policy to mitigate the effects of the pandemic on the populace, but also in counteracting incorrect narratives depicted by popular figures and the media as part of the anti-vaccine movement (Kreps and Kriner, 2020). Public trust in science is required in order for science communication to be effective (Intemann, 2023), but this trust can be eroded by scientific scandals, like academic dishonesty as in the recent case of Jonathan Pruitt, counteracting scientific opinions like those of Bjorn Lomborg (Schoenbrod, 2002), or wilful misuse of scientific knowledge and expertise for personal gain, as in the case of Andrew Wakefield (Leshner, 2003). However, even in the face of a global pandemic which at times appeared to erode the public's trust in science (Intemann, 2023), some countries reported an increase in public trust in science compared to before the pandemic (Kreps and Kriner, 2020).

The importance of public engagement (PE), or the establishment of a dialogue between science and the public, is apparent, but the methods by which it occurs vary greatly, and with varying levels of effectiveness. Public engagement efforts can be more rigidly structured, for example public lectures, interviews, popular scientific publishing in books, magazines, and newspapers, and public debates, and can involve collaborations with NGOs and governments (Bauer and Jensen, 2011), or less strictly controlled through science festivals, comedy events, and social media (Stilgoe et al., 2014). Some PE researchers believe that PE efforts that do not set out to impact governance are less legitimate (Stilgoe et al., 2014), which in turn aids in the public perception that scientists take on a paternalistic stance when interacting with those outside their own fields (Leshner, 2003). However, PE efforts that aim to increase interest or enthusiasm about science are equally valid and can lead to increased uptake of scientific education or jobs, increased scientific literacy, and an increased level of trust within the targeted community (Intemann, 2023), which in turn can impact policy at a higher level. Less rigidly structure PE efforts can play an important role in facilitating this increased level of interest in science or specific scientific topics.

Public engagement involves an element of learning, and therefore it is worth considering educational practices which may apply equally well to PE efforts. Constructivist learning theory (Fernando and Marikar, 2017) may be particularly well-suited to certain types of PE. This theory describes learning as being an active process in which the learners construct knowledge and meaning from their experiences, rather than relying on rote memorization (Bada, 2015). This type of learning relies heavily on hands-on experimentation and real-world problem-solving, with the instructors acting like facilitators or guides. Learning groups tend to be smaller and more heterogeneous than in traditional classroom settings (Bada, 2015). One way in which constructivist techniques can be used in both educational and PE settings is through game-based learning (GBL) (Tobias et al., 2014). A long-term study by Bolstad and McDowall (2019) in New Zealand showed that GBL aided students in the development of critical thinking, problem solving, cultural acceptance, and technological skills. Subject-specific GBL was implemented in a variety of subjects, and was found to work best when the game play or design directly linked to the subject knowledge (Bolstad and McDowall, 2019).

Tabletop role-playing games (TRPGs) are a specific type of game which allow multiple players to assume imaginary characters and interact with an imaginary environment with some degree of freedom, often facilitated and guided by a game master (GM) (Boysen et al., 2023). The narrative of the game is developed collaboratively by the players and GM and requires elements of exploration, improvisation, and composition of the story development through character actions. TRPGs are generally played using pen and paper and verbal roleplaying, although they can be enhanced through the use of dice and props. Players learn to rapidly switch between in-character performance and out-of-character discussion (Daniau, 2016). TRPGs have been used in various levels of education to promote different learning outcomes (Boysen et al., 2023) as well as in PE, including education of the English language (Cook et al., 2016), Latin (Gellar-Goad, 2014), robotics (Collins and Sabanovic, 2021), cyber security (Hart et al., 2020), and engineering (Ross and Hall, 2023). TRPGs could be especially beneficial for individuals who may be less likely to engage with more traditional forms of engagement, as the gaming element helps to remove the perception that academic research requires advanced learning to understand. By placing research in a more accessible fantasy setting which the participants control, it allows them to interact with the research on a less formal basis, which may inspire them to explore the subject further.

TRPGs are a potential method for educating the public about animal behaviour and ecology. Increased knowledge and understanding of species vulnerable to climate change, habitat destruction, and extinction can assist in increasing conservation efforts towards those species and their environments (Bennett et al., 2015; Fukano et al., 2021). Archerfish are not widely known worldwide, but they inhabit vulnerable ecosystems, mangrove forests, that are at increased risk of disappearing (Polidoro et al., 2010). Raising awareness of archerfish, their behaviour, and their environment could lead to increased public funding to help maintain mangrove habitats worldwide through a method known as the use of a “flagship species” (Smith and Sutton, 2008).

The aim of this study was to develop a TRPG that could be used to educate the public about archerfish. I developed the game based on various aspects of archerfish ecology and created a multiple-choice quiz to test the participants’ knowledge of archerfish before and after they played the game. Here I report my findings on the creation and utilization of this game for the purpose of spreading awareness of my study species.

Methods

This study design consisted of multiple components: game design, survey design, and learning outcomes. The learning outcomes guided the design of both the game and the survey.

I established a list of twenty facts relating to archerfish behaviour and ecology, ranging from facts which (from my experience with science communication) could be considered common knowledge ("archerfish spit water at insects") to highly specific ("archerfish modulate the force of their water jets to reach six times the force generated by the muscles at the moment of impact" (Vailati et al., 2012)). This list of facts then influenced both the game design and the survey design (See Appendix 1 for the archerfish fact sheet which included the 20 facts, which was provided to participants after the completion of the study). I decided success would be measured by the number of questions the participants answered correctly after playing the game in comparison to the number they answered correctly before the game. There were 10 questions in total, and the participants were shown the same questions both times.

Game Design

The inspiration for my game design came from a TRPG system called "Honey Heist" by game designer Grant Howitt (Howitt, 2017). This game system is based on the use of several statistics ("stats" from here on) which describe the player characters' abilities and the use of a six-sided dice to determine the characters' success at various tasks.

I identified three behavioural traits which would be appropriate as stats for the archerfish characters in the game. The first trait was boldness, which has been studied across the animal kingdom (Toms et al., 2010). Boldness determines how likely an animal is to approach or interact with a novel object (Blaszczyk, 2017), and individual archerfish have been shown to vary in the amount of time spent in the open, which corresponds to their rate of learning about novel objects (Jones et al., 2021b). The second and third stats were decision speed and accuracy, which are related in archerfish through a trade-off: archerfish that make decisions faster are less likely to choose the correct, rewarded, target when given a choice between multiple targets (Jones et al., 2020). This relationship between speed and accuracy made these aspects of archerfish behavioural ecology well-suited for the game format. Each of these stats ranged from 1 to 6, depending on what the player rolled on the dice.

Finally, to provide each player with a unique characteristic, I created a list of six “personalities”. Some of these personalities were based on personal observations of archerfish over the past four years (e.g., “always hungry”, “highly aggressive”) and others on scientific facts (“archerfish will take longer before shooting if under observation by a conspecific” (Jones et al., 2018)). One “personality” related to gouramis *Trichogaster* spp. Block & J. G. Schneider, 1801, which are also capable of hunting by spitting, although their height reached is significantly lower than that of archerfish (Jones et al., 2021a) (See Appendix 2 for the personality table).

For the gameplay, I created six potential problems and multiple challenges which the players could face. Most of the problems and challenges were based on mangrove or archerfish ecology. Throughout the game, I would provide the players with relevant information about archerfish ecology, depending on the challenges they faced and the players’ actions. For a full description of game mechanics and instructions, including a list of all possible problems and challenges, please see Appendix 2.

I tested the game design using five volunteers who were ignorant of archerfish ecology and adapted the game to increase the clarity of the instructions per their suggestions. I also tested the surveys during this playtest, to ensure that the incorrect answers were viable options.

Survey Design

After the creation and playtesting of the game, I determined which facts regarding archerfish were most likely to be incorporated into the gameplay, either through the character design, scenarios, or challenges which the participants may encounter. This was largely based on my own experience, as TRPGs rely on improvisation and thus I could not be certain exactly which facts would come up during each game. I constructed ten multiple choice questions which incorporated these facts to test the participants knowledge of archerfish before and after the game.

To determine the participants' perception of the study and game design, I constructed a Likert-scale based survey (Jebb et al., 2021) with ten statements which the participants could rate as "agree", "neither agree nor disagree" and "disagree". I also provided two write-in questions: "what did you enjoy most about this game?" and "what would you improve?" in order to allow the participants to provide written feedback.

Finally, I requested the participants' age and how they identified themselves in relation to science communication and TRPG experience, from a list of options. For the full survey, see Appendix 3.

Recruitment

Participants were recruited through several online PE and TRPG networks. After I determined each participant's availability, I divided the respondents into groups of three to five, expecting that not all respondents would participate, resulting in group sizes of between two and four. Sessions lasted between forty-five minutes and one hour. For recruitment materials please see Appendix 4.

