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**The Functional Response
of
Invertebrate Predators
to Prey Density**

by

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INTRODUCTION

During the interval between 1923 and 1935 a remarkable amount of activity was directed to developing mathematical models of animal populations (Lotka 1923, Thompson 1924, Volterra 1931, Gause 1934, Nicholson and Bailey 1935). These models, and the approach used to develop them, for the first time seemed to provide the population biologist with the same powerful tools that had proved so effective in analyzing processes in physics. The models attempted to express with great precision the action and interaction of a number of processes that affect animal numbers, and significant and important generalizations emerged from them concerning the gross behaviour of populations. But if the ultimate test of the usefulness of an approach lies in the power the resulting theories provide to manipulate events, these early applications of mathematics are not notably successful. It is still largely true that any animal population that affects man economically must still be approached as a unique entity. There are few detailed principles that can be usefully exploited to manipulate a variety of situations.

Part of the difficulty lies in the inherent complexity of population events — a complexity that arises from the large number of components involved, as well as from the unique interactions between them. It has already been pointed out (Holling 1964) that these complex events must be approached with conceptual and analytical tools specifically suited to handle the complexity. The early population models lacked these tools, since they were developed using methods borrowed from the classical physics of 50 years ago. Consequently, the models are basically similar to the physicist's model, having the same neat, well-structured form, the same language of expression (largely differential calculus) and the same logical structure. By accepting this language, the biologist is forced to adapt his image of the process to the severe limitations imposed by the language. If the process is fairly simple in structure then this can be done with great profit. But if the process is as complex as population processes are, the simple approach and language can be applied only by sacrificing reality.

It would therefore be an entertaining and potentially profitable undertaking to analyze the various processes that affect animal numbers — e.g. predation, competition, and parasitism — by initially ignoring the limitations imposed by the restrictions of traditional mathematical models and emphasizing the need for a realistic explanation. Once the analysis is complete it might then be possible to express the explanation in a precise mathematical form without sacrificing reality. In this way the process itself would dictate the form of the model rather than some arbitrarily chosen mathematical language.

The first population process chosen for analysis was predation, and this paper presents the results of an analysis of the effects of prey density on attack by invertebrate predators. The paper represents a particularly important step, for it is the first time in this program of research that a process of significant complexity has been investigated. The analysis should therefore show whether it is possible, in principle, to develop specific mathematical models of population processes that are not only precise but biologically realistic.

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THE APPROACH

Although the achievement of reality and precision are fundamental aims, two additional requirements must also be considered in developing an adequate approach. The first is the need for an analysis of a whole system rather than of isolated fragments of the system. While it is useful to know, for example, the maximum consumption of a predator, its speed of searching, or its attack success, it is considerably more useful to know how these fragments interact with each other and with the many other fragments of the predation process. The essence of any complex process often lies in the interaction between fragments as much as in the action of the fragments themselves — the whole is greater than the sum of its parts. The analysis of a whole system realistically and precisely gives great depth. But breadth is just as important. It would be most disappointing, for example, to devise an analysis of great depth and discover that it had very specific and limited application. Hence the final desirable attribute required is generality.

The analytical approach should be designed to satisfy the need for four attributes: realism, precision, wholeness, and generality. It might well be possible, however, that complex biological processes are so diverse or intricate that these four are mutually exclusive; that it is impossible or unprofitable, for example, to deal with whole systems realistically, or to develop realistic specific models that have general application. Nevertheless, if we assume, *a priori*, that such is the case we simply guarantee failure. The possible rewards justify the effort.

The approach finally devised has been termed an experimental components analysis and has been described in detail elsewhere (Holling 1963). It is based on the belief that the characteristics of any specific example of a complex process can be determined by the action and interaction of a number of discrete components. Some of these components are shared by all examples of the process and can be called basic, in that they underlie all manifestations of the process. Others are present in some situations and not others and can be termed subsidiary. By initially dividing the components into universally occurring, or basic ones, and sporadic, or subsidiary ones, generality of a high order becomes at least theoretically possible. Some of the features of every example of the process will arise from the action of the basic components and some from the action of various combinations of the subsidiary ones.

