

DEFENSIVE STRATEGIES OF SCHOOLING PREY
UNDER PREDATORY STRESS

by

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ABSTRACT

The strategy and tactics of avoiding a predator by a schooling prey are examined using the specific example of rainbow trout (Salmo gairdneri) chasing single and schooling sockeye salmon (Oncorhynchus nerka) . Three general rules of defensive strategy are developed from the examination of predation as a process and from parallels in modern aerial warfare.

The first rule is based on prey vigilance.

Rule 1. The best strategy from the prey point of view is not to be detected by a predator, and to detect the presence of a predator as soon as possible, preferably before detection. It is best to avoid a chase, which can be achieved by hiding, or moving away, so as to increase the distance from the predator.

The second rule is based on group cohesion.

Rule 2. Individuals and strays from groups are more vulnerable to predators, and school size and structure is limited by signal loss between individuals, therefore, the group should become more compact in spacing when attacked by predators. This will allow the execution of group manoeuvres with minimal group disintegration.

The third rule is based on tactical manoeuvre considerations.

Rule 3. The best manoeuvre that the group can perform, if it detects the predator at a distance that enables the manoeuvre to be executed, is to turn toward the direction of the predator. This enables the individuals to move around the predator when it engages the group. This results in positioning the predator behind and heading away from the group.

The predator was found to use path prediction as an interception strategy and prey used rapid turning manoeuvres as a defensive strategy. The first response of schooling prey was to move away from the path direction of the predator while forming a more compact school. The second response of the school was to turn toward the path of the predator. The third response was rapid school disintegration as each individual turned rapidly and accelerated to a high linear velocity and oscillating angular velocity. Schooling by prey confuses and limits the ability of the predator to path predict. Consequently, predator capture success is greater when chasing single prey.

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INTRODUCTION

Most predation studies have concentrated on the effects of predation rather than investigating its mode. There have been few attempts to define and synthesize the behavioural components of predator-prey systems, contrasted to the many that have described ecological effects. Curio (1976) points out that ecological models of predator-prey systems suffer from unrealistic assumptions concerning behavioural parameters, and that the models could gain immeasurably in realism, precision, and generality by integrating behavioural findings with ecological theory.

This study was aimed at examining one of the least investigated facets of predator-prey systems; the strategy and tactics of avoiding a predator.

The aim was to evolve general rules applicable widely to predation systems, by examining in detail : (1) the evolution and importance of formalized communication behaviour and information handling systems, (2) the components which define the predation process, and (3) the evolution of evasion strategy and tactics. From these examinations, hypotheses generated by synthesis of these theoretical concepts could then be tested by experimental analysis of a predation process.

Observations were made of a predatory fish (rainbow trout (Salmo gairdneri)) attacking schooling and single prey (sockeye salmon (Oncorhyncus nerka)). Also, a study was made of computer designed, gaming simulations of modern air warfare, from which many of the hypotheses concerning evasion strategy and tactics were conceptualized.

ASPECTS OF PREDATION AS A PROCESS

I. Components

Specific types of predator prey interactions, or prey capture/predator avoidance strategies, depend upon the relative importance of basic components of the process. Predation can be considered to be driven by a number of internal factors, such as motivation and physiological status in respect to energy needs (hunger), and has four operational components that can be measured and evaluated with respect to prey capture. These four basic components are (1) search (or perception or awareness), (2) stalk, (3) attack, and (4) subduing of prey. The parameters that define the actions and interactions of these components determine the relative importance of each to any predation strategy. For gregarious prey species, the components that determine predator avoidance and escape strategies are, (1) the perception of predators (vigilance), (2) effect of group structure on defensive manoeuvres, and (3) group re-formation.

It is important that the parameters that define each component be identified, and considered in terms of their interactions and relative importance to the object of prey capture. Parameters which are responsible for prey capture have been defined and examined by Holling (1965), Elliot (1972), Curio (1976), and others. Brock and Riffenburgh (1960),

Howland(1974), Radakov(1973), and Partridge(1980, 1982) are the only researchers (to my knowledge) to date, that have begun to identify and measure parameters that relate to predator avoidance or escape strategies. In order to make hypotheses regarding predator avoidance or escape strategies, the identification of the parameters within each predation component, and their effect on the component interactions, is necessary. To accomplish this end, the level of generality of the study must first be defined.

II. Levels of Generality

The reaction of gregarious prey species to predator stress can be divided into 3 levels of generality .

At the highest level, the group, or school of animals can be considered as an intelligent (capable of directed movement) patch of food for a predator within some environment. The patches can contain different amounts of energy as functions of their mass and quality. The primary concern of studies at this level, relative to predation, rests on the concept of patch detection by predators, their exploitation, and considerations of search times between successful patch detection. These studies have contributed to optimal foraging and optimal patch use theories. In respect to the prey species, optimal predator avoidance strategies are based on functions of predator and prey densities, and environmental heterogeneity (Paloheimo 1971 for example) .

A second and lower level of generality is characterized by studies that focus on the relative behaviour of the predator and prey, once the predator has detected a patch and prepares to utilize the patch for food (attack and subdue). From the predator's point of view, the important considerations are; (1) distance to the patch, (2) probability of approaching the patch undetected (stalk), (3) reaction distance of the patch to the presence of the predator , (4) when to execute an attack with a

high probability of success , (5) relative risk of failure, and consequent energy loss due to capture effort, and (6) relative risk of damage from defensive mechanisms of the patch. An optimal attack strategy can be expressed in terms of maximizing the probability of net energy gain. From the point of view of the gregarious prey species, the important considerations are; (1) distance to the predator, (2) timing of defensive manoeuvres that reduce probability of detection by the predator, (3) timing of manoeuvres that effect structural cohesion of the group, (4) pattern of change with increasing proximity of danger, and (5) timing of manoeuvres that will lead to minimum losses for the group. Optimal evasion or escape strategies can be expressed as group behaviours that optimize an individual's escape probability.

The third level of generality, the most particular, deals with the situation when a predator has detected a group and begins an attack on a selected individual, or a selected portion of the group. At this level the primary concerns are the tactics of escape, or capture. The important considerations at this level are : (1) group structure, relative to the aims of the group and the predator, (2) relative orientation of the prey to the predator at the time of the attack, and to the other members of the prey group, (3) relative distance, velocities ,and acceleration capabilities of both predator and prey, (4) effects of the foregoing on manoeuvrability of predator and prey, (5) reaction distance to the predator or prey, (6) handling time per

prey for the predator, and (7), the contribution of learned components to the behaviour of both predator and prey. The expression of escape or capture tactics depends on the relative importance of these parameters in the context of maximizing the probability of escape or capture. The focus of this investigation is on this third level of generality.

III. Components of Attack and Escape Behaviour

1. Search

It is assumed that all strategies and tactics of predation hinge on whether a predator, or prey can track the other. We can hypothesize therefore that selection has maximized sensory perception or awareness distance, such that the relative positions, and direction of movement of each can be tracked by the other. Conversely; selection has minimized the signals released by predator or prey such that it is more difficult for the other to track it. For example, the crouching behaviour of a lion stalking its prey acts to minimize signals that the prey can perceive.

From the point of view of the prey, the ability to detect and track the predator is mandatory if it is to implement avoidance and escape strategies and tactics. Furthermore, the implementation of such strategies must occur as soon as necessary to maximize escape (or avoidance), probabilities.

From the predator viewpoint, it is necessary to detect prey before being detected, enabling selection of a victim and directing the focus of attack such that detection and defensive manoeuvres by the prey are minimized.

To detect prey, or predators , there has been a great development in searching and vigilance behaviours and mechanisms. From the predator viewpoint, search behaviour can be considered active, in the sense that motor patterns, and scanning of signals are designed to maximize detection of prey. Prey species may not necessarily actively seek out predators, but they also need to detect the presence of a potential predator as soon as possible. This behaviour of prey is termed vigilance (Brown 1975, Smith 1977).

The first rule of defensive strategy is prey vigilance.

Rule 1. The best strategy from the prey point of view is not to be detected by a predator, and to detect the presence of a predator as soon as possible, preferably before detection. It is best to avoid a chase, which can be achieved by hiding, or moving away, so as to increase the distance from the predator.

Presumably, if prey are unable to detect a predator, and are themselves detected, the probability of escape is decreased (this is the basic strategy of ambush predators). If both predator and prey detect each other, then alternative strategies are necessary to ensure capture or escape. Pursuits, such as lions chasing wildebeast, or bass chasing minnows, arise from mutual predator/prey detection.

Habitat heterogeneity is an important component in the

response and evolution of strategies. In open environments, such as grasslands, open waters, and skies, there is little interference to block perception between predators and prey. It would therefore be expected that prey species that evolved in such environments would have developed excellent mechanisms for perception of predators. Pursuit appears to be found primarily in such environments. In heterogenous environments, with complex habitat structure, a predator may lose track of a prey due to the convergence and obscuring of environmental signals with prey signals. Ambush predators evolve in such environments, and prey species evolve cryptic tactics to avoid predation (Edmunds (1974), and Robinson (1969)).

Hamilton (1971) proposed that gregariousness arose as a response of animals in open environments to predation. His rationale is that each animal would seek to hide behind another animal, putting another animal between the predator and itself, reducing the personal risk of capture. Theoretical work by Triesman (1975a, 1975b) and Vine (1971, 1973) support and expand this idea.

The hypotheses that emerge from these concepts, with respect to the defensive strategies and tactics of schooling prey species under predator stress are :

- (1) the structural configuration of schools is constrained by vigilance behaviour.
- (2) the structure of schools functions to a) eliminate blind

spots such that the members on the periphery monitor the complete area around the school, and b) present the least possible target to a searching predator.

Though peripheral members of a school may not consciously monitor for predators, their position enables them to act in this manner. Breder (1976), Lighthill (1975) and Weihs (1973), point out that hydromechanical considerations alone can be used to describe observed structure of schools, but do not explain the observed behaviour of the groups. Breder (1967), Brock and Riffenburgh (1960), and van Olst and Hunter (1970) point out that the spherical shape of schools presents a minimum surface area and that this configuration enables comprehensive monitoring of the surrounding environment.

In gaming simulations of modern air warfare, scenarios which begin with both sides out of contact in a particular airspace, and proceed such that only the aircraft of one side detects the opposing aircraft, always result in loss to the side that does not detect the other. Historically, Johnson (1964) reports that 80% of the 352 aircraft shot down by a German ace during WW II, never saw the enemy aircraft until it was too late.

The environment of earlier air warfare scenarios was relatively open, which led to the belief that only groups of

aircraft could succeed in their missions by employing mutual support. The modern air warfare environment is highly heterogeneous. With the advances in technology, electronic countermeasures (ECM) of modern aircraft function to introduce structural heterogeneity. Thus single aircraft, or pairs, can perform their missions with a minimum of mutual support.

Animals and aircraft have analogous Information Handling Systems (IHS). There are mechanisms that are used to detect predators or prey at long ranges (hearing, olfaction = radar), and short ranges (eyesight= infrared detectors), and mechanisms that maintain contact between individuals (specific displays, physiological adaptations = radio). The ECM of aircraft act to confuse and mislead the signals perceived by the enemy IHS, in a fashion similar to the effect of structural heterogeneity of habitat, interfering with tracking signals between prey and predator. The general rule regarding search and detection aims also applies to aircraft in air warfare scenarios. It is interesting to note that the strategies of air warfare have evolved in an analogous manner to the evolution of gregariousness, with respect to environmental heterogeneity.

2. Group Cohesion

Animals that travel in organized groups must to some extent be able to communicate with, or at least track each other to have cohesive movements. Even in non-hierarchical systems, nearly spontaneous executions of manoeuvres occur, such as turning. Assuming that signals for these responses are generated and travel from individual to individual, and if the IHS model holds, lag times will occur for the evaluation of signals and the execution of decisions. The size of groups of animals living in open environments may be a function of lag time. An adaptation to overcome this problem is moving closer together, decreasing the distance between individuals when important manoeuvres are to be made. Fish schools and bird flocks are known to respond to predation by decreasing the distance between individuals (Radakov 1973).

For example, the author has observed a flock of aggregating starlings split into smaller flocks when rapid turning manoeuvres were initiated by lead elements of the flock. Sometimes the smaller flocks reform into a large flock; but rapid manoeuvres continue to split up large flocks. The splitting is probably due to the signal loss phenomenon. Above a certain group size, the signal loss from the lead elements to the following elements is such that some part of the group will be " out in front " before they realize that the leading elements have turned. High speed films of the manoeuvres of

large flocks could be used to measure the lag times between signal generation to signal loss by the unresponding elements. Recent observation by the author of fish schools consisting of many individuals reveals the same phenomenon.

Presumably, similar problems of signal loss face any gregarious species whose group is large, when it is subjected to predation. If the signal loss causes partial disintegration of group structure such that individuals, or small groups of individuals stray from the main group, the predator would benefit, as smaller groups, or individuals have a reduced escape success in open environments. Adaptations that reduce signal loss, and function to maintain group cohesion are to be expected. Specific inter group displays and communication, reduction of inter individual distance, and observed size limits of groups, can be considered such adaptations (Smith 1977).

Predators try to force strays when attacking groups, (Curio 1975, Elliot 1972), suggesting that strays have reduced escape probabilities. Lions often try to force sick individuals or calves away from herds of wildebeast (Elliot 1972). To reduce the chance of becoming a stray, an animal must be able to respond quickly to sudden manoeuvres of the group. In this respect, the spatial organization of the group is of importance. For the group to act cohesively, the organisms must be able to simultaneously track each other within the group , and some at least must track the predator.

The second rule of defensive strategy is based on group cohesion.

Rule 2. Individuals and strays from groups are more vulnerable to predators, and school size and structure is limited by signal loss; therefore, the group should become more compact in spacing when attacked by predators. This will allow the execution of group manoeuvres with minimal group disintegration.

The manoeuvres of schools in response to predators are also a function of the approach direction of the predator. Radakov (1973) points out that in head on situations, school response is to simply avoid collision with the predator. Individuals in the path of the predator displace to a species specific characteristic angle and distance from the predator as it passes through the school. These displacements affect the school structure by forcing similar displacement of the individuals throughout the remainder of the group. This results in the splitting of the school just ahead of the predator, and its re-formation behind it.

The same strategy is employed in airwar simulations to avoid missiles or intercepting aircraft. The defending aircraft (the " prey ") move into the path of the missile or interceptors (" the predator"), as the missile or interceptor

and the defending aircraft are about to come together, the defender rolls away from the attacker. This is identical in form to the fish example and presumes that the predator has been spotted. The manoeuvre functions to increase separation distance between prey and predator.

If the predator attacks the school from any position relative to the school, and if the prey have detected the predator at a distance that enables them to execute a response, the response to the threat is to face the predator.

Rule 3. The best manoeuvre that the group can perform , if it detects the predator at a distance that enables the manoeuvre to be executed, is to turn toward the direction of the predator. This enables the individuals to displace around the predator when it engages the group. This results in positioning the predator behind and heading away from the group direction. Before the predator can turn around, the separation distance between prey and predator, and the prey awareness of the threat, can make further attacks by the predator unlikely.

The hypotheses that emerge from these considerations are :

- 1) School size is limited by the signal loss phenomenon.
- 2) The signal loss is measurable, and is important in the regulation of group cohesion.

- 3) The group tends to remain together, and inter-individual distance is decreased under predator stress, because lone individuals have a higher risk of capture in open environments.
- 4) Predator attack direction has direct consequences on the manoeuvres and orientation of the group.
- 5) Rules 2 and 3 are universal phenomenon applicable to all analogous predation situations.
- 6) Perception and awareness through physical mechanisms is optimized to function such that the time between detection of the predator, and the execution of defensive manoeuvres is maximized.
- 7) The manoeuvre of facing toward, and displacing around the predator may act to confuse the predator by flooding the IHS with a large number of tracking problems simultaneously. This may partially explain why lone individuals are more vulnerable to predation in open environments.

3. Individual Tactics

Group disintegration occurs when the predator succeeds in getting so close to the group that detection was not made before

the attack commenced. In such cases, the capture success probability of the predator is very high .

The group's best response in such a circumstance is to disperse away from the predator. The dispersal is usually performed without order, and the group appears to disintegrate as a cohesive structure. The group can however, subsequently reform.

If the predator has not yet captured a prey individual when the group disintegrates, the disorderly movement could incidentally act to confuse predator tracking of the selected target. When this confusion occurs, the predator must locate and track another target. This usually results in the classic scenario of a predator chasing a desperately manoeuvring prey, as described by Howland (1974) for example.

Howland (1974) pointed out that the tactics of defense in this situation are based on the relative ability of prey and predator with respect to speed and manoeuvrability. These are the result of the structural components that function together to describe the characteristic locomotion pattern, or kinematics, of the organism.

If a predator is chasing a prey individual, presumably it is tracking the prey position relative to itself and further, the predator must anticipate the direction that the prey will

take. To solve this tracking problem the predator must have a capacity to evaluate a lead pursuit function. The lead pursuit tactic defines a point that is ahead of the prey and the predator aims for this point. As the distance between the predator and prey decreases, the lead point converges to the prey. Capture is at the convergence of the lead point and the prey.

The prey has several defensive options: 1) decouple itself from the predator IHS by hiding, or manoeuvre into a position such that the predator cannot track it. 2) outrun the predator, or 3) stop and fight the predator.

In open environments it is not often possible to hide from a chasing predator unless the prey species finds some cover that is impassable to the predator. Predators have co-evolved with their prey; speed advantages by prey are accordingly rare. Further, for fish species, the prey is usually smaller, and for physical reasons is slower but more manoeuvrable. Many animals that have the capability to fight their predators do so only as a last resort, no doubt because of the high risk of injury or death, the greater likelihood of fatigue, and the possibility that the predator can continue to track the prey. The best defensive tactic by the prey is to outmanoeuvre the predator. The results of a successful defensive manoeuvre is that the prey is in a position that (1) decouples it from the predator's IHS, and (2) reduces the probability of a successful attack if the

predator regains its perception of the prey.

If the prey has a greater maximum velocity, acceleration, and endurance, the simple, and optimal manoeuvre is movement directly away from the predator at the maximum velocity. In such a case, the predator will never catch the prey (if there was any distance that initially separated them). If the predator is capable of greater acceleration, velocity, or endurance, then the straight ahead run of the prey is not an effective anti-capture tactic, for the predator will always catch up with the prey. The straight ahead manoeuvre is rarely seen in nature, probably because predators would learn from experience not to chase species whose ability for sustained maximum velocity and acceleration are greater than theirs.

Observations of chase scenarios often reveal desperate turning manoeuvres by both prey and predator as they attempt to gain a position of advantage. The position of advantage for the prey is that which maximizes the escape probability. Conversely, the position of advantage for the predator is the position that maximizes the probability of prey capture.

Howland (1974) states that the relative turning ability of the predator and prey is the critical factor in determining the outcome of an attack. If the prey can turn more sharply, and if the initial separation is large, the prey will always escape. If the predator has a better relative turning ability, the prey

will never escape. These conclusions are too simplistic and unrealistic. It is more critical to know when to execute a turning manoeuvre than to have the ability to turn sharply.

When an animal (aircraft, or any other moving object) begins a turning manoeuvre, the centripetal forces needed to maintain a circular path result in loss of momentum and velocity. Thus, the decision to execute a turning manoeuvre must be made with care. The result of sustaining a turn is that velocity will drop to some level that is a function of the forces necessary to maintain that turn; and is far below the maximum linear velocity. If the turn is attempted too soon, the decrease in prey velocity makes the closure rate of the predator much greater; or enables the predator to decelerate and match the turn of the prey. This negates any defensive advantage and probably decreases the probability of escape.

There are at least four basic defensive turning manoeuvres that were conceived in air warfare simulations, and that are also observed in animals. The first manoeuvre is called the maximum performance turn and is executed by entering, and sustaining the minimum possible circular path at some constant velocity. The timing of this manoeuvre is difficult to judge; improper timing can be disadvantageous (for the reasons stated in the previous paragraph).

The second manoeuvre is called the defensive turn. As the

predator approaches the prey, the prey begins to turn slowly away from the predator. As the predator approaches, the prey continues to turn at a greater rate; but still in the same direction. When the predator is almost in a position for capture; the prey turns at a maximum rate. If the predator is travelling at a greater velocity than the prey, and was maintaining a lead pursuit, there is a high probability that it will "overshoot" the prey when the maximum turn portion of the manoeuvre is executed. This can effectively place the prey in a position of advantage. The timing for executing the different phases of this manoeuvre is critical and depends on the relative kinematic parameters of the particular predator and prey. While turning, the prey also has the advantage of being able to continually track the predator. Presumably this allows the prey to judge closure rates and other parameters relative to proper timing.

The third manoeuvre is called the reversal. If the predator detects that the prey has begun a defensive turn, it may decelerate in order to continue the lead pursuit and match the prey turning manoeuvre. If the prey realizes the predator counter tactic, it can wait until the predator has committed itself to the turn. Then as the predator closes with the prey; the prey can execute a turn 180 degrees to the previous direction. Properly executed, this manoeuvre will cause the predator to "overshoot", and face in one direction while the prey faces another, and usually opposite direction. The ability

of the prey to continually track the predator is of importance to the judicious timing of the manoeuvre. Poorly timed, the prey will be in the same difficulty as with the maximum performance turn.

The fourth manoeuvre is called the scissors. This is a series of reversals and results in a zig-zag course, characteristic of many chase scenarios. This manoeuvre is used to counter a predator that correctly anticipates the original reversal. Again, timing is critical. The zig-zagging of the prey may also function to confuse the predator. The scissors manoeuvre quickly establishes a pattern, making anticipation easier for the predator. The cessation of the manoeuvre by the prey and the beginning of an unanticipated manoeuvre (with respect to the predator), can result in tracking loss by the predator.

The testing of these hypothesized manoeuvres rests on the analysis of velocity and turning performances in a chase sequence.

METHODS AND MATERIALS- GENERAL

I THE PREY

The prey used throughout were juvenile sockeye salmon (Oncorhyncus nerka), laboratory reared at 9 C in freshwater and fed Oregon Moist pellets daily. For experimental purposes, fish of total length 75 to 100 mm were used.

The first series of observations consisted of transferring a single fish from the rearing container (45 gal. Fibreglass tank), to the predation arena. The fish was left for 3 days to acclimate. For the second series of observations , 6 to 12 fish were introduced to the arena and left for 3 days to acclimate. After filming, the fish were removed to a 45 gal. tank.

II THE PREDATOR

The predator used throughout were adult rainbow trout (Salmo gairdneri), that prey naturally on juvenile sockeye salmon. The trout were taken from a laboratory reared population and ranged from 300 to 350 mm in total length. Three predators were used in the experiments. They were held separately and fed exclusively on both dead and live juvenile sockeye.

One trout at a time was placed in the holding portion of the filming tank. Over a period of two weeks, the trout were conditioned to accept and chase juvenile Sockeye. Before filming, a trout was not fed for 3 days.

III APPARATUS

1) The Predation Arena

The predation arena was a large (300 x 240 x 30 cm) fiberglass aquarium that was divided into two sections of 225 x 240 x 30 cm and 75 x 240 x 30 cm by a white plexiglass barrier. The predator-prey interactions were observed and filmed in the larger section, while the smaller section was the predator holding area. The walls of the arena were constructed of translucent fiberglass while the bottom was uniformly white fiberglass to provide contrast between fish and background. The predator could be released into the arena via a sliding plexiglass door on the barrier.

Viewing and filming was accomplished indirectly via a large mirror mounted at 45 degrees. A wide angle (10 mm) lens on a Bolex 16 mm Reflex camera was used to record the entire 225 x 240 x 30 cm arena on one frame of 16 mm film with minimal

distortion (Fig. 1).

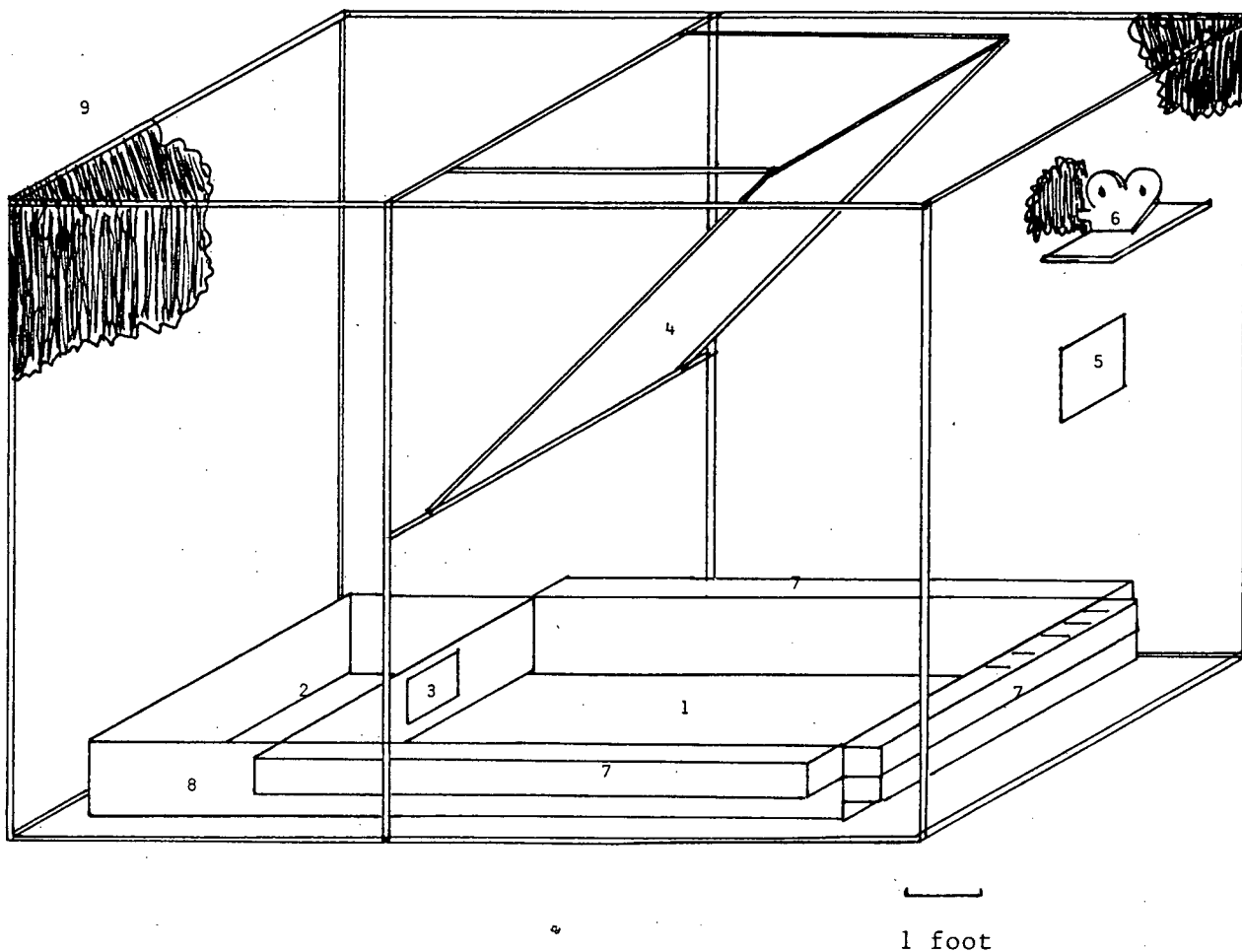
Filming was run at 24 frames per sec., at f 2.8 , using a Body Motor drive mounted on the camera. This was the maximum filming speed possible with the Bolex Motor. The lens to water surface distance was 3.2 m. PLUS -X reversal film of 400 ASA at normal processing was used to record the interactions.

Three banks of 240 cm flourescent lights in groups of four were constructed along the translucent sides of the arena and covered with light baffles to eliminate stray reflections. These lights provided even, diffuse illumination throughout the arena. The entire arena was housed in a steel frame and covered with black felt. This eliminated stray light and reflections into the arena, and provided a barrier between the fish and experimenter.

Water level was maintained at 10 cm to make the interactions essentially two dimensional, and kept at 9°C by the use of an automatic flowthrough system and recirculation pump. The systems were shut off and the tank left to stabilize for one hour before any filming was done in order to eliminate any effects of water currents.

Preliminary observations indicated that both predator and prey would react to the noise from the camera. To alleviate this problem, the fish were trained to ignore the camera noise by running the empty camera during regular feeding schedules.

Figure 1 The Arena for observing predation of sockeye salmon (Oncorhynchus nerka) by rainbow trout (Salmo gairdneri)



- 1 interaction arena
- 2 Predator holding area
- 3 Sliding release door
- 4 Mirror
- 5 one-way glass Viewing port
- 6 Camera
- 7 Light Banks
- 8 8 ft x 10 ft Fibreglass tank
- 9 Light proof felt covering entire arena

2) Filming

When it was judged that all factors were stabilized, the predator was released into the arena via the sliding door. The camera was switched on when the experimenter felt that a chase was imminent. From previous observations, the experimenter was able to predict with accuracy when chases would occur.

3) Analysis Of Film

All films were examined on a PCD-16 MOTION ANALYZER with a Vanguard 16 mm Projection Head. A PCD Digitizer and Techtran Disk Drive attached to a Hazeltine 1500 terminal were used to record directly onto disk the frame by frame x and y coordinate position data for predator and prey.

For each chase sequence the x and y positions of the predator and prey from a standard reference point were measured using the cross-hair viewfinder of the digitizer. The cross-hair was placed on the central axis of each fish, approximately $1/3$ of the body length from the snout. This position was chosen because it is close to the body center of gravity, least effect from the natural oscillations of swimming motion. Twenty chase sequences were filmed for each observational series. The

sequences ranged from 75 to 150 frames in length providing 150 to 300 x-y position observations per sequence. The time interval between each frame was $1/24$ sec. For the second series of experiments 6 to 12 fish were used, yielding up to 2400 observations per sequence.

To reduce edge effects, only those interactions that occurred near the center of the arena were used in data analysis. The x,y position data were read onto tape and disk by a PDP-11 computer and the relative kinematic data ie. Position, velocity, acceleration, orientation, and closure distance were calculated by computer programs written in Fortran IV. Some data were analysed on the APPLE II Plus micro-computer, programmed in Basic.

IV Measurement of Variables

1) Position Variables

At any time t , X_1, Y_1 refer to the predator position relative to a reference point, defined as $X_r = 0, Y_r = 0$, the bottom left corner of the predation arena. X_2, Y_2 refer to the prey position from the same reference point. C , the closure distance was then calculated as

$$C = \{ (X_2 - X_1)^2 + (Y_2 - Y_1)^2 \}^{1/2} \quad (1)$$

and measures the straight line distance between predator and prey (Fig. 2) .

The predator direction angle (θ_1), is measured relative to the reference point as the direction along the X axis equal to 0.0 degrees/radians. At each time interval θ_1 is calculated by

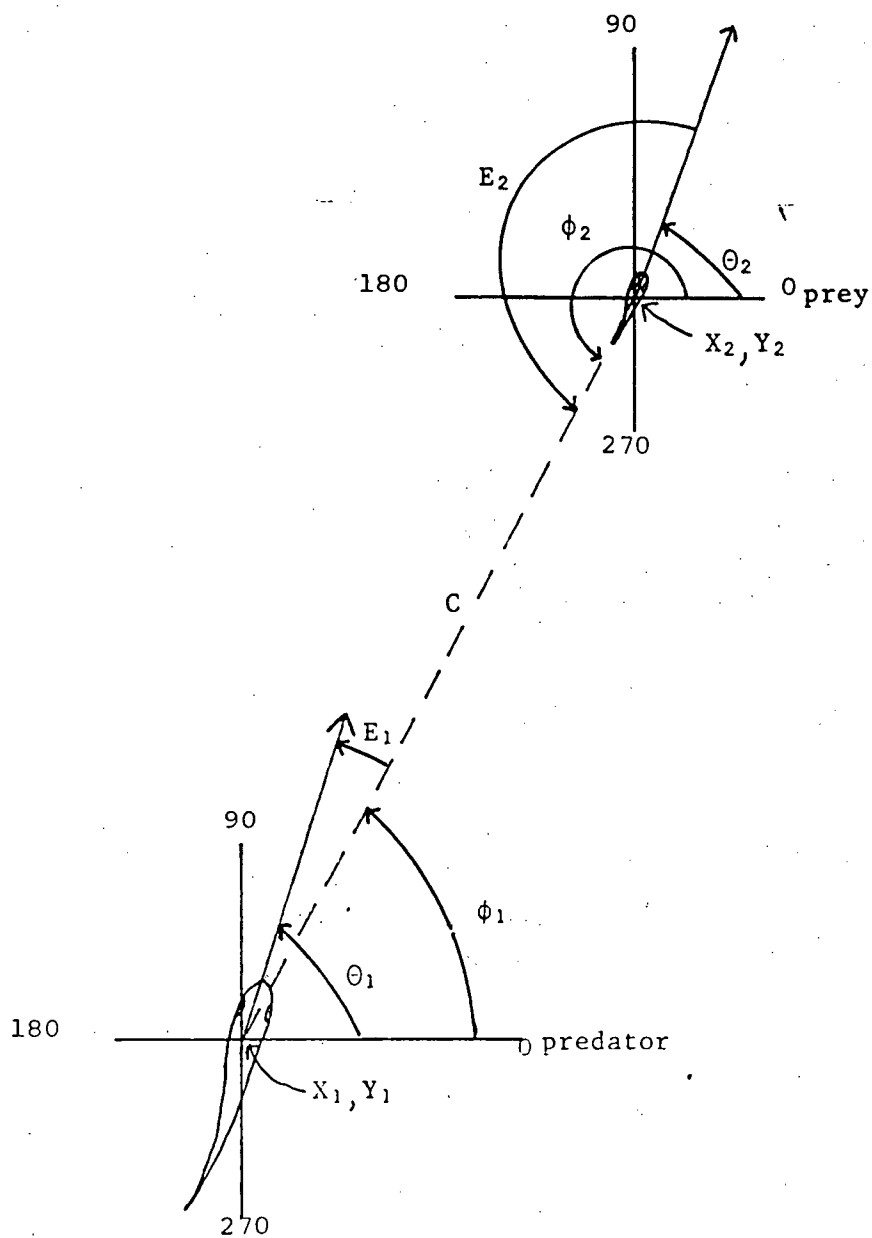
$$\theta_{1(t)} = \tan^{-1} \left[\frac{Y_{1(t)} - Y_{1(t-1)}}{X_{1(t)} - X_{1(t-1)}} \right] \quad 360^\circ > \theta_{1t} > 0^\circ \quad (2)$$

The prey direction angle (θ_2) was calculated similarly using the prey co-ordinate data.

ϕ_1 is the prey position angle and is the angle between the straight line from predator to prey and the reference direction.

Figure 2 Position variables measured at each time frame.
X1,Y1 and X2,Y2 refer to the coordinates of the predator and prey respectively. θ_1, θ_2 are the direction of travel for predator and prey. E_1, E_2 are the error tracking angle and offset angle. ϕ_1, ϕ_2 are the direction angles for predator and prey.

Figure 2. Position variables measured at each time frame.



C is the Closure Distance

This is the direction the predator would be facing if it pointed directly at the prey. It is calculated by

$$\phi_{1(t)} = \tan^{-1} \left(\frac{Y_2(t) - Y_1(t)}{X_2(t) - X_1(t)} \right) \quad 360^\circ > \phi_{1t} > 0^\circ \quad (3)$$

ϕ_{2t} is the predator position angle and is the angle between the straight line from prey to predator and the reference direction. ϕ_2 is calculated by

$$\phi_{2(t)} = \tan^{-1} \left(\frac{Y_1(t) - Y_2(t)}{X_1(t) - X_2(t)} \right) \quad 360^\circ > \phi_{2t} > 0^\circ \quad (4)$$

This is the direction the prey would face if it faced directly at the predator. E_1 is the tracking error angle (also called lead angle) and is defined as the angular difference between the predator current heading and the prey position angle. This is a measure of the angular difference between where the predator is heading and where the prey is. E_1 is calculated as

$$E_1(t) = \{ \theta_1(t) - \phi_{1(t)} \} \quad 180^\circ > E_1 > -180^\circ \quad (5)$$

This value was adjusted such that if the prey was to the right of the predator, (ie. $\phi_{1(t)} > \theta_1(t)$) then E_{1t} was multiplied by minus 1. Negative values of $E_{1(t)}$ indicate that the prey was to the right of the predator, positive values of E_{1t} indicate that the prey position was to the left of the predator. This convention was adopted to measure changes in the predator heading in response to prey position. Thus, $\Delta\theta_1$ was negative for

right turns and positive for left turns.