Analysis

I constructed a binomial general linear mixed model to compare the response for each question in the quiz (correct or incorrect) to when the question was answered (before or after the game) and group size, with session identity (which group the participant was in) and question number as random effects. Final group sizes were between two and four and given that this was a collaborative role-playing game it was possible that the number of participants per session affected how much and what was learned. As the game play varied between sessions, I included session as a random effect to account for differences between sessions due to their unique mixes of players, and I included question number as some questions may have been less likely to be answered during the sessions. I attempted to nest participant identity within session for the random effects, but this model resulted in a singular fit. Separating the model into two separate models, one including session as random effect and one including participant identity, resulted in nearly identical results with AIC values within 1 of each other. I decided that session was the more meaningful characteristic as the information about archerfish provided was determined by the scenario and challenges and the participant's questions during each session and therefore included that variable instead of participant identity. All analysis was conducted in R version 4.2.2.

Results

In total, thirty-nine people participated in this study across thirteen sessions. Participants were between 19 and 56 years old, with an average age of 31.7. Twenty-two participants described themselves as a game master, seventeen each as a science communicator or scientist, and thirty-three as a TRPG player. Six people also identified themselves as "other", including game designer, writer, engineer, and educator.

Participants were more likely to answer questions correctly after playing the game than before (Table 5.1, Figure 5.1A), regardless of group size. The median number of correct questions increased from four to eight, the minimum number correct from two to five, and the maximum from seven to ten (Figure 5.1B). Only one out of the thirty-nine participants did not improve their score after the game, getting six questions correct on both attempts.

The majority of the responses to the Likert scale questions were positive, with all of the participants indicating they enjoyed the game and learned new information about archerfish.

Most participants would play the game again, play a similar game about a different animal, run a session of the game themselves, or use a similar game in their own science communication (Table 5.2). The written responses to the question, “What did you enjoy most about this game?” mentioned the storytelling aspect, the way the characters’ abilities related to archerfish ecology, and my abilities as a game master. Only twenty-five participants answered the question “What would you improve?”. They spoke largely of streamlining and expanding the game design, but the majority of the comments were still positive overall.

Table 5.1: Model results for the binomial glmer comparing the likelihood of providing a correct answer to the time when it was asked (before or after the game). Significant results are emboldened.

Likelihood of answering a question correctly in relation to when the question was answered and group size.	
Fixed terms	**Coefficient ± SE**
Intercept	0.154 ± 0.316
Time Answered = Before	**-1.804 ± 0.173**
Group Size = 3	0.294 ± 0.229
Group Size = 4	0.120 ± 0.227
Random terms	**Variance ± SD**
Session	1.254e-06 ± 0.001
Question Number	0.607 ± 0.779

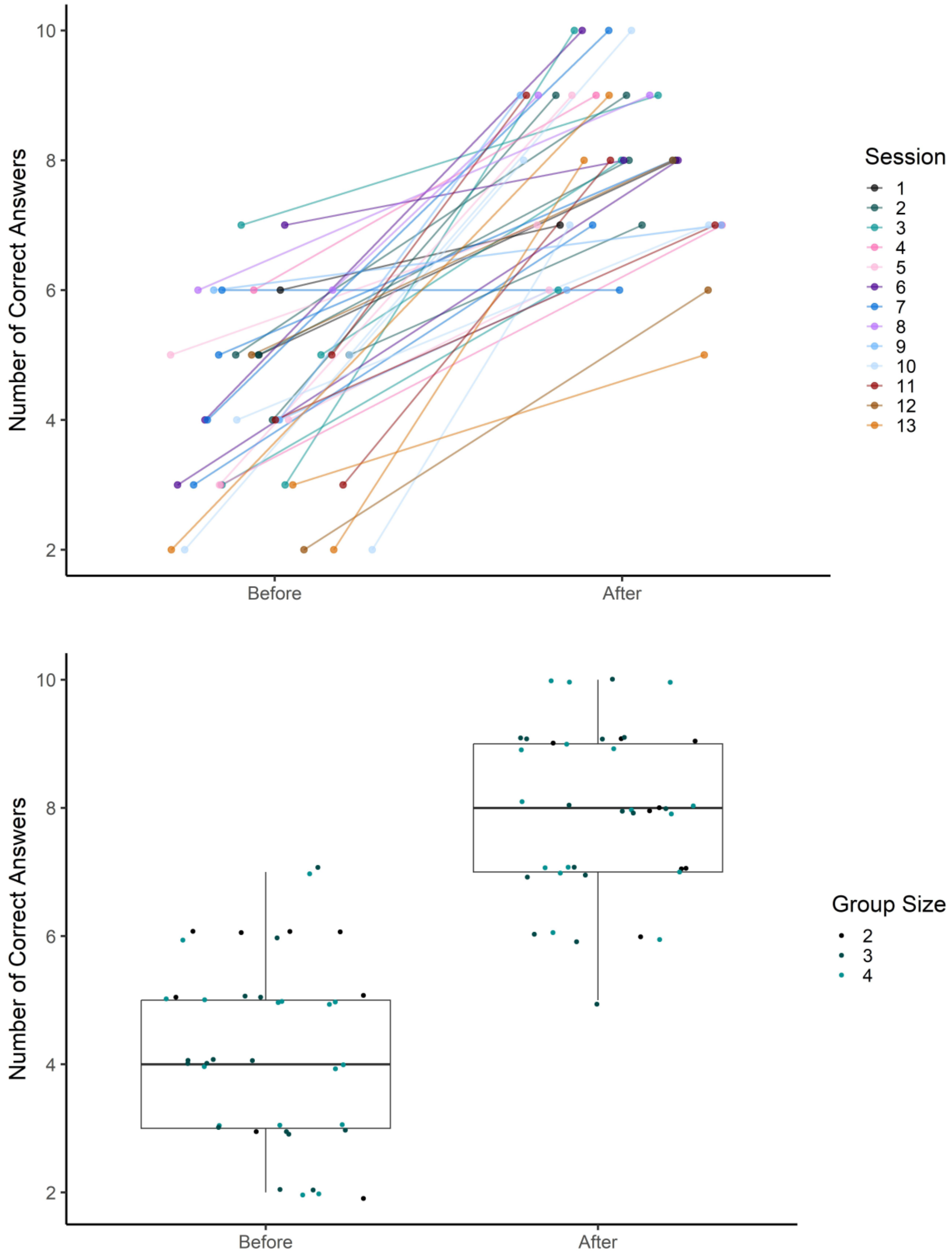

Figure 5.1 A: Number of correct answers before and after playing the TRPG. Each set of points indicates one participant. The colours indicate the session number. **5.1 B: Median correct responses per group size.** Points indicate participants.

Table 5.2: Likert Scale responses to the survey questions.

Statement	Agree	Neither Agree nor Disagree	Disagree	Not Applicable
I enjoyed playing the game	39	0	0	0
I would play the game again	37	1	1	0
I feel confident that I could run this game myself	27	5	5	0
I feel this is an effective manner of communicating facts about archerfish ecology	38	1	0	0
I have learned new information about archerfish	39	0	0	0
I am interested in using a similar game in my own science communication	24	8	1	6
I am interested in playing a similar game about a different animal	36	3	0	0
I feel my enjoyment of this game was linked to the abilities of the Game Master	33	4	2	0
I feel that the written handouts help my understanding of the game	36	3	0	0
I feel that the written handouts help my understanding of archerfish	29	9	1	0

Discussion

Out of the thirty-nine participants, only one failed to improve their test score after playing the TRPG. All participants indicated they enjoyed the game, and that they learned new information about archerfish ecology that they had not known previously. All but one participant agreed that the TRPG was an effective method of communicating information about archerfish ecology. These highly positive results indicate that TRPGs are a viable method of science communication and that they can be used to increase levels of PE with specific scientific topics, which is consistent with previous qualitative research into the same topic (Ross and Hall, 2023).

Most PE studies that look at the use of TRPGs consider only qualitative responses, as their primary goal tends to be to raise awareness of a subject area (Collins and Sabanovic, 2021; Boysen et al., 2023; Ross and Hall, 2023). By asking my participants to complete a quiz testing their knowledge of the subject area both before and after, I was able to directly measure the impact of the game on the participants' knowledge. Although I did not test how this compared to information gained in a more traditional manner (for example, a video or presentation about archerfish ecology), this study was not meant to test whether using TRPGs are a better form, but merely whether it is a viable form of science communication. Given that, from personal observation during the study, the participants enjoyed themselves and became invested in their characters and the storyline, regardless of whether they had previous experience with this format of gaming, the use of TRPGs could potentially be used to reach audiences not typically reached using more rigid forms of PE.

The participants were all adults, but their ages ranged from 19 to 56. This is a far broader range of ages than previous studies on the efficacy of TRPGs for PE and learning, and also skews older (with a mean age of 31.7) than previous studies (Gellar-Goad, 2014; Cook et al., 2016; Bolstad and McDowall, 2019; Ross and Hall, 2023). My results suggest that TRPGs are more widely applicable to PE than previously considered, appealing to adults as well as younger audiences. The participants in this study also did not appear to be limited in their learning or enjoyment by the fact that they played with strangers, people from different countries or cultures, and ages. TRPGs potentially provide a way to engage a varied audience not just with research, but also with each other. Future research could investigate whether more diverse groups of participants experience any additional benefits over more homogenous groups.

