A CONSIDERATION OF THE CONCEPTS OF GENERALITY AND COMPLEXITY, AS USED IN EXPERIMENTAL COMPONENTS ANALYSIS

by

Wilf Cuff

B. Sc., University of Manitoba, 1966
M. Sc., University of Western Ontario, 1967

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY in the Department of ZOOLOGY

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

August, 1972
In presenting this thesis in partial fulfilment of the requirements for
an advanced degree at the University of British Columbia, I agree that
the Library shall make it freely available for reference and study.
I further agree that permission for extensive copying of this thesis
for scholarly purposes may be granted by the Head of my Department or
by his representatives. It is understood that copying or publication
of this thesis for financial gain shall not be allowed without my
written permission.

Department of Zoology

The University of British Columbia
Vancouver 8, Canada

Date July 21, 1972
ABSTRACT

Two features of experimental components analysis (Holling, 1966) are considered. A method of writing general functions is proposed and verified with some observations from hydra. An analytical method of studying certain features of a simulation model of attack is then proposed and tested.

The method proposed to attain generality of functions is a strategic one. Operationally, one need only determine a strategy used by many animals, uncover some opposing variables which may have been important in its development, and predict on the basis of these antagonistic forces some characteristic response of the strategy. It is suggested that this characteristic response is a broadly applicable as is the strategy.

The dynamic response of a number of modes of searching through volume is predicted to be of shorter duration the larger the hunger threshold to which the mode responds. This is found to be the case for hydra. A similar hypothesis, that the steady states of these searching modes be directly related to the hunger thresholds of the modes, does not give as clear results. It is suggested that an additional strategy must be considered to give a better picture. These results are then used to write a model for the time which an animal spends searching for food.

The sensitivity analysis of the attack simulation model attempts to formalize the conventional method: going through the block diagram and picking out what seems to be important. A Boolean expression is written to describe all possible paths through the model. This expression is used to tabulate the various forms of the equation of the dependent variable, the attack rate. These forms of the attack rate are used to illustrate how one might analyze a complex, non-linear model.
## TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABSTRACT</td>
<td>i</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>iv</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>vi</td>
</tr>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>viii</td>
</tr>
<tr>
<td>GENERAL INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td><strong>PART I</strong></td>
<td></td>
</tr>
<tr>
<td>THE PROBLEM OF GENERALITY</td>
<td></td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>2</td>
</tr>
<tr>
<td>THE PROPOSAL</td>
<td>6</td>
</tr>
<tr>
<td>HYDRA STUDIES: IDENTIFICATION OF THE SEARCH MODES AND PRELIMINARIES ON THE MODEL</td>
<td>14</td>
</tr>
<tr>
<td>HYDRA STUDIES: A MODEL OF VOLUME SEARCHED</td>
<td>30</td>
</tr>
<tr>
<td>HYDRA EXPERIMENTATION: THE APPROACH</td>
<td>43</td>
</tr>
<tr>
<td>HYDRA EXPERIMENTATION: TENTACLE LENGTHENING</td>
<td>49</td>
</tr>
<tr>
<td>HYDRA EXPERIMENTATION: WALKING</td>
<td>63</td>
</tr>
<tr>
<td>HYDRA EXPERIMENTATION: FLOATING</td>
<td>72</td>
</tr>
<tr>
<td>A TEST OF THE HYPOTHESIS</td>
<td>77</td>
</tr>
<tr>
<td><strong>PART II</strong></td>
<td></td>
</tr>
<tr>
<td>A TIME SPENT SEARCHING FUNCTION FOR HYDRA</td>
<td></td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>79</td>
</tr>
<tr>
<td>METHODS AND RESULTS</td>
<td>80</td>
</tr>
</tbody>
</table>
DISCUSSION FOR PARTS I AND II ........................................ 94
Searching by Animals ...................................................... 94
Strategical Models ......................................................... 101

PART III
SENSITIVITY ANALYSIS OF A MODEL OF ATTACK

INTRODUCTION ................................................................. 108
The Approach ............................................................... 108
TECHNIQUES FOR WRITING LOGICAL EQUATIONS ..................... 111
REDUCTION OF THE LOGIC OF THE ATTACK MODEL ................. 118
DEDUCTIONS ................................................................. 124
DISCUSSION FOR PART III ............................................... 140

GENERAL DISCUSSION ...................................................... 142
LIST OF SYMBOLS .......................................................... 144
BIBLIOGRAPHY ............................................................... 145

APPENDICES

I. Some observations on hydra in Beaver Creek ...................... 151
II. Partial evaluation of the equations of the model ................ 165
III. Effect of parameter values on the conclusions of PART II .......... 168
IV. Flow graph of the attack model ..................................... 171
### List of Tables

<table>
<thead>
<tr>
<th>Table I.</th>
<th>Parameter estimates for the following equation:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>[ L(t) - L(t_{\text{min}}) = \frac{L(t_{\text{max}})}{1 + \exp(s) / \exp(r \times t)} ]</td>
</tr>
<tr>
<td></td>
<td>Page 58</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table II.</th>
<th>The results of four runs of a three-level, nested ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Page 59</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table III.</th>
<th>Distance moved per time interval by <em>Chlorohydra viridissima</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Page 65</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table IV.</th>
<th>Percentage of hydra which moved per hour, for successive hours after hour of first step</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Page 68</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table V.</th>
<th>A factorial Analysis of Variance Table: the effect of food and hydra density on the time which hydra take to begin floating</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Page 74</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table VI.</th>
<th>The various forms, with controlling logic, of the function of time spent in digestive pause (TD) included in the attack model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Page 126</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table VII.</th>
<th>The various forms, with controlling logic, of the function of time spent searching (TS) included in the model of attack</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Page 127</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table VIII.</th>
<th>The various forms, with controlling logic, of the function of time spent pursuing prey (TP) included in the attack model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Page 129</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table IX.</th>
<th>The various forms, with controlling logic, of the function of time spent eating the prey (TE) included in the model of attack</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Page 130</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table X.</th>
<th>The various forms of TI. The attack rate (A) is defined as (24 / TI)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Page 131</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table XI.</th>
<th>The parameters of the attack rate, by type of function</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Page 134</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table XII.</th>
<th>The totality of types of hunger equations outputted at the end of the i-loop of the attack model. Controlling logic is given</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Page 137</td>
</tr>
</tbody>
</table>
Table I of Appendix I
Density of *Hydra carnea* (number/cm²) in Beaver Creek ......................... 155

Table II of Appendix I
Relationship between the density (numbers/quadrat) of *Hydra carnea* in Beaver Creek and the depth of the water above the quadrat (A) and the surface water velocity (B) ............... 158

Table III of Appendix I
Percentage of hydra and percentage of substrate type, by substrate types, for each of five sites ......................................................... 160

Table IV of Appendix I
Percentage of hydra with one or more buds and percentage of hydra with one or more testes as a correlate of the density of the hydra .... 162
<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Figure 1</td>
<td>Various types of volume searched by a hydra. The effect of prey movement is included</td>
<td>32</td>
</tr>
<tr>
<td>Figure 2</td>
<td>A number of individual Chlorohydra graphs of tentacle length as a function of time of food deprivation</td>
<td>53</td>
</tr>
<tr>
<td>Figure 3</td>
<td>Mean tentacle and stalk length as a function of time of food deprivation</td>
<td>56</td>
</tr>
<tr>
<td>Figure 4</td>
<td>The time that hydra take to egest food-remains as a function of the size of their last meal</td>
<td>62</td>
</tr>
<tr>
<td>Figure 5</td>
<td>The time that Chlorohydra viridissima polyps take to walk for the first time, as a function of the size of their last meal</td>
<td>71</td>
</tr>
<tr>
<td>Figure 6</td>
<td>The time that hydra take to detach and begin to float as a function of the size of their last meal</td>
<td>75</td>
</tr>
<tr>
<td>Figure 7</td>
<td>A simulated result of the searching rate of a hydra which has been pre-fed with 3 Artemia nauplii, as a function of food deprivation. VY=0.0 mm/minute, VPF=0.50 mm/minute, and DMT=2.0 mm</td>
<td>86</td>
</tr>
<tr>
<td>Figure 8</td>
<td>A simulated result of the searching rate of a hydra which has been pre-fed with 3 Artemia nauplii, as a function of food deprivation. VY=VPF=100 mm/minute, and DMT=300 mm</td>
<td>87</td>
</tr>
<tr>
<td>Figure 9</td>
<td>A simulated result of the searching rate of a hydra which has been pre-fed with 3 Artemia nauplii, as a function of food deprivation. VY=500.0 mm/minute, VPF=100 mm/minute, and DMT=0.0 mm</td>
<td>88</td>
</tr>
<tr>
<td>Figure 10</td>
<td>A simulated result of the searching rate of a hydra which has been pre-fed with 3 Artemia nauplii, as a function of food deprivation. VY=VPF=10,000 mm/minute and DMT=150 mm</td>
<td>90</td>
</tr>
<tr>
<td>Figure 11</td>
<td>A simulated result of the searching rate of a hydra which has been pre-fed with 3 Artemia nauplii, as a function of food deprivation. VY=10,000 mm/minute, VPF=100 mm/minute, and DMT=0.0 mm</td>
<td>91</td>
</tr>
</tbody>
</table>
Figure 12. Median activity of chicks, rabbits, guinea pigs, and hamsters as a function of days of deprivation (from Campbell et al, 1966) .......... 96

Figure 13. A FORTRAN IF ... statement from the flow graph of Appendix IV ............................... 112

Figure 14. An equivalent form for the conditional statement of Figure 13 ................................ 112

Figure 15. A logical flow graph, with operators A and B ... 112

Figure 16. A logical flow graph, with operators Q, D, and C .................................................. 114

Figure 17. A logical flow graph, with operators Q, D, C, and E .................................................. 114

Figure 18. The logic for the flow diagram of Appendix IV ........................................ 119

Figure 19. The logic for the DEFG part of the flow graph of Appendix IV ............................... 120

Figure 20. The logic for the flow diagram of Appendix IV. The DEFG and HI parts are modified from the form given in Figure 18 ..................... 123

Figure 1 of Appendix I
A map of the field study area ......................... 152

Figure 1 of Appendix IV
A flow graph of the attack model .................... 172
I am grateful to Dr. C.S. Holling for his advice during this study. Suggestions by P. Larkin, N. Gilbert, and C. Wehrhahn are appreciated.

A number of other people have been of service at various stages. My thanks to T. Gossard, R. Harger, D. McPhail, and N. Wilimovsky.
The original intent of this study was to replace the section of the predation model of Holling that describes competition (see Griffiths and Holling, 1969) with a section that included more explanatory content. The techniques of experimental components analysis (Holling, 1966) were to be applied to the process of competition.

In considering experimental components analysis and its bedpartner, simulation, I became aware of two inadequacies. First, this approach produces such large and intricate models that complexity of the model becomes a problem in its own right. It is a difficult task to relate in detail Holling's model of predation to Beukema's (1968) model of stickleback predation to Ware's (1971) model of trout predation.

Secondly, Holling's method of writing functions which describe the activity of many species is not as generally useful as one might wish. In the end it was decided to concentrate on methods to achieve both generality and simplicity using predation as the focus.

The problem of jointly achieving both are fundamental quests in science. It is not my presumption to fully answer such difficult questions in this thesis, but any step that can be made in that direction is significant.
Holling (1966) suggested that a model should have the attributes of realism, precision, wholeness, and generality. Whether these goals were to guide decisions concerning variables, functions, or structure of systems was not made clear. I examined these attributes at each level.

The attributes of realism and generality are applicable at the level of the variable. Holling (op. cit.) achieved realism and generality at this level by invoking the concept of component and by classifying components by their degree of universality. The word component tends to mean membership in a classification scheme; however, the choice of component influences directly the variables used in the model. When his study of the process of predation began, Holling (op. cit.) first chose a dependent variable and then listed all processes which could influence this variable. These were termed components and separated into basic (shown by all species) and subsidiary (shown by some species). Each component was then subdivided again and again. This procedure was continued until each component was expressed in terms of a set of realistic variables. Each set reflected the subsidiary or basic nature of the component from which it was derived.

At the level of structure, the attributes of wholeness and generality apply. Holling (op. cit.) achieved the technological potential for wholeness by using simulation, rather than analytic, models. Generality was achieved by using the universal attack cycle as the core of the model.
At the level of the function, the attributes of realism, precision, and generality apply. By "function" is meant the relationship between the dependent and the independent variables. From this point of view, realism has been achieved by conducting experiments for the form of the relationship and by seeking an explanation for this relationship from the literature. Precision has been achieved by combining precise experimentation with theoretical diversions and by translating biological explanations from English to the more rigorous language of mathematics.

Two methods of achieving generality of functions have been attempted. First, where it was possible, Holling (1966) considered biological processes in physical terms. When dealing with the visual field of mantids, Holling (op. cit.) wrote the area of perception as a linear function of the square of the distance to its outer boundary. The physical basis is that area is a function of some distance squared.

Secondly, generality of functions was obtained by making simplified explanations of the causative mechanism. Holling (1966; page 68) suggested that the validity of this method would be confirmed or refuted as further evidence accumulated. Some has been accumulated in the case of the hunger equation.

Dethier (1969) found that blowflies, *Phormia regina*, do not continue to eat until the gut is full of food. The flies stop eating upon advice based upon sensory adaptation. Hubbell (1971), in his study of the isopod *Armidillium*, found that gut capacity is not a physical quantity but a function of the overall health of the isopod. Beukema (1968), in his study of the stickleback *Gasterosteus aculeatus*, found that the pattern of presenting and withholding food was of some significance in dictating the form of the hunger equation. The work of Beukema and of Hubbell suggest that the causative explanation might
be incomplete. I cannot determine from their papers whether this incompleteness is trivial or not. The work of Dethier does not find gut capacity to be an important determinant of hunger in blowflies. It is no longer a simple problem of incompleteness.

These examples suggest the sort of problems that this method of formulating functions might entail. What is the most important causative feature? Is there a most important cause? This is the inadequacy to which I referred in the GENERAL INTRODUCTION.

In Holling's model of predation there are four essential equations: time spent digesting prey (TD), time spent pursuing prey (TP), time spent searching for prey (TS), and time spent eating prey (TE). The function for the time spent digesting prey (TD) is based on a causative explanation. It is a rewording of the hunger equation which, in turn, is based on an abstraction of the gut as a size-limited bag. The functions for the time searching for and pursuing prey (TS and TP) are both based mainly on physical explanations. The exception is the function relating the size of the reactive field to hunger. This function is based on a simplified explanation of the physiological structure of the eye. The function for time spent eating a prey (TE) incorporates the causative explanation. Thus each of the four equations of the attack cycle incorporates the causative explanation.

The functions for time spent digesting prey (TD), time spent pursuing prey (TP), and time spent eating prey (TE) are all explicit functions. Each fits into the complete simulation model as a small module, complete within itself and with a well defined boundary. On the other hand, the function for time spent searching for prey (TS) is an implicit one and is solved iteratively in the simulation model of
predation. It is solved using two internal loops; these loops contain eight internal choice statements (the FORTRAN statement: IF a n_1, n_2, n_3) resulting in seven possible functions for time spent searching. Some of these functions are used as parts of the arguments of three separate choice statements. The effect of these choice statements is, in two cases, to determine the function for time spent pursuing prey (TP) and, in the other case, to introduce a major modification in the searching function (TS) itself.

The function for time spent searching (TS) is simulated in such a way that it can be modified only with great difficulty. The other three functions are included in the simulation model as distinct modules and so are easily modifiable in specific cases. Thus it was decided that the time spent searching variable (TS) would be an appropriate one for testing a strategic method of writing general functions. This method will be introduced in the next section. An additional attempt will be made to write an explicit function for time spent searching (TS).
The initial formulation by Holling (1966) of the time spent search-in function, as well as a second unpublished version, are derived from

\[ NA = \left[ 2t \times RD \times \sqrt{VD^2 + VY^2} + \pi \times RD^2 \right] \times NO \]  

where \( VD \) is the velocity of the predator during searching; \( VY \) is the average velocity of the prey; \( RD \) is the reactive distance of the predator; \( NO \) is the prey density; and \( NA \) is the number of prey attacked in time \( t \). This equation is written more generally as

\[ NA = VS(t, VD, VY, RD) \times NO \]  

where \( VS \) is the volume searched by the predator. (The bracketted part of \( I \) was expanded from area to volume by Watt, 1968.) This volume was modified for the effects of prey movement. If time \( t \) can be separated from the right hand side of this equation, then it becomes identically the time spent searching for prey, \( TS \). The job of writing an explicit \( TS \) function is reduced to one of finding a \( VS \) function from which \( t \) may be separated.

In attempting to find such a function for the volume searched by a predator, I reasoned from the fact that a limited amount of generality has been obtained by using causative, or tactical, arguments. Yet a large number of tactics can be combined under the umbrella of a more limited number of strategies. Thus it seemed valuable to explore some properties of the tactical-strategical concepts. Following economic and military etymology, I will use the word tactic as a synonym for method and strategy as a synonym for goal.

The concept of strategy has a subtle relationship to that of tactic. It is possible for a single process to be viewed either as a strategy or as a tactic. A trivial example will serve to clarify what is meant.

Dr. S. Hubbell has invented a monopoly-type game of "ecological
warfare". Each player becomes a species who, during the game, attempts to survive longer than all other contestants. The player who survives the longest wins. The goal, or strategy, of each player is to stay in the game as long as possible.

Consider the case where one contestant shares a trophic level with two other players. He is a superior competitor in every respect except that the other players have a habit of killing his young by stepping on them. The contestant can foresee that his recruitment is too low to insure survival and that he is going "extinct". His immediate concern is to find a way to protect the young from the feet of his competitors. This is a goal, a strategy.

Thus there are at least two strategies: to stay in the game as long as possible and to keep the feet of the competitors off the heads of the young. But the second strategy is one way of insuring that the first will be accomplished. This makes a strategy a tactic.

One way of distinguishing between the two types of strategies in this example is to consider the first as the ultimate strategy and the second as a proximal strategy. Thus it is necessary to talk of strategies at various levels. Since strategies can be viewed as tactics, it is clear that tactics can also be defined at various levels.

These levels can be viewed as hierarchical. The ultimate strategy of ecological systems is often thought to be survival of the species. Survival is ensured by population processes such as reproduction, dispersal, and so on. These processes, in turn, would not develop unless there had developed earlier a process of energy intake (predation in a broad sense). There are three levels mentioned here.

Each of these processes can be thought of as a strategy: unless an animal takes in energy it will die, unless it disperses it may eliminate
itself by density dependent processes, unless it reproduces it will go extinct in one generation, and unless it survives it will not be part of the ecological system. Yet the individual acts of energy accumulation, reproduction, dispersal, and survival are concrete processes - tactics.

The various subprocesses that combine to make up a process constitute the elements of another kind of hierarchical scheme. For example, the process of predation has been subdivided into search, approach, capture, and preparation-ingestion subprocesses (De Ruiter, 1967). Each of these subprocesses as discussed is a tactic. This is not the only possible view. For example, later in the thesis various search strategies used by animals will be considered. In this type of hierarchical scheme the components at one level work together to produce the process at the next level.

The main points of the last few paragraphs are: 1) any-process can be viewed either as a tactic or as a strategy; 2) the tactical-strategical concept does apply at various levels on naturally occurring hierarchical schemes.

Other authors have already used strategical concepts in writing general functions. Space limits their consideration here. The subject will be taken up in the discussion.

Some data are available which relate to the subject of writing strategical functions. They indicate that the responses of species tend to produce behaviour which seems to the observer to be that expected if the animals use behaviour that is optimal in their current habitats (Brett, 1965; Milsum, 1966). Without going into examples, I will assume that this is true. The strategical method proposed for writing general functions follows from this assumption. The method is first to define a strategy, then to delimit a few general opposing forces, and finally to look at the
effects of the forces on the strategy and to attempt to see certain features which seem "desirable". It is suggested that these features will represent general methods for achieving a given goal.

It is assumed that animals searching for food attempt to cover as much volume as is needed in order to catch enough prey to return hunger to some level. One such level might be the "eat threshold" (Holling, 1966). This assumption is the strategy chosen for study in the thesis.

One general force acting upon this strategy is starvation. A response to this, and only this, factor would be a volume searched during some time interval (a searching rate) that is always greater than the volume occupied by those prey that are necessary to return the hunger of the predator to the eat threshold. A lower searching rate would result in a hungry predator. The hungrier the predator the more likely it is to starve to death.

It is difficult to say how much greater the actual volume covered per time interval in the future will be over that needed in current habitats and under current fluctuations in prey abundance. However, during a period of exceptionally low prey abundance, the higher the volume covered per time interval, the more likely will be survival. (It is assumed that the animal is not able to sidestep the issue; the animal can't leave the area during a period of low prey abundance.) Thus there should be a tendency for search rates to increase as evolution proceeds. However, as the volume covered per time interval increases the animal becomes less fit under periods of high prey abundance. An animal that wastes time reacting to prey it will not eat or eating prey it cannot use, and so runs the risk of destroying its food supply or of becoming more vulnerable to its predators, is not an effective competitor.
This animal, being less fit than others, would tend to be replaced by organisms with a lower search rate. This replacement would tend to depress over time the average searching rate of the species.

(It may be useful to emphasize that the argument is based on an evolutionary time scale, not a short time scale. It supposes that each organism inherits some searching rate. Over a long time period some searching rates will be more fit than others. The fittest rates will survive and replace the others, and so the average search rate of the species will change. The reduced-efficiency force is, from this viewpoint, a measure of the likelihood of an animal with some searching rate being outcompeted by one with a different search rate. This force can be viewed from a minimum of one generation.)

One might expect that animals would tend to use a searching rate that lies somewhere between those extremes produced by separate consideration of the starvation and the reduced-efficiency forces.

Let hunger be measured as the amount of food required to return an animal to its "eat threshold" (Holling, 1966). When measured for mantids, hunger was found to be directly related to the time of food deprivation (op. cit.). I have suggested that the volume searched per time interval is closely associated with hunger. The hypothesized control is the antagonistic action of two forces. It follows from this argument that the search rate is directly related to the time of food deprivation. This statement does not seem to be profitably testable as stated. It becomes more so when we consider that many animals use more than one searching method (see the discussion). Two and sometimes three methods are used. Each method has its own responsiveness to hunger and each has its own searching rate function.

The magnitude of the starvation force is directly related to the time of food deprivation. The likelihood of an animal starving to death
increases with the length of time it is deprived of food. The magnitude of the reduced-efficiency force is assumed to be independent of the time of food deprivation. This implies that any method of searching that is initiated at low hunger levels will be molded more strongly by the reduced-efficiency than by the starvation force. Any method of searching that is initiated at high hunger levels will be molded more strongly by the starvation than by the reduced-efficiency force.

For each search mode, I assume that the function relating volume searched per time interval to the time of food deprivation will take the following form: a minimum steady rate of searching to a certain hunger level, then an increasing rate of searching, and finally a maximum steady rate of searching. (Henceforth, I will use the jargon: dynamic and steady state responses. A dynamic response is a non-stabilized response. A steady state response is a stabilized response. The minimum and the maximum steady rates of searching are steady state responses. The increasing rate of searching is a dynamic response.)

Any search mode which begins its rise from the minimum rate - which is "initiated" - at low times of food deprivation will possess a dynamic response operating over a long time interval. If the duration of the dynamic response approaches zero, then too much food may be contacted too soon. Conversely, any searching mode which is initiated after a long interval of food deprivation will possess a dynamic response operating over a short time interval. If the duration of the dynamic response is large, then the animal may not search through enough volume soon enough to prevent its death. The animal may starve to death only because the search mode does not reach its full potential at a low enough hunger level. In general, the duration of the dynamic response of a searching rate function should be inversely related to the function's threshold of initiation. PART I of this thesis
is directed towards testing this hypothesis.

Two further points need elaboration. In equation 12 the volume searched variable is written as a function of \( VD, RD, t, \) and \( VY \). Yet, prey velocity \( (VY) \) has been mentioned only indirectly. This is because the volume to which I have referred thus far is an effective volume, where prey velocity is incorporated as a component of predator movement. In this way prey are considered to be fixed in space. Secondly, information about the values of the maximum search rates is also necessary in order to formulate a function for the volume searched by a hydra. PART II will take up this problem.

In order to test the proposed relationship it is necessary to choose a suitable species with which to work and to make a list of its search modes. The hypothesis is in terms of volume searched per time interval, as a function of time of food deprivation. Thus it is necessary either to measure an index of volume searched for each search mode or to model what seems to be the volume searched by each search mode. The latter approach is chosen, as it is difficult to measure directly the volume searched by an animal. When the model is evaluated, it is used to obtain estimates of the searching rate for each search mode, as a function of time of food deprivation. It is then left only to place the search modes on the food deprivation axis, to measure the initiation threshold of each search mode.

A suitable experimental animal was deemed one which searches in a manner more or less unaided by directional cues from the prey. This type of searching is expected to be predominant in primitive organisms. They often have a restricted set of sensory organs with which to detect the presence of prey. One of the simplest known multicellular animals, the hydra, might be a suitable experimental animal.

Hydra are readily cultured and reproduce asexually, thereby allowing
one to work with a clone. They can attain a substantial rate of population increase by means of asexual reproduction. Some brown hydra in my laboratory took less than five days to double their numbers.
In this section the search modes are identified and the model which is used to calculate a measure of the volume searched by each search mode is introduced. A literature survey opens the section; those behaviours which seem to have any relationship to searching are identified and described. Our definition of search mode is restricted to one of volume searched per time interval. Thus, after all possible search modes are identified some are eliminated. Those that do not contribute to searching through volume are eliminated. This process leads naturally into a discussion of the ways in which volume is searched by the various modes. It is thus appropriate to describe in a preliminary way the overall structure of the model, presented in detail in the next section.

Some field observations were also conducted. The reader not familiar with hydra may wish to familiarize himself with a broad description of various aspects of the ecology of a hydra population by reading the results of a field study as presented in Appendix I. Some aspects of the distribution and abundance of *Hydra carnea* as they occurred in Beaver Creek (Stanley Park, Vancouver) are described. These results are related to some observations on the searching of *Chlorohydra viridissima* and a tentative life history formulation is constructed for hydra in Beaver Creek. Various aspects of these results from the field will be referred to from time to time; however, the results have been put in an appendix so as not to interfere with the flow of testing the hypothesis of the relative durations of the dynamic responses of the search modes.

We return to identification of the search modes, and begin with the
literature survey. Hydra were first reported on by Leeuwenhoek in a letter to the Royal Society in 1703 (Ewer, 1949). However, the first serious studies were done by Abraham Trembley around 1740. Trembley published the first detailed description of what may be our first search mode, locomotion.

Locomotion became the object of study again, about 150 years later. Trembley's original observations were verified and extended. Such authors as Jennings (1906), Wagner (1905), and Wilson (1891) agreed with Trembley that a hydra moves by attaching itself to the substrate alternately by its foot and by its anterior end. The hydra first bends its anterior end to the substrate. It attaches the tentacles to the substrate and detaches its foot. The foot is brought up and set down close to the tentacles. In this way the animal moves forward almost its own length, very much as a caterpillar or leech does. Trembley noted this form of locomotion to be the usual one. This mode was described by Jennings (1906) as: "In the commonest method the animal places its free end against the substratum, releases its foot, draws the latter forward, reattaches it, and repeats the process, thus looping along like a measuring worm". This mode of locomotion has become known as "stepping" (Ewer, 1949) or "looping" (Ewer, 1947b).

Trembley also described a second, less frequent type of locomotion. The foot is not merely brought up to the tentacles but is swung over them and attached well in advance, so that the animal moves forward almost twice its own length. This mode of locomotion has become known as "somersaulting" (Ewer, 1947b).

