



Presence of an audience and consistent interindividual differences affect archerfish shooting behaviour

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ARTICLE INFO

Article history:

Received 7 December 2017

Initial acceptance 2 February 2018

Final acceptance 9 April 2018

MS. number: 17-00965R

Keywords:

archerfish
consistent individual differences
foraging
kleptoparasitism
producer–scrounger
social foraging

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 interindividual 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 interindividual 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.

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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

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ways that mitigate intraspecific foraging competition (Alanärä, Burns, & Metcalfe, 2001; Carothers & Jakić, 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 (A. 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 × 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

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