

Refraction and the Spitting Behavior of the Archerfish (*Toxotes chatareus*)

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Summary. 1. Archerfish (*Toxotes chatareus*) spit droplets of water at aerial insect prey, knocking them onto the water surface to be eaten. Since the fish's eyes remain completely below the water surface during sighting and spitting the fish must deal with potentially severe refraction effects at the air-water interface. High speed (200 f.p.s.) motion picture films of 480 spitting sequences were analyzed to determine the magnitude of the refraction effect and to suggest how the fish compensate for it.

2. *T. chatareus* do not shoot from a position directly below the prey, but can correctly set their spitting angle to compensate for the refraction unique to a variety of positions (Fig. 6). The fish can correct (Fig. 14) for large refraction effects on the prey's apparent elevation (Fig. 12) or apparent height (Fig. 13). They may be enabled to do so by a rather precise linear relationship between the real elevation of the prey from the nose and the apparent elevation from the eye which exists during sighting (Fig. 15) and spitting. However, spitting accuracy decreases with increasing prey height (Fig. 7) or range (Fig. 8).

3. The archerfish must also correct for significant curvature of the water droplet's trajectory (Fig. 10). Since shot velocity is relatively constant (Fig. 9) the fish must make this correction via their spitting angle, but the stage in the spitting process at which this occurs is unknown.

Introduction

The archerfish are a family (Toxotidae) of freshwater fish who have the ability to spit water droplets at aerial insects (either on the wing or resting on surfaces above the water), knocking them onto the water surface to be eaten. Since the eye of the fish remains entirely below the surface during positioning and shooting, the archerfish has a potentially serious optical problem which it must correct for, i.e., refraction at the air-water interface.

When a ray of light from the prey strikes the water surface, it is bent

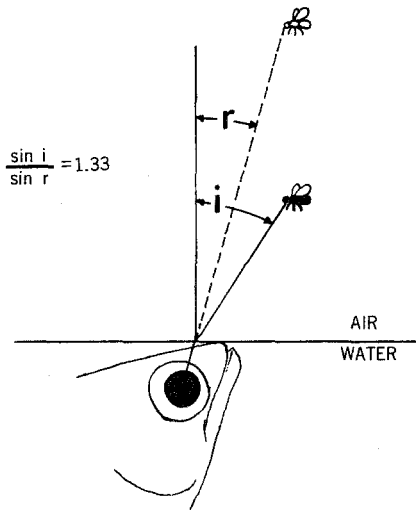


Fig. 1. Refraction at the air-water interface. The incident ray is bent and the fly appears along the projection of the refracted ray, above its true position. The angles of incidence (i) and of refraction (r) are related according to Snell's law

from its original line of travel in accordance with Snell's Law. The sine of the incident ray divided by the sine of the refracted ray equals 1.33, the refractive index of (pure) water (Fig. 1). The prey will appear to be somewhere along the projection of the refracted ray, i.e., somewhat higher than it actually is. How much higher will depend upon the size of the angle of incidence, which depends in turn upon the height of the prey, the distance between the eye and the prey in the horizontal plane and, to a small extent, the depth of the eye below the water surface. It is less easy to state at what distance along this line the prey will be seen by the archerfish. If the incident rays are thought of as a pencil, the refracted pencil will be astigmatic. Different parts of the prey will be focused at different distances from the eye (Jenkins and White, 1950). Unless the fish's eye is constructed in such a way as to correct for this astigmatism, then the entire prey will not be in clear focus and parts of it will appear fuzzy. In what follows, it is assumed for convenience that the prey appears to be exactly above its true position. The error introduced by this assumption to the calculation of the distance from the eye to the apparent position of the prey will nowhere exceed 5% (Leigh Palmer, pers. comm.). A somewhat smaller error will be introduced to the calculation of apparent elevation.

Lüling (1963) reported that the archerfish *Toxotes jaculatrix* shot from a position almost directly below its prey, and concluded that:

“When the archerfish is directly below its prey or nearly so, there is no refraction, or extremely little, of the light rays reflected from the quarry and reaching the archer's eye. The eyes, in any case, are so close to the surface of the water that refraction can hardly be much of a problem”

This explanation of how the archerfish corrects for refraction has been confirmed by Bekoff and Dorr (1976) and been widely accepted. However,

some preliminary observations of another species of archerfish, *Toxotes chatareus*, suggested that it could not explain the accuracy of this species, which consistently shot from positions which were far from being directly under the prey (also reported by Timmermans, 1975 and pers. comm.). The main purpose of the work reported here was to measure the extent of the refraction problem and to examine the behavioral tactics used by *T. chatareus* to overcome that problem.

Materials and Methods

The four specimens of *T. chatareus* used in these experiments were obtained from a tropical fish importer. They ranged from 7.0 to 8.0 cm fork length, and therefore were probably not quite mature (Smith, 1945). Unfortunately, the extent of their previous spitting experience was unknown.

