Presence of an audience and consistent inter-individual differences affect archerfish shooting behaviour

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Abstract

The social environment can play an important role in shaping the foraging behaviour of animals. In this study we investigated whether archerfish, *Toxotes jaculatrix*, display any behavioural changes in response to the presence of an audience while using their specialized foraging tactic of shooting, spitting precisely aimed jets of water, at prey targets. As any prey items shot down are potentially available to competitors, we hypothesized that shooting fish would be sensitive to the presence of potential competitors, especially given the suggestion that, in the wild, this species shows intraspecific kleptoparasitism and faces interspecific competition. We found that in the presence of another fish, archerfish took longer to shoot, made more orientations (aiming events) per shot, and tended to be closer to the target at the time of shooting. Additionally, archerfish showed high inter-individual differences in latency to shoot, and these differences were consistent across contexts, with and without an audience. Our results show that archerfish are sensitive to, and adjust their shooting behaviour in response to, the presence of an audience and highlight the importance of social context in this fish species. We also suggest that inter-individual differences may play an important role in archerfish shooting behaviour. This study highlights the importance of social effects and competition on foraging behaviour and decision making. Further work in this species could explore whether differences in competitive foraging ability are linked to sensitivity to the presence of an audience.

Keywords

archerfish; consistent individual differences; foraging; kleptoparasitism; producer–scrounger; social foraging;

Introduction

An animal’s social environment can influence its behaviour in many ways, and social effects on behaviour are frequently studied within the context of foraging. Social cues can be used by an individual to determine, for example, when, where and what to eat (Galef & Giraldeau, 2001). Rates of foraging success and related foraging efficiency at the individual level may increase with social foraging, through for example processes of social enhancement (Baird, Ryer, & Olla, 1991) or indirect benefits of social living such as reduced need for predator vigilance in groups (Lima, 1995). However, rates of foraging can also be negatively affected by the presence of others through within-group competition (Cresswell, 1997; Goss-Custard, 2002) and effects of social inhibition as observed in social hierarchies (Baker, Belcher, Deutsch, Sherman, & Thompson, 1981).

One of the more subtle ways in which social context can affect the behaviour of an individual is through the mere presence of an another individual (Zajonc, Heingartner, & Herman, 1969). In foraging contexts it is well documented that the presence of an ‘audience’ of one or more individuals can affect the behaviour and decision making of an individual forager (Giraldeau & Caraco, 2000). For example, individuals may shift from one foraging site to another to avoid competition (Alatalo, 1981). Individual foragers can suffer reduced foraging rates through what is known as indirect or passive interference competition (Cresswell, 1997; Maniscalco, Ostrand, Suryan, & Irons, 2001; Shealer & Burger, 1993), also called cryptic interference (Bijleveld, Folmer, & Piersma, 2012). This and other forms of competition are considered to be especially important in situations where behaviour may make resources publicly available to others, such as in the caching behaviour of ravens, *Corvus corax* (Heinrich & Pepper, 1998) and/or where the cost of competition can be particularly high, where competitors can engage in physical attack or where the likelihood of kleptoparasitism is high (Ward & Webster, 2016). In such competitive situations timing and positioning may be important, and it has been suggested that animals can adjust the timing of certain behaviours in ways that mitigate intraspecific foraging competition (Alanärä, Burns, & Metcalfe, 2001; Carothers & Jaksić, 1984).

Fish have been shown to actively manage the competing demands of vigilance and competition in a group (Ryer & Olla, 1996), use social information to develop more efficient foraging techniques (Reid, Seebacher, & Ward, 2010) and adjust the level of cooperative foraging (Pinto, Oates, Grutter, & Bshary, 2011). There have also been studies of kleptoparasitism and producer–scrounger systems in fish species showing that the costs and benefits of the producer and scrounger roles are affected by group size, and suggesting that individual fish may be able to use social cues to adjust their role (Hamilton & Dill, 2003). Fish in general have long been considered good laboratory models for understanding foraging competition (Ashley, Ward, Webster, & Hart, 2006) as they are typically more tractable species for experimental work than other vertebrate taxa. Archerfish offer particular benefits as an experimental fish system as they can be relatively easily trained to shoot at targets for food rewards (Newport, Wallis, & Siebeck, 2015; Schuster, 2007; Timmermans, 2000).

Archerfish, *Toxotes* spp., are a particularly interesting group in which to study social effects on foraging decisions. When foraging, archerfish spit water to down prey such as insects in vegetation overhanging the water. While their shooting ability allows them to target prey mostly unavailable to other fish, it also has the potential disadvantage of being an inherently conspicuous behaviour. It provides a clearly visible cue to competitors for the imminent arrival of food at the water's surface. When shooting at a potential prey item, archerfish tend to hold position in a stereotypical alignment, 'aiming' or orienting towards the target (Bekoff & Dorr, 1976; Timmermans & Souren, 2004) with their gaze fixated at that target (Ben-Simon, Ben-Shahar, & Segev, 2009). The orientation and posture of a hunting archerfish may therefore act as inadvertent cues, providing information about where and when a shot is likely to be made to any potential competitor. Other fish may be able to take advantage of the impending arrival of a food item such that a shooting archerfish becomes an obvious resource provider, and other fish, acting on this information, can act as scroungers or kleptoparasites. Thus, archerfish provide an example of a foraging system with inherently public resource provision in a producer–scrounger system. This, combined with the intense competition archerfish are exposed to in the wild (Rischawy, Blum, & Schuster, 2015) suggests that archerfish should be selected to pay attention to social conditions and associated competitive risk while foraging.

Many other aspects of archerfish shooting behaviour have been studied, from how they shape and control their shots, learn to hit moving targets and discriminate between targets (Dewenter, Gerullis, Hecker, & Schuster, 2017; Gerullis & Schuster, 2014; Karoubi, Leibovich, & Segev, 2017; Newport et al., 2015; Newport, Wallis, Temple, & Siebeck, 2013; Schuster, 2007; Wöhl & Schuster, 2007). However, little is known about their behavioural responses to differing social contexts. Given the potential for competition and kleptoparasitism, archerfish are likely to be sensitive to the presence of an audience and this may result in a change in their behaviour. Indeed, archerfish perform rapid but directed bursts of speed (‘c-starts’) that enable them to quickly reach downed prey, and there is some evidence that the latency to perform c-starts decreases in groups (Schlegel & Schuster, 2008). Similarly, juvenile archerfish were shown to jump more frequently for food, a tactic with lower kleptoparasitism risk, as group size increased (Davis & Dill, 2012).

While jumping may reduce the threat of kleptoparasitism, it only works for prey that are close to the water surface as archerfish are unable to jump as high as they can effectively shoot (Shih, Mendelson, & Techet, 2017). In situations where an archerfish must shoot, nearby conspecifics are likely to affect the decision making of the shooting fish. Given the importance that related factors of distance, speed and time are likely to play in competing for a shot-down prey, where scroungers may be able to get closer to the prey than the shooter in social foraging situations, we expected that orientation and distance between fish and the target may be important parameters governing shooting behaviour strategies. We aimed to determine whether latency to shoot changed when a fish was exposed to a visual audience in the form of a size-matched conspecific. We also anticipated that archerfish would react to the presence of a conspecific by changing their positioning or other aspects of their shooting behaviour. As any single foraging decision can be affected by many factors, but notably levels of satiation (Morgan, 1988; Riddell & Webster, 2017), we used a repeated measures approach, testing each fish multiple times in each experimental context.

