OPERANT CONDITIONING OF SPITTING BEHAVIOUR IN THE ARCHER FISH (TOXOTES JACULATOR)

BY
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ABSTRACT

The archer fish, *Toxotes jaculator*, has the ability to knock insects out of the air by spitting at them. Although many studies have been done using the archer fish, it has never been considered from the operant conditioning perspective. In the wild the fish does not always get the prey at which it spits. Therefore, it is possible that a Variable Ratio (VR) schedule of reinforcement is involved in the spitting process. In an effort to understand this behaviour, one must first demonstrate operant conditioning with the spitting response. This hypothesis was tested in the laboratory with three fish in three indentical tanks, each with a target apparatus, an automatic food dispenser; all were attached to a PET computer to control the schedules and to record responses and reinforcements. All three fish were successfully shaped to spit at the target and all came under control of a Continuous Reinforcement (CRF), a Variable Ratio 3, 5, 8, and 10 schedule of reinforcement. I also found that the fish showed greater resistance to extinction following a VR 10 schedule relative to CRF. The results of this experiment suggest operant learning principles can be used to control the spitting behaviour of the archer fish.

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Method

ARCHER FISH

The freshwater fish of the genus Toxotes (Greek word for archer) has the ability to knock insects out of the air by spitting at them (Gill, 1909). There are six species of Toxotes of which *Toxotes jaculator* (Pallas) and *Toxotes chartareus* (Hamilton) are the most common (Luling, 1964), and all exhibit this behaviour in varying degrees.

Archer fish range from south eastern Asia to the northeastern tip of Australia and are mainly found in the brackish water of mangrove swamps and estuaries (Sterba, 1963; Luling, 1964). The fish usually are found in schools and consequently, when feeding, a number of fish may spit at the same prey (Fletcher, 1968). The fish eat a variety of food including cockroaches, crickets, grasshoppers, mosquitoes, flies, ants, gnats, dragon-flies, beetles, moths, caterpillars, ephemerids, spiders, flower buds and shrimp all of which can be found floating on the surface of the water, or in some cases on over hanging vegetation or flying over the water's surface (Smith, 1936,1945, Allen, 1978). They are usually inactive at night and feed at the surface during the day, (Allen, 1973) or during bright moon-lite nights (Gill, 1909).

The fishes colouration is interesting because it's normal silver background with dark patches or bars (Luling, 1964) may change depending on the circumstances. Gill (1909) noted that the fish are sensitive to weather and water temperatures and that these variables were associated with the disappearance of the bands or spots and change of overall body colouration. Herald (1965) also found a sensitivity to changes in illumination which could disturb feeding behaviour. Their black stripes also become more defined with the advance of the shooting sequence (Bekoff & Dorr, 1976).

Considering the unique characteristics of the archer fish, it is surprising that relatively little has been done on the behavioural capabilities of this animal. The majority of the studies on the archer fish are concerned with the anatomical, physiological, and optical mechanisms involved in spitting. These will be reviewed first and will be followed by a discussion of the behavioural aspects of the spitting response.

During the act of spitting the nose breaks the water surface (Dill, 1977) and a single jet of water is ejected which immediately breaks into a number of smaller droplets (Hediger and Heusser, 1961). Milburn and Alexander (1976), using high speed film and muscle stress calculations, determined that the spit has an average velocity of 3.8 m $\sec^{(-1)}$, a volume of 140 $mm^{(3)}$ or 2-3 % of the body volume. The spit requires 28 msec and occurs at an average of 78^{o} to the horizontal. Elshoud and Koomen (1985) also simplified the description of the spitting procedure noting three basic movements 1) levation of the mouth bottom 2) adduction of the lateral sides and 3) levation of the jaws. The shortest time between spits was found to be 0.41 seconds.

Models of the Spitting Mechanism: The actual mechanism which allows the fish to propel a stream of water with relative accuracy up to a metre has received considerable attention. After careful dissection and study of the fishes mouth, Smith (1936, 1945) and Myers (1952) describe the structure as analogous to a blowpipe. They found that the oddly shaped tongue fits a narrow slot in the roof of the mouth and hence a tube of less than 1.5 mm in diameter is formed resembling a blowpipe. This account was further popularized by Luling (1964).

The exceptional intrinsic speed of the adductor muscle (comparable only to a mouse limb or rat extrinsic eye muscle) was noted by Milburn and Alexander (1976). Through dissection and measurements of the muscles operating during spitting the strain rate was found to be highter than the expected muscle stress. Milburn and Alexander (1976) concluded that the bones surronding the muscles must somehow act as a spring and are released during spitting. These authors thus proposed a catapult mechanism rather than the accepted blowpipe theory.

With the use of electromyography and computer modelling to construct an accurate three dimensional mathematical model, both the blowpipe and catapult postulations have been rejected (Elshoud and Koomen, 1985). The mouth valves are apparently closed by water pressure except for the rostral tip which is kept open by the septa. This formation resembles a pressure tank with a small aperture through which a water jet can be emitted.

Perceptual Considerations: The eyes of the archer fish and their special refractory adaptability are also an intergral part of the spitting response. The unique ability to adjust for the refraction between air and water provoked Luling (1964) and later Bekoff and Dorr (1976) to note that the fish swam to a point directly below its prey before spitting. This they felt minimized the refraction at the air-water interface and allowed the fish to overcome optical distortions. However, Timmermans (1975) and Dill (1977) rejected the 90^o hypothesis as they observed varied positions being used by the fish and an incredible ability to compensate for each different refraction effect. With the use of high speed photography it was found the fish makes certain behavioural adjustments to deal with each refraction problem (Dill, 1977). The fish will use its binocular vision to locate and judge the distance of the prey while remaining motionless for a few seconds at a fixed body angle near the water surface. The close-up high-speed its body angle to a steeper position. Dill (1977) found a strong correlation with this final body angle and prey elevation but a weak correlation with the prey elevation and the initial body angle.