The fish were kept individually in 13.2-l aquaria maintained at 23° C. The prey used in these experiments was a plastic fly 1.0 cm long, suspended above the edge of the aquarium by a nylon monofilament thread. Shots at this prey at heights of 10, 15, 20, 25, and 30 cm above the water surface by each fish were filmed. (Fish 3 refused to shoot at the 10-cm high prey after four days, and these were replaced by 35-cm prey).

Each day an attempt was made to film ten shots per fish, two at each of the five heights presented in random order. This procedure was followed for 15 days in the case of two of the fish, and ten in the case of the other two, who died before the series could be completed. Occasionally fish would refuse to shoot and consequently a total of only 480 shots were filmed.

Filming was conducted at 200 frames/s with a Ciné-8 camera (Visual Instrumentation Corp., Burbank, California) and Super-8 mm color film (Kodak Ektachrome, ASA 160) using light provided by a Colortran Flood lamp. These films were analyzed on a PDQ II Motion Analyzer (Photographic Analysis Co., Wayne, N.J.). Distance (DIST), body angles (α , Ω) shot angle (δ) and droplet velocity (VELOC), were measured for each shot filmed (Fig. 2). The body angle was measured twice: when the fish took up its initial position at the water surface (α) and just as the shot left the mouth (Ω). The shot angle increment (γ) was calculated from δ and Ω . The distance from the nose to the center of the eye, and the angle of the eye beneath a line from the nose to the fork of the tail (β) were measured on close-up pictures of each fish. These allowed calculation of the depth of the eye at any body angle, and from this the position of the prey image on

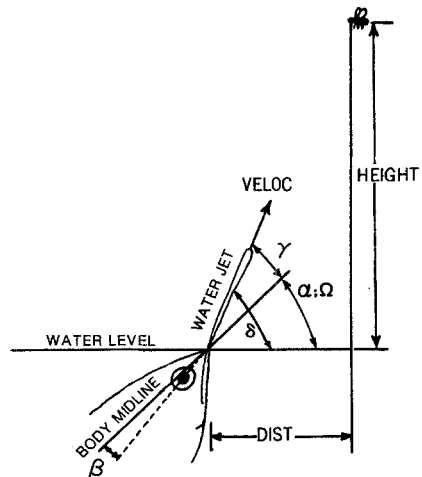


Fig. 2. The parameters of spitting measured from the films. Height (HEIGHT), distance (DIST), velocity (VELOC), initial body angle (α), final body angle (Ω), and shot angle (δ) were measured for each sequence. β is a constant, and was measured once per fish

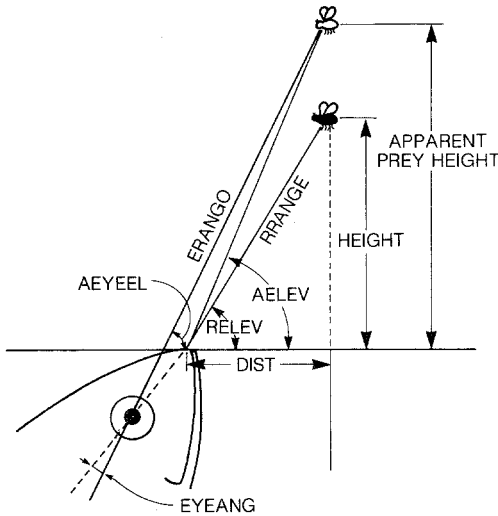


Fig. 3. The prey position parameters which were calculated from the measured spitting parameters shown in Figure 2. *RELEV* and *AELEV* are the elevations from the nose to the prey and apparent prey position, respectively. *AEYEEL* is the elevation of the apparent prey position from the eye. *RRANGE* is real range (nose-to-prey distance); *ERANGO* the distance from the eye-centre to the apparent prey position. *EYEANG* is the angular position of the prey image on the retina (see text). Apparent prey height is calculated as $DIST (\tan AELEV)$

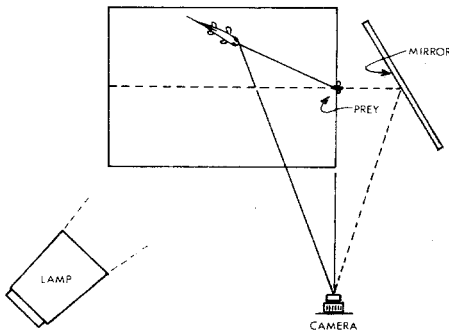


Fig. 4. Overhead view of the aquarium, showing how the mirror reflected a light ray perpendicular to the centre of the tank. This allowed calculation of the fish's position in the third dimension (see text)

the retina (*EYEANG*, degrees below the eye center-nose tip line) and the apparent position of the prey. *EYEANG* and several other distances and angles characterizing the real and apparent prey positions are shown in Figure 3. For a variety of reasons (e.g., camera started too late) not all measurements could be obtained for every shot filmed.