Methods

Subjects and animal husbandry

Eight archerfish of unknown sex (archerfish are monomorphic) and age (the archerfish were wild caught) participated in this experiment. At the time of the experiment, the fish were estimated to be 8–16 months old and were 8–10 cm long. They were sourced from an accredited ornamental fish retailer. The fish were housed in the St Andrews fish laboratory as a single group in a glass tank (180 × 45 cm and 35 cm deep) and under a 12:12 h light:dark cycle, with water temperatures between 24.5 and 25 °C. Water quality parameters (pH, nitrite, ammonia and nitrate concentrations) were measured weekly, and levels were kept within a range appropriate for archerfish as per Newport et al. (2013). The fish were fed daily with an alternating mixture of commercial fish food (Tetra Cichlid Sticks) and freeze-dried bloodworms.

Experimental set-up

Three tanks of equal dimensions (55 x 55 cm and 45 cm deep) were set up side by side with a 0.5 cm gap between them (Fig. 1). A 3 mm thick black opaque plastic barrier was inserted between each tank which could be easily slid in or out to block or allow vision between tanks. These barriers were used to create three different experimental conditions (hereafter ‘treatments’, see below), by controlling the visibility of the side tanks, and thus audience fish, during trials. Each tank had an immersion heater to ensure temperatures were kept at 24.5 ± 0.5 °C and a small internal filter (Eheim 305), a 1 cm deep gravel bottom, and plastic plants positioned to provide structure and refuge but allow a clear view of neighbouring tanks. The water in all three tanks was maintained at the same level (± 1 cm).

The middle tank was used for the focal fish and had three plastic plants (to provide cover) positioned at the rear of the tank. For all trials a clear Plexiglas ‘target platform’ 10 cm wide and 54 cm long was placed (15 ± 2 cm) above the water level of the focal tank. The tanks to each side of the focal tank were designated as audience tanks; each was identical to the focal tank but the three plastic plants were positioned at the side of the tank furthest from the focal tank, to provide a clear view between tanks, and there was no target platform. A camera (ELP 2 Megapixel USB webcam) was positioned 0.7 m above the tank set-up such that all three tanks could be remotely observed from a top down perspective.

Experimental Procedure

The size of each fish was estimated at time of capture from the stock tank using a ruler while holding the fish in the net against the side of the tank. Fish were then size matched as closely as possible (differences in length no larger than 0.5 cm total length) and tested in pairs. For each pair, one fish was randomly assigned as the focal fish and the other as the audience fish. The audience fish was randomly assigned to one of the side tanks, and the two fish were transferred to the experimental tanks and left for 24 h to acclimatize before the experiment started. Audience fish were always fed with the barriers in place to ensure that the focal fish never observed them eating. The experiment consisted of two phases: training and testing. To avoid potential stress and disruption to the focal fish the audience fish remained in their respective tank throughout both training and test phases for the focal fish.

For the initial 24 h, the barriers were removed, and the focal fish was able to see both the empty tank and the tank with the conspecific (hereafter ‘audience tank’) except during feeding. Both the focal and audience fish received daily food rations after all trials for each day were complete to maximize hunger levels immediately prior to training or testing.

During the training phase each focal fish was trained to shoot a novel target (black square shape) within 3 min of presentation. This was to ensure that the fish had properly acclimatized to the tank set-up and had reliably learnt to shoot the target to gain a food reward. During training sessions, the opaque barriers were set in place, so all shooting was done without an audience. There were two training stages, each consisting of three sessions with up to 10 trials per day. Each trial consisted of an opportunity for the fish to shoot at a target placed on the Perspex platform. Trials began as soon as the target was placed on the platform and ended when a shot hit the target or after a maximum trial duration if one was imposed (see below). A food reward was delivered after each successful shot and successive trials were begun between 30 and 45 s after the previous trial had ended. Shots could easily be seen, as water jets hit the platform and left a water splash. During training, fish were only rewarded for shots where the splash hit the Perspex within 5 mm of the target. Fish were never rewarded for jumping, nor for shooting anything except the presented target.

Training stage 1

Initially, the focal fish was presented with a known food item, a large pellet, as a target on the platform for each trial. Three sessions were conducted for each fish per day. Each session lasted until the fish had successfully completed 10 trials, or for 1 h if the fish did not achieve this. Once a fish had shot at the pellet 10 times in three consecutive sessions, it was considered ready for the second training phase.

Training stage 2

The fish was presented with a novel square black plastic shape (10 × 10 mm and 2 mm thick), and once each fish had shot at this target consistently (shooting at least 10 times in a single 1 h session) a maximum trial time of 180 s was imposed. If a fish failed to shoot within the 180 s, the trial was terminated, and a new trial was begun after 30 s. Once a fish had shot the target within 180 s per trial in at least eight of 10 trials per session in three consecutive sessions in a single day, it was considered trained. After fish had achieved this second training criterion, training was continued for a further three sessions (another full day) to ensure the fish was shooting consistently, and experimental sessions were started the following day.

Trial phase

1. After achieving training criterion, each fish entered the trial phase in which experimental treatments were introduced. Here visible access to neighbouring tanks was manipulated using barriers to create one of three treatments: Baseline: both barriers were in place such that neither of the neighbouring tanks were visible to the focal fish as per training conditions.
2. No Audience control: one barrier was removed so that an empty tank was visible
3. With Audience: one barrier was removed such that the tank with a conspecific fish was visible

The baseline condition was included as well as the no audience condition to account for any potential differences in behaviour of the focal fish in response to potential distraction due to a changed environment that could occur in the no audience condition.

Each fish received 90 experimental trials, with testing run for 3 days for each fish, and three sessions per day. Each session consisted of 10 trials and was randomly assigned to a treatment, such that each subject was exposed to one session of each treatment per day. Sessions were set within consistent time periods to account for diel variation in hunger or shooting motivation. Morning sessions were begun between 0900 and 1000 hours, with a minimum of 3 h between successive sessions. Test trials lasted until a fish shot or until 360 s had elapsed without any shot being made. At no point did any of the audience fish ever attempt a shot at the target, given the position of the platform and the dimensions of the target it is unlikely they could see the target, and any shot would have been obstructed by the glass of the aquarium walls.

Measurement of variables

Each session was recorded with the video camera from above. Variables were scored during video playback using the Solomon software package (Péter, 2017), version 17.03.22. Latency (s) to shoot was recorded for each trial, where a trial started as soon as the target had been placed on the platform and ended once the fish had shot at the target (or the trial time limit was reached), with the water jet hitting the platform.