This study also showed that the archer fish compensates for the force of gravity and aims to rectify the curvature the spit accords over distance. These behavioural adjustments may account for the 69% success rate of the spits found over a range of heights from 10 to 35 cm (Dill, 1977). Timmermans (1975) also noted that the maximal distance for spit accuracy increased with body length remaining constant at about 10 times an individual's length.

Electron microscopic analysis of eye tissue revealed that the archer fish does indeed have very unique eyes, including a mosaic pattern of cones which facilitates the ability of the retina to gather moving visual stimuli (Braekvelt, 1985a, 1985b, 1985c). Enhanced visual acuity and ability to correct for the refraction can also be considered important because spitting is sometimes replaced by jumping out of the water in an attempt to capture prey (Smith, 1945, Allen, 1973, Gill, 1909). Larger members of the species (15-17 cm) may reach heights of 30 cm when jumping for food (Herald, 1965).

Behavioural Studies: Only two behavioural studies have been done using archer fish. Bekoff and Dorr (1976) were primarily concerned with ethological aspects of spitting, particularly the behavioural components involved in accurate responding. In their experiment, an insect was stationed 30 cm above the water surface using a piece of thread until a shot was taken. If a direct hit occurred the fish were allowed to consume the insect. They found that *Toxotes jaculator* were successful in shooting at suspended prey 25.5% of the time. Also of importance in their study was that a sequence of five acts preceded each deliberate shot at the prey. These behaviours included; orient, swim, rotate vertically (twice), leap, and shoot.

The second behavioural study, and the only one specifically concerned with learning, was done on auto-shaping in the archer fish (Waxman & McCleave, 1978). This experiment light, with a fruit fly presentation. This contingency eventually brought the squirt response under control of the light. The three fish used began to spit at the light after 43 to 52 light-insect pairing. When the red light was hit by the spit the experimenter, using an aspirator, blew in the fly. A control group of two fish had random presentations of light and fruit fly but yielded no responses.

The experiment on auto-shaping was particularly interesting because it suggests that conditioning mechanisms may play a critical role in understanding the dynamics of this unusual foraging behaviour. The classical conditioning component suggests that stimuli combined with food may come to release the spitting response while the operant aspect suggests the critical role of consequence in maintaining behavior. It is along these lines that the present and further research will procede. Before describing the conditioning research to be done in this thesis some comments about the existing studies are in order.

Although both of these experiments provide important information on the behaviour of the fish they exhibit the methodological problems encountered when first experimenting with a new species. The method used by Bekoff and Dorr (1976), suspending the insect (moth or cricket) by a piece of thread and immediately cutting it for the fish to consume introduces potential experimenter effects that could affect the outcome of the experiment. Waxman and McCleave's (1978) experiment on auto-shaping exhibited many of the same problems since methodologically, the experiment lacked a dispensing method that automatically provided the fish with reinforcement when the target was hit. This limitation constrains the range of operant studies that might otherwise be investigated.

The rationale for auto-shaping is interesting because it combines both classsical and operant conditioning in that a CS-US stimulus pairing generates classical conditioned behaviour; since a response to the CS also generates reinforcement, the CS also becomes the discrimintive stimulus which can set the occasion for operant behavior (Brown &

Jenkins, 1968). One obvious implication of this is that both classical conditioning and operant conditioning can be demonstrated as independent processes in this fish. The purpose of this study is to provide an objective demonstration of operant conditioning in Toxotes. The problems encountered in the aforementioned experiments will be rectified using a fully automated operant conditioning system.

It was noted that the archer fish tends to swim in schools (Fletcher, 1968), or in small, loose companies (Gill, 1909) making feeding a communal affair. Since a group member can often learn where and what to eat by observing fellow foragers (Krebs, 1978), the grouping strategy for the feeding archer fish makes good evolutionary sense. Crook (1965) also points out that group foraging often allows members to locate food easier than isolates, a phenonomen referred to as local enhancement. Social foraging also may allow group members to be considerably safer, since predators can usually be detected faster than in solitary situations (Pulliam and Caraco, 1984).

There are some obvious advantages of social foraging but when the whole school of archer fish spits at an unsuspecting prey only one fish will get the meal unless that particular insect is very large (Fletcher, 1968). The social feeding behavior of the archer fish suggests that the fish are not always reinforced for each individual spit and that an individual foraging in a group may have it's spitting controlled by a socially induced variable-ratio (VR) schedule of reinforcement (Goldstein, 1981). Luling (1964) and Smith (1936) also noted that individual archer fish will often hit their prey with the spit but that the force is so great that the prey would often end up being knocked out of reach, onto the creek or river bank. In addition, the inverse relationship between prey distance and spitting accuracy also creates a VR schedule for the predator. Thus, regardless of whether the archer fish was foraging in a social situation or feeding alone, a variable-ratio schedule of reinforcement appears to characterize it's spitting activity. For this reason the operant study to be performed here will focus on the ability of a VR schedule to control spitting. Ratio schedules have been demonstrated with several different fish including goldfish (Rozin and Mayer, 1964), three-spined sticklebacks (Sevenster, 1968), and Siamese fighting fish (Hogan et al., 1970), but never with archer fish.

EXPERIMENT 1

Before an operant study could be carried out, it was necessary to ascertain specific behavioural information about the fish to facilitate the design and set-up of the apparatus. Specifically the first experiment was designed to discover the height at which the operant target should be set to maximize spitting and minimize jumping.

Method

Subjects: Subjects were 15 *Toxotes jaculators* obtained through a fish retail outfit in Toronto (the fish were native to southeastern India.) The fish were 7-8 cm long and were housed in four aquaria containing slightly brackish water at 26-27^{o} C. One fish was in a 38 L tank, two fish were in another 38 L tank, four fish were in 120 L tank, and eight fish were in a 190 L tank. (The fish had all demonstrated previous acustomed to laboratory conditions before any experiments were begun. Their actual age was unknown. Sex of the fish was also unknown since no indentifiable secondary sexual characteristics have been established in the scientific literature. The fish were fed frozen bloodworms during the experiment.