This game focussed on archerfish ecology, but the majority of participants indicated they would be interested in playing a similar game themed around a different animal. A simple TRPG like the one used in this study appears to be a good way to utilize constructivist learning theory and game-based learning (Bada, 2015; Bolstad and McDowall, 2019), and would allow the educator to link specific topics to the game play and design (Bolstad and McDowall, 2019). Potentially, it could even be used in classroom settings, where TRPGs have previously been used to great success (Gellar-Goad, 2014).

One drawback of this study is that it does not test long-term information retention and long-term changes in attitude and behaviour. A follow-up study could be conducted to test knowledge retention and behavioural changes, such as buying more eco-friendly certified products, over a longer period of time, potentially also in comparison to more traditional forms of science communication, as well as a study which could test long-term exposure to a scientific topic through TRPGs similar to that used by Gellar-Goad (2014) to increase engagement and knowledge retention of Latin. Repeated testing has been shown to improve long-term knowledge retention better than repeated study (Larsen et al., 2009), and as learning-by-doing is an proven method of increasing understanding of new concepts to various audiences (Roussou, 2004; Sevli et al., 2013), playing a TRPG relevant to a specific topic over a number of weeks or months could greatly enhance awareness and understanding of said topic.

It should be noted that the majority of the participants in this study had experience playing TRPGs, as only six out of the thirty-nine did not describe themselves as a TRPG player or game master. The participants also self-selected, so it is likely that the six inexperienced participants had some level of interest in playing TRPGs. Therefore, I cannot say that TRPGs are an effective method of science communication for every person or circumstance. However, interest in TRPGs has greatly increased in recent years, with the player base expanding due to the popularity of "Actual Play" shows like *Critical Role* and *Dimension 20*, online video streams of *Dungeons and Dragons* games, and prevalence of TRPGs in other popular media, like the tv show *Stranger Things* (Sidhu and Carter, 2020). Although it is very difficult to put an exact number on how much the TRPG industry is growing, and how many people are interested in TRPGs, the use of TRPGs for science communication and outreach has the potential to reach a very broad audience. The age range of the participants in this study suggests that, although previous studies on the use of TRPGs in educational settings have focussed on school- and university-aged students, it could also be highly beneficial to older participants. Although TRPGs will not always be preferential over other, potentially simpler, forms of PE, they could be especially beneficial to interdisciplinary subjects for they provide a broad scope, and given the interactive nature of TRPGs they lend themselves well to use with larger, heterogenous groups. Incorporating TRPGs into outreach programmes could help to broaden the reach of said programme, as it is possible that people who would not attend a public lecture on a scientific topic would attend or participate in an Actual Play centred around the same topic, and it would be interesting to investigate this in future research.

The most prevalent feedback received for improving the TRPG was that the instructions could be more streamlined, and the game expanded further to include other species. I believe there is certainly scope to collaborate with professional game designers to both increase the clarity of the instructions and to expand the game beyond the one-page instructions. This could potentially allow for education on topics relating to fish ecology and biodiversity beyond archerfish and could provide a valuable template for similar PE endeavours. Educational resources using TRPGs exist, most notably those provided by *Dungeons & Dragons* publisher Wizards of the Coast, but these resources generally focus on improving critical thinking and problem solving, rather than educating on a specific topic. This study, however, suggests that TRPGs can be for this purpose also, and personal experience from performing at science festivals and in online gaming streams has shown me that TRPGs can be easily based around a variety of science and science history topics, including the digestive system, cloning, conservation, chemical pollution, evolution, and more. The use of TRPGs for PE and science communication is worthy of increased study to determine the best manners in which it can be applied to assist both scientists and the public.

Chapter 6 – General discussion

> *"You're brave, to admit you don't know everything and then do something about it."*

Tamora Pierce, The Woman Who Rides Like a Man

Summary

In this thesis, I investigated several aspects of archerfish social behaviour. The main conclusion I can draw from the research I have conducted is that the social behaviour of archerfish is more complicated than previously thought. Whether archerfish are capable of social learning remains an open question. There is no reported evidence of social learning in this genus with the exception of a single study conducted by Schuster et al. (2006). In fact, it is possible that archerfish may be hampered in their learning when in the presence of conspecifics, for they are more hesitant to shoot as well as making other behavioural changes (Jones et al., 2018; Jones, 2020; Jones et al., 2021b). Archerfish appear to be capable of learning about new stimuli in isolation, so they may not have a need for social learning in the wild.

Below, I will summarise the research I conducted during my PhD and what my findings mean for archerfish research and the wider field of animal behaviour.

Archerfish social behaviour

In chapter 2, I showed that archerfish foraging success is not impacted by the perceived threat of kleptoparasitism, even though it did affect their behaviour as fish decreased the time spent aiming when more conspecifics were present. The reason for this remains somewhat unclear but could be related to the fact that aiming is a conspicuous behaviour that may cue potential competitors to the presence of food. This hypothesis is corroborated by research which indicates archerfish respond most to the earlier stages of a robot archerfish's hunting sequence (Brown et al., 2021b), but this does not rule out other explanations, for example that the increased aiming duration is due to the shooter scanning for predators. My findings provide additional evidence that archerfish alter their foraging behaviour in the presence of conspecifics, as previous work by Jones et al. (2018) discovered that archerfish which are under observation by a conspecific take longer to shoot, and undertake more orientation movements, which is part of the aiming process. However, this study incorporated orientation movements which did not result in shots, while my study only considered those that did, and my study did not compare aiming duration in groups to aiming duration when solitary. Even when considering a single orientation movement, the time spent aiming increased when in the presence of more individuals, suggesting that archerfish are aware not only of the presence of conspecifics, but also of the increased threat of kleptoparasitism when more conspecifics are present.

In chapter 3, I took the first steps towards understanding how archerfish perceive videos of conspecifics but was unable to determine whether archerfish will respond to a video conspecific in the same manner as they do a real conspecific. My experiment only consists of one half of the necessary study, and I therefore can't say whether video demonstrators and stimuli will be an effective tool for archerfish research. However, there are now multiple studies which suggest archerfish do not behave in an adverse manner towards a video of an archerfish in relation to other stimuli, be they a neutral video stimulus, a mirror, or an empty fish tank (Austin, 2020). Their response to a video stimulus in relation to a live stimulus remains to be tested, but another potential dynamic stimulus, a robotic archerfish, has recently been tested and provided interesting results (Brown et al., 2021a; Brown et al., 2021b). Real archerfish responded to the robotic stimulus by approaching it when it initiated a hunting sequence, although whether archerfish respond in a similar manner to a hunting conspecific has not yet been tested. Regardless, if archerfish do not respond to video stimuli as they do to live conspecifics (Schuster et al., 2006; Jones et al., 2018), stationary images (Leadner et al., 2021), or a robot conspecific (Brown et al., 2021a; Brown et al., 2021b), those other options may work well for studies on archerfish cognition and social behaviour.

Archerfish as a model for social learning

In chapter 4, I attempted to discover whether archerfish learn to shoot novel targets faster in groups by exposing them to a dual-choice experiment in groups and solitarily. However, despite my experimental design being similar to previous work (Newport et al., 2013; Karoubi et al., 2017; Leibovich-Raveh et al., 2021), the archerfish did not learn to distinguish between the rewarded and unrewarded targets in any treatment, and exposure to the training phase in a group did not alter the shooting behaviour of those who shot the least when testing them individually. I can only speculate as to why; it is possible that the fish did not have enough time to learn the difference between the targets, were relying on faulty information provided by the dominant shooters (Cook and Mineka, 1989), or did not have sufficient time to reach a group consensus (Kao et al., 2014). Archerfish that take less time before shooting are more likely to choose the lower-reward or unrewarded target in a choice experiment (Jones et al., 2020), so it is possible that the faster shooters are simply less reliable demonstrators. The fish tested individually may not have shot because the targets were too close to the water (Jones, 2020), at which point jumping is a more energy efficient tactic (but was prevented due to the tank cover being in the way) (Shih et al., 2017). I did observe fish jumping during this study, but I did not record the frequency of this behaviour and thus can only suggest this as a future avenue for research.

The development, over time, of one or two dominant shooters in the group treatments could suggest the existence of dominance hierarchies in archerfish groups, or the existence of a producer-scrounger relationship. In his thesis, Jones (2020) reported that archerfish exhibit temporal resource partitioning, with individuals changing their levels of foraging activity during a single feeding session to create a hierarchy of sorts. The manner by which this temporal resource partitioning is maintained in archerfish has yet to be determined, but could be related to levels of aggression or differences in cognitive styles and personality (Jones et al., 2020). It is also possible, given that in both my study and the work by Jones (2020) described above, there were individuals which shot rarely or not at all, some fish rely on alternate hunting methods like jumping and hunting underwater in lieu of shooting, or scrounge food downed by conspecifics. Many questions remain on the subject of archerfish social behaviour and how individual differences affect this.

One of my main questions throughout my time researching archerfish has been whether they are capable of social learning. Although Schuster et al. (2006) claimed archerfish could learn to down moving targets by observing a trained conspecific, no further studies have been published on the question of whether archerfish can learn socially. Although they certainly pay attention to social cues (Brown et al., 2021a; Brown et al., 2021b; Leadner et al., 2021), their rate of learning does not appear to be accelerated by the presence of trained conspecifics (Jones et al., 2021b). Now, seventeen years after the first claims of social learning in archerfish were made, it appears that we are still unable to say one way or another whether it is true.