Looping and somersaulting have tended to be described separately (Ewer, 1947b). Ewer found no clearcut distinction between these two types of locomotion. Trembley had noted this lack of clearcut distinction
but misleading distinctions had crept into the textbooks by 1947. Ewer found the latter form to be only an extreme form of the former. He let P1 designate the position of a hydra's foot and A designate the position at which the anterior end of the hydra is set down. The foot is then lifted and the body contracted to a little lump on the top of the tentacles. The foot is then set down at any point on a circle of small diameter P2, with A its centre. If the body is not properly contracted then the foot is set down at a considerable distance from A, but again at any point on a circle, P3, of larger diameter than P2. The difference between the two forms of locomotion is thus the degree to which the body contracts during the repositioning of the foot. Ewer discovered that the hydra placed its foot anywhere on the locus of circle P2 or P3. Early analogies to caterpillars, leeches, and measuring worms are somewhat prosaic. Fortunately, Ewer used a composite name for this behaviour, the word "walking". In this thesis we also use the word "walking". Hydra will take "steps".

Walking has some obvious relationships to searching. It will be included as a tentative searching mode. The detailed relationship between walking and volume searched will be given in the next section.

Wagner (1905) describes a form of locomotion where the foot is not detached but simply is pulled towards the tentacles. To my knowledge this behaviour has not been observed by anyone other than Wagner. For example, Ewer (1947b, 1949) deals in considerable depth with walking, but does not mention this form. My observations on *H. littoralis* and *Chlorohydra viridissima* have not confirmed its presence. This form of locomotion will be mentioned again in later sections only because there it will be shown that foot attachment is not relevant to volume searched. This behaviour is treated as just another step.
Jennings (1906) noted that a hydra had been observed to attach itself by its tentacles, release its foot, and then use its tentacles like legs. I have never seen this behaviour in my observations of hydra and have never seen it referred to in any other publication. It is difficult to imagine how this behaviour operates. To move in some direction, the hydra must move all tentacles in the direction of movement. Tentacle contractions have been studied from an electrophysiological viewpoint by Rushforth and Hofman (in press; also see abstract by same authors, 1966). The neural correlates of tentacle contractions do not suggest the degree of sophistication necessary to move all tentacles in the direction of movement.

Ewer (1947b) shows that only 10 or fewer nematocysts are used to anchor each tentacle during locomotion and that a period of 10 seconds of mild pressure is necessary to discharge the small glutinants. It is conceivable that the investigator to which Jennings referred saw a hydra which made repeated attempts to anchor its tentacles firmly to the substrate. This form of locomotion will not be considered further as a potential search mode because it has only been reported once, because I could not observe it in my hydra, because current information does not suggest the existence of a mechanism sophisticated enough to control such a behaviour, and because an alternate explanation of the behaviour is available.

"A still different form of locomotion has been described, in which the animal is said to glide along on its foot; how this is brought about is not known." (Jennings, 1906). Jennings is presumably referring to the work of Wagner (1905). Wagner noted that a Chlorohydra moved by gliding on its foot. He writes that the movement is very slow and noticeable only on very close observation, but contends that considerable
distances can be covered in this way. To my knowledge this behaviour has not been seen by anyone other than Wagner. In fact, Brien (1960) notes that the region of the basal disc does not participate in digestion and has a slow metabolic rate. Gastrodermal cells in a state of disintegration are continuously being evacuated through the aboral pore of the basal disc. The epidermal cells of the basal disc similarly die and are sloughed off. It is difficult to see how such a region could control the behaviour described by Wagner. This is considered sufficient evidence to eliminate this behaviour as being either non-existant or not very frequent. Nevertheless, it will be considered as a possible search mode since it will be shown that this mode does not contribute to searching through volume.

In summary, there are two possible search modes in the area of locomotion. They will be referred to as walking and gliding. We turn to another set of behaviours, collectively referred to as "spontaneous movements" (Jennings, 1906).

A hydra which has not been recently fed does not remain still, but reorientates its stalk in "a sort of rhythmical activity" (Jennings, 1906). After remaining in a certain position for a given time, the hydra contracts. The hydra then bends to a new position, and re-extends its stalk. In this new position the hydra remains for a few minutes, then it contracts, changes its position and again extends. Jennings suggests that thereby "the animal thoroughly explores the region about its place of attachment and largely increases its chance of obtaining food".

These movements have been referred to as "column contractions" by more recent authors (Passano and McCullough, 1963; Rushforth, 1971). Reis (1953) challenged the observations of the earlier workers regarding strict temporal rhythmicity of column contractions in hydra. Using
Pelmatohydra oligactus, he failed to find any trace of a temporal rhythm. By ignoring time and concentrating on sequences of movement, he did discover "rhythmic" behaviour. About 75% of the behaviour sequences took one of three forms. Suppose we let a letter designate the increase in stalk length of a hydra when it elongates from a contracted position. For example, the letter b could designate some increase in stalk length. Then the three sequences which appeared most frequently were: aaabbbccc, abcdabcd, abba. In the first sequence a large number of elongations of different magnitude are repeated successively in series. In the second sequence expansions of equal extent do not occur successively in a block, but patterns (abcd) are repeated. In the third sequence patterns are also repeated, but in reversed order, thereby producing a mirror image effect. Arhythmical sequences occurred less than 10% of the time. Thus Reis showed that the sequence of column contractions do follow definite patterns, but that these patterns are not spaced rhythmically in time.

Reis' results have not had widespread effect on the belief of rhythmicity of column contractions. His results have been overpowered by the discovery of a rhythmicity in electrical activity, correlating to a degree with column contractions (Passano and McCullough, 1963). Two regions of rhythmical "pacemaker systems" of electrical activity control column contractions. While their paper is not primarily concerned with strict behavioural rhythmicity, Passano and McCullough note that "polyps usually show regular contraction bursts. Every 5-10 min they shorten into a tight ball, and then re-elongate their column and tentacles". Rushforth (1971) quotes these authors in saying that contractions of the body column and tentacles in hydra is a "rhythmically recurring behavioral" event. In fairness to Rushforth it must be noted that his interests, like
those of Passano and McCullough, are mainly at the physiological, and not at the behavioural, level.

We conclude that patterned sequences of contraction-and-elongation do occur in hydra but not in fixed temporal patterns. Roughly speaking, Passano and McCullough (1963) find the frequency of column contractions to be once per 5-10 minutes. Rushforth and Hofman (in press) find a rate of 4.1 contractions per 15 minutes (SE=0.2, n=20) for H. littoralis, of 4.4 contractions per 15 minutes (SE=0.3, n=20) for H. pseudoligactis, and of 9.3 contractions per 15 minutes (SE=0.4, n=20) for H. pirardi.

Another kind of spontaneous movement is that of tentacle contraction (Wagner, 1905). Rushforth and Hofman (in press) write: "In unstimulated hydra, spontaneous activity of the tentacles consist primarily of single contractions of individual tentacles, or bursts of contractions of one or more tentacles". Rushforth (in press) shows that there is an increased frequency of such contractions before the contraction of the body column of hydra. Rushforth and Hofman (in press) show that there are 1.5 tentacle contractions per 15 minutes for H. littoralis, 1.6 per 15 minutes for H. pseudoligactis, and 7.9 per 15 minutes for H. pirardi. With 15 observations per mean, standard errors are 0.2, 0.4, and 0.4 respectively.

To the spontaneous movements of tentacle and stalk contractions we add two additional observations from Wagner (1905). "The extended Hydra may also change the direction of its long axis without a general contraction, by mere flexion of the expanded body. Sometimes a change from one oblique position to another is brought about by first swaying to the vertical and then to the new oblique position. Quite as often, however, it occurs through circumnutation around the attached foot. In this case there appears first a contraction of the ectoderm on one side near the
foot. This contraction then travels towards the hypostome in slightly spiral form. The Hydra, in this manner, slowly swings around, the body curved into a complete loop or even beyond." This is the only published account of these two behaviours. It is interesting that in three years of hydra-watching, I saw the swaying behaviour once. It is this and other reasons that make me suspect that the frequent lack of confirmation of many behaviours observed by Wagner is a credit to his patience and his powers of observation. His novel additions to the repertoire of hydra behaviour patterns are probably real, but rare. We add the swaying and circumnutation behaviours to the list of possible search modes.

To summarize, there are four possible search modes under the title of spontaneous movement. We now turn to another of Trembley's observations, that hydra are often found hanging from the surface film of the water.

Floating occurs when hydra "produce a bubble of gas beneath their pedal disk. When the bubble is sufficiently large it floats to the surface of the water, with the Hydra hanging from it. The bubble typically bursts at the surface, leaving the Hydra suspended by its pedal disk from the surface film". "The floating Hydra may remain hanging from the surface for several days." This quote is from Lomnicki and Slobodkin (1966).

Two methods of suspension of the hydra from the surface film are described by Wagner (1905). In one case a large air-bubble is attached to the basal disc, the bubble apparently keeping the hydra afloat. In the other case, the typical one according to the above quote, the basal disc of the hydra rests at the base of a capillary depression of the surface film. The basal disc, however, is above the surface film and dry. Wagner notes that sometimes it is easy to dislodge a hydra from
the surface, but at other times it is extremely difficult. He does not say which method of suspension makes it easy to dislodge the hydra.

Wilson (1891) ascribes floating behaviour to oxygen deficiencies in the lower reaches of the water. His conclusions were based on circumstantial evidence; he did not measure oxygen concentration (Ewer, 1947a). Ewer studied young buds and found a gravity, but no oxygen, response. He does caution the reader against interpreting his data as a demonstration "that Hydra has no reaction to oxygen concentration".

Lomnicki and Slobodkin (1966) may have provided a better explanation to Wilson's observations when they showed that the "fraction of Hydra that will float is related to the degree to which they are crowded by other hydra". The mechanism of floating may be related to the finding that water "conditioned" by the presence of other hydra will elicit floating. Nevertheless, these authors also showed a relationship between hunger and the tendency to float. Thus floating may well be a search mode.

This takes us to "a remarkable cycle of behavior in hungry yellow Hydras. Hydras usually remain, as we have seen, in the upper layers of the water, on account of the oxygen there found. But when the crustacea on which the animals feed have become scarce, so that little food is obtained, Hydra detaches itself, and with tentacles outspread sinks slowly to the bottom. Here it feeds upon the debris, often gorging itself with this material. It then moves towards the light, and at the lighted side again upward to the surface. Here it remains for a time, then sinks again and feeds upon the material at the bottom. This cycle may be repeated indefinitely, requiring usually some days for its completion." (Jennings, 1906; from Wilson, 1891). This story is puzzling from a number of aspects: first, reactions of hydra to oxygen concentration
have not been confirmed after the initial postulation in 1891.

Second, hydra have not been noted to be able to detach themselves.

Third, the work of Loomis (1955) and of Lenhoff (1961) have shown the
"feeding reflex" of the hydra to be chemically induced by the presence
of the chemical glutathione.

As pointed out previously, the reaction of hydra to oxygen con-
ccentration has not been adequately demonstrated. In recent times
Lomnicki and Slobodkin (1966) have shown relations between floating and
crowding of hydra and hunger. Ewer (1947a) has shown a relation between
upward movement in detached buds and gravity. Regarding hydra detaching
themselves from the surface film, we note that Lomnicki and Slobodkin
(1966) suggest that hydra detach and sink when a wave rides over their
foot. Wagner (1905) did note that at times hydra are relatively easy
to detach from the surface. A wave might be sufficient. In Appendix I
of this thesis evidence is presented to suggest that hydra quit floating
when they bang into something solid. The results of this process are seen
in the laboratory when hydra, known to have been floating, are found
attached to the container wall at the level of the water surface. Loomis
(1955) notes that Trembley, in 1744, observed that hydra feed exclusively
(emphasis his) on living animals. Hyman (1940; see Loomis, 1955) showed
that hydra will feed on a wide variety of species - but only on the living
members, not on dead specimens of the same species. Even Wilson (1891)
noted that Greenwood, in a paper published in 1888, found hydra to be
essentially carnivorous. Finally, Wilson notes that the length of the
cycle may vary from one day to several weeks and that in order to see
this cycle it is necessary to observe large numbers of animals. Wilson
observed groups of hydra from five hundred to a thousand strong. Wilson
observed this behaviour in H. fusca, but could not find it in H. viridis
(Chlorohydra). One is thus tempted to dispute Wilson's observation, but the behaviour was confirmed by Welch and Loomis (1924) for H. oligactis. Hydra began this behaviour after 5 days of starvation and almost all were "muck feeding" (Welch and Loomis, 1924) at the end of 10 days. Thus we consider this as another possible search mode.

The following search modes have been suggested: two forms of locomotion (walking and gliding), four forms of spontaneous movements (column contractions, tentacle contractions, swaying, and circumnutation behaviour), floating, and "muck feeding". Some of these search modes aid in locating prey by moving the hydra from one location to a different one. Others contribute to locating prey by searching through volume. Some do both. The hypothesis tested in the thesis deals only with the second aspect, searching through volume. Thus for any one of the eight search modes to be included they must result in some reactive volume being traversed.

In order to ascertain the relevance of these behaviours to the hypothesis it is useful to construct an idealized view of the searching hydra. In this regard we find a sentence in Wagner (1905): "In Hydra viridis the tentacles, also moderately expanded, extend obliquely outward and forward, forming the framework of a sort of funnel with the hypostome at the bottom". Also, Jennings (1906) refers to the "normal" position of an unstimulated hydra: foot attached, head not attached, comparative straightness of the body, and tentacles outspread.

The hypothesis to be tested concerns an animal trying to locate prey organisms. We assume that other factors do not interfere with the animal trying to find prey. Thus the normal position in hydra is a suitable idealized state from which to construct a model. The funnel is a useful geometric idealization from which to begin. We use only the
top part of the funnel - the cone. The basic volume searched by the hydra is taken to be the volume contained in the cone of tentacles by a hydra in the normal position.

The volume of "volume searched per time interval" is a reactive volume - the volume within which a prey's chance of being captured differs from unity only by the probability of a successful recognition (SR) of the prey by the predator, of a successful pursuit (SP) of the prey by the predator, and of a successful strike (SS) at the prey by the predator. This definition is suggested by the work of Holling, 1966.

The volume of the cone of tentacles is such a reactive volume for hydra. Yet, small prey can slip through the tentacles undiscovered or a prey can enter the cone from the top, move almost to the hypostome, turn around and leave without being captured. It should be noted that hydra feed on many different species - nematode and annelid worms, crustacea, insect larvae, arachnids, and even such vertebrates as tadpoles and newly-hatched fish (Loomis, 1955). To a small fish the whole cone is the reactive volume, but to a small crustacean the inside region of the cone is not reactive volume. The model may be of such a nature as to apply only to a specific prey species, or it may be of a less precise nature. The hypothesis to be tested regarding the duration of the dynamic responses of the search modes is qualitative; it is necessary only to show that the duration of the dynamic response for one mode is greater or less than that for another. If the volume of the cone overestimates the actual volume searched by one mode, it will do likewise for all other modes. This follows from the fact that the cone will be shown to be an integral part of the volume measure of all the search modes. The reader should thus bear in mind that our attempts do not relate to a description of the searching behaviour of hydra but only to testing a qualitative
hypothesis.

The stimulus needed for nematocyst firing is not constant, but a function of time of food deprivation (Ewer, 1949; Wagner, 1905). This is of no concern here because we deal only with reactive volume, as defined a few paragraphs ago. Variation in nematocyst firing relates to variation in SS, the probability of a successful strike. Thus variation in nematocyst discharge is not dealt with in the thesis. Variation in elicitation of the feeding reflex (Lenhoff, 1961) is not considered for the same reason.

The basic model of volume searched is that of a cone enclosed by the tentacles of a hydra standing in the normal position. Many people have noted that tentacles change length (Jennings, 1906; Hegner, 1933). It is now clear that changing tentacle length may change the volume covered by hydra. Thus this behaviour, not mentioned in the literature survey, is a component of volume searched by hydra. It is a search mode. Tentacle length can easily be shown to be a function of time of food deprivation. If a hydra is fed to satiation, it contracts its tentacles and stalk. The stalk becomes a round ball and the tentacles shorten into stubs. The hydra lengthen their tentacles over a matter of hours.

We now return to the study of the eight possible search modes identified previously. The first form of locomotion, walking, has the cone of tentacles moving through space as the hydra moves its tentacles from the normal position to the substrate, and as the hydra lifts its tentacles back to the normal position. It is thus a search mode. (Note that it is irrelevant whether or not the foot is detached from the substrate after the tentacles have been attached. Thus the type of walking where the foot is not detached does not have to be considered separately from the usual kinds.)
The second form of locomotion results in a slow gliding of the hydra in normal position. The volume of a moving cone must be considered with regard to the velocity of the prey movement. By letting prey be considered fixed in space and then by letting the hydra's velocity of movement be converted to relative velocity, we can interpret volume searched by hydra. Relative velocity can be approximated, for any direction of prey movement, by the square root of the sum of the prey velocity squared and the predator velocity squared (Holling, 1966; after Skellam, 1958). Thus the effect of a slowly moving cone is approximately that of a non-moving cone. The gliding movement is thus not worthwhile including, especially in light of its observation by only one person. We do not consider it as a search mode.

Spontaneous movements may be search modes. Column contractions do not result in volume covered because when the animal in normal position is about to contract its stalk, it also contracts its tentacles. Thus when the animal is in contracted position, its tentacles are withdrawn. This is shown in the drawing of the behaviour given in Jennings (1906) and Hegner (1933). I have noted tentacle withdrawal in my observations of hydra. Column contractions serve to move the reactive cone to a different spatial position, with the possibility that the prey density is higher in the new position.

Tentacle contractions will not be dealt with because they serve only to modify slightly the shape of the reactive volume from the cone to some other form. They occur only at a rate of once per 10 minutes for H. littoralis - one of the species used in the experimental section of the thesis. My observations suggest that each tentacle contraction lasts only a short time; the tentacle is quickly withdrawn and, in a few seconds, lengthened.
Finally, we come to the spontaneous movements called swaying and circumnutation behaviour. These behaviours are so infrequent in the hydra which are studied here, *Hydra littoralis* and *Chlorohydra viridissima*, that none of them could be found to study. As noted previously, I saw swaying only one time in three years of observation. These behaviours are not included because they are not used very often by hydra.

Floating seems to cover volume in a number of ways. Just after hydra detach, they float to the surface with tentacles extended. When hanging from the surface, hydra do so with tentacles extended (my observation). Hydra floating in this manner do take prey. Thus hydra cover reactive volume by floating to the surface and by floating along the surface. Floating will be included as a search mode.

Lastly, we consider "muck feeding". A relevant aspect of this behaviour is that hydra feed on debris on the bottom. Our hypothesis does not relate to where the animals feed, or on which kinds of foods. Volume is covered only by the animal getting to the surface and falling back down again. But the hydra either use previously described modes of locomotion or floating to do so. Thus this behaviour need not be considered outside of locomotion and of floating studies. This argument may be unnecessary as Wilson (1891) could not find this behaviour in *Chlorohydra*, our main laboratory hydra. Neither could I. This behaviour will not be considered, outside of its possible effects on walking and floating.

The search modes have been chosen in a somewhat arbitrary fashion. To be more objective would require an even more detailed survey of hydra behaviour than that given. It is important to notice, therefore, that the hypothesis does not require that all search modes are studied. It requires
only that for those studied, the greater the initiation threshold
of the search mode the shorter its dynamic response. We emphasize again
that the objective is to test the hypothesis, not to study hydra behaviour
for its own sake.

Tentacle lengthening, walking, and floating have been chosen as
being worthy of study. In the next section a model is constructed which
describes the volume components of each of these three search modes.
It is more terse and detailed than that model already described.
In the previous section the various search modes that are used by hydra were identified. It was concluded that concern will focus on only the three search modes of tentacle lengthening, walking, and floating. In this section a model is constructed to translate certain aspects of these behaviours into a measure of volume searched by a hydra in some time interval.

**Tentacle Lengthening.** The volume delimited by the tentacles of a hydra is that of a cone with the hypostome region of the hydra describing the apex of a cone and the tips of the tentacles describing the circle at the base of the cone. Once a prey moves into this cone, its chances of being captured are rather large.

It is suggested that the effect of tentacle lengthening is to increase the volume of the cone. The definition of a right cone is

$$\frac{\pi r^2 h}{3}$$  \hspace{1cm} (13)

where \( r \) is the radius of the cone, and \( h \) is the height. If we know the mean tentacle length, \( L(t) \), and the angle, \( \alpha \), at the apex of the cone, then \( r \) is

$$\sin (\alpha/2) \times L(t)$$  \hspace{1cm} (14)

and \( h \) is

$$\cos (\alpha/2) \times L(t)$$  \hspace{1cm} (15)

Substituting (14) and (15) in (13), one gets an equation of the volume searched by a hydra at time \( t \):

$$\frac{\pi}{3} \sin^2 (\alpha/2) \times \cos (\alpha/2) \times L^3 (t)$$  \hspace{1cm} (16)

The equation describes the actual volume searched by the hydra at time \( t \). As stated previously, we do not want the actual but the
effective volume searched - the actual volume searched, modified by the effects of prey movement. This modification of I6 follows.

The cone of the hydra is assumed not to move through space at this stage. Thus in any interval of time T, a prey moves in the direction of the cone a distance equal to the product of T and the velocity of the prey towards the cone. (Since the hydra is assumed not to move at this stage, we do not have to study relative velocities.) It makes no computational difficulty to let the prey be fixed in space and to let the cone move towards the prey. By doing this the effect of prey movement on the cone of tentacles can be included by extending the cone through space in some direction and by letting the tentacles lengthen as the cone moves (Figures 1A and 1B).

It is too limiting to specify a certain direction of prey movement, relative to the cone. We thus write two equations for each search mode: a minimal effect of prey movement and a maximal effect. Then it is possible to determine the volume searched for any angle of prey movement relative to predator movement by choosing between the two extremums given. We now determine the angles of prey movement which result in extremum values of effective volume searched.

It can be shown that extension of the cone in that direction illustrated in Figure 1A gives a minimal effect of prey movement on volume searched by the hydra; and that extension of the cone in that direction illustrated in 1B gives the maximal effect of prey movement on the volume searched by the hydra.

The magnitude of the effect depends directly on the area of the cone which is extended. This area is triangular in Figure 1A and circular in Figure 1B. This means that if one can show that the triangular area is a minimal area and that the circular area is a maximal one, then
Figure 1. Various types of volume searched by a hydra. The effect of prey movement is included. The direction of prey movement is shown by the arrows.

Figures 1B and 1C overlap only for purposes of economy of space. In figure 1B, the cone is pulled upwards and the tentacles allowed to lengthen as the cone extends upwards. In figure 1C, a series of cones move sideways. The first part is the demi-cone of figure 1B. For more detail on figure 1C, see text.
equivalent volume relationships can be assumed. (This is only strictly true if the incremental volume due to tentacle lengthening is the same for models of Figures 1A and 1B. It will be shown that the area of the circle is 5 times as large as that of the triangle. Thus, ignoring the differences in incremental volume is probably not important for our purposes.)

The cone can be extended in three ways: from the top (circular area), from the side (triangular area), and from any angle between these two views. The last view is of a triangle with height less than that of the triangle viewed from the side and of a demi-ellipse whose major axis is equal to the diameter of the circle and whose semi-minor axis is less than the radius of the circle viewed from the top of the cone.

Consider the equation of a right cone:
\[
\frac{x^2}{a^2} + \frac{y^2}{a^2} - \frac{z^2}{c^2} = 0
\]
Equation 17 can be changed to an equation for a circle at the base of the cone by letting \( z = h(t) \). From this equation parameters \( a \) and \( c \) can be estimated. The equation is
\[
\frac{x^2}{a^2} + \frac{y^2}{a^2} = \frac{h^2(t) \cdot a^2}{c^2}
\]
where \( h(t) \) is the height of the cone of tentacles. The parameter \( h(t) \) is dependent upon estimates of \( \alpha \) and \( L(t) \) for its evaluation (see 15). The angle \( \alpha \) has been measured to be equal to \( 112 \pm 25 \) (SD) degrees \((n=102)\) for Chlorohydra. Let \( L(t) = 1 \) mm. Then the parameter \( h(t) \) is equal to 0.5592.

From 18 and 14 we can write
\[
0.5592 \cdot \frac{a}{c} = \sin(56) \cdot L(t) = 0.8290
\]
Let \( c \) be arbitrarily set to value of 1 and so \( a = 1.48 \). Thus \( c^2 = 1 \) and \( a^2 = 2.20 \). These parameter estimates are all we need in order to write the equation which describes the cone of tentacles as follows:
\[ \frac{x^2 + y^2 - z^2}{2.20} = 0 \]

Now consider the three cases. An equation of the area extended in Figure 1A is obtained by letting the x-coordinate (or the y-coordinate) have zero value:

\[ z = \frac{y}{1.48} \]

If only that part of the coordinate system for \( z \geq 0 \) is considered, then II10 describes two straight lines which meet at the origin. These lines may be visualized as a triangle centered along the z-axis, with vertex at the origin. Let each line terminate at the same z-coordinate, at \((z, \pm y)\). At this point we have \( \sqrt{z^2 + (\pm y)^2} = L(t) \). Then the z-coordinate represents the height of the cone of tentacles and the y-coordinate represents the radius of the cone. This means, by II10 that \( r(t)/1.48 = h(t) \). The area of the triangle, \( r(t) \times h(t) \), may thus be written as \( 1.48 \times h^2(t) \).

The second case to be considered is that shown in Figure 1B. An appropriate equation results from I9 by letting \( z = h(t) \); the equation is written as I8. Since this is an equation of a circle we may write \( r^2(t) = 2.20 h^2(t) \). The area of the circle, \( \pi r^2(t) \), may thereby be written as a function of \( h(t) \): \( 2.20 \pi h^2(t) \) or \( 6.91 h^2(t) \).

Consider the final case. The largest conceivable area is that of a demi-ellipse whose area is equal to one half of that of the circle at the base of the cone, \( \text{vis.} \), \( 3.45 h^2(t) \), and a triangle whose area is equal to that of the triangle of II10, \( \text{vis.} \), \( 1.48 h^2(t) \). The sum of these areas is equal to \( 4.93 h^2(t) \). This area is less than that of the circle alone. This means that the extension of the cone in that direction illustrated in Figure 1B gives the maximum effect of prey movement on volume searched by the hydra.
The ratio of the area of the circle to the triangle is about 5:1. This ratio suggests that mixes of areas of triangle and demi-ellipse will be larger than the area of a triangle alone. Thus the direction of prey movement illustrated in Figure 1A will be considered to be that producing a minimal effect of prey movement. This completes a rather long diversion of thought away from the model building.

It is still left to describe the volume covered as in Figures 1A and 1B. Consider 1A. At time \( t_0 + nT - T \) the hydra occupies the volume

\[
\frac{\pi}{3} \sin^2(\alpha/2) \cos(\alpha/2) \cdot \frac{3}{L (t_0 + nT - T)}
\]

and at time \( t_0 + nT \) it occupies the volume

\[
\frac{\pi}{3} \sin^2(\alpha/2) \cos(\alpha/2) \cdot \frac{3}{L (t_0 + nT)}
\]

These equations simply state that tentacle length changes over time. The volume between these two (demi-) cones is due to prey movement and describable as:

\[
V_Y \cdot \sin(\alpha/2) \cdot \cos(\alpha/2) \int_{t_0 + nT - T}^{t_0 + nT} dt \left[ L^2(t) \right]
\]

An approximation to this integral which is in line with the measurements available is

\[
V_Y \cdot \sin(\alpha/2) \cdot \cos(\alpha/2) \cdot \frac{T}{2} \left[ \frac{L^2(t_0 + nT - T) + L^2(t_0 + nT)}{2} \right]
\]

Combining one half of each of equations I11 and I12 with I14, we have an equation for the minimal volume covered by the predator between time \( t_0 + nT - T \) and time \( t_0 + nT \):
\[
\frac{\tau}{6} \sin^2(\alpha/2)\cos(\alpha/2) \left[ L^3(t_o+nT-T) + L^3(t_o+nT) \right] + \\
\frac{VY}{2} \sin(\alpha/2)\cos(\alpha/2)T \left[ L^2(t_o+nT-T) + L^2(t_o+nT) \right]
\]

Similarly, we may describe the volume as portrayed in Figure 1B as

\[
\frac{\tau}{3} \sin^2(\alpha/2)\cos(\alpha/2) L^3(t_o+nT-T) + \frac{\tau}{2} VY \sin^2(\alpha/2)T \\
\int_{t_o+nT-T}^{t_o+nT} \left[ L^2(t) \right] \, dt
\]

Making an approximation for the integral as previously, we get an equation for the maximal volume covered by the predator between time \( t_o+nT-T \) and time \( t_o+nT \):

\[
\frac{\tau}{3} \sin^2(\alpha/2)\cos(\alpha/2) L^3(t_o+nT-T) + \frac{\tau}{2} VY \sin^2(\alpha/2)T \\
\left[ L^2(t_o+nT-T) + L^2(t_o+nT) \right]
\]

In summary, equations 115 and 117 give estimates of the minimal and the maximal values of the volume searched by the cone of tentacles during the time \( t_o+nT-T \) to the time \( t_o+nT \).