$E_2(t)$ is a measure of the threat angle, or angle off, and is calculated by

$$E_2(t) = \{ \theta_2(t) - \phi_2(t) \} \quad 180^\circ > E_2 > -180^\circ \quad (6)$$

This value measures the angular difference between the prey heading and the predator position angle. This value was adjusted such that if the predator was to the right of the prey, E_2 was negative. The rationale for this adjustment was the same as that for E_1 .

2) Kinematic Variables

For each frame at time t , velocity of both predator and prey (V_1t and V_2t) were calculated by

$$V_1(t) = \{ (\Delta X_1)^2 + (\Delta Y_1)^2 \} / \Delta t \quad (7)$$

$$V_2(t) = \{ (\Delta X_2)^2 + (\Delta Y_2)^2 \} / \Delta t \quad (8)$$

where $\Delta X = X(t+1) - X(t)$ and $\Delta Y = Y(t+1) - Y(t)$ and t is the time difference between frames. For this study,

$t = .01467$ sec., or $1/24$ sec., and is the reciprocal of filming speed.

Angular velocities of predator and prey (W_1 and W_2) were calculated by

$$W_1(t) = \{ \Delta \theta_1 / \Delta t \} = \{ \theta_1(t+1) - \theta_1(t) \} / \{ (t+1) - t \} \quad (9)$$

$$W_2(t) = \{ \Delta \theta_2 / \Delta t \} = \{ \theta_2(t+1) - \theta_2(t) \} / \{ (t+1) - t \} \quad (10)$$

where θ_1 and θ_2 are the direction of travel of predator and prey. Acceleration was calculated by

$$a_1(t) = \{ \Delta V_1 / \Delta t \} = \{ V_1(t+1) - V_1(t) \} / \{ (t+1) - t \} \quad (11)$$

$$a_2(t) = \{ \Delta V_2 / \Delta t \} = \{ V_2(t+1) - V_2(t) \} / \{ (t+1) - t \} \quad (12)$$

and angular acceleration by

$$\dot{\omega}_1(t) = \{ \Delta W_1 / \Delta t \} = \{ W_1(t+1) - W_1(t) \} / \{ (t+1) - t \} \quad (13)$$

$$\dot{\omega}_2(t) = \{ \Delta W_2 / \Delta t \} = \{ W_2(t+1) - W_2(t) \} / \{ (t+1) - t \} \quad (14)$$

The time to maximum velocity K^{-1} was calculated from

$$X_t = X_0 + V_m t - (V_m - v_0) (1 - e^{-kt}) / k \quad (15)$$

(Okubo 1980, Elliot et al 1977). $X(t)$ is the displacement in

time t , V_m is the maximum velocity , V_o is the starting velocity, and X is the starting position.

3) Interception Variables (Fig. 3)

At each frame , from position and kinematic variables, the intercept coefficients A and B , the lead angle BA , cross track angle AA , and orientation angle CA were calculated as follows:

At time $t + 1$ the predator position can be described as

$$\begin{aligned} X_{t+1} &= X_t + B \cos \theta_{1t} \\ Y_{t+1} &= Y_t + B \sin \theta_{1t} \end{aligned} \quad (16)$$

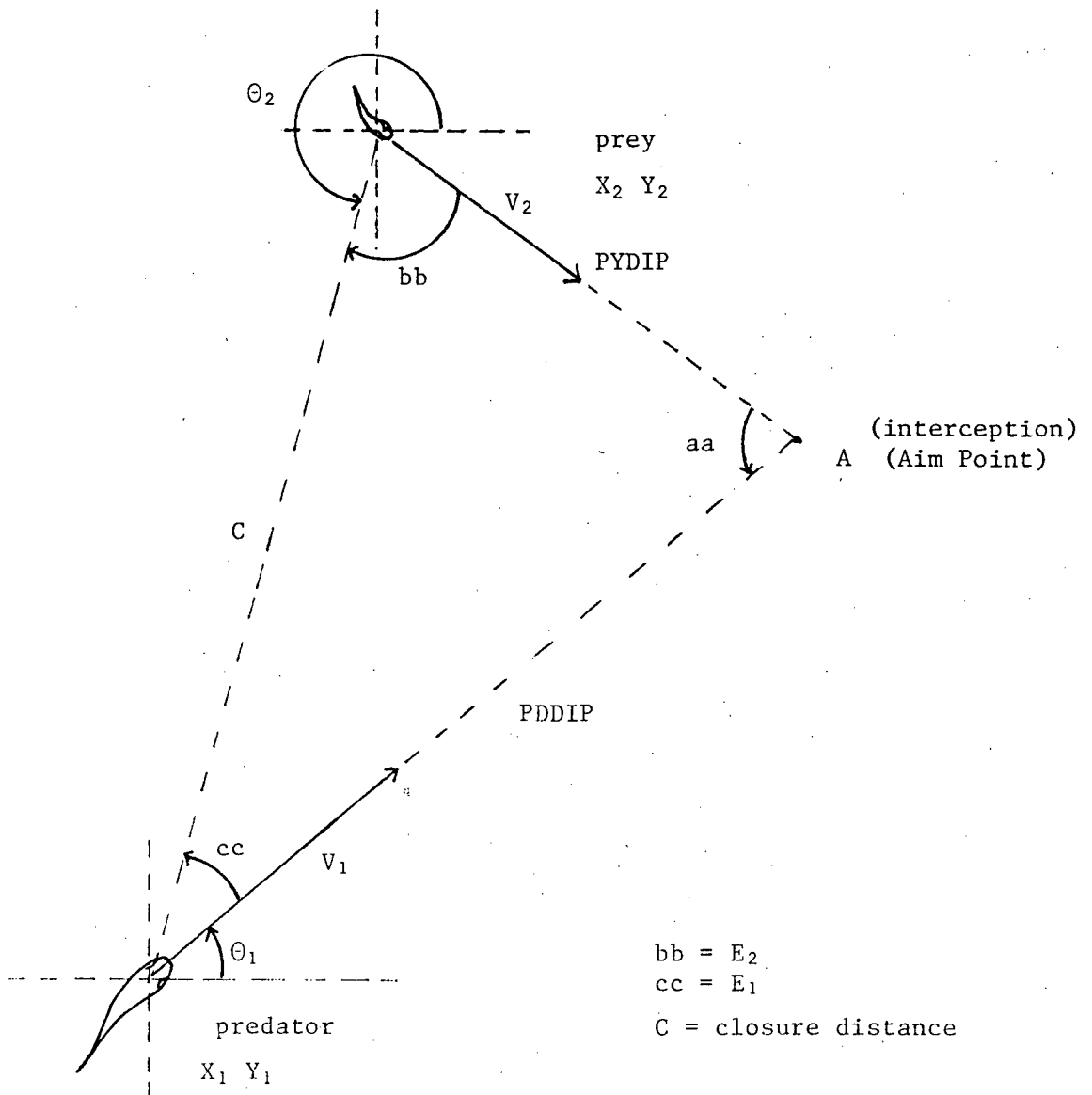
and the prey position as

$$\begin{aligned} X'_{t+1} &= X'_t + A \cos \theta_{2t} \\ Y'_{t+1} &= Y'_t + A \sin \theta_{2t} \end{aligned} \quad (17)$$

If the predator is to capture the prey, then their paths should cross such that

Figure 3 Interception variables calculated at each time frame. V_1, V_2 are the respective linear velocity vectors for predator and prey. C is the closure distance. Point A is the intercept point and PDDIP is the predator distance to the intercept point, PYDIP is the prey distance to the intercept point.

Figure 3. Interception Variables Calculated at each time frame.



$$X_t = X_t'$$

$$Y_t = Y'_t$$

(18)

At this point

$$X_t + B \cos \theta_{1t} = X'_t + A \cos \theta_{2t}$$

$$Y_t + B \sin \theta_{1t} = Y'_t + A \sin \theta_{2t}$$

(19)

Solving for B and A (Appendix 1).

$$B_t = \{ (X'_t - X_t) \sin \Theta_{2_t} + (Y_t - Y'_t) \cos \Theta_{2_t} \} / \{ \sin(\Theta_{2_t} - \Theta_{1_t}) \} \quad (20)$$

$$A_t = \{ (X_t - X'_t) \sin \Theta_{1_t} + (Y_t - Y'_t) \cos \Theta_{1_t} \} / \{ \sin(\Theta_{1_t} - \Theta_{2_t}) \} \quad (21)$$

The point where the paths cross (if it exists) is

$$Ax_t = X_t + B_t \cos \Theta_{1t} = X'_t + A_t \cos \Theta_{2t}$$

$$A y_t = Y_t + B_t \sin \Theta_{1t} = Y'_t + A_t \sin \Theta_{2t}$$

(22)

The values of A and B may be interpreted as follows;

both positive:

intercept at some subsequent time
(aim point A_x, A_y ahead of prey)

A positive B negative

intercept point behind predator

(predator moving away from prey)

A negative B positive

intercept point behind prey

both negative

aim point behind both predator
and prey (moving away from each
other) .

The angles BA and CA are equal respectively to E1 (tracking angle) and E2 (threat angle) .

At each frame, the Time to Closest Approach and Distance at Closest Approach were calculated from the positions of the predator and prey. The predator position in each frame may be represented as

$$\begin{aligned} X_{t+1} &= X_t + U_1 t \\ Y_{t+1} &= Y_t + V_1 t \end{aligned} \quad (23)$$

where U_1 is the velocity component in the X direction and V_1 is the velocity component in the Y direction. Similarly, the prey position in each frame may be represented as

$$\begin{aligned} X'_{t+1} &= X'_t + U_2 t \\ Y'_{t+1} &= Y'_t + V_2 t \end{aligned} \quad (24)$$

where U_2 and V_2 are as above but refer to the prey.

At time t , the distance between predator and prey is

$$D_t = \{ (X_t - X'_t)^2 + (Y_t - Y'_t)^2 \}^{1/2} \quad (25)$$

Taking the first derivative of this equation with respect to t , we find

$$\frac{d(D^2)}{dt} = \left\{ \{ (X_t + U_1 t) - (X'_t - U_2 t) \}^2 + \{ (Y_t - V_1 t) - (Y'_t - V_2 t) \}^2 \right\} \quad (26)$$

when $d(D^2)/(dt) = 0.0$ the Time to Closest Approach is

$$t^* = \frac{\{ -(X_t - X'_t)(U_1 - U_2) - (Y_t - Y'_t)(V_1 - V_2) \}}{\{ (V_1 - V_2)^2 + (U_1 - U_2)^2 \}} \quad (27)$$

By substituting t^* in equation 23 the point at closest approach is

$$\begin{aligned} X_{t+1}^* &= X_t + U_1 t^* \\ Y_{t+1}^* &= Y_t + V_1 t^* \end{aligned} \quad (28)$$

Similarly the quantities X'^* and Y'^* can be calculated, and the Distance at Closest Approach is

$$D_t^* = \{ (X_{t+1}^* - X'_{t+1}^*)^2 + (Y_{t+1}^* - Y'_{t+1}^*)^2 \}^{1/2} \quad (29)$$

(appendix 2 gives the derivation of t^* and D^*).

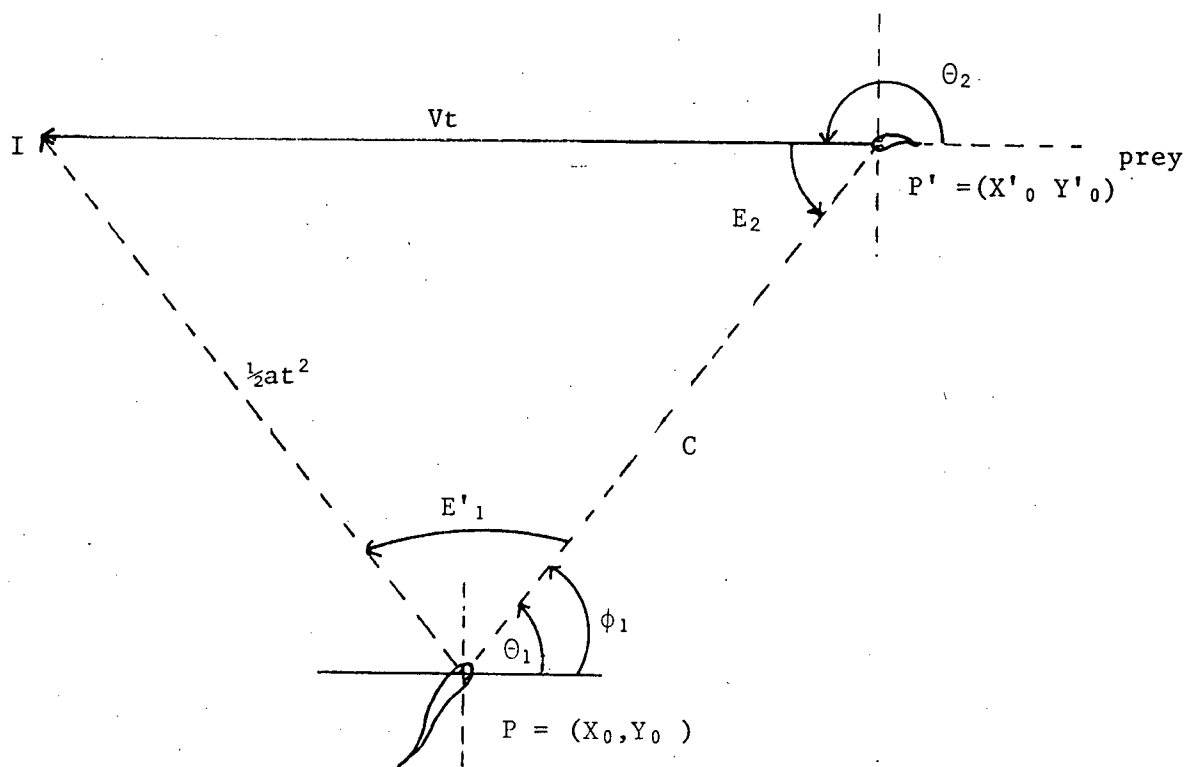
Regardless of the model used to analyze predator-prey kinematics, the concepts of Time to Closest Approach and Distance at Closest Approach are the most important. The Time to Closest Approach can be interpreted as the time at which the distance between the predator and prey will be minimized, given the current position, orientation, and kinematics of both. The Distance at Closest Approach is the distance between predator and prey at this time. If a predator is to capture the prey, then at some time in the future, the distance between them must be minimized to some prey non-escape threshold. Regardless of t^* , if D^* is at 0 or some minimum, then there is indication that the predator is tracking the prey and is adjusting its kinematics accordingly. Theoretically, capture should occur when both t^* and D^* are 0 ; predator and prey are at the same point at the same time.

4) Analysis of Chase Sequences

There are 3 possible intercept strategies that a predator may employ to converge with an intended prey. The first and simplest is for the predator to calculate the quarry flight path, using information integrated upon first sighting, and then to calculate an interception course. The geometry and kinematics for this strategy are presented in Fig. 4, using the

Figure 4 Interception geometry for strategy I. Notation is as in figures 2 and 3. See text for full explanation.

Figure 4. Interception Geometry for Strategy I.



C = Closure Distance

At point I : $(X_t, Y_t) = (X'_t, Y'_t)$

angular conventions presented earlier. To achieve an interception course, the predator needs to know at first sighting, in addition to its own kinematic ability :

- (1) the angular position of the prey ϕ_1 .
- (2) the angular velocity of the prey relative to the predator (dE_2/dt).
- (3) the linear velocity (V_2) of the prey.
- (4) the distance to the prey, CLD.

Assuming that the predator begins with $V_1 = 0.0$ and is oriented toward the prey ($\phi_1 = \theta_1$) then the angular velocity of the prey relative to the predator can be measured as (Fig 5)

$$g^* = \{ V_2 \sin E_2 / CLD \} \quad (30)$$

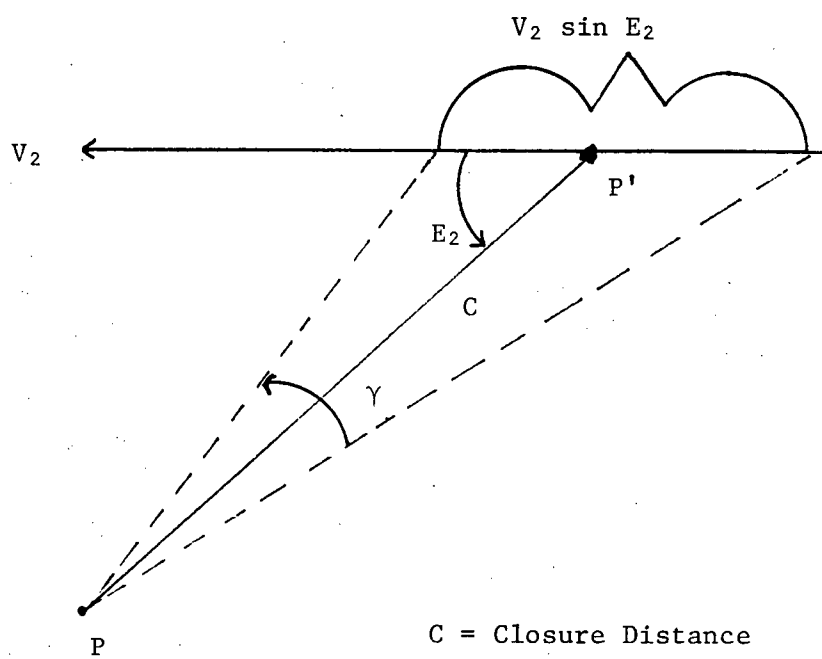
If V_2 remains constant the predator has a direct measurement of the relative course of the prey by

$$E_2 = \sin^{-1} \{ g^* \cdot CLD / V_2 \} \quad (31)$$

If $\theta_1 \neq \phi_1$ then the predator can orient its position to equalize these quantities.

Figure 5 Determination of prey angular velocity . See text
for full explanation.

Figure 5. Determination of prey angular velocity.



To successfully intercept, the predator must travel PI in the same time as the prey travels P'I, arriving at I. To accomplish this, it is necessary for the predator to calculate E'2 and to change orientation such that $\theta_{t+1} = E'2$.

This is done by first calculating the time to interception given E2 at first sighting and the kinematic parameters. By applying the cosine rule to triangle PP'I (Fig. 4), the time to intercept is calculated as

$$P'I^2 = (P'I^2 - 2P'IP'P\cos E_2)^{\frac{1}{2}} \quad (32)$$

Since $P'I = V_2t$, $PI = At^2/2$ and $P'P=C$, then

$$0.0 = \frac{\{ V^2t^2 + (CLD)^2 - .25 a^2t^4 \}}{\{ 2V (CLD) t \}} - \cos E_2 \quad (33)$$

There may be several roots to this equation; but it is assumed that a predator would wish to minimize the time to intercept the prey in order to minimize the detection probability and energy consumption. For this reason, the shortest possible time for the intercept is used. The necessary orientation change E'1 is then calculated by the application of the sine rule to PP'I

$$E'_1 = \sin^{-1} \{ (2V/at) \sin (E_2) \} \quad (34)$$

The course $\theta_{1t} + E'1$ is that which the predator must take to

intercept the prey. Collett and Land (1978) show that this method of interception is used by houseflies (Eristalis) to catch conspecific mates.

With this strategy there is no tracking involved and it therefore can be considered a closed loop solution (Fig. 6). The predator uses the initial kinematic assessment of the prey to determine an interception point, then makes a 'go', 'no-go' decision, and if 'go', turns away from the prey and proceeds toward that point with the proper kinematics for interception. We would expect a predator using this strategy to show little deviation in orientation during movement to the interception point, high acceleration rates, and high velocities. The interception point occurs at some point along the projected prey path.

The second interception strategy involves an open loop system (Fig. 7). The predator receives constant information about the prey kinematics and relative position and uses this information to alter its own position and kinematics such that it continually points toward the prey throughout the chase. The predator must assess both prey orientation and kinematics and accordingly adjust its own orientation, including presumably, an allowance for its response time.

This process may be modeled in the same manner as the first strategy but where $\theta_1 = E_1$ is the new predator course such that

Figure 6 Tracking strategy I . (i) The predator uses the initial kinematic assessment of the prey to determine an interception point, and then turns away from the prey and proceeds toward that point with the proper kinematics for interception. (ii) Typical predator-prey trajectory with this strategy.

Tracking Strategy I

i)

Prey Initial Position



Assess Prey Kinematics

Calculate New Orientation
and Interception PointMotor Activity → Alter orientation
and kinematics to arrive at calculated
interception point at the same time as
prey.

ii)

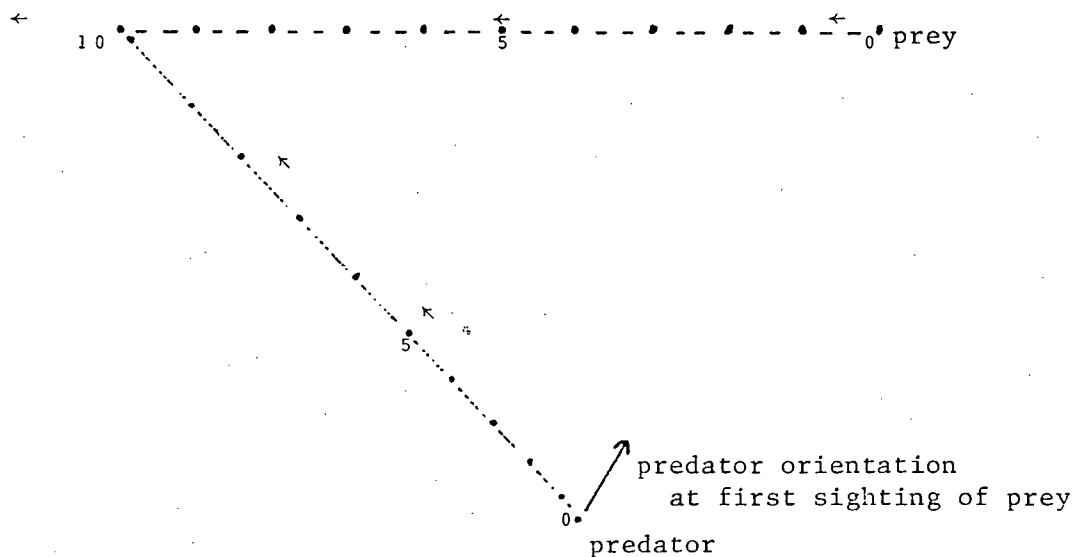


Figure 7 Tracking strategy II . (i) The predator receives constant information about the prey kinematics and relative position and uses this information to alter its own position and kinematics such that it continually points toward the prey throughout (ii) Typical predator-prey trajectory with this strategy.

Tracking Strategy II

i)

Prey Initial Position
at First Sighting



Assess Prey kinematics, orientation
and new projected prey position



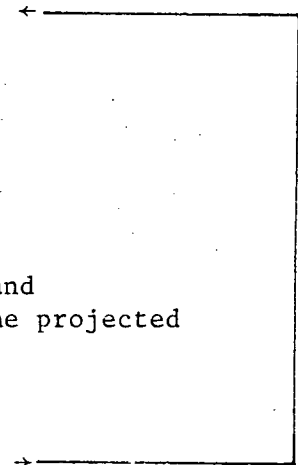
Calculate new Predator orientation
to point toward prey.



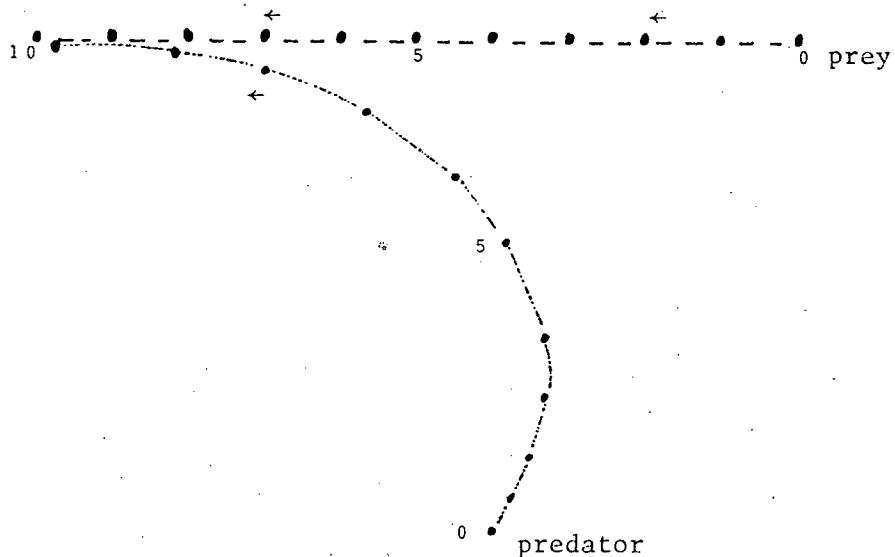
Motor Activity → Alter orientation and
kinematics to move toward prey at the projected
orientation to the prey position.



Time Interval + Time Step



ii)



at time t , $\theta_1 t = \phi_1 t$, and E_1 is constantly evaluated to give the current prey position. The calculated interception point will coincide with the prey current position at all times.

If the prey has better manoeuvrability, it can wait until the predator is very close, then execute a high deceleration and rapid turning manoeuvre to escape. Howlands (1974) simple model of the turning gambit is an explicit evaluation of this situation; if the square of the normalized velocity $(V_2/V_1)^2$ is greater than the normalized turn radius $(R_2/R_1)^2$ then the prey will escape. This relationship yields optimal normalized starting distances for the turn X_0 .

Turning ability is a function of velocity and the control surfaces needed to apply the required force; therefore, there should be significant kinematic adjustments in a predator responding so as to keep E_1 at zero.

The third strategy for interception can be considered a variation of the second with more complexity. It is termed the lead pursuit and was defined earlier. It is an open loop system (Fig 8) in which the predator receives constant information about prey kinematics, relative position and orientation. Using this information the predator alters its own kinematics and orientation such that it is pointing to a point where the paths are intersecting. The predator is path predicting and tracking. Regardless of the current predator/prey kinematics and

Figure 8 Tracking strategy III . (i) The predator receives constant information about the prey relative kinematics, relative position, and orientation to alter its course and kinematics such that it is pointing to an interecption point ahead of the prey. (ii) Typical predator-prey trajectory with this strategy.

Tracking Strategy III (Path Prediction)

i)

Prey Initial Position
at First Sighting



Assess Prey kinematics and orientation
and new position in future (aim point)



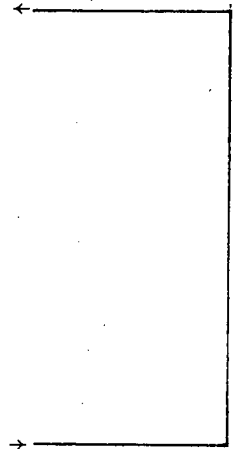
Calculate Aim Point as a function of
prey-predator orientation and kinematics



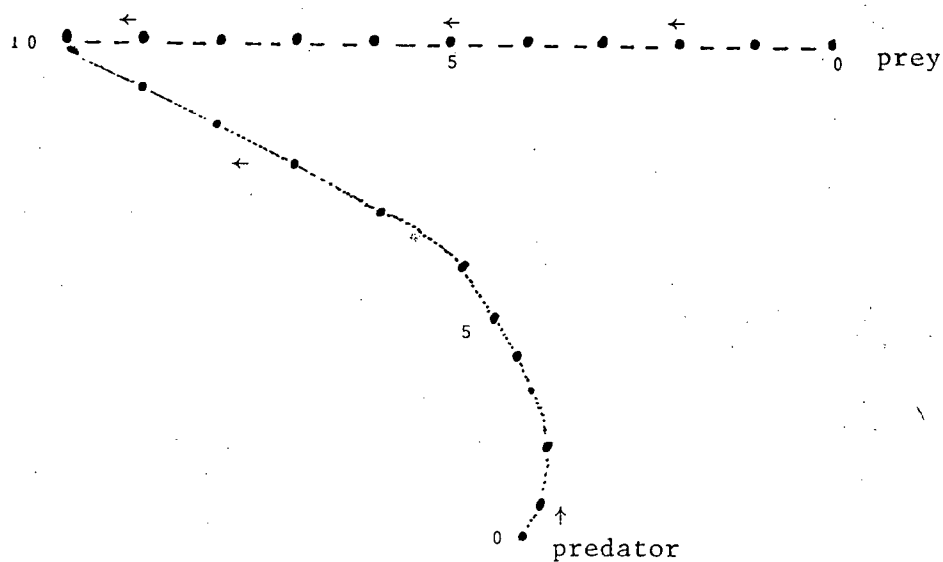
Motor Activity → Alter orientation and
kinematics to move toward Aim Point



Time Interval + Time Step



ii)



orientation, the Distance at Closest Approach (DCA) will theoretically be zero until capture. In practice the Distance at Closest Approach will probably never be zero because of prey avoidance behaviour and lags in the predator response. This process may be modeled in the same manner as the first where at time t , $|\phi_{1t} - \theta_{1t}| = E_{1t}$ and E_{1t} is the lead angle pointing to the intercept point calculated by the predator given the prey kinematics and orientation.

Not only are the manoeuvre type and timing important for a prey attempting to survive attack, the predator is also constrained in its timing of the attack. The prey must by definition be within a tracking range, and the predator should time the attack to be effective in minimizing energy consumption and fatigue, and still capture the prey.

RESULTS

I Single Predator - Single Prey Interactions

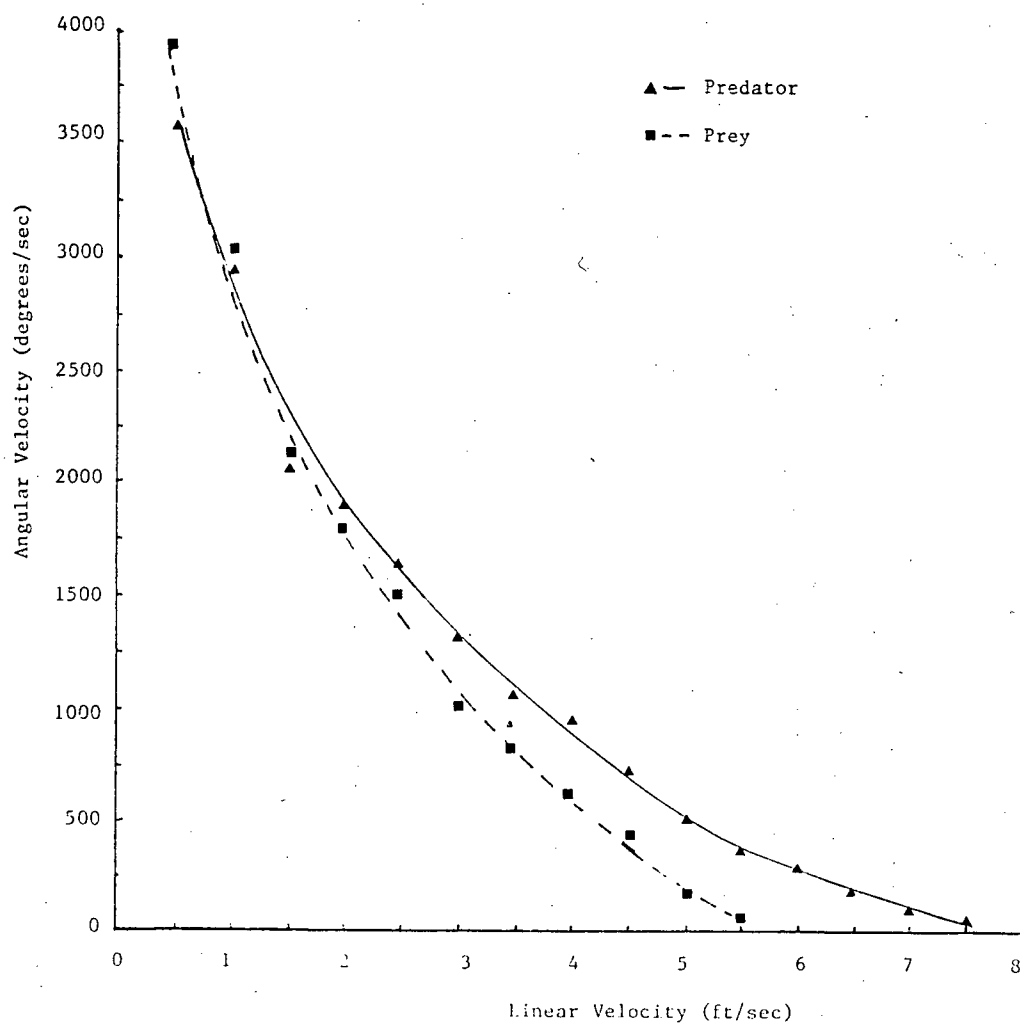
1) Kinematic Attributes.

The maximum recorded linear velocity found in 20 chase sequences for the trout in these experiments was 7.3 ft/sec, that of the sockeye 5.65 ft/sec. These results are not unexpected because larger fish should be able to swim faster than smaller ones (Howland 1974, Bainbridge 1976). The mean of the maximum linear velocity recorded in each sequence was 4.98 ft/sec for the trout and 4.76 ft/sec for the sockeye. Webb (1975) reported overall maximum velocities of 8.5 ft/sec for rainbow trout (Salmo gairdneri) with burst velocities of up to 20 ft/sec. Mean overall acceleration rates were calculated as 2.32 ft/sec² for the predator and 1.98 ft/sec² for the prey; with burst accelerations of 6.03 ft/sec² and 4.7 ft/sec² for predator and prey respectively.

Angular velocity and linear velocity are plotted in Fig 9. The data may be interpreted as maximum turning ability in degree/sec at the initial linear velocity before execution of a turn and show that the predator had a higher turning ability than the prey at higher velocities. Up to velocities of 1.75

Figure 9 Angular velocity and linear velocity of predator and prey).The angular velocity is the mean maximum angular velocity recorded at the indicated linear velocity for 20 chase sequences. Angular velocities for linear velocities less than 0.5 ft/sec were not observed.

Figure 9. Angular Velocity vs Linear Velocity.



ft/sec, predator and prey turned equally well, but at higher velocities, the predator changed direction faster than the prey. However, the minimum turning radius of the predator at all velocities was greater than that of the prey. This minimum radius was found by setting the centrifugal force acting on the fish equal to the force available for the turn and solving for the radius.

Parameters to satisfy equation 15 (Time to Maximum Velocity) were taken from 15 chase sequences where the predator and prey initial velocities were below 0.2 ft/sec and reached their respective maximum velocities for that chase. The mean value of K was $0.566 \text{ sec} \pm .12$ for the predator and $0.3059 \pm .08$ for the prey. These values differ significantly (t-test, $t=6.37$ ($P<.01$) $n=15$), indicating that the prey reaches maximum velocity faster than the predator.

To summarize the kinematic attributes of predator and prey:

- (1) The predator achieves a higher linear velocity than the prey.
- (2) The prey reaches maximum velocity in nearly half the time of the predator.
- (3) The predator achieves a higher angular velocity at high linear velocity, but at the cost of a higher

turning radius.

- (4) The linear acceleration of the predator is higher than that of the prey.

2) Example chase sequence- single predator-single prey

In many respects the 20 chase sequences showed considerable similarity. It is convenient to begin the presentation of these results with a detailed description of a typical sequence. Chase sequence [4] was chosen to illustrate a single predator-single prey sequence in which the predator successfully captured the prey.

Time trajectories of chase sequence [4] are presented in Fig. 10. Kinematic measurements are presented in Figs. 11 to 16. At the beginning of the sequence, predator and prey were 3.15 ft apart, travelling in almost opposite directions. From frame 1 to 13, the predator executed a turn to the left. The angular velocity was moderately high and ranged from +600 deg/sec to -500 deg/sec. The linear velocity of the predator remained nearly constant, with a slightly increasing trend. The prey meanwhile continued in an unaltered direction of travel with a nearly constant linear velocity (Fig. 11).