Once the basic components and some of the subsidiary ones are tentatively identified on the basis of general observation and experimentation, a simple example is selected that includes only the basic components. Preliminary experiments suggest hypotheses to explain the action of each component, and these postulates are then tested experimentally in the classical scientific manner. When a set of postulates is finally proved adequate, they are then expressed in a mathematical form and the equations synthesized to produce a model of the basically simple example chosen. This provides a base from which to explore more complex examples where additional, subsidiary components operate, for these new components can be analyzed in the same way and the basic model expanded to include them. In this way a more and more complex structure is built, each progressive step being taken only when a valid explanation has been obtained for the previous step.

This approach provides at least the hope that the four qualities mentioned earlier will be retained. Wholeness is achieved since each step is not considered as an end in itself but is combined with other steps so that progressively more and more of the process is considered. Reality is ensured by the intimate union established between theory and experiment, with experiment dictating theory and

theory suggesting experiments in many small, successive steps. Precision is assured because the demands of the mathematics forces us to cast the explanation in a form precise enough to permit testing of its adequacy. Finally, a degree of generality is achieved by classifying each example by the universality of the components.

In practice, of course, the experimental program does not have quite the logical inevitability that it would appear to have from the above outline. This arises because individuals of only one species usually serve as the experimental animal at any one step in the analysis — a species chosen because it lends itself, for practical reasons, to the particular experimental manipulation required. Hopefully, this species may serve as an accurate analogue of all examples of the particular components being investigated, but in fact it very often represents a limiting condition of a general case. The present study, for example, largely concerns one species of praying mantid. This predator, like many, is an ambush type that waits for prey to come to it. As a result, one subcomponent, the speed of movement of the predator, is zero, thereby representing a limiting case of a general condition. This means that any interaction between speed of movement and other subcomponents cannot be explored. Nevertheless, a place is kept for such an interaction in the final model, so that when the form is finally discovered, it can be readily added. In practice, therefore, it is important to cast the explanation of the action of one species in as general a form as possible and to support the data wherever possible by additional information obtained from a variety of species.

COMPONENTS OF PREDATION

It has been argued elsewhere (Holling 1959a, 1961) that of the many variables that affect predation, prey and predator density must be considered as inevitable features of every predator-prey situation in which population effects are the main concern. Since these two variables are universal, the responses to them will represent the basic components of predation. Two main kinds of response are important, since the total number of prey destroyed by predators is the product of the number killed per predator and the number of predators that are present. Solomon (1949) has aptly proposed two terms to describe this twofold nature of predation: the functional response, concerning prey consumption, and the numerical response, concerning the density of predators. Thus the basic components arising from the two universal variables can be considered as the functional responses of the predator to prey and predator density, and the numerical response. Since the numerical response is largely the outcome of the effects of food consumption on reproduction, immigration, emigration and mortality, it follows that the functional responses, which are measured in terms of food consumption, are of central importance. A large part of the predation process will therefore be explained by an analysis of the functional responses to prey and predator density. As a start, then, it is logical to concentrate on the functional responses.

A number of components of the functional responses have been identified (Holling 1961) and are shown in Fig. 1. The components that occur in real situations are shown in the first row of the figure. If a particular component is present in all situations, i.e. is basic, only a "yes" occurs, but if a component is subsidiary, or present in some situations and not in others, both a "yes" and "no" are noted. The connecting lines indicate all possible combinations that can occur in different examples of the response and since there are five subsidiary