Bringing science to the people

My inclusion of a research chapter testing the efficacy of a specific method of public engagement is perhaps unexpected in a thesis which focuses on group behaviour in archerfish. However, the results of chapter five speak for themselves: tabletop role-playing games are an effective and enjoyable method of engaging the public with scientific research. This study was a culmination of outreach work I have been conducting as part of my broader post-graduate training. I developed the idea of combining my hobby of playing Dungeons and Dragons with public engagement work in the autumn of 2021, and have since produced over 200 hours of video content merging the two. Developing my own TRPG and using it to test the efficacy of using TRPGs for public engagement has, for me, confirmed that the public engagement work I have conducted over the past two years was beneficial. Since conducting the study detailed in chapter 5, I have applied my findings to improve the game and design new ones and used them to run workshops for public engagement professionals and shows at science festivals.

Public engagement work is critically important for educating the public about advances in scientific research and for increasing public trust in science (Bromme et al., 2022), but the distribution of who participates is skewed. Amongst scientists, senior researchers and researchers who teach are more likely to engage in PE work, possibly due to increased job stability providing the time to do more work outside of the institutions and increased experience (Bauer and Jensen, 2011). A lot of public engagement work continues to be conducted in more rigidly-organized manners, backed by large organizations and governments (Stilgoe et al., 2014), and thereby less accessible to those not already interested in science. All this combined means that only certain people will access scientific information provided through PE efforts, and only specific information will be disseminated to the public, usually by older, male, white scientists (Dudo et al., 2018). However, with the advent of social media and less rigorously organized public engagement efforts like independently produced podcasts and blogs, PE work is becoming more accessible for both researchers and the public (Menlove et al., 2019). One of the greatest barriers that still exists to increased participation from scientists at all levels of their career is the lack of recognition from institutions that “unofficial” public engagement work has value (Calice et al., 2022).

As a part of my funding agreement for this PhD, I was required to spend three months working outside of academia on a placement. I spent that time working at a museum in the Netherlands, Naturalis Research Center, conducting research using museum specimens while participating in their LiveScience exhibit. This exhibit is a free, open-plan museum space where museum employees and volunteers can conduct their research in public, so that the visitors can engage directly with the work. This exhibit allowed people at all levels of education and every social class to learn about the research which occurs at the museum and was incredibly beneficial for me to experience. The fact that I was able to have face-to-face conversations with the visitors allowed me to directly explain my work, inspire those I spoke to, and persuade them as to why scientific research is important. It also led me to gain new insight into my own work, open myself up to new theories and viewpoints, and discover new meaning behind my work. Scientists must do more to remove themselves from their institutions and directly engage with the public, for without disseminating our work outside of our own fields it will be of little use.

Future Work

In this thesis, I have made some advances in understanding the social behaviour of archerfish, but many questions still remain. I will outline below some of the most pressing gaps that remain in our knowledge and potential ways to tackle them. Lastly, I will touch upon the future of game-based public engagement.

Archerfish behaviour in the wild

A significant amount of research has been conducted on archerfish since the mid-twentieth century. We know a significant amount about their vision (Newport and Schuster, 2020), their neurology (Karoubi et al., 2016; Sillar et al., 2016), their hunting behaviour (Schuster, 2018), and increasingly more about their social behaviour as well (Jones, 2020). However, almost no research has been conducted on archerfish behaviour in the wild. Although unpublished reports on this topic do exist (see (Schuster, 2018)), published research is limited to a single study on behavioural adaptations to interspecific kleptoparasitism (Rischawy et al., 2015).

Although lab-based research is incredibly valuable and allows for more controlled experimentation than in the field, the lack of field-based research on archerfish means that lab-based research makes assumptions about archerfish ecology which are not necessarily confirmed in wild individuals. Observation of archerfish in the wild, and a closer look at their social structures in the wild, would be greatly beneficial. Archerfish are currently considered to be facultatively social, but whether they congregate at feeding patches due to local enhancement (Perez-Cembranos and Perez-Mellado, 2015) or actively seek out others for anti-predator benefits (Wrona and Jamieson Dixon, 1991). Whether archerfish in the wild also experience the temporal resource partitioning reported by Jones (2020) is also unknown, as is the structure of any groups which may form. Do archerfish have dominance hierarchies? We don't know, but it is a distinct possibility that the social behaviour seen in the lab is not identical as that seen in the wild, as was the case for the famous "alpha wolves" study (Mech, 1999). The first studies conducted on wolf pack hierarchies were done on unrelated captive wolves *Canis lupus* Linnaeus, 1758 and found that one male and one female (the "alphas") were the dominant individuals; future research on wild populations instead showed that wolf packs are nuclear families, and the alphas merely the parents (Mech, 1999). Captive animals can behave very differently than their wild counterparts, and these changes in behaviour must be taken into consideration when reporting results (Webster and Rutz, 2020). Research on animals' social behaviour in the wild is critical if we are to draw accurate conclusions in future lab-based studies, and this holds true for archerfish as well.

Archerfish as a model for sophisticated social learning

The initial purpose of my thesis had been to discover whether archerfish could be used as a model for sophisticated social learning. They are well-suited to social learning studies, as their method of hunting is conspicuous, they are aware of, and possible observe, conspecifics, and any social learning involving a novel shooting task could only be observed visually. The observers would not be able to interact with the product of the learning, or any other cues like odour, to rule out types of social learning like local enhancement in studies focussing on more complex tasks like imitation.

Whether or not archerfish are capable of any form of social learning, including imitation, remains unknown. A recreation of the experiment conducted by Schuster et al. (2006), this time focussed on examining how the observers learn, rather than whether archerfish can learn, to down moving targets would be incredibly beneficial to the field of social learning research. This experiment would use a similar premise, teaching naïve archerfish to shoot down a moving target, but would implement the use of ghost demonstrator (Hopper, 2010) to determine if the archerfish are truly observing the live demonstrator or merely the movement of the target. The experimenters could then, using robot archerfish, alter aspects of the demonstrator's movements, like angle and positioning, while shooting to determine which, if any, the naïve individual copies. This experiment would be a good start towards understanding how archerfish interpret social cues and learn to down moving targets.

If archerfish can be proven to be capable of imitation, they may prove to be a good model genus alongside primates. Non-human primates have long been thought to be the only non-human animals capable of imitation, but recent research suggests that birds are also capable of imitation (Zentall, 2022). Fish are relatively inexpensive to keep, require less space than primates and birds, environmental or social conditions are easier to manipulate for fish, and many species have faster reproduction rates than apes. Furthermore, if fish are capable of imitation, it will help us determine the breadth of this trait as well as increasing our knowledge of how ecology influences the evolution of cognition. Archerfish would be well-suited for studies on imitation as their practice of spitting water at their prey means the observers would not be able to interact with any odour or audio cues left on or near the target, thus eliminating anything except visual cues. Other species may be well-suited to studies on imitation in non-mammalian species, for example bumblebees which have been shown to perform better at novel tasks after exposure to a real demonstrator rather than a ghost demonstrator (Loukola et al., 2017). Non-social species may also provide insights into the development of social learning, as some species like Port Jackson sharks *Heterodontus portusjacksoni* (F. A. A. Meyer, 1793) have been shown to be capable of learning novel behaviour by observing conspecifics (Vila Pouca et al., 2020; Webster, 2023). Non-mammalian and non-social species can provide valuable information on the evolutionary origins of, and mechanisms behind, social learning, and they warrant increased research.

Working with non-model organisms

One of the struggles of working with non-model species is the need for designing new or adapting existing methodologies. For my studies on video model recognition and group learning, I spent significant amounts of time designing, adapting, and testing various methodologies. I could not assume that archerfish can interpret moving images on a screen in the same way as humans, or even as other fish do, thus I needed to first determine how the fish responded to such a stimulus in relation to control cues before I could compare it to their response to live conspecifics. I attempted to use one-shot video object segmentation (Caelles et al., 2017) and automated tracking using the TRex software (Walter and Couzin, 2021) to analyse the resultant data prior to conducting the planned second part of my experiment. Due to the archerfish's preference for dim lighting and gravel substrate, this failed as the software was unable to detect the fish against the background. By the time I had coded the videos by hand, the fish I had used in the first part of the experiment had died, and my new stock was of a different species of archerfish.

Given the wide geographical range that archerfish inhabit, we cannot assume that each species act identically. Published research on archerfish primarily uses *Toxotes chatareus* and *T.*

jaculatrix, but due to supply complications outside of my control the majority of my stock was *T. blythii*. This species has a relatively narrow range, being found only in freshwater bodies in Myanmar, and although they do exhibit the same spitting behaviour as their more well-researched sister species, it is unclear what behavioural differences they may exhibit. Little has been published about archerfish behaviour in the wild in general, and inter-species comparisons have not yet been made. However, given the stress the *T. blythii* exhibited when isolated from their conspecifics, evidenced by their behaviour (hiding, reluctance to feed), it is possible that this species is perhaps more social than others. The process of designing my final archerfish experiment gave me greater insight into the importance of understanding individual species, and individual animals, as what was meant to be a study on social learning instead resulted in my archerfish never learning to distinguish between two targets, which the literature suggests they should have learned to do in days (Newport et al., 2013).