Although the angular velocity (Fig. 12) of the prey showed

some spikes (notable at frame 6 and 7), these may have been movements unrelated to the predator. If the predator was detected at this point , a change in the linear velocity of the prey should have been seen. The predator had detected the prey, and this conclusion is supported by the intercept co-efficients and error tracking angle (Fig 15 , Fig 14). The error angle deviated slightly around the zero position, and the intercept co-efficients indicate that the intercept point was fluctuating from ahead to behind the prey.

Fig. (16) indicates the distance to the intercept point for both predator and prey. Large spikes appeared up to frame six, indicating that the predator had detected the prey and was altering orientation to follow or get an accurate "fix" on the kinematic parameters of the prey. Between frames 6 and 12, the intercept parameters indicate that the predator path was intersecting ahead of the prey. The error tracking angle (Fig. 14) for frames 6 to 12 showed an adjustment at frame six and a flattening out at frame 10 to 12. The plateau coincided with an error angle E1 of approx. -20 degrees (the prey was 20 degrees to the right of the predator path). The offset angle E2 for frames 6 to 12 shows little variation, indicating a relative constant predator offset angle of approx. 50 degrees (the predator was approx. 50 degrees to the left of the prey path). This is further indication that the prey might not as yet have been aware of the predator's presence.

The closure distance (Fig. 13) between frames 1 and 12 slowly decreases as the predator and prey were traveling toward each other. The Distance at Closest Approach also decreased indicating tracking by the predator.

Frames 13 and 14 show a direction change by the prey, and the response by the predator. Figure 12 shows a large spike at frame 13 for the prey and the predator. The reason for the prey change of direction in frame 13 is unclear, but, the result of the move was to momentarily break the tracking by the predator.

The intercept co-efficients (Fig. 15) for frame 13 indicate that the interception point was behind the prey. Additionally, the distance to the interception point for both predator and prey (Fig. 16) shows an increase, rather than the expected decrease if tracking was still in progress.

Tracking of the prey by the predator resumes at frame 14 and continues to frame 27 (Fig. 15). The high angular changes of the prey in frame 13 and 14 appeared to "trigger" a quick response by the predator. The predator clearly was aware of the prey and responded by accelerating to a high linear velocity (Fig 11), peaking at frame 20 and maintained to frame 27. From Fig. 10 it is quite clear that the predator was not heading toward the prey, but was path predicting. This is further indicated in Figure 14 where for frames 14 to 26, the tracking error is constant at approx. -20 degrees, and Figure 12 where

the angular velocity for the predator is small.

As the linear velocity of the predator increased, the rate of closure increased, and this is reflected in Figure 13 , where the slope of the closure distance increases sharply at frame 20. The Distance at Closest Approach continues to decrease from frame 14 with decreased oscillations. At frame 20, the Distance at Closest Approach is nearly zero and is maintained at a very low value until frame 25. This indicates that the predator was tracking the prey by path prediction.

In contrast, the prey linear velocity decreased from frame 14 to 24 (Fig. 11), and the offset angle E2 (Fig. 14) slightly increased, indicating a moving away trend by the prey. Prey awareness of the predator may have occurred in frame 14 as shown by the velocity decrease and moving away trend. The responses clearly show a change in pattern of the prey kinematics to the awareness of some object.

Frames 25 to 40 demonstrate the prey escape response. Beginning at frame 25, the prey accelerated to maximum linear and angular velocity (Figs. 11 ,12), turning away from the predator. The offset angle E2 drastically changes (Fig. 14) and the error tracking angle E1 also increases, indicating a loss of tracking by the predator. This is further supported by the intercept co-efficients (Fig. 15) for frames 26 to 32. The linear velocity of the predator decreased as the angular

velocity increased (Figs. 11, 12 frame 27) as a turning manoeuvre was attempted to match the turning response of the prey. The predator was partially successful as it responded to the prey increases (frame 26 to 35). The predator appeared to regain tracking of the prey (frames 32 to 37) as indicated by the decreasing Distance at Closest Approach , closure distance, Predator Distance to Intercept Point (PDDIP), and Prey Distance to Intercept Point (PYDIP) (Fig. 16), despite the fact that the intercept point is oscillating from ahead to behind the prey (Fig. 15).

The high angular velocity of the prey at frame 35 resulted in the prey crossing the path of the predator. At frame 36 the prey turned to the left as the predator turned to the right in response to the high angular velocity of the prey. This "scissors" manoeuvre by the prey was successful in that high angular velocities in opposite directions can effectively break tracking by the predator.

In frames 40 to 43 and from Figures 15 and 10 the predator and prey were moving away from each other. The Distance at Closest Approach and closure distance (Fig. 13) both increase as does the PDDIP and PYDIP (Fig. 16) indicating that the predator had "lost" the prey.

At frame 44 the predator responded to the prey position as tracking was re-established. The high predator angular velocity

toward the prey position at frame 44 clearly indicates a response. From frame 45 to 50, the intercept co-efficients indicate path prediction and the closure distances decreased as the predator linear velocity increased (Fig. 13). At frame 47 the Distance at Closest Approach clearly decreased as did the PDDIP, indicating that the predator was once again tracking the prey.

At frame 52, the prey turned away from the predator and accelerate to maximum velocity; momentarily causing disruption of tracking. The predator response was to decelerate and at frame 53, was once again able to track the prey. Prey capture occurred at frame 57 as indicated by the zero E1 (error angle) and the -180 degree E2 (offset angle) . In frames 58 to 60 the prey was carried in the mouth of the predator. The total time elapsed for this entire sequence was 2.5 sec.

Chase sequence [4] was instructive in that the prey initially decoupled from the predator tracking with a turning manoeuvre followed by a scissors (frames 25 to 41), but at frame 47, a turn in the " wrong " direction by the prey enabled the predator to re-acquire tracking that eventually led to prey capture at frame 57.

This sequence also illustrated predator tracking from head on and stern positions. From Figures 10 and 16, it is quite clear that the predator did not directly head toward the prey,

but appeared to orient such that the paths of predator and prey intersected ahead of the prey; and this path prediction was used regardless of direction of approach.

The sequence discussed in the foregoing was typical of all the sequences in types of behaviour exhibited by both predator and prey. Of particular interest was the methodology the predator employed to track the prey. All single predator-single prey sequences showed remarkable similarity in the pattern of intercept variables. The slope, or closure rate, remained nearly constant (frames 1 to 16). There was a marked increase in slope indicating an increased closure rate, due to an increase in predator velocity (frames 17 to 26). The closure rate remained very low or nearly zero due to either defensive manoeuvres by the prey, or to the predator losing tracking (frame 27 on). This pattern was seen in all chase sequences. The average closure distance at the point where the slope of the closure distance showed a marked increase (C1) was $2.13 \pm .28$ ft (SE, $n=10$). The average closure distance at the point where the Distance at Closest Approach became less than 0.1 feet (C2) and the predator was maintaining tracking (as indicated by the intercept coefficients) was found to be $1.01 \pm .09$ feet ($n=10$). The average velocity of the predator at this point was $4.26 \pm .36$ feet/sec ($n=10$).

In all chase sequences the Distance at Closest Approach up to point C1 was characterized by large oscillations around a

decreasing trend line. None of the oscillations was greater than the closure distance. Between point C1 and C2, the Distance at Closest Approach showed a marked decrease in oscillations. From C2, the Distance at Closest Approach remained small relative to the closure distance until either the prey executed a defensive manoeuvre or was captured.

It appears that the predator undergoes three phases when tracking. The first phase up to point C1 is marked by a low but slightly increasing linear velocity and large oscillations in the Distance at Closest Approach and angular velocity. During this phase, the predator orientation changes such that it is in the general direction of the prey, and the oscillations of the Distance at Closest Approach, $E1$ and angular velocity indicate adjustment of the kinematic parameters of the predator to establish tracking. This procedure may be akin to stalking and target acquisition.

The second phase, between C1 and C2, shows dampening of angular velocities, $E1$, Distance at Closest Approach values, and an acceleration to a high linear velocity resulting in an increased closure rate.

From earlier arguments, an hypothesis was presented that once a predator has acquired a target and alters orientation and kinematics to intercept prey, the best strategy is to accelerate rapidly so as to minimize time to interception. This would

decrease the time in which the prey can react to the approaching predator as well as placing the predator nearer the prey. The second phase functions to accomplish these aims.

The third phase, from point C2 to when the prey is captured or escapes shows Distance at Closest Approach values near zero, indicating tracking, low variation in tracking error angle ($E1$), and linear and angular velocities of the predator changing in an attempt to match the prey kinematics. Unfortunately, the filming speed proved to be too slow to detect meaningful predator reaction times to prey movement during tracking.

The error tracking angle $E1$, was found to be independent of Distance at Closest Approach or closure distance during tracking, and as stated earlier, remained nearly constant during tracking segments. From Figure 4 if $E1$ is constant, as the closure distance decreases, the triangle ABC shrinks resulting in the movement of the aim point (the point where the predator and prey paths cross) toward the actual position of the prey (decreasing the prey distance to intercept point , PYDIP). The predator distance to intercept point (PDDIP) (Figs. 12) and prey distance to intercept point (PYDIP) show similar trends to the closure distance and Distance at Closest Approach (Fig. 16). For the segments where the intercept coefficients indicate that the paths are crossing in the future, (frames 14 to 24 in sequence [4] for example), there is an almost perfect match between closure distance and PDDIP and between DCA and PYDIP.

This further supports the hypothesis of a constant (plus error) tracking error by the predator.

For all chase sequences, the mean error angle $E1$ was calculated for those segments where the intercept coefficients indicated tracking (Table 1). A Watson and Williams test (Mardia 1972) was used to test the null hypothesis that there was no difference among the $E1$ values. An F_s value of 1.156 ($P [F_s=1.156] > .25$, $df= 5,54$) indicates the acceptance of the null hypothesis.

The grand mean ($E1$) was found to be 13.37 degrees. A Modified Rayleigh test (Mardia 1972) was used to test the null hypothesis that the preferred error tracking angle was equal to zero (ie. The predator always heads toward the prey). A calculated V' value of 57.34 ($P << .05$, $df=60$) indicates a rejection of the null hypothesis. However, as closure distance decreases, the prey distance to intercept point decreases as does the predator distance to the intercept point. Figs. 17 and 18 show that for points where the intercept co-efficients indicate path prediction, there is a linear relationship between the predator distance to the intercept point and the closure distance; and the prey distance to the intercept point and closure distance. At any given closure distance, the prey is closer to the intercept point than the predator is. At closure distances less the 1.0 feet (approx point C2), the point of interception nearly coincides with the prey position. This

Table 1

Error angle (E_1) where the intercept coefficients indicate tracking.

I) test of H_0 : No significant difference among Error angles.

H_1 : There exists a significant difference among Error angles.

Sequence	4	5	6	7	8	9	Total
$\Sigma \sin E_1$	3.23	1.39	.701	.927	3.46	3.92	13.63
$\Sigma \cos E_1$	10.36	8.77	4.94	5.91	12.02	15.33	57.34
n	11	9	5	6	13	16	60
r	.987	.987	.997	.996	.962	.989	.982
R	10.85	8.88	4.99	5.98	12.51	15.83	58.94
$\bar{E}_1$	17.32	8.97	8.07	8.93	16.04	14.53	13.37

Using Watson and Williams test (Mardia 1972)

$$\therefore F_c = 1.156 \quad (df = 5, 54)$$

$$\therefore P (F_c = 1.156) > 0.25 \quad \text{Accept the Null Hypothesis}$$

2) test of H_0 : Preferred direction is 0.0° in Error angle (Predator points toward prey)

H_1 : Preferred direction is not 0.0° in Error angle.

$$E_p \text{ (preferred angle)} = 0.0 \text{ degrees}$$

Using the Modified Rayleigh Test (Mardia 1972)

$$V' = R \cos(\bar{E}_1 - E_p)$$

$$V' = 57.338$$

$$P (V' = 57.338) \ll 0.05 \quad \therefore \text{Reject the Null Hypothesis}$$

suggests that at small closure distances, the predator may switch tracking strategy from path prediction to pointing at the prey. The measurement errors involved in digitizing the film sequences may have masked this switching. From a tactical point of view, to capture the prey, the predator must be at the same point at the same time as the prey; therefore, at some time the predator must be pointing at the prey (+ some angular strike distance).

Figure 10 Time trajectory chase sequence [4] . The predator (+) and prey (x) are plotted for each frame; representing $1/24$ second time intervals. 0 indicates the relative starting position for the predator and prey. Predator path prediction is easily seen in frames 15 to 20, where the predator path is intersecting ahead of the prey path. The defensive manoeuvre by the prey can be seen at frames 25 to 30. Prey capture by the predator is seen at frame 57. The axis are normalized units from the reference X_0, Y_0 position and are used to scale the trajectory plots.

Figure 10 Time Trajectory Chase Sequence (4)

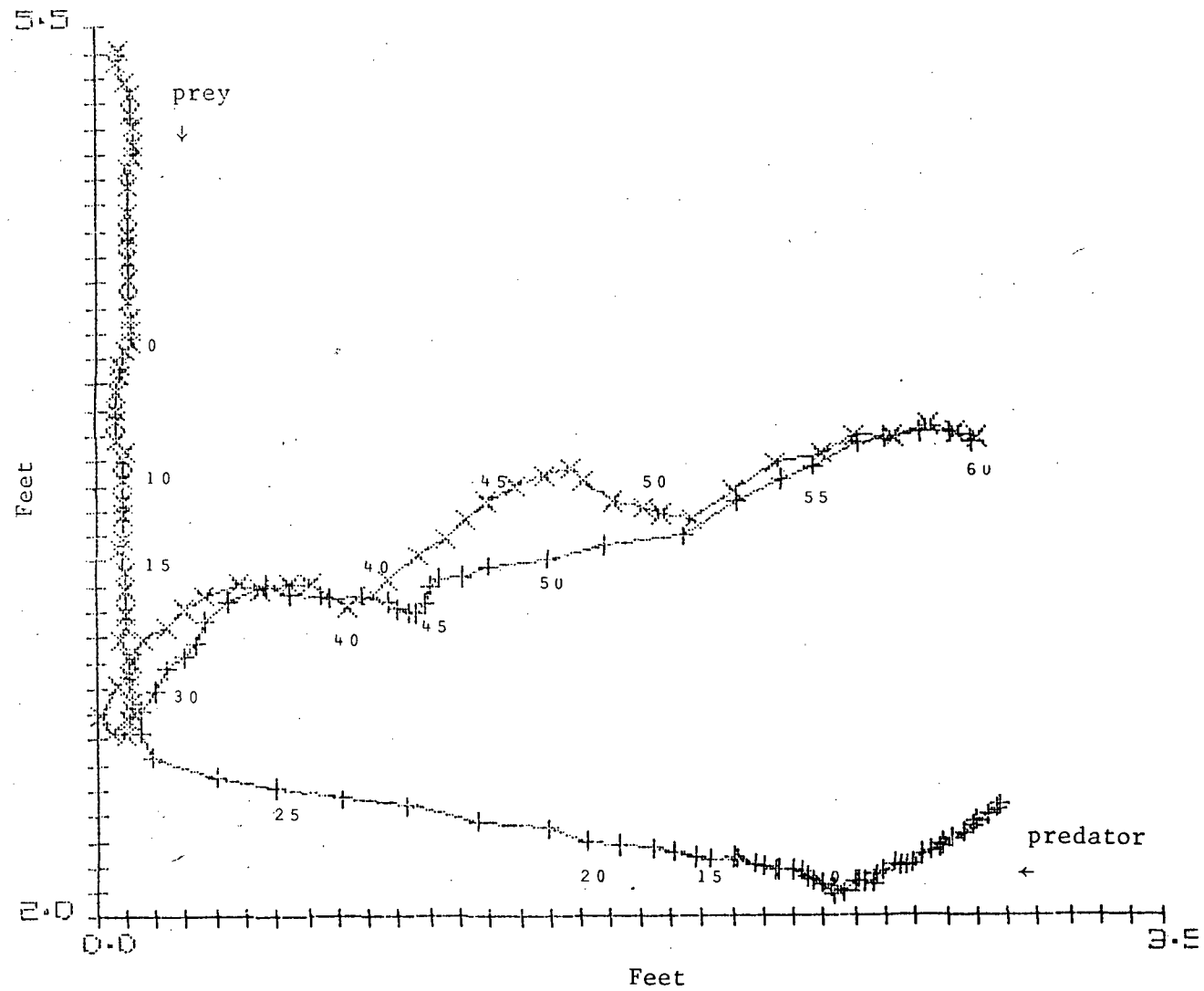
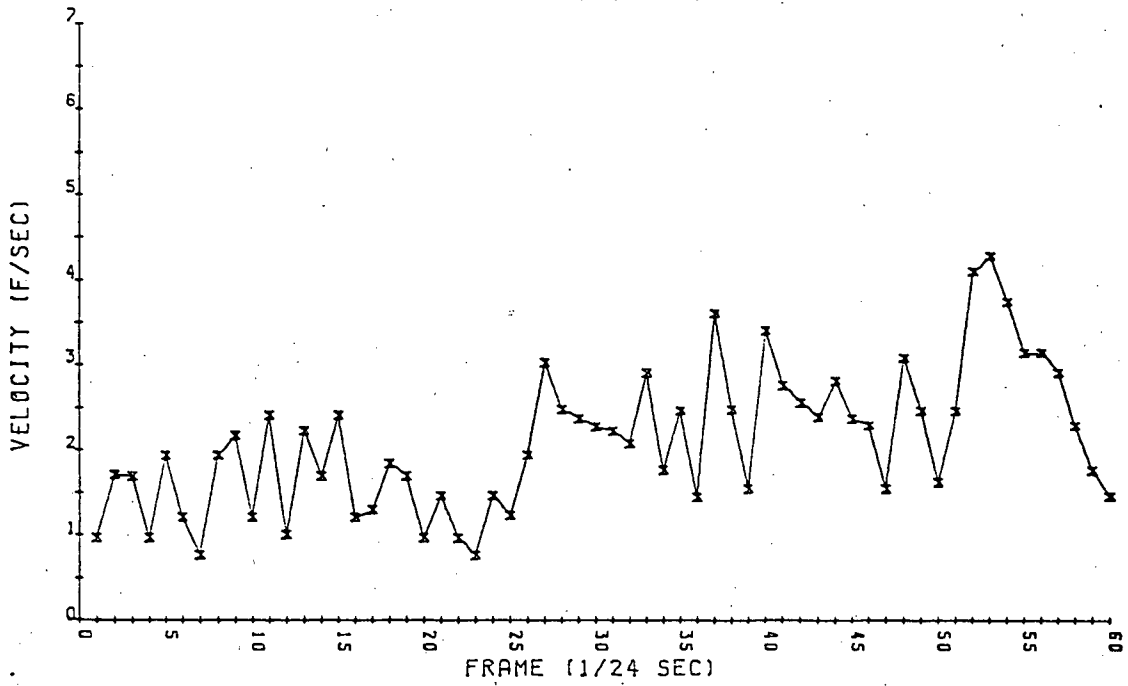


Figure 11 Linear velocity of predator and prey over time .
The predator response to the prey can be seen at frames
15 to 20 and 45 to 50 as increases in linear velocity.
The prey velocity shows an increasing trend from frames
25 to capture at frame 57.

Figure 11
PREY VELOCITY CS-4



PREDATOR VELOCITY CS-4

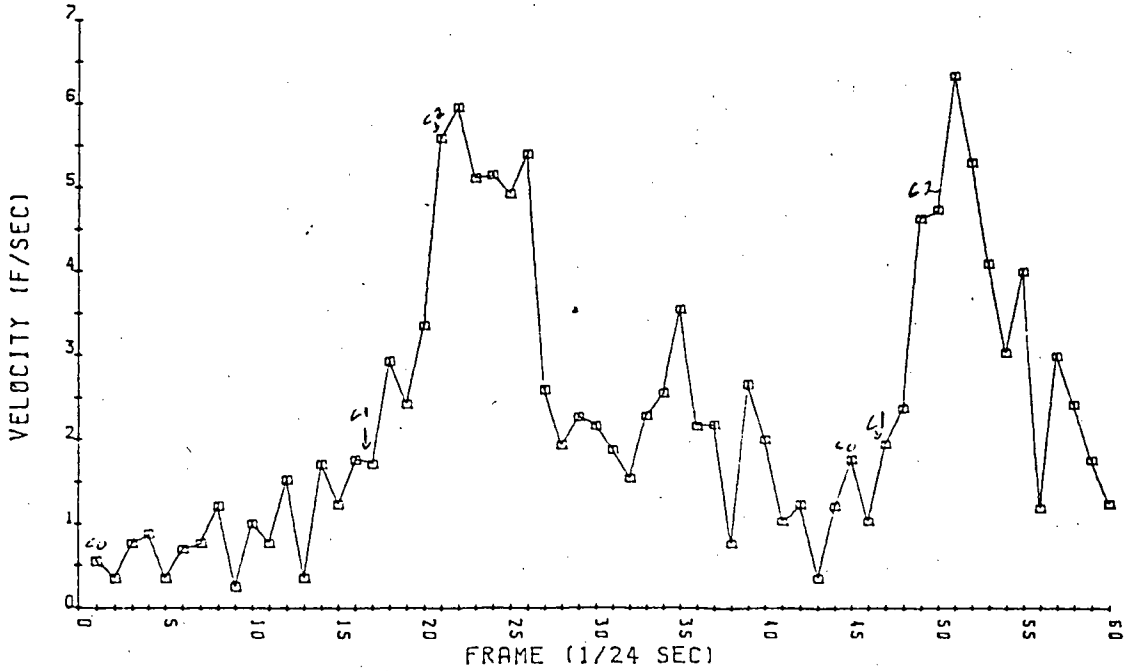
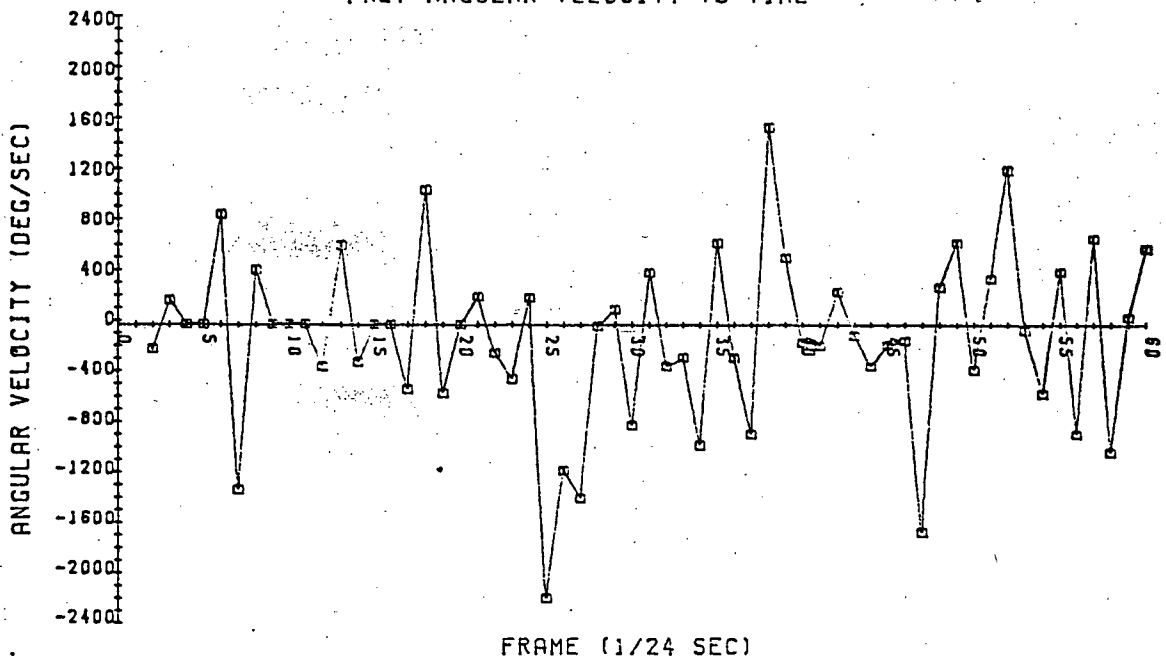


Figure 12 Angular velocity of predator and prey over time .
The defensive turning manoeuvre by the prey can be seen as the increase in angular velocity at frame 24 to 25. The predator attempts to match this manoeuvre at frames 26 to 27. Negative values of the angular velocity indicate a turn to the right.

Figure 12
PREY ANGULAR VELOCITY VS TIME



PREDATOR ANGULAR VELOCITY VS TIME

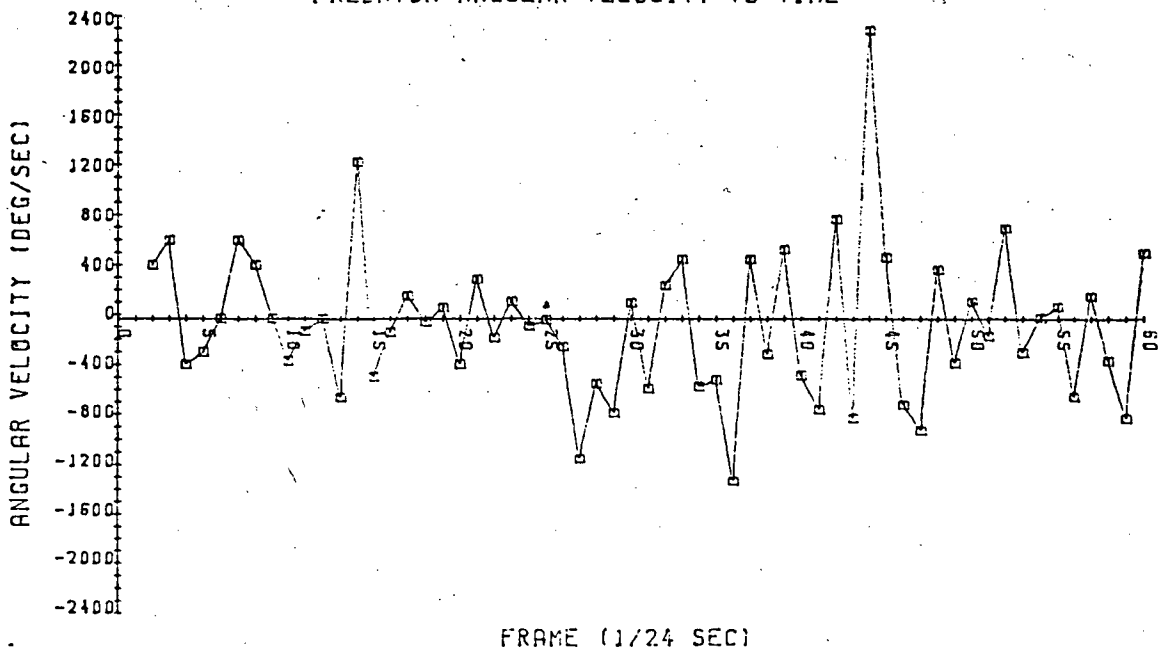
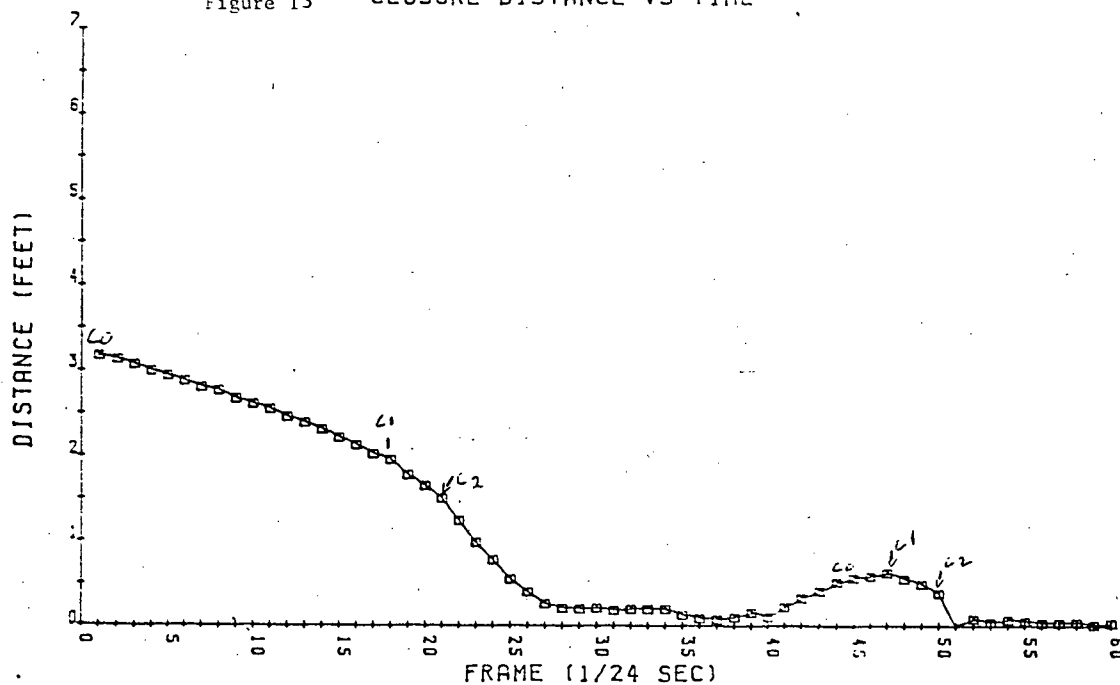


Figure 13 Closure distance and Distance at Closest Approach over time . The form of the closure distance is characteristic of all single predator-single prey chase sequences. Path prediction by the predator is clearly seen in frames 20 to 25 and 49 to 52 of the distance at closest approach graph.

Figure 13 CLOSURE DISTANCE VS TIME



DISTANCE AT CLOSEST APPROACH VS TIME

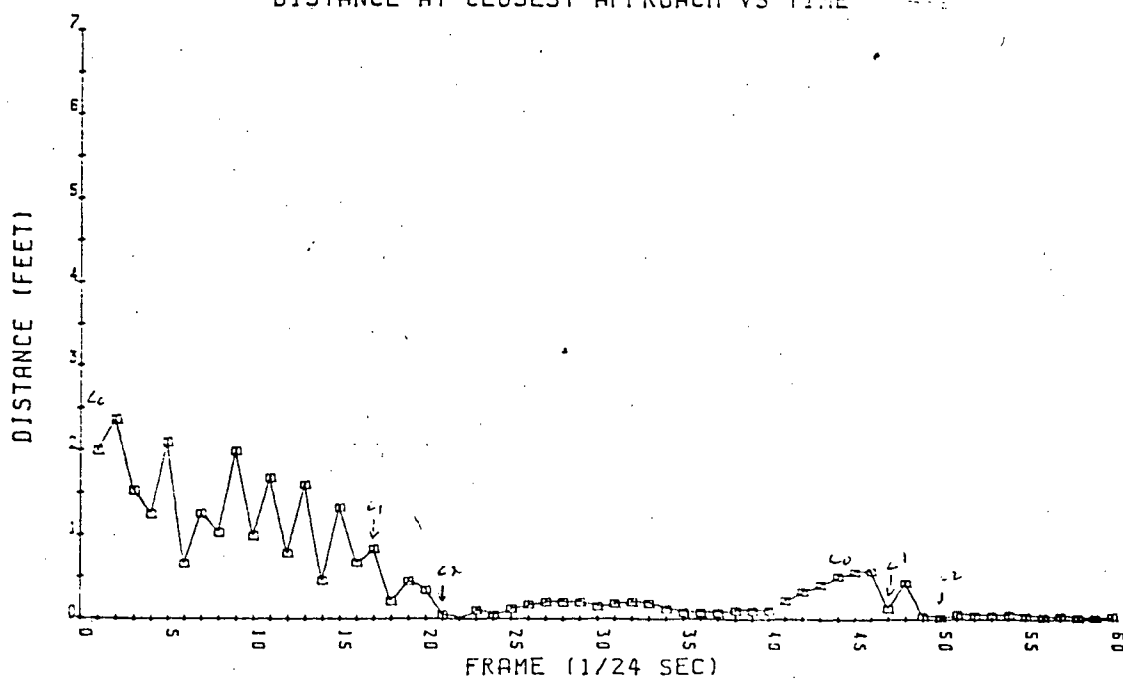


Figure 14 Error tracking angle and offset angle over time .
The error tracking angle shows a marked increase at frame 26 indicating tracking loss caused by the defensive manoeuvre of the prey. The corresponding offset angle shows the characteristic moving away trend from the start of the sequence to frame 25 and the effect of the defensive manoeuvre at frame 26.

Figure 14
ERROR TRACKING ANGLE

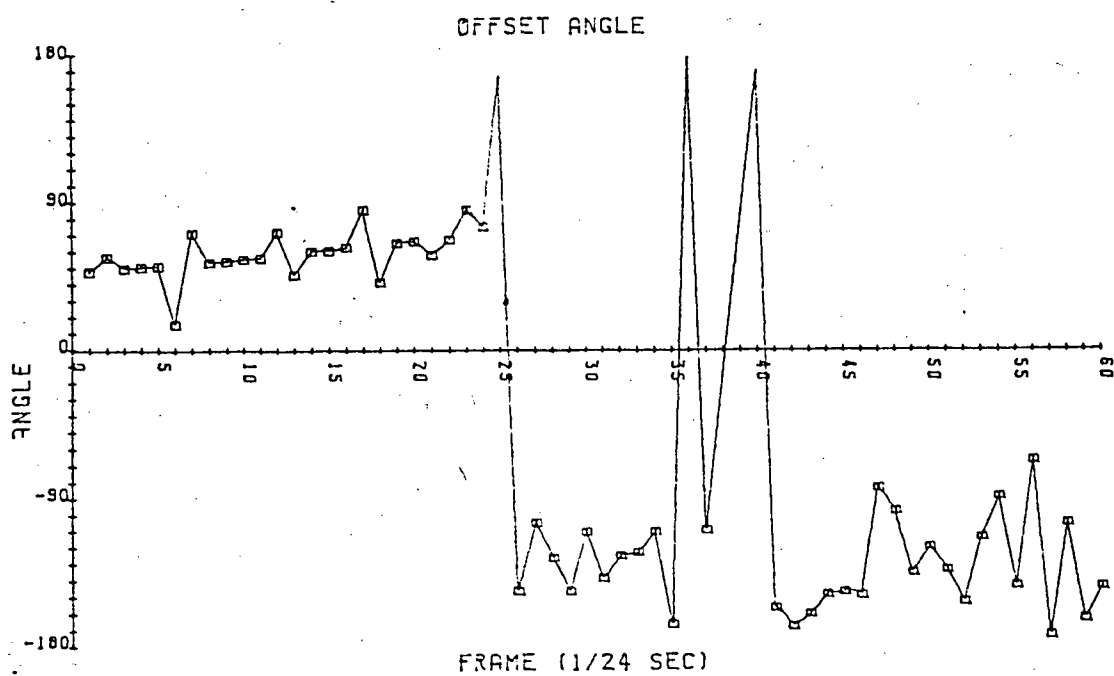
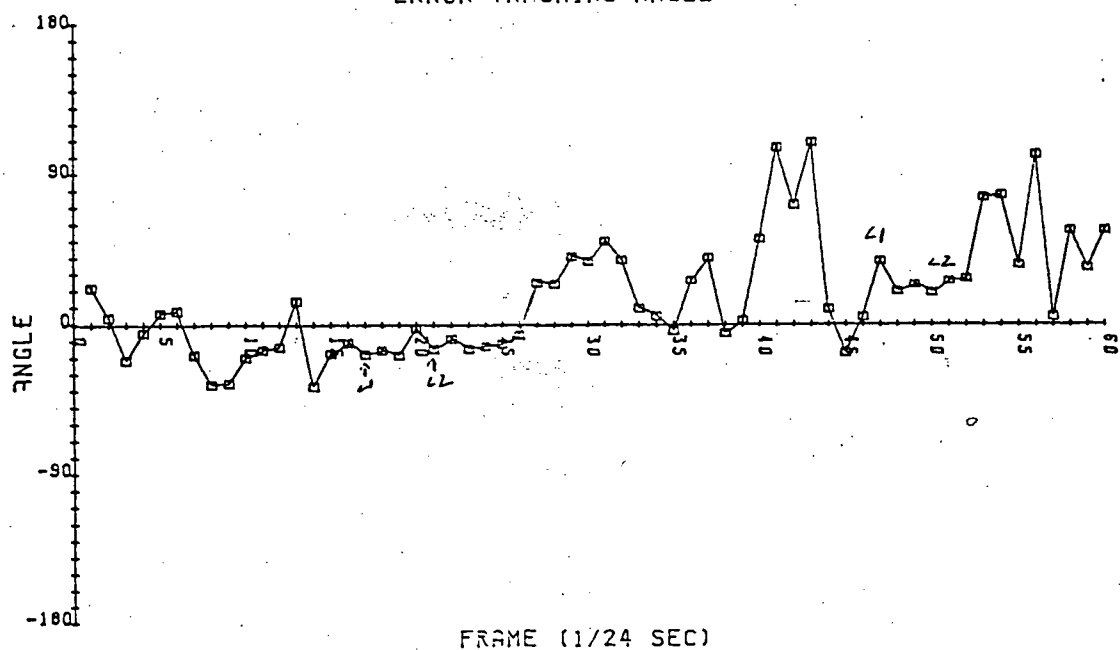


Figure 15 Interception coefficients over time . Where the coefficients are both positive indicates path prediction by the predator. Where the coefficients are both negative , predator and prey are moving away from each other. Where A is positive and B is negative, the predator is moving away from the prey. Where A is negative and B is positive, the interception point is behind the prey.