A first surface mirror was mounted behind the prey in such a way that the long axis of the aquarium was reflected directly into the camera lens (Fig. 4). In each filmed sequence the droplet of water shot by the fish could be seen traversing this mirror since the water and mirror were filmed simultaneously. The angle of its ascent, together with the distance of the fish from

the mirror, allowed calculation of the fish's position in the tank with respect to the tank's longitudinal axis. All measured angles and distances could then be converted to real values in the plane connecting fish and prey.

If a shot was successful, the fish was immediately rewarded with a large flake of commercial fish food (Tetramin). Otherwise the fly was quickly removed and then presented at the next pre-selected height. At least 1 h after filming, those fish which had missed shots were given enough food to bring their total daily ration up to ten flakes (the same as those fish which were successful with every shot). Thus, all fish were in the same state of hunger at the start of each day's testing, but fish were not rewarded immediately for missing the fly. It is perhaps worth noting that when a fish hit the fly it did not seem aware that the reward was not the object spat at, as is also the case for *T. jaculatrix* (Lüling, 1958).

Results

1. General Description of Spitting Behavior

The spitting behavior of *T. chatareus* is similar in many respects to that reported for *T. jaculatrix* (Lüling, 1963). Upon reaching the water surface the fish remains motionless for a few seconds at a fixed body angle (α). During this period the eyes may be seen to rotate in the dorsoventral plane and to converge. This binocular fixation of the prey would allow its correct placement along the extension of the fish's longitudinal axis. It may also allow the archerfish to judge the prey's distance. The fish then very quickly pitches to a new body angle (Ω) which is steeper than α . In one fish for which close-up high-speed films of spitting were obtained, the pivot point for this rotation was the base of the pectoral fins. A short forward movement of the body then occurs which causes the tip of the nose to just break the water surface. A single jet of water is released, which begins to break up into a major stream and a number of smaller droplets when a few cm from the mouth, just as reported for *T. jaculatrix* (Hediger and Heusser, 1961). However, unlike *T. jaculatrix*, *T. chatareus* has completed its body pitching and is motionless in the water when the shot is released.

The initial body angle (α) is not very precisely related to the prey elevation (Fig. 5; $r=0.41$), but the final body angle (Ω) is very strongly correlated with prey elevation (Fig. 6; $r=0.84$). Although both correlations are significant ($p<0.01$), it seems obvious that the fish obtain some information during initial sighting which allows them to set their final body angle more precisely. In fact the final body angle is very nearly that required to hit the prey if γ were a fixed angle (Fig. 6).

2. Effect of Prey Height on Spitting Success

As prey height increased, the proportion of spitting attempts which were successful progressively declined (Fig. 7). Two lines are shown on this figure. The first (A) represents the first eight shots fired at prey at each of the five heights by each of the four test fish, i.e., it represents the data from the first four days of the experiment. The second line (B) represents all attempts made by

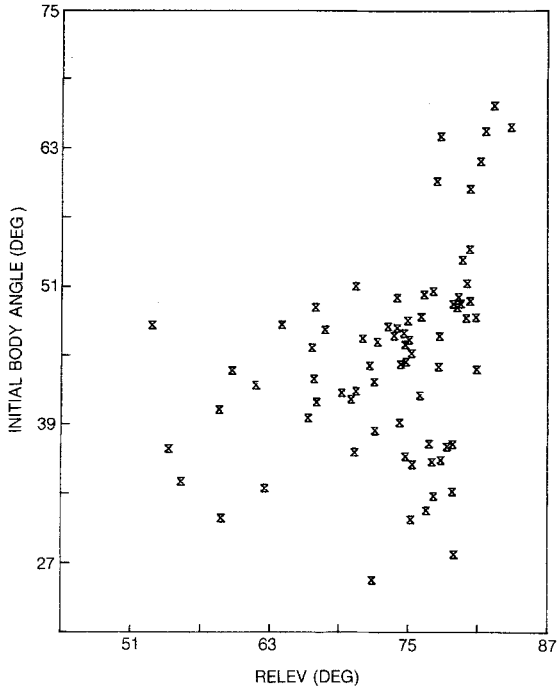


Fig. 5. The relationship between the archerfish's initial body angle (α) and the real elevation of the prey (*RELEV*). Fish 3 data only