In addition to latency to shoot we recorded the frequency of orientation (aiming) events per trial and distance between target and fish at the time of each shot. This behaviour was defined and categorized based on descriptions of orientation during shooting behaviour given in previous studies (Bekoff & Dorr, 1976; Ben-Simon et al., 2009). Fish were considered to be orienting towards the target when they positioned themselves such that the target was directly ahead of them and they maintained this orientation while swimming slowly or remaining motionless for at least 2 s. The distance between the target and the fish at the time of each shot was measured as the number of body lengths apart, which was split into two categories: close, where fish shot from a position directly under or within a single body length of the target, or far, more than one body length between fish and target. Latency to shoot per trial was recorded for all eight fish in all trials; however, for one fish (fish 7) the other variables were not included in the analysis. This was due to a technical issue affecting the camera that meant that we were unable to clearly view movements of the fish in some parts of the tank, although shots hitting the shooting platform were still clearly visible and are included in the analyses for latency to shoot.

To assess the reliability of the data we extracted from the videos, 25% of the videos were rescored by a hypothesis-naïve observer. To estimate interobserver agreement an inter-rater reliability test was run to compare principal (N.J.) and secondary scorer, for the latency to shoot (irr package in R, Gamer, Lemon, Fellows, & Singh, 2012). A high interobserver agreement was found with an interclass correlation between observers of 0.98–0.99, with a mean of 0.986; $F_{139,140} = 141$, $P < 0.001$). Similarly, scores for frequency of aiming events and distance at time of shot had high interobserver agreement, with interclass correlation between observers of 0.913–0.954 (mean of 0.937; $F_{139,140} = 30.8$, $P < 0.001$) and of 0.830–0.909 (mean of 0.875; $F_{139,140} = 30.8$, $P < 0.001$), respectively.

Data Analysis

Only data from trials in which a shot was made were included in analysis, but this was the case for most of the 90 trials per fish. Those trials where the 180 s cut-off was reached were not included in the analysis as the lack of a shooting attempt could not be attributed to any single cause. However, the time limit was reached in only 8.5% of the 720 trials, and the occurrences were spread evenly across the treatments (baseline: N=16; no audience: N= 23; with audience: N = 26).

Latency to shoot

All statistical analyses were performed using R Studio 1.0.136/R version 3.2.3 (R Core Team, 2017) using a mixed model approach. Before any models were interpreted we checked that the model assumptions of normality and homoscedasticity of residuals was met, as determined by visual inspection of diagnostic plots. We set latency to shoot at a presented target (latency) as the response variable, and log transformed it to reduce skew. We then fitted a linear mixed-effects model (Bates, Mächler, Bolker, & Walker, 2015) to test whether the latency to shoot varied with treatment. Thus, treatment was a fixed factor, and as this was a repeated-measures design we included the subject identity (FishID) as a random factor to account for within-subject variation. To account for any variation that occurred across days and within days across sessions we included day and session as random factors. As trials were consecutive for each session and trial order might be expected to account for some variation in the model it was also included as a random factor. These terms were nested, specifically trial nested within session within day to account for potential correlations within sessions and days. Thus, the full model built using the 'lmer' function (in R lme4 package) was:

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lmer (logLatency~ Treatment + (1|FishID)  + (1| Day) +(1| Day:Session) + 
(1|Day:Session:Trial))
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To test for the significance of each random factor included in the model, we built a reduced model without that random factor and ran a likelihood ratio test (LRT) where we compared the full model with the reduced model using the 'anova' function in the R 'stats' package (Quinn and Keough, 2002). If these two models were not significantly different we assumed that the random effects were not important; only random factors that were significant in the model were retained. (See the Supplementary material for tables of null models.) For the main fixed effect of treatment, we ran an LRT to calculate the significance of the fixed factors. For these, and all other, models, where appropriate, we conducted post hoc pairwise comparisons using the 'lsmeans' function in the R lsmeans package (Lenth, 2016) with *P* values adjusted for multiple comparisons (Tukey method), using the default Satterthwaite method to estimate degrees of freedom. As some focal fish were used as an audience prior to being tested as a focal fish there might have been an effect of experience on latency to shoot. We included an order term in the model to account for this. We used a two-level categorical factor based on whether the focal fish been an audience member before being a focal fish or not. This term did not significantly improve model fit (Table 1) and was not included in the final model. This lack of an experience effect was not unexpected as each focal fish required significant training time and this appeared independent of experience as an audience.

Individual differences in latency to shoot

While not an initial aim of this study, the repeated-measures approach afforded us the chance to examine whether archerfish showed any consistent individual differences across experimental contexts. Consistent individual differences have been shown for many species, expressed in a variety of different measures of behaviour, and can have strong effects on speed and accuracy of foraging decisions (Wang, Brennan, Lachlan, & Chittka, 2015), and these differences may also affect or be affected by social context (Jolles, Taylor, & Manica, 2016). The training periods for the fish suggested that individuals might exhibit consistent differences in time to reach training criterion and tendency to shoot (Appendix Table A1) As such, although we had no a priori hypothesis, we attempted to quantify whether these observed tendencies to shoot at the individual level were evidence of consistent individual differences. The formal method of quantifying whether a behavioural trait is influenced by consistent inter-individual differences is to analyse the behaviour for repeatability. A behaviour is repeatable where individuals behave consistently through time and or different contexts and when individuals behave differently from each other within those contexts (Bell, Hankison, & Laskowski, 2009). To test this and assess whether the individual differences in latency to shoot are repeatable in archerfish, we compared latency to shoot across the three treatment contexts. We used the approach described by Biro et al. (2010) where a random intercept model describes the extent to which the rank order of individual scores is maintained across contexts. We compared the full model we used to quantify the effect of treatment on latency (as above), where fish identity was specified as a random effect, with a null model, where the individual identity was removed, using an LRT with the ‘anova’ function. A significant difference between the two models indicates that there are consistent differences in behaviour at the individual level across the three treatments. To explore and ensure that these differences were consistent across experimental treatments, repeatability ‘R’ was calculated as has been used in similar analysis of repeatability of behaviour (Krause, Krüger, & Schielzeth, 2017) using the ‘rptR’ package in R. This package builds on the functions developed for mixed-model analysis with the addition of parametric bootstrapping to provides reliable estimates for ‘R’ and the uncertainty surrounding these estimates (Stoffel, Nakagawa, & Schielzeth, 2017).

Orientation frequency

A generalized linear mixed model was fitted to compare the frequency of orientation events per shot across treatments. We compared the frequency of orientations between treatments using a Poisson family model. The model used was:

glmer (Orient~ Treatment + (1|FishID) + (1| Day) +(1| Day:Session) + (1|Day:Session:Trial), family ="poisson")

After fitting this model, we ran the dispersion_glmer function in the lmer package (as per Bates et al, 2015) to ensure there was no overdispersion in the model fit.