**Walking**. It is assumed that the effect of walking is to move the cone of tentacles through space for a certain distance during a given time.

Walking, described earlier in the thesis, occurs as follows: the hydra begins to move: it bends over, attaches its tentacles to the substrate, and by contracting its stalk, pulls its foot free of the substrate. Then it resets its foot in a new location, attaches it, pulls the tentacles free by contracting its stalk, and then assumes again the upright position. Let the amount of time spent moving during the time interval \( T \) be denoted as \( T_m \) and the amount spent not moving and fixed by \( T_u \). The term \( T_m \) is measured as the time it takes the hydra
to bend the cone of tentacles to the substrate plus the time it takes the hydra to resume the normal position after detaching. However, $T_u$ need not be measured experimentally as it can be calculated from the equation: $T = T_m + T_u + T_a$. $T_a$ is the time of tentacle attachment to the substrate.

Consider the case where prey move towards the predator in such a way as to give minimal effect to the volume searched by the cone of tentacles. During $T_m$ this will be where the prey and predator move in the same direction, at the same speed. We now consider relative velocity, equal in this case to zero. This makes the effective volume searched equal to the actual volume searched ($j_6$). However, in order to explore various field-like situations it is not desirable to specify the magnitude of prey velocity. Thus, the minimal case will be considered the one where the prey and predator move in the same direction, with speed unspecified. The relative velocity is $(|V_Y-V_{PL}|)$, where $V_{PL}$ is the velocity of the walking hydra.

To describe this case with a model, we will describe the $T_m$ and the $T_u$ parts separately. During $T_u$ the situation is describable by I15 with the term $T$ replaced by $T_u$. Later in the thesis it will be shown that $T_u \sim T$; thus tentacle length was allowed to run from $L(t_o+nT-T)$ to $L(t_o+nT)$ in I15. During $T_m$ the situation is also describable by I15, but with the term $T$ replaced by $T_m$ and $V_Y$ replaced by the absolute value of $(V_Y-V_{PL})$. There are other changes, resultant from the fact that $T_m \sim 0$. The integral of I13 now has limits of $t$ to $t+T_m$, with $t$ being some time value within $T$. But $t$ may be any value within $T$, from $t_o+nT-T$ almost to $t_o+nT$. Thus the integral was approximated by the product of a two-point-average tentacle length and the time interval $T_m$. When this is done, the integral of I13 becomes the corresponding
term of I14. A similar argument for equations I11 and I12, relative to their form in I15, results in the first term of I15 becoming

$$\frac{\pi}{24} \sin^2(\alpha/2) \cos(\alpha/2) \left[ L(t_o + nT - T) + L(t_o + nT) \right]^3.$$  

At the time junction between $T_m$ and $T_u$, the two models share a cone. Thus one of these cones is eliminated in the construction of the overall model.

The equation for the minimal effect is thus:

$$\frac{\pi}{24} \sin^2(\alpha/2) \cos(\alpha/2) \left[ L(t_o + nT - T) + L(t_o + nT) \right]^3 +$$

$$\left[ VY \cdot T_u + (|VPL - VY|) \cdot T_m \right] \sin(\alpha/2) \cos(\alpha/2) \left[ L^2(t_o + nT - T) + L^2(t_o + nT) \right].$$

I18

Next we consider the case where the prey moves towards the predator in such a way as to give maximal effect. The degree of cone extension can vary greatly as a function of the direction in which the prey approaches the moving hydra. Extension is maximal if predator and prey move directly towards each other. Suppose this is so. Then relative velocity is equal to $(VY + VPL)$ and the equation is like I18. However, the hydra moves with its side first. The minimal area of the cone is thus projected forward. At low $VY$ values this case would not be maximal - the increase in the distance over which the minimal area is projected would not compensate for the fact that the area extended is the minimal area.

The movement that is being discussed is one with the cone moving towards the substrate. It seems that prey do not often emerge from the substrate. This makes the case describable by a modified I18 one which one is unlikely to find in the field. Therefore the equation of maximal effect will be developed on the basis of the maximal area extended, and not on the basis of the maximal distance extended. The
situation to be modelled is shown in Figure 1C.

Hydra are visualized as moving in steps. The hydra stays in some position for time $\Delta t$ and then moves on to the next position. While a hydra occupies a certain position, prey are moving down onto the cone at a velocity $V_Y$. This results in a volume component due to prey movement. This component is cylindrical, of height $V_Y \Delta t$.

During $T_m$ that part of the volume which is covered by the cone of tentacles itself (actual volume covered) can be described by II5 with $V_Y$ replaced by $V_{PL}$ and the term $T$ replaced by $T_m$. Since $T_m \to 0$, and average tentacle lengths are most appropriate, modification in term one of II5 is again in order.

That part of the volume which is due to the effect of prey movement on the moving cone of tentacles can be described as follows:

$$\frac{T_m}{4} V_Y \sin^2(\alpha/2) \Delta t^* \left( L(t + nT) + L(t) \right) +$$

$$\int_t^{t+T_m} dt \left[ 2V_Y \sin(\alpha/2) V_{PL} \Delta t^* L(t) \right]$$

with $\Delta t$ defined as

$$\frac{T_m}{V_{PL} \frac{T_m}{T_m}} \left[ 2r(t) \right] = \frac{2}{V_{PL}} \sin(\alpha/2) L(t)$$

By way of explaining II9, the first term describes the demi-cylinders to the right and left of Figure 1C. Because $T_m$ is small, I again constructed the model only as a function of average tentacle length. The second term of II9 describes the volume contained between the two demi-cylinders. We can approximate the integral once again as the product of the mean tentacle length and $T_m$.

From the alterations of II9, we get
\[
\frac{\pi}{4} \sin^3(\alpha/2) \cdot VY \left[ L(t_o+nT-T) + L(t_o+nT) \right]^3 + 2VY \sin^2(\alpha/2) \cdot T^* \cdot T_m
\]

During \(T_u\) the volume covered can be described by 117, with the term \(T\) replaced by \(T_u\). Tentacle length was allowed to run from \(L(t_o+nT-T)\) to \(L(t_o+nT)\) in 117.

As before, the \(T_m\) and \(T_u\) models share a cone. The same solution is adopted.

The equation for the maximal effect is thus

\[
\left[ \frac{\pi}{48} \sin^2(\alpha/2) \cdot \cos(\alpha/2) + \frac{\pi}{4} \sin^3(\alpha/2) \cdot \frac{VY}{VPL} \left[ L(t_o+nT-T) + L(t_o+nT) \right]^3 + 
\]

\[
+ \frac{\pi}{6} \sin^2(\alpha/2) \cdot \cos(\alpha/2) \cdot L^3(t_o+nT-T) + 2VY \cdot T^* \cdot \sin^2(\alpha/2) + 
\]

\[
\frac{\pi}{2} VY \cdot T_u \cdot \sin^2(\alpha/2) + \frac{T_m}{2} \cdot VPL \cdot \sin(\alpha/2) \cdot \cos(\alpha/2) \right] \left[ L^2(t_o+nT-T) 
\]

\[
+ L^2(t_o+nT) \right]
\]

In summary, equations 118 and 122 give the estimates of the minimal and the maximal values of the volume searched by the cone of tentacles during the time \(t_o+nT-T\) to \(t_o+nT\), during which walking is assumed to take place.

**Floating.** It will be assumed that the effect of floating is to move the cone of tentacles through space for a certain distance during a given time. It is further assumed that at the beginning of some interval of time, the hydra detaches from the substrate and begins to float. Let this interval be designated as \(t_o+kT\). For all subsequent intervals of time, the hydra is assumed to remain floating.

When a hydra detaches, it floats vertically to some level and then horizontally along it. This vertical movement occurs only
during the hour described as $t_o + kT$. During this interval the volume covered is

$$\pi * DMT * \sin^2(\alpha/2) * L^2(t_o + kT)$$

where $DMT$ is the distance of vertical movement. The vertical movement is completed so quickly that the effects of $VY$ will be small enough to be ignored.

The horizontal movement finds the hydra floating upside down, but with the tentacles extended and ready to capture prey. The effects of prey movement during this time can be considered in the usual way.

Consider the case where the prey moves towards the predator in such a way as to give minimal effect. This will be described by equation I15, with $VY$ replaced by the absolute value of $(VY - VPF)$. $VPF$ is the velocity of hydra movement during floating.

Consider now the case where the prey moves towards the predator in such a way as to give maximal effect. There are two possible situations, already discussed in the walking section. The horizontal floating movement is entirely due to water motion. It does not seem likely that prey of a size usable by hydra will often swim upstream. They will tend to use the same currents that the hydra use. The maximal effect will again be modelled on the basis of the maximal area extended. The situation is that of Figure 1C.

The model is a sum of two equations: I15 with $VY$ replaced by $VPF$ and I21 with $VPL$ replaced by $VPF$ and $T_m$ replaced by $T$.

Combining I23 with the modified I15, we get an equation for the minimal volume searched during interval $T$:
Combining I23 with the modified I21 and the modified I15, we get an equation for the maximal volume searched during the time interval $T$:

\[
\begin{align*}
\Pi \sin \left(\alpha/2\right) \cdot DMT^2 \cdot L(t_0^k + T) + \frac{\Pi}{6} \sin \left(\alpha/2\right) \cdot \cos\left(\alpha/2\right) \cdot \left[ L(t_0^o + T) \right] + T \cdot \left| VY - VPF \right| \cdot \sin \left(\alpha/2\right) \cdot \cos\left(\alpha/2\right) \cdot \left[ L(t_0^o + T) \right] + \\
L(t_0^o + T) + T^* VPF \cdot \sin \left(\alpha/2\right) \cdot \cos\left(\alpha/2\right) \cdot \left[ L(t_0^o + T) \right] + L(t_0^o + T)
\end{align*}
\]

In summary, equations I24 and I25 give the estimates of the minimal and the maximal values of the volume searched by the floating cone of tentacles during the time $t_0^o + T$ to $t_0^o + N T$. 
In the previous section a set of equations for each of tentacle lengthening, walking, and floating has been developed. Each set of equations consisted of two equations: one describing the effective volume searched by a hydra when prey moved in such a direction as to have minimal effect on the actual volume searched by the hydra, and the other describing the effective volume searched by a hydra when prey moved in such a direction as to have maximal effect on the actual volume searched by the hydra. To test the dynamic response hypothesis it is necessary to relate each of these equations to time of food deprivation. The equations, as written, are not functions of time of food deprivation. It is thus necessary to make them functions of food deprivation by expanding those terms of the equations that are sensitive to food deprivation. It is also necessary to obtain estimates of the parameters of these equations. Only then is it possible to relate volume searched per time interval (the model) to time of food deprivation. The hypothesis also requires that the initiation threshold of each search mode be known. Measuring the variables of the equations as functions of time of food deprivation, estimating the parameters, and determining the initiation threshold of each search mode is the purpose of the following HYDRA EXPERIMENTATION sections. The purpose of this section is to explain certain aspects of the approach which is to be followed in these sections.

The HYDRA EXPERIMENTATION: TENTACLE LENGTHENING section begins with a restatement of equations I15 and I17. The HYDRA EXPERIMENTATION: WALKING section begins with a restatement of equations I18 and I22. The HYDRA EXPERIMENTATION: FLOATING section begins with a restatement of equations I24 and I25. I say "restatement" because the equations are
presented in a slightly evaluated form. The basics of these alterations are given in Appendix II.

The prime reason for beginning each experimental section with a model is to set the stage for the section. Experiments are conducted only to evaluate the equations. Variables are measured as functions of time of food deprivation. Parameters are estimated. Initiation thresholds are set. By the end of the section all necessary experimental observation is completed; the model is ready to yield all information necessary to determine the duration of the dynamic response. The model is ready to be placed on the time of food deprivation axis.

After the equations are introduced, the terms of the equations which are sensitive to food deprivation are identified. Then the bulk of each section is given to determination of the relationship between these variables and time of food deprivation. This job is more difficult that it appears at first glance.

It will be shown that there is only one variable sensitive to food deprivation in each set of equations. This being the case, the duration of the dynamic response of the searching rate equations will be equivalent to the duration of the dynamic response of the variables in these equations. For example, tentacle length is the variable of equations 115 and 117. The duration of the dynamic response of 115 and 117 is that of the tentacle length graph as a function of food deprivation. It is thus essential that the duration of the dynamic response of the variables be measured accurately.

Suppose some variable has an S-shape over time of food deprivation. Now suppose we measure this relationship for a number of animals. Each animal gives the S-shaped relationship. However, the function for some animal begins its S-shaped rise at some abscissa value and the function
for another animal at a somewhat different abscissa value, and soon. Then, if all data are plotted, means and variances calculated, and a best fit line drawn, the duration of the dynamic response of this graph would be larger than the real duration! Those animals whose function is pushed along the abscissa will tend to delay the maximum; and those animals whose function is initiated earlier than the average will prematurely pull the line up from the minimal value.

We will encounter this problem in the following sections. This variability existed in spite of a number of attempts to minimize it. Hydra were fed only with newly hatched brine shrimp (*Artemia salina*). Hydra stocks were fed 24 hours before experimental feeding. Only hydra of "average" size were used. Yet this variation persisted. This variation will be shown to be due to the shape of the prey, relative to the way in which they are ingested by the hydra. Again, it is not practical to force the hydra to eat a prey in a certain manner and not convenient to raise *Chlorohydra* on other prey organisms. Likewise it is too time consuming to artificially inject non-living food into hydra, although the technique for doing so is available (Claybrook, 1961). This is especially so considering the amount of replication needed for the experiments of this thesis. It was decided to accept the variation and to find a way to compensate for the variation. The solution adopted was to overlap all functions by moving them along the time of deprivation axis as required to meet a certain criterion. This criterion is that least variation should occur in the region where the graph rises from the minimum to the maximum value. This criterion gives the best estimate of the duration of the dynamic response.

The substantial job of measuring those variables sensitive to hunger as functions of time of food deprivation is followed by a brief description
on estimating the values of the parameters of the equations.

Then emphasis shifts to the second major job: to measure the initiation threshold of the model. We have already noted that there exists only one variable in each set of equations. Thus the initiation threshold of each searching equation is that of the variable. We measure the initiation threshold of each variable over an abscissa of time of food deprivation.

An indicator of the approximate time of the transition from the minimum value of the variable to the increasing range is chosen. This indicator is measured as a function of the amount of food pre-fed to the hydra. One might expect that it is necessary only to measure the initiation threshold from satiation. A range of pre-feeding levels was used to make certain that the initiation thresholds of the various search modes held fairly constant positions relative to the others. The hypothesis does not require a strict relationship between the initiation thresholds of the search modes. It requires only that the search modes can be ranked and that this ranking be the same over all pre-feeding levels. If this is not possible, then one cannot relate the duration of the dynamic response to the initiation threshold in any general fashion. It would be possible that the hypothesis would hold at some pre-feeding levels and not at others.

Measurement of the initiation threshold completes each section. The tentacle lengthening search mode is followed by the walking search mode, which is followed by the floating search mode. Then the data from these three sections are co-related and the hypothesis tested in

A TEST OF THE HYPOTHESIS.

It may be useful to add a note on the degree of accuracy needed for the experiments. Earlier it was assumed that each search function takes
the following form: a minimum steady rate of searching to a certain hunger level, then an increased rate of searching, and finally a maximum rate of searching on a time of food deprivation axis. The model representing the search rate function contains only one variable for each search mode. Thus the specifications for the search function are specifications for the function of the variable. When the variable is measured over time of food deprivation, a detailed accurate description of the relationship is not needed. We have occasion to determine in some detail a function of tentacle length over time of food deprivation. The reason, however, relates to overlapping the data from individual animals in such a way as to estimate the dynamic response as accurately as possible. Also, measurement of initiation thresholds is based on the choice of a criterion of the approximate threshold value. Further accuracy is not needed; it will be shown that the search modes are sufficiently separated along the food deprivation axis that crude estimates of the initiation thresholds are all that are needed to rank the search modes.

We now turn to a brief description of the experimental methods. As the comments are applicable to experiments on each of tentacle lengthening, walking, and floating, it is felt that they are well placed as preliminary comments.

The species *Chlorohydra viridissima* is used most often for the experimental work but *Hydra littoralis* is also used. Stocks of each species were begun from animals obtained from a biological supply house. Stocks were kept in circular, disposable petri plates of 9 cm in diameter and of 1 cm in depth. The hydra were maintained in a medium which consisted of 3,765 mls of tap water modified by 17 mls from each of two solutions. The first of these consisted of 20 grams of NaHCO₃ and 10 grams
of "Versene" dissolved in tap water to make 1 litre of solution. The second of these consisted of 9.513 grams of CaCl₂ dissolved in tap water to make 1 litre of solution.

Stocks were removed once daily from the controlled temperature chamber and fed. The food consisted of live brine shrimp nauplii, hatched daily at a temperature of 25-28 deg C.
The equations which follow describe the effective volume covered by a hydra which stands upright with tentacles outstretched, but not walking or floating. They represent the lower and upper limits of the volume searched by a hydra within a time interval, $T$, from $t_o+nT-T$ to $t_o+nT$. The equation for the lower limit is as follows:

$$0.20 \left[ L^3(t_o+nT-T) + L^3(t_o+nT) \right] + 13.90VY \left[ L^2(t_o+nT-T) + L^2(t_o+nT) \right]$$

The equation for the upper limit is as follows:

$$0.40 \left[ L^3(t_o+nT-T) \right] + 64.76VY \left[ L^2(t_o+nT-T) + L^2(t_o+nT) \right]$$

The constant $t_o$ is time equal to zero, dependent upon the amount of food pre-fed to the hydra; $n$ is a constant which designates the number of $T$ intervals which have passed; $T$ is an interval of time chosen to suit experimental practicalities, in minutes; $L(t_o+nT)$ is the mean tentacle length, in millimeters, at time $t_o+nT$; and $VY$ is the prey velocity, in millimeters per minute, in the direction of the hydra.

We deal first with the variable of tentacle length. It will be studied as a function of time of food deprivation. Stalk lengths will be measured at the same time, even though they are not used in the equations. They will have a role in understanding the controlling mechanism behind tentacle lengthening.

Any point can be localized in space by observing it from two perpendicular directions. When viewing the point from one direction the object is to obtain estimates of the $x$ and $y$ coordinates and when viewing it from the other direction the object is to get estimates of the $x$ and $z$ coordinates. The point becomes localized as a set of $(x,y,z)$
coordinates. The usual distance formula can be used to calculate the distance between any two points. I measured tentacle lengths by noting the spatial position of the hypostome and the position of the distal part of each tentacle. The stalk length was measured by noting the position of the foot and by using the measure of the hypostome position already collected.

A plexiglass container was constructed and filled with the medium in which hydra live. A small plexiglass stand was set into this container. The temperature of the medium was kept between 20 and 22 deg C. The container was set on a cement table that minimized vibrations. One camera was mounted directly over the stand (to measure the x and y coordinates) and another was mounted directly in front of the stand (to measure the x and z coordinates).

Two 35 mm Nikon cameras, each mounted with bellows extension and equipped with 135 mm lens, were used. The cameras were loaded with "Tri-X" film whose stated ASA of 400 was effectively raised to 1200 by developing the negatives in "Acu-1" developer. This allowed the use of a relatively low light intensity of about 50 foot-candles.

A typical green hydra, Chlorohydra viridissima, was taken from a stock which had been fed 24 hours previously. This hydra was pre-fed a set number of newly hatched brine shrimp nauplii and introduced into the container. The hydra was placed on the stand and allowed to attach. If the hydra did not attach within 15 minutes, I proceeded as if it had. A picture was taken from the top of the hydra at the same time as one was taken from the side. Photographing at a rate of once per hour was sufficient to capture the essence of the process. This means that the parameter $T$ of equations 126 and 127 is to be set at 60 minutes. The hydra was photographed for 12 hours at the rate of once per hour.
The film so produced was coded for spatial positions with the use of a "Vanguard" Motion Analyzer. This machine magnifies an image a constant amount and allows one to measure two dimensional coordinates with respect to some arbitrary reference point. The hypostome was chosen as the reference point for both tentacle and stalk length calculations. This gave for each hourly photograph a reading of the coordinates of the tip of each tentacle and of the foot. This information was used to calculate stalk and tentacle lengths for each hydra, once per hour over a 12 hour interval.

The distance calculation involved one minor complexity. Each hourly record consisted of two photographs: one with a series of \((x,y)\) coordinates and the other with a like series of \((x,z)\) coordinates. There was no immediate way of determining which \((x,y)\) tentacle went with which \((x,z)\) tentacle. This had to be done correctly in order to calculate distances. A computer program was devised which, for each record, ordered by magnitude of \(x\) values each \((x,y)\) coordinate pair from smallest to largest. It did the same for each \((x,z)\) pair. The program then matched the first \((x,y)\) pair with the first \((x,z)\) pair, the second \((x,y)\) pair with the second \((x,z)\) pair, and so on. When the positions of certain \(x\) coordinates were changed, the corresponding \(y\) or \(z\) coordinates were changed in the same manner.

Certain tentacles were not held out evenly when the picture was taken. Furthermore, hydra do not possess a rigid skeleton and periodically change their typical tentacle and stalk lengths for short periods by contracting a tentacle or by retracting their whole body. Hourly photographs were taken when the hydra was not contracted. Unexpected data that was due to either of these two sources was eliminated from the calculations. Only the mean tentacle length of
the hydra is used in further considerations of the data and in the model.

When the data were plotted, they indicated that tentacle length is an S-shaped function of time of food deprivation (Figure 2). Although the form of the tentacle length graph appears to be the same from animal to animal, the time axis has considerable inconsistency. This is especially so where the hydra were pre-fed with two brine shrimp nauplii. The consequences of this inconsistency have already been discussed. The reason for it was explained briefly in the previous section. We go into more detail here regarding the reason for the inconsistency. Some information of the biology of hydra will help to explain the reason.

Hydra is a two layered animal: a layer of epidermal cells and a layer of endodermal cells. Between these layers there is a mass of gel and fibres (mesoglea). Both the epidermal and the endodermal cells have their bases drawn out into a pair of processes running in opposite directions. Lying between the base of each cell and the mesoglea is the contractile element, the myoneme. The terminal branches from one epidermal cell contact the myoneme-containing terminal branches from several adjacent cells and form a continuous contractile network. The myonemes of the epidermis lie longitudinally and form part of the system responsible for the contraction of the polyp. The myonemes of the endodermis are organized in a circular fashion and are the antagonists of the epidermal myonemes.

Haynes et al (1968) suggest that the fibres of the mesoglea may be organized in a spiral pattern. The spiral acts much like a spring - it can be stretched and it can be compressed, but it always holds its shape. This property of the mesoglea seems to be involved in the maintenance of the normal position of a hydra.

It is suggested that in the unfed polyp the longitudinally orientated epidermal muscles are relaxed. The length of the polyp is
Figure 2. A number of individual *Chlorohydra* graphs of tentacle length as a function of time of food deprivation. In the top graph, data from four individual hydra are presented. Each hydra had been pre-fed with two newly hatched brine shrimp. In the bottom graph, data from three individual hydra are presented. Each hydra had been pre-fed with six newly hatched brine shrimp.

The lines through the data represent my feeling for the pattern of the data. The reason for drawing this particular locus is discussed in the text. The darkened portions of the line represent the time within which the food-remains were egested.
Time of Food Deprivation (hours)

Length (mm)

Tentacle
determined by the characteristics of the mesogleal spiral. It is suggested that in the fed polyp the circular muscles are relaxed. This gives the surface area necessary to surround the food in the gut. As the circular muscles relax the antagonistic system of longitudinal muscles contracts. The contraction of these muscles results in the shortening of both the stalk and the tentacles. As digestion proceeds the food packet becomes smaller and more densely packed. This allows the spiral to recoil and the circular muscles to contract a certain amount. As the circular muscles contract, the antagonistic longitudinal muscles relax and the hydra lengthens. When the food packet is finally emitted, maximum tentacle length and stalk length are rapidly regained. I am suggesting that the release of the food packet is the mechanism which produces body lengthening.

Figure 2 shows that those hydra which ate two nauplii each released the undigested food packet later along the S-shaped curve than did those which ate six nauplii each. The smaller packet of the former case would, before egestion, allow the hydra considerable contraction of the circular muscles whereas the larger packet would allow less. (The smaller packet would crumble faster than the densely packed, large food packet.)

Hydra eat nauplii head first, tail first, or side first. The amount of gut distension immediately after feeding could be quite different, dependent upon the way that the nauplii were eaten. If two nauplii were eaten in such a way that the first prey was head down and the second tail down a very small packet could be achieved. Gut distension would be slight at any one point. The tentacle length at time of food deprivation equal to zero (Figure 2) would be quite far into the S-shaped graph. If the two nauplii were stuffed into the gut cross-wise at right angles to each other, the cross sectional area of the packet would be considerable.
The tentacle length at time of food deprivation equal to zero would either not have entered the S-shaped graph (e.g., open circles of Figure 2) or not be very far into the graph.

If this explanation is correct, then standardizing the functions of tentacle lengths any further might prove a considerable difficulty. Yet, as explained in the previous section, the variability of the tentacle length function along the time axis has serious effects on the estimation of the duration of the dynamic response of the tentacle length search mode. The solution adopted is to overlap all functions by moving them along the time of deprivation axis such that least variation occurs in the region of the point of inflection. This is a more specific criterion for overlap than that given in the previous section; and the reason for postulating the S-shaped graph is to estimate in an accurate way the duration of the transient response. The resultant graph is shown in Figure 3.

The overlapping of stalk length data follows the pattern applied to the tentacle length data. The composite graph of stalk lengths is shown in Figure 3. Similarities exist between stalk length and tentacle length data.

The physiological mechanism proposed to explain variation in the time axis of Figure 2 suggests that there is a single mechanism for the control of body length. The similarities between the tentacle length and stalk length data will be studied to see how closely the data conform to this suggestion.

A logistic function was fit to each of the tentacle and the stalk length data (Figure 3). The non-linear logistic function was chosen in preference to the similar linear decaying exponential function because I believe the initial slow rise in the data is real. As a hydra digests its food certain amounts of packing can be expected. As this packing occurs, the extent of the distension of the circular muscles will be lessened and
Figure 3. Mean tentacle and stalk length as a function of time of food deprivation. The lower line is a logistic fit to the tentacle length data. The upper line is a logistic fit to the stalk length data. The means are ranged by one standard deviation of the mean. The sample size varies from three at the extremes to seven at the central phase.
the tentacles and stalk will become slightly longer.

The parameters of best fit to the logistic function are given with standard deviations in Table I, for each of tentacle and stalk length data.