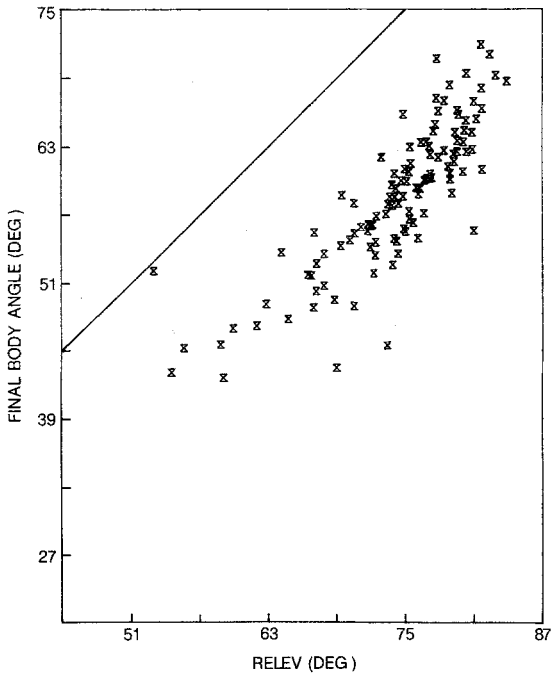


Fig. 6. The relationship between the archerfish's final body angle (Ω) and the real elevation of the prey (*RELEV*). Fish 3 data only. The one-to-one line is also shown

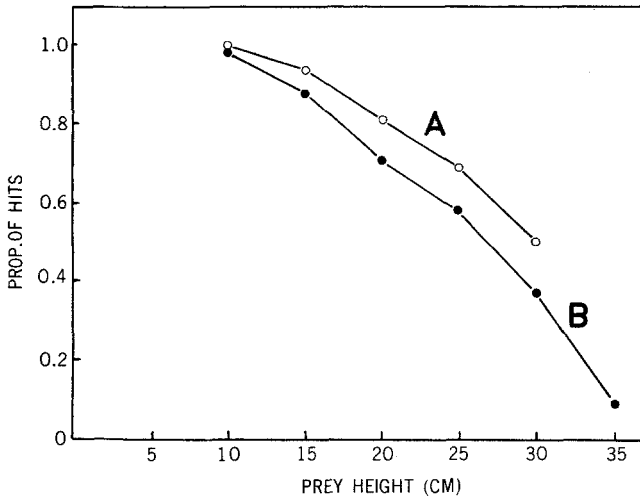


Fig. 7. The effect of prey height on spitting success. *A*, Spits recorded during the first four days: (4 fish \times 5 heights \times 4 days \times 2 replicates per day); *B*, All spits which occurred during the experiment

the archerfish (sometimes more than one per film sequence) during the course of the experiment. The shots at 35-cm-high prey were by fish 3 only. In all, 531 shots are represented here, ranging from 11 directed at the 35-cm-high prey to 111 directed at the 20-cm-high prey. The difference in the levels of the two curves is primarily due to the fact that fish 6 became less accurate as the experiment progressed. However, the shapes of the two curves are essentially the same. Overall, 69% of the shots were successful.

Fish shooting at prey at a particular height did so at various distances from the prey along the water surface, i.e., they did not take up positions directly below the prey as described by Lüling. Consequently the distance from the fish's mouth to the prey was not constant for any prey height. As this resultant distance increased, the proportion of successful shots declined (Fig. 8).

Lüling (1958) reported that most misses by *T. jaculatrix* were the result of shooting to one side or another of the prey, not above or below. Such a breakdown was not attempted for the present data. However, it was clear that the shots rarely missed by more than a few centimeters, and were not 15–20 cm off the mark as Bekoff and Dorr (1976) reported for *T. jaculatrix*.

3. Ballistics

Although the water droplet was released at an increasingly higher velocity (measured during the first 0.015 s after release) as the distance from the eye to the apparent position of the prey increased (Table 1), the effect was small and the variability great (Fig. 9). The average velocity recorded was 355.9 cm/s ($n=402$), a value very similar to that observed by Milburn and Alexander (1976). According to Lüling (1958) *T. jaculatrix* also spits with constant force.

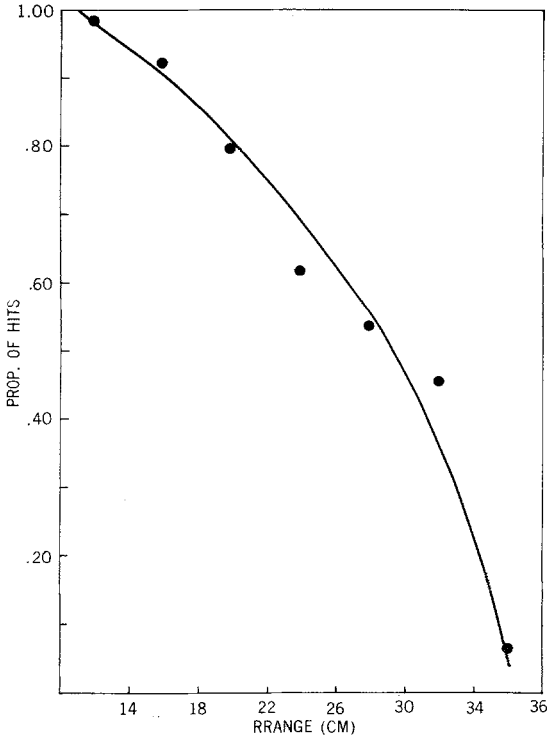


Fig. 8. The effect of the distance from the tip of the nose to the prey (*PRANGE*; see Fig. 3) on spitting success. The data are divided into seven groups according to *RRANGE* values: 10–14 cm ($n=77$), 14–18 ($n=67$), 18–22 ($n=69$), 22–26 ($n=55$), 26–30 ($n=52$), 30–34 ($n=66$), 34–38 ($n=16$)

