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One shot, one kill: the forces delivered by archer fish shots to distant targets

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ABSTRACT

Archer fishes are skillful hunters of terrestrial prey, firing jets of water that dislodge insects perched on overhead vegetation. In the current investigation, we sought an answer to the question: are distant targets impractical foraging choices? Targets far from the shooter might not be hit with sufficient force to cause them to fall. However, observations from other investigators show that archer fish fire streams of water that travel in a non-ballistic fashion, which is thought to keep on-target forces high, even to targets that are several body lengths distant from the fish. We presented targets at different distances and investigated three aspects of foraging behavior: (i) on-target forces, (ii) shot velocity, (iii) a two-target choice assay to determine if fish would show any preference for downing closer targets or more distant targets. In general, shots from our fish (*Toxotes chatareus*) showed a mild decrease (less than 15% on average) in on-target forces at our most distant target offered (5.8 body lengths) with respect to the closest target offered (2.3 body lengths). One individual in our investigation showed slightly, but significantly, greater on-target forces as target distance increased. Forces on the furthest targets offered were found to double that of attachment forces for 200 mg insects, even for individuals whose on-target forces showed mild decreases with increases in target distance. High-speed video analysis of jet impact with the target revealed that the shot was traveling in a non-ballistic manner, even to our most distant target offered, corroborating previous suppositions that on-target forces should remain high. Fish were able to accomplish this without large changes to shot velocity, but we did find evidence that the water jets appeared to differ in the timing of their acceleration as target distance increased. Our two-target choice experiment revealed that fish show preference for downing the closer target first, even though impact forces on distant targets only showed mild decreases. Our overall findings (and the findings of others) suggest that archer fish modulate many aspects of their shooting behavior: from target selection to active control over the water jet that allows the fish to deliver reliably forceful impacts to prey over a wide range of distances.

1. Introduction

Archer fishes (Toxotidae) are a small family of perciform fishes that inhabit the mangroves of southeast Asia and northern Australia (Lüling, 1963; Schuster, 2007). Archer fishes forage using an unusual tactic: upon spotting terrestrial prey (typically small insects, such as ants; Simon et al., 2009) on overhead foliage, the fish spits a stream of water from its mouth that can dislodge the prey, causing it to fall onto the surface of the water. When the fish is preparing to spit, the long axis of the body is rotated vertically, so that the snout protrudes above the surface of the water, while the eyes of the fish remain beneath the surface (Lüling, 1963; Bekoff and Dorr, 1976; Dill, 1977; Timmermans and Souren, 2004). The stream of water is propelled from the mouth by the actions of the adductor operculi and the geniohyoideus muscles (Elshoud and Koomen, 1985), which adduct the gill covers and the floor of the mouth, respectively, compressing the buccal cavity. Sniped prey are then grabbed at the water surface and consumed.

The task of aiming at and hitting an aerial target while submerged is complicated by the fact that a target above the water, when viewed from beneath the surface, appears to be in a different location than it actually is, due to the change in refractive index as light moves through the air–water interface (Dill, 1977). The discrepancy between where the target is actually located and where it appears to be depends in part on target height; the critically important correct calculation of the distance to the target is thought to be dependent on torsion of the eyes in the orbit as the fish rotates its body vertically (Lüling, 1963; Dill, 1977; Timmermans and Souren,

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2004), which keeps the prey image focused on an area in the ventro-temporal region of the retina with high spatial resolution (Temple et al., 2010). When the intended prey item is struck by a shot from an archer fish and falls, the fish can accurately predict where it will land, using the height of the target, the target speed, and direction of movement, all of which are obtained during the first 100 ms of free fall (Rossel et al., 2002). Information about target height is clearly important in several aspects of archer fish foraging; however, the relationship between impact forces and target distance has not been explored. Therefore, the focus of the current investigation examines the relationship between target height and impact force.

In their natural habitat, archer fish are expected to encounter terrestrial targets at a variety of distances above the water, due to the structural complexity of overhead vegetation. Early investigations into the spitting behavior of archer fish postulated that the water stream would only be effective if prey were within a few centimeters of the water surface (Lüling, 1963). However, it has been documented that the stream of water is capable of traveling at least 15 body lengths (BL) away from the fish firing the shot (Elshoud and Koomen, 1985); field observations have found that the fish is capable of striking targets as far away as 2 m (Gerullis and Schuster, 2014), equivalent to approximately 13 BL for a large archer fish. The fact that the jet of water is capable of traveling considerable distances from the fish prompted the question: how forceful is the fired stream on a distant target? If the water jet fired by the fish is assumed to be ballistic, gravitational acceleration would convert the upward kinetic energy of the shot into potential energy, given by the following equation:

$$\text{total energy} = \frac{1}{2}mv^2 + mgh, \quad (1)$$

(where m = shot mass, v = shot velocity, g = gravitational acceleration, and h = target height) and the shot would slow down as it approaches the apex of its flight. Because the acceleration of the water stream imparted by the fish would be progressively countered by gravity as the stream travels, on-target forces would be expected to show an inverse relationship with target distance: high forces for targets in close proximity, lower forces for distant targets. Using empirical values of shot volume (0.1 ml, mass = 0.1 g for pure water) and shot velocity (3.5–4.5 m/s) from a 67 mm standard length (SL) *Toxotes jaculatrix* (from Vailati et al., 2012), we find that under the assumption of a ballistic projectile, the kinetic energy of the shot decreases between 12 and 24% for each increase in target height of 0.1 m. This would suggest that distant targets are not very practical foraging choices, especially for smaller individuals.