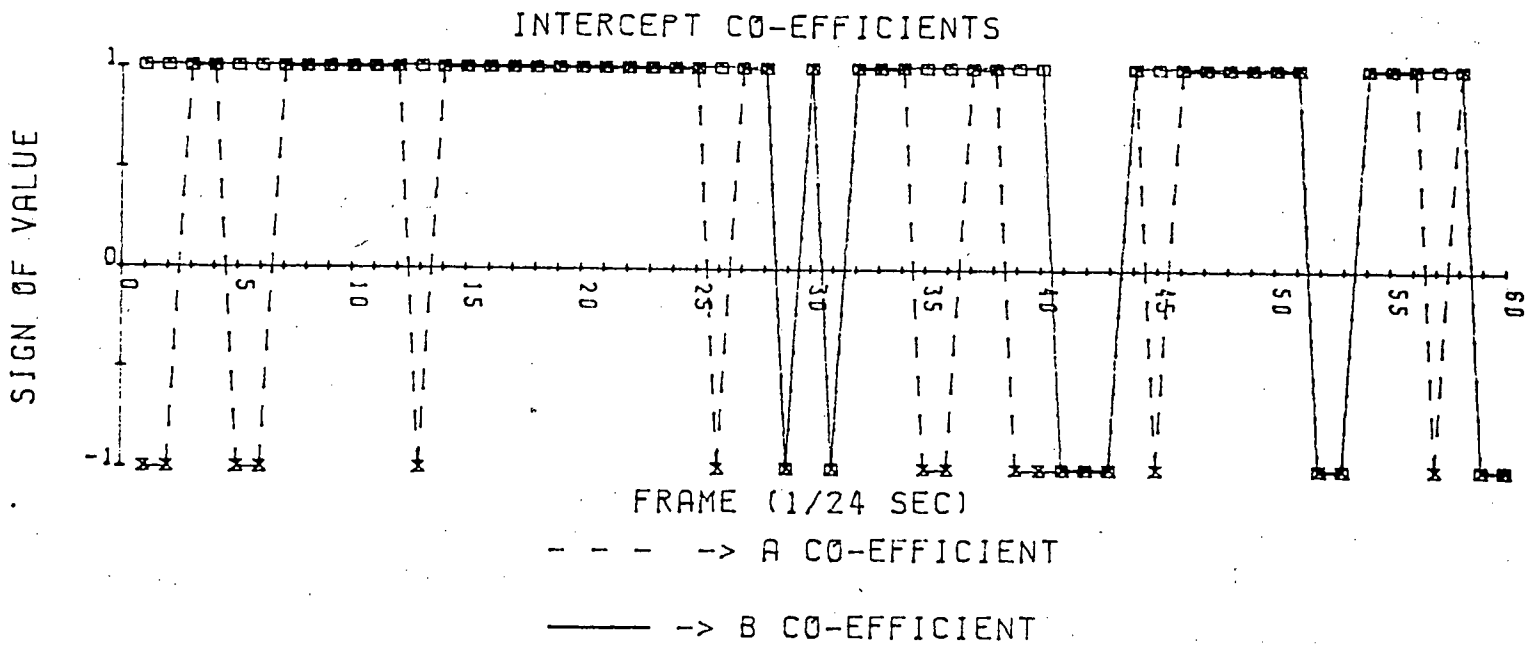
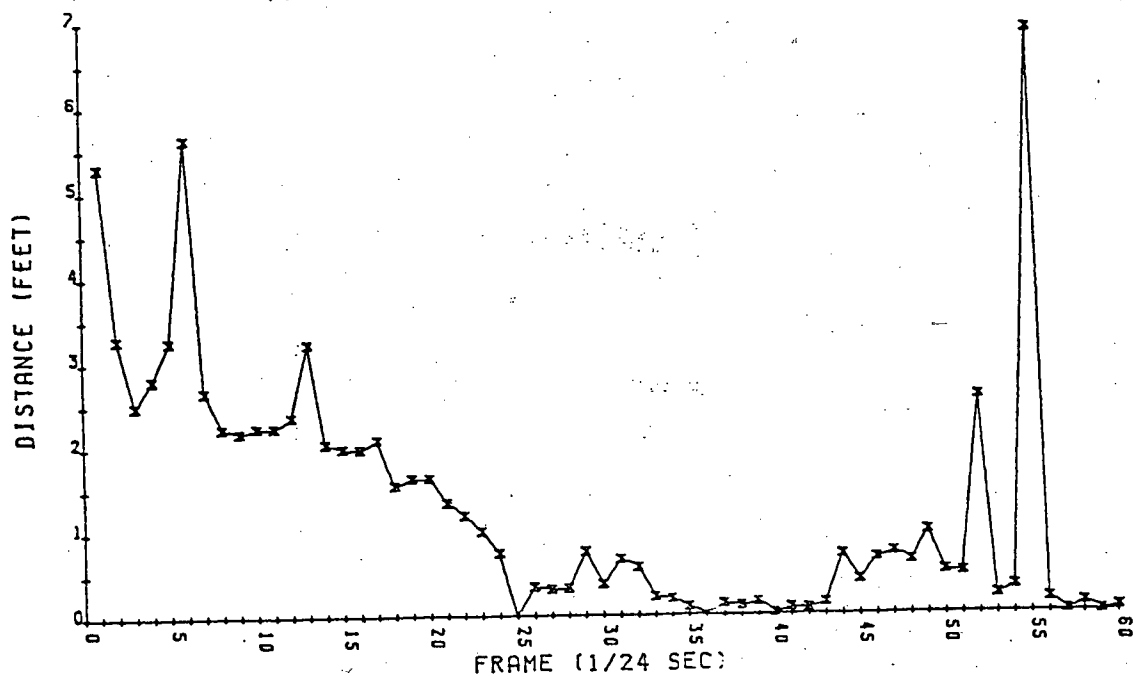


Figure 15

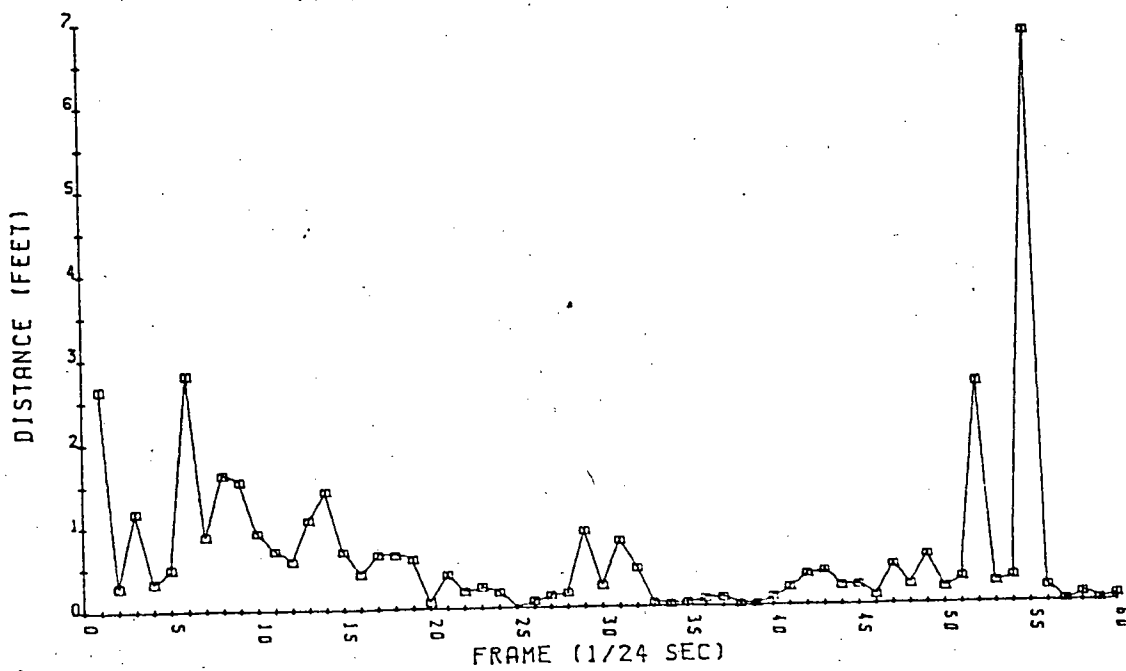
Figure 16 PDDIP and PYDIP over time . The predator and prey distance to intercept point graphs show similar trends to the closure distance and distance at closest approach graphs respectively. This was common in all single predator-single prey chase sequences.

Figure 16

PREDATOR DISTANCE TO INTERCEPT POINT



PREY DISTANCE TO INTERCEPT POINT



II Single Predator - Schooling Prey

1) Example Sequences

Three chase sequences of a single predator attacking schooling prey are presented to illustrate typically observed predator-school interactions. Sequence [1S] illustrates an attack by the predator on a cohesive school. Sequence [2S] illustrates an attack on a cohesive school in which one individual became separated from the school. Sequence [3S] illustrates a situation when one member of the school was separated from the other school members at the beginning of the chase sequence. In all three cases the school was composed of six individuals.

Time trajectories of chase sequence [1S] for the predator and one of the prey (prey 5) (the time trajectories for the other school members were similar) are presented in figure 1S.1 . The kinematic parameters for the predator and prey 4, 5, and 6, are presented in figures 1S.2 to 1S.10 .

The data for sequence [1S] is indicative of schooling as a defensive strategy. The linear and angular velocity of the predator remained relatively constant through the sequence and

Figure 1S.1 time trajectory school : sequence 1S , prey 5.
Only prey 5 is plotted as the others were similar. The
axis are normalized units from the reference X_0, Y_0
position and are used to scale the trajectory plots.

Figure 1S.5
Time Trajectory : Sequence 1S prey 5

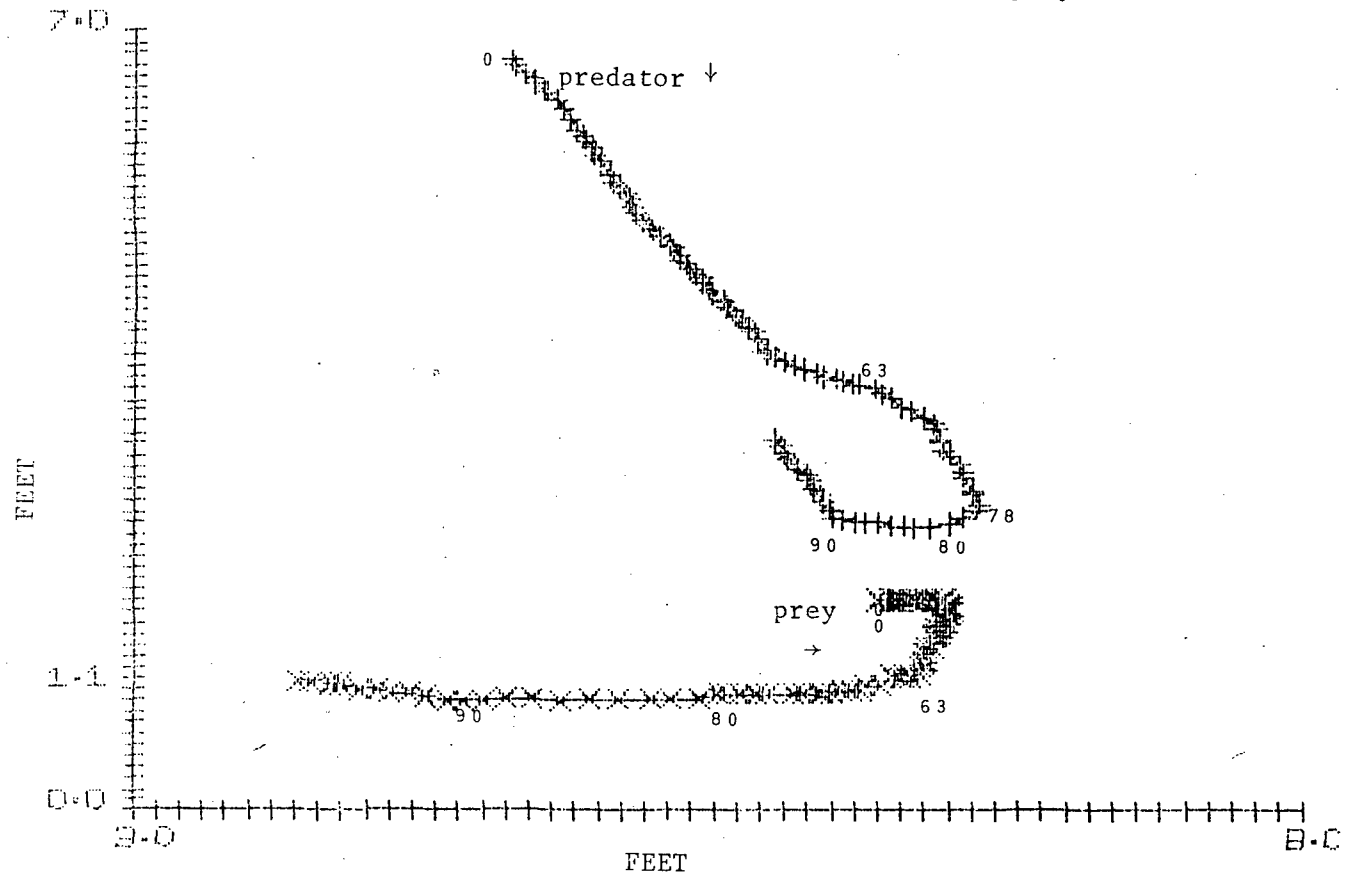


Figure 1S.2 predator linear and angular velocity : sequence 1S
. See text for interpretation.

Figure 1S.2

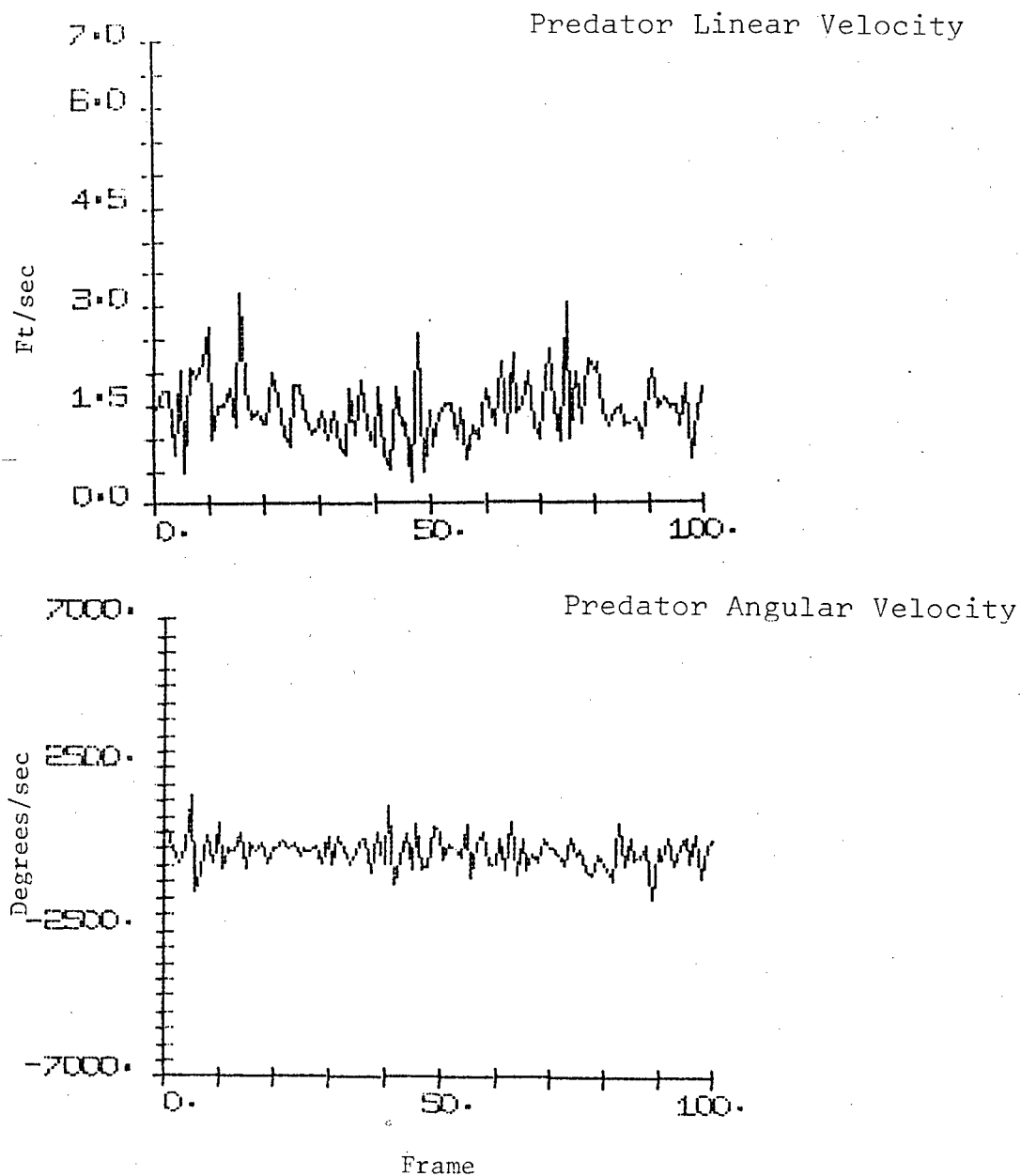


Figure 1S.3 closure distance over time : sequence 1S for prey 4,5 and 6. Note the concave and similar response for all three prey. See text for interpretation.

Figure 1S.3

Cld vs Time (frame)

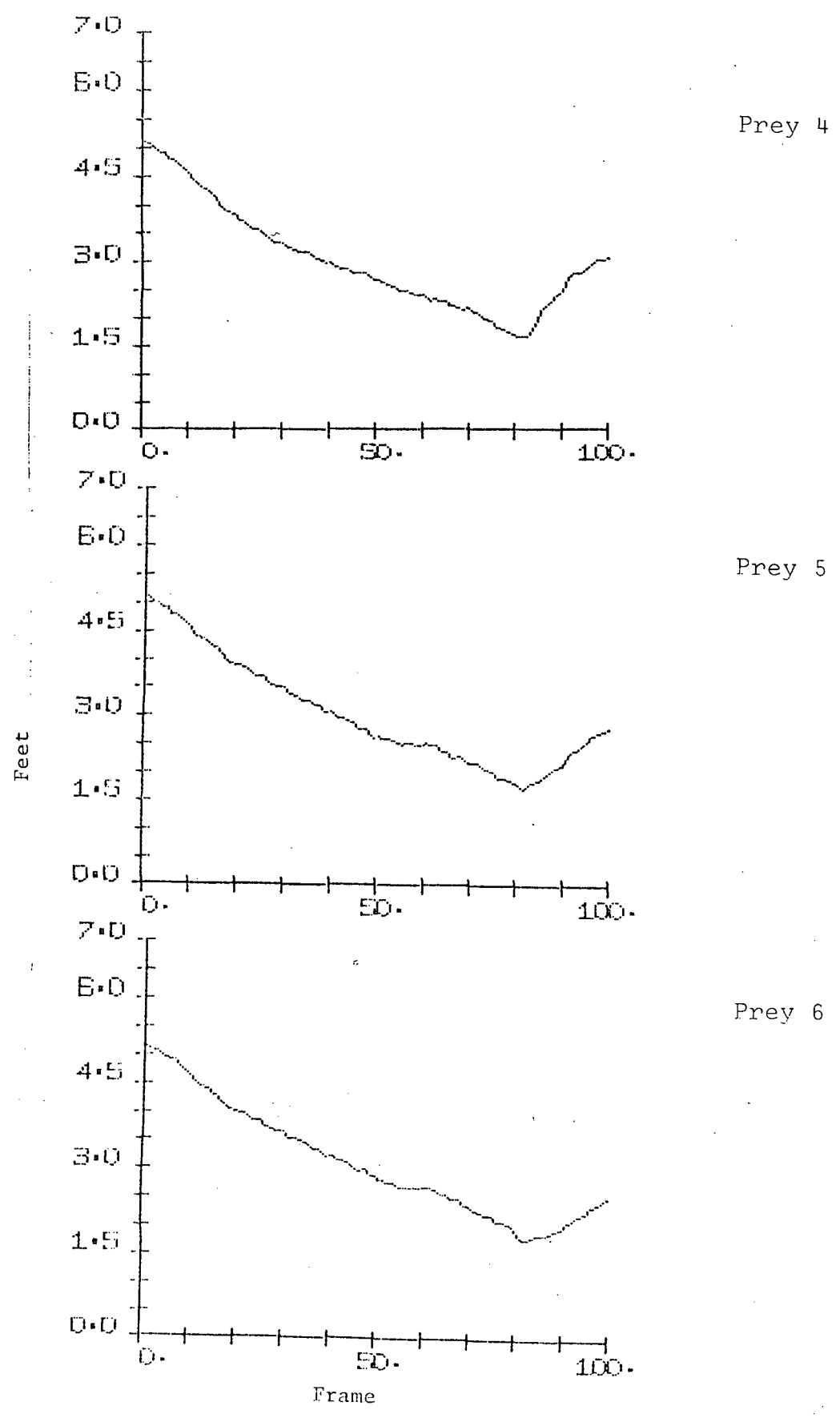
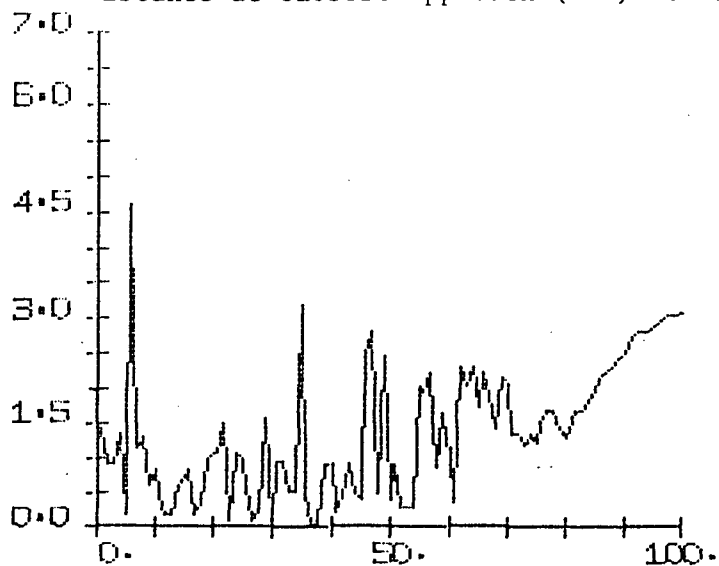


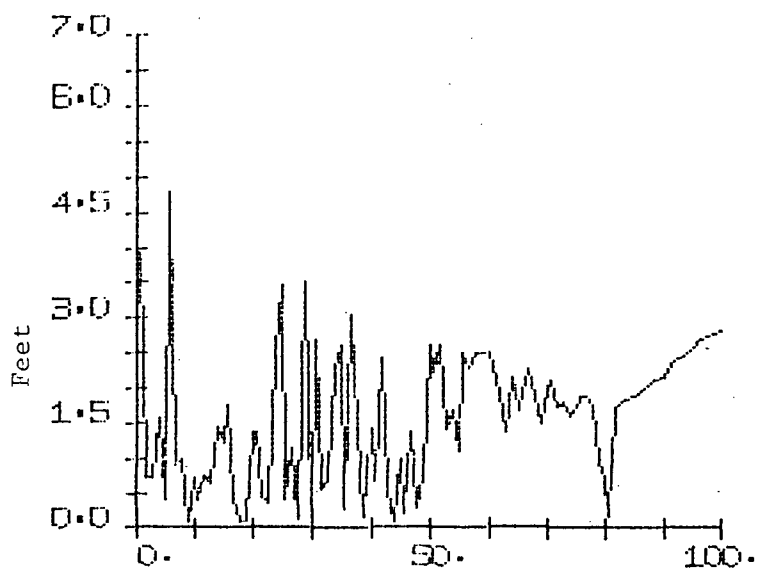
Figure 1S.4 Distance at Closest Approach over time : sequence 1S for prey 4,5 and 6. Note that there is no indicated path prediction by the predator.

Figure 18.4

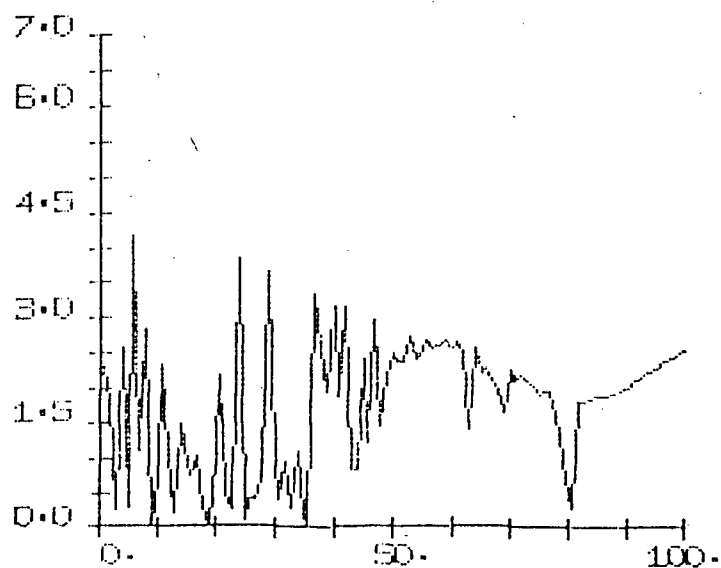
Distance at Closest Approach (DCA) vs Time (frame)



Prey 4



Prey 5



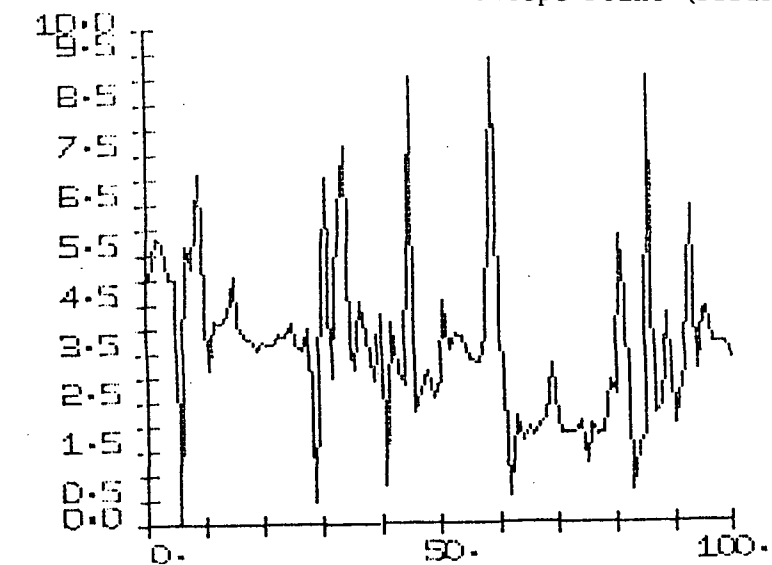
Prey 6

Frame

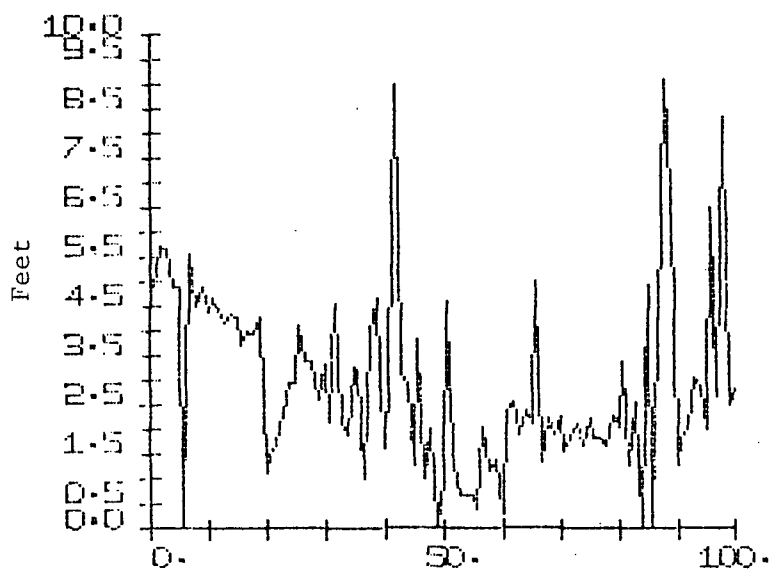
Figure 1S.5 PDDIP over time : sequence 1S for prey 4,5 and 6.

Figure 1S.5

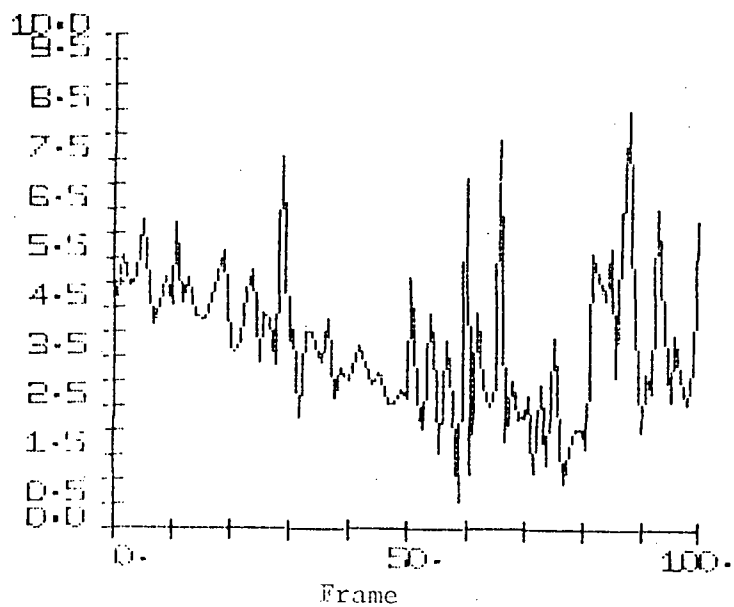
Predator Distance to Intercept Point (PDDIP)



Prey 4



Prey 5

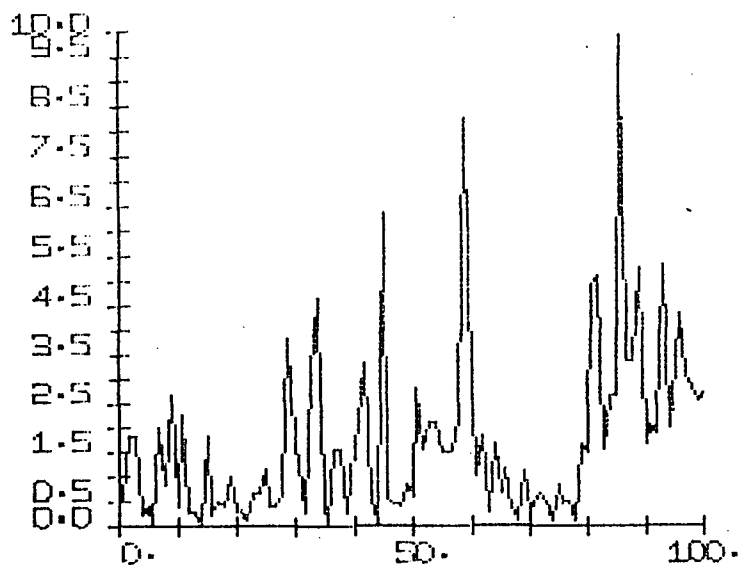


Prey 6

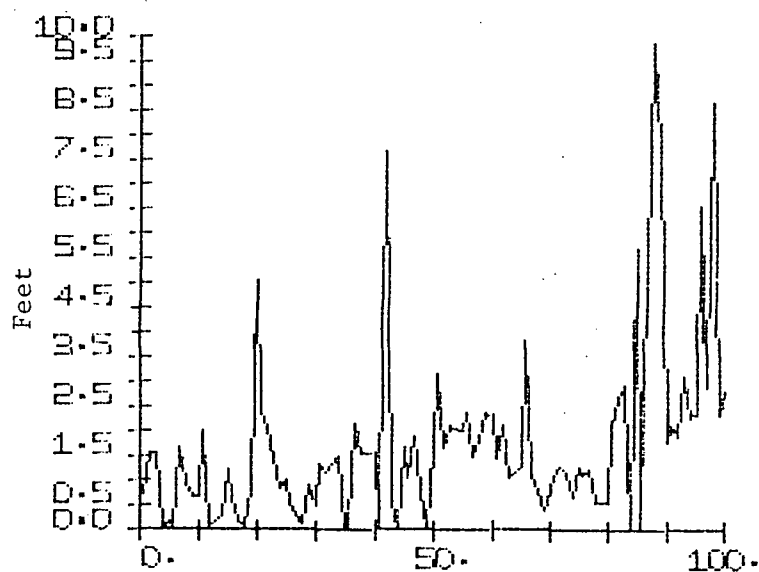
Figure 1S.6 PYDIP over time : sequence 1S for prey 4,5 and 6.

Figure 1S.6

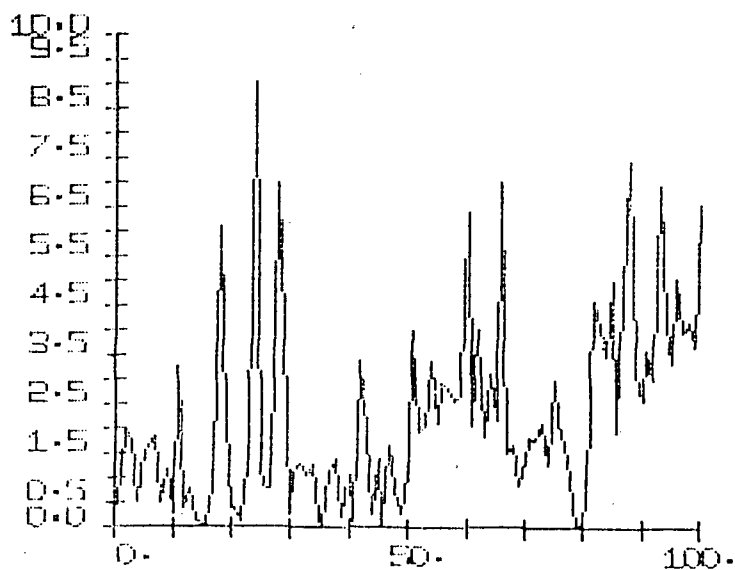
Prey Distance to Intercept Point (PYDIP) vs Time (frame)



Prey 4



Prey 5



Prey 6

Frame

Figure 1S.7 error tracking angle over time : sequence 1S for
prey 4,5 and 6.