Distance from target

To investigate whether the audience had an effect on the distance between the shooting fish and target at the time of the shot we categorized the distance between fish and target as either close (within one body length) or far (fish more than one body length from the target). We used body length as the unit of measurement to standardize between fish with different lengths. To analyse these data, we fitted a mixed-effects model to estimate the probability of shooting from further than one body length (Far). The model was fitted as a binomial glmm model:

glmer (Orient~ Treatment + (1|FishID) + (1|Day) + (1|Session) +(1| Day:Session) + (1|Day:Session:Trial), family ="poisson")

Ethical Note

This research was approved by the University of St Andrews Animal Welfare and Ethics Committee (AWEC). No procedures required U.K. Home Office licensing. All tanks were enriched with gravel and plastic plants for cover. All fish were retained in the laboratory after the study period to be used in future projects. Handling was kept to a minimum, and when fish had to be moved between tanks they were caught using two large hand nets to reduce the likelihood of extended capture periods. In the experimental tanks fish were kept singly in a volume of at least 125 litres. Archerfish are not considered a social species. There are no published studies on the effects or preference for any social context and or isolation in this species, but multiple previous studies have maintained archerfish in isolation with no reported ill effects or perceived likelihood of stress. During our study we closely monitored each fish, specifically for signs of reduced feeding rate, responsiveness, stereotypic behaviour and colour changes. We observed few instances of these signs, only post transfer between tanks, and all effects were temporary.

Results

Training

All fish achieved both training criteria but required a lot of time to reach them. The number of trials required to achieve criterion differed markedly across fish (Appendix Table A1). There appeared to be a positive relationship between time to criterion and latency to shoot in baseline settings, and this may relate to a general sensitivity to risk but we did not formally quantify this given the small number of fish (Appendix Table A1).

Latency to shoot

Focal fish took longer to shoot when exposed to a visible audience than when exposed to an empty tank or when neither tank was visible (Fig. 2, Table 2). Latency to shoot was influenced by audience treatment (LRT: $\chi^2_2 = 13.642$, $P = 0.001$; Table 2). The differences in latency were due to the audience: post hoc contrasts between the treatments with and without an audience when the barrier was removed were statistically significant (lsmean: $t_{536.92} = -2.641$, $P = 0.023$). There was no statistically significant difference between the baseline and no audience treatments (lsmean: $t_{456.99} = -0.875$, $P = 0.066$).

Inter-individual differences

The fish identity term within the model accounted for up to 47% of the variance explained by the random effects, indicating that there was important variation between individual fish. Indeed, during both training and testing, individual fish displayed notable differences in latency to shoot. Across the three treatments individual repeatability 'R' in mean latency to shoot was high ($P < 0.001$; Table 3), with lower repeatability at the level of treatment. Similarly, median (Fig. 3) and mean (Table 4) latencies to shoot for each fish across all trials show that individual archerfish had relatively consistent latencies to shoot that persisted across contexts. Median latency to shoot varied between individuals by a factor of eight or more from under 10 s to over 70 s.

Orientation

Fish did not always shoot even after orienting or 'aiming' at a target, and would sometimes disengage and switch to other behaviours, or reposition before reorienting at the target. The mean number of orientation events per shot increased in the presence of an audience (LRT: $\chi^2_2 = 26.674$, $P < 0.001$; Fig.4, Table 5). There were significant differences in the frequency of orientation events between the audience and no audience conditions (lsmean: $z = -4.173$, $P < 0.001$). Fish did not show different frequencies of orientation in the baseline and no audience treatments (lsmean: $z = -0.513$, $P = 0.872$).

Distance from target

Treatment had an overall effect on where fish shot from (close/far; LRT: $\chi^2_2 = 8.614$, $P = 0.013$; Table 6), and fish were less likely to shoot from further away when there was an audience than in the no audience control (lsmean: $z = 2.873$, $P = 0.011$; Fig. 5).

Discussion

Archerfish increased their latency to shoot a target for a food reward when observed by an audience member in a neighbouring tank, which suggests that, when shooting, archerfish are sensitive to the visual presence of other fish and modify their behaviour in response to that presence. Moreover, given the change in other aspects of their behaviour when exposed to a conspecific, with the increase in mean number of aiming events per trial and the tendency to make fewer shots from further distances from the target, our results are consistent with archerfish modifying their behaviour to reduce the potential risk of kleptoparasitism. This interpretation is especially likely given that Davis and Dill (2012) observed behavioural changes in the context of high kleptoparasitism rates in groups of juvenile archerfish. Being aware of, monitoring and reacting to potential competitors with behavioural tactics to reduce the chances of kleptoparasitism have been reported for a variety of animals with some classic examples from corvids (Heinrich & Pepper, 1998) and kelp gulls, *Larus dominicanus* (Hockey & Steele, 1990). Although the actual time difference between treatments was small it was functionally significant given how fast archerfish make foraging decisions when shooting and intercepting prey, with fish capable of making complex decisions in as little as 0.04s (Schlegel & Schuster, 2008). Even small increases in latency can be important in such systems.

Foraging events with long handling times can lead to higher rates of kleptoparasitism (Steele & Hockey, 1995). Given that shooting represents an investment of time in a specific prey item akin to handling time, it may be expected that archerfish would attempt to reduce kleptoparasitism by shooting more quickly, reducing this ‘handling’ time, when exposed to a potential competitor. Our results fit the theory that in systems where there is very aggressive competition and/or high rates of kleptoparasitism, animals will attempt to avoid or mitigate such competition. The change in position and the increased frequency of orientation events we describe may represent such avoidance techniques, similar to the evasive behaviour when caching displayed by grey squirrels, *Sciurus carolinensis* (Leaver, Hopewell, Caldwell, & Mallarky, 2007), ravens (Heinrich & Pepper, 1998) and blue gouramis, *Trichopodus trichopterus* (Hollis, Langworthy-Lam, Blouin, & Romano, 2004). Our results may also be partly due to the conditions of the experiment: with a consistent food cue a single audience member may represent a ‘manageable’ threat, so positioning and timing are enough to reduce the threat of kleptoparasitism. It is likely that archerfish would respond differently if less predictable food cues were used and/or if there was more than one potential competitor. Animals that forage in groups may experience multiple types of interspecific competition. Broadly, three types of competition are possible: interference, scramble and contest (Ward et al., 2006). A single competitor may represent a form of interference competition which, as shown in studies of blackbirds, *Turdus merula*, suggests competitive foraging can reduce foraging efficiency (Cresswell, 1997). Even in systems where direct kleptoparasitism is low, interference competition, such as that observed in blackbirds, can have a powerful effect on foraging behaviour, reducing foraging efficiency, as monitoring of intraspecific competitors may reduce any benefits, at the individual level, of group foraging (Cresswell, 1997). Our results underline the importance of interference competition, where the threat of kleptoparasitism acts as a powerful driver of behaviour.

While not the primary aim of this study, our results also suggest that individual differences may play a role in responses to an audience. Such individual differences are a central and active field of research (Bell et al., 2009; Dall, Bell, Bolnick, & Ratnieks, 2012; Magurran, 1986; Réale, Reader, Sol, McDougall, & Dingemanse, 2007). They can play a major role in numerous aspects of animal behaviour including collective behaviour (Jolles, Boogert, Sridhar, Couzin, & Manica, 2017) and foraging performance (Bergvall, Schäpers, Kjellander, & Weiss, 2011). Individual behavioural differences can often be correlated with different strategies of coping with risk; for example, more ‘proactive’ animals show less sensitivity to risk (Ioannou & Dall, 2016), including levels of competition risk. Archerfish shooting behaviour is inherently risky, with the threats of kleptoparasitism and predation, as the fish may be exposed to both aerial and aquatic predators while positioning and aiming their shots. Although somewhat speculative at this point, given the individual differences observed in our study, archerfish may have different sensitivities to competition at the individual level and this may result in different levels of response to the presence of others; however, this will need to be examined by further studies specifically designed to test this effect.