The parameter values for the two cases are very similar, with the major difference between tentacle and stalk length functions occurring in the maximum length parameter. This difference is not due to a possible difference between the rise factors, since it would produce the opposite effect. Thus the difference between maximum length parameters is due to the length of time over which the tentacles expand relative to the length of time over which the stalk expands. Figure 3 shows that tentacle length increases over a longer period of time than does stalk length. Since tentacle length is controlled by one factor (longitudinal muscles) rather than the two which control stalk length (longitudinal and circular muscles), this observation follows.

Furthermore, it can be shown, by calculating $r^2$, that 73% of the variation in stalk length can be explained by variation in tentacle length.

The variance found in the tentacle length data was partitioned into three sources. This was done as a check on the experimental technique. It was assumed that the variance could be due to technical problems associated with the camera, motion analyzer, and so on; to variation within individuals, between tentacles; and to variation between individuals. The variation due to technical errors was measured by partitioning the variation between the two readings of the x-coordinate. The expected sums of squares for the tests are given in Table II. Four analyses were conducted. Each corresponded to some time of food deprivation. Compilations were made of the percentages of variation explained by each of the three sources. These percentages are given in Table II. This table shows that the technical sources of error were adequately
Table I. Parameter estimates for the following equation:

\[ L(t) - L(t_{\text{min}}) = \frac{L(t_{\text{max}})}{1 + \exp(s)/\exp(r*\tau)} \]

The estimates were obtained by fitting this equation to data with the use of a non-linear least squares routine.

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>TENTACLE LENGTH</th>
<th>STALK LENGTH</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(10^{-2}) mm</td>
<td>(10^{-2}) mm</td>
</tr>
<tr>
<td>Minimum length, (L(t_{\text{min}}))</td>
<td>58.00</td>
<td>159.00</td>
</tr>
<tr>
<td>Maximum length, (L(t_{\text{max}}))</td>
<td>161.00 ± 4.70</td>
<td>125.00 ± 7.20</td>
</tr>
<tr>
<td>Lag factor, (s)</td>
<td>1.10 ± 0.14</td>
<td>1.30 ± 0.45</td>
</tr>
<tr>
<td>Rise factor, (r)</td>
<td>0.23 ± 0.03</td>
<td>0.31 ± 0.11</td>
</tr>
</tbody>
</table>

1: arbitrarily fixed
Table II. The results of four runs of a three-level, nested ANOVA.

Each test contained readings from five individuals. Tentacle length was recorded by x-coordinate, by tentacle, and by individual. Three tentacles per individual and two x-coordinate readings per tentacle were used.

TECHNICAL DETAILS OF ANALYSIS:

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>EXPECTED MEAN SQUARES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Individuals</td>
<td>$\sigma_I^2 = n_1 \sigma_{TI}^2 + n_0 \sigma_I^2 + \sigma^2$</td>
</tr>
<tr>
<td>Tentacles</td>
<td>$\sigma_T^2 = n_0 \sigma_{TI}^2 + \sigma^2$</td>
</tr>
<tr>
<td>Measuring Equipment</td>
<td>$\sigma_n^2 = \sigma^2$</td>
</tr>
</tbody>
</table>

PERCENTAGE OF VARIATION EXPLAINED:

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>DATA SETS</th>
<th>MEAN OVER SETS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ns</td>
<td>1</td>
</tr>
<tr>
<td>Individuals</td>
<td>7.99</td>
<td>35.66</td>
</tr>
<tr>
<td>Tentacles</td>
<td>89.93</td>
<td>57.45</td>
</tr>
<tr>
<td>Measuring Equipment</td>
<td>2.08</td>
<td>6.89</td>
</tr>
</tbody>
</table>

1 : $p=0.088$
ns : not significant at $p=0.05$
*** : significant at $p=0.001$
An estimate of prey velocity, $V_Y$ is also necessary in order to use equations 126 and 127. In Beaver Creek, prey velocity was identical to water velocity. Thus estimates may be obtained from Appendix I.

This completes the first of two objectives set for this section. The attempt is now made to find the relationship between the time of initiation of equations 126 and 127, and the amount of food pre-fed to the hydra. The initiation threshold of these equations is measured in terms of the tentacle length graph. A suitable indicator of the approximate time of logistic growth is chosen. This indicator is related to amount of food pre-fed to the hydra.

Some hours after eating, hydra emit a packet of undigested food-remains. The darkened areas of the graphs of Figure 2 represent the time range within which this egestion occurred. When hydra eat few nauplii they egest the food-remains near the top end of the logistic growth phase of tentacle length. When hydra eat to satiation, they egest the food-remains near the beginning of logistic growth. Egestion always occurs during the phase of logistic growth. Thus, this easily measurable characteristic is a suitable indicator of the approximate time of logistic growth.

An experiment was devised to measure the time of egestion as a function of the amount of food pre-fed to the hydra. Since Hydra littoralis is larger than Chlorohydra, it emits a larger, more visible food packet. Hydra were used in the initial stages of this experiment. The form of the graph obtained was then checked with some Chlorohydra observations. The brown hydra were fed at levels of 6, 11, 16, and 21 Artemia nauplii per hydra and placed in petri plates of 5 cm in diameter. The petri plates containing hydra were placed within a square arrangement on a cement table that minimized vibrations. The plates were banked on
each of two sides by a neon light, giving a light intensity over the plates of 50 to 100 foot-candles. Temperature averaged 20 deg C.

Hydra were checked at hourly intervals for egestion. The results of this experiment are shown in Figure 4. The data are presented in two ways: first as a cumulative percentage of the total number of Hydra observed which have egested the food-remains (reached criterion) and, in the inset, as the time to egestion. The lower set of points in the inset describes the expected time that the first hydra will take to egest the food remains. The top set of points describes the expected time that the last hydra will take to egest the food-remains. Note the 3 hour difference between the two lines in the inset. This result is interesting in light of the problems encountered in trying to set up Figure 3. Some data allowed me to fit an approximate abscissa for Chlorohydra.

The graphs of the inset give a true reflection of the time of logistic growth only if egestion occurs at the same position on the function, regardless of the amount of food pre-fed to the hydra. But egestion does not occur at the same position on the function. As the amount of food pre-fed to the hydra increases, the position of egestion shifts back along the function. Thus the linear relationship shown in the inset underestimates the true slope. Using the data of Figure 2 one can infer that the maximum amount of shifting of egestion along the logistic function is of the order of 4 hours. This correction would result in the slope being revalued from 1.3 to 2.3 hours/nauplii for Chlorohydra and from 0.2 to 0.4 hours/nauplii for Hydra.

I will now turn to the model building and the relevant measurements for the second searching behaviour, walking.
Figure 4. The time that hydra take to egest food-remains as a function of the size of their last meal. In the lower graph the lines represent data from Hydra pre-fed at levels of 6, 11, 16, and 21 Artemia/hydra.

If the points of the lower graph are assumed to lie along a straight line, then each set of points in the inset represents the 0% and the 100% levels of the abscissa. The points in the inset are a translation of the data below for Hydra littoralis (n= 69, 8, 55, 20). The open circles represent data for Chlorohydra viridissima (n= 15, 18, 12).
The equations which follow describe the upper and the lower limits of the volume searched by a hydra which steps at least once within an interval of time from \( t_0 + nT - T \) to \( t_0 + nT \). The equation for the lower limit is

\[
0.05 \left[ L(t_0 + nT - T) + L(t_0 + nT) \right]^3 + \left[ 0.23T_u \times VY + 0.23T_m \times (|VY - VPL|) \right] \\
\left[ L^2(t_0 + nT - T) + L^2(t_0 + nT) \right]
\]

The equation for the upper limit is

\[
\left[ 0.03 + 0.45 \frac{VY}{VPL} \right] \left[ L(t_0 + nT - T) + L(t_0 + nT) \right]^3 + 0.20 \left( t_0 + nT - T \right) \\
+ \left[ 1.37T_m \times VY + 1.08T_u \times VY + 0.23T_m \times VPL \right] \left[ L^2(t_0 + nT - T) + L^2(t_0 + nT) \right]
\]

Those terms not defined in the previous section are defined as follows:

- \( T_m \) is the amount of time in the interval \( T \) that involves hydra movement;
- \( T_u \) is the amount of time in the interval \( T \) that does not involve hydra movement; and
- \( VPL \) is the velocity of the movement of the cone of tentacles, as occurs when the hydra is walking.

Parameters \( T_m \) and \( VPL \) will be estimated. The term \( T_u \) can be easily calculated once \( T_m \) is known. The terms \( L(t_0 + nT) \) and \( VY \) were discussed in the previous section.

The frequency of stepping changes with time of food deprivation. Thus \( T_m \) is better written as \( T_m(t_0 + nT) \). The major job attempted in this section is the measurement of \( T_m \) as a function of hunger.

It is not experimentally convenient to measure \( T_m(t_0 + nT) \) in terms of time. A distance measure is more suitable. The parameter \( T_m \) is equal to the product of the average time to complete one step and the number of steps completed. The variable of number of steps can be
measured in terms of distance if the average distance moved per step is known.

The distance moved by a hydra in one step was measured experimentally. Two *Chlorohydra* polyps were each given two *Artemia* nauplii. The hydra were then placed in the experimental container described earlier. They were put on the small plexiglass stand and allowed to attach. The position of each hydra was recorded at intervals of 35 minutes. This time interval was chosen because the probability of a hydra moving more than once within it is low. Thus most movements will be single steps. A frequency diagram of distance moved per 35 minutes will define a step.

The position of hydra was recorded with the aid of a camera system placed directly over the hydra. This measuring equipment was identical to that used for body length measurements, except that picture taking at 35 minute intervals was fully automated. The position of each hydra was photographed both day and night. Hydra were kept in the range of the camera by darkening all areas of the experimental container which were outside of the desired area. The area within which hydra moved was illuminated at an intensity of 100 foot-candles. In each photograph the camera recorded the position of each hydra. Estimates of the \((x,y)\) coordinates for the position of the hydra were obtained from the motion analyzer. Estimates of the distance moved per hydra were obtained from the usual distance formula.

The results of these measurements are shown in Table III (FREQUENCY per 35 minutes). The frequency classes of 01-02 and of 00-01 mm were omitted in setting up this table. Movement of less than 2 mm was found to be due to experimental error. Most data centers around the mode of 05-06 mm. This observation relates to the previous observation that the
Table III. Distance moved per time interval by *Chlorohydra viridissima*. Only those animals which moved were considered.

<table>
<thead>
<tr>
<th>DISTANCE MOVED (mm)</th>
<th>FREQUENCY per 35 minutes</th>
<th>FREQUENCY per 60 minutes</th>
</tr>
</thead>
<tbody>
<tr>
<td>02-03</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>03-04</td>
<td>11</td>
<td>14</td>
</tr>
<tr>
<td>04-05</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>05-06</td>
<td>16</td>
<td>33</td>
</tr>
<tr>
<td>06-07</td>
<td>10</td>
<td>26</td>
</tr>
<tr>
<td>07-08</td>
<td>6</td>
<td>12</td>
</tr>
<tr>
<td>08-09</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>09-10</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>10-11</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>11-12</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>12-13</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>13-14</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>14-15</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>15-16</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>16-17</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>17-18</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>18-19</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>19-20</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>20-21</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>21-22</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>22-23</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Total: 63 103
maximum stalk length is about 3 mm (Figure 3). The two types of walking discussed by Ewer (1947b) are visible; there is a peak at each of the 03-04 and the 05-06 classes. Those hydra movements of more than 6 mm might relate to my observation that hydra tend to elongate before walking.

A step is defined as a position change of 3-8 mm in length. I recognize that two position changes of 3 mm or two of 4 mm would be counted as one step. However, when vibrations are minimized, Chlorohydra move at low rates even when deprived of food for a long time. This makes it unlikely that a hydra will move more than once in any of the time intervals used in this study.

The distance moved per hour by individual Chlorohydra polyps was measured as a function of hunger. The interval T was chosen to be 1 hour because equations 128 and 129 are functions of $L(t_0+nT)$ as well as of $T_m(t_0+nT) - L(t_0+nT)$ is measured only at discrete intervals of 1 hour's duration. Polyps were chosen from the Chlorohydra stock. They were fed and then deprived of food. Each polyp was fed with three newly hatched nauplii. Sets of four polyps which had been treated in this manner were placed in each of six petri plates. The plates were 60 mm in diameter. They were placed on a stand elevated from the top of a cement table that minimized vibrations. Once every hour the petri plates were marked from the bottom for the position of each hydra. This began immediately after feeding and continued for 12 successive hours. The plates were plastic and could be easily scratched with a sharp probe. When a hydra moved from one position to another, I marked the new position and drew a line from the former to the new position. Records were taken in the same way for another 12 hours, beginning the next morning - and again the next day. In this way the paths of the hydra were traced during times of deprivation of 1 to 12
hours, of 24 to 36 hours, and of 48 to 60 hours. A total of 96 hydra were followed in this manner. An additional set of 96 hydra were treated as above, except that they were fed in the evening, with recording begun the next morning. This allowed observations of hydra behaviour during times of deprivation of 12 to 24 hours, of 36 to 48 hours, and of 60 to 72 hours. A continuous 72 hours of recording was obtained by combining this set of data with the other set.

Certain aspects of the relationship between the distance covered per hour by a hydra and the time of food deprivation emerged from these data. The distance covered/hydra/hour retains a minimum value until about 27 hours after feeding. To this time, the probability of a hydra walking during an interval of 1 hour is 0.4%. Then the distance covered/hydra/hour increases to a larger, but variable, maximum. The probability of a hydra walking during an interval of 1 hour is 5.9%. The standard deviation is 3.5%.

The duration of the dynamic response between the minimum and the maximum value is not clear because of the variability around the maximum response. Practically no hydra moved more than once in any one hour interval: of 103 movements, 94 were of single steps (Table III). This means that if the dynamic response is to be greater than 1 hour (the inter-record interval), then the probability of a hydra stepping at the rate of once per hour must increase as hunger increases. Thus, all hydra data were standardized to the time of first step. The probability of a hydra moving was calculated for each hourly interval after the time of the hydra's first step.

Table IV gives the percentage of hydra which moved per hour for all hours in which data from 20 or more hydra were available. The data do not indicate a relationship between the probability of a hydra
Table IV. Percentage of hydra which moved per hour, for successive hours after hour of first step.

<table>
<thead>
<tr>
<th>HOURS AFTER FIRST STEP</th>
<th>TOTAL NUMBER HYDRA OBSERVED</th>
<th>NUMBER HYDRA MOVED</th>
<th>PERCENTAGE HYDRA MOVED</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>77</td>
<td>4</td>
<td>5.2</td>
</tr>
<tr>
<td>2</td>
<td>62</td>
<td>4</td>
<td>6.5</td>
</tr>
<tr>
<td>3</td>
<td>69</td>
<td>4</td>
<td>5.8</td>
</tr>
<tr>
<td>4</td>
<td>75</td>
<td>10</td>
<td>13.3</td>
</tr>
<tr>
<td>5</td>
<td>54</td>
<td>4</td>
<td>7.4</td>
</tr>
<tr>
<td>6</td>
<td>34</td>
<td>2</td>
<td>5.9</td>
</tr>
<tr>
<td>7</td>
<td>28</td>
<td>3</td>
<td>10.8</td>
</tr>
<tr>
<td>8</td>
<td>29</td>
<td>1</td>
<td>3.5</td>
</tr>
<tr>
<td>9</td>
<td>24</td>
<td>1</td>
<td>4.2</td>
</tr>
<tr>
<td>17</td>
<td>21</td>
<td>1</td>
<td>4.8</td>
</tr>
<tr>
<td>18</td>
<td>26</td>
<td>3</td>
<td>11.5</td>
</tr>
<tr>
<td>19</td>
<td>32</td>
<td>6</td>
<td>18.8</td>
</tr>
<tr>
<td>20</td>
<td>34</td>
<td>3</td>
<td>8.8</td>
</tr>
<tr>
<td>21</td>
<td>30</td>
<td>4</td>
<td>13.8</td>
</tr>
<tr>
<td>22</td>
<td>37</td>
<td>3</td>
<td>8.1</td>
</tr>
<tr>
<td>23</td>
<td>48</td>
<td>5</td>
<td>10.4</td>
</tr>
<tr>
<td>24</td>
<td>52</td>
<td>8</td>
<td>5.4</td>
</tr>
<tr>
<td>25</td>
<td>35</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>26</td>
<td>28</td>
<td>3</td>
<td>10.7</td>
</tr>
<tr>
<td>27</td>
<td>35</td>
<td>1</td>
<td>2.9</td>
</tr>
<tr>
<td>28</td>
<td>35</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>29</td>
<td>26</td>
<td>1</td>
<td>3.9</td>
</tr>
</tbody>
</table>
moving and the time after it first steps. The dynamic response will be chosen as less than or equal to 1 hour.

The data of Tables III and IV will now be converted into a time measure of $T_m(t_o+nT)$. The probability of movement to hour 27 is 0.004. The probability of movement rises quickly 1 hour later to 0.059. Each movement is one step. The time which a hydra takes to bend over and attach its tentacles to the substrate and then to pull up the tentacles is about 0.75 minutes per loop. Thus 0.00300 minutes is the average $T_m(t_o+nT)$ for time less than 27 hours. For time greater than 27 hours the average $T_m(t_o+nT)$ is 0.04435 minutes.

The parameter $T_u$ can be calculated as the total time $T$ minus $T_m$, the time spent moving. Since the time spent moving is so small, an additional term will be subtracted from $T$. This term is $T_a$, the time during a step that the hydra has its tentacles attached to the substrate. $T_a$ has been measured to be about 1 minute per step. When modified for the probability of looping, $T_a$ equals 0.004 minutes for time less than 27 hours and 0.059 for time greater than 27 hours. Thus, for time less than 27 hours, $T_u$ is 59.9930 minutes and for time greater than 27 hours, $T_u$ is 59.8968 minutes.

The terms $T_u$ and $T_m$ are not accurate to six significant figures. However, we keep these small differences to see how such differences can affect the volume searched equations. $T_m$ might well be larger in the field than shown here. Wagner (1905) notes that vibration can elicit various behaviours. However, in order to determine the effect of only hunger on $T_m$, a vibration-minimizing table was used for these experiments.

The final parameter necessary to be estimated is VPL. An approximate value is 60 mm per minute.

Finally, $T_m(t_o+nT)$ will be related to the amount of food pre-fed to
the hydra. The time of first step will be the criterion which will be related to the time of food deprivation.

**Chlorohydra** polyps were fed at levels of 1, 3, and 6 newly hatched nauplii and then deprived of food. The polyps were placed in petri plates. These plates were set on the stand used in the most recently described experiment. The position of each hydra was marked by scratching the underside of the plate. The number of hydra not standing on their mark was recorded each hour until all hydra had moved at least one time.

The results are shown in the customary manner in Figure 5. There is a 34 hour difference between the two lines in the inset.

This completely fulfills the objectives of this section. I will turn to the model building and the analogous measurements of the final searching behaviour, floating.
Figure 5. The time that *Chlorohydra viridissima* polyps take to walk for the first time, as a function of the size of their last meal. In the lower graph the lines represent data from hydra pre-fed at levels of 1, 3, and 6 *Artemia* per hydra.

If the points of the lower graph are assumed to lie along a straight line, then each set of points in the inset represents the 0% and 100% levels of the abscissa. Each set of points in the inset is based on a sample of 24 hydra.
The equations which follow describe the upper and lower limits of the volume searched by a hydra from \( t_0 + nT - T \) to \( t_0 + nT \) for all intervals of \( T \) after and including that in which the hydra detaches and begins to float. The equation for the lower limit is

\[
10.36 \cdot DMT + 0.20 \left[ L^3(t_0 + nT - T) + L^3(t_0 + nT) \right] + 13.91 * (|VY - VPF|) * \\
\left[ L^2(t_0 + nT - T) + L^2(t_0 + nT) \right]
\]

For the upper limit:

\[
10.36 \cdot DMT + 0.20 \left[ L^3(t_0 + nT - T) + L^3(t_0 + nT) \right] + 13.91 \cdot VPF * \left[ L^2(t_0 + nT - T) + L^2(t_0 + nT) \right]^3 + 82.47 * VY * \\
\left[ L^2(t_0 + nT - T) + L^2(t_0 + nT) \right]
\]

Those terms not defined previously are defined as follows: \( DMT \) is the distance the hydra floats vertically before beginning to be swept horizontally. \( DMT \) is equal to zero for all time not equal to \( t_0 + kT \). \( VPF \) is the velocity of hydra movement during floating.

The only unmeasured parameters of these equations are \( DMT \) and \( VPF \). Neither is a function of the time of food deprivation. Much of the form of the floating function is clear without the necessity of data collection. Before detaching, the hydra covers no volume through the use of the floating behaviour. Suddenly the hydra detaches and begins to float. Thus the duration of the dynamic response is less than 1 hour (the inter-record interval). After detaching, the hydra continues to float. It covers volume as a function of \( VPF \). The assumption is made that the hydra continues to float indefinitely, at constant \( VPF \). The parameter \( DMT \) took values up to 30 cm for \( Hydra carnea \) populations in Beaver Creek. The parameter \( VPF \), as
reflected by the water velocity, ranged up to 30 cm/second.

This short exposition completes the first of two objectives which have been set for this section. The form of the floating function has been described. The time of initiation of this function will now be related to the amount of food pre-fed to the hydra. The criterion of initiation is detaching and begin-floating.

Detaching, with subsequent floating, has been hypothesized to have a duality of cause: food and density (Lomnicki and Slobodkin, 1966). The joint effects of food and density were studied to ascertain the relative importance of each factor. A number of \textit{Hydra littoralis} were pre-fed at levels of 1, 6, and 16 newly hatched nauplii per hydra. The hydra were then placed at densities of 1, 2, and 8 hydra per 20 cc medium in petri plates of 5 cm in diameter. The petri plates were set on a cement table that minimizes vibration and were illuminated with a light intensity of 50-100 foot-candles. Temperature averaged 20 deg C.

The number of hydra floating was recorded at 12 hour intervals. The result of this experiment showed that density is the minor factor (Table V). Thus all density data were combined. The cumulative percentage of hydra which were floating was calculated as a function of time of food deprivation and of the amount of food pre-fed to the hydra. The data are presented in the usual fashion in Figure 6. There is a 32 hour difference between the two lines of the inset.

In Figure 4 it was shown that the graph of the time to criterion as a function of the amount of food ingested was the same for both \textit{H. littoralis} and \textit{C. viridissima}. The two graphs were overlapped when the maximum number of \textit{Artemia} eaten by each species was lined up together along the abscissa. Maximum ingestion is 32 newly hatched nauplii for \textit{H. littoralis}. For \textit{C. viridissima} it is six \textit{Artemia}. The assumption
Table V. A factorial Analysis of Variance table: the effect of food and hydra density on the time which hydra take to begin floating.

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>DEGREES OF FREEDOM</th>
<th>SUM OF SQUARES</th>
<th>MEAN SQUARE</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Food (F)</td>
<td>2</td>
<td>27,241</td>
<td>13,621</td>
<td>51.00 (p &lt; 0.001)</td>
</tr>
<tr>
<td>Density (D)</td>
<td>2</td>
<td>241</td>
<td>121</td>
<td>0.45 (p &gt; 0.50)</td>
</tr>
<tr>
<td>F X D</td>
<td>4</td>
<td>79</td>
<td>20</td>
<td>0.07 (p &gt; 0.75)</td>
</tr>
<tr>
<td>Error</td>
<td>297</td>
<td>55,590</td>
<td>269</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>215</td>
<td>83,151</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 6. The time that hydra take to detach and begin to float as a function of the size of their last meal. In the lower graph, the lines represent data for hydra pre-fed at levels of 1, 6, and 16 *Artemia* nauplii/hydra.

If the points of the lower graph are assumed to lie along a straight line, then each set of points in the inset represents the 0% and the 100% levels of the abscissa. In the inset the points represent data collected for *Hydra littoralis* (n = 24, 24, 24). The open circles represent data for *Chlorohydra viridissima* (n = 10, 10, 10).
Time to Criterion (hours)

Hydra littoralis

Chlorohydra

Number Nauplii Pre-fed

Cumulative Percent Criterion

Time of Food Deprivation (hours)
is made that the same relationship holds for the floating criterion. A Chlorohydra axis was set to Figure 6.

Then some data was collected to test this assumption. The only unusual experimental condition was that the hydra were subjected to a diurnal light cycle of 12 hours of light (5 foot-candles) and 12 hours of darkness. The results are shown as open circles in the inset of Figure 6.

This completely fulfills the objectives of this section. It also completes the data necessary to test the searching rate hypothesis.
A TEST OF THE HYPOTHESIS

The hypothesis to be tested is that the duration of the dynamic response for some searching mode is inversely related to the time of food deprivation which initiates searching by that mode. Hydra use three searching modes: tentacle lengthening, walking and floating.

The searching behaviour which is initiated first on a time of food deprivation axis is tentacle lengthening. The searching function appropriate to this behaviour is that for which equation 126 is the lower limit and for which 127 is the upper limit. In these equations only tentacle length is responsive to the time of food deprivation. Thus, it is clear from the form of 126 and 127 that the duration of the dynamic response of these functions is the duration of the dynamic response of the tentacle length graph (Figure 3). One can see from this figure that the approximate duration is 5 hours.

The searching behaviour which is initiated next on a time of food deprivation axis is walking. The lower and upper limits to this function are given by I28 and I29 respectively. In these equations both tentacle length and the frequency of walking ($T_m$) are responsive to the time of food deprivation. However, as shown in Figures 4 and 5, tentacle length reaches its maximum value before walking begins. Thus, it is clear that the duration of the dynamic response of these functions will be the duration of the dynamic response of the $T_m$ function. This duration, as noted in the section called HYDRA EXPERIMENTATION: WALKING is less than or equal to 1 hour.

The searching behaviour which is initiated last on a time of food deprivation axis is floating. The lower and the upper limits to this function are given by I30 and I31 respectively. In these equations only
tentacle length is responsive to the time of food deprivation. However, as shown in Figures 4 and 6, tentacle length reaches its maximum value before floating is initiated. Thus, these functions are not sensitive to time of food deprivation, other than being switched on at some hunger level. The duration of the dynamic response of these functions is in terms of a few seconds.

If my hypothesis is correct, then the duration of the dynamic response for tentacle lengthening should not be less than that for walking, which should not be less than that for floating. We find that the duration of the transient response for tentacle lengthening is of length 5 hours; for walking of length less than 1 hour; and for floating, of length much less than 1 hour. These data do not contradict my assumption. I conclude that there may be some validity in the use of strategical hypotheses in the formulation of general functions.
PART II

A TIME SPENT SEARCHING FUNCTION FOR HYDRA

INTRODUCTION

In PART I a relationship between the duration of the dynamic responses of various searching modes was formulated and tested. The hydra behaved as predicted. The concern of this section is with searching by hydra, and only indirectly with strategical hypotheses.

Much data has been collected on searching by hydra. The data has been used only to test a transient response relationship. However, enough data has been gathered in order to formulate a complete function for volume searched (VS) by hydra. To do so requires the additional knowledge of the steady state searching rates of the various searching modes used by hydra. When this information is combined with the dynamic response information of PART I, it will allow one to write an overall searching rate function. From this it is possible to derive a function for time spent searching (TS) by hydra.

This work was separated from that of PART I so as not to confuse the somewhat interrelated objectives of PARTS I and II. In the first PART the objective was to see if strategic hypotheses have value in formulating general functions. In the second PART the objective is to formulate a VS function for hydra and to use this function in writing an explicit time spent searching function (TS).
The relationship between the steady state searching rate of a searching mode and the initiation threshold of that mode will be studied by exploring the behaviour of the searching model.

The equations of minimal effect for body lengthening and looping will be studied first. We may write equation I28, relative to I26, as follows:

\[
100 \left[ \frac{6.40 + 0.23(V_Y - 60.0)}{4.26 + 134.55V_Y} \right] - 100 III
\]

This gives the percentage increase of the minimal volume searched per hour by a walking hydra over one that does not move. Estimates of VPL, T_u, T_m, and of maximum tentacle length were obtained from Chlorohydra data.