Figure 1S.7

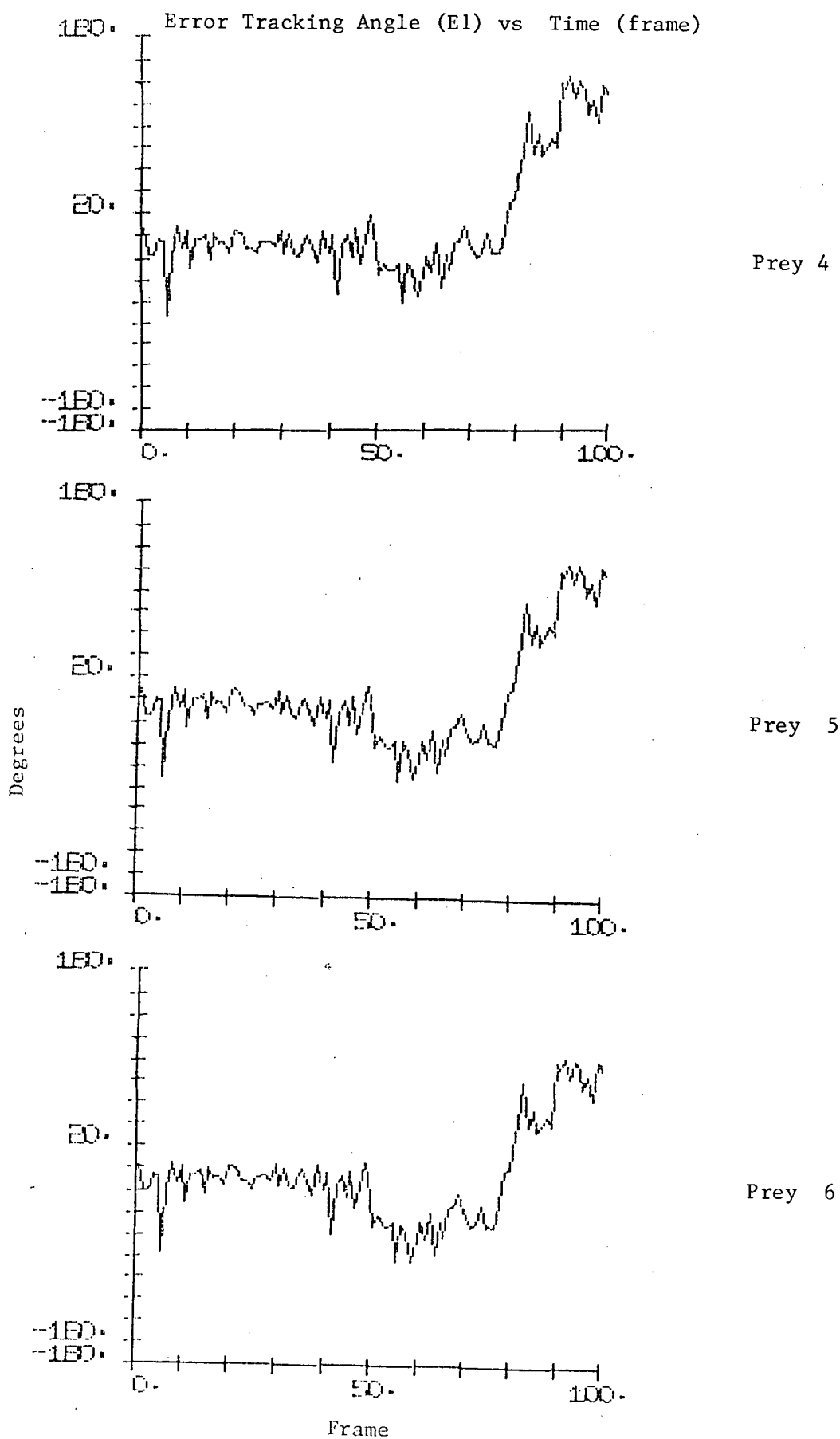


Figure 1S.8 offset angle over time : sequence 1S for prey 4,5
and 6.

Figure 1S.8

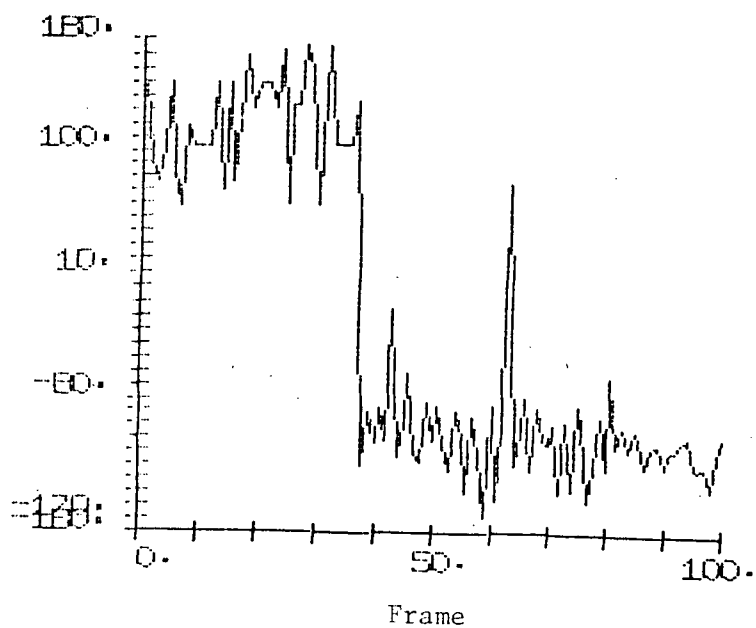
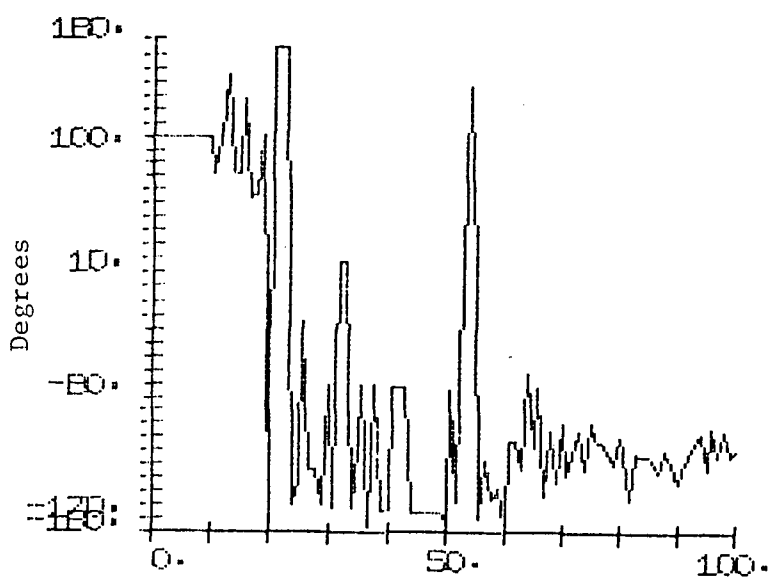
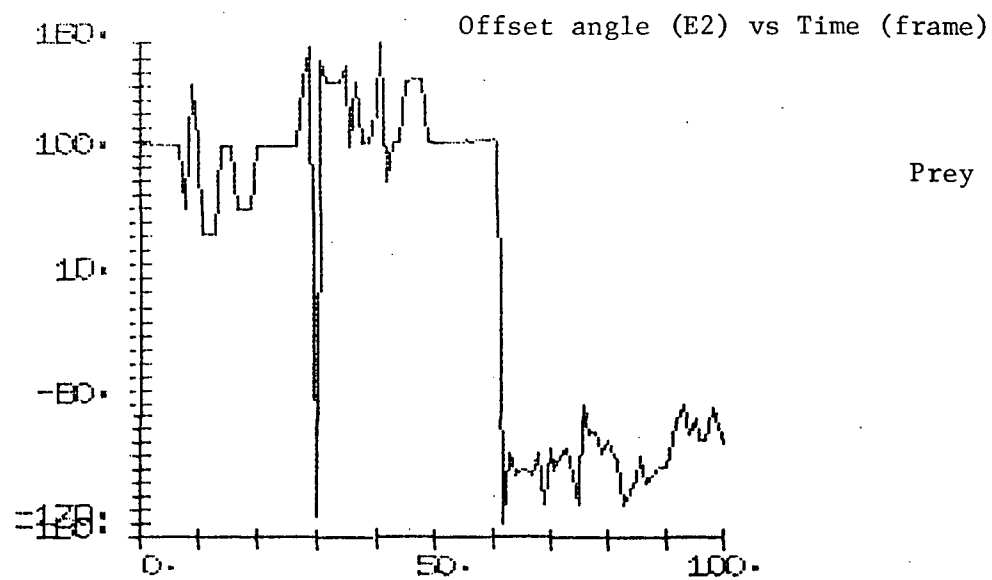


Figure 1S.9 prey linear velocity over time : sequence 1S for
prey 4,5 and 6.

Figure 1S.9

Prey Linear Velocity

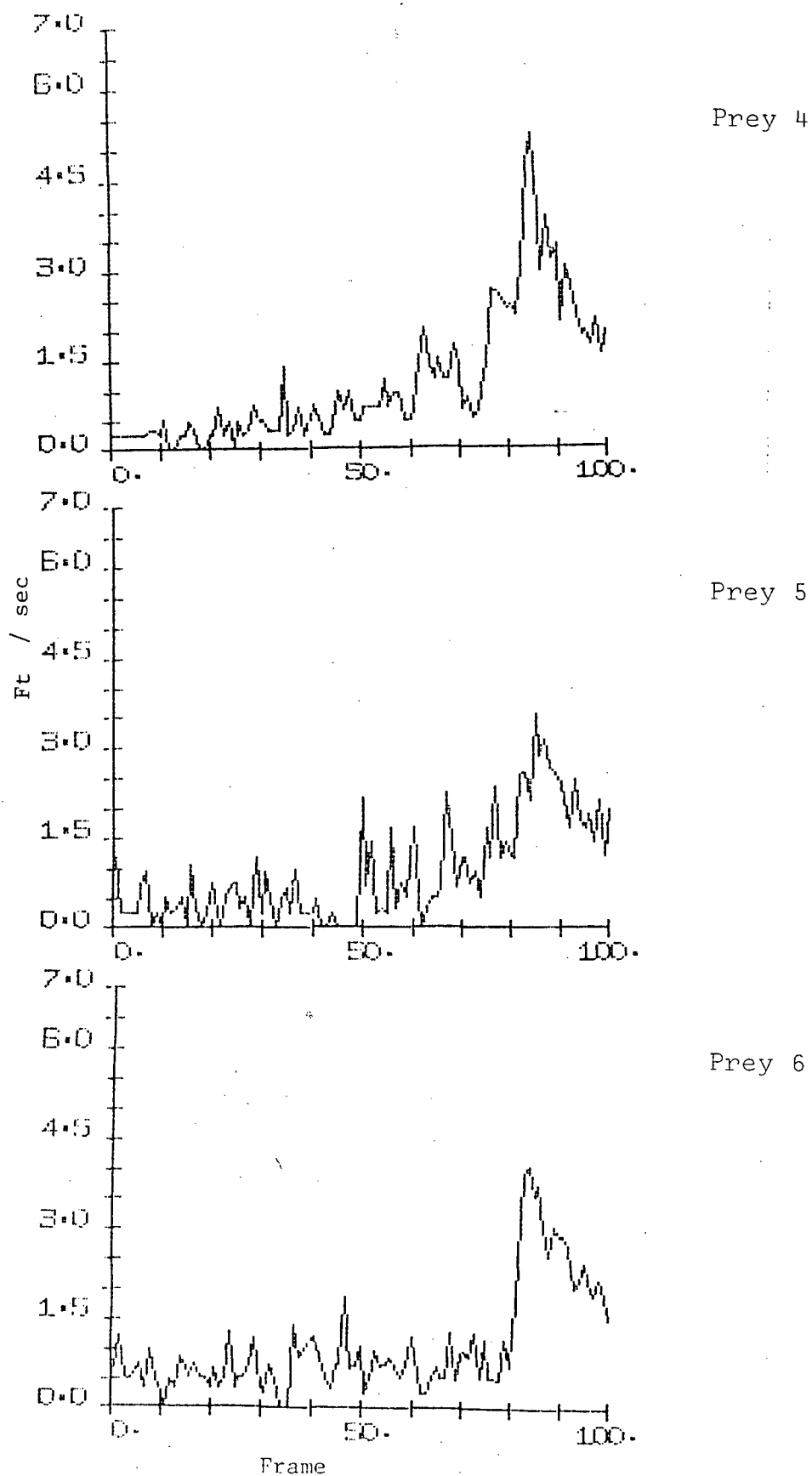
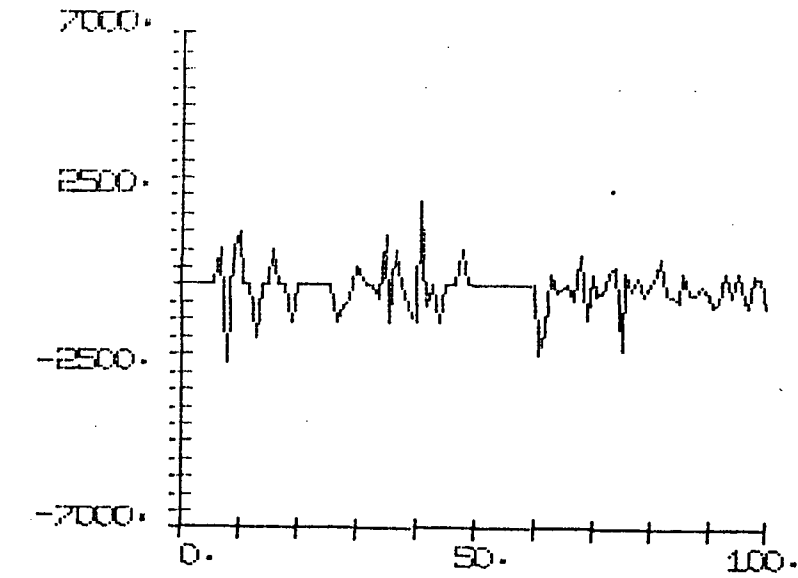


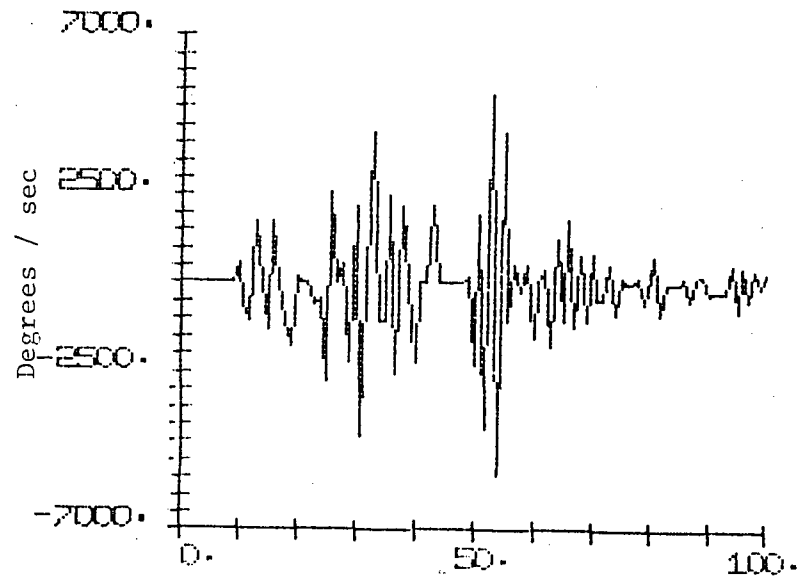
Figure 1S.10 prey angular velocity over time : sequence 1S for
prey 4,5 and 6.

Figure 1S.10

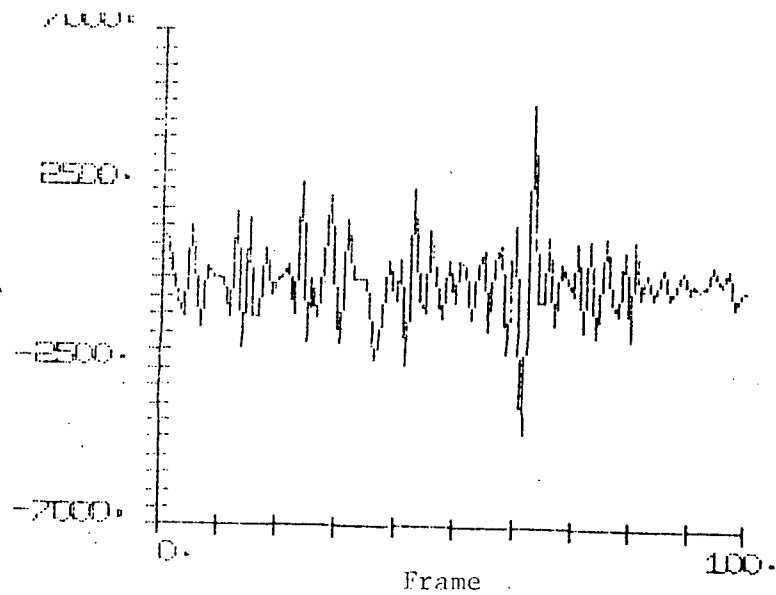
Prey Angular Velocity vs Time (frame)



Prey 4



Prey 5



Prey 6

the closure distance curves show a concave response indicating a decreasing rate of closure. The Distance at Closest Approach (DCA) for each prey individual exhibits large fluctuation through the sequence. Furthermore, none of the decreasing DCA response trends seen in the single predator - single prey sequences were evident. The intercept coefficients are not plotted, but these showed no regular pattern that would indicate path prediction. The large noise components in the DCA graphs would indicate that the predator was unable to "lock" onto a particular target fish in the school. Target switching by the predator could not be directly assessed because of these noise components.

In sequence [1S] the prey remained close together and responded similarly and almost instantaneously with respect to each other as the predator approached. This is especially evident in the angular and linear velocity graphs of the prey where trends and peaks were very similar. The sharp increase in linear velocity coincided with the closest distance to the school achieved by the predator at frames 80 to 82. The offset angles (E2) of all the prey showed an increasing trend to frame 60 for prey 1,3,and 4, and to frames 40-45 for prey 2 and 6. Prey 5 showed a response beginning at frame 20 indicating a moving away from the predator trajectory. For all prey, high angular velocities commenced at frame 13 and continued with increasing amplitudes through the sequence with peaks corresponding to the changes in the offset angles (E2). The high

angular velocities exhibited by the prey early in the sequence while the predator was relatively distant may have functioned to confuse prey tracking. Prey 5 responded in frame 20 by turning almost 180 degrees from the predator trajectory. Prey 6 responded in frame 30 with a similar manoeuvre. At these frames, prey 5 and 6 were not the closest to the predator. During frames 20-30 prey 1-4 showed increased angular velocities but no drastic changes in overall heading. However, at frames 55-62 all prey exhibited a drastic change in direction and angular velocity. At this point, the mean predator distance was 2.31 ft. The DCA, PDDID, and PYDID data indicate that no tracking by the predator was occurring. From frames 65-80 the prey continued moving away from the predator in the same general direction as indicated by the offset angles (E2). At frames 81-82 the predator achieved minimum closure distance and at that point, all prey responded by increasing linear velocity through frame 90. The predator then turned away from the school.

Similar patterns were exhibited in kinematic data for both predator and prey in all sequences in which the prey remained relatively close together and turned in the same direction, maintaining close contact and similar angular and linear velocities. The prey began turning away from the predator trajectory with increasing angular velocity oscillations. This increase in oscillating angular velocity without a corresponding major direction change has been termed "dithering" behaviour by Holling (pc). At a mean closure distance of $2.4 \pm .3$ feet,

major directional change followed by increased linear velocity were seen. In these sequences, no measurable tracking by the predator were seen, and closure rates showed concave responses. Predator linear velocity remained relatively constant and low instead of the expected increase if tracking to intercept occurred. The data indicates that "dithering" and close proximity of the prey individuals serve to confuse the predator, destroying the predator tracking solution.

Time trajectories of chase sequence [2S] for the predator and two of the prey (prey 4 and 5) are presented in figures 2S.1a and 2S.1b. The corresponding kinematic parameters for the predator and prey 4,5, and 6, are presented in figures 2S.2 to 2S.10.

Sequence [2S] is of interest because the predator attack results in one prey individual , designated prey 5 , becoming separated from the school.

The linear velocity of the predator showed an immediate increase to a maximum by frame 40, resulting in a convex closure distance pattern similar to that observed in single predator-single prey interactions. The closure distance graphs indicate that the minimum closure distance occurred at frame 48-55. Prey 5 was closest to the predator at frame 48. From the prey linear angular velocity graphs for prey 5, a response can be seen at this point. Up to frame 48, the prey exhibited a characteristic

Figures 2S.1a and 2S.1b time trajectory school : sequence 2S
the predator and prey 4 and 5.

Figure 2S.1a

Time Trajectory Sequence 2S : prey 4

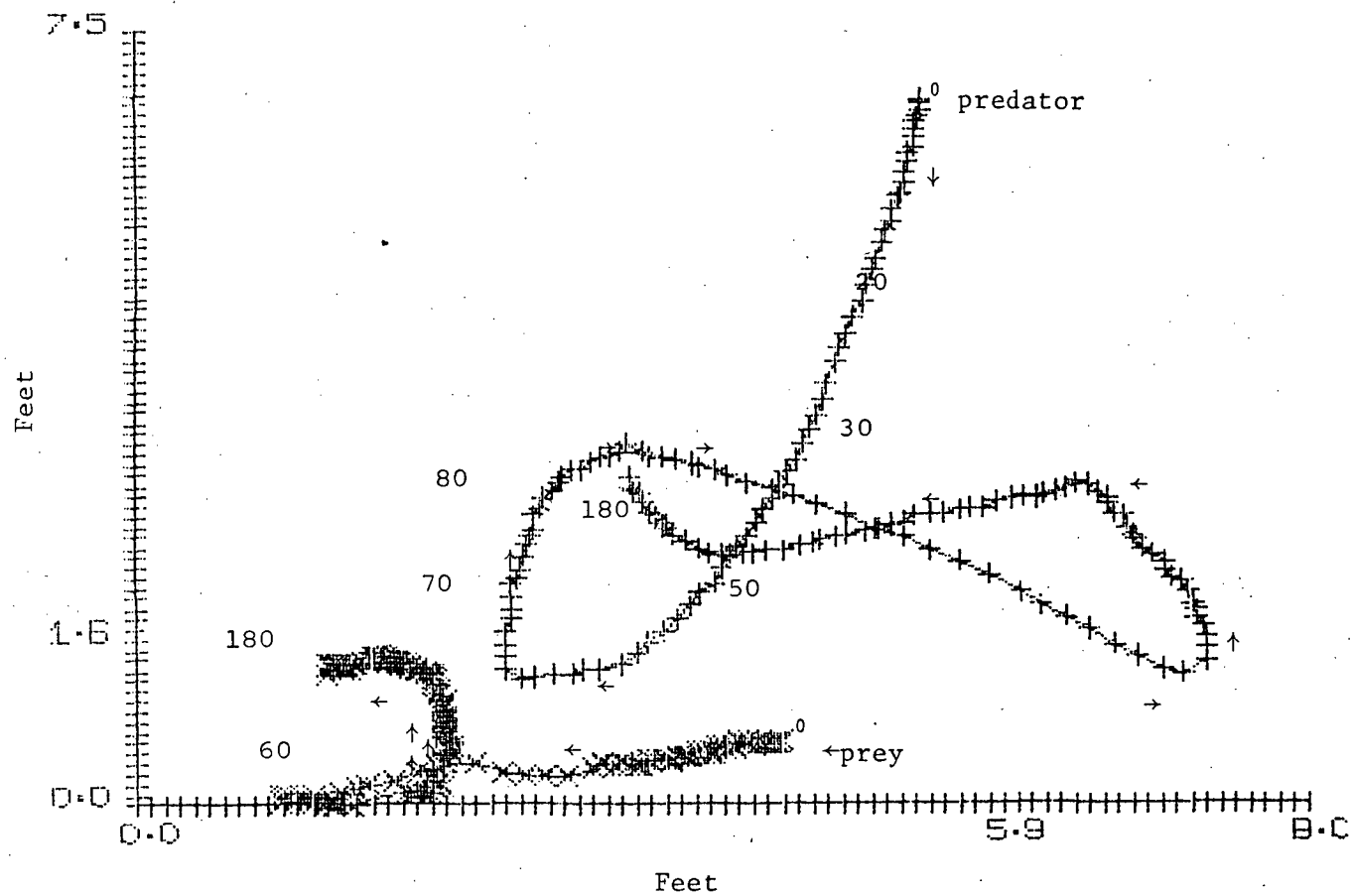


Figure 2S.1b

Time Trajectory Sequence 2S : prey 5

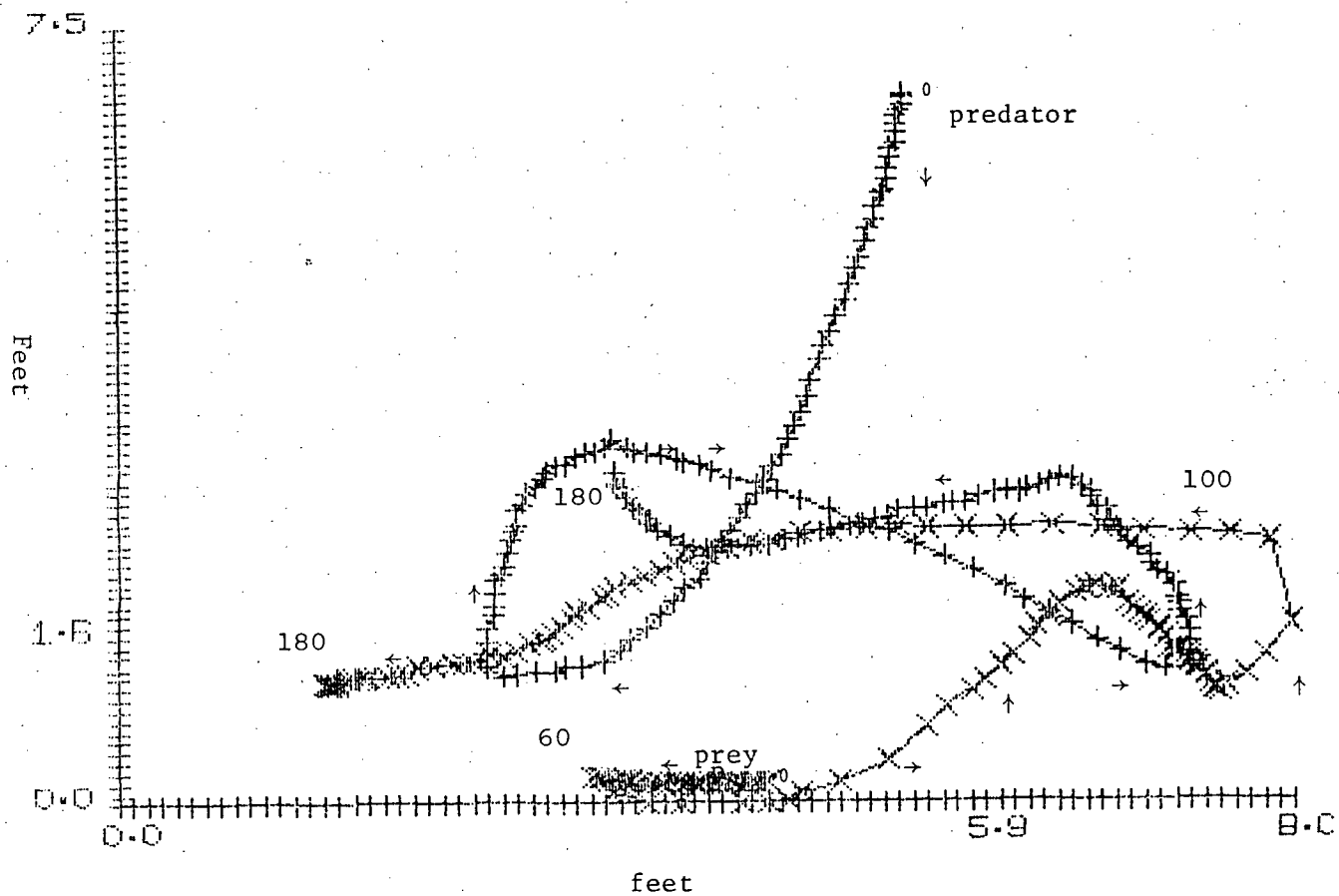


Figure 2S.2 predator linear and angular velocity : sequence 2S

Figure 2S.2

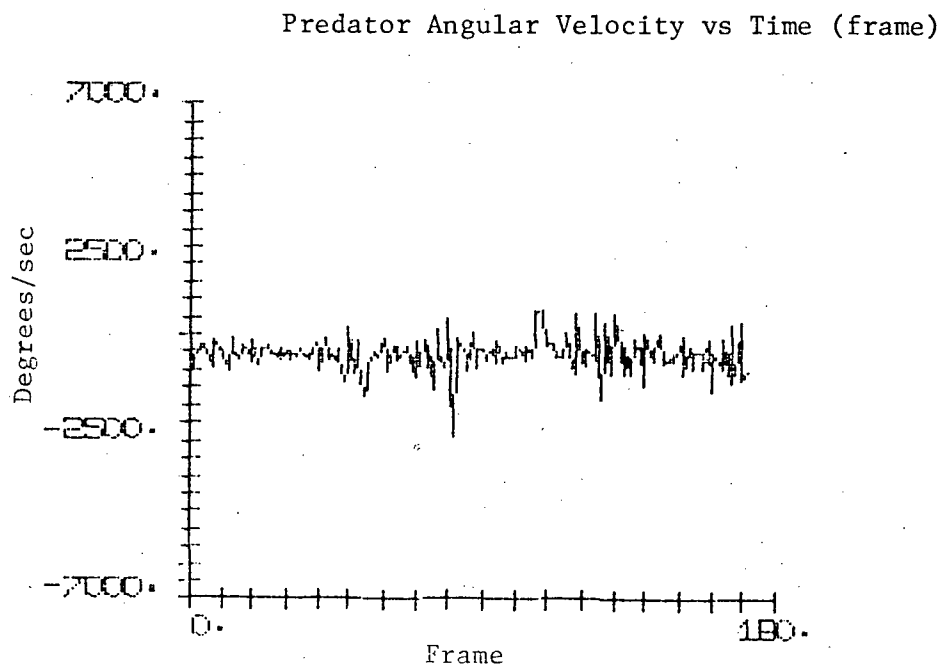
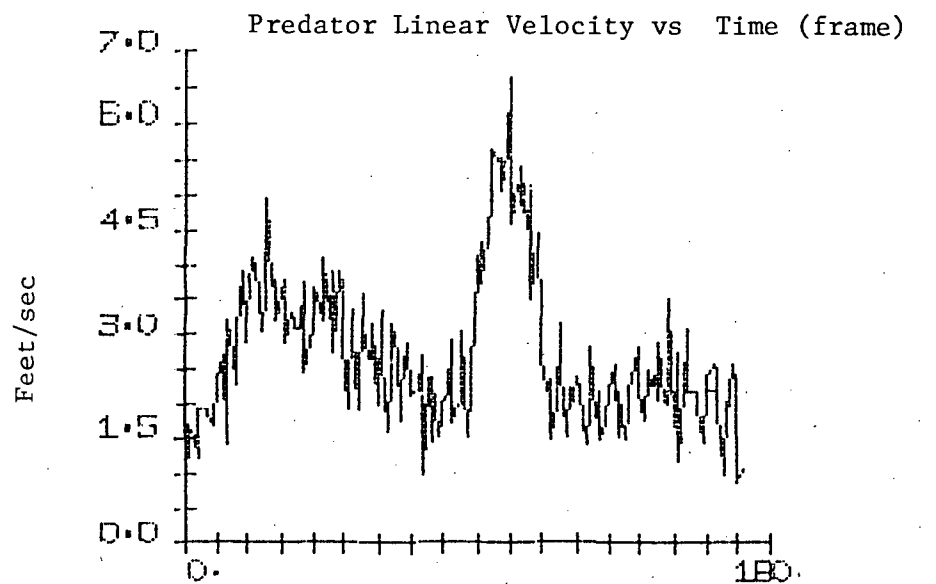
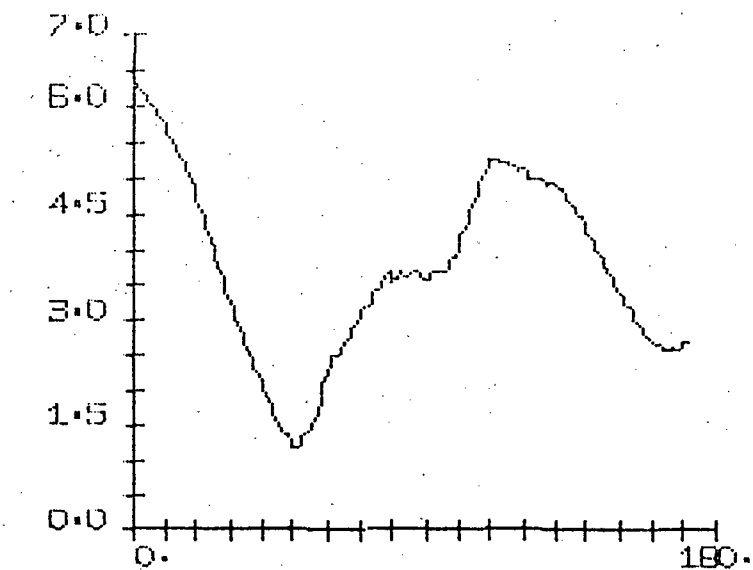


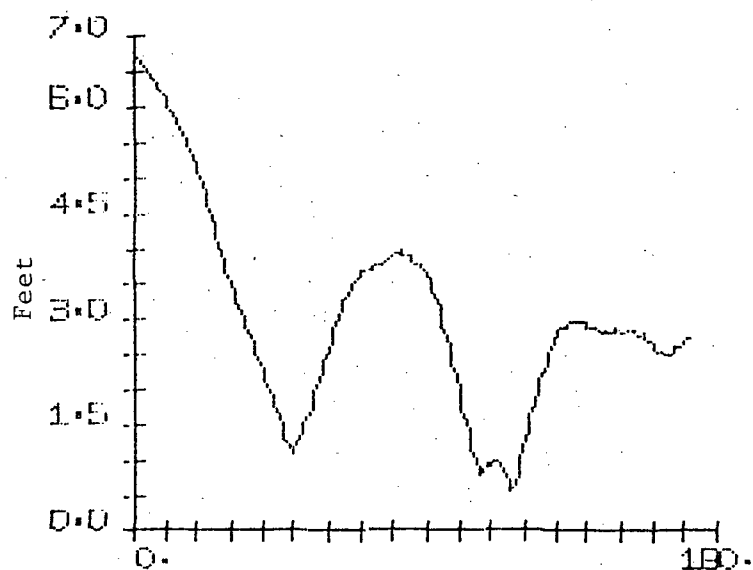
Figure 2S.3 closure distance over time : sequence 2S for prey 4,5 and 6. Note the convex response for prey 5, frames 90-110.