Measured individual differences in behaviour may also be attributed to ecological niches within a population, size or developmental differences. Studies of similar producer–scrounger systems with intense competition have shown that individual differences can play a role in the development and use of foraging tactics such as kleptoparasitism and related scrounging behaviours (Beauchamp, 2001; Morand-Ferron, Giraldeau, & Lefebvre, 2007). At the ecological level there is some interest in the interconnected effects of individual differences and foraging ecology (Bolnick et al., 2003; Toscano, Gownaris, Heerhartz, & Monaco, 2016). Theoretical work has explored the effects of different roles in a producer–scrounger game, specifically categorizing some individuals as more or less resistant to kleptoparasitism (Grundman, Komárková, & Rychtář, 2009). Empirical work has shown that individual differences can affect competitive foraging behaviour and competitive ability in a number of ways, for example dietary wariness (McMahon, Conboy, O’Byrne-White, Thomas, & Marples, 2014) or foraging decisions (Toscano et al., 2016). Given the individual consistencies we have shown in latency to shoot in the presence of an audience, we expect that further work on this system may contribute to the understanding of the connections between individual differences, sensitivity to social context and ecological roles or foraging tactics employed within producer–scrounger systems.

Further studies on social context on archerfish shooting behaviour are likely to reveal different social factors that affect shooting behaviour and responses to the presence of others. Dominance and social rank can have a large impact on the use of alternative foraging tactics and may also be related to individual differences and shape the competitive effects on behaviour (Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014). While there are no direct studies of dominance in archerfish, it has been described in captivity (Davis & Dill, 2012) and dominance and social hierarchies can have strong effects on kleptoparasitic systems (Baker et al., 1981; Barta & Giraldeau, 1998; Hollis, Langworthy-Lam, Blouin, & Romano, 2004b; LeSchack & Hepp, 1995). Similarly, the number, size and density of competitors are likely to strongly impact behaviours of a shooting fish. Density is known to affect animal behaviour in competitive contests and has been shown to affect food resource defence and competition in fish species such as the swordtail, *Xiphophorus* sp. (Kaiser et al., 2013). More subtle factors may also be worthy of investigation; for example, levels of familiarity may also affect rates of kleptoparasitism (Webster & Hart, 2007).

Overall, our results add to the body of evidence showing that animals can be sensitive to their social environment when making foraging decisions and respond in a manner that presumably increases their individual success. We have shown that archerfish are sensitive to, and respond to, an audience while foraging. Our results also suggest that there may be consistent individual differences in levels of sensitivity to, or strategies to cope with, an audience in archerfish. This needs to be confirmed with studies specifically designed to test this effect. Such studies could also examine the effects of dominance hierarchies on inter-individual differences in archerfish shooting behaviour.

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Appendix

Training criterion data

See table A1. For the training trials required to achieve criterion for each fish.

Tables

Table 1. Results from the likelihood ratio test for effect of test order on the model fit

	df	AIC	BIC	LogLik	Deviance	χ^2_1	*P*
Without order term	8	2163.2	2199.2	1073.6	2147.2		
With order term	9	2163.9	2204.4	1072.9	2145.9	1.334	0.248

The order term relates to whether the fish was an audience or focal fish first. AIC: Akaike information criterion; BIC: Bayesian information criterion.

Table 2. Summary of results for the mixed-model analyses of latency to shoot

		Estimate	SE
Fixed effects	(Intercept)	2.409	0.418
	Treatment no audience	0.102	0.117
	Treatment with audience	0.408	0.114
Random effects	Day*Session*Trial	0.063	0.251
	Day*Session	0.037	0.193
	FishID	1.291	1.137
	Day	0.009	0.096
	Residual	1.336	1.156

Table 3. Summary of results for the repeatability ‘R’ analyses in latency to shoot, using 1000 bootstraps

Grouping variable	R	SE	Lower CI	Upper CI
FishID	0.467	0.136	0.163	0.675
Treatment	0.011	0.007	0.003	0.03

CI: confidence interval.

Table 4. Mean and SD latency to shoot per fish per treatment

	Baseline		No audience		With audience	
FishID	Mean	SD	Mean	SD	Mean	SD
1	2.03	0.38	4.23	1.42	13.57	5.05
2	7.73	1.1	8.63	1.40	7.8	1.38
3	23.9	6.4	15.37	3.83	85.1	14.0
4	127.4	22.47	259.2	23.02	172.13	26.11
5	60.03	9.45	71.43	9.58	87.03	14.46
6	48.67	15.28	54.17	14.49	175.5	26.92
7	13.17	3.29	6.67	1.32	15.37	7.63
8	19.55	4.43	35.7	7.80	34.4	6.19

Table 5. Summary of results for the mixed-model analyses of frequency of orientation per trial

		Estimate	SE
Fixed effects	(Intercept)	0.685	0.163
	Treatment no audience	0.037	0.075
	Treatment with audience	0.33	0.071
Random effects	Day*Session*Trial	0.001	
	Day*Session	0.001	
	Session	0.005	
	FishID	0.167	
	Day	0.001	

Table 6. Summary of results for the mixed-model analyses of distance at time of shot

		Estimate	SE
Fixed effects	(Intercept)	-0.486	0.357
	Treatment no audience	0.381	0.249
	Treatment with audience	-0.371	0.275
Random effects	Day*Session*Trial	0.318	
	Day*Session	0.0001	
	Session	0.14	
	FishID	0.767	
	Day	0.027	

Table A1. Number of training trials required to achieve criterion for each fish and respective median latency to shoot in the baseline treatment

	Number of trials to achieve training milestones			
Fish	Trials to criterion 1	Trials to criterion 2	Total	Median latency
1	91	130	221	1.0
2	60	107	167	6.0
3	160	125	287	9.0
4	603	250	853	56
6	200	517	717	40
7	54	80	134	7.0
5	250	350	600	8.0
8	100	110	200	14.0

Also see Table 4, which presents mean values.

Figures

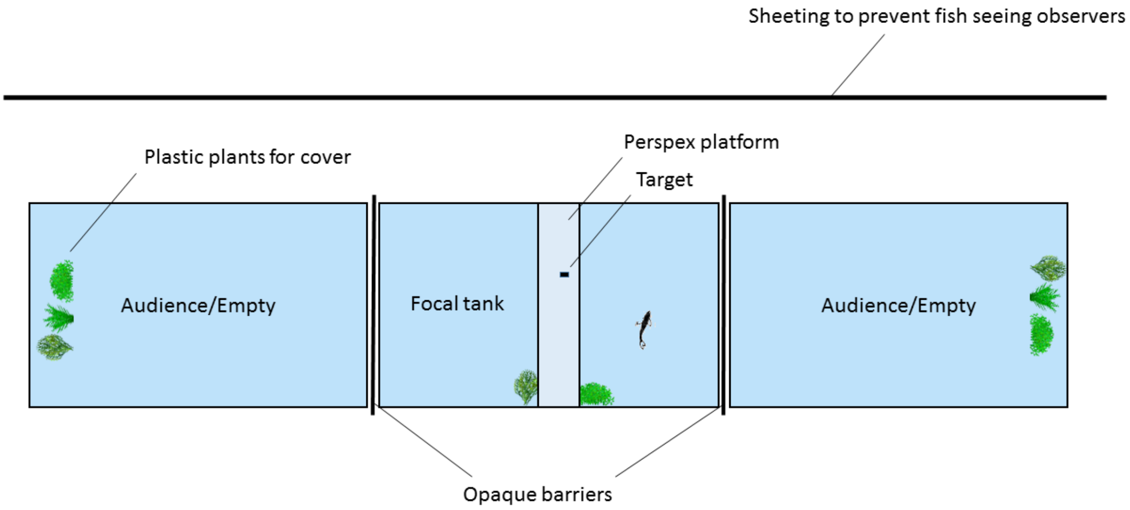

Figure 1. Experimental set-up, top down view, as recorded by the camera above the tank. The focal fish ($N = 8$) was always tested in the middle tank; the side tanks were randomly assigned to house either an audience fish (with audience) or remain empty (no audience) for each focal fish (see Supplementary material for video of a trial).