Table 1. The effect of *ERANGO* (distance from eye to apparent position of prey) on the initial velocity (first 0.015 s after release) of the water droplet

<i>ERANGO</i> (cm)	n	<i>VELOC</i> (cm/s)	
		Mean	Standard Deviation
12–19	76	340.1	38.36
19.1–25	71	341.4	37.33
25.1–31	76	355.7	39.84
31.1–37	62	365.6	51.81
37.1–43	73	363.0	39.82
43.1–51	44	381.9	34.82

The observed velocities are such that the trajectories of the water droplets curve downward significantly. The height that each droplet falls during the course of its travel from the fish’s mouth to the vertical plane of the prey (Fig. 10A) may be calculated from the relationship:

$$FALL = \frac{g}{2} \left[\frac{DIST}{VELOC(\cos \delta)} \right]^2 \tag{1}$$

where g is the accelerating force of gravity (981 cm/s^2).

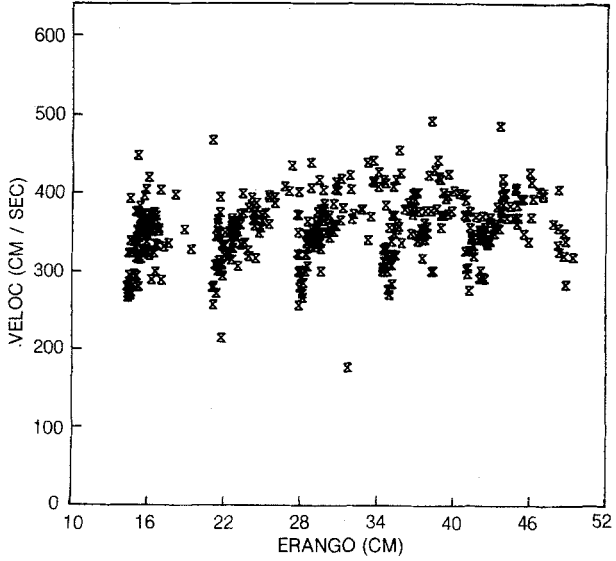


Fig. 9. Droplet velocity (*VELOC*) as a function of the distance from the archerfish's eye to the apparent position of the prey (*ERANGO*; see Fig. 3)

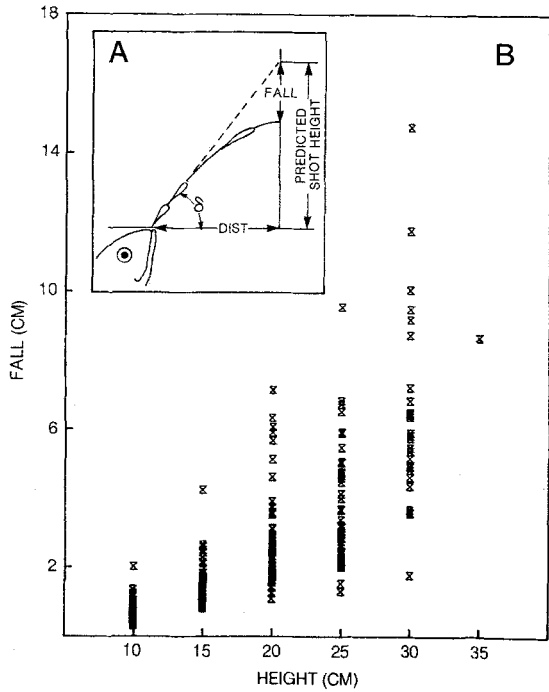


Fig. 10. A Predicted shot height is that height at which a water droplet traveling in a straight line would strike the vertical plane of the prey and is calculated as $DIST (\tan \delta)$. However, gravitational forces cause the droplet trajectory to curve. The height difference between the straight and actual trajectories at the vertical plane of the prey is designated *FALL* and defined in the text. **B** The correction (cm) which the archerfish must make for trajectory curvature as a function of prey height. Successful shots only