However, the jets of water fired by archer fish behave much differently than simple ballistic projectiles. The power of the shot is amplified by a mechanism external to the fish, but intrinsic to the properties of how a pulsed jet (i.e., a jet fired from an archer fish) travels (Vailati et al., 2012). When the stream is fired, the "tail" of the stream (the water that leaves the mouth aperture last) has a higher velocity than the "head" end of the stream (the water that left the mouth aperture first), which causes the axial length of the stream to become shorter as it travels, and expands the radius of the rounded "head" of the stream (Vailati et al., 2012). As long as the jet remains intact, this expansion is the result of the transfer of the mass, velocity, and momentum from the "tail" to the "head" (Vailati et al., 2012; Gerullis and Schuster, 2014) resulting in a non-ballistic phase for the jet. The widening of the head of the jet, combined with the effects of surface tension on the stream itself, which favors a jet with as little surface as possible, contributes to the destabilization of the stream (termed Rayleigh–Plateau instabilities) to a point where it will eventually fragment into small droplets (Vailati et al., 2012). The motion of each droplet (including the large rounded "head") after the stream has broken up could then be treated as ballistic. The non-ballistic phase of the jet is particularly important: streams only composed of small droplets or elongated intact streams would not be very effective at transferring energy to a target, because both scenarios result in long momentum transfer times to the target (Vailati et al., 2012). A more effective projectile would be a single, large projectile that transfers its momentum to the target in a short amount of time, which is what the gathering of water at the "head" of the stream accomplishes. This gathering of the projectile is the amplification mechanism alluded to earlier, and as a result, on-target power is nearly six times greater than the maximum power known to be produced by skeletal muscles accelerating that projectile (Vailati et al., 2012). In their study, Vailati et al. (2012) investigated jet formation for jets directed at targets less than two body lengths distant from the fish (where SL = 67 mm), which is in relatively close proximity to this smaller individual of *T. jaculatrix*. This still leaves the question of whether the jet is effective when directed at more distant targets. Building upon the findings of Vailati et al. (2012), Gerullis and Schuster (2014) have more recently found that large individuals of *T. jaculatrix* (SL 130–140 mm) are capable of controlling the stability (that is, controlling the non-ballistic merging phase) of the jet over a range of target distances (0.2–0.6 m, relative distance 1.5–4.5 BL). Their data show that the jet of water completes its merging at the "head" of the stream just moments before contact with the target (Gerullis and Schuster, 2014), even when the target is located at a variety of distances from the fish. The fish (specifically *T. jaculatrix*) appears to modulate the velocity of the water within different parts of the jet with respect to target distance: the fish can control the difference between the speed of the water released first (the "head" of the jet) and the speed of the water released last (the "tail"; see Gerullis and Schuster, 2014). This changes the velocity profile of the tip of the jet over time. Fine tuning of water velocity within the jet, along with other factors (such as controlling the duration of mouth opening and closing during spitting), appears to contribute to the overall stability of the jet when target distance is variable (Gerullis and Schuster, 2014). Although animal length, target distance, and shot velocity (Vailati et al., 2012 = 4 m/s, Gerullis and Schuster, 2014 = 6 m/s) were quite different in the two studies, some generalizations from the observations of both Vailati et al. (2012) and Gerullis and Schuster (2014) can be made. Taken together, their findings suggest that distant targets are practical foraging choices. The non-ballistic phase of jet travel allows mass and momentum to build up in the "head" end of the stream over time during its travel to the intended target, and the timing of the buildup of mass and momentum at the "head" of the jet is matched to target distance. The fish does not simply spit a small, rounded, ballistic projectile.

The primary goal of our investigation was to determine how target distance and impact forces are related. We developed two competing hypotheses. From the findings of Vailati et al. (2012) and Gerullis and Schuster (2014), we predicted (hypothesis 1): on-target forces would be consistent across a variety of target distances. This would be a result of the control by the fish of the non-ballistic phase of jet travel across all target distances presented, so that jets would be equally merged (and presumably, deliver equivalent on-target force), no matter the distance. Alternatively, it could be possible that the on-target forces would show a pattern predicted for the kinetic energy of ballistic projectiles (hypothesis 2): high impact forces for proximal targets, low impact forces for distant targets, especially if the jet merged early on, then fragmented, with a single large droplet or droplets then traveling in a ballistic manner. To test these ideas, we measured on-target forces delivered by 85–90 mm SL individuals of *Toxotes chatareus* and imaged the impact of the stream with the target using high-speed video.

We also used high-speed video to record the jet of water as it left the mouth of the fish. We wanted to determine if *T. chatareus*