Figure 2S.3

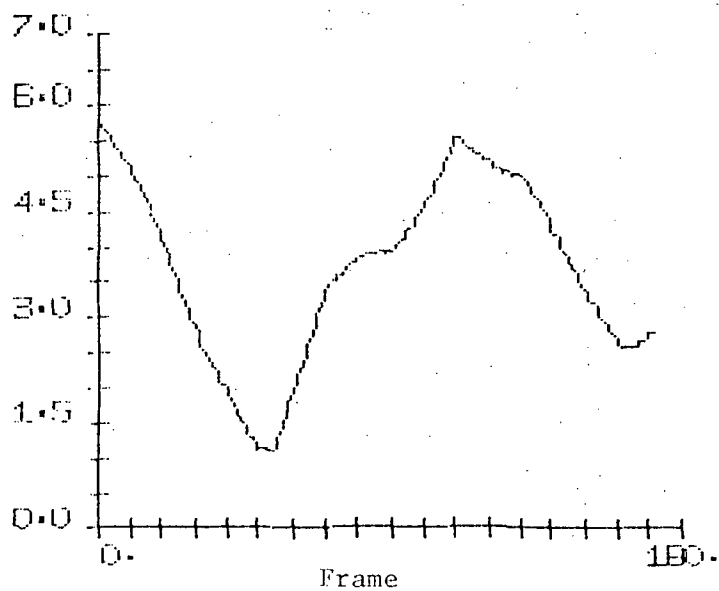
Closure Distance (CLD) vs Time (frame)



Prey 4



Prey 5

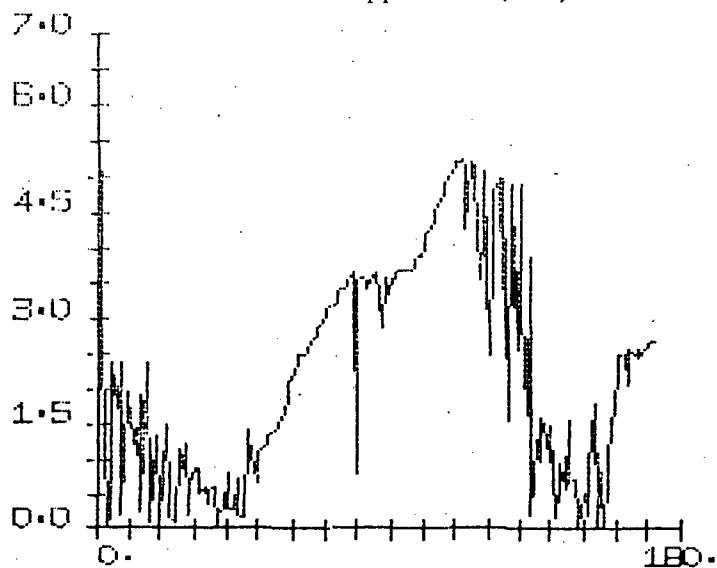


Prey 6

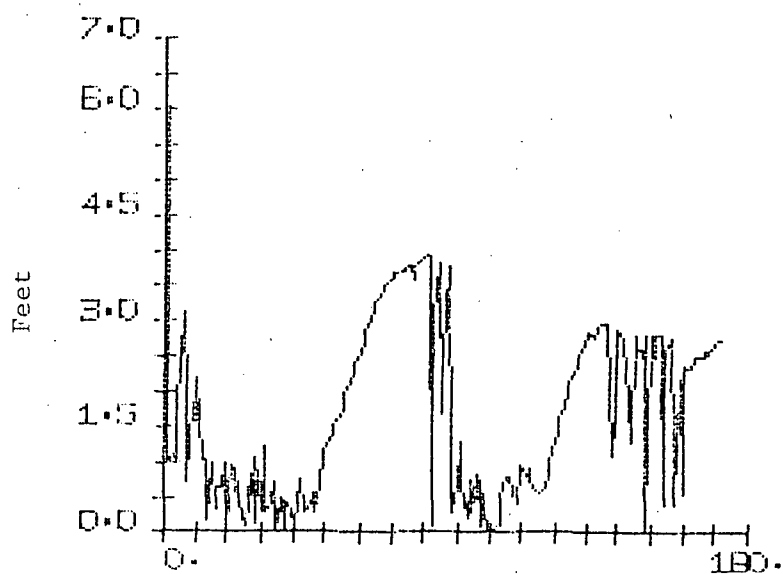
Figure 2S.4 Distance at Closest Approach over time : sequence 2S for prey 4,5 and 6. Path prediction by the predator can be seen for prey 5, frames 90-110. See text for full explanation.

Figure 2S.4

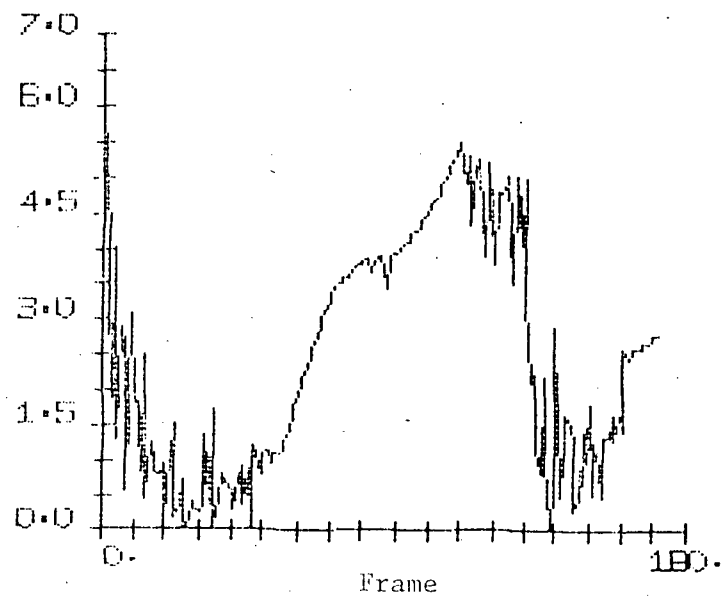
Distance at Closest Approach (DCA) vs Time (frame)



Prey 4



Prey 5

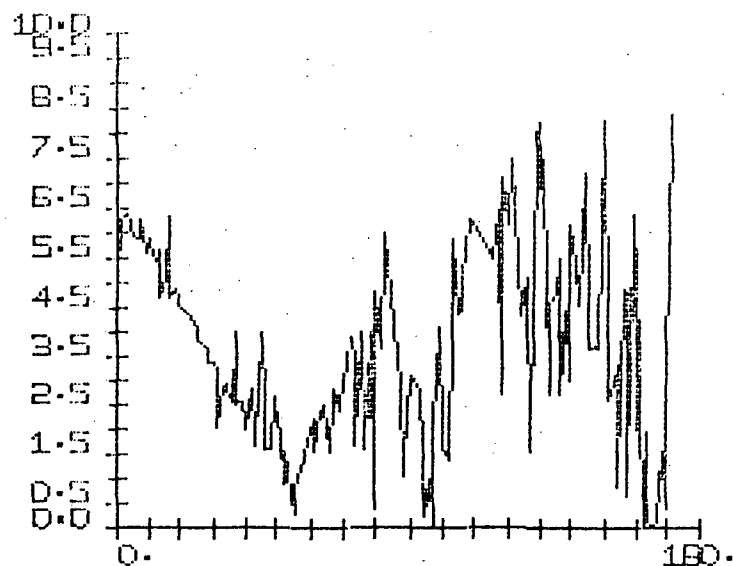


Prey 6

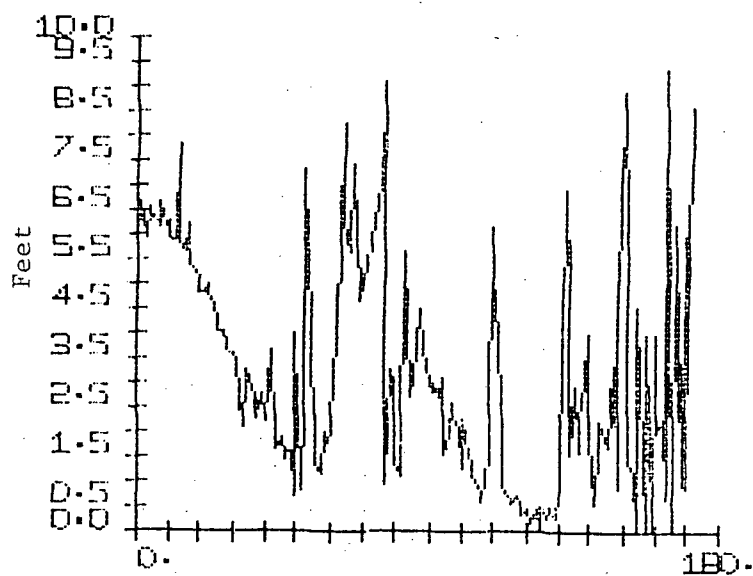
Figure 2S.5 PDDIP over time : sequence 2S for prey 4,5 and 6.

Figure 2S.5

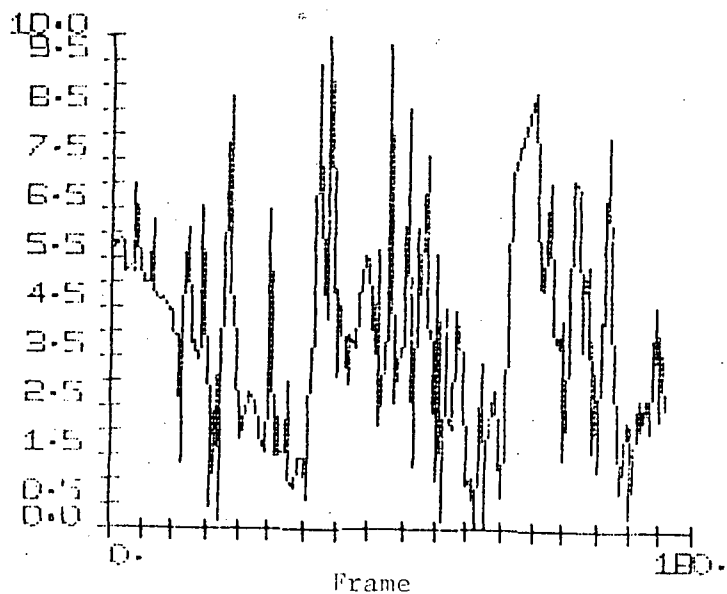
Predator Distance to Intercept Point (PDDIP) vs Time (frame).



Prey 4



Prey 5

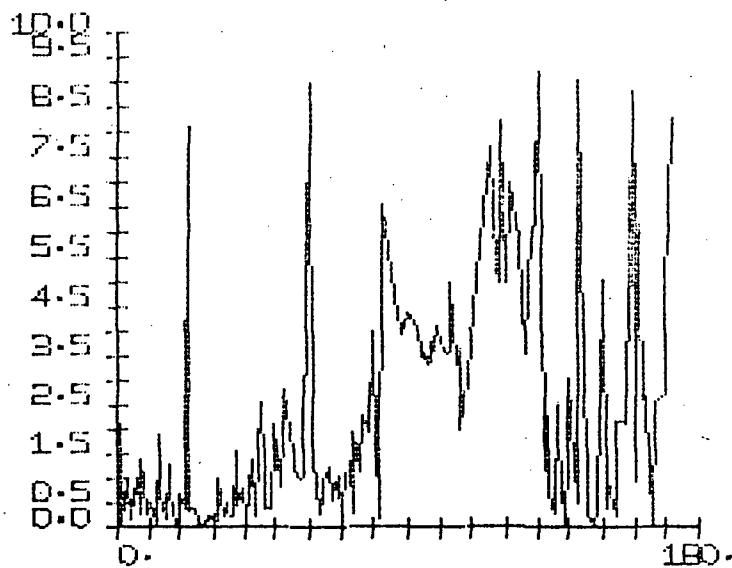


Prey 6

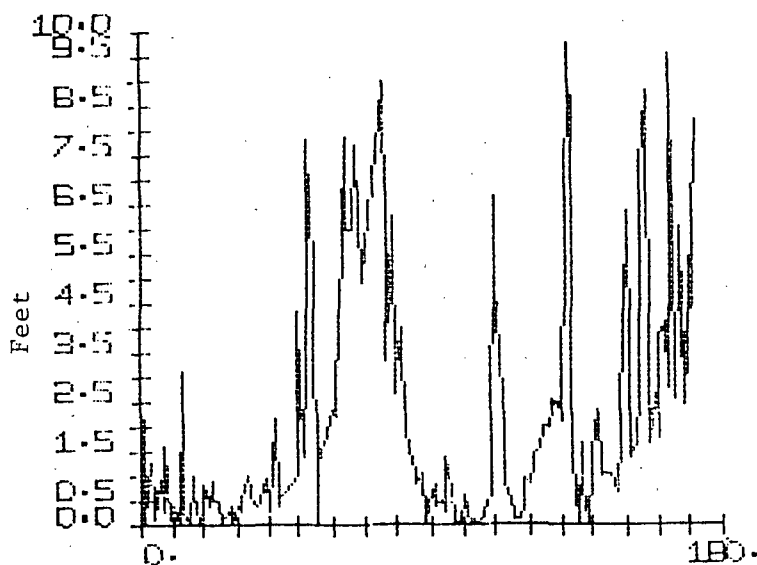
Figure 2S.6 PYDIP over time : sequence 2S for prey 4,5 and 6.

Figure 2S.6

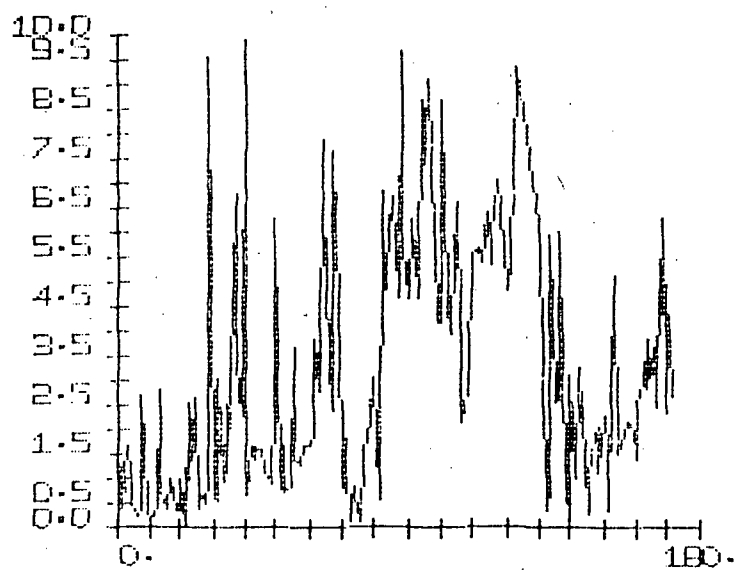
Prey Distance to Intercept Point (PYDIP) vs Time (frame)



Prey 4



Prey 5



Prey 6

Frame

Figure 2S.7 error tracking angle over time : sequence 2S for prey 4,5 and 6. Defensive manoeuvres by the school can be seen as the large fluctuations in tracking error. See text for full explanation.

Figure 2S.7

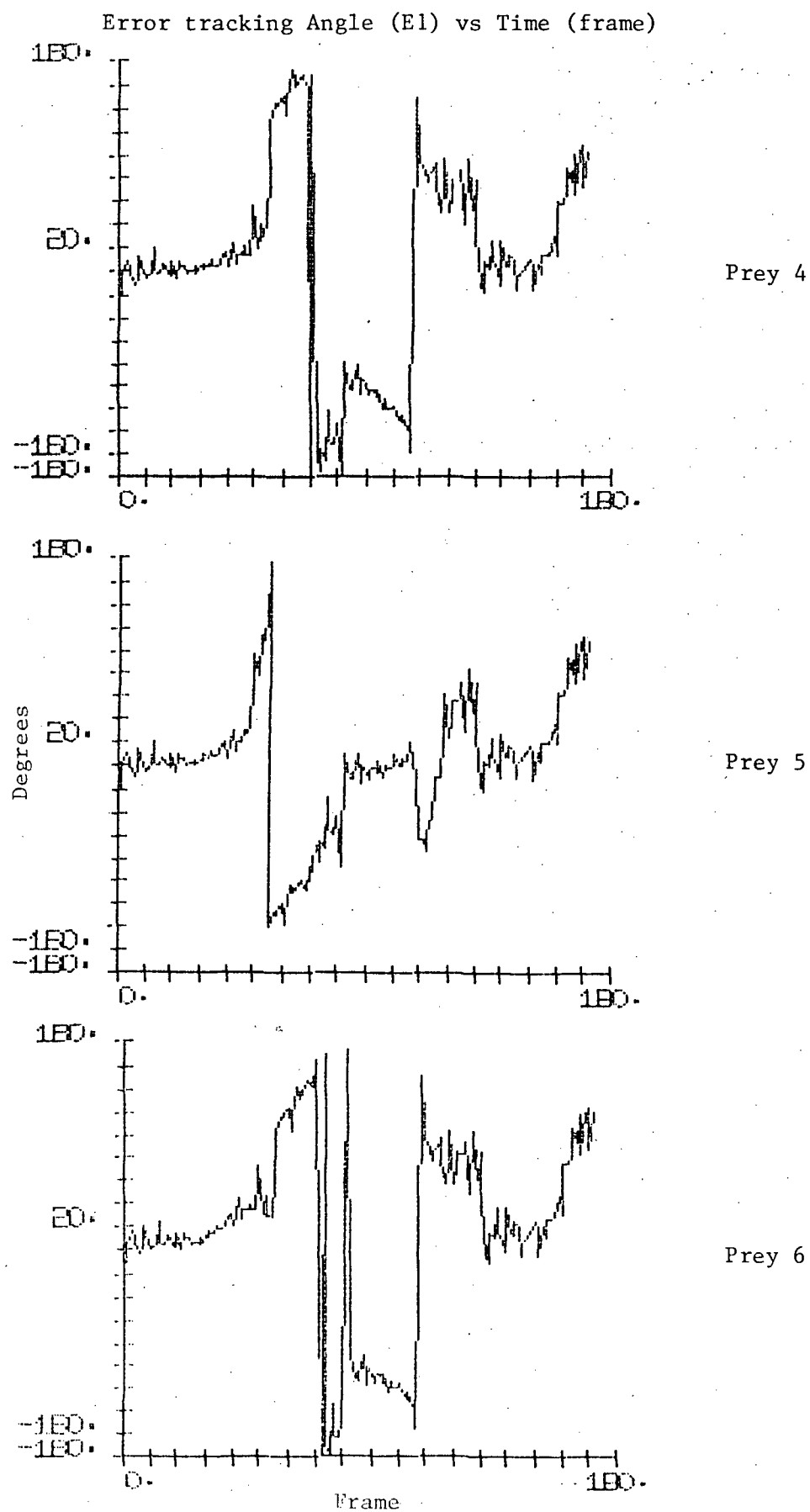
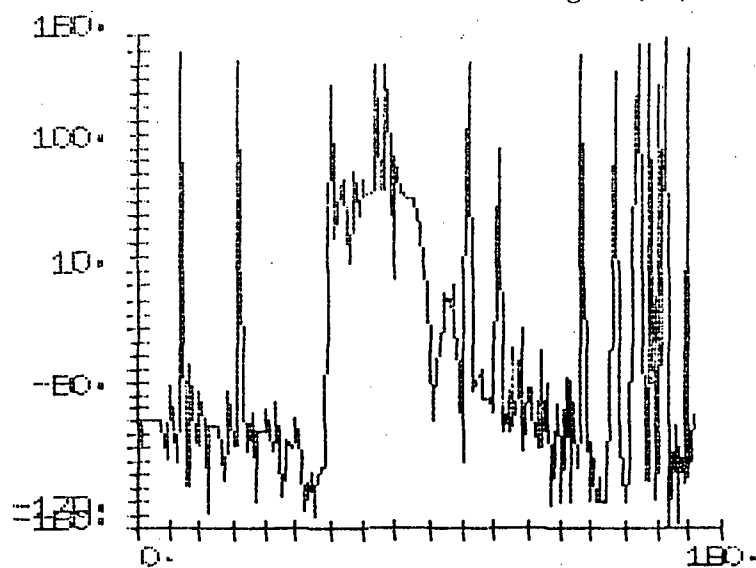


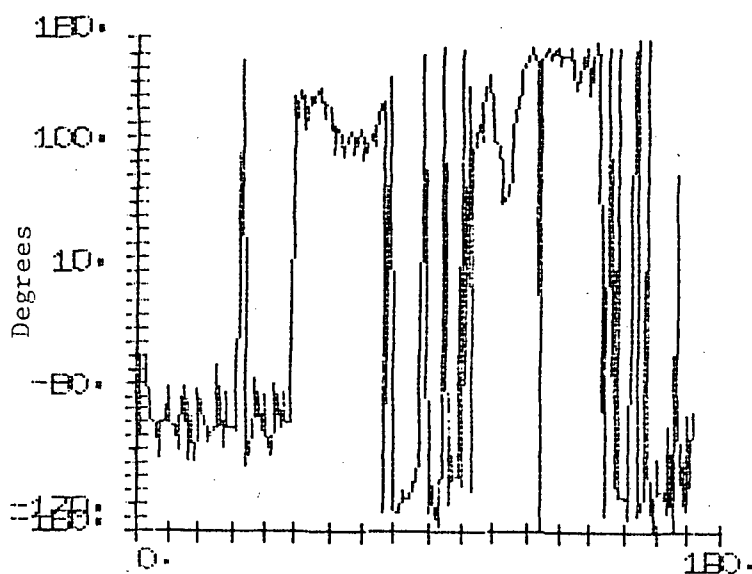
Figure 2S.8 offset angle over time : sequence 2S for prey 4,5
and 6.

Figure 2S.8

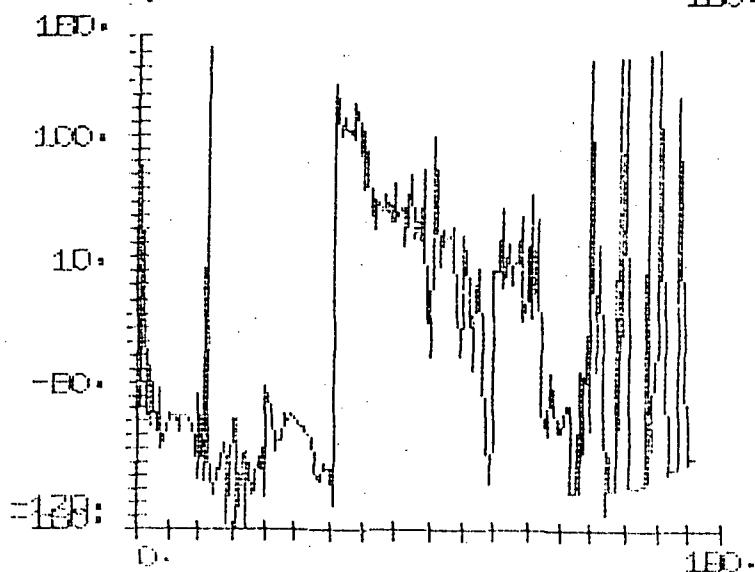
Offset Angle (E2) vs Time (frame)



Prey 4



Prey 5



Prey 6

Frame

Figure 2S.9 prey linear velocity over time : sequence 2S for
prey 4,5 and 6.

Figure 2S.9

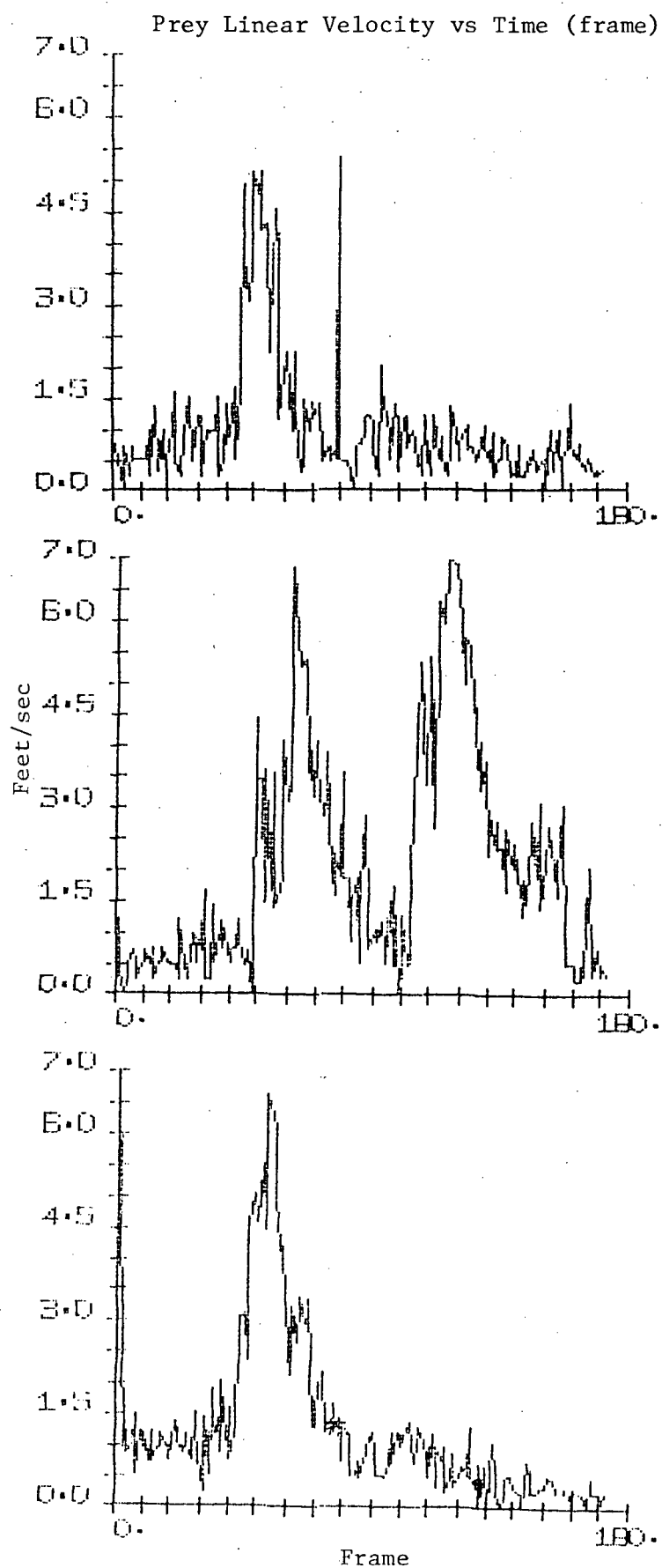
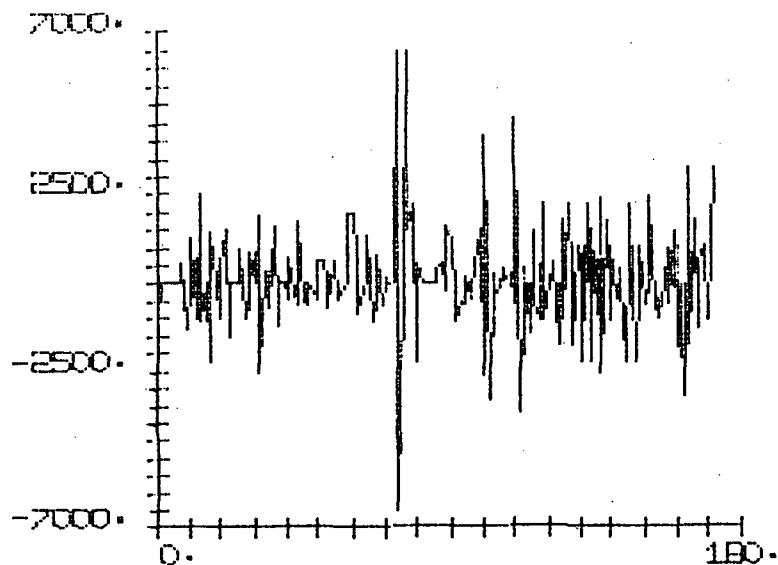


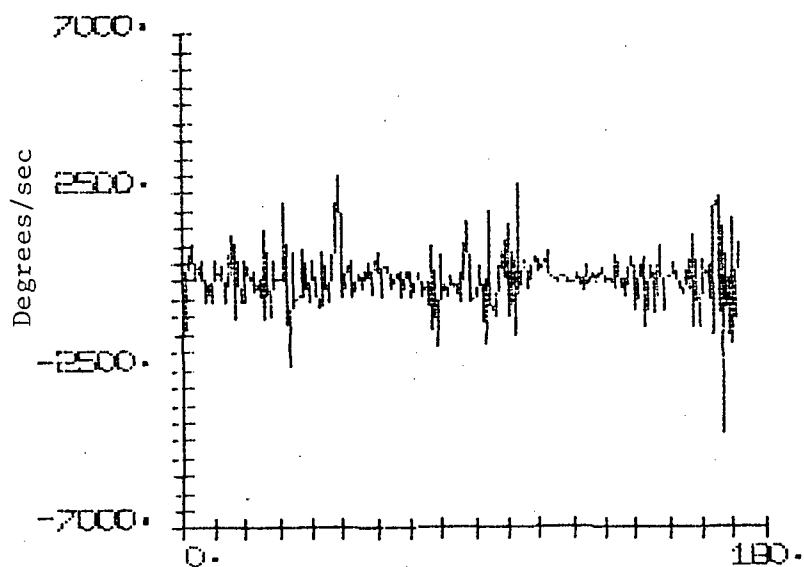
Figure 2S.10 prey angular velocity over time : sequence 2S for
prey 4,5 and 6.

Figure 2S.10

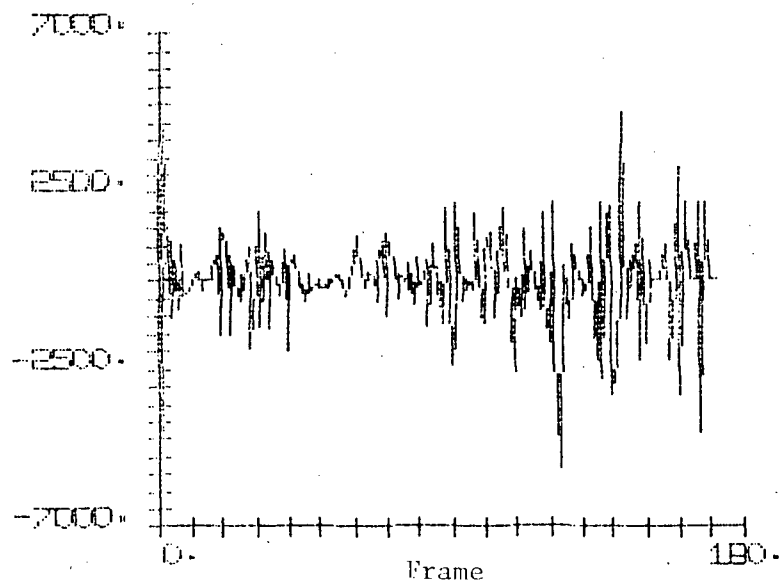
Prey Angular Velocity vs Time (frame)



Prey 4



Prey 5



Prey 6

moving away from the predator trajectory as indicated in the offset angle (E2) graphs. Prey 5 was the first to respond by a quick turn to the left. This is indicated in the error angle (E1), angular velocity, and offset angle (E2) graphs. Up to frame 48 the DCA data, and the corresponding PDDIP, PYDIP, and error angle (E1) data for prey 5 showed less fluctuation than those of the other school members, suggesting that prey 5 was the target prey. The DCA data showed large fluctuations and were however, not as "clean" as those for single predator-single prey interactions. The turning manoeuvre at frame 48 by the prey resulted in the predator losing tracking and turning away. From the linear velocity graphs of the prey, it can be seen that prey 5 maintained a higher linear velocity for a greater length of time than the other school members. As prey 1,2,3,4, and 6 slowed down and turned gently to the left, reforming the school, prey 5 continued in the opposite direction. From the closure distance and DCA data, it is quite clear that the predator responded to prey 5, and initiated a new attack. The predator response appears at frame 80 and continues to frame 117. At minimum closure distance, prey 5 responded with a quick left turn and approached the reformed school. The kinematic data indicate tracking by the predator for a short time, but the large oscillations in DCA, PDDIP, and PYDIP indicate eventual tracking loss. As in sequence 1S, the prey in 2S exhibited increased angular velocities ("dithering") and moving away from the predator trajectory. At frame 160, the predator moved away from the school.

Time trajectories of the predator and prey 1 and 2 for chase sequence [3S] are presented in figures 3S.1a and 3S.1b. The corresponding kinematic parameters for the predator and prey 1,2,and 3 are presented in figures 3S.2 to 3S.10 .

The linear and angular velocity data of the predator show the characteristic response of attack indicated by the rapid linear acceleration. The closure distance data also show the characteristic attack pattern. From the DCA,PDDIP, PYDIP, and error angle (E1) data, it is quite clear that prey 1 was the target and that the predator was tracking this individual. At a distance of 2.35 feet at frame 30, prey 1 responded with an increased linear velocity ; turned away from the predator and headed toward the school. Up to frame 30, the angular and linear velocity of the school remained low and the offset (E2) shows an increasing trend indicating a moving away from the predator trajectory. As prey 1 approached the school in frames 30-40, the school responded with an increased angular and linear velocity leading to loss of tracking by the predator. By frame 55, the predator moved away from the school. The DCA,PDDIP, PYDIP, and error angle (E2) data show that from frames 40-50 there may have been tracking by the predator, but it is unclear as to which prey is tracked. The tracking error increased for all individuals of the school from frame 46 onwards. Up to frame 38 the error angle for prey 1 showed little deviation and was a constant response, similar to that seen in single predator-

Figures 3S.1a and 3S.1b time trajectory school : sequence 3S
the predator and prey 1 and 2.