The derivative of III, with respect to V_Y, shows a positive slope. The slope at V_Y=0 is rather large but it falls quickly to less than 1 %-minute/mm by V_Y=2.91 mm/minute. For all larger V_Y values, equation III keeps almost the same value. At V_Y=3 mm/minute, it has value of -2.84. Water velocity in Beaver Creek was observed to vary from 0 cm/sec to 30 cm/sec (18,000 mm/minute). Thus, the effect of walking on the minimal volume searched per hour is slightly negative over most of the water velocities in which hydra have been observed. The searching time not used when the tentacles are attached (T_a) to the substrate is not compensated for by the extended volume covered due to the combined effects of moving the cone through space (V_Y and VPL).

Analogous to III, an equation for the percentage increase of the maximal volume searched per hour by a walking hydra over one that does not move may be written as follows:
The derivative of this equation, with respect to VY, shows a negative slope. Although at VY= 0 there is a large slope, by VY= 2.03 mm/minute the slope descends to less than 1 %·minute/mm. Thus over almost the whole range of VY values, the magnitude of equation 112 is constant, at +1.15%. Walking at the rate of 0.059 times per hour is not very beneficial to the hydra, at least in terms of volume searched.

The experiment from which the walking rate was calculated was set up to minimize vibrations. This was done so that the effects of hunger alone could be determined. In field situations with substantial water velocities, I observed that hydra waved vigorously with the changing motion of the water. In the laboratory, I noted that a common stimulus for walking was when the tentacles of an upright hydra contacted the substrate with some force. The stepping rate in the field may be larger than that measured in the laboratory. It is not unreasonable to suggest the possibility of walking contributing some slight amount to the searching rate.

Next the effects of floating will be examined. The percentage increase of the minimal volume searched by a floating hydra over one which does not move is as follows:

\[
100 \left( \frac{325.06 + 134.65 \times (|VY-VPF|)}{4.26 + 134.55 \times VY} \right) - 100
\]

The parameter DMT was given the value of 30 mm. (Note that DMT occurs only during time \( t_0 + kT \). The first term of the numerator of 113 must be subtracted when time is not equal to \( t_0 + kT \).

If the assumptions that \( VY \geq VPF \) and \( VPF > 2.3 \) are made, then the derivative of 113 with respect to VY has a positive slope. For values of VY near to VPF, the equation has a relatively large slope. This
slope falls to less than 1 %-minute/mm by $V_Y=28$ mm/minute, for $V_{PF}=10$ mm/minute; by $V_Y=99$, for $V_{PF}=100$; and by $V_Y=223$, for $V_{PF}=500$.

The stream situation might well be approximated when prey velocity ($V_Y$) is set equal to water velocity, which is set equal to the floating speed ($V_{PF}$) of hydra. Floating hydra have no apparent means of propelling themselves. In streams, independent means of locomotion of prey might well be counteracted by water movement. Equation 113 was evaluated for $V_Y=V_{PF}=100$ mm/minute. It took the value of -97.9%. This value could be made less negative only during the time interval, $t_o+\kappa T$, by adjusting the value of $D_M T$ upward; however, the equation would always remain negative in value. On the other hand, the value could be pushed to -100% by letting $V_Y=V_{PF}$ take larger values. The persistent negative effect of floating arises because the floating hydra loses the prey velocity component it had when attached. That is to say, the volume searched by a hydra floating in a stream is the actual, not the effective, volume searched.

Estimation of the amount that the volume searched per time interval is reduced by a floating hydra requires knowledge of the length of time which the hydra floats before reattaching. Where the water ran quickly in Beaver Creek, the hydra were swept not along the surface of the water but only a few millimeters from the substrate. Thus one might expect that they do not float for long times before running into some protuberance and re-attaching.

Another complicating factor has arisen. In Beaver Creek the floating hydra which I saw moved down the creek with tentacles outspread. However, Slobodkin has seen hydra floating down a stream with tentacles fully withdrawn (communicated to me by Bill Clark). When this occurs, the volume searched by a floating hydra might be substantially reduced.
over the volume searched by a non-floating hydra.

The lake situation might be approximated when the absolute value of \((VY - VPF)\) is set equal to the value of \(VY\). This is because in a lake environment water velocity and consequently \(VPF\) is about zero. On the other hand, prey movement is often a function of self propulsion, rather than a function of water movement. In this situation the minimal volume searched per time interval remains identical with that of the attached hydra. One exception is the initial jump in searching rate during time \(t_0 + \kappa T\). This addition becomes more substantial with increases in \(DMT\).

The percentage increase of the maximal volume searched by a floating hydra over one which does not move is as follows:

\[
100 \left( \frac{4.26 + 10.36 DMT + 798.31 VY + 134.65 VPF + 38.33 \frac{VY}{VPF}}{4.26 + 627.88 VY} \right) - 100
\]

\(II4\)

Simply by looking at this equation, one gets the impression that the effect of floating is going to be substantial. The constants modifying the \(VY\) values are much larger in the numerator than in the denominator. The derivative of \(II4\), with respect to \(VY\), has a negative slope. For values of \(VY\) which are not too large, the equation has a substantial slope. The rate of stabilization is about the same or slightly faster than that of equation \(II3\).

As an example, let \(DMT = 30\) mm and \(VPF = 100\) mm/minute. These are modest estimates of the parameters as they occurred in Beaver Creek. The slope of \(II4\) falls to less than 1 \(\%\)-minute/mm by \(VY = 47\) mm/minute. It is noteworthy that the equation holds a rate stabilized value of \(+50\%\).

Enough information is now available to draw some conclusions about
the relationship between the maximum searching rate of some searching mode and its initiation threshold. The minimal effect of walking on the volume searched is slightly negative. The minimal effect of floating is either no change (when the absolute value of \((V_Y-V_{PF})V_Y\)) or very negative (when \(V_Y=\text{water velocity}=V_{PF}\)). On the other hand, the maximal effect of walking on the volume searched is slightly positive but the maximal effect of floating is very positive.

These results have been drawn from a deterministic model. The conclusions also follow from a "stochastic" model; see Appendix III.

I had expected the maximum rate of searching volume to be related to hunger in a similar manner as was hypothesized for the transient responses. Although this was so for the maximal effect data, it was not so for the minimal effect data. The consequences are studied in the discussion.

Simulation was used in studying searching by hydra. Equations 126 to 131 were programmed; see Figures 7 to 11 inclusive. In all graphs the volume searched per hour by a hydra is presented as a function of time of food deprivation. Volume searched is in the units of \(\text{mm}^3/\text{hr}\).

Each graph is composed of three sections. Between 0 and 26 hours, equations 126 and 127 are plotted. These equations begin their rise from the minimum to the maximum value at about 6 hours after being pre-fed with three *Artemia* nauplii. This is so because those observations recorded in Figure 4 show that a hydra pre-fed with three nauplii egests food-remains from 5 to 8 hours after feeding. It is implied in these figures that at 26 hours, equations 126 and 127 are replaced by equations 128 and 129. This is because walking is considered a sufficient addition to the volume searched activity to be considered separately. One component of this behaviour is tentacle length. The placement of 128 and 129 is related to the data of Figure 5. The dynamic responses of these
equations are shown as instantaneous. This conclusion formed part of the results of PART I. The maximum value of these equations does not show the variability of the previous equations. This is because the fitted maximum value of tentacle length (Table I) was used, rather than the actual data as was done for equations I26 and I27. Finally, at hour 60, equations I30 and I31 began as I28 and I29 dropped out. The time of transition was according to data of Figure 6. The dynamic response was made instantaneous, again in agreement with data of PART I. In the various simulations, DMT and VY were varied.

In Figure 7 the actual volume searched by a hydra (VY=0) is portrayed. The difference between the minimal and the maximal effects of any search mode is small, relative to the differences between modes. The parameter VPF took the small value of 0.50 mm/minute instead of the value zero. This value was given in order to avoid the problem of dividing by zero in the term VY/VPF of equations I30 and I31. A larger value of VPF would serve to increase the effects of floating. DMT was given the small value of 2.0 mm.

If one were to describe this graph with a continuous function, he might well choose the exponential function. The exponential function has an exponential derivative; and one should note that the volume searched during the floating period is larger than that during the walking period by an amount much greater than the volume searched during the walking period is larger than that during the tentacle lengthening stage.

In the next two figures, searching by hydra in a slow stream (Figure 8) and in a lake (Figure 9) are shown. Prey are assumed to move slowly. In the stream, prey are allowed to move only as a function of water velocity, at 100 mm/minute. In the lake, prey movement is set at 500 mm/minute. A feature of interest is that even at the modest VY of 100, the effect of DMT is masked; thus the large hump shown in
Figure 7. A simulated result of the searching rate of a hydra which has been pre-fed with 3 Artemia nauplii, as a function of food deprivation. \( V_Y = 0.0 \) mm/minute, \( V_PF = 0.50 \) mm/minute, and \( DMT = 2.0 \) mm.

Because \( V_Y = 0.0 \) the result estimates the actual volume searched per hour, as a function of time of food deprivation.

Minimum and maximum estimates of the volume searched for each search mode are given. These extremum estimates are based on the direction of prey movement relative to the hydra.
Figure 8. A simulated result of the searching rate of a hydra which has been pre-fed with 3 *Artemia* nauplii, as a function of food deprivation. \( V_Y = V_{PF} = 100 \text{ mm/minute} \), and \( D_{MT} = 300 \text{ mm} \).

In a stream, prey movement may be passively controlled by water movement. Floating by hydra is entirely the result of water movement. Thus when \( V_Y = V_{PF} \), as here, the results estimate the searching rate of a stream dwelling hydra. Since the water moves at a velocity of only 0.16 cm/sec, the stream is a slow one.

Minimum and maximum estimates of the volume searched for each search mode are given. These extremum estimates are based on the direction of prey movement relative to the hydra.
Figure 9. A simulated result of the searching rate of a hydra which has been pre-fed with 3 *Artemia* nauplii, as a function of food deprivation. $V_Y = 500.0$ mm/minute, $VPF = 100$ mm/minute, and $DMT = 0.0$ mm.

In a lake situation independent means of prey locomotion may not be overridden by water velocity. Thus when $V_Y > V_PF$, as here, the results estimate the searching rate of a lake dwelling hydra.

Minimum and maximum estimates of the volume searched for each search mode are given. These extremum estimates are based on the direction of prey movement relative to the hydra.
Figure 7 is restricted to situations with very small $V_Y$. The hump is only barely visible in Figure 8.

More importantly, these figures show that with increasing values of $V_Y$ over zero the minimal effects spread rather far from the maximal effects for any searching mode. This difference tends to expand with time of food deprivation. The volume searched drops to the actual volume searched for minimal effect floating in the stream situation.

The situation for hydra searching in a quickly flowing stream (Figure 10) and in a lake (Figure 11) are shown. Prey are assumed to move quickly. Except for covering much more volume, the hydra search in a similar pattern.

These results show that the exponential searching rate which was hypothesized for the actual volume searched graph (Figure 7) does not hold for the various effective volume searched graphs (Figures 8 to 11). The primary searching mode, in terms of effective volume searched per time interval, is tentacle lengthening. One might suggest, however, that the effective searching rate is initially exponential and then constant or slightly increasing.

For reasons of simplicity, I will consider only the exponential section of the searching function. This assumption will underestimate the maximal effect floating rate by about 20%. On the other hand, for those situations where the effective volume is very close to the actual volume, the exponential function may be applied over all three searching modes.

Thus, we write

$$\frac{\Delta V_S}{\Delta t} \approx \frac{d V_S}{d t} = e^{a*t}$$

II5
Figure 10. A simulated result of the searching rate of a hydra which has been pre-fed with 3 *Artemia* nauplii, as a function of food deprivation. $VY=VPF=10,000$ mm/minute and $DMT=150$ mm.

For reasons like those given in the legend of Figure 8, the situation here is for a stream dwelling hydra. As water velocity is about 17 cm/sec, the stream is a fast one.

Minimum and maximum estimates of the volume searched for each search mode are given. These extremum estimates are based on the direction of prey movement relative to the hydra.
Figure 11. A simulated result of the searching rate of a hydra which has been pre-fed with 3 *Artemia* nauplii, as a function of food deprivation. \( V_Y = 10,000 \text{ mm/minute}, \ V_{PF} = 100 \text{ mm/minute}, \) and \( D_MT = 0.0 \text{ mm}. \)

For reasons like those given in the legend of Figure 9, the situation here is for a lake dwelling hydra. Prey move much more quickly in this figure (10,000 mm/minute) than in Figure 9 (500 mm/minute).

Minimum and maximum estimates of the volume searched for each search mode are given. These extremum estimates are based on the direction of prey movement relative to the hydra.
The time which tentacle length takes to begin its rapid increase is variable (Figure 4). The time is a function of the amount of food pre-fed to the hydra. Equation II5 can be made to fit all levels of pre-feeding by adding to the exponent a variable representing the amount of food pre-fed to the test animals. This variable would delay the function without affecting its form when the function is finally executed.

It is assumed that when hydra are satiated, the variable to be added to the exponent equals zero. The value could be different from zero without affecting the subsequent argument. It was chosen equal to zero because this value was simplest to work with.

Suppose a hydra gets a meal which is sufficient only to return the hunger of the animal to some time of food deprivation, TFl, but not to satiation, time zero. The hydra does not search at rate \( \exp(a*0) \) but at rate \( \exp(a*TFl) \). At some time later, say T, the animal will be searching at the rate, \( \exp(a*TFl + a*T) \). This simply increments time by T units. The variable T is a variable of time since last meal, not of time since satiation.

A function of volume searched per unit time, from time of last meal to some time later, is as follows:

\[
\frac{dVS}{dT} = e^{a*TFl} \left[ e^{a*T} \right]
\]

By integrating II6 over T, from \( T=0 \) to \( T=TS \), we get an equation of the total volume searched by a predator from the time of last meal to some time TS later.

\[
VS(TS) = \frac{e^{a*TFl}}{a} \left[ e^{a*TS} - 1 \right]
\]

In this equation \( VS(0)=0 \).
The variable \( TFl \) is written as a function of hunger with the use of results from Holling (1966):

\[
TFl = \frac{1}{AD} \ln \left[ \frac{HK}{HK-HO} \right]
\]

The parameter \( HO \) is the hunger at time \( TFl \).

Substituting equation 118 for \( TFl \) in 117, we get

\[
\text{VS}(TS) = \left[ \frac{a*TS}{e - \frac{1}{a}} \right] \left[ \frac{HK}{HK-HO} \right] a/AD
\]

From equation 12 (\( NA = VS*NO \)), it follows that

\[
TS = \frac{1}{a} \ln \left[ \frac{a*NA*(HK-HO)}{NO*(HK)} + \frac{1}{a/AD} \right] a/AD
\]

If the terms for predator inefficiency are included as a means of reducing prey density (op. cit.), we have

\[
NO = NO*SR*SP*SS
\]

The parameter \( SR \) is the success of prey recognition, \( SP \) is the success of prey pursuit, and \( SS \) is the success of prey capture. When incorporated in 119, we get

\[
TS = \frac{1}{a} \ln \left[ \frac{a*NA*(HK-HO)}{NO*SR*SP*SS*(HK)} + \frac{1}{a/AD} \right] a/AD
\]
DISCUSSION FOR PARTS I AND II

The data base is the same for PARTS I and II. The objectives of PARTS I and II are related in some respects but are very different in other respects. PART I attempts to test a method for writing general functions. PART II attempts to formulate an explicit function for time spent searching (TS) by hydra.

A short review of searching by animals will open the discussion. Emphasis will be placed on the form of the volume searched function. This function plays a dominant role in determining the form of the function for time spent searching (TS). This review will be followed by evidence concerning the dynamic response relationships of searching modes for several species. A discussion of optimality and strategic models will terminate this section. In PART I it was mentioned that previous authors have used strategic hypotheses in writing general functions. The work of these scientists will be reviewed in the discussion.

Searching by Animals. In this thesis, searching invariably means searching through volume. Searching by changing location and thereby changing prey density is not considered. (Its omission is not meant to reflect on its importance relative to searching through volume.)

Searching and locomotion have often been treated as closely related (De Ruiter, 1967). This relationship was once elevated to pedantic levels (Campbell et al., 1966). The classical notion was that locomobile activity is driven by some discomforting activity, called drive. Campbell et al. (1966) compared the activity of a number of
species as a function of the time of food deprivation. Various methods of measuring locomobile activity were used. Stabilmeter activity was measured. The results showed that chicks increase their activity with increasing hunger; that hamsters move about at the same rate until 7 hours of food deprivation and then move at a decreasing rate; and that guinea pigs and rabbits show a continual drop in activity with increasing time of food deprivation. However, when wheel activity was measured, it was found that guinea pigs and hamsters increased their activity for a while (Figure 12). The authors conclude that "the range and variety of stimuli which elicit activity ... vary enormously from species to species as a result of evolutionary development" (their page 127). This conclusion is important in that it warns against taking too narrow a view of searching. It is also relevant to my thesis as it supports a major contention: that tactical approaches are unlikely to yield as much generality as strategical approaches.

Pianka (1966) refers to those animals which do not move when searching for prey as "sit-and-wait" predators. These types of animals have also been referred to as "ambush" predators (Holling, 1966). Examples of such species are some hawks (Haverschmidt, 1962), lizards of the family Iguanidae (Pianka, 1966), and dragonfly larvae, mantids, certain spiders, frogs, and chameleons (Pritchard, 1965).

Mantids effectively search through increasing amounts of volume by increasing their distance of reaction to prey with increasing hunger. If the reactive distance is designated as $r_0$, then the area searched by the mantid is $0.8064 r_0^2$ (Holling, 1966). The area searched as a function of time of food deprivation follows from a description of
Figure 12. Median activity of chicks, rabbits, guinea pigs, and hamsters as a function of days of deprivation (from Campbell et al., 1966).
\( r_0 \) as a function of time of food deprivation (TF). The area searched then becomes \( 0.8064 \times G^2 \left[ -HT + HK(1 - \exp(-AD \times TF)) \right]^2 \) for hunger greater than the threshold HT (op. cit.). For hunger less than HT, the area searched is zero. The form of the area searched function, from satiation to some time of food deprivation, might be suitably described by an exponential function and then a linear function \( = 0.8064 \times G^2 (HK - HT)^2 \). This means that searching by mantids might be adequately described for some purposes by equation II5.

The attempt to fit the mantid data to equation II5 points to a shortcoming of the strategic method of writing general functions. The method does not incorporate a specific and testable explanation. Arguments are devised to predict certain characteristics of a relationship. However, in the case of the volume searched strategy the characteristics were not sufficient to permit choice among a number of descriptive equations. The form of a relationship can be predetermined from strategic arguments. Realism of the parameters cannot be attained. This means that when the predicted equation is tested for a number of species, it must be treated almost as an empirical equation.

Data useful to our purpose on the searching biology of other sit-and-wait predators is not available. Haverschmidt (1962), in describing some natural history of the Grey Hawk \((Butea nitidus)\), notes that it "hunts lizards mostly as a 'still hunter' from a perch". He also refers to the Laughing Falcon \((Herpetotheres cachinnans)\) as a "still hunter". Kennedy (1956) notes a few observations made regarding the Rusty Lizard, \(Sceloporus olivaceus\). In the morning and evening the lizard climbs onto a tree trunk and looks down, chasing after prey when they happen by. Pianka (1966) notes that the Iguanid lizard, \(Callisaurus\),
stands up on its forelegs, thereby increasing "the area covered and maximizing the efficiency of utilization of the open spaces".

Those animals which do move when searching for food might be referred to as active predators. *Drosophila melanogaster*, an active searcher, has been studied by Haynes and Sisojević (1966). They starved flies from birth through to death and measured an index of the actual volume swept by the flies by recording the number of contacts with an artificial spider (their Figure 20). The data followed a monotonically increasing function which rose at an increasing rate with time: at 0 hours of food deprivation the number of contacts was less than one; at 24 hours, equal to one; at 48 hours, between one and two; at 70 hours, about 13; and at 72 hours, about 23. Death occurred at about 72 hours.

Another dipteran, *Phormia*, has been extensively studied from a viewpoint relevant to my studies (see Dethier, 1969; Green, 1964). Dethier (1969; page 254) cites earlier work by Green to the effect that under conditions of constant light and of starvation, an emerging fly is more or less quiescent during the first 72 hours. "At 72 hours activity begins in earnest, increases to a maximum at 84-94 hours, then begins to wane, foreshadowing death." The results are similar to those obtained for *Drosophila*, except that *Phormia* do not die at the maximum rate of searching. My model of time spent searching (TS) is likely to be applicable to *Phormia* only during the first 80% of the starvation response.

A second searching mode used by *Phormia* involves the acceptance threshold of the fly to various concentrations of sugar solutions (Dethier, 1969). Lowering of the acceptance threshold of the feeding response is in effect increasing the reactive distance; thus, it is
analogous to increasing the visual distance of the mantid. Evans and Dethier (see Figures 24-27 of Dethier, 1969) have measured changes in glucose and fucose (6-desoxygalactose) thresholds as functions of time of food deprivation, following satiation on glucose (Figure 24), on fucose (Figure 25), on mannose (Figure 26), and on lactose (Figure 27). In the first test a linear decrease over time was found; in the second and fourth tests approximate negative exponentials were found; and in the third test a threshold that kept its value for a time and then fell quite rapidly was found. In all cases the threshold fell with time of food deprivation. It is assumed that the acceptance threshold is inversely related to the distance of reaction. The volume searched is a cubic function of the reactive distance. Thus we might expect that the volume searched is an accelerating function of time of food deprivation.

The threshold of initiation for the first searching mode used by Phormia depends upon the type of food given to the fly. It is zero hours for the change in glucose acceptance threshold when the fly is pre-fed with glucose and 10-20 hours for the fucose threshold when the fly is pre-fed with fucose. The initiation threshold for the locomobile searching mode is about 72 hours, when the flies are fed to repletion on 1M sucrose.

The acceptance threshold varies less than one order of magnitude with hunger, whereas activity varies up to three orders of magnitude with hunger. It appears that the major searching component is locomotion. The overall searching rate function might well be described by equation II.5. However, this brief consideration of searching by Phormia by no means proves this to be the case.
A few pages back, I noted my expectation that the steady state searching rate be related to hunger in a manner similar to that hypothesized for the dynamic responses. This expectation was not verified in the case of the minimal effect data for hydra. One explanation which may account for this discrepancy follows from the observation that hydra search not only be covering volume but also by changing locations. By changing locations, the hydra may increase the density of prey organisms which they contact. Walking and floating may serve this role in addition to that of searching through volume. If two strategies are interacting, then this fact suggests the need to study more than one strategy at a time.

We now turn to the question of the dynamic response relationship. Ideally, it should be checked for a wide variety of species other than hydra. Unfortunately, although much has been written about searching in a variety of species, it is usually not possible to calculate the duration of the dynamic responses.

One exception is the work on the blowfly by Dethier and co-workers (Dethier, 1969). They found that the duration of the dynamic response of the glucose threshold, following ingestion of 2.0 M glucose, is about 60 hours. They found that the duration of the dynamic response of the fucose threshold, following ingestion of 1.0 M fucose, is about 25 hours. They tested a number of combinations of sugars - eg., pre-fed mannose, tested fucose threshold - and got a number of responses. Dethier cites a paper by Green (1964) in which is given a figure of the activity of Phormia after being fed various amounts of sucrose. The duration of the dynamic response of activity as a function of time of food deprivation is 40 to 50 hours. Dethier notes in his paper that the threshold search mode is initiated at lower hungers than the activity mode. Comparison of the glucose threshold to the sucrose activity data shows
that the dynamic response of the former is 60 hours long and that the dynamic response of the latter is 40 to 50 hours long. This is as predicted. Comparison of the fucose threshold to the sucrose activity data shows that the dynamic response of the former is 25 hours long and that the dynamic response of the latter is 40 to 50 hours long. This is not as predicted. It is unfortunate that the same sugars were not used in conducting both the threshold and the activity tests.

Strategical Models. It was noted in the section referred to as THE PROPOSAL that previous attempts have been made at using strategical, or related, concepts in model building. Space prohibited their discussion in that section.

The strategical approach is inherent in the philosophy of many biologists: that nature is purposive. This view has been used in asking the question: if some hypothetical behaviour can be defined - and an example of it found in nature - can statements be made about it which will apply to the animals which use this behaviour?

Such biologists as Rashevsky (1961) and Rosen (1967) stress the importance of optimality principles in biological systems. Strategical models as proposed in this thesis express ideas that have been previously pointed out by these authors. Rosen (1967) writes that "in order to find an optimal solution to a particular design problem, three things ... are required: (a) to determine the class of all possible solutions to the problem, (b) to assign to each such solution a certain number, which represents the cost it involves, and (c) to search among the set of costs to find that which is least".

Although Rosen does write optimality models, he does not deal with strategic models. The difference between these two approaches has to
do with the way in which the problem is formulated. Rosen uses a
tactical formulation. He describes a problem in a mechanistic way and
then applies optimality principles to this description.

Bioengineers have used optimization technologies in the biomedical
area. Experimental observation has been shown to relate well to theoretical predictions based on the minimization of performance criteria based
on energy (power consumption) or on force (total muscular effort; average inspiratory force). Some examples are given in Milsum's (1966) book. The examples are all at the physiological level of biological complexity.

To my knowledge, one of the earliest attempts at writing not only optimality, but strategic models of ecological systems is by MacArthur and Pianka (1966). This coincided with a paper by Emlen (1966) on the same subject. These models are called strategic because each of them defines a goal or strategy for the animal; both papers optimize time and energy budgets for a predator feeding on a range of prey types. MacArthur and Pianka consider only time, in terms of searching and pursuing time of prey in a fine-grained environment and in terms of hunting and travelling time in a coarse-grained environment. Emlen proposed an abstract model which suggests that a predator will continue to eat increasing types of prey so long as the energetic returns are positive. Thus, the original approaches to strategic models tried to partition prey types to a predator feeding optimally in terms of energy and time variables.

This approach has been continued up to and including a recent work: Schoener (1971). In his review of strategic models of feeding, Schoener expands the range of optimal models from the previous area of optimal diet to three other areas - optimal foraging space, optimal
feeding period, and optimal foraging-group size.

The strategic models reviewed by Schoener present a number of predictions in areas of ecological concern. Since Schoener's (1971) review is quite up-to-date, we will work from his article. The most well thought out area is that of optimal diet, with some strategic work completed in the area of optimal foraging space. No formal theory has been worked out for optimal placing of feeding periods over the activity cycle and only qualitative hypotheses exist for optimal foraging-group size. Within the area of optimal diet, predictions cluster into categories of "range of items eaten" by an animal; "food size and distance from the predator"; and "optimal kinds of feeders". Within the area of optimal foraging space, predictions cluster into categories of "home range size", "patch utilization", and "home range overlap and defense". We discuss the major deductions in each of these categories:

1) Range of items eaten - Models by MacArthur and Pianka (1966), Emlen (1966), Schoener (1971), and others all predict that the lower the absolute abundance of food, the greater the range of items (prey types) taken. Schoener (1971) reviews supporting evidence found in fish, weaverbirds, blackbirds, swifts, and Conus molluscs.

MacArthur and Pianka (1966) suggest that if some kinds of items are reduced differentially, then the range of items taken either increases or remains the same. Using his model, Schoener reaches the same conclusion. Oriens and Horn (see Schoener, 1971) have some indirect evidence for this contention.

Finally, Schoener's model predicts that an increase in the energy requirements of an animal has the same effect as a decrease in food density on selectivity. Schoener notes that birds select large prey from the habitat to feed young, and that the number of small prey brought
to the nest may increase with brood size. Hunger is proposed as the short term mechanism whereby animals monitor small temporal perturbations in food availability.