Apparatus: All tanks had water levels set at 2 cm from the top. A 50.5 cm x 26.5 cm x 24 cm Plexiglas frame was designed to fit the rim of the two 38 L aquaria. Two other frames of equal dimensons cross-fitted the end of each of the larger tanks (See figure 1). Slots were cut in the middle of the 50.5 cm sides of the frame at 2 cm, 6 cm and 14 cm from the bottom which would fit a 32 cm x 8 cm x 0.5 cm piece of Plexiglas (the feeding plate). All open sections of the tanks were covered with glass. A 3 channel event recorder, (Gerbrands) was used to record jumping, spiting and eating. A video tape was taken of each experimental session with the use of a VHS camera and a time lapse video cassette recorder (EVT-801).

Procedure: The thawed bloodworms were put on the middle of carefully drained allowing the bloodworms to remain attached to the plate when it was turned upside down and fitted into the Plexiglas slot. This allowed the fish to either jump or spit at the feeding plate. The five experimental heights studied were 2cm (the feeding plate laid directly on the aquarium top), 4 cm, 8 cm, 16 cm, and 24 cm (the top of the frame). Approximately 1 gm of bloodworms was used per fish. The insertion of the feeding platform into the frame marked the beginning the 30 min experimental session. When the fish would either jump or spit at the bloodworms the response was recorded on the appropriate channel of the event recorder.

Each of the four groups were tested in 30 min testing intervals at the same height, on the same day. Three methods of testing were employed; ascending, descending and random. In the ascending method the height was first set at 2 cm and then on each subsequent day raised to 4 cm, 8 cm, 16 cm, and finally 24 cm. In the decending method the five day order began at 24 cm and descended to 2 cm. Finally, in the random method the order for the five experimental days was determined by reference to a table of random numbers. A two day break occurred between each ordering method. All experimental sessions were video taped.

Results

The average amount of spitting and jumping when combining all three orders of presentation at each of the five experimental heights are shown in figure 2. The data show that irrespective of height, spitting is the predominant mode of foraging. An inverted u-shaped relationship was found to exist between spitting and height with 8 cm being the optimum spitting height. The jumping response decreased from 2 cm to 4 cm and was non-existent by 8 cm. Thus it was found that 8 cm was the height that maximum spitting and minimum jumping occurred.

Since the population size was different for the four tanks, spitting and jumping were also examined as a function of population size. The average amount of spitting and jumping when combing all three orders of presentation for each of the four experimental groups are exhibited in figure 3. The greatest total amount of spitting occurred with a group size of four. However, it should be noted that when mean spits per fish are considered a group size of one produces the highest amount of spitting. The jumping response reached its peak amount with a group size of two archer fish. The lone archer fish did not jump at any height.

Discussion

The results suggest that the height of the food source does in fact influence the amount of spitting and jumping engaged in by the archer fish. The results also show that population size influences the amount of spitting and jumping. It is known that the archer fish prefers initially to jump for food if it is close enough to the water surface (Luling, 1964, Herald, 1965, Bekoff and Dorr, 1976), but for our purposes it was necessary to know the specific height at which the fish would not jump. This study found that jumping did not occur past 4 cm and that jumping was dependent on population size. The fact that the archer fish maintained in isolation did not jump was important, since in the operant study fish were to be tested in isolation.

That jumping peaked with two fish and decreased to almost zero with eight fish suggests that a small amount of competition stimulates jumping as compared to no competition or a lot of competition.

The inverted u relationship between spitting and height indicated that beyond a certain height (8 cm), the fish no longer responded with the same intensity. Dill (1977) found that spitting accuracy decreased with increased food heights. Increased height obviously makes it harder for the fish to visually locate the food and, together with decreasing accuracy, may account for the decrease in spitting. Since spitting range is related to fish size (Timmermans, 1975) the generality of the findings are, of course, confined to fish in the 7-8 cm range. The fact that the amount of spitting per fish was highest for the lone fish compared to the groups, suggests that not all fish spit in a group situation or that spitting per fish dramatically decreases through group foraging. This might possibly indicate that a variable ratio schedule does control foraging.

spitting response will be involved and that this height will also facilitate optimum spitting.

Experiment 2

This study attempted to bring the spitting response of the archer fish under operant control and to also demonstrate that a VR schedule of reinforcement could be established with the fish.

Method

Subject: The subjects were three *Toxotes jaculators* obtained through a fish retail outfit in Toronto who imported wild specimens from southeastern India. The fish had demonstrated previous spitting behaviour and were involved in experiment 1. The fish were 8-11 cm long and were housed in aquariums containing slightly brackish water at 26-27^{o} C. The fish had been in the laboratory for 14 months prior to the start of this experiment, by this time they ranged in size from 8 to 11 cm long.

Apparatus: The description of the apparatus is divided into three sections; operandum, computer mechanism, reinforcement device (See figure 4).

Operandum: The target was a disk with a 2.5 cm diameter and was covered with a transparent plastic cover which extended 0.5 cm beyond the border of the target. The disk was a piezo electric transducer (30v273-073, Radio Shack) with variable gain and operated in conjunction with a detecting circuit. It was sensitive to any possible impact the archer fish could generate by spitting. A right angle brace (16 cm x 2 cm) projected the target 8 cm above the water surface and 8 cm from the back edge of the aquarium.

Computer control mechanism: The target and control circut were attached to a PET microprocessor which recorded and analyzed all responses and reinforcements. It also controlled the schedules of reinforcement. Hardware and software details can be found in Goldstein, Blekkenhorst & Mayes (1982).

Reinforcement device: The dispenser was a conveyor belt mechanism attached to a stand and operated by a stepping motor. Evenly spaced on the belt were 30 small vials. The vials were attached to the conveyor belt with Velcro that was glued to the vial bottoms and to the surface of the belt. Each vial was capable of holding the reinforcers, mealworms, or frozen bloodworms. Activation of the piezo electric circuit ultimately resulted in the advancement of the belt by an amount sufficient to discharge the contents of one vial into the test aquarium.

Three identical units set up in three individual stalls in the fish laboratory. The three 38 L aquaria were equipped with identical features; a side mounted mini aquaclear filter, a bottom air filter and a heater. The water level was maintained at 4 cm from the top of the tank. A glass top was used to cover the aquarium when experimental sessions were not being conducted. A 15 cm square piece of cardboard was put over the glass directly below the target. Visual obstruction of the target prevented spitting between experimental session.