Figure 3S.1a

Time Trajectory Sequence 3S: prey 1

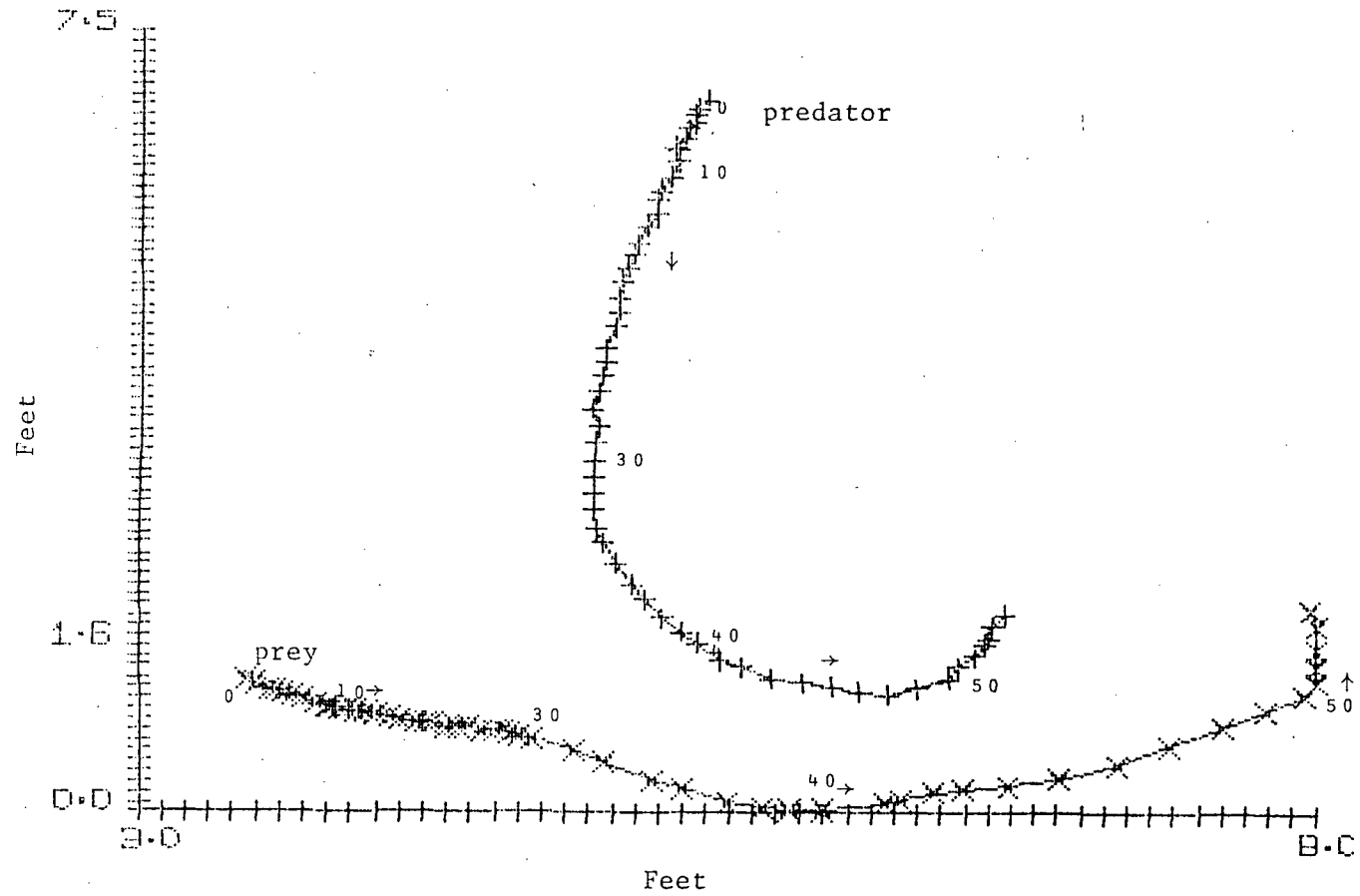


Figure 3S.1b

Time Trajectory Sequence 3S: prey 2

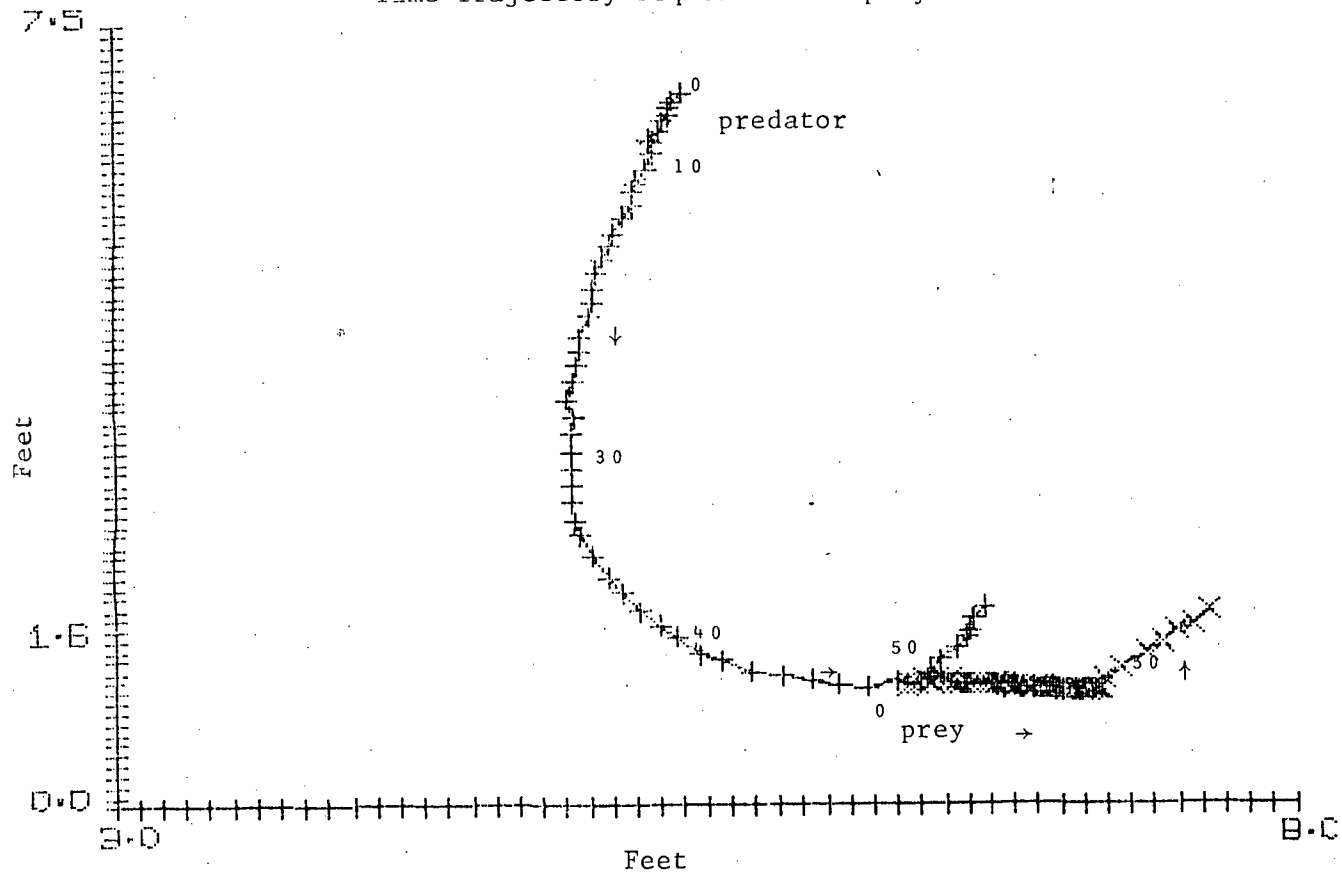


Figure 3S.2 predator linear and angular velocity : sequence 3S

Figure 3S.2

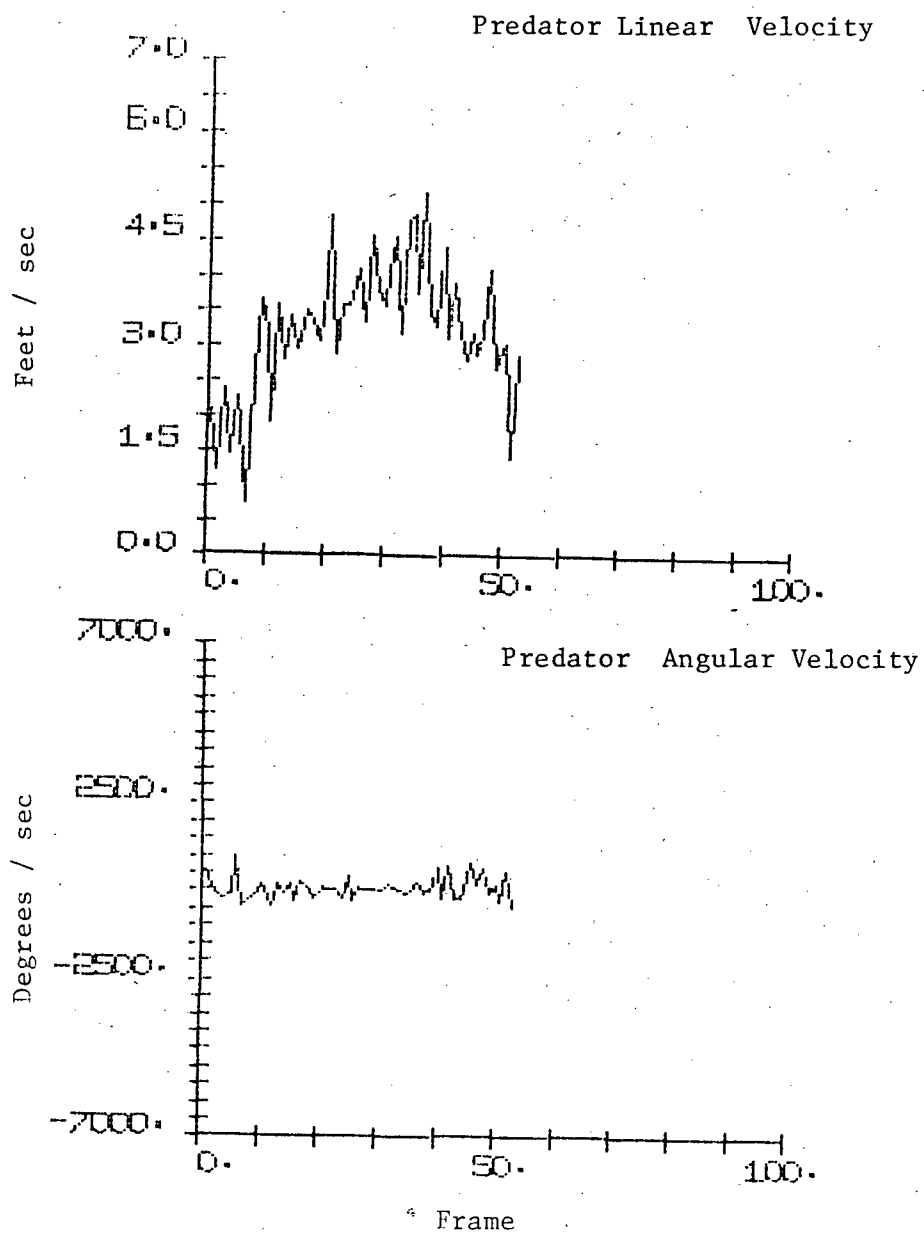
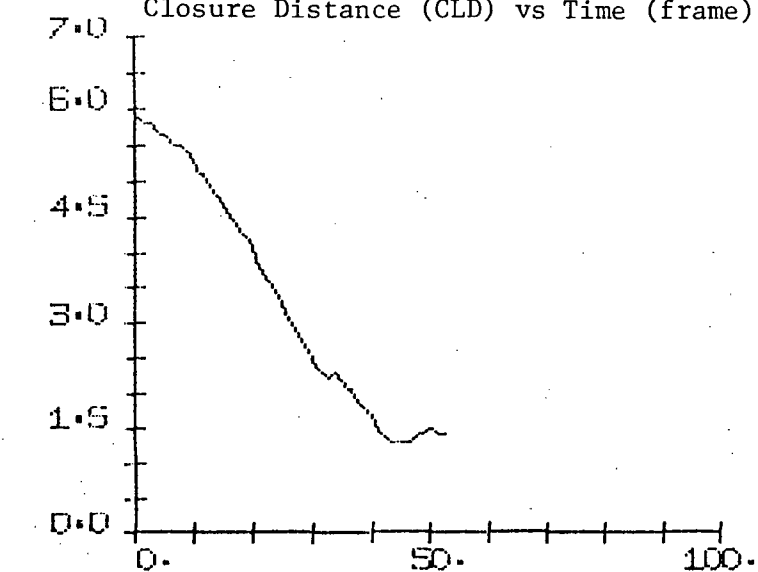


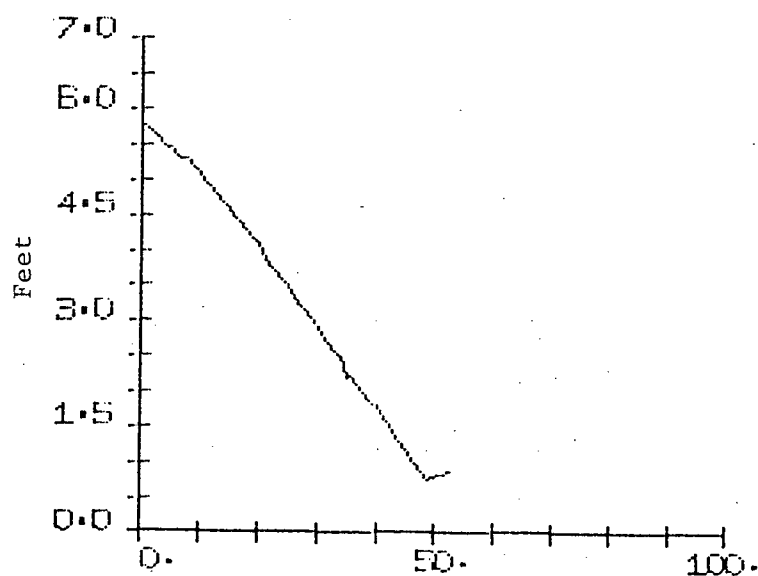
Figure 3S.3 closure distance over time : sequence 3S for prey
1,2 and 3.

Figure 3S.3

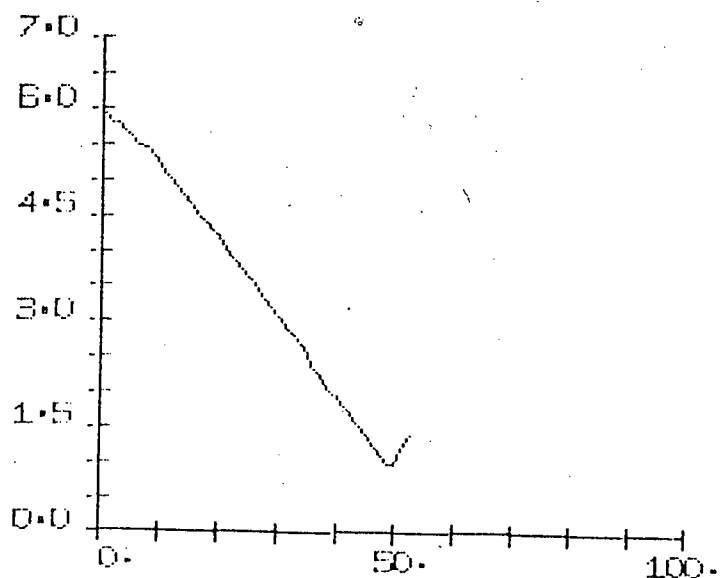
Closure Distance (CLD) vs Time (frame)



Prey 1



Prey 2

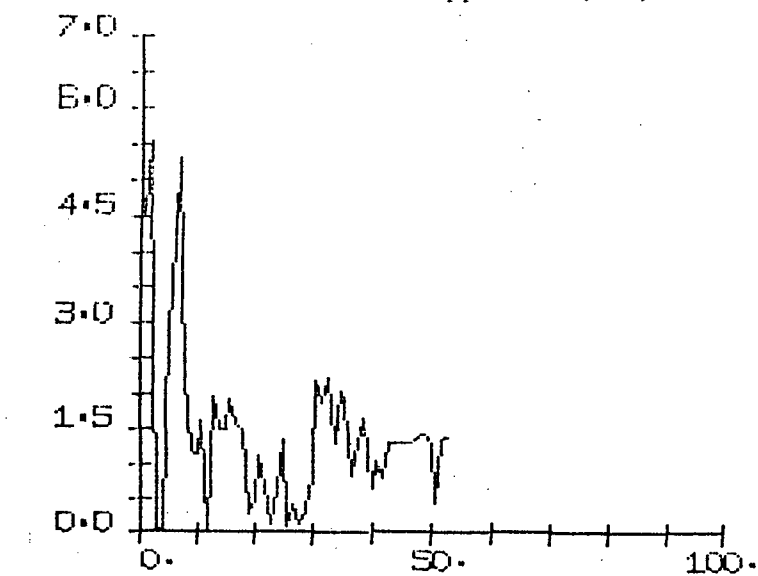


Prey 3

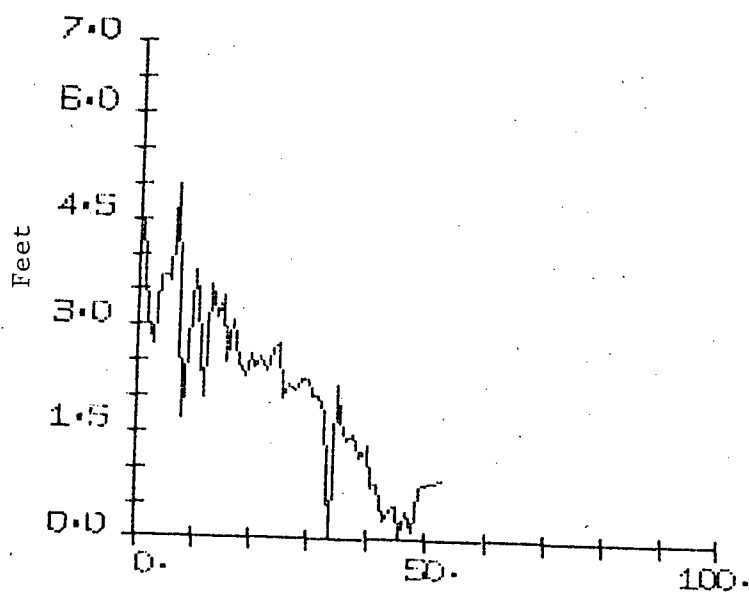
Figure 3S.4 Distance at Closest Approach over time : sequence
3S for prey 1,2 and 3. Note the attempted path
prediction for prey 1 by the predator.

Figure 3S.4

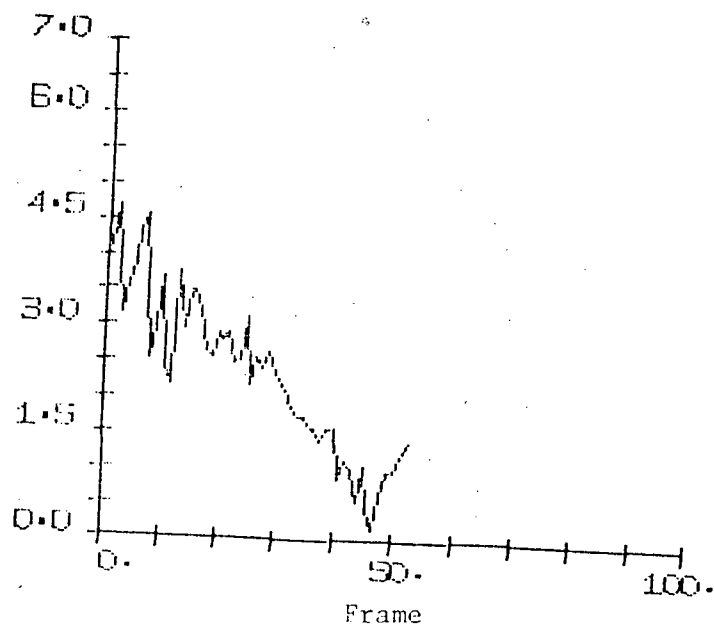
Distance at Closest Approach (DCA) vs Time (frame)



Prey 1



Prey 2



Prey 3

Figure 3S.5 PDDIP over time : sequence 3S for prey 1,2 and 3.

Figure 3S.5

Predator Distance to Intercept Point (PDDIP) vs Time (frame)

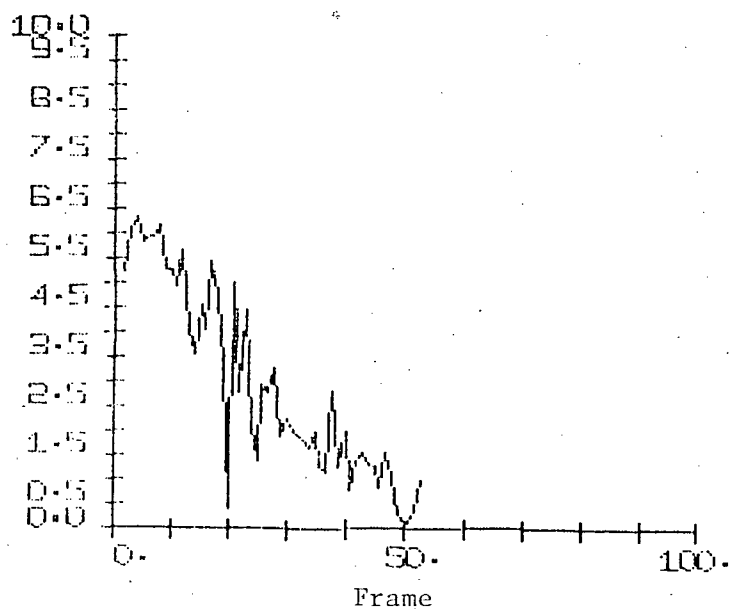
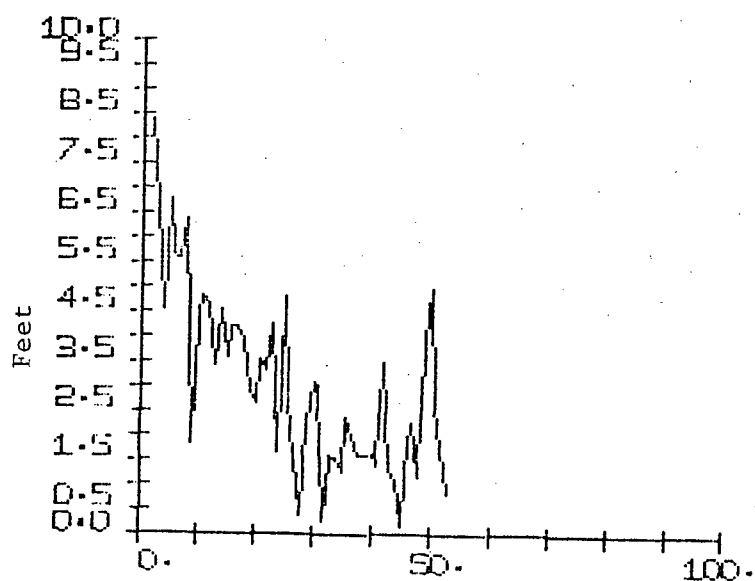
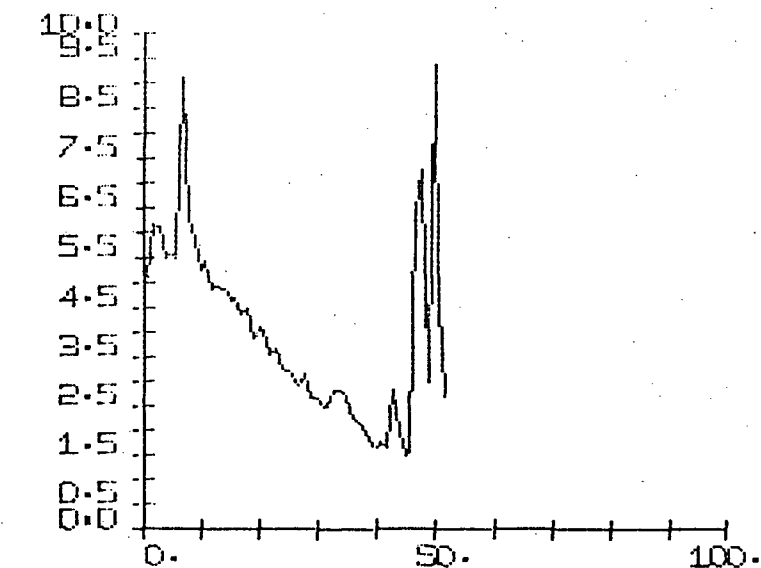


Figure 3S.6 PYDIP over time : sequence 3S for prey 1,2 and 3.

Figure 3S.6

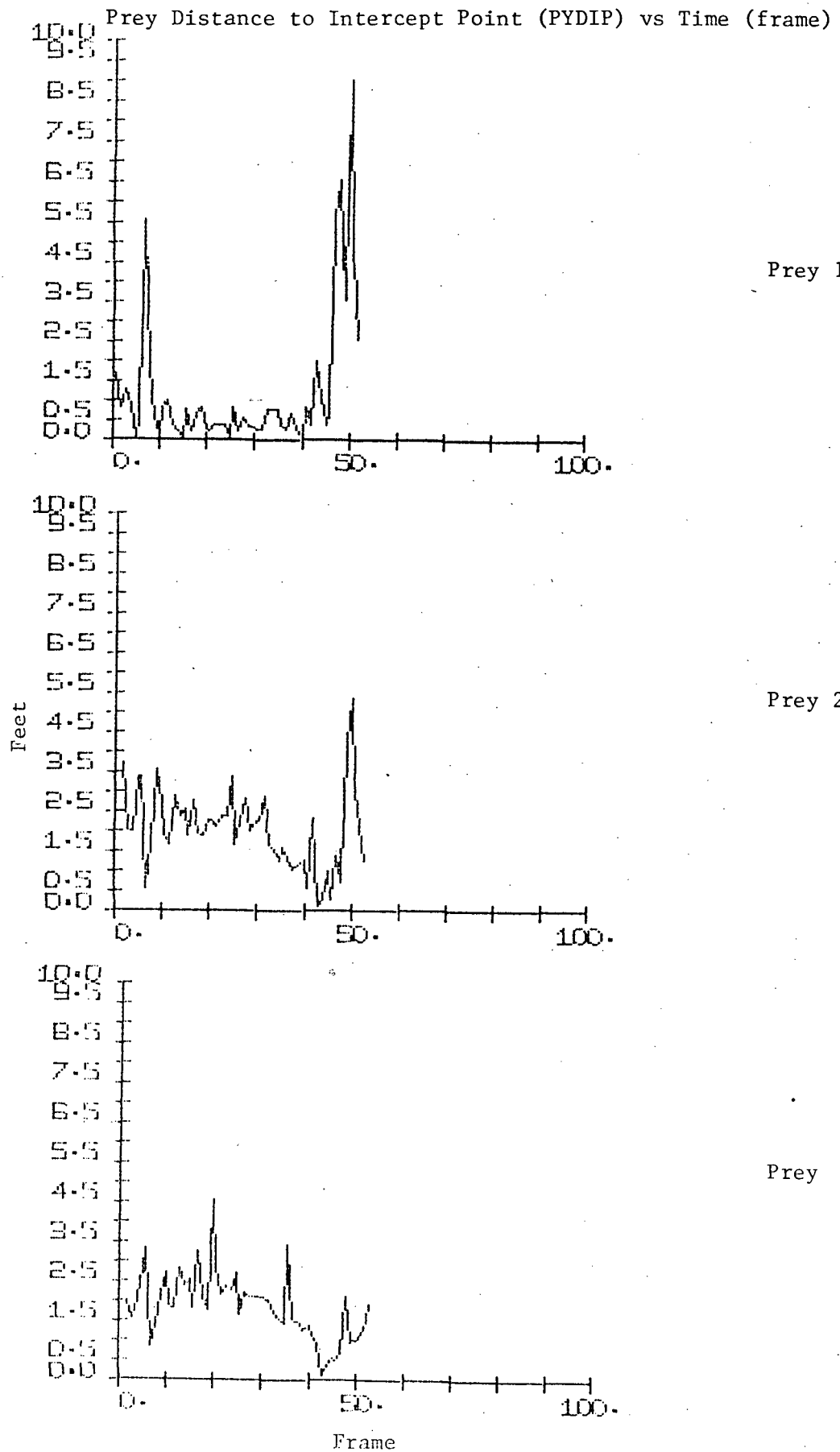
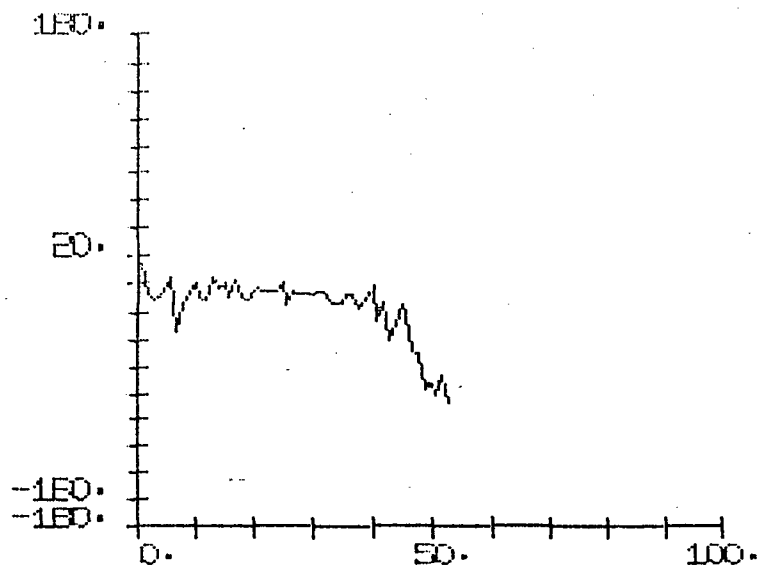


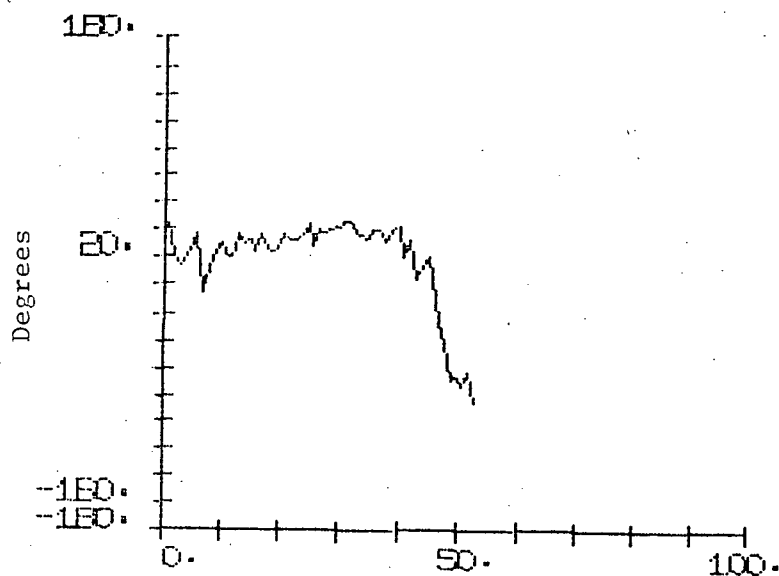
Figure 3S.7 error tracking angle over time : sequence 3S for
prey 1,2 and 3.

Figure 3S.7

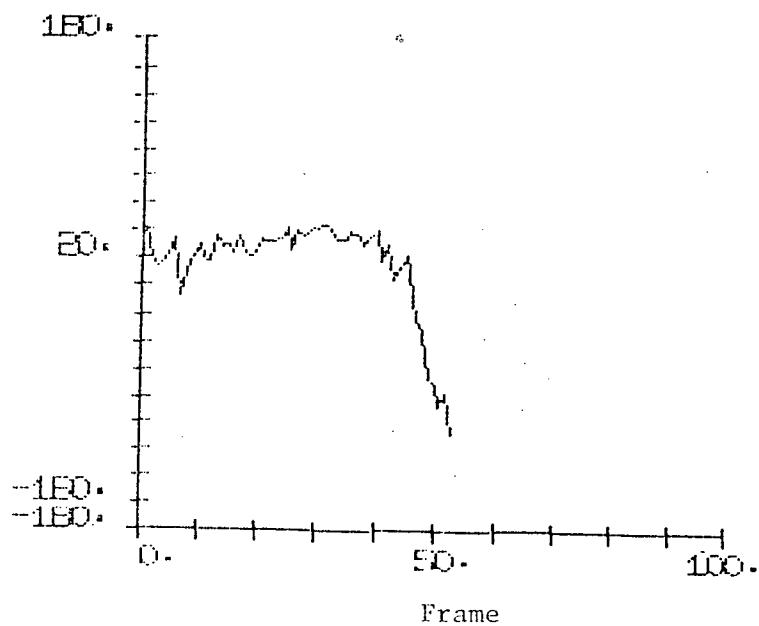
Error Tracking Angle (El) vs Time (frame)



Prey 1



Prey 2

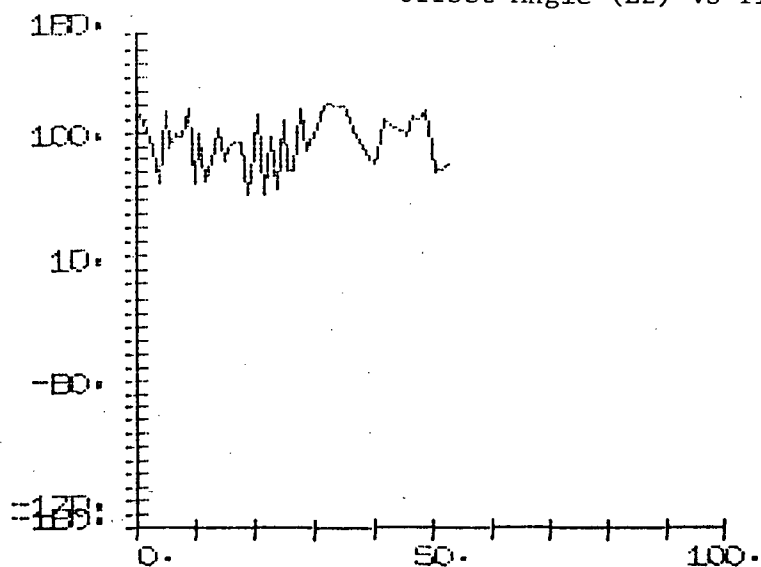


Prey 3

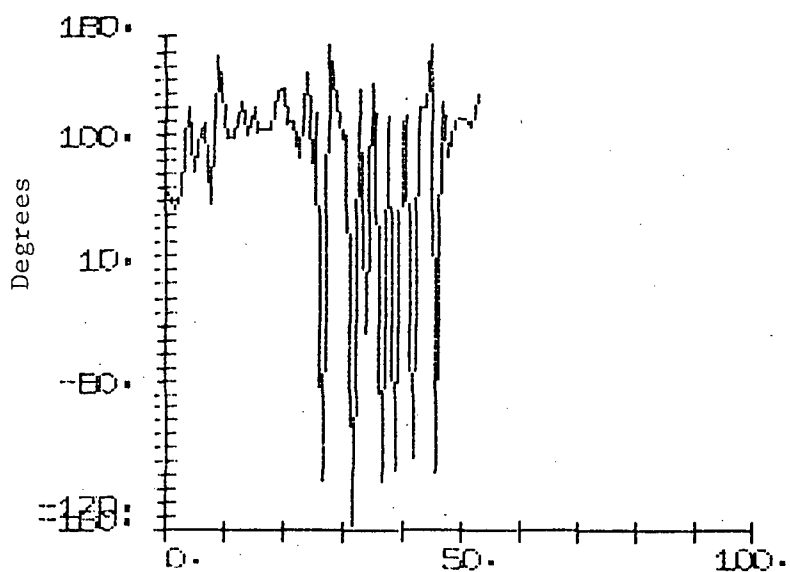
Figure 3S.8 offset angle over time : sequence 3S for prey 1,2
and 3.

Figure 3S.8

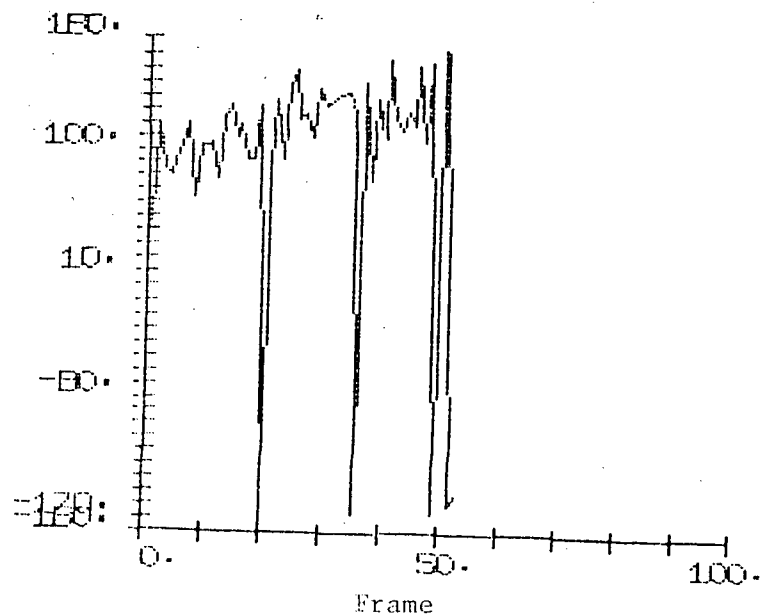
Offset Angle (E2) vs Time (frame)



Prey 1



Prey 2

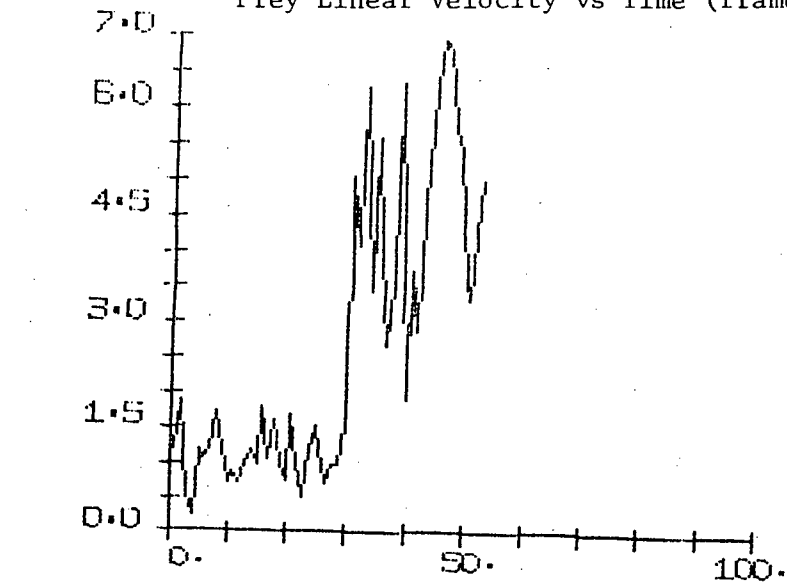


Prey 3

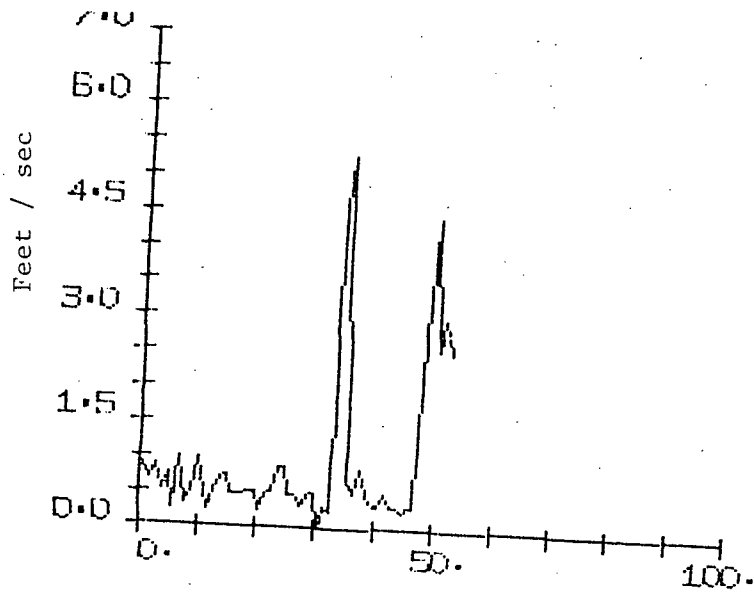
Figure 3S.9 prey linear velocity over time : sequence 3S for
prey 1,2 and 3.