We cannot assume that methodologies which work for one species will work equally well for others. In a recent study which tested capuchins Cebinae Bonaparte, 1831 and cleaner wrasse *Labroides* sp. Bleeker, 1851 performance in a task based on cleaner wrasse ecology, the wrasse, perhaps unsurprisingly, outperformed capuchins (Salwiczek et al., 2012). A follow-up study found that the capuchins performance was dependent on the cue presented (food colour versus plate colour), and whether the food was visible, whereas the wrasse performed equally well regardless of the presented cues (Prétôt et al., 2016). We must take differences in species ecology into consideration when designing studies to test performance and cognition, and when we do not have a good grasp on a species ecology, we must endeavour to learn what we can.

Gamifying science

I have already mentioned the importance of scientists engaging directly with the public, but more can be said in the manner in which such engagement can occur. Public engagement does not have to involve formal settings, complex set-ups, or high-budget productions. In fact, more relaxed PE efforts have the potential to draw in people who would not normally interact with scientific research. By gamifying public engagement, the audience gains the opportunity to interact in a new, playful, and enjoyable manner with scientific research. This can not only help reach new audiences, but learning-by-doing is a well-known method of increasing knowledge retention (Roussou, 2004; Bada, 2015). Why should we not use similar methods for public engagement work?

The next steps for the use of tabletop role-playing for public engagement is to determine whether it is an effective method for longer-term knowledge retention. It would also be beneficial to test its utility for subjects outside ecology. TRPGs are a versatile tool for communicating various topics, and their use for public engagement work does not need to be limited.

Conclusion

This thesis has provided new information regarding archerfish social behaviour. I hope it will be beneficial to future studies on archerfish ecology and help move the research towards investigating whether archerfish can be used as a model for sophisticated social learning. I have discovered that archerfish alter the time spent aiming at a target depending on group size, but that this does not impact their shooting success, and found evidence contradicting the literature on the relationship between kleptoparasitism and group size. I took the first steps into establishing whether video stimuli can be used for studying archerfish behaviour. I attempted to discover whether archerfish could learn socially, but instead found no evidence of learning of any form. Lastly, I tested a novel method of public engagement using tabletop role-playing games and found it to be a highly effective method of educating the public about archerfish ecology. Many questions still remain, however. Do archerfish exhibit dominance hierarchies?

Does a producer-scrounger relationship exist? Do archerfish respond to video conspecifics in the same manner they do to live conspecifics? And can any species of archerfish learn socially? Future research, incorporating ecology and cognition, comparing behaviour in the wild and in the lab, will tell, for this species, and for others.

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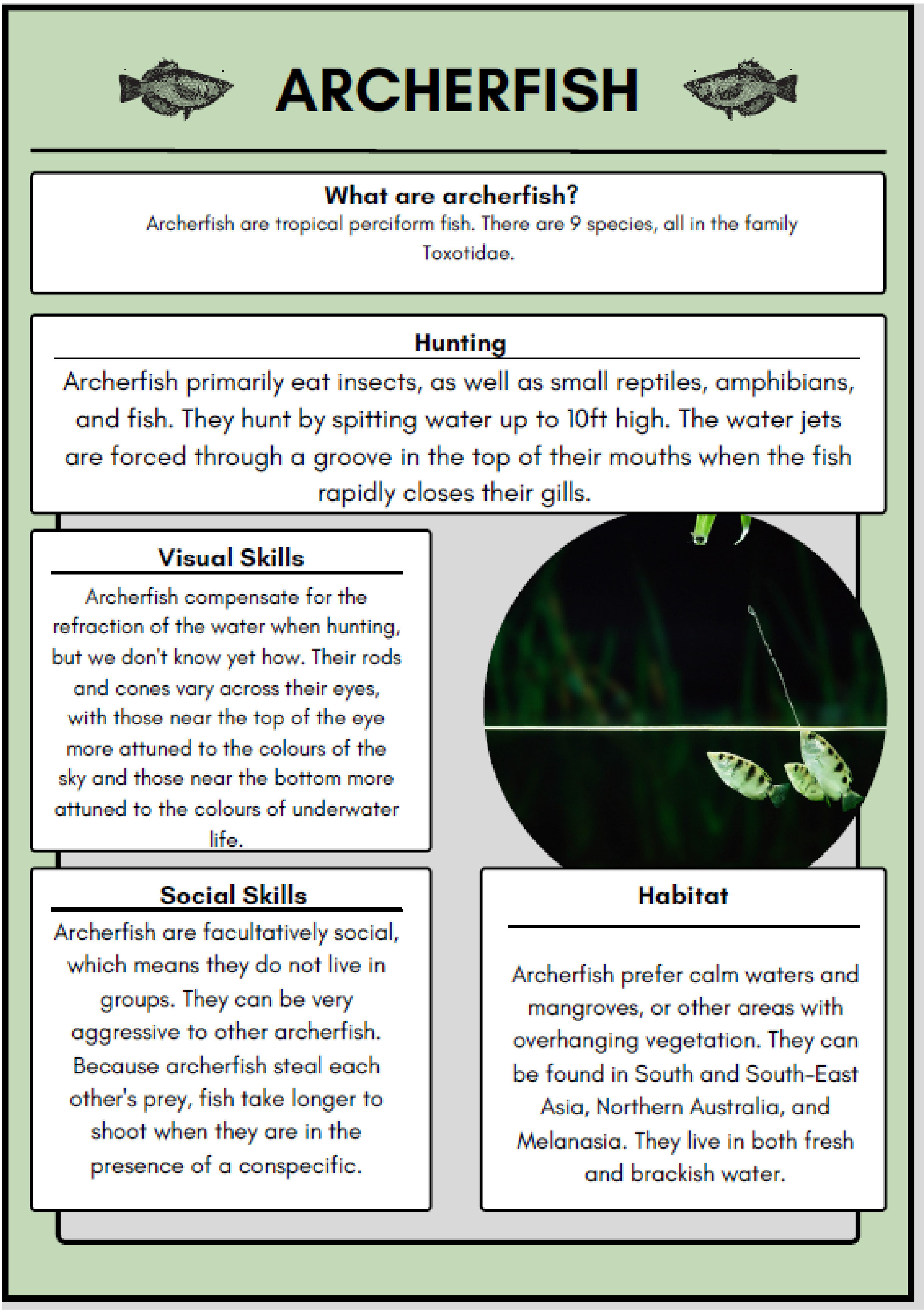
Appendix 1 – Archerfish fact sheet used for game design



ARCHERFISH

What are archerfish?

Archerfish are tropical perciform fish. There are 9 species, all in the family Toxotidae.

Hunting

Archerfish primarily eat insects, as well as small reptiles, amphibians, and fish. They hunt by spitting water up to 10ft high. The water jets are forced through a groove in the top of their mouths when the fish rapidly closes their gills.

Visual Skills

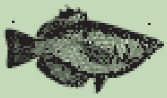
Archerfish compensate for the refraction of the water when hunting, but we don't know yet how. Their rods and cones vary across their eyes, with those near the top of the eye more attuned to the colours of the sky and those near the bottom more attuned to the colours of underwater life.

Social Skills

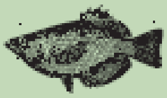
Archerfish are facultatively social, which means they do not live in groups. They can be very aggressive to other archerfish. Because archerfish steal each other's prey, fish take longer to shoot when they are in the presence of a conspecific.

Habitat

Archerfish prefer calm waters and mangroves, or other areas with overhanging vegetation. They can be found in South and South-East Asia, Northern Australia, and Melanasia. They live in both fresh and brackish water.



ARCHERFISH



Inhibition of Return

Archerfish were the first non-primate to show "inhibition of return". This means that, when archerfish are searching for prey above the water, they remember where they have already looked . This is the same way that humans search, but archerfish manage to do this without a visual cortex!

Speed-Accuracy Tradeoff

Archerfish have different "cognitive styles", or personality types. Some fish, when presented with multiple targets, will shoot at the first one they see. Others will take their time to investigate each target before making a decision. This means that, if only one of the targets provides a food reward, the fish that spend more time investigating are more likely to pick the correct target. We call this a "speed-accuracy tradeoff".

C-Starts

A "c-start" is an escape mechanism used by fish to quickly get away from potential threats. The fish bends its body in a "C" shape to change direction, and then accelerates away from the threat. Archerfish, however, also use c-starts to reach their prey. They calculate where the prey will land, and then reach it at the moment it hits the water.

Hydrodynamics

The speed of the jet is controlled by the opening and closing of the fish's mouth. The water that leaves the mouth first is the slowest, so the water behind it pushes it forward, increasing the momentum. At the point of impact, the force can be more than 6 times higher than the initial force generated by the muscles.

Facial Recognition

Archerfish can recognize more than 40 different human faces, despite lacking a neocortex. They can even generalize faces they've only seen from one angle so that they recognize it when shown a different angle. They are capable of this because they have very good pattern recognition skills.

Appendix 2 - “Archerfish in Troubled Water” game instructions

Character creation

Each character will have four stats. Boldness, Speed, Accuracy, and Personality. Boldness determines how brave you are when encountering unfamiliar things. Speed determines how quickly you react to events (not your physical speed). Accuracy determines how likely you are to pick the correct option when given a choice.