2) Food size and distance from the predator - Schoener's models predict that "Food sizes should decrease with decreasing predator size, but asymptotically"; that "A predator at a given distance should take prey both larger and smaller than any at a greater distance, but the large size limit should decline less with increasing distance than the small size limit should increase"; and that "Distributions of prey sizes eaten by a predator from a uniform size-abundance distribution of available prey should be more negatively skewed ... if the predator pursues its prey over greater distances or is relatively large than if the predator pursues its prey less or is relatively small". Schoener presents some supporting evidence.

3) Optimal kinds of feeding - Discussion is limited to the relative merits of specialist versus generalist feeders, and of large versus small animals. Predictions are not explicitly stated.

4) Home range size - It is predicted that, if "home range size is proportional to maximum distance travelled for food for a vantage area", then "relatively efficient pursuers should have larger home ranges than others of the same size". The suggestion is made that this may be why mammals have smaller home ranges than similarly size birds.

5) Patch utilization - In this section a "compression hypothesis" has arisen: "when competitors differentially reduce food density, the range of patches utilized should shrink because some patches are then worse than others, but range of food types within patches should not decrease and in fact may expand".

6) Home range overlap and defence - If invasion rate is proportional
only to the density of the invaders, then if it is economical to defend a territory at a given food density, it is also so at all lower food densities. If invasion declines to a level proportional to food density, then an initial lowering of food density will favor switching from a lack of defense to defense, while a further lowering will result in switching back to no defense.

All of the predictions describe certain consequences of an individual organism, while looking for food and while defending its territory. The deductions are readily interpreted in terms amenable to field observation. They are in spheres of ecological concern — predation, home range. Thus these examples, unlike those in Milsum's (1966) book, are at the ecological level of biological complexity.

The strategic approach used by previous authors has concentrated heavily on energy and time, on cost-benefit types of economic analyses. The approach tends ultimately to be characterized in a function of cost per unit effort to achieve some goal. Yet "cost" is a multi-faceted concept and this feature has lead to difficulties. It is necessary in Schoener's (1971) model to determine the energetic costs of pursuit, and of handling and eating the prey. It is also necessary to know the number of calories that the animal can extract from a food item after having eaten it. These are difficult determinations, and some rather substantial simplifying assumptions (op. cit.) have been made in an attempt to express these quantities.

This thesis suggests that organisms not only act efficiently in the form of an integrated unit, but that all biological processes are, more or less, well-adapted. It is suggested that strategies can be defined at various levels. Low-level strategies are suggested as one way to avoid the nebulous formulations of previous strategic models.
Thus, even though searching is a component of the energy/time performance criterion of Schoener, it is considered in this thesis as an independent unit. It is suggested that searching "fitness" can be considered independently of the overall fitness of the animal.

It was suggested in the introduction to PART I that if one could guess the goal of some particular tactic(s) and list some of the major forces which have shaped its development, then various types of behaviour could be imagined. Some types would be more efficient in reaching the goal than others. The assumption was made that if the goal as defined were the only one which the species had to deal with, then the most efficient type of behaviour would be the one used. It was further assumed that the difference between predicted behaviour and observed behaviour relates to the degree to which the species has had to compromise optimality in one area for increased efficiency in a different one. A specific example was taken and the method was tried. By not contradicting the prediction, this test gave some assurance that compromise will not cloud the simple predictions made on the basis of a single strategy.

In review, we have shown how strategic hypotheses arose from optimality considerations. We have noted that strategic models have concentrated at the level of the individual. It has been suggested that one need not work only at this level. Now we talk briefly about some implications of this approach.

The notion behind my work is that ecological processes might be profitably studied by dealing with their parts. This is, of course, a view often expressed in experimental components analysis. By showing that strategic models exist and (may) have some validity at a number of biological levels, this thesis has provided another way of formulating general functions for use in a model built under the dictates of experim-
ental components analysis. This approach works at various levels of biological complexity. Its aim is to provide a detailed theoretical view of predation, useful at the ecological level. Yet the approach delves readily to the physiological level. Hunger (physiological level) and prey density (population level) are both variables in the same model (Holling, 1966). For the strategic approach to be useful in writing functions for experimental components analysis, it must be useful for the hunger variable as well as the prey density variable. Thus the implications of my work are closely bound up in those of experimental components analysis.
PART III

SENSITIVITY ANALYSIS OF A MODEL OF ATTACK.

INTRODUCTION

In this part, an attempt is made to deal with the problem of complexity. In the GENERAL INTRODUCTION it was noted that experimental components analysis produces such large and intricate models that complexity of the model becomes a problem in its own right. The technique to be proposed to deal with this problem is most easily applied if all functions in the simulation model are explicit; and PART II was aimed at making the time spent searching function (TS) explicit.

A frequently used method of learning about the properties of a simulation model is by doing a "sensitivity analysis". A model is simply run in enough different ways until an intuitive understanding of the model is obtained. A group of computer based search techniques is available to speed up the process (Watt, 1968). This approach is time consuming. It leads to difficulties in comparing one simulation model to another simulation model. This section will address itself to finding an analytical way of studying the sensitivity of a complex flow graph.

The attempt will relate quite specifically to the model of attack as given in Appendix IV. Only a brief discussion of the breadth of applicability of the method will be attempted.

The Approach. Engineers have dealt with computer simulation of complex systems longer than biologists. A survey was conducted of their techniques as they relate to the problem studied here. It was found
that a basic approach used by control systems engineers is reduction
of the block diagram to equation form (Watkins, 1969). The equations
are usually differential or difference equations. There is now a
large body of theory relating to these forms of equations. Consequently,
engineers have been able to find common ground between many diverse
types of simulation models.

Block diagram manipulation techniques are linear techniques.
Engineers often manufacture their parts to fit linear models.
Biologists are not so fortunate. A great deal of non-linearity
occurs in biological systems.

Some non-linearities can be dealt with in such a way as to
make block diagram manipulation techniques applicable. It is
possible to linearize around singular points (Watkins, 1969).
It is also possible to deal in certain ways with flow graphs which
are linear in all but a few elements (Chua, 1969; Kain, 1962; and
others). Unfortunately, block diagrams for biological systems
tend to be mostly non-linear, with a few linear elements. More
than this, biological models incorporate an additional kind of
problem. This problem has been called a "threshold effect" (Holling,
1965). Our functions are, at best, "piecewise continuous".

Engineers have dealt with an analogous situation by dealing with
switches. They have developed certain tricks, but not much theory,
to deal with switches. The language used is Boolean Algebra (see

I assume that it would be desirable to reduce biological flow
graphs to equation form. The model of attack given in Appendix IV
is being considered in this PART. It is assumed that it would be
desirable to write an explicit equation for the attack rate (A),
one whose predictions are identical to those from the simulation model.

There are 10 conditional statements in the flow graph of the attack model. If each combination of these conditional statements were to produce a different attack rate function, then there would be $2^{10}$ different functions. This assumes no feedback exists in the model and that each conditional statement has only two outflowing paths. (Such a conditional statement would be an IF (a) $n_1, n_2, n_3$, where any two $n_i$ took the same value.) There is a great deal of feedback in the attack model. Thus the possibility is very real of far more than $2^{10}$ different functions.

Each combination of conditional statements does not produce a different attack rate function. The number is still likely to be large. Yet almost all attack rate functions result from changes in the intensity of the independent variable, hunger. These changes do not affect the parameters or the structure of the function.

Only those changes which result in structural modification in a function will be considered. All functions which are structurally different will be tabulated. From such tables it should be possible to extract some knowledge about the sensitivity of the simulation model.

An attempt was made to go through all the paths of the block diagram, writing the various forms of the attack rate function as they arose. Invariably, I became confused. It was difficult to determine when all the paths had been covered. Thus, an expression was developed which denoted all the potential paths through which flow can move through the block diagram. Then it became a simple job to go through all the paths, writing the various forms of the attack rate function as they arose.
Consider a block diagram, such as the one in Appendix IV, only in terms of its conditional statements. Then a resemblance to the classical linear flow graph can be seen. Operators, nodes, and paths are all identifiable.

The operators are not constants, but are inequalities. Each conditional statement has been decomposed into a number of inequalities, corresponding to the number of paths flowing from it. We let each inequality be viewed as a switch. When the inequality corresponds to the actual situation, the switch is considered to be closed. When it does not, the switch is considered to be open. Using Boolean Algebra, we may designate a closed switch by value one, and an open switch by value zero. In this way the operators of the "logical flow graph" become constants.

For example, in Appendix IV there is a conditional statement, reproduced in Figure 13. This statement can be decomposed into two separate inequalities: $TP > 0$ and $TP \leq 0$. When these inequalities are represented as switch-operators, the situation may be redrawn as in Figure 14. The state $TP \leq 0$ has been designated by the switch-operator $A$. The state $TP > 0$ has been designated by its complement function, $\overline{A}$. (Technical terms are used as explained in Wickes (1968) and Zehna and Johnson (1962).) The logical flow graph of Figure 14 is describable by the expression, $A + \overline{A}$. It describes the totality of paths through which flow may occur through to the a-node. The expression should be read as follows: for flow to reach the a-node, either the path through $A$ or through $\overline{A}$ must be used. The "or" referred to is the Boolean-OR. We will also have occasion to refer
Figure 13. A FORTRAN IF ... statement from the flow graph of Appendix IV.

Figure 14. An equivalent form for the conditional statement of Figure 13.

Figure 15. A logical flow graph, with operators A and B.
to the Boolean-AND.

The rest of this section will be used to introduce enough complexities to allow manipulation of the flow graph of Appendix IV. Consider the case drawn in Figure 15. This case is like that of Figure 14, except that there are a couple of repeated units. Flow through to the a-node is describable by the expression \((A + \overline{A}) \cdot (B + \overline{B})\), where the elevated dot is one symbol for the Boolean-AND. Often no AND symbol will be used; this is equivalent to the way which multiplication symbols are often omitted.

The form of this expression is called the "standard product form" (Wickes, 1968). Another form of this expression is \(AB + A\overline{B} + \overline{A}B + \overline{A}\overline{B}\). It is called the "standard sum form". The meaning of an expression is often more visible from the standard sum form. The above expression states clearly that flow may get to the a-node via the AB path, the \(A\overline{B}\) path, the \(\overline{A}B\) path, or the \(\overline{A}\overline{B}\) path. Because much use is made of complement functions in this expression, it is possible for flow to follow only one of these paths at a time.

The word "equation" has been fastidiously avoided in the above discussion. Boolean algebra has been used to define expressions, not equations. It is not my purpose to enumerate these expressions. They are to serve only as a short-hand description of the totality of paths through the model. The expressions should be treated more as sentences than as equations, more as symbolic language than as mathematics.

Case 2 introduces feedback. It is drawn in Figure 16. This flow graph, to the a-node, is describable by the expression, QDC. The path QDC is not realized because if flow ever entered the \(\overline{C}\) path, it would never emerge to the a-node. In this Figure
Figure 16. A logical flow graph, with operators Q, D, and C.

Figure 17. A logical flow graph, with operators Q, D, C, and E.
the state of a switch-operator is not allowed to change.

Now suppose that operators D and C may change their state, as a function of the number of times that flow passes around the feedback loop. Let the variable of iteration, or counter, be designated as i. Then we indicate that C and D are functions of i by writing $C_i$ and $D_i$. The set of i over which switch-operator C is closed will be called the domain of C. A like definition will be used for $D_i$.

We now consider the logical flow paths for the times when C is closed for $i=1, 2, 3, \ldots$. When C is closed for $i=1$, the appropriate expression is $QD_i=1C_i=1$. This statement may be read as: flow enters the graph and passes through the Q operator, the D operator for $i=1$, and the C operator for $i=1$ to get to the a-node.

When C is open for $i=1$ (and so $\overline{C}$ is closed for $i=1$) and C is closed for $i=2$, the appropriate expression is $Q\left[\prod_{i=1}^{2} D_i\right] \overline{C_i=1} C_i=2$. Boolean-AND's are implied between each term. The term for $D_i$ introduces a new symbol, $\prod$. It is used to AND a number of $D_i$'s. This term would be equivalent to writing $D_i=1D_i=2$. Much use will be made of this symbol in the next few pages. Nevertheless, the above expression reads: flow enters the system, passing through a closed Q operator-switch, a closed D operator-switch, and a closed $\overline{C}$ operator during $i=1$. As flow re-entered the forward path from the feedback loop, i was incremented to value 2. Flow then passed through a closed D operator and a closed C operator to reach the a-node.

When C is open for $i=1, 2, 3, \ldots$ but closed for $i=1$, the appropriate expression is $Q\left[\prod_{i=1}^{i=1} D_i\right] \overline{\prod_{i=1}^{i=1-1} C_i} C_i=1$. If $i=1$, then the $\overline{C}$ term is nonsensical; when this is the case, we define $\overline{C}$ to be closed.

Let the b-node of Figure 16 flow into the path of the a-node at a level beyond the C operator. Where C and D are not functions of i,
the appropriate expression is $Q_{DC} + Q_{D}$. Where $C$ and $D$ are functions of $i$, the appropriate expression is

$$Q \left\{ \sum_{i=1}^{i_1} D \right\} \left[ \sum_{i=1}^{i_1-1} C_i \right] C_{i=i_1} + Q_{D} \left\{ \sum_{i=1}^{i_2-1} D_i \right\} \left[ \sum_{i=1}^{i_2-1} C_i \right]$$

This expression states that the flow to the $a$-node follows if either operators $Q; D$ for all $i$'s, such that $1 \leq i \leq i_1$; $C$ for all $i$'s, such that $1 \leq i \leq i_1$; and $C$ for $i=i_1$ are closed, or operators $Q; \bar{D}$ for $i=i_2$; and $D$ and $\bar{C}$ are closed for all $i$, such that $1 \leq i \leq i_2$.

Two paths may thus be followed to the $a$-node. However, many more functions than two may be outputted at the $a$-node, depending upon the values of $i_1$ and $i_2$. That is to say, if flow goes out the $\bar{Q}D$ path and if the equation which is outputted at the $a$-node (and not shown, of course, in the logical diagram of Figure 16) is a recursion equation, then it will be structurally modified with each cycle through the $D\bar{C}$ feedback loop. Similar dependencies occur when flow emerges from the feedback loop to the $a$-node via the $QDC$ path.

Now we turn to consideration of the third and final case. This is where feedback loops occur within other feedback loops. A simple example is shown in Figure 17. Note that in this case $D_i$ might be a function of $j$ as well as of $i$. To indicate this, I will write $D_i$ as $D_{ji}$. To be completely accurate, one should write both the range of the $i$ and the $j$ values for which $D$ is closed. However, as the range of the outer $j$ loop will be specified in other terms, its statement here would be redundant. Thus $D_{ji}$ and $C_{ji}$ will specify the range of the $i$ values only. $E_{ji}$ will specify the range of the $j$ values.

As a first step to writing an expression for the flow graph of Figure 17, we recall that the feedback loop, QCD has already been described. (The loop specified as QDC is simply that loop that contains
the Q, D, and C operators.) The logic for the QDC loop is set as an operator-switch, \( X_{ji} \). Then the flow graph of Figure 17 becomes

\[
X \mathbf{E}_{ji} = \prod_{j=1}^{j_1-1} E_j. \]

If we substitute \( X_{ji} \) in this expression, we get the following expression:

\[
E_{ji} = \prod_{j=1}^{j_1-1} E_j \left\{ Q \left[ \prod_{i=1}^{i_2-1} D_{ji} \right] \left[ \prod_{i=1}^{i_1-1} C_{ji} \right] \right\} D_{ji, i=i_2-j} + Q \left[ \prod_{i=1}^{i_2} D_{ji} \right] \left[ \prod_{i=1}^{i_1} C_{ji} \right] C_{ji, i=i_2-j} \}
\]

In this expression, \( i_2 \) and \( i_1 \) are written as functions of \( j \) by writing \( i_2-j \) and \( i_1-j \). This means that the number of times through the feedback loop depends upon the number of times that flow has gone through the outer feedback loop.

These are the only techniques used in writing a complete expression for the totality of paths which flow may take through the attack model.
The first step is to set up the logical flow graph for the model of Appendix IV. This is given in Figure 18. In constructing the Figure, I have assigned individual IF ... statements labels such as described in the previous section. It has been necessary to define three counters or variables of iteration: i, j, k. The feedback loop that is designated by the counter j involves only the D, E, F, and G operators. It will be referred to as the DEFG loop. The HI loop is designated by counter k, while the ABCDEFGIJ loop is designated by counter i.

Consider the DEFG loop. There are three paths into this loop, viz., B, BC, and BC. They need not be considered at this stage. Likewise, the output from this loop will not be considered at this time.

The internal section of the DEFG loop can be collapsed to give the flow graph of Figure 19. In this graph \( \alpha_j \) is a function of operators \( \overline{D} \), \( E \), and \( F \). Assume that flow can emerge from the path \( \ldots G \) at \( j = j_2 \) or from the path \( \ldots D \) at \( j = j_1 \). Output from the loop is thus describable as follows:

\[
G_j = \sum_{j=1}^{j_2} \left[ \frac{j_2 - 1}{j - 1} \overline{G}_j \right] \left[ \frac{j_1 - 1}{j - 1} \overline{\alpha}_j \right] + \sum_{j=1}^{j_1} \left[ \frac{j_1 - 1}{j - 1} \overline{G}_j \right] \left[ \frac{j_1 - 1}{j - 1} \overline{\alpha}_j \right]
\]

The \( \alpha_j \) are structurally the same in each term, but have differing domains. If we elaborate on these terms, we get the following expression:
Figure 18. The logic for the flow diagram of Appendix IV.
Figure 19. The logic for the DEFG part of the flow graph of Appendix IV.
The expression completely describes the logic of the DEFG loop. Note the complex, $\overline{E} + EF + Ef$ above. The domains are from 1 to $j_2$ for the first appearance and from 1 to $j_{l-1}$ for the second. The first appearance of this complex should be read: for $j=1$ either $E$, or $\overline{EF}$, or $\overline{EF}$ must be closed; and for $j=2$ again; and for $j=3$ again, etc. The point is that if $E$, say, is closed for $j=1$, it need not be closed for all larger $j$.

We now consider the HI loop. Because of the way in which the DEFG loop was treated, there is only one path into the HI loop. This is via the above expression. In the HI loop only the $H$ operator is a function of the iteration variable, $k$. The operator $I$ is a constant. There are two paths from the HI loop. The $I$ controlled path is described by the expression $H_{k=1}I$. The operator-switch $H$ is closed only for $k=1$ because $I$ is a constant - for any program, $I$ is either open or closed. The other path is appropriately described by the expression $H_{k=1}I$. This is not entirely true, for when $k=1$, the state of $I$ is irrelevant. To show this, I let the condition $I$ be written as $H_{k=1}I$, without the subscript $k$. An expression for the HI loop follows by OR'ing the two statements:

\[
H_{k=1}I + H_{k=1}I
\]
A simpler flow graph of the attack model may now be drawn
(Figure 20). That part of the flow graph within the \( i \)-loop may be
written without definitions of domains as \( (A + A)(BC + BC + B) \beta_j \gamma_k \).
The problem of nested loops is met here for the first time. Recall
that the method needed to deal with this problem was developed as
the last step of the previous section. Applying the rules developed
there, we get the expression:

\[
\begin{align*}
J_{i=1} & \left[ \frac{i-1}{i} \mathbf{J} \right] \beta_{ij} \gamma_{ik} \left\{ \left[ \frac{i}{i} A \right] + \left[ \frac{i}{i} A_i \right] \right\} \left\{ \left[ \frac{i}{i} B \right] + \right. \\
& \left. \left[ \frac{i}{i} B \right] \right\} \left[ \frac{i}{i} C \right] + \left[ \frac{i}{i} B_i \right] \left[ \frac{i}{i} C_i \right] 
\end{align*}
\]

This expression is a complete description of the logic contained
in the flow graph of Appendix IV. A more useful form would be with
\( \beta_{ij} \) and \( \gamma_{ik} \) written out in full. When this is done we have the
following Boolean expression.

\[
\begin{align*}
J_{i=1} & \left[ \frac{i-1}{i} \mathbf{J} \right] \left\{ \left[ \frac{i}{i} \mathbf{H} \right] + \mathbf{H} \right\} \left\{ \left[ \frac{i}{i} \mathbf{H}_{ik} \right] + \mathbf{H}_{ik} \right\} \\
& \left\{ \left[ \frac{i}{i} \mathbf{G}_{ij} \right] + \mathbf{D}_{ij} \right\} \\
& \left\{ \left[ \frac{i}{i} \mathbf{F}_{ij} \right] + \mathbf{E}_{ij} \right\} \\
& \left\{ \left[ \frac{i}{i} \mathbf{F}_{ij} \right] + \mathbf{E}_{ij} \right\} \\
& \left\{ \left[ \frac{i}{i} \mathbf{A}_i \right] + \left[ \frac{i}{i} \mathbf{A}_i \right] \right\}
\end{align*}
\]
Figure 20. The logic for the flow diagram of Appendix IV. The DEFG and HI parts are modified from the form given in Figure 18.
DEDUCTIONS

The logic-expression developed in the previous section will be used to direct the search for the various forms of the attack rate function. The method which will be used to find the various forms of the attack rate relates to the way in which the logic-expression has been written. It is in the standard product form, where each "term" is surrounded by braces. There are five of these terms: an A term, a BC term, a DEFG term, an HI term, and a J term.

The various paths of the J term will be checked against the block diagram of Appendix IV in order to determine their relevance with respect to changing the form of the attack rate function. If this term is not relevant then it will be omitted from further considerations. We will proceed to the HI term. This procedure will be continued through to the A term. Whenever a distinct form of the attack rate function is found, the form and its accompanying logic will be recorded and tabulated. This explains the procedure.

The use of this procedure will now be considered. The attack rate is a linear combination of the TD, TS, TP, and TE functions. Each of these functions will be considered separately and then together.

Consider the TD variable. The J term regulates only the hunger, the independent variable. It does not affect TD structure. A study of the block diagram reveals that the next term, the HI loop, does affect the form of the TD function. There are two paths out of the HI loop (see the two OR'ed terms of the logic-expression). The function generated when flow passes as \( H_{i,k=1}^{1} \) is the same as that which enters the HI loop. Call this TD as TD\((k=1)\). On the other hand, the second path through the HI loop generates a function that
depends on the value of \( k_{l_1} \) according to the following equation:

\[
TD(k=1) + (k_{l_1}-1) \times \text{RECAD} \times \text{LN} \left( \frac{HK}{HK-HTE} \right)
\]

The obvious task is to determine the various forms of \( TD(k=1) \). We thus move to the next term of the logic-expression, the DEFG term. But \( TD \) is not considered here and so we go on to the BC term. It is also not relevant. The A term, however, is of importance. Here we find that \( TD(k=1) \) can take two forms: 0 and \( \text{RECAD} \times \text{LN} \left( \frac{HK-HO}{HK-HTE} \right) \). Each of these two functions must be combined with those of the HI loop to produce four forms of the TD function. The logic which controls the generation of each form of TD is readily obtained by AND'ing the appropriate HI logic with the appropriate A logic, as implied by the standard product form of the logic-expression. From this we obtain a list of functions and the logic appropriate to each function (Table V). In this table the HO variable has been changed to H; this variable is meant to designate some undefined value of hunger. (The variable H used in one place may or may not equal an H used in some other place.)

We now turn to the TS function. TS is first defined in the DEFG loop. In this function, SP is not a constant. SP is defined in various forms in both the DEFG and the BC terms. Regardless of where SP is defined, it always has two forms. When these forms are included two forms of the TS function emerge. These forms, along with the controlling logic, are given in Table VII. Also in this table a slight novelty was introduced: we write \( D_{i_1,j_1} = j_{l_1} \geq 1 \). This says that operator \( D \), as a function of \( i \) and \( j \), is closed for some \( i \) values and for some \( j \) value equal to \( j_{l_1} \), such that \( j_{l_1} \) is greater than one.
Table VI. The various forms, with controlling logic, of the function of time spent in digestive pause (TD) included in the attack model.

<table>
<thead>
<tr>
<th>FUNCTION GENERATED</th>
<th>CONTROLLING LOGIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. $\text{RECAD*LN} \left[ \frac{\text{HK-H}}{\text{HK-HE}} \right]$</td>
<td>$A_{i=1}^{i=1} H_{i,k=1}^i$</td>
</tr>
<tr>
<td>2. 0</td>
<td>$A_{i=1}^{i=1} H_{i,k=1}^i$</td>
</tr>
<tr>
<td>3. $\text{RECAD<em>LN} \left[ \frac{\text{HK-H}}{\text{HK-HE}} \right] + (k_{11} - 1) \text{RECAD</em>LN} \left[ \frac{\text{HK}}{\text{HK-HE}} \right]$</td>
<td>$\bar{A}<em>{i=1}^{i=1} H</em>{i,k=1}^i$, $k_{1}^{1-1}$ $H_{i,k}^i$ $k_{2}^{1-1}$ $I_{i,k}^i$</td>
</tr>
<tr>
<td>4. $(k_{11} - 1) \text{RECAD*LN} \left[ \frac{\text{HK}}{\text{HK-HE}} \right]$</td>
<td>$\bar{A}<em>{i=1}^{i=1} H</em>{i,k=1}^i$, $k_{1}^{i-1}$ $H_{i,k}^i$ $k_{2}^{i-1}$ $I_{i,k}^i$</td>
</tr>
</tbody>
</table>
Table VII. The various forms, with controlling logic, of the function of time spent searching (TS) included in the model of attack.

<table>
<thead>
<tr>
<th>FUNCTION GENERATED with CONTROLLING LOGIC</th>
</tr>
</thead>
</table>

1. \[ \frac{1}{a} \ln \left( \frac{a^{*}N^{*}(H-K-H)}{N^{*}S^{*}R^{*}S^{*}S^{*}(H-K)} \right) + 1 \]

\[ D_{i,j} = \begin{cases} \frac{j_{2i} - 1}{\hat{T} \hat{T}} G_{i,j} + \frac{1}{\hat{T} \hat{T}} \bar{E}_{i,j} \bar{F}_{i,j} \quad \text{if } j_{1i} > 1 \\ \frac{j_{2i} - 1}{\hat{T} \hat{T}} \bar{D}_{i,j} \quad \text{otherwise} \end{cases} \]

2. \[ \frac{1}{a} \ln \left( \frac{a^{*}N^{*}(H-K-H)}{N^{*}S^{*}R^{*}S^{*}S^{*}(H-K)} \right) + 1 \]

\[ D_{i,j} = \begin{cases} \frac{j_{2i} - 1}{\hat{T} \hat{T}} G_{i,j} + \frac{1}{\hat{T} \hat{T}} \bar{E}_{i,j} \bar{F}_{i,j} \quad \text{if } j_{1i} > 1 \\ \frac{j_{2i} - 1}{\hat{T} \hat{T}} \bar{D}_{i,j} \quad \text{otherwise} \end{cases} \]
We now turn to the TP function. As with the previous function, TP is determined in the DEFG and the BC paths. There are two forms, given in Table VIII.

We now turn to the TE function. As for all previous functions, the J term does not affect the form of TE. The HI complex does. If the $h_{1,k=1}I$ path is used, then $TE = -RECAD*LN\left[\frac{HK-RECAD/AKE}{HK-RECAD/AKE-H}\right]$. If the other path is chosen, then a number of possible functions seem to be generated according to the function:

$$-(k-1)*RECAD*LN\left[\frac{HK-RECAD/AKE}{HK-RECAD/AKE-H}\right] + AKE*W + (k-1)*RECAD*LN\left[\frac{HK-RECAD/AKE}{HK-RECAD/AKE-H}\right]$$

The first and third terms cancel out, leaving only $AKE*W$. Thus there are only two forms of TE, shown with the logic appropriate to each in Table IX.

The various forms and controlling logic have now been described for each of TD, TS, TP, and TE. The logic may be combined into sets, to give the various types of attack rate functions. The results are shown in Table X. In this table TS1 refers to equation 1 of Table VII, whereas TP2 refers to equation 2 of Table VIII, etc. There are eight types of functions of the attack rate included in the simulation model of Appendix IV.