Procedure: The operant experiment involved an initial three day period in which the fish were allowed to become accustomed to the aquarium, dispenser and the target. During this time any spitting or other contact responses were automatically was shaped until a steady state (a consistent rate of spitting per session for a period of 3 days) of responding was reached at each particular schedule for each fish.

The vials were loaded with bloodworms and water before the session began with the glass top and cardboard cover in place. The schedule was set on the computer, the bottom air filter was turned off, the glass top was removed, and the timer was started, begining each 30 minute training session. The computer recorded each spit response and reinforcement. All experimental sessions were run between 2:00 and 4:00 pm and lasted for exactly 30 minutes for each fish.

Shaping: The normal method of feeding the archer fish in the fish laboratory was to put bloodworms on the underside of the glass cover so that they could be spit off. Therefore the inital shaping procedure was to put bloodworms on the underside of the glass cover directly below the location of the target. After these were spit off, the next shaping step was to place the worms on the underside of the target itself during the experimental time period. When the fish hit the worms on the target two consequences followed. First the worms fell off into the water and second, the dispenser discharged a vial of worms. For each subsequent spit at the unbaited target the fish were reinforced on a continuous reinforcement schedule (CRF) during the 30 minute session. Following that shaping step a small amount of bloodworms were placed on the transparent upperside of the target which allowed the fish to see the bloodworms. When the fish spit at the target no bloodworms fell except through the dispensing system. The next shaping step involved no bloodworms on the target but with the fish still being continuously reinforced for each spit.

A minimum of 7 days was used to establish responding on the initial period of continuous reinforcement (CRF). When a steady rate of spitting was achieved for a period of 7 days the fish were brought through an extinction period where spitting was not reinforced with food. Extinction lasted for a minimum of 3 days or until no responding occurred in a session. The fish were then returned to CRF using a very small amount of bloodworms on the underside of the target as an initial reshaping or priming technique.

Following this the fish's spitting behaviour was brought under control of a variable ratio 3, (VR 3) schedule in which every third response on average was reinforced for a period of 3 days or until a steady state of responding was achieved. The fish was then brought up to a VR 5 schedule, a VR 8 schedule and finally a VR10 schedule using the same transitional requirements. Upon completion of VR 10 the fish were once again placed on extinction and then returned to continuous reinforcement until spitting returned to baseline levels. Video tapes were made of the CRF, EXT, and VR conditions to provide a pictorial record of behaviour.

Results

All three fish showed operant conditioning of the spitting response (Fig. 5, 6, and 7). In the three day treatment free baseline the fish did no spitting at the target. After shaping, the graphs show that the fish responded not only to the CRF contingency but also to VR 3, VR 5, VR 8, and VR 10. In addition all three fish successfully underwent extinction following initial exposure to CRF and upon completion of the VR 10 schedule. Following both periods of extinction, the three fish rapidly returned to pre-extinction CRF levels in one session with only minimal priming.

Two of the fish reached peak responding during VR 10 (see fig. 6 and 7). The reinforcement level during VR was similar to that established during CRF. The other fish reached peak responding during VR 3 and VR 5 (see fig. 5). For this fish the reinforcement level during VR 8 and VR 10 was stable but below the established amount for CRF, VR 3 and VR 5.

Table 1 shows that for extinction two fish required three experimental sessions following both CRF and VR 10. The other fish required five sessions for extinction after CRF and four sessions after VR 10. However the number of responses during extinction was higher after VR 10 relative to CRF for all three fish. Fish one had total extinction responses of 21 after VR 10 and 11 after CRF, fish two had totals of 209 after VR 10 and 181 after CRF, and fish three had total responses of 60 after VR 10 and 45 after CRF (see table 1).

Discussion

The aim of the experiment was to bring the spitting response of the archer fish under operant control in a laboratory setting. This is the first step necessary to support the hypothesis that a VR schedule might in fact control spitting behaviour in the wild. In this experiment all three fish came under the operant control of a VR schedule.

The archer fish under control of a VR schedule in the wild may be a result of social foraging. Fletcher (1968) notes that the fish that spits does not always get that specific food reinforcement. The archer fish feeding in groups of two, four and eight in experiment number one did in fact exhibit this behaviour. It was also found that in the group situations that sometimes only one or two of the archer fish would do the spitting which provided the necessary food for the entire foraging group. Luling (1964) observed that the fish often hit its prey but with such force that the insect was knocked clear out of reach. This was also observed in experiment number one and in the shaping portion of experiment number two where by the archer fish would directly hit the bloodworm but knock it completely out of the aquarium. Thus the archer fish when foraging alone also appears to be controlled by a VR schedule in the laboratory.

Operant conditioning in the archer fish is interesting because unlike the situation found when training a rat to bar press, the operant response is the consummatory response. This is similar to conditioning a hamster to face wash (Shettleworth, 1973), chaffinches to perch or peck (Stevenson-Hinde, 1973), or a pigeon to peck (Brown and Jenkins, 1968).

During operant conditioning in which rats are exposed to ratio schedules of reinforcement, compensation for schedule increments is complete or almost complete at low ratios but gradually fails at higher ratios (Collier et al., 1972). A lack of adjustment, or breaks in response rate, are said to be due to ratio strain (Ferster and Skinner, 1957). Other animals such as guinea pigs and rhesus monkeys react in a similar manner to a ratio schedule (Hogan and Roper, 1978). Hogan and Roper (1978) in their comparative look at food as a reinforcer show that fish develop earlier signs of ratio strain relative to rats .

In Siamese fighting fish, Hogan et al., (1970) found that the number of responses increased so that the number reinforcements remained constant for a fixed ratio schedule (FR) from FR 1 to FR 6. Rozin and Mayer (1964) found that goldfish make the same adjustment from FR 1 to FR 10 but a gradual decline in the reinforcement rate occurred from FR 10 to FR 100. Two of the archer fish showed this same elastic type compensation for VR 3 through VR 10. The third fish demonstrated a difficulty to adjust past VR 5. This inability to compensate for an increase of ratio size may be due to this particular fish's spitting style.