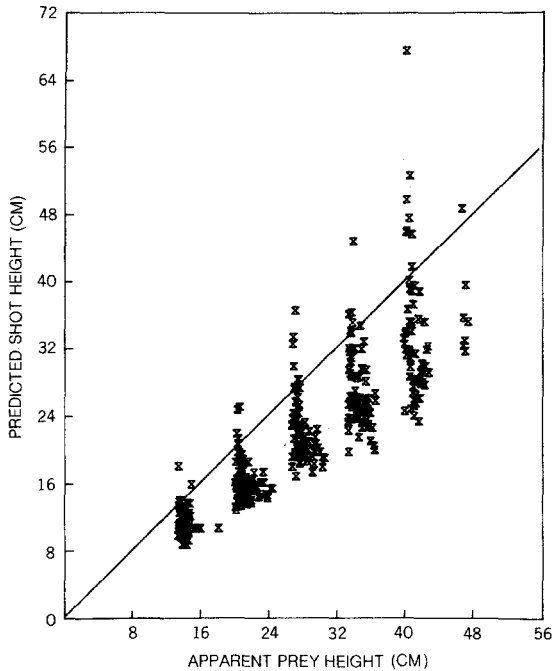


Fig. 11. The height at which shots were predicted (from their initial angle) to cross the vertical plane of the prey (see Fig. 10A), compared to the apparent prey height (see Fig. 3)

The reduction in height due to trajectory curvature was calculated for all successful shots and is plotted against prey height in Figure 10B. It is obvious that the archerfish is able to compensate successfully for the force of gravity when spitting. That hits are not the accidental results of droplets aimed at the apparent image (and striking the lower prey due to trajectory curvature) can be seen by comparing the predicted shot heights to the apparent prey heights (Fig. 11). Predicted shot height is the height at which a droplet traveling in a straight line would strike the vertical plane through the prey (see Fig. 10A). It can be seen from Figure 11 that the archerfish were aiming below the apparent position of the prey. (If the prey appears to lie somewhat closer than assumed here, then predicted shot heights differ even more from apparent prey heights. This is due to the fact that the tip of the nose is not coincident with the position of the eye.)

The fish are not reducing FALL by greatly increasing the velocity of shots directed at more distant prey. They are therefore presumably correcting for the effect by varying the shot angle (γ). Either mechanism would require that the fish estimate the distance to the prey which, as noted above, they can presumably do during binocular fixation.

4. Magnitude of the Refraction Problem

There are two ways of expressing the magnitude of the problem caused for the archerfish by refraction: either in terms of the angular correction or the

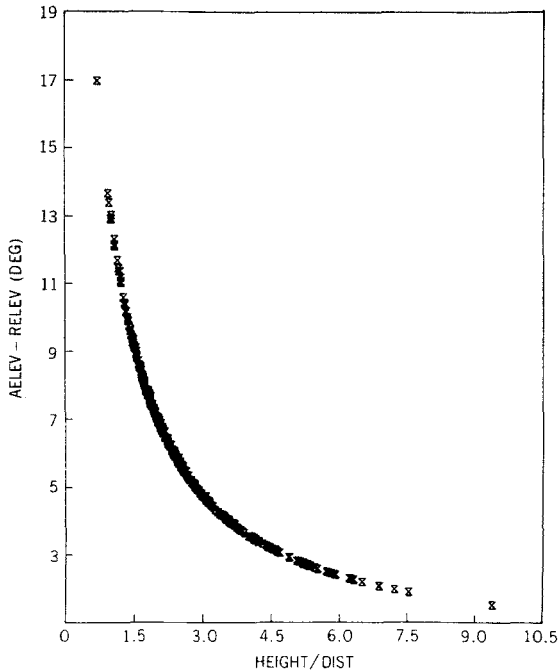


Fig. 12. The angular correction which the archerfish must make for refraction ($AELEV-RELEV$) as a function of the height of the prey divided by the distance from the nose to the prey in the horizontal plane ($HEIGHT/DIST$). $AELEV$ is the elevation of the apparent prey, $RELEV$ that of the prey itself. These are determined by the archerfish's position in relation to the prey

height correction which the fish must make. The required angular correction (apparent elevation minus real elevation, both measured from the tip of the nose) is shown in Figure 12. Notice that this required correction may reach almost 14° when the angle of incidence is high ($HEIGHT/DIST$ is low), showing that refraction is not a trivial problem. Figure 13 shows the required height correction (apparent prey height minus prey height). This may exceed 13 cm for high (30–35 cm) prey, and even for 10 cm prey is never less than 3.5 cm (35%). Each curve in Figure 13 corresponds to a different prey height and the range of observed $HEIGHT/DIST$ values shows the variability in shooting distance and angle for prey at a given height. In summary, refraction is a nontrivial problem which the archerfish overcome in some way other than by positioning themselves directly beneath the prey. Rather, the fish can shoot from a variety of positions, correctly setting their spitting angles to compensate for the refraction effect unique to that position.