It is towards the development of Table X that the work has been directed. If the procedure developed is to be useful, then insight into the operation and control of the attack rate should be available through the use of information presented in this table.

The first four functions of Table X differ in logical control from the last four by the behaviour of the HI loop. (More specifically,
Table VIII. The various forms, with controlling logic, of the function of time spent pursuing prey (TP) included in the attack model.

<table>
<thead>
<tr>
<th>FUNCTION</th>
<th>GENERATED</th>
<th>CONTROLLING LOGIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. TX</td>
<td>same as for TS1 @</td>
<td></td>
</tr>
<tr>
<td>2. $TX + \frac{KA\times HONP\times (L + EYE)\times (H-HTP)}{VP} - DS$</td>
<td>same as for TS2</td>
<td></td>
</tr>
</tbody>
</table>

@ Since this table was constructed, it has been discovered that the logic for TP is not exactly the same as that for TS. In term 2 of TS1, the expression, $E + EF$, holds for $j=j_{2i}$, and not for $j=j_{2i}-1$. In term 2 of TS2, the expression, $EF$, holds for $j=j_{2i}$ and not for $j=j_{2i}-1$. 
Table IX. The various forms, with controlling logic, of the function of time spent eating the prey (TE) included in the model of attack.

<table>
<thead>
<tr>
<th>FUNCTION GENERATED</th>
<th>CONTROLLING LOGIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. (-\text{RECAD}^*\text{LN}\left[\frac{\text{HK-RECAD/AKE}}{\text{HK-RECAD/AKE-H}}\right])</td>
<td>(H_{i,k=1}^{1})</td>
</tr>
<tr>
<td>2. (\text{AKE}^*W)</td>
<td>(\overline{H}<em>{i,k=k</em>{1}}^{1}\left[\frac{k_{1}^{1}}{l_{1}^{1}} H_{i,k=1}^{1}\right])</td>
</tr>
</tbody>
</table>
Table X. The various forms of TI. The attack rate (A) is defined as 24/TI.

FUNCTION GENERATED

1. $\text{RECAD}^*LN \left( \frac{(HK-H) (HK-\text{RECAD}/\text{AKE}-H)}{(HK-\text{HTE}) (HK-\text{RECAD}/\text{AKE})} \right) + TS_1 + TX$

2. $\text{RECAD}^*LN \left( \frac{(HK-H) (HK-\text{RECAD}/\text{AKE}-H)}{(HK-\text{HTE}) (HK-\text{RECAD}/\text{AKE})} \right) + TS_2 + TP_2$

3. $-\text{RECAD}^*LN \left( \frac{HK-\text{RECAD}/\text{AKE}}{HK-\text{RECAD}/\text{AKE}-H} \right) + TS_1 + TX$

4. $-\text{RECAD}^*LN \left( \frac{HK-\text{RECAD}/\text{AKE}}{HK-\text{RECAD}/\text{AKE}-H} \right) + TS_2 + TP_2$

5. $\text{RECAD}^*LN \left( \frac{HK-H}{HK-\text{HTE}} \right) + (k_1 - 1) \text{RECAD}^*LN \left( \frac{HK}{HK-\text{HTE}} \right) + AKE^*W + TS_1 + TX$

6. $\text{RECAD}^*LN \left( \frac{HK-H}{HK-\text{HTE}} \right) + (k_1 - 1) \text{RECAD}^*LN \left( \frac{HK}{HK-\text{HTE}} \right) + AKE^*W + TS_2 + TP_2$

7. $\text{RECAD}^*(k_1 - 1) \text{LN} \left( \frac{HK}{HK-\text{HTE}} \right) + AKE^*W + TS_1 + TX$

8. $\text{RECAD}^*(k_1 - 1) \text{LN} \left( \frac{HK}{HK-\text{HTE}} \right) + AKE^*W + TS_2 + TP_2$

CONTROLLING LOGIC

1. $A_{i=1}^{H_i,k=1} \left\{ D_{i,j=1} \left( B_{i=1}^{i=1} + \bar{B}_{i=1}^{i=1} \right) \right\} + \ldots \text{ see TS}_1 \text{ logic}$

2. $A_{i=1}^{H_i,k=1} \left\{ D_{i,j=1} \bar{B}_{i=1}^{i=1} \bar{C}_{i=1}^{i=1} \right\} + \ldots \text{ see TS}_2 \text{ logic}$

3. $\bar{A}_{i=1}^{H_i,k=1} \left\{ D_{i,j=1} \left( B_{i=1}^{i=1} + \bar{B}_{i=1}^{i=1} \right) \right\} + \ldots$

4. $\bar{A}_{i=1}^{H_i,k=1} \left\{ D_{i,j=1} \bar{B}_{i=1}^{i=1} \bar{C}_{i=1}^{i=1} \right\} + \ldots$
Table X continued.

5. \( A_{i=il} H_{i,k=kl} \left( \sum_{k=1}^{kl-1} I_{ik} \right) \left( \sum_{k=2}^{kl} I_{ik} \right) \) \( D_{i,j=1} \left( B_{i=il} + B_{i=il} C_{i=il} \right) + \ldots \)

6. \( A_{i=il} H_{i,k=kl} \left( \sum_{k=1}^{kl-1} I_{ik} \right) \left( \sum_{k=2}^{kl} I_{ik} \right) \) \( D_{i,j=1} \left( \bar{B}_{i=il} + \bar{B}_{i=il} C_{i=il} \right) + \ldots \)

7. \( A_{i=il} H_{i,k=kl} \left( \sum_{k=1}^{kl-1} I_{ik} \right) \left( \sum_{k=2}^{kl} I_{ik} \right) \) \( D_{i,j=1} \left( B_{i=il} + B_{i=il} C_{i=il} \right) + \ldots \)

8. \( A_{i=il} H_{i,k=kl} \left( \sum_{k=1}^{kl-1} I_{ik} \right) \left( \sum_{k=2}^{kl} I_{ik} \right) \) \( D_{i,j=1} \left( \bar{B}_{i=il} + \bar{C}_{i=il} \right) + \ldots \)

@ The foot-note to Table VIII (page 106) changes this table. The forms of TI are not 8, as given, but 16. Table X was constructed under the assumption that TP logic and TS logic are identical. Thus TS1 logic occurred in association with TP1 logic and TS2 logic occurred in association with TP2 logic. The modifications necessary to correct this table are: to change TI1 by letting TP2 replace TP1, and then adding this equation as a new form of TI; to change TI2 by letting TP1 replace TP2, and then adding this equation as a new form of TI; and so on through TI8.

The rest of this section does not incorporate this change. The section is valid in so far as it goes. The effects of the additional 8 forms are ignored, of course.
the first differs from the fifth, the second differs from the sixth, etc.) The logic describing that path through the HI loop that generates TE2 (Table IX) may be stated as follows - if for some captured prey, the predator is hungry enough to eat the complete prey all at once; or if not, eat all it can, leaving to digest the food, but returning to the carcass to eat again and again until the prey is completely consumed and then going away for good.

Thus there are two distinct tactics included in this model. This is an interesting characteristic of the model since it increases the breadth of applicability by introducing various cases, control being channeled to the appropriate case by a switch (I) which is not a function of any variable of iteration.

This characteristic has been noted, among other reasons, to illustrate how one can begin to break up an otherwise complex model into cases. Logical sets of attack rate equations 1, 2, 5, and 6 could be compared to the set of 3, 4, 7, and 8 equations. In this case the division is on the basis of types of functions of time spent in digestion (TD). In the first set, the predators do spend some time digesting food; in the second case, they do not. The animals operating under 1, 2, 5, and 6 equations might be less prone to predation. The effects of predation on the predator might well be studied from the first set of equations.

One might study the possible effects of changes in parameter values on the value taken by the attack rate. It might be of interest to know which parameters occur in which functions and which are held in common in all functions, as well as the purpose the parameters fill in the functions. In Table XI the first two points are answered. Only the parameters HK, AD, AKE, TX, a, NO, SR, and SS are parts of all forms of the attack function. In fact, the last four parameters relate only
Table XI. The parameters of the attack rate, by type of function.

An X designates the presence of the parameter in the model of a certain number.

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>MODEL NUMBER</th>
<th>PARAMETERS IN COMMON</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1  2  3  4  5  6  7  8</td>
<td></td>
</tr>
<tr>
<td>HK</td>
<td>X X X X X X X X</td>
<td>X</td>
</tr>
<tr>
<td>HTE</td>
<td>X X X X X X X X</td>
<td>X</td>
</tr>
<tr>
<td>AD (RECAD)</td>
<td>X X X X X X X X</td>
<td>X</td>
</tr>
<tr>
<td>AKE</td>
<td>X X X X X X X X</td>
<td>X</td>
</tr>
<tr>
<td>k l i</td>
<td>X X X X X X X X</td>
<td>X</td>
</tr>
<tr>
<td>W i l</td>
<td>X X X X X X X X</td>
<td>X</td>
</tr>
<tr>
<td>TX</td>
<td>X X X X X X X X</td>
<td>X</td>
</tr>
<tr>
<td>a</td>
<td>X X X X X X X X</td>
<td>X</td>
</tr>
<tr>
<td>NO</td>
<td>X X X X X X X X</td>
<td>X</td>
</tr>
<tr>
<td>SR</td>
<td>X X X X X X X X</td>
<td>X</td>
</tr>
<tr>
<td>SS</td>
<td>X X X X X X X X</td>
<td>X</td>
</tr>
<tr>
<td>AM</td>
<td>X X X X</td>
<td></td>
</tr>
<tr>
<td>KA</td>
<td>X X X X</td>
<td></td>
</tr>
<tr>
<td>HONP</td>
<td>X X X X</td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>X X X X</td>
<td></td>
</tr>
<tr>
<td>EYE</td>
<td>X X X X</td>
<td></td>
</tr>
<tr>
<td>HTP</td>
<td>X X X X</td>
<td></td>
</tr>
<tr>
<td>DS</td>
<td>X X X X</td>
<td></td>
</tr>
<tr>
<td>VP</td>
<td>X X X X</td>
<td></td>
</tr>
</tbody>
</table>

1  0 1 0 1 1 1 1 1 1 0  number of parameters
9  9 7 8 6 1 9 1 9 8 parameters
to that part of the TS function held in common -

\[
\frac{1}{a} \ln \left( \frac{a^{a \cdot \text{NA} \cdot (\text{HK} - H)}}{\text{NO} \cdot \text{SR} \cdot \text{SS} \cdot (\text{HK})} + 1 \right)
\]

The parameter SP takes two values, dependent upon the logical control (Table VII). Thus SP was not incorporated in the above function.

HK and AD (=1/RECAD) parameters occur in common places within the function

\[
\text{RECAD} \cdot \ln \left( \frac{f_1(\text{HK}, H)}{f_2(\text{HK}, H)} \right)
\]

The parameter TX holds a common position in the various functions. However, AKE occurs in more than one place in the various functions.

Control of the value taken by the attack rate might be suitably achieved by concentrating attention on HK, AD, TX, a, NO, SR, and SS. The position of each is according to the following general form of the attack rate function:

\[
\text{TX} + \text{RECAD} \cdot \ln \left( \frac{f_1(\text{HK}, H)}{f_2(\text{HK}, H)} \right) + \frac{1}{a} \ln \left( \frac{a^{a \cdot \text{NA} \cdot (\text{HK} - H)}}{\text{NO} \cdot \text{SR} \cdot \text{SS} \cdot (\text{HK})} + 1 \right)
\]

The rate of digestion, AD, is directly related to the attack rate. The parameter TX, a hoarding parameter, has an inverse relationship with the attack rate. The parameter a, the searching rate parameter, also has a direct relationship with the attack rate. The parameter HK, the maximum hunger, has both direct and inverse relationships with the attack rate. It is also clear that parameters a, TX, and AD have the greatest effect on the above function. This is because all other parameters operate as arguments of log functions.

The value taken by the attack rate can also be influenced by
the level of the independent variable, hunger. The totality of types of hunger functions included in the block diagram are listed in Table XII. All types of hunger functions were listed in this table because the number of them is small.

Hunger has a simple direct relationship with each of TE, TS, and TP. The longer the predator pursues a prey, the longer it looks for a prey, and the longer it takes to eat the prey, the hungrier it will be after eating the prey. There is a direct relationship between AKE, the feeding rate, and hunger. There are both direct and inverse relationships between AD and hunger.

It is not only necessary to know how to control hunger, but to know how hunger affects the value of the attack rate. Looking back at Tables VI through IX, we find that hunger is directly related to TP2; inversely related to TD1 and TD3, to TS1, and to TE1; both directly and inversely related to TS2; and not related to TD2 and TD4, to TP1, and to TE2. Thus hunger can affect the attack rate in numerous ways. It is concluded that the response of the system to a directional change in hunger is not easily predictable.

It has been shown that the value of the attack rate is effectively modified by altering the values of the AD, a, and TX parameters. Yet the parameter AD has been shown to have both direct and inverse relationships with hunger. Thus the parameters a and TX are the basic ones that will elicit a predictable response that will show regardless of the state of the rest of the system.

This concludes the attempt at finding an analytical way of studying the sensitivity of a complex flow graph to changes or variation in its parameters. In conclusion, we attempt to use this technique in anticipating the form of simulated output and in helping to explain
Table XII. The totality of types of hunger equations outputted at the end of the i-loop of the attack model. Controlling logic is given.

**FUNCTION GENERATED**

1. \( 0 \)
2. \[
\begin{align*}
\text{HK-RECAD} & \left( 1-e^{\text{AD} \cdot \text{TE}} \right) + \left( \text{HO}(i-1) - \text{HK} \right) e - \text{AD}(\text{TP}+\text{TE}) \\
\text{AKE} & 
\end{align*}
\]
3. \[
\begin{align*}
\text{HK-RECAD} & \left( 1-e^{\text{AD} \cdot \text{TE}} \right) + \left( \text{HTE} - \text{HK} \right) e - \text{AD}(\text{TP}+\text{TE}) \\
\text{AKE} & 
\end{align*}
\]
4. \[
\begin{align*}
\text{HK-RECAD} & \left( 1-e^{\text{AD} \cdot \text{TE}} \right) + \left( \text{HO}(i-1) - \text{HK} \right) e - \text{AD}(\text{TS}+\text{TP}+\text{TE}) \\
\text{AKE} & 
\end{align*}
\]
5. \[
\begin{align*}
\text{HK-RECAD} & \left( 1-e^{\text{AD} \cdot \text{TE}} \right) + \left( \text{HTE} - \text{HK} \right) e - \text{AD}(\text{TS}+\text{TP}+\text{TE}) \\
\text{AKE} & 
\end{align*}
\]

**CONTROLLING LOGIC**

1. \( H_{i,k=1} \)
2. \[
\begin{align*}
\text{H}_{i,k=kl} & \left[ k_{1 \cdot 1} \right]^{T}_{k=1} \text{H}_{ik} \left[ k_{1 \cdot 1} \right]_{i=1} \text{D}_{i,j} \left[ j_{1 \cdot 1} \right]_{j=1} \text{D}_{ij} \left[ j_{1 \cdot 1} \right]_{j=1} \text{G}_{ij} \left[ j_{1 \cdot 1} \right]_{j=1} \text{E}_{ij} + \\
& \ldots \text{see logic-expression of previous section. A-term only of } \overline{\text{A}}_{i=il}. \\
\end{align*}
\]
3. logic as for 2, with \( \overline{\text{A}}_{i=il} \) replaced by \( \text{A}_{i=il} \)
4. \[
\begin{align*}
\text{H}_{i,k=kl} & \left[ k_{1 \cdot 1} \right]^{T}_{k=1} \text{H}_{ik} \left[ k_{1 \cdot 1} \right]_{i=1} \text{G}_{i,j} \left[ j_{1 \cdot 1} \right]_{j=1} \text{...} \\
& \text{use only the } \overline{\text{A}}_{i=il} \text{ part of the A-term, as above} \\
\end{align*}
\]
5. logic as for 4, with \( \overline{\text{A}}_{i=il} \) replaced by \( \text{A}_{i=il} \)
certain features of simulated output that are not clear.

Holling (1966) presents a plot (his Figure 31) of the time spent in the digestive pause (TD) as a function of the number of flies per square centimeter (NO). Using the table of the various forms of the TD function, we can see that no TD function includes NO as a parameter. Thus the effects of NO on TD must occur through the hunger variable.

The hunger generated at the end of the i-loop is directly related to TS (Table XII). NO is inversely related to TS (Table VII). Therefore, NO is inversely related to hunger, H. The variable H is related to TD as a log function in such a way that TD=0 when H=HTE. The variable TD, as a function of NO, is strictly a log function. The relationship operates via hunger, through changes in TS.

Holling mentioned (1966; page 62) that the magnitude of this function is very sensitive to changes in some of the parameters. It is clear that parameters AD and HTE are the only two that affect TD directly. Others may operate through hunger and the parameter AKE is the most obvious.

"In the H. crassa - housefly system, for example, the 'digestive' pause did not appear even at the highest density that was simulated. This occurred mainly because the size of the prey (W) relative to the size of the predator (HK) was very much smaller in the H. crassa than in the M. religiosa one." (Holling, 1966; page 62). This statement is equivalent to \( \bar{H}_{i,k=kl_{i}}=1 \), which is part of the logic pertaining to TD4 (Table VI). The reason given in the quote may well be the main reason, but the logic of TD4 states that \( \bar{A}_{i=1} \) is also necessary.

That is, the hunger of the predator just after its preceding meal had to be greater than or equal to the eat threshold, HTE.

A possibility for eliminating the digestive pause that was not mentioned above is given in TD2. This is where the size of the prey
is irrelevant because the predator is not very hungry and will not return to the carcass when it becomes hungrier.

The last question to be considered is whether the technique can be of value in anticipating the form of simulated output. Qualitative aspects of simulated output seem to follow readily from Table X. It is easy to say something about the behaviour of A as H changes; or to say something about the behaviour of A as RECAD, or TX, or AKE change. One can say whether all functions operate more or less in the same manner, or whether some operate very differently from the others. To be quantitative in one's predictions, however, is quite another matter. This is because a generalized hunger term, H, has been used in preference to, say, hunger referred to that at the beginning of the i-loop. Each H term could, of course, be referred to this point, but at the expense of expanding Table X. . . Even then, in order to predict output, one would have to go iteration by iteration, each time updating hunger in the equations of Table X. But then one would almost be doing what the computer is doing.

It has been suggested that perhaps this technique, developed for studying analytically the sensitivity of a model, might itself be programmed. As an aid to following the internal working of this program it might be useful to expand Table X, referring all hungers to the hunger at the beginning of the i-loop. If during a simulation run these hungers were being continuously printed, one could use this knowledge along with the Table to understand and control the program.
The approach which has been developed illustrates that complex, highly non-linear models are not completely intractable to analytical methods. By dealing with qualitative, as opposed to quantitative changes in the model, it is possible to delineate the various forms of the output variable. This was so even when there was more than $2^{10}$ different possible output equations. From this set of equations a set of parameters which serve a common role in all equations could be listed. Where the equations of the set differed greatly, it was possible to compile subsets of similar equations; the controlling logic was clear. It was shown how the independent variable varies over the iterations of the program. It was also possible to explain simulated output - by a more organized form of the method usually used. Because of this organization it was possible to know when the full explanation was at hand, and to know when there was more than one explanation.

The method is useful mainly in that it tells the investigator when all cases have been considered. If one simply moves haphazardly through the model seeking explanations, he may well overlook some important details. This possibility is less likely using my method because, in the attack model, the logic-expression developed for the block diagram of Appendix IV and Table X describe the totality of cases.

Because of the organized form that this method produces, various simulation models may be compared and contrasted. It is possible to compare this model of attack with that by Ware (1971) and that by Beukema (1968). This comparison is, however, another task and is not attempted in this thesis.

The method is unable to deal with the iterative nature of simulation
models: the value of the dependent variable in one iteration depends upon the value of the independent variable of the last iteration; but the value of the independent variable during that iteration depended upon the value of the dependent variable of the previous iteration. This seemed to be the major problem in determining the exact form of simulated output from the attack model of Appendix IV.
This study attempted to deal with two inadequacies of experimental components analysis. It is, perhaps, appropriate to end this thesis with an appraisal of the methods proposed and tested.

The problem of generality was studied from a strategic, rather than from a tactical, viewpoint. An hypothesis was formulated regarding the duration of the dynamic responses of various searching modes. Hydra were used to test this hypothesis.

Searching behaviours were identified through the joint use of the literature and my own observations on Chlorohydra viridissima and Hydra littoralis. Those behaviours which changed in frequency over time of food deprivation were regarded as searching behaviours. It was also necessary that those behaviours could be interpreted in terms of searching through volume. Three search modes were identified: tentacle lengthening, walking, and floating.

It was shown that over all hunger levels, the typical response for hydra is to lengthen the tentacles first, then to begin to walk, and lastly to detach and begin to float. Furthermore, it was shown that the duration of the dynamic response of a search mode is inversely related to the hunger level at which the mode is initiated.

These results on hydra suggest that the strategic hypothesis may have some usefulness in writing general functions. The initial hypothesis was based on an argument which was independent of the specific characteristics of hydra.

An explicit function for time spent searching (TS) was written. This function was formulated in an attempt to simplify the implicit TS function by Holling (1965, 1966). Both equations rely on the
parameters HK, AD, SP, SS, and SR. The equation developed in this thesis adds the parameter called "a" while Holling's equation adds the parameters VR, AKRGM, HTS, HTO, and AF.

In Holling's (1966) paper the results of some simulations are presented. His Figure 31 presents a graph of the time spent searching, as a function of the density of prey (NO). On the whole it takes a form reminiscent of that produced by the expression $e^{-ct}$. Most of the change takes place over small NO values. Thus in the equation II10, we might ignore the second term of the argument of the log term, to get $1/a \left[ \ln(f) - \ln(g*NO) \right]$, where $f = a*N*\left(\frac{A}{H} - H\right)$ and $g = \frac{A}{H}$. If $\ln(f) > \ln(g*NO)$, the resultant of the difference between a constant TS and a log function resembles the graph simulated by Holling.

The problem of model complexity was approached simply by identifying the various kinds of equations of the outputted variable that were included in the simulation model. These forms of the outputted variable were listed. From this list certain deductions were made. A serious problem with this approach is that of omission; the interesting problem of how to deal with the iterative feature of simulation models could not be dealt with.
LIST OF SYMBOLS

The logical symbols of PART III will not be included. These symbols may be checked by referring to Appendix II.

For PARTS I and II, the symbols are as follows:

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a$</td>
<td>a parameter associated with the rate of searching</td>
</tr>
<tr>
<td>$AD$</td>
<td>rate of digestion</td>
</tr>
<tr>
<td>$DMT$</td>
<td>distance of vertical movement during floating</td>
</tr>
<tr>
<td>$HK$</td>
<td>maximum hunger level</td>
</tr>
<tr>
<td>$HO$</td>
<td>hunger level just after a prey is consumed</td>
</tr>
<tr>
<td>$t_{0+kT}$</td>
<td>time interval in which hydra detach and begin to float</td>
</tr>
<tr>
<td>$L$</td>
<td>mean tentacle length</td>
</tr>
<tr>
<td>$NA$</td>
<td>number of prey attacked</td>
</tr>
<tr>
<td>$NO$</td>
<td>prey density</td>
</tr>
<tr>
<td>$n$</td>
<td>a time counter for difference equations</td>
</tr>
<tr>
<td>$RD$</td>
<td>reactive distance</td>
</tr>
<tr>
<td>$t$</td>
<td>unspecified time</td>
</tr>
<tr>
<td>$t_0$</td>
<td>time zero for difference equations</td>
</tr>
<tr>
<td>$T$</td>
<td>time interval for difference equations</td>
</tr>
<tr>
<td>$TF$</td>
<td>time of food deprivation timed from a condition of complete satiation</td>
</tr>
<tr>
<td>$TD$</td>
<td>time taken in a digestive pause after a prey is eaten</td>
</tr>
<tr>
<td>$TE$</td>
<td>time spent eating prey</td>
</tr>
<tr>
<td>$TP$</td>
<td>time spent pursuing each prey</td>
</tr>
<tr>
<td>$TS$</td>
<td>time spent pursuing each prey</td>
</tr>
<tr>
<td>$T_m$</td>
<td>time in $T$ in which hydra move</td>
</tr>
<tr>
<td>$T_u$</td>
<td>time in $T$ in which hydra are fixed and not moving</td>
</tr>
<tr>
<td>$T_a$</td>
<td>time in $T$ in which hydra have tentacles attached to the substrate</td>
</tr>
<tr>
<td>$VD$</td>
<td>average velocity of predator during searching</td>
</tr>
<tr>
<td>$VY$</td>
<td>average velocity of prey</td>
</tr>
<tr>
<td>$VPL$</td>
<td>average velocity of the looping hydra</td>
</tr>
<tr>
<td>$VPF$</td>
<td>velocity of the floating hydra</td>
</tr>
<tr>
<td>$VS$</td>
<td>volume searched per time interval</td>
</tr>
</tbody>
</table>
BIBLIOGRAPHY

Beukema, J.J. 1968  Predation by the three-spined stickleback 
   (Gasterosteus aculeatus L.): The influence of hunger 

Brett, J.R. 1965  The swimming energetics of Salmon. Sci. Amer. 
   213(2):80-85.


Campbell, B.A., N.F. Smith, J.R. Misanin, and J. Jaynes 1966 
   Species differences in activity during hunger and thirst. 

Chua, L.O. 1969  Introduction to nonlinear network theory. 

   In: The Biology of Hydra and of Some Other Coelenterates. 
   H.M. Lenhoff and W.F. Loomis (Editors). University of 
   Miami Press, Coral Gables, U.S. of A.

   D.S. Lehrman, R.A. Hinde, and E. Shaw (Editors). 

Emlen, J.M. 1966  The role of time and energy in food preference. 
   The Amer. Nat. 100:611-617.


A field study was initiated in an attempt to determine the distribution and abundance of a hydra population. Emphasis was placed on the feeding biology of the population. As the data are observational, the results are only tentative. This program was judged necessary in order that laboratory studies could be related to circumstances arising in a natural habitat.

The study area was the outlet creek from Beaver Lake. This lake is located in Stanley Park, Vancouver (Figure 1). The hydra were studied in various parts of the creek, but always between the lake and the Pipe Line Road. Very few hydra were found in the rest of the stream.

Beaver Creek is approximately 15-30 cm deep. The creek is exposed to fluctuations in depth, as it is supplied with water which enters via a spillway from Beaver Lake. The mainstream flow of the creek is around 30 cm/sec. Near the shore, where populations of hydra were readily observable, flow varied from less than 2 cm/sec to the mainstream flow. Bottom type is variable: mud, sand, gravel, gravel covered by filamentous algae, intricate interlacing of a tubular weed, and human refuse were all observed. The period of study was two weeks in late August. Afternoon water temperature was between 19 and 20 deg C.

**Taxonomy of Beaver Creek Hydra.** Using the taxonomic key of Forrest (1959), I identified the hydra collected from Beaver Creek as *Hydra carnea*, L. Agassiz. The most important features of this species are:

a) Nematocysts: those types of nematocysts called penetrants were measured to be between 11 and 15 microns. They are between 9 and 19
Figure 1. A map of the field study area. The enlarged portion of the map shows Beaver Creek more clearly.

The darkened arrows indicate the location of the substrate, or core, samples. The open arrows indicate the location of the grid samples.
microns in length for *H. carnea*. The large (streptoline) glutinants are of narrowly oval form of 10 microns in length. Those of *H. carnea* are of 10 microns in length. The small (stereoline) glutinants are of oval form but, unlike the large forms, are pointed at one end and of 7 to 8 microns in length. Those of *H. carnea* are about 9 microns long. The volvents were measured to be between 6 and 7 microns long. Those of *H. carnea* are between 6 and 8 microns in length.