Herald (1965), noted that archer fish display different spitting behaviours from individual to individual. Herald makes the analogous comparison to rapid shot machine gun types and single shot artillery types. The three fish demonstrated these differences with Fish 1 being of the single shot variety and

Fish 2 and Fish 3 being of the machine gun type. During experimental sessions, Fish 2 and Fish 3 were observed moving to the water surface and shooting up to six times in succession from the one position with about a half a second to a second between spits. These differences were confirmed by consulting the video tapes. Fish 1 would spit and then would usually swim away in a circle of varying circumference before returning to spit again. This method is obviously slower and less productive than the type employed by Fish 2 and 3. Fish 1, using the single shot method, did not achieve the response levels of the other two fish and since the experiment involved time restricted sessions, the fish could not adjust to the higher schedules and hence ratio strain became evident.

In many circumstances VR schedules promotes more persistence during extinction than CRF (Macintosh, 1974). In the study of extinction in fish this effect is still under consideration and must be qualified (Wertheim and Singer, 1964, Gonzalez et al., 1962). Wertheim and Singer (1964) compared extinction in goldfish after CRF and a Variable

Interval (VI) schedule and found more resistance to extinction following VI but only when the whole period of extinction was considered. If only the first session of extinction was to be considered, a contrasting conclusion might be adopted due to a higher response strength after CRF relative to VI. When looking at extinction in the archer fish it was found that there was greater resistance to extinction for VR as compared to CRF for both the first session responses and total responses. During extinction the archer fish would often spit at the empty vials on the underside of the belt displaying a generalized response characteristic of extinction in rats (MacIntosh, 1974)

The fish demonstrated a real accuracy with its spitting in both experiments one and two and clearly supported Dill's (1977) findings that the spits rarely missed, and only by a few centimeters when they did. The experiments with the archer fish exhibited their unique ability to adjust for air-water refraction and supported Timmermans (1975) and Dill's (1977) findings that many different spitting angles are used and for each case the refraction difficulties are overcome.

Many circumstances in the environment were associated with a change of the archer fish's colours (Gill, 1909, Herald, 1965). In our work it was noted that the fish adapted to its background, a dark or black background resulted in the fish becoming consistently darker in colour and a light background resulted in a relatively lighter exhibition of it's natural colours. Bekoff and Dorr's (1976) observations that the fish's black stripes became more defined as the shooting sequence advanced was witnessed many times during these experiments.

The experiments with the archer fish did not procede without difficulties which are worth noting for future research. An attempt was made to monitor eating behaviour as well as spitting and jumping in experiment number one. However, it was found that a food source other than bloodworms was needed. The bloodworms were too small and often one spit would knock down several worms which confused our attempt to follow each individual spit to decide which fish received the reward.

The conveyor belt apparatus was situated over the aquarium and would often cause the fish to spit at the empty vials on the underside of the belt instead of the target. This occurred rarely but was especially noted during extinction when the fish was not being reinforced. Perhaps to avoid any possible indiscriminant spitting, a dispensing method which did not directly hang over the tank should be employed.

The archer fish and its unique characteristics are excellent subjects for the study of behaviour. The basic operant and ethological information that has come from this study should facilitate future studies involving the archer fish.

While there are potentially a large number of avenues along which future research might procede, two of the more obvious ones will be mentioned.

First, the successful demonstration of VR control of spitting suggests the need to investigate the effects of other basic schedueles of reinforcement on spitting. Such an analysis will provide further evidence on the generality of schedule effects. In addition, the two types of spitting styles observed in this study may interact differentially with schedule type. For example, fish exhibiting the single shot approach would be more likely to come under the effective control of interval, rather than ratio schedules, since the former favor the production of longer intervals between successive responses. This could be easily determined by exposing both types of spitters to interval contingencies.

A second line of research might utilize the present methodology (with some modifications) to study how the variability of spitting is affected by exposure to reinforcement conditions. It is well known, for example, that response characteristics exhibit increased variability under conditions of extinction(Ferster and Skinner, 1957). The spitting response has at least two characteristics which might show this variability; intensity and accuracy. It would then be a rather straight forward matter to generate data relevant to the question of schedule induced response variability. Such data would serve to address both the generality and comparative aspects of the question.

In conclusion, it now appears that the spitting response of the archer fish can come under operant control, and further, that this response can come under control of a variable ratio schedule of reinforcement. The demonstration of VR control of spitting provides a fact which helps explain why foraging in the natural environment persists when only a portion of spits are reinforced.

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FIGURE LEGENDS

Figure 1. Spitting and jumping apparatus.

Figure 2. Jumping and spitting as a function of height.

Figure 3. Jumping and spitting as a function of population size.

Figure 4. Operant conditioning apparatus.

Figure 5. Response and reinforcement as a function of schedule. Fish 1.

Figure 6. Response and reinforcement as a function of schedule. Fish 2.

Figure 7. Response and reinforcement as a function of schedule. Fish 3.

Table 1. Responses in Extinction.