5. Correcting for Refraction

The fact that archerfish are reasonably successful at hitting prey even when the amount of refraction is considerable suggests that they do make appropriate

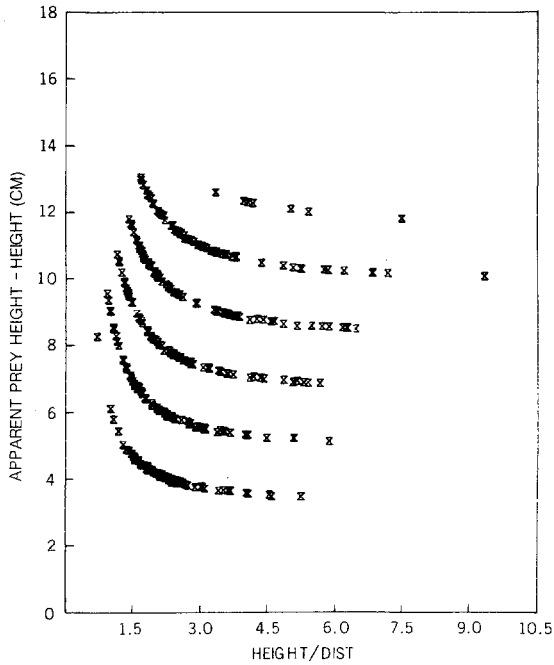


Fig. 13. The height correction which the archerfish must make for refraction (*APPARENT PREY HEIGHT-HEIGHT*) as a function of *HEIGHT/DIST*. Each curve represents one prey height

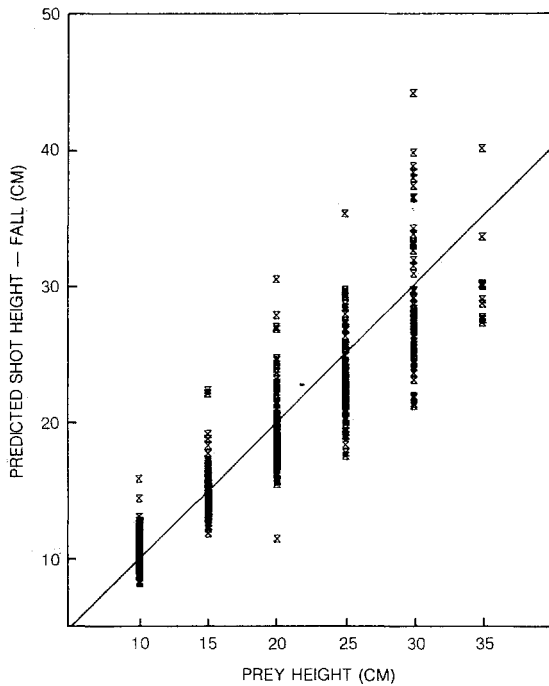


Fig. 14. The height at which shots were predicted (from their initial angle and velocity) to cross the vertical plane of the prey (see Fig. 10A), compared to the prey's actual height

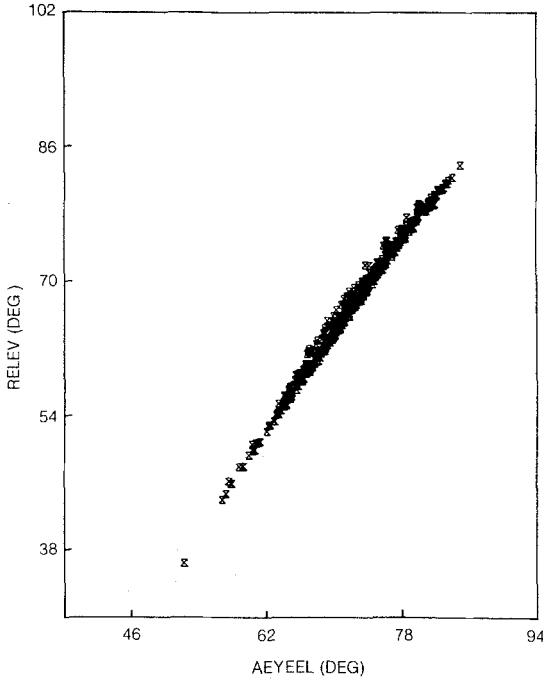


Fig. 15. The measured relationship between the apparent elevation of the prey from the eye (*AEYEEL*) and its real elevation from the nose (*RELEV*) during initial sighting (at body angle α)

corrections for this optical phenomenon. The water droplet is aimed at the prey from the start, corrections apparently having been made for the force of gravity (Fig. 14). Examination of the films confirms this: the prey is hit by the main water droplets, not by smaller droplets which have followed a lower trajectory.