As specified for *H. carnea*, the Beaver Creek animals showed three or four transverse or obliquely-transverse coils of thread within the large glutinants.

b) Tentacle arrangement: during tentacle formation on a bud of *H. carnea*, the first protuberance occurs on one side of the hypostome. This protuberance is followed by the growth of other tentacles. A typical arrangement is with the older tentacles on one side of the hypostome, the younger ones on the other side, with some tendency for alternation of longer and shorter tentacles. These patterns were shown in the field hydra.

c) Number of tentacles: a sample of 2,317 hydra from the field showed 45% with five tentacles, 45% with six tentacles, and 5% with four tentacles. Animals with one, two, three, seven, eight, or nine tentacles were recorded infrequently.

d) Gametes: testes of the field species were small, mammiform, and with nipples. None of the hydra specimens which were collected had eggs attached to them. However, two eggs were collected from substrate samples. These eggs were spherical, with small spines emerging from the theca. This is typical of *H. carnea*.

Some Observations on the Distribution and Abundance of *Hydra carnea* in Beaver Creek. Preliminary observation had indicated that hydra
occurred in a great many places along the stream. The hydra were often found in such densities that it was impossible to estimate their densities directly. Thus the habitat, with adhering hydra, was sampled. Measurements were obtained from the preserved hydra.

To this end a syringe of 16 mm diameter was modified to produce a bottom sampler. The tip of the syringe was removed, leaving a cylinder with its plunger. In using this sampler, I set it over a section of the bottom and pushed it into the substrate. This resulted in a core of substrate at the bottom of the cylinder. Retracting the plunger moved the core further up into the cylinder. The core sample was then transferred to a collecting bottle, and preserved in a formalin solution.

This technique allowed me to sample known areas of the substrate in each of six locations. The locations were situated at various distances from the spillway (see black arrows of Figure 1). Five samples were taken at each location. They were not chosen at random, but stratified in such a way as to indicate the ranges in hydra density present. I simply looked around each location for various densities of hydra. (Also, some bottom substrate was collected and examined in the laboratory. These collections were made where the water was too deep, or the current too swift, or the bottom of unsuitable texture to collect in the previous manner. The objective was to ascertain only the presence or absence of hydra. In each of five samples taken, hydra were found. There were many hydra in two samples but only a few in the rest of the samples.)

The data from this sampling exercise is presented in terms of numbers of hydra per cm$^2$ of substrate (Table I). The data is presented such that location 1 of Table I corresponds to the most upstream black
Table I. Density of *Hydra carnea* (numbers/cm²) in Beaver Creek. The data are given for groups of five samples per location, with locations numbered from the most upstream to the most downstream (see Figure 1).

Sample size is the total number of hydra counted in all five samples per location.

<table>
<thead>
<tr>
<th>LOCATION</th>
<th>DENSITY (number/cm²)</th>
<th>SAMPLE SIZE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2 12 12 16 33</td>
<td>150</td>
</tr>
<tr>
<td>2</td>
<td>29 51 58 80 88</td>
<td>612</td>
</tr>
<tr>
<td>3</td>
<td>0 3 16 42 110</td>
<td>342</td>
</tr>
<tr>
<td>4</td>
<td>17 19 24 28 132</td>
<td>442</td>
</tr>
<tr>
<td>5</td>
<td>12 57 75 84 136</td>
<td>729</td>
</tr>
<tr>
<td>6</td>
<td>5 6 8 13 16</td>
<td>96</td>
</tr>
</tbody>
</table>
arrow of Figure 1; location 2 of Table I corresponds to the next black arrow of Figure 1; etc. Thus location 6 of the table corresponds to the most downstream black arrow of Figure 1. It is readily observable that no straightforward relationship exists between the density of hydra in a locality and the distance of that locality downstream from the spillway. However, it has been noted that few hydra were found downstream from the Pipe Line Road. A large amount of variation in density of hydra exists in individual sections of the stream (see data from location 5).

Next the distribution of *H. carnea* within small areas was studied. A grid of 1 foot to each side was constructed. It was subdivided into 576 quadrats, each of them being 1.6 cm² in area. A hundred quadrats were then selected at random, under the restriction that each one-quarter of the grid had to contain one-quarter of the selected quadrats.

In using the grid, I placed it over an area of the bottom of the stream and counted the number of hydra in each of the 100 selected quadrats. For each quadrat the composition of the substrate, the depth of the water, and the surface water velocity were also noted. This procedure was followed in each of five different sites (see Figure 1; open arrows). The sites were chosen in such a way as to illustrate the various types of habitats: 1) an even water depth of 30-50 mm; with a fast water flow of 30 cm/sec; and with mixed gravel and filamentous algal substrate; 2) an uneven water depth of 30-60 mm; with a medium water flow of 10 cm/sec; and a mixed mud and weed substrate; 3) an uneven water depth of 6-35 mm; with a variable water flow of 2-30 cm/sec; and with mixed mud, silt, weed, and gravel bottom; 4) an uneven water depth of 20-60 mm; with a fast water flow of 30 cm/sec; and with mixed mud and weed substrate; and 5) an even water depth of 20-37 mm; with a
slow water flow of 4 cm/sec; and with mixed mud and weed substrate.

The order of data presentation in Table II is from the most upstream site to the most downstream site. It is visible in Figure 1 that the area designated as location 1 is the same area as site 1. Likewise it may be observed that location 2 was taken in the same area as site 2 and that location 6 was taken in the same area as site 5. Location 4 was taken more or less in the same area as site 3. Location 3, location 5, and site 4 were all taken in unique areas of the creek.

The density of hydra was correlated with the depth of the water, the water velocity at the surface, and the substrate type. The data are analyzed separately for each site. The sites were not chosen at random. They were chosen deliberately to illustrate the variety of habitats present. Thus an appropriate error distribution cannot be assumed for data lumped from all sites.

The data suggest that over a range of depths from 8 to 30 mm, hydra density is directly related to water depth (site 3 of Table IIA). At greater depths the relationship may be negative (sites 1, 4, and 5 of Table IIA).

In three of the five sites water velocity was uniform over the whole grid. Thus correlations were run for the data from the remaining two sites. The results are given in Table IIB. They suggest that over low velocities (7-10 cm/sec) there is a negative relationship between density of hydra and water velocity, and that over higher velocities (2-30 cm/sec) there is no relationship.

A relationship was found between the density of hydra and the substrate type. For each quadrat the number of hydra per quadrat and the substrate type were recorded. The dominant substrate types were mud, mud and weeds, weeds, weeds and gravel, gravel, gravel and
Table II. Relationship between the density (numbers/quadrat) of *Hydra carnea* in Beaver Creek and the depth of the water above the quadrat (A) and the surface water velocity (B).

### A.

<table>
<thead>
<tr>
<th>SITE</th>
<th>RANGE OF DEPTHS (mm)</th>
<th>REGRESSION COEFFICIENTS</th>
<th>CORRELATION COEFFICIENTS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>SLOPE</td>
<td>INTERCEPT</td>
</tr>
<tr>
<td>1</td>
<td>30-45</td>
<td>-0.004</td>
<td>+0.76</td>
</tr>
<tr>
<td>3</td>
<td>08-30</td>
<td>+0.087</td>
<td>-0.36</td>
</tr>
<tr>
<td>4</td>
<td>31-52</td>
<td>-0.545</td>
<td>+29.03</td>
</tr>
<tr>
<td>5</td>
<td>20-37</td>
<td>-0.077</td>
<td>+0.51</td>
</tr>
</tbody>
</table>

### B.

<table>
<thead>
<tr>
<th>SITE</th>
<th>RANGE OF VELOCITIES (cm/sec)</th>
<th>REGRESSION COEFFICIENTS</th>
<th>CORRELATION COEFFICIENTS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>SLOPE</td>
<td>INTERCEPT</td>
</tr>
<tr>
<td>2</td>
<td>07-10</td>
<td>-1.006</td>
<td>+15.41</td>
</tr>
<tr>
<td>3</td>
<td>02-30</td>
<td>+0.006</td>
<td>+0.75</td>
</tr>
</tbody>
</table>

**ns:** not significant at p=0.05  
** ***: significant at p=0.001
algae, and algae. The number of hydra in a given quadrat was characterized by the substrate type of that quadrat. Then it was possible to calculate the percentage of hydra by substrate type. For comparative purposes, calculations were made of the percentage of various substrate types. As 100 quadrats were counted at each site, these calculations were done simply by counting the number of quadrat types. This latter calculation was then considered to be the percentage of hydra by substrate type, if the hydra were distributed entirely on the basis of substrate type. The results are given in Table III. The actual numbers of hydra found are given to the left of each pair of numbers while the expected numbers are given to the right of each pair of numbers.

It is clear from Table III that the number of hydra expected on the mud bottom is consistently higher than the number actually present. The opposite situation is shown for weedy substrates. The mud and weed substrate data show the intermediate situation, with the data from three locations behaving as for the weed covered substrates and the data from one location behaving as for the mud substrate.

The frequency distribution of hydra within each site was studied. Indices of dispersion ($s^2/\bar{Y}$) were calculated (Pielou, 1969). The expected value of this ratio is one when individuals are dispersed at random. It is greater than one when individuals are distributed contagiously. For sites one through five coefficients took values of 3.18, 5.03, 2.09, 10.60, and 4.38 respectively. These indices suggest that the hydra are distributed contagiously.

One would expect on the basis of the data given in Table III that the clumping might be due to the distribution of the weeds within the grids. The distributions were analyzed for only the weed covered
Table III. Percentage of hydra and percentage of substrate type, by substrate types, for each of five sites. Blanks in the table should be read as zeros.

<table>
<thead>
<tr>
<th>SUBSTRATE TYPE</th>
<th>SITE</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>% Hydra</td>
<td>% Sub. Type</td>
<td>% Hydra</td>
<td>% Sub. Type</td>
<td>% Hydra</td>
<td>% Sub. Type</td>
</tr>
<tr>
<td>mud</td>
<td>00-01</td>
<td>00-01</td>
<td>07-22</td>
<td>10-36</td>
<td>40-74</td>
<td></td>
</tr>
<tr>
<td>mud and weeds</td>
<td>19-31</td>
<td>21-12</td>
<td>42-25</td>
<td>46-18</td>
<td></td>
<td></td>
</tr>
<tr>
<td>weeds</td>
<td>71-55</td>
<td>40-24</td>
<td>39-32</td>
<td>04-02</td>
<td></td>
<td></td>
</tr>
<tr>
<td>weeds and gravel</td>
<td>19-17</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>gravel</td>
<td>07-14</td>
<td>02-01</td>
<td>00-01</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>gravel and algae</td>
<td>76-62</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>algae</td>
<td>15-20</td>
<td>00-01</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>other</td>
<td>02-03</td>
<td>08-11</td>
<td>13-24</td>
<td>09-07</td>
<td>10-06</td>
<td></td>
</tr>
</tbody>
</table>

Number of hydra per site

<table>
<thead>
<tr>
<th>Site 1</th>
<th>Site 2</th>
<th>Site 3</th>
<th>Site 4</th>
<th>Site 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>59</td>
<td>641</td>
<td>112</td>
<td>543</td>
<td>265</td>
</tr>
</tbody>
</table>
quadrats at sites two, three, and four. The other sites did not contain enough data. The indices were 4.63, 1.59, and 3.62 for sites two, three, and four respectively. The distributions still seem to be contagious. However, the degree of clumping is consistently less when only the weedy substrates are considered than when all substrate types are considered.

Some information on the reproductive activity of hydra was collected from the core samples. Table IV gives the percentage of hydra with reproductive organs, correlated with hydra density. These data suggest that budding is low at densities of 0 to 24.5 hydra/cm$^2$ and that it is also low at densities greater than 75 hydra/cm$^2$. At intermediate densities budding is about twice as frequent. Sexual reproduction appears to be low below 50 hydra/cm$^2$ and high above this density.

Some Observations on the Searching of Chlorohydra viridissima as Performed in the Laboratory. Hydra carnea is not used in these laboratory studies as it is difficult to culture in artificial medium. Chlorohydra viridissima is used. This species performs readily the usual behavioural repertoire of hydra (Hegner, 1933).

The behaviour patterns of the hydra were identified by feeding the hydra to satiation and then depriving it of food and watching what it did. Each hydra was assumed to be satiated when a freshly killed brine shrimp, Artemia, placed near its mouth, was not eaten.

The behaviours whose frequency of occurrence changed with hunger were considered searching behaviours. When fed to satiation the hydra contracts its tentacles and stalk. The stalk becomes a round ball and the tentacles, stubs. During the first few hours of food deprivation, the hydra lengthens its tentacles and stalk. Later, the hydra begins to move: it bends over, attaches its tentacles to the substrate, and by
Table IV. Percentage of hydra with one or more buds and percentage of hydra with one or more testes as a correlate of the density of the hydra. One standard deviation is also presented.

Results were derived from the core samples of the substrate of Beaver Creek.

<table>
<thead>
<tr>
<th>DENSITY (numbers/cm²)</th>
<th>NUMBER HYDRA CORES SAMPLED</th>
<th>NUMBER SAMPLED</th>
<th>PERCENT BUDDING</th>
<th>PERCENT WITH GAMETES</th>
</tr>
</thead>
<tbody>
<tr>
<td>00-24.5</td>
<td>365</td>
<td>16</td>
<td>6.85 ± 8.96</td>
<td>0.85 ± 2.13</td>
</tr>
<tr>
<td>25-49.5</td>
<td>263</td>
<td>4</td>
<td>14.61 ± 6.83</td>
<td>0.75 ± 0.90</td>
</tr>
<tr>
<td>50-74.5</td>
<td>332</td>
<td>3</td>
<td>15.66 ± 8.18</td>
<td>1.45 ± 1.32</td>
</tr>
<tr>
<td>75-99.5</td>
<td>650</td>
<td>4</td>
<td>8.76 ± 7.89</td>
<td>2.82 ± 1.83</td>
</tr>
<tr>
<td>100 up</td>
<td>749</td>
<td>3</td>
<td>9.58 ± 2.92</td>
<td>1.59 ± 1.11</td>
</tr>
</tbody>
</table>
contracting its stalk, pulls its foot free of the substrate. Then it resets its foot in a new location. After its foot is attached, the hydra pulls its tentacles free by contracting its stalk, and then assumes again the upright position. Usually a few hours later the hydra detaches from the substrate and floats upside down to the surface. Here it remains floating with foot on the surface of the water and stalk and tentacles extending down into the water.

A Tentative Life History Formulation for Hydra. The field and laboratory data give a qualitative picture of the behaviour of hydra. It is assumed that *Hydra carnea* data can be taken as a complement of the *Chlorohydra viridissima* data. My observations suggest that this is not an unreasonable assumption.

Hydra which have not eaten recently stand with outspread tentacles and elongated stalk. When a prey comes by and brushes against a tentacle, nematocysts discharge, holding the prey to the tentacles. The tentacles are retracted and the prey is eaten (Hegner, 1933). If the prey is large enough to reduce the hunger level of the hydra, the hydra shortens its tentacles and stalk. Searching begins a few hours later when the tentacles and stalk begin to lengthen. Provided that no prey chances along, the hydra begins to move about and eventually detaches and floats somewhere in the water column (laboratory observations).

I have observed in Beaver Creek some hydra floating from the surface of the water. However, many hydra were swept along the creek just slightly above the bottom. As the hydra float downstream with the water perhaps they reattach when they run into some protuberance (such as a weed bed, or a stick) up from a relatively flat substrate (such as mud). Such a mechanism would be in agreement with the data of Table III.
High densities of hydra were observed in the field (Table I). Such densities might result from a limited number of hydra budding at a high rate. Low-medium densities of hydra do show rapid budding activity (Table IV). As densities become medium-high, the rate of asexual reproduction falls while the rate of sexual reproduction increases (Table IV).
APPENDIX II

PARTIAL EVALUATION OF THE EQUATIONS OF THE MODEL

Equations I15, I17, I18, I22, I24, and I25 are repeated in the text in a partially evaluated form as equations I26, I27, I28, I29, I30, and I31 respectively. Here the basics of the evaluation for each equation are provided.

Expression I26 was derived from I15. We write

\[ 0.20 = \frac{(3.1416)(0.8290)^2(0.5592)}{6} = \frac{\pi \sin^2(56) \times \cos(56)}{6} \]

where 0.20 is the evaluated part of the first term of I26 and

\[ \frac{\pi \sin^2(56) \times \cos(56)}{6} \] is an equivalent form from I15. This explains only one half of the enumeration of I15. We also write

\[ 13.90 = \frac{(0.8290)(0.5592)(60.0)}{2} = \frac{\sin(56) \times \cos(56) \times T}{2} \]

where 13.90 is the evaluated part of the second term of I26 and

\[ \frac{\sin(56) \times \cos(56) \times T}{2} \] is an equivalent form from I15. This completely describes the evaluation of I15, as given in I26. This technique will be followed for the other equations.

Expression I27 was derived from I17. We write

\[ 0.40 = \frac{(3.1416)(0.8290)^2(0.5592)}{3} = \frac{\pi \sin^2(56) \times \cos(56)}{3} \]

and

\[ 64.76 = \frac{(3.1416)(0.8290)^2(60.0)}{2} = \frac{\pi \sin^2(56) \times T}{2} \]

Expression I28 was derived from I18. We write

\[ 0.05 = \frac{(3.1416)(0.8290)^2(0.5592)}{24} = \frac{\pi \sin^2(56) \times \cos(56)}{24} \]

and

\[ 0.23 = \frac{(0.8290)(0.5592)}{2} = \frac{\sin(56) \times \cos(56)}{2} \]
Expression 128 was derived from 122. We write
\[
0.03 = \frac{(3.1416)(0.8290)^2(0.5592)}{48} = \frac{\pi \sin^2(56) \cdot \cos(56)}{48}
\]
and
\[
0.45 = \frac{(3.1416)(0.8290)^3}{4} = \frac{\pi \sin^3(56)}{4}
\]
and
\[
0.20 = \frac{(3.1416)(0.8290)^2(0.5592)}{6} = \frac{\pi \sin^2(56) \cdot \cos(56)}{6}
\]
and
\[
1.37 = (2.0)(0.8290)^2 = 2 \sin^2(56)
\]
and
\[
1.08 = \frac{(3.1416)(0.8290)^2}{2} = \frac{\pi \sin(56)}{2}
\]
and
\[
0.23 = \frac{(0.8290)(0.5592)}{2} = \frac{\sin(56) \cdot \cos(56)}{2}
\]

Expression 130 was derived from 124. We write
\[
10.36 = (4.80)(0.8290)^2(3.1416) = L^2(t_o + kT) \cdot \sin^2(56) \cdot \pi
\]
and
\[
0.20 = \frac{(3.1416)(0.8290)^2(0.5592)}{6} = \frac{\pi \sin^2(56) \cdot \cos(56)}{6}
\]
and
\[
13.91 = \frac{(60.0)(0.8290)(0.5592)}{2} = \frac{T \cdot \sin(56) \cdot \cos(56)}{2}
\]

Expression 131 was derived from 125. We write
\[
10.36 = (4.80)(3.1416)(0.8290)^2 = L^2(t_o + kT) \cdot \pi \cdot \sin^2(56)
\]
and
\[
0.20 = \frac{(3.1416)(0.8290)^2(0.5592)}{6} = \frac{\pi \sin^2(56) \cdot \cos(56)}{6}
\]
and
13.91 = \frac{(60.0)(0.8290)(0.5592)}{2} = \frac{T\sin(56)\cos(56)}{2}

and

0.45 = \frac{(3.1416)(0.8290)^3}{4} = \frac{T\sin(56)^3}{4}

and

82.47 = (2.0)(0.8290)^2(60.0) = 2\sin^2(56)T

This series of equalities completely expands all of the constants of equations I26-31 back to their original forms.
APPENDIX III

EFFECT OF PARAMETER VALUES ON THE CONCLUSIONS OF PART II

In PART II the model is studied as a function of time of food deprivation. Parameters VY, VPF, and DMT are varied to determine their effects on the volume searched per time interval. However, parameters \( \alpha, T_u, T_m, VPL, \) and L (tentacle length) are fixed in advance. Yet these parameters are biological quantities, and exhibit variability. The variability in parameters can affect the conclusions regarding the steady state search rates. We attempt to determine the effect of variability in parameters \( \alpha, T_u, T_m, VPL, \) and L on the following conclusions.

1. The minimal effect of walking on the volume searched by a non-moving hydra is slightly negative;
2. the minimal effect of floating on the volume searched by a non-moving hydra is either no change (when the absolute value of \((VY-VPF)\alpha VY\)) or very negative (when \(VY=\text{water velocity}=VPF\));
3. the maximal effect of walking on the volume searched by a non-moving hydra is slightly positive;
4. the maximal effect of floating on the volume searched by a non-moving hydra is very positive.

Parameter \( T_u \) was measured in the text to be very close to \( T \) (=60 minutes). Since \( T = T_u + T_m \), the parameter \( T_m \) is very close to zero. The walking equations (I18,I22) reduce to the tentacle lengthening equations (I15,I17) when \( T_u=T \); and \( T_u \) was never more than 0.1 minutes from 60 minutes (T). No evidence was collected to suggest that \( T_m \)
ever wanders far from $T$. Thus we dismiss the effects of variation in $T_m$ and $T_u$ on the conclusions drawn in PART II.

Parameter VPL operates only during $T_m$. Since $T_m$ is so small, it is unlikely that VPL will have much of an effect on the conclusions. Its effects are considered to be unimportant.

It is suggested that the effect of walking on volume searched by a non-moving hydra is minimal regardless of expected variation in parameters $T_m$, $T_u$, and VPL. Conclusions 1 and 3 are not greatly changed by variation in these parameters. We now consider the effects of $\alpha$ and $L$ on conclusions 2 and 4. Consider conclusion 2. We compare equation I15 to I24. In I15, parameter $T=60$ and $VY$ may take values up to 18,000 mm/minute. It is thus frequently the case that term one is much less important than term two. We write $I15 \simeq VY \sin(\alpha/2) \cos(\alpha/2) \times T \left[ L^2(t_o+nT) + L^2(t_o+nT-T) \right]$. The major effects of I24 are due to $T$, $VY$, and VPF. Term one is non-zero only for $t \neq t_o+kT$. Since we are comparing steady states, we ignore this term. Term two is ignored because it contains neither $T$, nor $VY$, nor VPF. Thus $I24 \simeq T \sin(\alpha/2) \cos(\alpha/2) \times (|VY-VPF|) \times \left[ L^2(t_o+nT) + L^2(t_o+nT-T) \right]$. The relative effect of I24 and I15 is $I24/I15$. Since the $L$ containing terms are the same in each of I24 and I15, it is clear that $L$ cannot change the conclusions. Likewise for the $\alpha$ terms.

Now consider conclusion 4. Equation I17 $\equiv \pi \sin^2(\alpha/2) \times T \times VY \times \left[ L^2(t_o+nT) + L^2(t_o+nT-T) \right]$. Term one and two of I25 are not considered for the same reasons that they were not considered for I24. Term four does not contain $T$, as do terms three and five. However, it contains $VY$, as $VY/VPF$. When $VY=VPF$, this ratio equals one and term four is small relative to terms three and five. In fact, it is only important when VPF becomes increasingly less than 1 mm/minute. This is a very small velocity
and so term four is eliminated. Thus \( I_{25} \leq \frac{T \times VPF \times \sin(\alpha/2) \times \cos(\alpha/2)}{2} \left[ L^2(t_o+nT) + L^2(t_o+nT-T) \right] + 2 VY \times \sin^2(\alpha/2) \times T \times \left[ L^2(t_o+nT) + L^2(t_o+nT-T) \right] \)

The ratio \( I_{25}/I_{17} \) must hold more or less constant as \( \alpha \) and \( L \) change for the conclusion 3 to remain valid. Since the same \( L \) containing term can be factored out of each of \( I_{25} \) and \( I_{17} \), \( L \) cannot affect the conclusions.

This conclusion does not hold for parameter \( \alpha \), since term two of \( I_{25} \) has \( \alpha \) as \( \sin^2(\alpha/2) \) to term one's \( \sin(\alpha/2) \times \cos(\alpha/2) \). If \( VPF \) tends to zero, then conclusion 4 is unaltered. This is also the case if \( VY > VPF \), since then the major volume covered by \( I_{25} \) is due to term two, as above.

The term \( \sin(\alpha/2) \times \cos(\alpha/2) \) has a relevant property. It has a maximum value at \( \alpha/2 = 45 \) degrees and falls monotonically from this peak to value zero at \( \alpha/2 = 0 \) and at \( \alpha/2 = 90 \) degrees. Conclusion 4 can be invalidated only by a decrease in the value of \( I_{25}/I_{17} \). This can occur only if \( \cos(\alpha/2) \times \sin(\alpha/2) \) takes a smaller value. Since the standard deviation of \( \alpha \) is 25 degrees, it must be 12.5 degrees for \( \alpha/2 \). The parameter \( \alpha/2 \) has to be less than 34 degrees before the \( \sin(\alpha/2) \times \cos(\alpha/2) \) term can take a smaller value than it has at \( \alpha/2 = 56 \) degrees. This low a value of \( \alpha \) is a rare event. Thus the \( I_{25}/I_{16} \) ratio can be decreased only as \( \alpha/2 \) is increased to 90 degrees.

It is clear from the expanded form of \( I_{25}/I_{16} \) that when \( \alpha/2 = 90 \), then the ratio will tend to value of one, or approximately so.

We conclude that parameters \( T_u \), \( T_m \), VPL, and \( L \) are formulated in such a way that variation in them does not affect to any significant degree the conclusions of PART II. The parameter \( \alpha \) may negate conclusion 4 only under the following conditions, and then only maybe. The conditions are: that \( VPF \) is not equal to zero, that \( VY \) is not much larger than \( VPF \), and that \( \alpha/2 \) approaches the value of 90 degrees.
In Figure 1 is a flow graph of the functional response of a predator to prey density (Holling, 1966). It has been modified slightly, by replacing his equation for time spent searching (TS) by predators by one developed in this thesis (equation II10).
Figure 1. A flow graph of the attack model.
\[ TP = \sqrt{\frac{\ln h_{o+H_T}}{a}}(H_{o-H_T}) \frac{a}{AD} \] 
\[ SP = \exp(-AM^2TP) \]

\[ TS = \frac{1}{\alpha} \ln \left( \frac{\alpha^*Na^*(H_T-H_0)^{\alpha}}{AD} + 1 \right) \]
\[ TP = TP_1 + TX \]
\[ H_1 = H + (H - H) \exp(-AD^2 TP) \]
\[ W_1 = W \]

\[ TP_1 = 0, SP_1 = 1 \]

\[ TP_1 = 0, SP_1 = 1 \]

\[ TEST8 = |SP - SP_1| \leq 0.02 \]
\[ TP = TP_1 + TX \]

\[ H_1 = H - (H - H) \exp(-AD^2 TP) \]
\[ W_1 = W \]

\[ TE = AKE^2W_1 \]
\[ AA1 = HCAD \]
\[ AA2 = HC - W_1 \]
\[ HO = HC - AA1 - (AA2 - AA1) \exp(-AD^2 TE) \]
$WE = W$
$WD = 0$
$TE = TE + TB$

3

$W = W / AE$
$WD = WI - WE$
$HO = 0$

$TE = -RECAD^{LH} LN \frac{Hk - RH1}{AA2 - AA1}$

$TD1 = 0$
$TE1 = 0$
$T1NEW = TD1 + TS + TP + TE$
$TEST1 = |T1NEW - T1| - 0.01 T1NEW$
$T1 = T1NEW$

$NWAST \geq 0$

$TE = TE1 + TE$
$TD1 = RECAD^{LN} \frac{Hk}{Hk - HTE}$
$TD = TD1 + TD$
$WI = WD$
$H1 = HTE$

1 \geq 0$

$A = 240 / T1$
$SWAE = WE^{*A}$

OUT