To determine your character’s stats, follow these instructions:

1. To determine Boldness, roll 1d6
2. To determine Speed, roll 1d6
3. To determine Accuracy, subtract your Speed stat from 6.
4. To determine Personality, roll 1d6 and the consult the table below:

Number	Trait	Description
1	Highly aggressive	Ignoring what you rolled for Boldness, when attacking other archerfish, this stat is 6
2	Always hungry	Ignoring what you rolled for Speed, when food is involved, this stat is 6
3	Shy	You won’t shoot if other fish are watching you
4	Drama queen	After every three rolls, your Speed and Accuracy stats switch
5	Deformed palate	None of your shots land on your target, regardless of your Accuracy stat
6	Secretly a gourami	Your stats remain the same, but you can only spit ~5 cm high

Playing the game

Each stat number comes with its own modifier. When the outcome of your actions is uncertain, you will roll 1d6 and add or subtract the modifier for the most relevant stat. The result of your roll will determine your success. The modifiers are listed in the table below.

Number	Modifier
1	-1
2-3	0
4-5	+1
6	+2

If you want to try and shoot at a target, roll a d6. Unless your personality dictates otherwise, you hit if you roll a 4 or higher. If there is more than one target for you to choose between, you must roll Accuracy to determine if you've shot at the correct target.

Instructions for the Game Master

Roll 1d6 to determine a scenario/story hook. The resolution is optional and can be changed if you come up with something you believe fits better. You can also invent your own scenario!

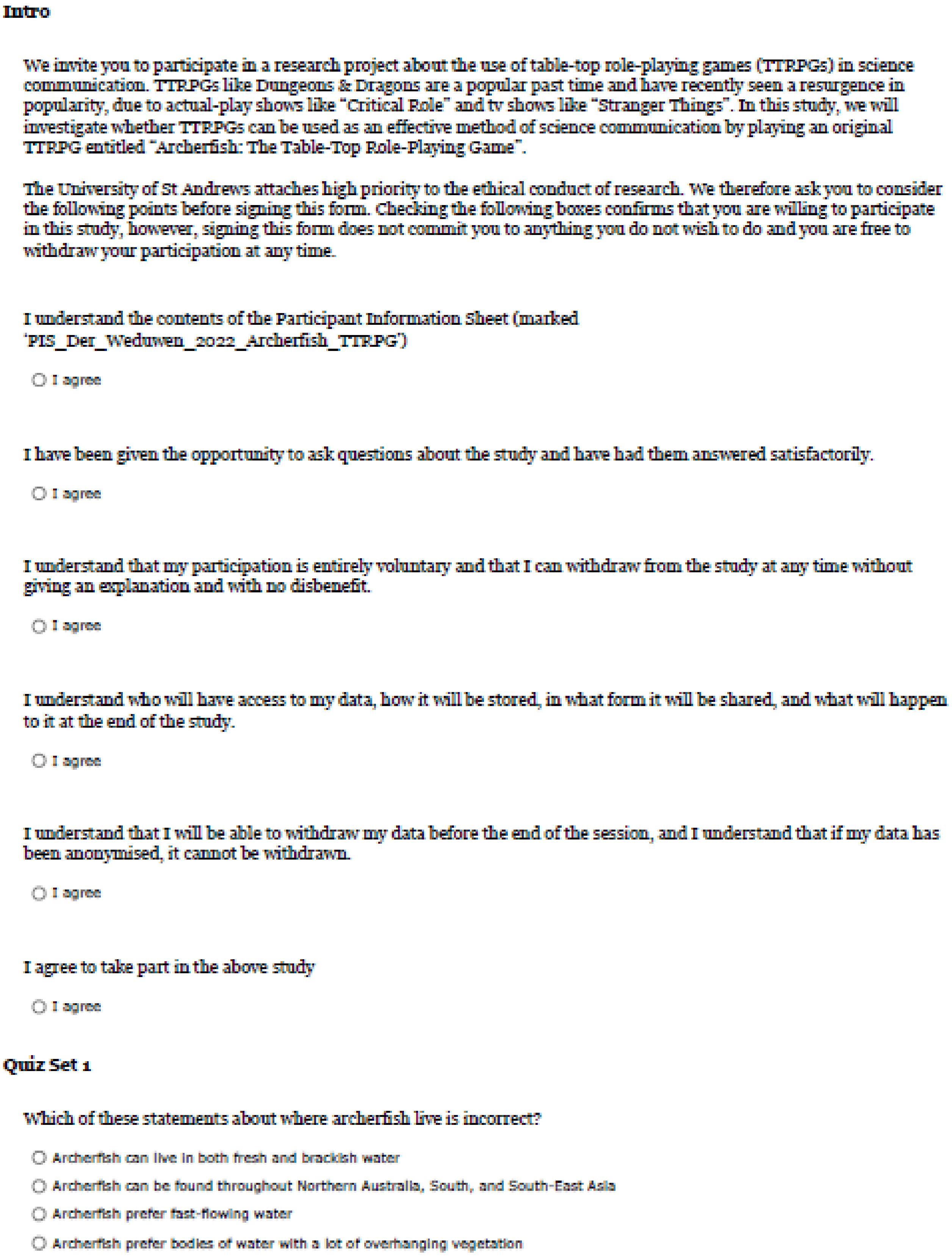
1. A rival archerfish gang has invaded your mangrove forest
    a. SOLUTION: The "rival" gang is just a big mirror
2. An archerfish child, Meno, has been kidnapped by pet shop employees
    a. SOLUTION: Meno asked to be kidnapped, as they want to travel and see the world
3. All the insects have disappeared
    a. SOLUTION: The insects have been eaten by small lizards, which are just as tasty (to archerfish) as insects
4. Humans are encroaching on your territory with big machines
    a. SOLUTION: The big machines are just camera equipment, and the humans are here to film a BBC documentary about archerfish

5. The water level in the forest has lowered overnight
    a. SOLUTION: It’s just the tide. The water will come back.
6. A scientist has arrived to ask invasive questions about your lifestyle
    a. SOLUTION: The scientist confused archerfish and anglerfish, and is in the wrong habitat

To determine the challenges the players will face, roll 2d6 (or pick from the list). You can roll fewer, or more, if you so choose.

1. A bird of prey attacks
2. A hatch blocks the river, and the lever/button to open it is really high up
3. CCTV cameras
4. Polluted water
5. Rapids
6. The mangrove crabs demand toll

Appendix 3 – Public engagement questionnaire and quiz



Intro

We invite you to participate in a research project about the use of table-top role-playing games (TTRPGs) in science communication. TTRPGs like Dungeons & Dragons are a popular past time and have recently seen a resurgence in popularity, due to actual-play shows like “Critical Role” and tv shows like “Stranger Things”. In this study, we will investigate whether TTRPGs can be used as an effective method of science communication by playing an original TTRPG entitled “Archerfish: The Table-Top Role-Playing Game”.

The University of St Andrews attaches high priority to the ethical conduct of research. We therefore ask you to consider the following points before signing this form. Checking the following boxes confirms that you are willing to participate in this study, however, signing this form does not commit you to anything you do not wish to do and you are free to withdraw your participation at any time.

I understand the contents of the Participant Information Sheet (marked 'PIS_Der_Weduwen_2022_Archerfish_TTRPG')

○ I agree

I have been given the opportunity to ask questions about the study and have had them answered satisfactorily.

○ I agree

I understand that my participation is entirely voluntary and that I can withdraw from the study at any time without giving an explanation and with no disbenefit.

○ I agree

I understand who will have access to my data, how it will be stored, in what form it will be shared, and what will happen to it at the end of the study.

○ I agree

I understand that I will be able to withdraw my data before the end of the session, and I understand that if my data has been anonymised, it cannot be withdrawn.