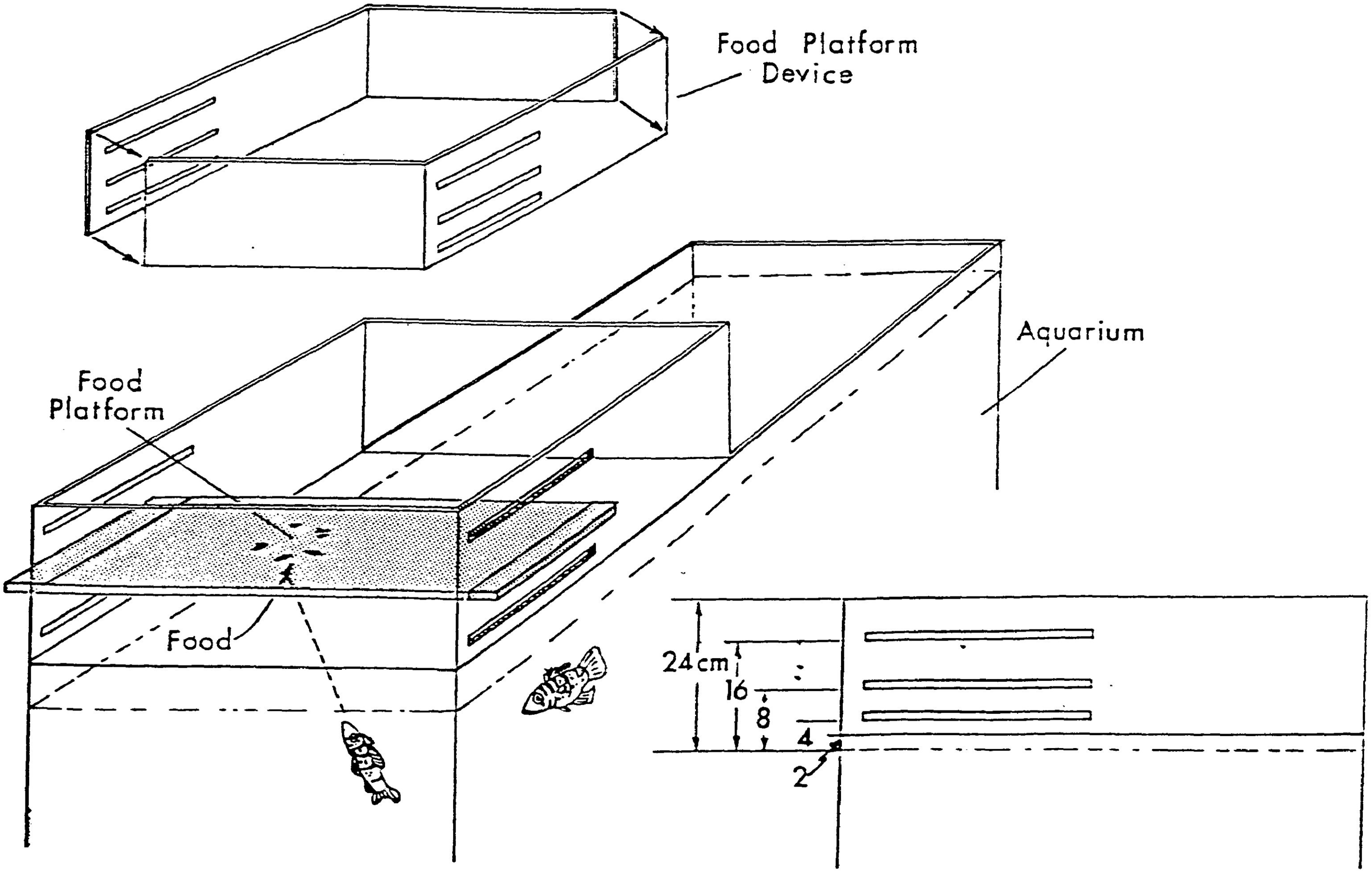

FIG. 1. SPITTING AND JUMPING APPARATUS

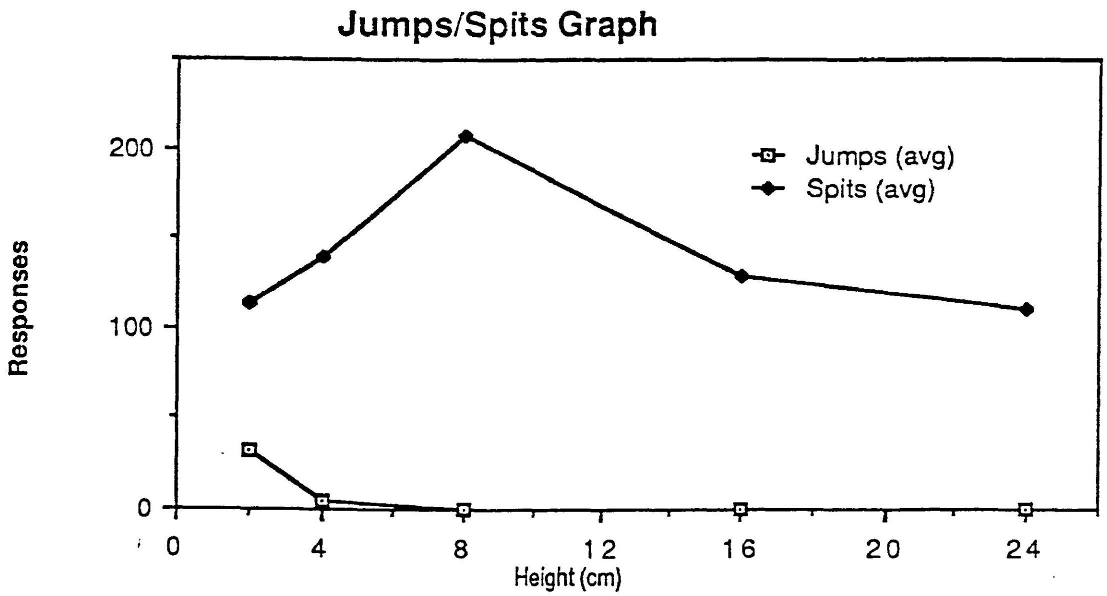

Fig. 2. Jumping and Spitting as a Function of Height

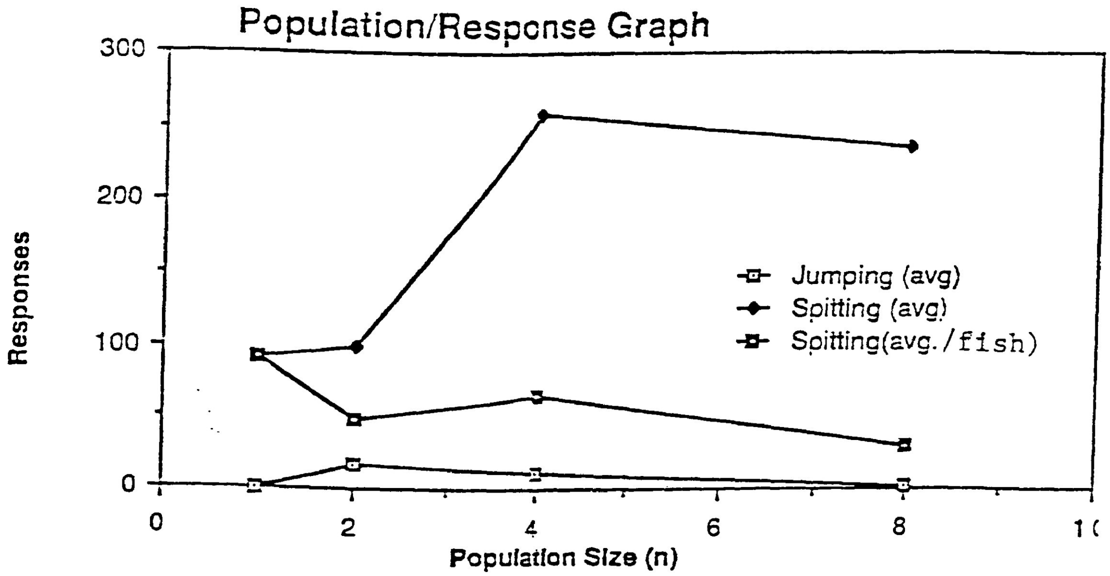

Fig. 3. Jumping and Spitting as a Function of Population Size

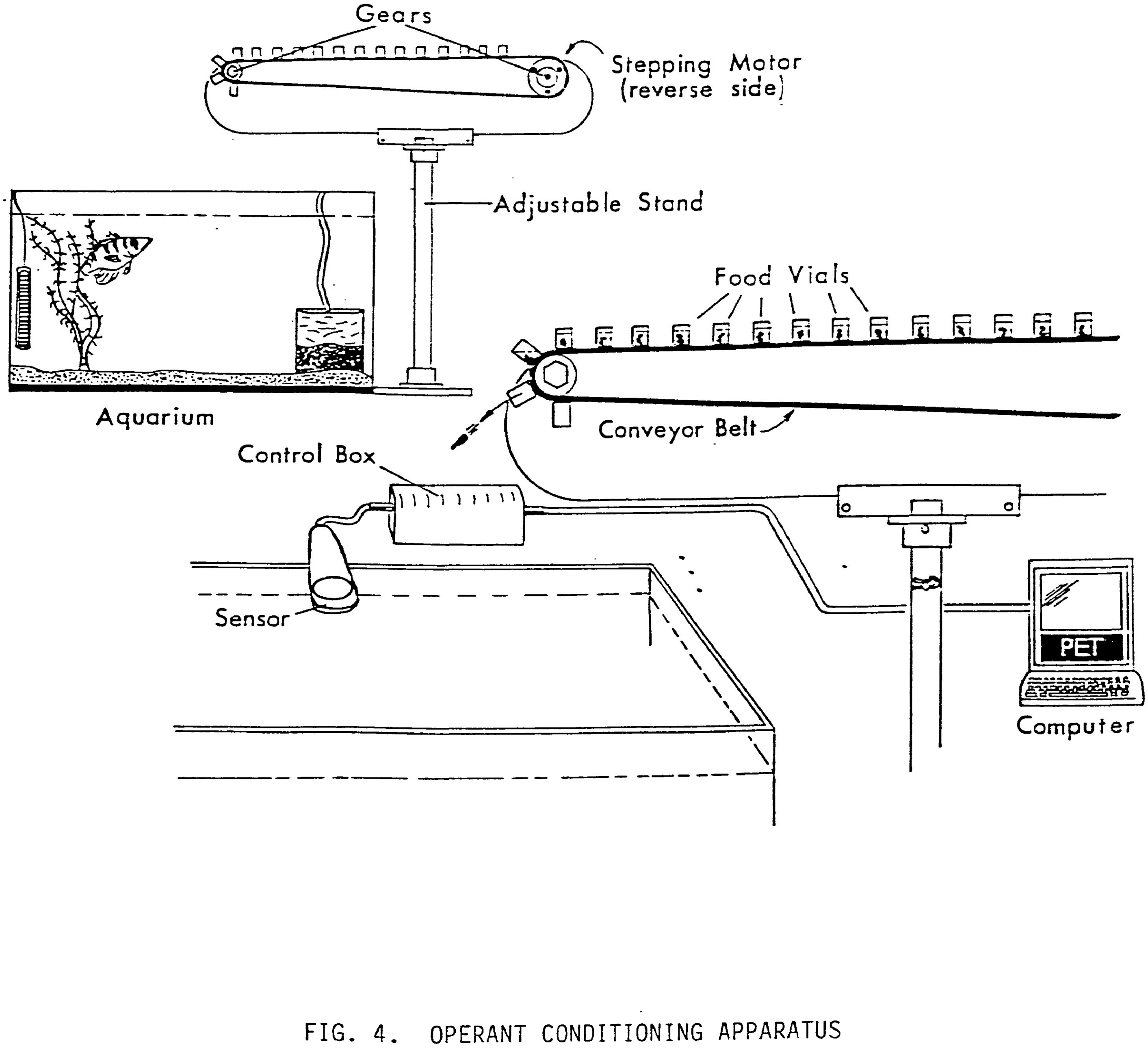