Figure 3S.9

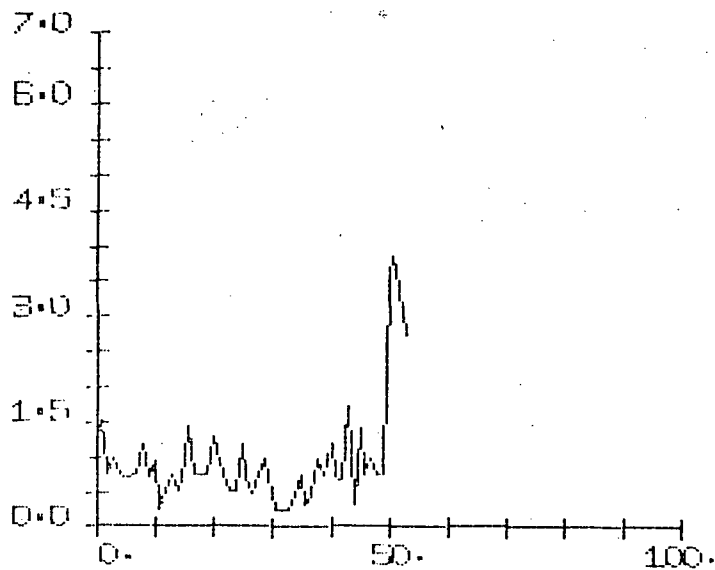
Prey Linear Velocity vs Time (frame)



Prey 1



Prey 2



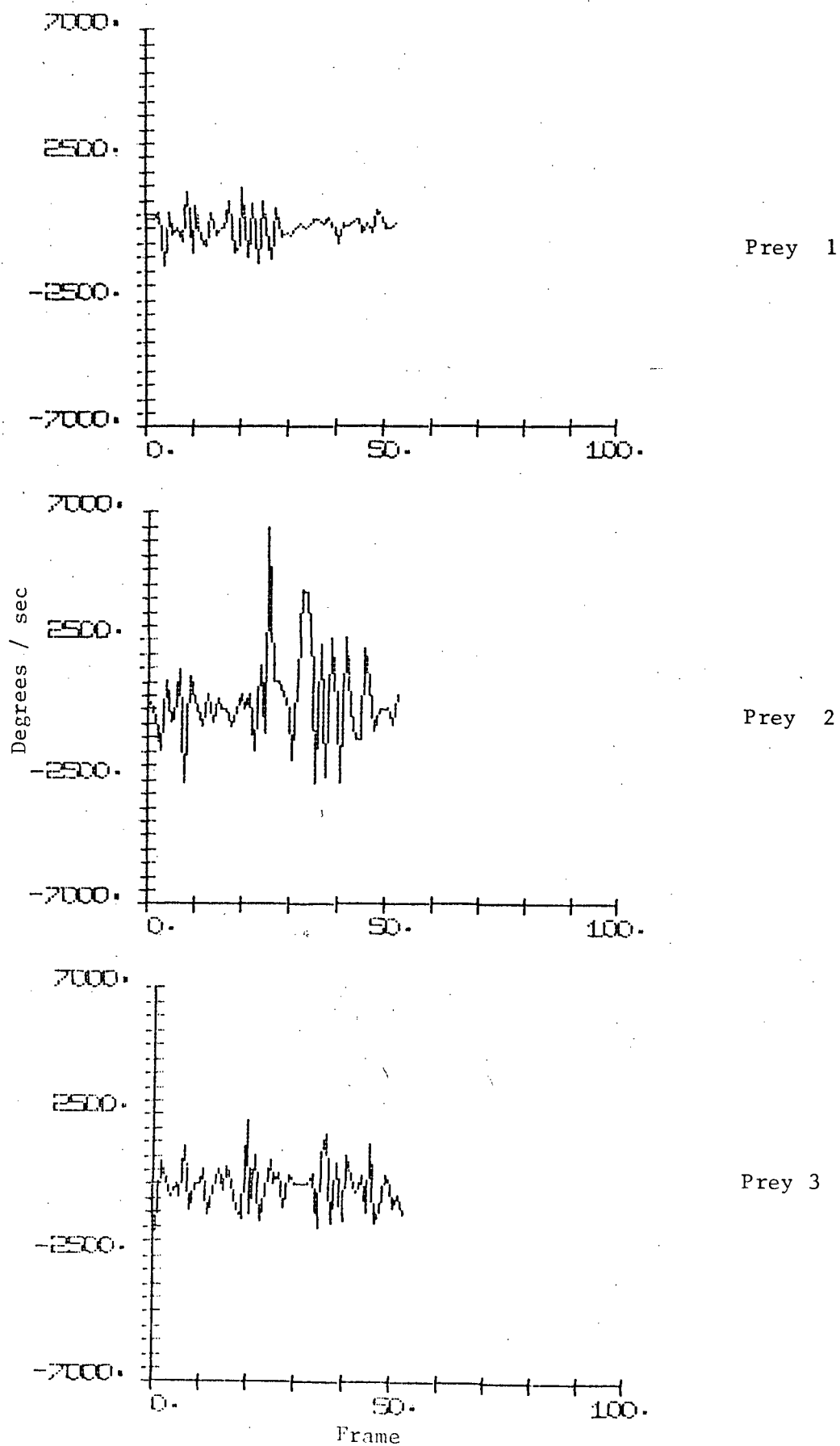
Prey 3

Frame

Figure 3S.10 prey angular velocity over time : sequence 3S for
prey 1,2 and 3.

Figure 3S.10

Prey Angular Velocity vs Time (frame)



single prey encounters.

Sequences 1S,2S,3S demonstrate that given a choice, a predator prefers to attack single individuals. In these attacks where individuals were separated from the school, it was not surprising that the kinematic variables showed similar patterns to those of single predator-single prey sequences. When the predator approached a school, the kinematic parameters for all the prey and the predator showed increased variance, and tracking was either not accomplished or lost.

It appears that when confronted by multiple targets the predator cannot maintain tracking even if a particular fish is initially the target. This is probably due to distracting movements of the other members of the school. The only captures observed in single predator-schooling prey sequences occurred when one or more individuals were separated from the school and swam alone.

Schooling prey demonstrated remarkably similar kinematic parameter values and executed similar manoeuvres almost simultaneously. As with single prey, the school initially responded to the predator by slowly moving away from the direction of attack. At a distance of 2.3 ± 0.4 feet, increased linear and angular velocities were initiated by the prey. The common escape response was the quick turn away from the predator, with increased angular oscillations ("dithering").

This response appears to be an effective tracking breaking mechanism. Fountain and flash expansion behaviours, as described by Partridge (1982) were rarely observed. This may be due to the small size of the schools used in these experiments. The relationships between kinematic variables found for single predator-single prey encounters were the same as those found in single predator-schooling prey sequences.

2) School Cohesion

In order to measure the two dimensional spatial structure of the school, the following approach from statistical theory was taken. At any frame (time interval), the members of the school can be considered as points on a surface. Within the minimum and maximum x,y coordinates of these points, there exists a point termed the center of mass. At this point, the mean sum of the distances from the center of mass to each of the points (fish coordinates) is a minimum. This distance was designated Z_m . As fish move closer together Z_m decreases, and as fish move farther apart Z_m increases. Computationally, finding Z_m is a minimizing least squares problem.

$$Z_m = \min \left[\sum_{i=1}^n \{ (X_i - C_x)^2 + (Y_i - C_y)^2 \}^{\frac{1}{2}} \right] \quad (35)$$

The coordinate of the center of mass CM_x, CM_y (where Z is a minimum) was found for each frame using a ravine search method (Bard 1974) over the Z response surface. Figure 17 illustrates the response surface for sequence 2S , frame 1. Plotting Z_m vs time for a school not subjected to predator attack is presented in figure 18, and for the first 80 frames of sequence 2S are presented in figure 19. The mean minimum distance from the center of mass for non-attacked schools was 0.36 feet which is slightly greater than the mean body length of the prey species. For schools that were attacked, the response of Z_m with time was

Figure 17 Z_m response surface : sequence 2S, frame 1. The inverse of Z_m is plotted to show it as a maximum for clarity. The center of gravity at point CM_x, CM_y is where Z_m is minimized over the response surface.

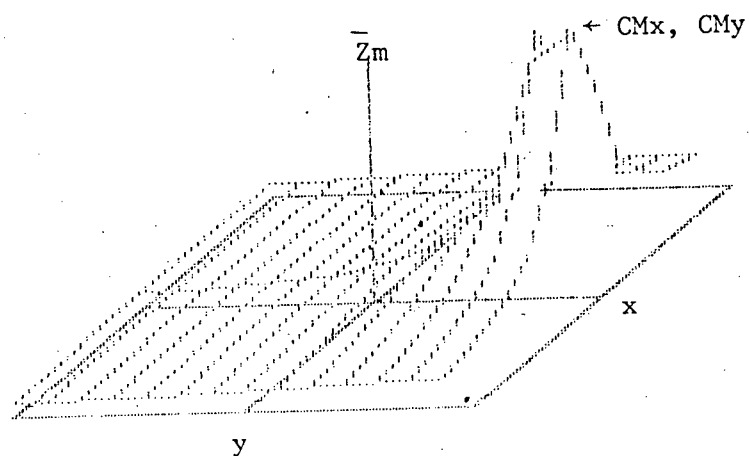


Figure 18 Zm over time : unattacked school . The response of Zm over time shows a relatively constant level at 0.36 ft which is slightly greater than the prey mean body length. This indicates a stable school structure.

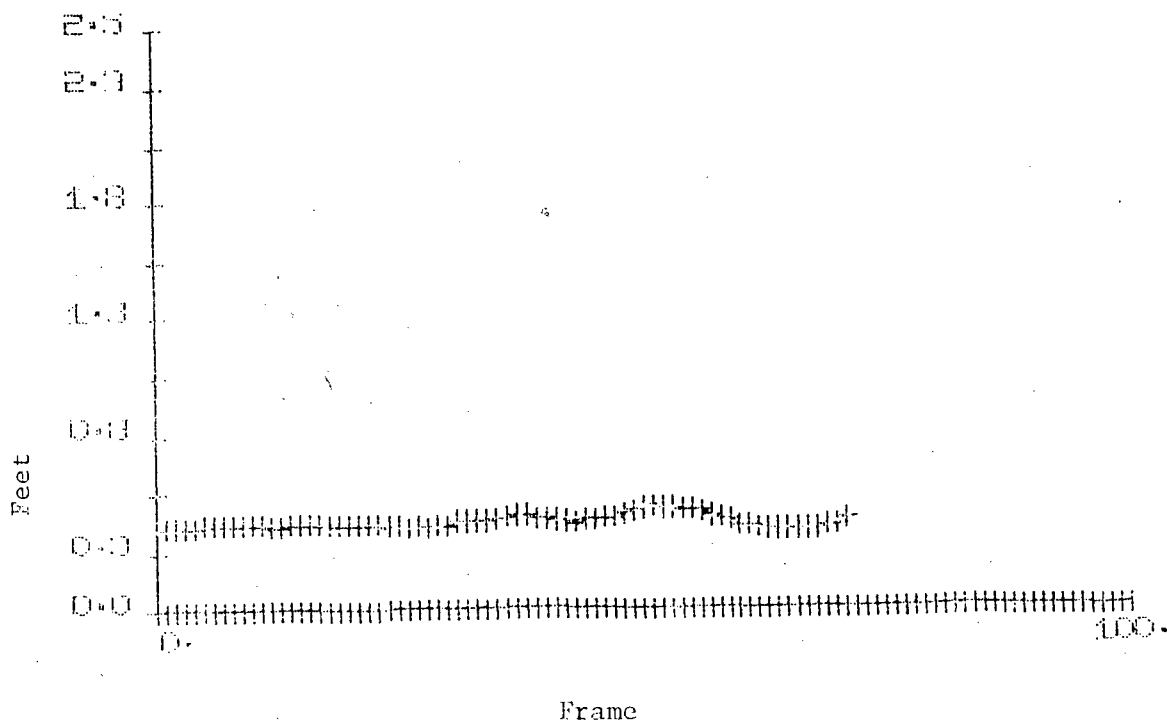
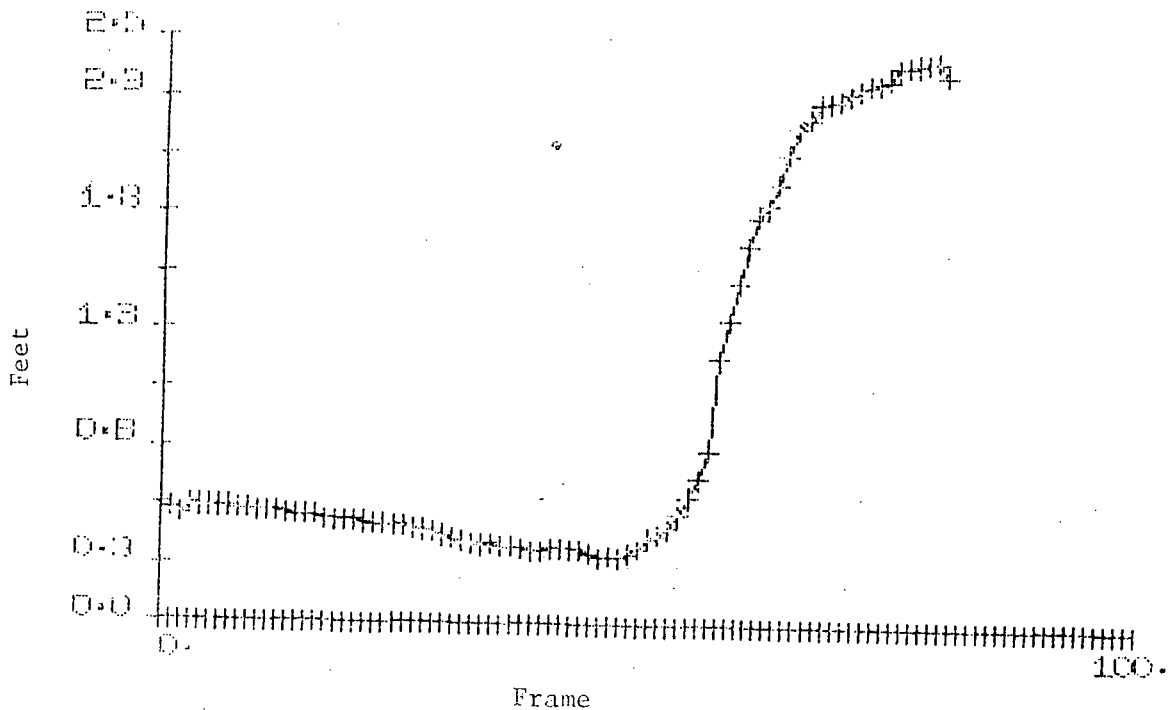


Figure 19 Z_m over time : sequence 2S, frame 1 to 80 . The Z_m response for sequence 2S is typical of the response for attacked schools. Z_m shows an initial decreasing trend indicating that the schooling members move closer together. The defensive manoeuvre by the school can be seen as the rapid increase in Z_m , indicating that the school members are moving away from each other.



remarkably similar, showing a decrease with closure distance of the predator. The minimum Z_m for these situations was found to be 0.26 feet or approximately $3/4$ of the mean prey body length. Figure 18 (for the first 80 frames of the school in sequences 2S) is typical of the response. The minimum Z_m was found to coincide with the minimum closure distance by the predator indicating that the schooling fish were closest together when the predator was at a close distance, just before active kinematic evasive manoeuvres were initiated by the school. The data supports the hypothesis that schooling fish move closer together when attacked by predators, or when a threat is perceived.

DISCUSSION

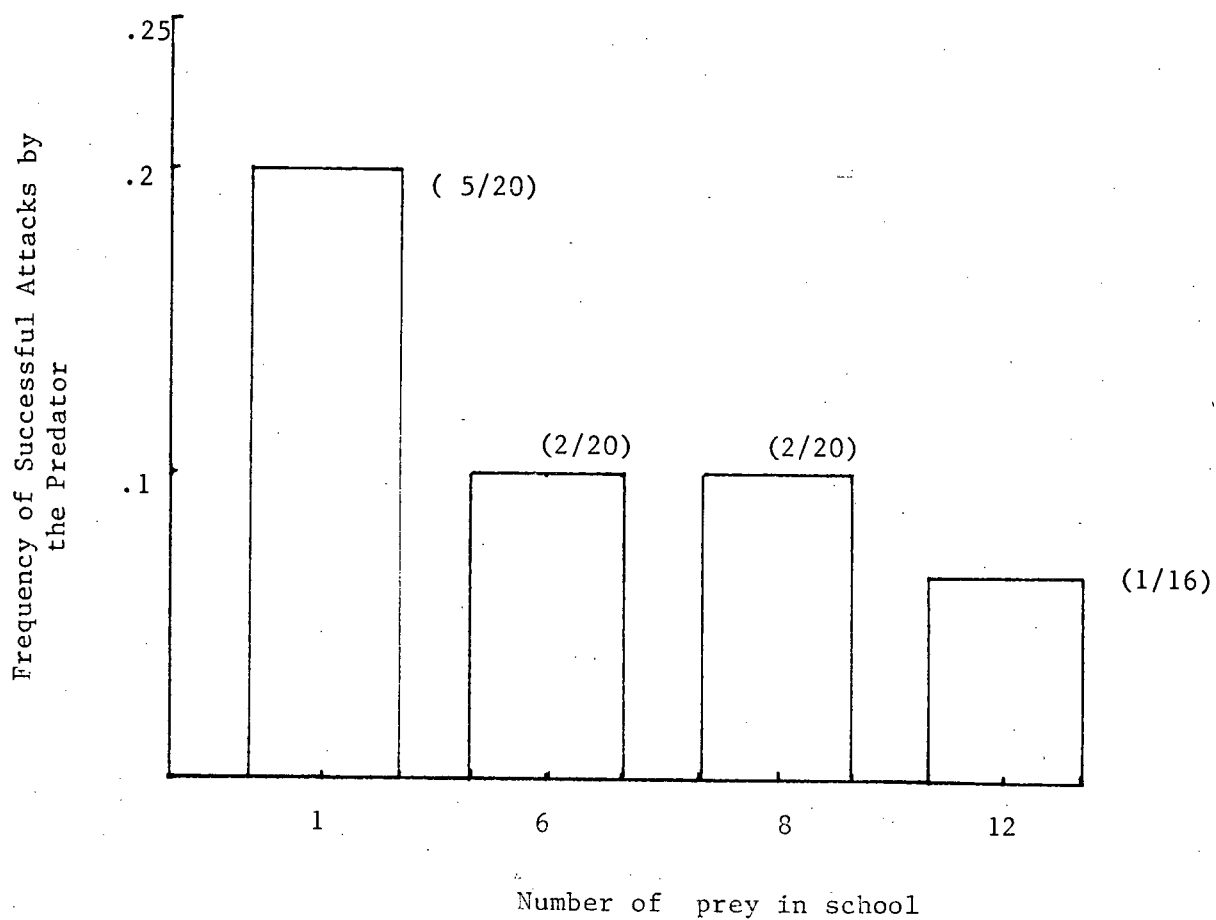
As noted by Partridge (1982) nearly half of all fish species school throughout or during some time of their lives. This behaviour suggests that some evolutionary advantage is gained by schooling; and it is thought to be primarily a protection from predators. The results of this analysis confirms that at least one of the functions of schooling as a defensive strategy leads to reduced predator success. Figure 20 presents predator success frequencies as a function of school size as revealed during this study. Significantly, those fish caught by the predator attacking schools were individuals that somehow became separated from the school and swam alone. No prey were observed caught during the initial attack by the predator on a school.

The mechanisms that reduce the success ratio of the predator on schooling prey are twofold: (1), the reduced detection probability of the school, which was not studied during this investigation, but is summarized by Partridge (1982), and (2) sensory confusion of the predator by multiple targets.

Presented earlier were three possible predator interception strategies. The first strategy consisted of the predator calculating the quarry flight path using information upon first sighting and then turn away from the prey and proceed to the

Figure 20. Predator success as a function of school size.

Success is defined as prey capture. The ratios are the (number of captures/total trials).



intersection point; adjusting its kinematics to arrive at that point at the same time as the prey.

The second interception strategy was for the predator to continually point at the prey throughout the chase. Howland's simple model of predator-prey interaction is based on the predator tracking the prey by constantly heading towards it. Another name for this strategy could be called zero-error positioning. The zero-error refers to a tracking system that attempts to reduce the lead angle E_1 to zero at each reaction time, effectively positioning the tracker toward the target. Sensed deviations from the zero position cause motor actions to re-establish zero-error positioning. Heat seeking missiles of the modern air combat environment work on this principle, homing onto the heat exhaust from jet engines. In the tactical situation, they are most successful when fired from behind and the target aircraft (prey) does not 'see' the missile coming. Statistics of air combat show that if a pilot sees a missile coming he can time his break (hard turn) to avoid the missile because aircraft, although slower, are much more manoeuvrable. Latest technological advances have introduced improved seekers and vectored thrusting to improve missile manoeuvrability (Preyss 1978, Millar and Dahlem 1978).

The third interception strategy is the lead pursuit. The predator receives and evaluates constant information about prey kinematics, relative position, and orientation. Using this

information, the predator kinematics are altered such that it is pointing to a point where the current paths are intersecting, ahead of the prey. The predator is path predicting and tracking. In open environments this strategy appears to be the best possible intercept strategy for the predator. Not only does the predator have greater freedom of response to prey evasive behaviour, but the problems associated with the second strategy are solved. The predator does not necessarily follow a greater path distance. The point of aim is ahead of the prey; therefore, the predator is predicting where the prey will be and can move toward that point. The prey can not always outguess the predator because the predator path is not pointing toward it, but to one of many possible points in the future. This implies that a more complex defensive strategy on the part of the prey is needed.

Radar Homing (RH) missiles of the modern air combat environment work on the lead pursuit principle. An enemy aircraft is first 'locked' by the attacker's radar. This means that the radar computer is continuously evaluating the target kinematics, position and relative attack parameters from the radar return signals. The RH missile is then launched and guided to the target by the radar. The radar evaluates an interception point ahead of the target (path predicting) and sends signals that alter the RH missile orientation such that the Distance at Closest Approach is theoretically zero throughout the chase. Statistics of modern air combat (Drendel 1974, Middleton 1976) show that in environments of low structural heterogeneity (low

ECM) the RH missile is the most effective air to air weapon.

As discussed previously, the aircraft must 'see' the incoming missile to avoid it. Modern aircraft carry an array of devices to introduce structural heterogeneity in the environment that act to disable the tracking functions of the attack radar.

This study shows that at least rainbow trout (Salmo gairdneri) employ path-prediction tracking when attacking prey. This method involves sophisticated integration of both predator and prey kinematics by the predator peripheral nervous system and IHS, but is an optimal tracking strategy. The data show however, that when attacking schooling prey, the predator is unable to maintain tracking of an individual prey, even if it was initially able to do so. Given a choice, the predator always prefers to attack individual prey that become separated from the school.

The strategy employed by the schooling prey to defeat predator tracking involves four tactics with increasing levels of kinematic, and consequently energetic, activity. The detection and reaction distance of the prey were found to be the same in individual and schooling situations. Once the predator or threat is detected, the first tactic of the school is to turn away from the attack trajectory with a slowly increasing turn rate. This was clearly seen in the offset angle (E2) data presented earlier. The second tactic, which occurs

simultaneously with the first, is the compression of the school.

The data suggest that the function of the first tactic is twofold. First, as a mechanism of threat evaluation. If the velocity and path of the threat object remain constant, then the moving away tactic is a prudent avoidance behaviour involving minimal energy expenditure. If the threat object velocity increases and the trajectory changes toward the school, this can then be interpreted as a genuine threat. Secondly, moving away from the object path forces the predator to follow an increasingly curved path, consequently increasing the time to intercept. The simultaneous tactic of school compression functions to decrease the area of the school and consequently, the detection surface.

Further, Partridge and Pitcher (1980) show that in schooling fish, visual clues are used to maintain angular and distance separation and lateral line sensors responding to water displacement are used to determine velocity and direction. The execution of evasive manoeuvres requires knowledge of the kinematics of other members of the school, or at least that of the nearest neighbours. This suggests that the compression of the school may also function to minimize signal loss.

A further benefit of compression, especially if the school is small, is that it may initially present a single target to the predator. The DCA data for some schools show possible

tracking by the predator on the school as a single unit, although large " noise " components appear in the graphs.

As the predator approaches the reaction distance of the school the third and fourth tactics of maximum turn and scissors ("dithering") occur, resulting in school disintegration. These tactics occur when the predator linear velocity and corresponding turn radius are high. At high linear velocities, the manoeuvre options of the predator are low. The data show that the expanding area of the school and the simultaneous increased angular and linear velocities of the individual prey resulting from these tactics defeat predator tracking.

Partridge (1982) has termed this loss of predator tracking as the confusion effect and compares it to a tennis player trying to hit several tennis balls at once. The mechanism for this effect probably lies within the peripheral nervous system of the predator and is the sensory confusion caused by the presence of multiple targets. This idea is supported by the data in sequence 3S. Initially, the predator clearly shows tracking of the individual that is away from the school. As this prey individual approached the school, tracking by the predator was lost and not re-established. The failure to re-establish tracking by the predator of any individual suggest confusion rather than simple target loss.

The advantage of schooling in reducing the chance of being

detected and confusing a predator once the school is found is primarily a function of the form of the school. The evasive tactics employed to defeat predator tracking are a function of co-operation of the school members. Radakov (1973) and Partridge (1982) describe two evasive tactics termed the fountain effect and flash expansion. In the fountain effect, the attacked school splits into two groups that flow behind the predator which is carried forward by its own momentum. The flash expansion is characterized by a rapid expansion in the form of a sphere by the members of the attacked school away from the predator trajectory. During these tactics, no collisions between school members were observed, indicating that each fish must "know" where its neighbour is going.

Although these tactics are most dramatic in large schools, they are also seen in small schools, flash expansion being most easily recognized. Sequence 3S is an example of flash expansion. The fountain effect was rarely seen in this investigation, and only with schools of 20 or more individuals. Moreover, this tactic was used only in head on or tail on approaches by the predator. Experiments with schools of large size were not conducted because of the limited size of the predation arena. Even with schools of 12 fish, edge effects and corner seeking occurred frequently. In general however, even when schools were close to edges or corners, the escape behaviours and evasive tactics exhibited followed the same pattern as seen in smaller schools and situations where the experimenter felt that edge

effects were not a contributing factor.

Analyses of school structure summarized by Partridge (1982) suggests that school structure is not fixed, ie. in a regular geometric form such as a cubic lattice (Shaw 1970,1976) characteristic of some crystals. Observations from this study indicate that the school structure is a loose, and as Partridge puts it, a probabilistic structure. Generally, the fish maintain an empty space around each individual and for sockeye salmon fry it is slightly greater than one body length. Individuals regularly change position in the school as a function of velocity and direction change. When attacked, the school initially exhibits a more rigid structure with respect to velocity and direction by compression. The preferred compressed individual spacing was $3/4$ of a body length. The possible adaptive significance of school compression was discussed earlier.

To summarize, the data support the three defensive strategy rules presented earlier and the hypotheses that emerged from the subsequent theoretical discussion.

Rule 1. The best strategy from the prey point of view is not to be detected by a predator, and to detect the presence of a predator as soon as possible, preferably, before detection by a predator. It is best to avoid a chase , which can be achieved by hiding, or moving away, so as to increase the distance from

the predator.

The data show that the first reaction of the school is to slowly turn away from the path of the approaching predator. As the threat approaches, the turn rate and velocity of the school is increased. The data supports the first rule.

Rule 2. Individuals and strays from groups are more vulnerable to predators, and school size and structure is limited by the signal loss; therefore, the group should become more compact in spacing when attacked by predators. This will allow the execution of group manoeuvres with minimal group disintegration.

The Z_m (minimum mean distance from the center of mass) data for all schools that were attacked showed an initial decrease as the predator approached the school. This data supports the hypothesis that schooling fish move closer together when a threat is perceived.

Rule 3. The best manoeuvre that the group can perform, if it detects the predator at a distance that enables the manoeuvre to be executed, is to turn in the direction of the predator. This enables the individuals to displace around the predator when it engages the group. This results in positioning the predator behind and heading away from the group direction. Before the predator can turn around, the separation distance

between prey and predator, and the prey awareness of the threat, can make further attacks by the predator unlikely.

This manoeuvre was rarely seen in this investigation. The primary reason for this may have been the limited size of the predation arena. The only occasions where the school turned to face the predator were after school reformation following an attack. Subsequent predator attacks were from head on, leading to the fountain effect manoeuvre. This suggests that turning to face a threat may be a secondary defensive strategy after an initial attack and the threat identified.

Sources of error in this analysis stem from three primary sources. First, the predation arena was of limited size and density effects may be significant. Although only those interactions that appear not to have been influenced by edge effects were used in the detailed analysis, it is virtually impossible to eliminate edge effects. The arena walls were well within the visual acuity range of the species used. With large schools, those greater than eight individuals, the individuals would often travel next to the walls after school re-formation following attack; or remain motionless in a corner. The interactions were constrained to two dimensions for technical reasons, and although schooling behaviour studied by Partridge (1980,1982) was in three dimensional situations, the findings concur with his work. The extent of the effect of the two dimensional constraint on escape behaviours is not known. Fish

however are optimized for rapid horizontal movement; the vertical dimension therefore may not have as much significance on the defensive manoeuvres per se. The attack approach by a predator relative to the school in the vertical dimension may determine the degree of defensive manoeuvres and school structure. Mathematically, the analysis techniques presented are applicable to three dimensions, and further work should be aimed at experimental situations where three dimensions of movement of the school and predator can be provided.

The second source of error comes from the filming speed used in this investigation. For technical reasons the fastest film speed available was 24 frames/second. Observations of the chase sequences show evidence that significant information loss may have occurred at the filming speed used. Subsequent work should be done at filming speed of at least 120 frames/second.

The third source of error came from the film digitizing apparatus. Every attempt was made to digitize the position data of each predator and prey with minimum error, but the recording scale of the apparatus relative to the size of the fish on the film frame may have produced as much as a 7 % position error. The lack of reliability of the equipment with respect to recording data to disk was a constant nuisance which required that each sequence be examined in detail for writing errors. Large errors in position data were easily spotted, but small errors may have escaped undetected, contributing to the variance

in the analysis.

The total contribution and confounding of these error sources is unknown but are obvious sources of concern. Smoothing techniques (Tukey 1979) were attempted but in all cases information was lost, especially in turning and evasive situations. Prey commonly changed heading by as much as 250 degrees in $1/24$ of a second, and smoothing data over such situations is not worthwhile. Presumably, at higher filming speeds smoothing may be useful.

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APPENDIX 1

Derivation of the Interception Coefficients.

At any time t , the predator position can be described as

$$\begin{aligned} X_{t+1} &= X_t + B \cos \theta_{1t} \\ Y_{t+1} &= Y_t + B \sin \theta_{1t} \end{aligned} \quad (A1.1)$$

and the prey position as

$$\begin{aligned} X'_{t+1} &= X'_t + A \cos \theta_{2t} \\ Y'_{t+1} &= Y'_t + A \sin \theta_{2t} \end{aligned} \quad (A1.2)$$

For the predator to capture the prey, their paths should cross such that

$$\begin{aligned} X_t &= X'_t \\ Y_t &= Y'_t \end{aligned} \quad (A1.3)$$

At this point

$$X_t + B \cos \theta_{1t} = X'_t + A \cos \theta_{2t} \quad (A1.4)$$

$$Y_t + B \sin \theta_{1t} = Y'_t + A \sin \theta_{2t} \quad (A1.5)$$

To solve for A ;

$$(A1.4) * \sin \theta_{1t}$$

$$X_t \sin \theta_{1t} + B \cos \theta_{1t} \sin \theta_{1t} = X'_t \sin \theta_{1t} + A \cos \theta_{2t} \sin \theta_{1t} \quad (A1.6)$$

$$(A1.5) * \cos \theta_{1t}$$

$$Y_t \cos \theta_{1t} + B \sin \theta_{1t} \cos \theta_{1t} = Y'_t \cos \theta_{1t} + A \sin \theta_{2t} \cos \theta_{1t} \quad (A1.7)$$

$$(A1.6) - (A1.7)$$

$$X_t \sin \theta_{1t} - Y_t \cos \theta_{1t} = X'_t \sin \theta_{1t} - Y'_t \cos \theta_{1t} + A \cos \theta_{2t} \sin \theta_{1t} - A \sin \theta_{2t} \cos \theta_{1t} \quad (A1.8)$$

$$= X_t \sin \theta_{1t} - X'_t \sin \theta_{1t} + Y'_t \cos \theta_{1t} - Y_t \cos \theta_{1t} = \sin(\theta_{1t} - \theta_{2t}) A \quad (A1.9)$$

Therefore

$$A_t = \{ (X_t - X'_t) \sin \theta_{1t} + (Y'_t - Y_t) \cos \theta_{1t} \} / \{ \sin(\theta_{1t} - \theta_{2t}) \} \quad (A1.10)$$

B is similarly solved by $(A1.4) * \sin \theta_{2t}$, $(A1.5) * \cos \theta_{2t}$ and subtraction.

$$B_t = \{ (X'_t - X_t) \sin \theta_{2t} + (Y_t - Y'_t) \cos \theta_{2t} \} / \{ \sin(\theta_{2t} - \theta_{1t}) \} \quad (A1.11)$$

APPENDIX 2

Derivation of Equations for Time at Closest Approach and
Distance at Closest Approach

For each time interval t , the position of the predator can be described as

$$\begin{aligned} X_{t+1} &= X_t + U_1 t \\ Y_{t+1} &= Y_t + V_1 t \end{aligned} \quad (A2.1)$$

where U_1 is the velocity component in the X direction and V_1 is the velocity component in the Y direction. Similarly, the prey position may be represented as

$$\begin{aligned} X'_{t+1} &= X'_t + U_2 t \\ Y'_{t+1} &= Y'_t + V_2 t \end{aligned} \quad (A2.2)$$

At time t , the distance between predator and prey is

$$D_t^2 = \{ (X_t - X'_t)^2 + (Y_t - Y'_t)^2 \} \quad (A2.3)$$

Expanding equation (A2.3)

$$D_t^2 = \{ (X_t - X'_t) + (U_1 - U_2)t \}^2 + \{ (Y_t - Y'_t) + (V_1 - V_2)t \}^2 \quad (A2.4)$$

Expanding equation (A2.4)

$$\begin{aligned} D_t^2 &= (X_t - X'_t)^2 + 2\{(X_t - X'_t)((U_1 - U_2)t)\} + \{(U_1 - U_2)^2 t^2\} + (Y_t - Y'_t)^2 + \\ &\quad 2\{(Y_t - Y'_t)((V_1 - V_2)t)\} + \{(V_1 - V_2)^2 t^2\} \end{aligned} \quad (A2.5)$$

At the point of Closest Approach, $d(D^2) / dt = 0.0$. From equation (A2.5)

$$\frac{d(D^2)}{dt} = \left[2\{(X_t - X'_t)(U_1 - U_2) + (Y_t - Y'_t)(V_1 - V_2)\} + 2t\{(U_1 - U_2)^2 + (V_1 - V_2)^2\} \right] \quad (A2.6)$$

When $d(D^2) / dt = 0.0$ the Time to Closest Approach is

$$t^* = \frac{\{ -(X_t - X'_t)(U_1 - U_2) - (Y_t - Y'_t)(V_1 - V_2) \}}{\{ (V_1 - V_2)^2 + (U_1 - U_2)^2 \}} \quad (A2.7)$$

The Distance at Closest Approach is then calculated by substituting t^* in equations (A2.1) and (A2.2) and solving for D_t^* .