○ I agree

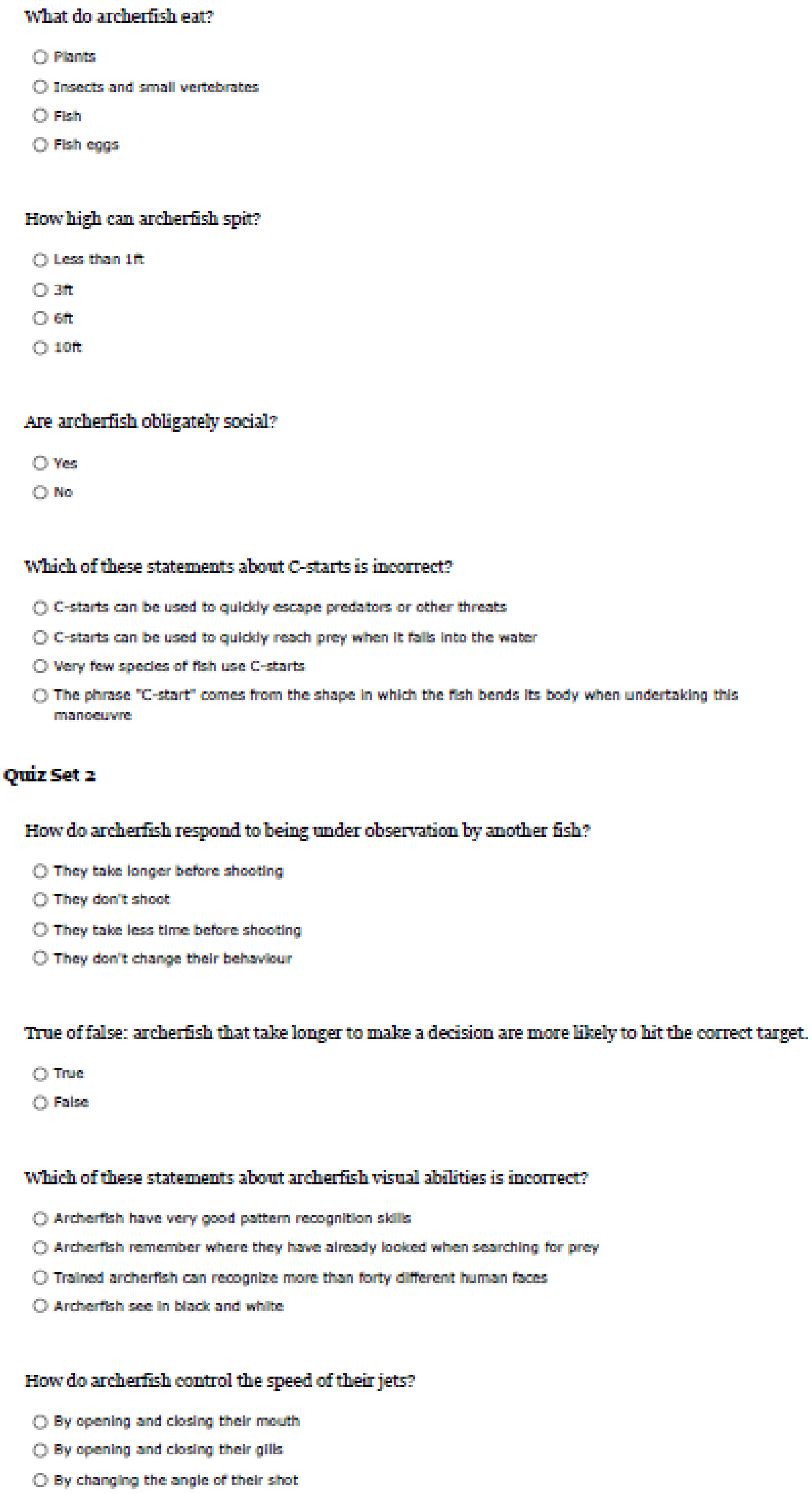
I agree to take part in the above study

○ I agree

Quiz Set 1

Which of these statements about where archerfish live is incorrect?

○ Archerfish can live in both fresh and brackish water
○ Archerfish can be found throughout Northern Australia, South, and South-East Asia
○ Archerfish prefer fast-flowing water
○ Archerfish prefer bodies of water with a lot of overhanging vegetation



What do archerfish eat?

○ Plants
○ Insects and small vertebrates
○ Fish
○ Fish eggs

How high can archerfish spit?

○ Less than 1ft
○ 3ft
○ 6ft
○ 10ft

Are archerfish obligately social?

○ Yes
○ No

Which of these statements about C-starts is incorrect?

○ C-starts can be used to quickly escape predators or other threats
○ C-starts can be used to quickly reach prey when it falls into the water
○ Very few species of fish use C-starts
○ The phrase "C-start" comes from the shape in which the fish bends its body when undertaking this manoeuvre

Quiz Set 2

How do archerfish respond to being under observation by another fish?

○ They take longer before shooting
○ They don't shoot
○ They take less time before shooting
○ They don't change their behaviour

True of false: archerfish that take longer to make a decision are more likely to hit the correct target.

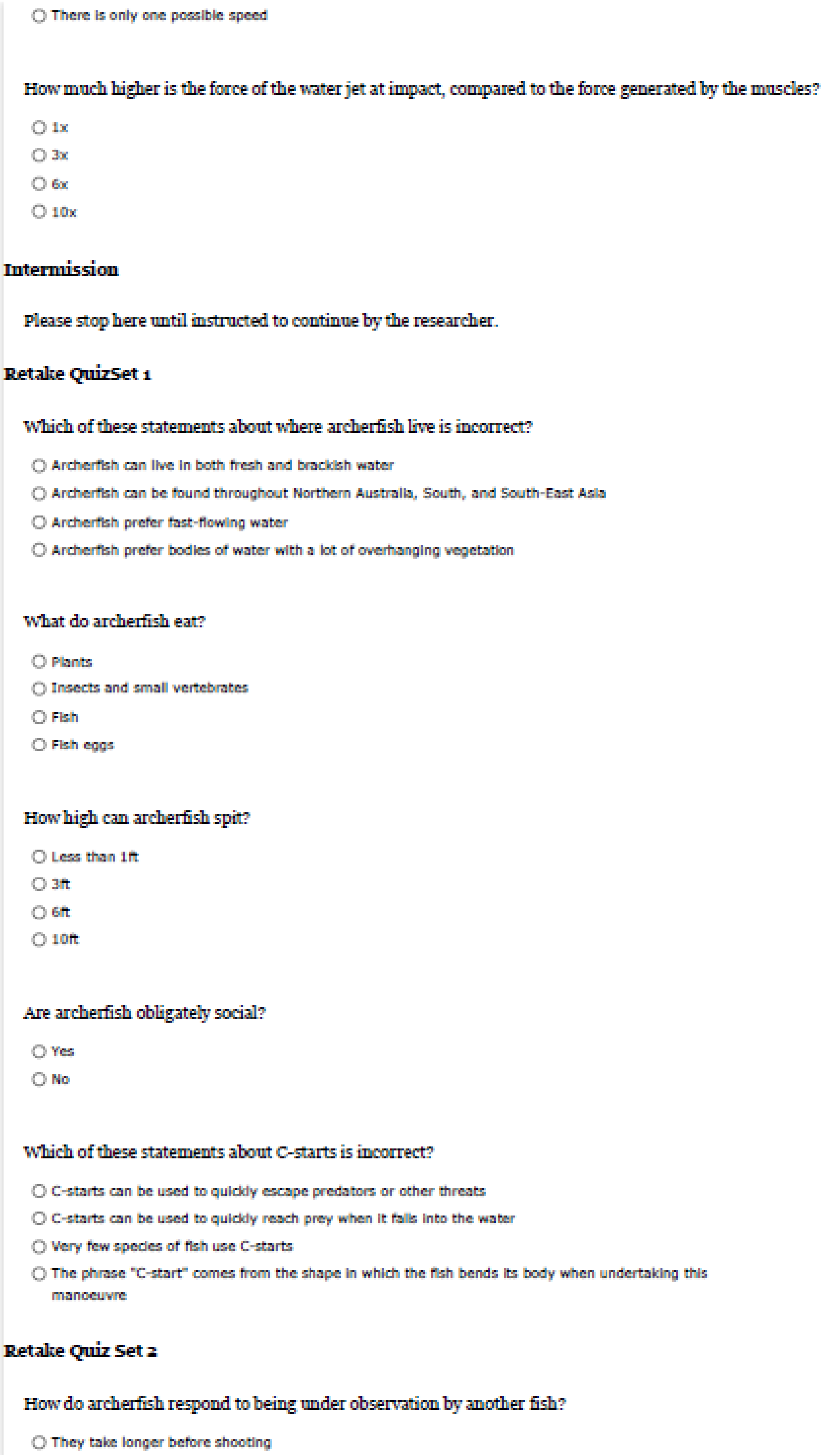
○ True
○ False

Which of these statements about archerfish visual abilities is incorrect?

○ Archerfish have very good pattern recognition skills
○ Archerfish remember where they have already looked when searching for prey
○ Trained archerfish can recognize more than forty different human faces
○ Archerfish see in black and white

How do archerfish control the speed of their jets?

○ By opening and closing their mouth
○ By opening and closing their gills
○ By changing the angle of their shot



○ There is only one possible speed

How much higher is the force of the water jet at impact, compared to the force generated by the muscles?

○ 1x
○ 3x
○ 6x
○ 10x

Intermission

Please stop here until instructed to continue by the researcher.

Retake QuizSet 1

Which of these statements about where archerfish live is incorrect?