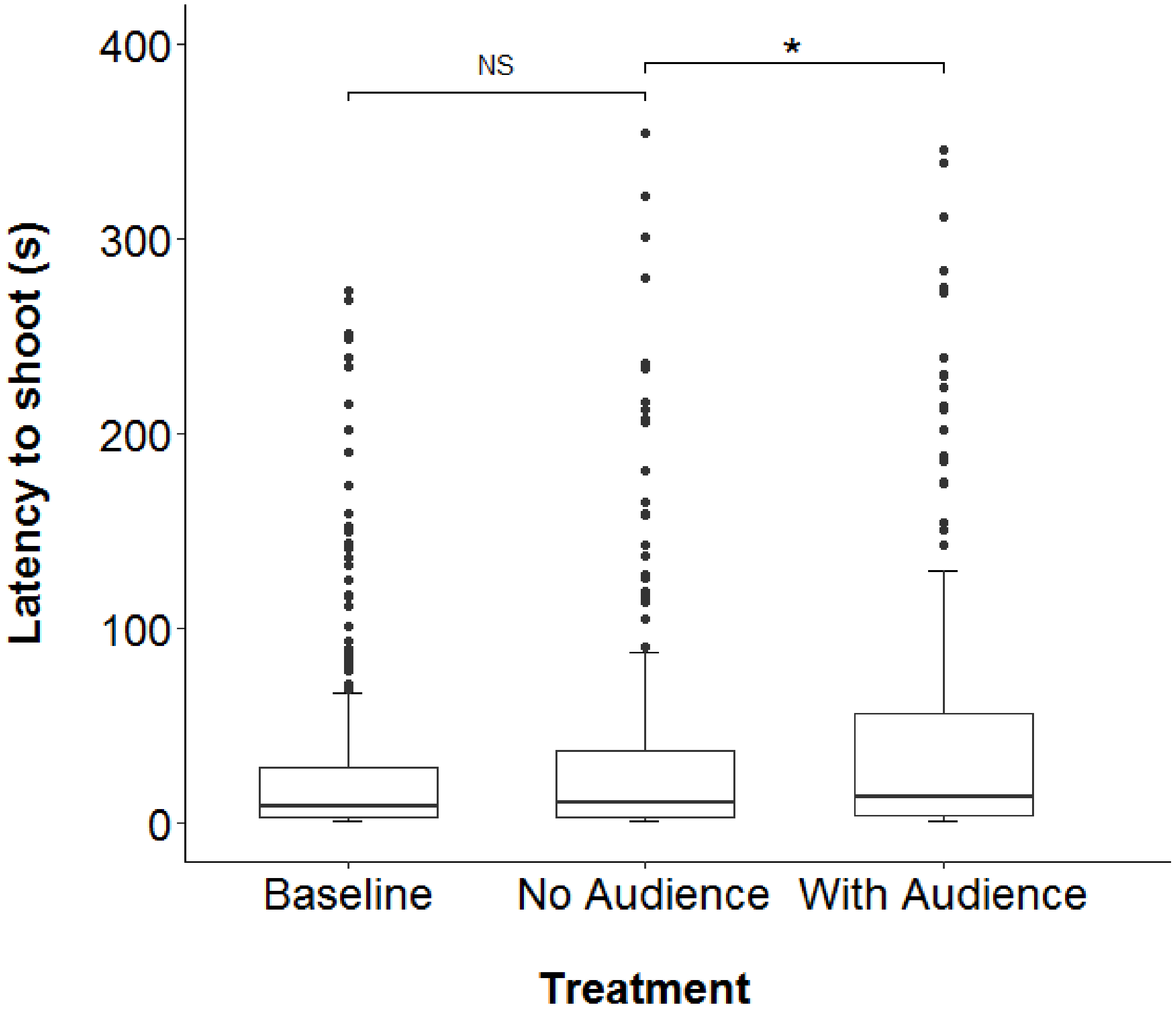

Figure 2. Latency to shoot for focal fish with three levels of conspecific audience as per experimental treatment ($N = 8$). The box plots show the median, 25th and 75th percentiles, and the whiskers extend to the data point that is no more than 1.5 times the length of the box as per the Tukey method (R package ggplot2). Points represent values outside of these limits. *$P<0.05$; post hoc multiple pairwise comparisons (with Tukey adjustment).