FIG. 4. OPERANT CONDITIONING APPARATUS

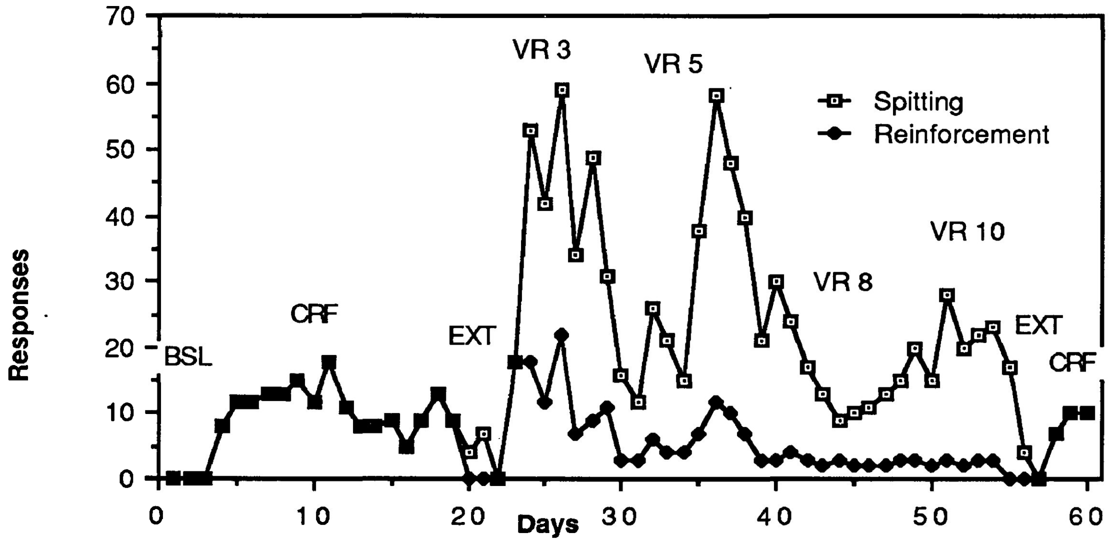

Fig. 5 Response and Reinforcement as a Function of Schedule. Fish 1

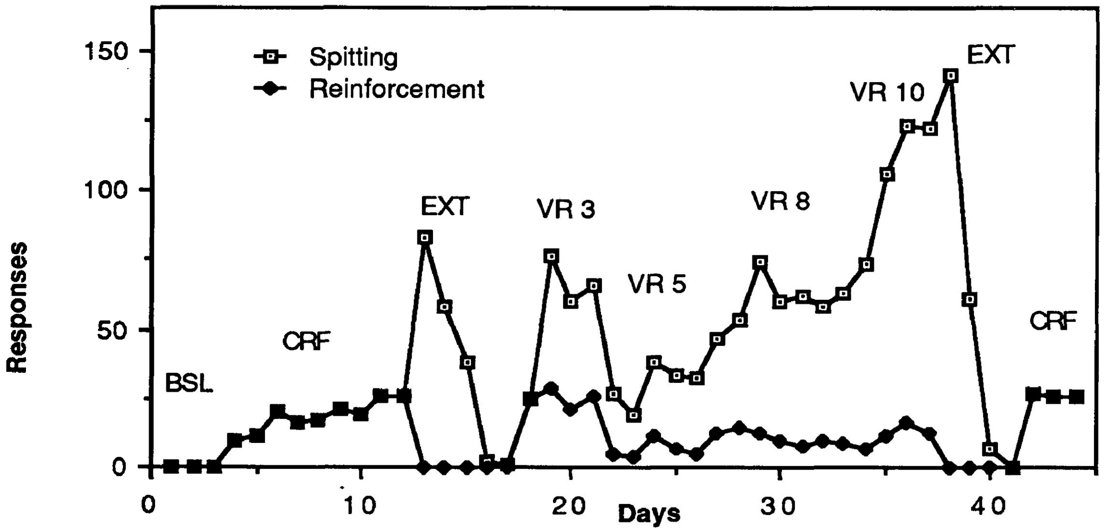

Fig. 6 Response and Reinforcement as a Function of Schedule. Fish 2

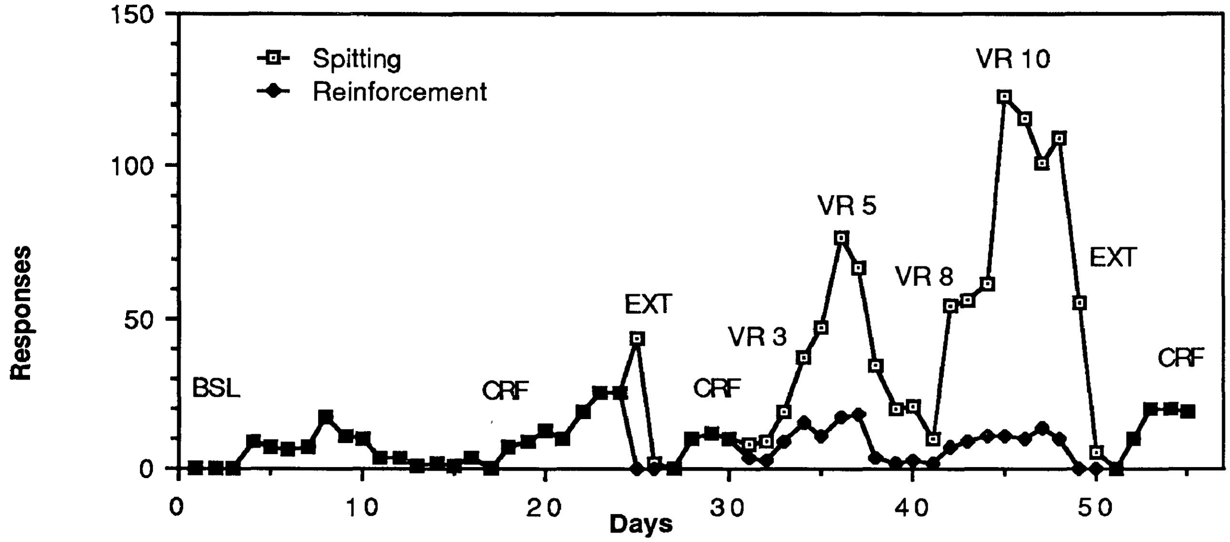

Fig. 7 Response and Reinforcement as a Function of Schedule. Fish 3

TABLE 1 RESPONSES IN EXTINCTION

Fish	Schedule	Day 1	Day 2	Day 3	Day 4	Day 5	Responses
Fish 1	CRF	4	7	0	-	-	11
	VR 10	17	4	0	-	-	21
Fish 2	CRF	83	58	38	2	0	181
	VR 10	141	61	7	0	-	209
Fish 3	CRF	43	2	0	-	-	45
	VR 10	55	5	0	-	-	60