○ Archerfish can live in both fresh and brackish water
○ Archerfish can be found throughout Northern Australia, South, and South-East Asia
○ Archerfish prefer fast-flowing water
○ Archerfish prefer bodies of water with a lot of overhanging vegetation

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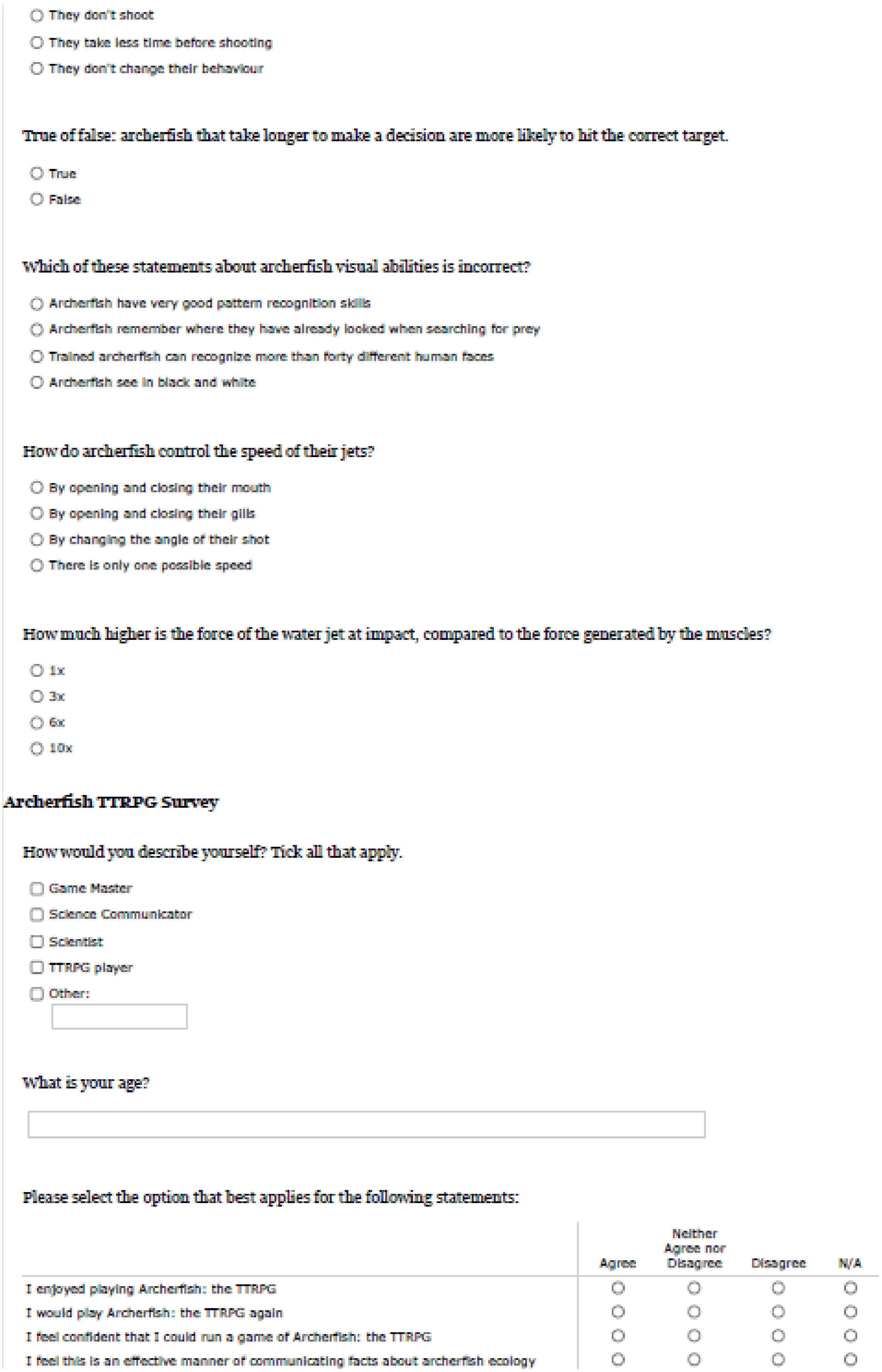
○ The phrase "C-start" comes from the shape in which the fish bends its body when undertaking this manoeuvre

Retake Quiz Set 2

How do archerfish respond to being under observation by another fish?

○ They take longer before shooting



○ They don't shoot

○ They take less time before shooting

○ They don't change their behaviour

True of false: archerfish that take longer to make a decision are more likely to hit the correct target.

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○ False

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○ By changing the angle of their shot

○ There is only one possible speed

How much higher is the force of the water jet at impact, compared to the force generated by the muscles?

○ 1x

○ 3x

○ 6x

○ 10x

Archerfish TTRPG Survey

How would you describe yourself? Tick all that apply.

☐ Game Master

☐ Science Communicator

☐ Scientist

☐ TTRPG player

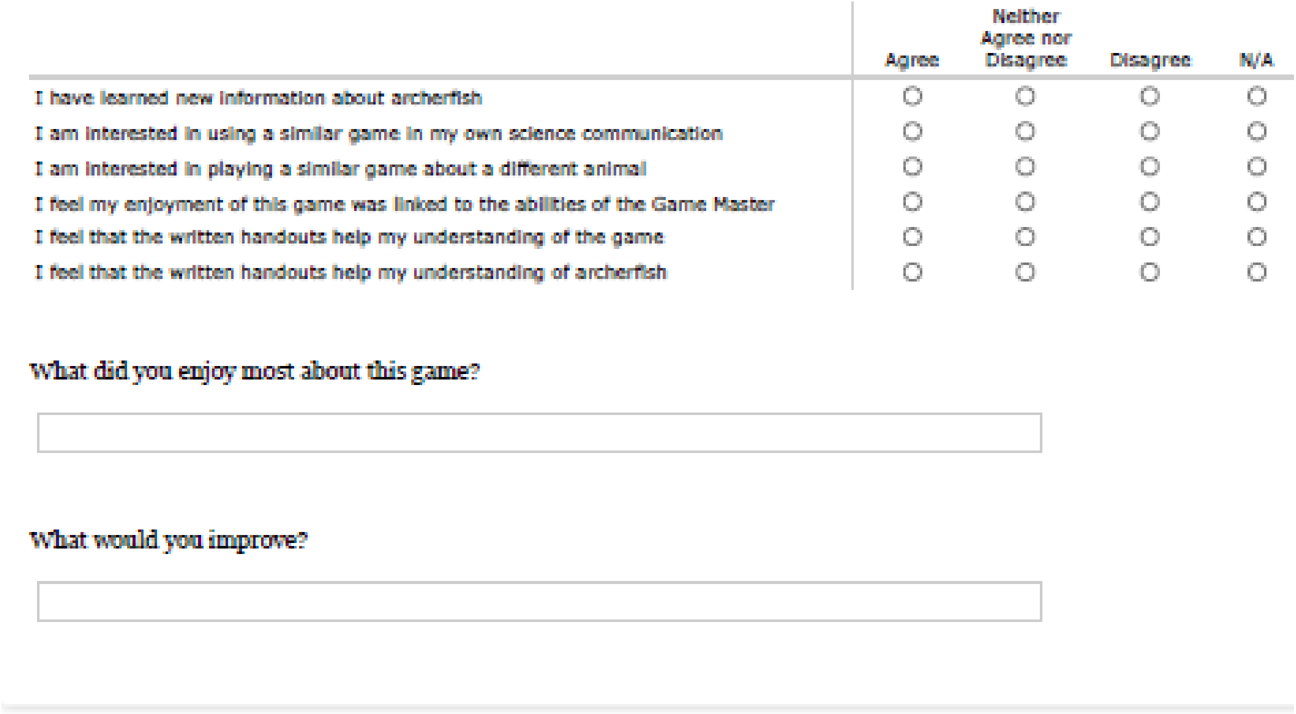
☐ Other: ________

What is your age?

____

Please select the option that best applies for the following statements:

	Agree	Neither Agree nor Disagree	Disagree	N/A
I enjoyed playing Archerfish: the TTRPG	○	○	○	○
I would play Archerfish: the TTRPG again	○	○	○	○
I feel confident that I could run a game of Archerfish: the TTRPG	○	○	○	○
I feel this is an effective manner of communicating facts about archerfish ecology	○	○	○	○



	Agree	Neither Agree nor Disagree	Disagree	N/A
I have learned new information about archerfish	○	○	○	○
I am interested in using a similar game in my own science communication	○	○	○	○
I am interested in playing a similar game about a different animal	○	○	○	○
I feel my enjoyment of this game was linked to the abilities of the Game Master	○	○	○	○
I feel that the written handouts help my understanding of the game	○	○	○	○
I feel that the written handouts help my understanding of archerfish	○	○	○	○

What did you enjoy most about this game?

What would you improve?

Appendix 4 – Recruitment materials for public engagement research

University of
St Andrews

PARTICIPANTS WANTED

Project Title

Investigating the efficacy of public engagement and science communication through table-top role-playing games.

This study is being conducted as part of my, Dagmar der Weduwen's PhD Thesis in the School of Biology at the University of St Andrews.

We invite you to participate in a research project investigating the efficacy of using table-top role-playing games (TTRPGs) for public engagement and science communication. This study will require you to play a simple, wholly original TTRPG entitled "Archerfish in Troubled Waters", in which you and other players take on the role of an archerfish in its native habitat. You will be required to overcome several challenges to solve a problem and will be guided in this by Dagmar der Weduwen. The study will also require you to take a short multiple-choice quiz to test your knowledge of archerfish before and after the game, and a brief questionnaire to gather information about the experience. At the end, you will be provided with all the instructions necessary to play the game at home.

If you are interested, please get in contact using the details below. You will then be given a Participant Information Sheet that further details my research and have the opportunity to ask questions, before being asked whether you consent to participate.

Contact Details

Researcher:	Dagmar der Weduwen, Luke Rendell (supervisor), Mike Webster (supervisor), Keith Sillar (supervisor)
Contact Details:	djdw@st-andrews.ac.uk

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