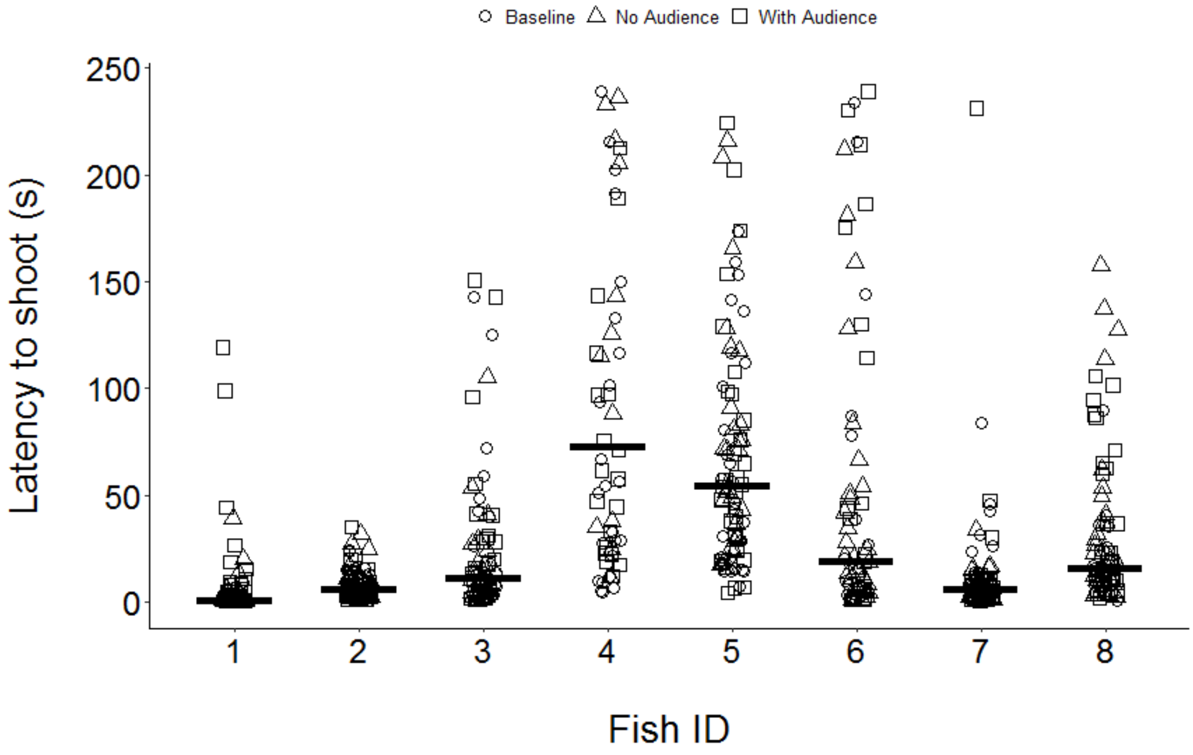

Figure 3. Repeatability of latency to shoot with observed latencies for each fish in each of the treatments (shown as differently shaped points). Median latency to shoot across all treatments (horizontal bars) is also included for each fish.

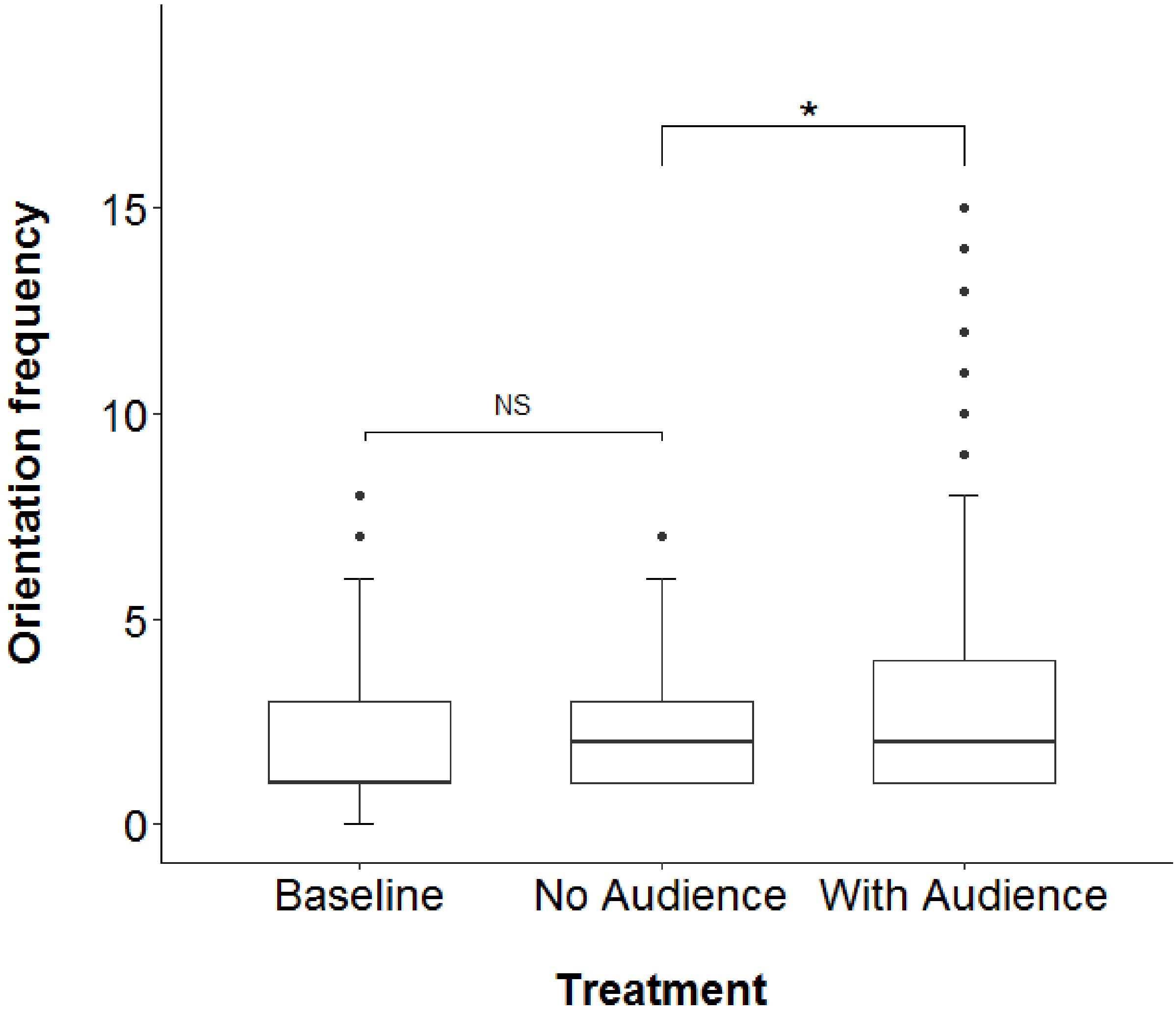

Figure.4. Frequency of orientation (aiming) events made per shot for all focal fish across the three treatments ($N = 7$). The box plots show the median, 25th and 75th percentiles, and the whiskers extend to the data point that is no more than 1.5 times the length of the box as per the Tukey method (R package ggplot2). Points represent values outside of these limits. $*P<0.05$; post hoc multiple pairwise comparisons (with Tukey adjustment).