The observation that the fish are very nearly properly aligned with the prey once they have assumed their final body angle (Ω , see Fig. 6) suggests that information concerning the true position of the prey is obtained during initial fixation at body angle α . This information is probably derived from a relationship which exists between the apparent elevation of the prey relative to the fish's eye (*AEYEEL*) and its true elevation relative to the tip of the nose (*RELEV*), as shown in Figure 15. The equation best describing this data (for *AEYEEL* greater than 60° , below which the line appears to curve slightly) is:

$$RELEV = -32.33 + 1.38 (AEYEEL). \tag{2}$$

Very few shots are taken when *AEYEEL* is less than 60° .

The fish can obtain *AEYEEL* from the relationship:

$$AEYEEL = EYEANG + \alpha + \beta \tag{3}$$

and having calculated RELEV, needs only to choose a combination of body angle and shot angle increment such that:

$$\Omega + \gamma = \text{RELEV}. \quad (4)$$

Either Ω or γ could then be further adjusted to compensate for the loss in shot height due to curvature of the trajectory. This hypothesis is attractive in that the archerfish need not "know" trigonometry, but only the equation of a line. Whether the equation is hard wired into the animal or acquired as a result of experience is unknown, but is largely irrelevant to the problem at hand.

The angle ($\alpha + \beta$) was measured using convenient landmarks on the exterior surface of the fish. It is presumed to be related in some simple way to that body angle (pitch) measured physiologically by the fish themselves. The only other thing that the archerfish need to measure is EYEANG (see Fig. 3). *T. jaculatrix* has an area on the retina analogous to a fovea (Lüling, 1958), and the archerfish might measure EYEANG by monitoring the amount of eyeball rotation required to place the prey image on this.

It is worth noting that γ is not predetermined, as might be expected, by the morphology of the mouth. The archerfish is able partially to determine the direction of the shot either with the lips, or more likely, the very thin tip of the tongue (Sterba, 1962). The ranges of γ values observed for the four fish were 10–30°, 6–25°, 4–21°, and 4–24° (cf. 10 to 40° in *T. jaculatrix* (Lüling, 1963)). Thus, although Ω seems to be chosen under the assumption that γ is fixed, the archerfish can change the direction of the shot at the last moment. This fine tuning mechanism can compensate for inaccuracy in the setting of body angle and might be adapted to spitting in moving water or at moving prey. *T. chatareus* can hit moving prey in the laboratory (model prey swinging along an arc, or in a circle above the aquarium). The mechanism might also be required because the position of the nose changes slightly during pitching (around the pectoral base) and RELEV needs to be redetermined. A linear relationship between AEYEEL and RELEV also exists at body angle Ω , allowing such recalculation. The constants in this equation are nearly identical to those in Equation (2). Finally, the variability in γ might be related to correction for trajectory curvature.

Discussion

While the archerfish is clearly unusual in its behavior, the problem which it must solve is by no means unique. Any animal which must operate through the interface of air and water must deal with the problem of refraction. Anything which can be learned about the archerfish's means of coping with the refraction problem may be applicable to other animals as well.

In the first place the Toxotids are not the only fish which spit at aerial prey. A number of Anabantids, especially of the genus *Colisa* also do this (Vierke, 1973). In addition, many fish jump through the air-water interface to capture aerial insects. Kalleberg (1958) has commented on this behavior

in juvenile salmon and trout, and noted that the fish need to correct for “refractive phenomena in the surface of the water”.

The spraying characid *Copeina arnoldi* has a similar problem. Pairs of these fish jump simultaneously out of the water and deposit their eggs on the underside of leaves. The male then tends the eggs for several days, using his tail to splash them regularly with water. Both in spawning and splashing the refraction problem is successfully overcome (Krekorian and Dunham, 1972).

Finally, many wading and diving birds must solve the refraction problem in reverse. Their underwater prey will appear closer to them than it actually is. Some of the diving birds (e.g., terns—Salt and Willard, 1971; Buckley and Buckley, 1974) solve this problem by plunging straight downward. Their line of sight is therefore normal to the water surface and refraction does not occur. The prey will appear on the correct line, but more shallow than is actually the case. Other diving birds, however, have an angle of attack which is not vertical, e.g., gannets (Godfrey, 1966), blue-footed boobies (Harris, 1975), and brown pelicans (Schreiber et al., 1975). Here again refraction must be dealt with, as noted by Phillips (1962).

The green heron, a wading bird, reportedly pecks short of food placed on the ground, evidence that this species has a built-in refraction correction mechanism (Ficken and Wilmot, 1968). These authors have suggested that the heron overcomes refraction by sighting along dark eye lines, which extend at an angle from the eye to above the tip of the bill. This explanation seems unlikely as it would only be effective if the prey were at a fixed distance below the water surface and in front of the bird's head, i.e., if the angle of incidence were constant. Furthermore, herons which occasionally forage on land, such as the blue heron, have no difficulty capturing prey, suggesting a more flexible prey-sighting mechanism. Perhaps thinking of the heron as a reverse archerfish will suggest a solution to this problem.

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