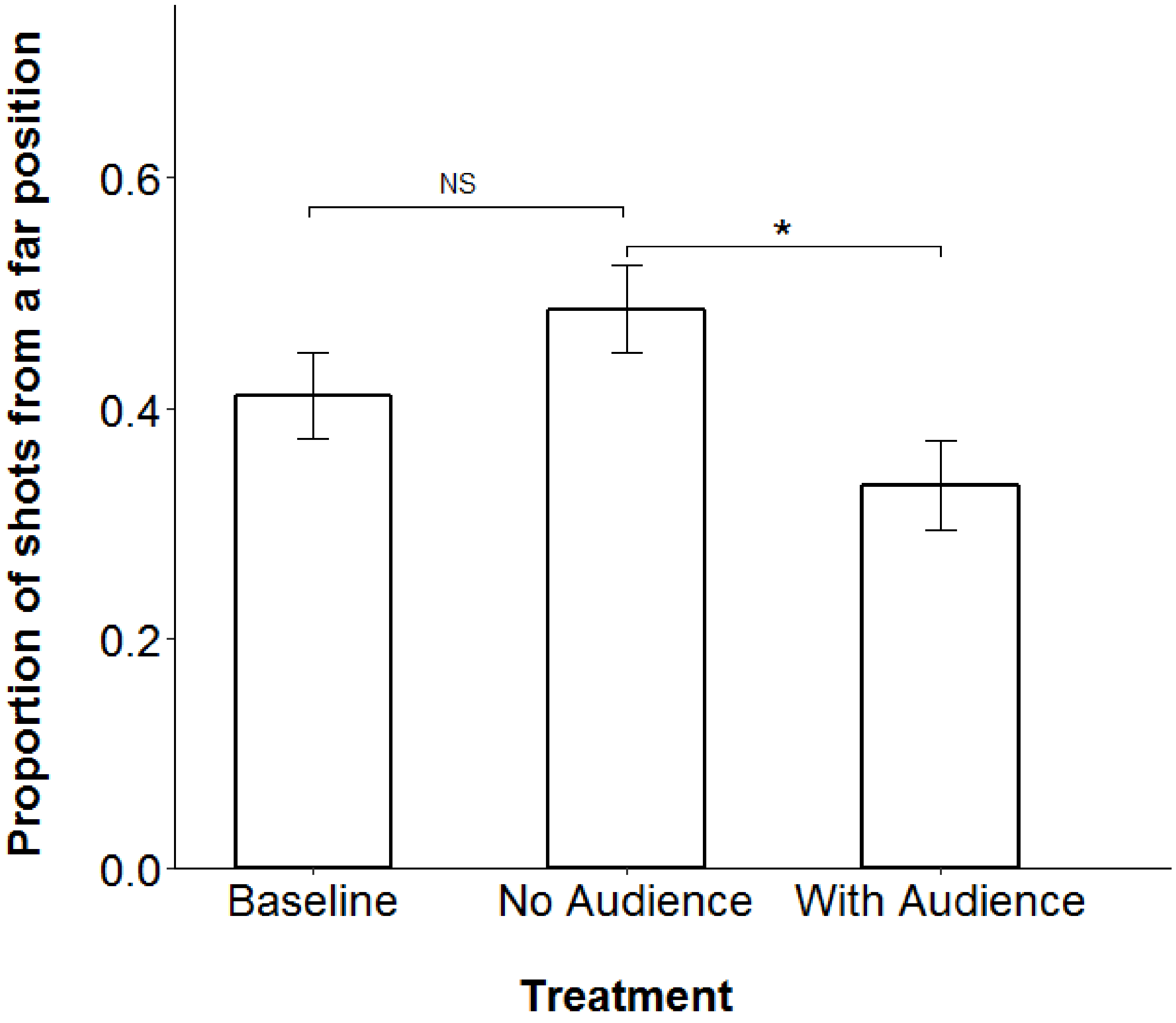

Figure.5. Mean (± SE) proportion of shots made from distances categorized as ‘far’ in each treatment (i.e. when the focal fish was more than one body length from the target). **P*<0.05; post hoc multiple pairwise comparisons (with Tukey adjustment).

Supplementary material

S.1 A video file of a trial is included.

S. 2 Data will be uploaded on Dryad after acceptance (they require publication before submission).

S. 3 Additional analysis details

Below is a list of the alternate null models for the analysis of latency data, these models differed according to the inclusion of different random variables and a comparison was run to ensure the selected model included the appropriate random variables see Table S.1 for comparison of anova comparison.

Table S. 1. Comparison of alternate null models for the analysis of latency data

Model	DF	AIC	BIC	LogLik	deviance	χ^2	Df	P
Ha1	8	2516	2552	-1250.9	2500			
Ha2	8	2162.8	2198.8	-1073.4	2146.8	353.126	0	0
Ha3	8	2162.8	2198.8	-1073.4	2146.8	0.005	0	0
Ha4	8	2166.3	2202.3	-1075.1	2150.3	0	0	1
Ha	9	2164.8	2205.3	-1073.4	2146.8	3.433	1	0.064

Similarly we have included a list of alternate models that were considered and compared for the analysis of orientation frequency and output from an anova comparison see Table S. 2.

```
null1 =glmer(Orient~  (1|FishID)  + (1| Day) + (1| Day:Session) + (1|Day:Session:Trial), data = PosData, family ="poisson")

null2 =glmer(Orient~  (1|FishID) +  (1|Session) +(1| Day:Session) + (1|Day:Session:Trial), data = PosData, family ="poisson")

null3 =glmer(Orient~  (1|FishID) +(1| Day) + (1|Session)  + (1|Day:Session:Trial), data = PosData, family ="poisson")

null4 =glmer(Orient~  (1|FishID) +(1| Day) + (1|Session) +(1| Day:Session) , data = PosData, family ="poisson")
```

Table S. 2. Comparison of alternate null models for the analysis of orientation frequency per shot

Model	DF	AIC	BIC	LogLik	deviance	χ^2	Df	P
null1	5	2048.4	2070.2	-1019.2	2038.4			
null2	5	2047.8	2069.6	-1018.9	2037.8	0.599	0	0
null3	5	2047.8	2069.6	-1018.9	2037.8	0	0	1
null4	5	2051.5	2073.3	-1020.7	2041.5	0	0	1
mod1	8	2027.2	2062	-1005.6	2011.2	30.334	3	0

List of null models, with different random variables excluded, that we considered for analysis of distance from target at time of shot. Table S.3 shows output of the anova comparison.

```
3.null = glmer(Far~ Treatment + (1|FishID) +  (1|Session)  +(1| Day:Session) +
(1|Day:Session:Trial) , data=PosData,family="binomial")

4.null = glmer(Far~  Treatment +(1|FishID) +  (1|Session) + (1| Day) +(1| Day:Session)  ,
data=PosData,family="binomial")

5.null = glmer(Far~ Treatment + (1|FishID)  + (1| Day) +(1| Day:Session) +
(1|Day:Session:Trial) , data=PosData,family="binomial")

6.null = glmer(Far~ Treatment + (1|FishID)  + (1|Session) + (1| Day) +
(1|Day:Session:Trial) , data=PosData,family="binomial")

7.null = glmer(Far~ Treatment + (1|FishID)   +(1| Day:Session) + (1|Day:Session:Trial) ,
data=PosData,family="binomial")
```

Table S. 3. Comparison of alternate null models for the analysis of distance from target at time of shot

Model	DF	AIC	BIC	LogLik	deviance	χ^2	Df	P
7null	6	624.12	649.35	-306.06	612.12			
6null	7	626.1	655.35	-306.05	612.1	0.022	1	0.882
3null	7	626.1	655.35	-306.05	612.1	0	0	1
4null	7	626.55	655.98	-306.28	612.55	0	0	1
5null	7	626.12	655.55	-306.06	612.12	0.43	0	0

Table S.4. Full output from repeatability estimate via bootstrap in Rptr

```
Repeatability estimation using the lmm method
Call = rpt(formula = logLatency ~ Treatment + (1 | FishID) + (1 | Day) + (1 | Day:Session) +
(1 | Day:Session:Trial), grname = c("FishID", "Fixed"), data = data1, datatype = "Gaussian",
nboot = 1000, npermut = 0, adjusted = FALSE)

Data: 665 observations
----------------------------------------
FishID (8 groups)
Repeatability estimation overview:
      R     SE   2.5%  97.5% P_permut  LRT_P
  0.467  0.136  0.163  0.675       NA      0

Bootstrapping and Permutation test:
            N   Mean Median   2.5%  97.5%
boot     1000  0.441  0.446  0.163  0.675
permut      1     NA     NA     NA     NA
Likelihood ratio test:
logLik full model = -1076.22
logLik red. model = -1252.916
D  = 353, df = 1, P = 3.87e-79
----------------------------------------
```