POSSIBLE COMPONENTS OF FUNCTIONAL RESPONSES TO PREY AND PREDATOR DENSITY										
ACTUAL COMPO- NENTS	RATE OF SUCCESS-FUL SEARCH	TIME EXPOSED	HAND-LING TIME	HUNGER	LEARNING BY PRED.	INHIBI-TION BY PREY	EXPLOI-TATION	INTERFE-RENCE BETWEEN PREDATORS	SOCIAL FACILI-TATION	AVOI-DANCE LEARNING BY PREY
	YES	YES	YES	YES	YES	YES	YES	YES	YES	YES
				NO	NO	NO			NO	NO
COMPONENTS INCLUDED IN OTHER PUBLISHED MODELS	LOTKA (1923) AND VOLTERRA (1931)	YES	—	—	—	—	—	—	—	—
	THOMPSON (1924)	YES	YES	—	—	—	YES	—	—	—
	NICHOLSON AND BAILEY (1935)	YES	YES	—	—	—	YES	—	—	—
	GAUSE (1934) AND IVLEV (1945, 1961)	YES	YES	—	YES	—	—	—	—	—
	RASHEVSKY (1959, equation 5)	YES	YES	—	YES	—	—	—	—	—
	WATT (1959)	YES	YES	—	YES	—	—	YES	—	—
COMPONENTS INCLUDED IN COMPONENT ANALYSES TO DATE	"DISC" EQUATION (HOLLING 1959)									
	"INVERT." F.R. MODEL (PRESENT PAPER)									
	"VERTEBRATE" F.R. MODEL (HOLLING IN PRESS)									

Fig. 1. The components of the functional response to prey and predator density, and the scope of various predation models.

components, there are five dichotomies and therefore 2^5 or 32 different kinds of responses to prey and predator density.

The first six components are involved in prey density effects, and the first three are basic to these effects, since every predator has to have a particular rate of search, has to be exposed to prey, and has to spend time handling prey if it is ever to catch them (Holling 1959b). Effects of the next component, hunger, were originally thought to be absent in at least some situations since some predators (e.g. cats) continue to attack and kill even though satiated. Once the analysis in this paper was completed, however, it seemed more likely that hunger still affects attack in these cases but in a restricted way. Nevertheless, since it is possible to devise an artificial predator-prey system (Holling 1959b) in which hunger definitely is not involved, this component will still be considered as subsidiary. The next two components are definitely subsidiary as a recent paper shows (Holling 1965). The learning component has been variously labelled as "development of a specific searching image" (Tinbergen 1960) and as "stimulation of specific searching by prey discovery" (Holling 1961) since some predators,

particularly vertebrates, learn to search specifically for those prey whose stimuli have become associated, through experience, with a palatable reward. The final, sixth component involved in the response to prey density assumes importance when prey, because of their unpalatability (Holling 1965) or energetic defence (Morris 1963), inhibit further attack for a time after a contact.

The remaining four components are involved in the effects of predator density. The exploitation component arises because predators compete for the same resource. Thus, as the density of predators increases, the chance that any predator will discover an unattacked prey decreases. Coupled with this is an interference component that becomes progressively more important as predator density rises and contacts become more frequent. Both these components of the functional response to predator density are probably universal, or basic, for all individual predators compete with others of the same species for the same resource and probably interfere with one another in so doing.

Exploitation and interference seem to be the only components involved in some examples of functional responses to predator density. They cause a regular decline in attack as predator density increases. In other cases, however, predation initially rises as predator density increases because contact with other animals of the same kind can stimulate a predator to eat more, to search more rapidly, or to capture prey more readily (Holling 1961, p. 173). This can be termed social facilitation, the ninth component in Fig. 1. The tenth and final component becomes important for those prey that can, through associative learning, learn to avoid a specific predator they have encountered before. The greater the density of predators, the greater will be the chance that each prey will have acquired an effective way of avoiding attack.

Figure 1 also provides a convenient way to demonstrate and compare the scope of various predation models published by other workers. All of these models consider the first two components, since it is impossible to even think about predation unless the predators are assumed to search for and to be exposed to prey. The basically similar functional response models of Lotka (1923) and Volterra (1931) do not go beyond this point so that the number of prey attacked is represented simply as a linear function of prey and predator density. Thompson (1924) and Nicholson and Bailey (1935) made a significant advance by including an exploitation component based on the assumption that predators search randomly. As Watt (1959) has shown, these latter two models are basically the same, as are models presented by Beverton and Holt (1957). The main assumption is that the rate of change of attack with respect to predator density is proportional to the density of undiscovered prey. That is,

$$\frac{dN_A}{dP} = a'(N_0 - N_A),$$

which integrates to

$$N_A = N_0(1 - e^{-a'P}),$$

where

N_A = number of prey attacked,

N_0 = density of prey,

P = density of predators,

a' = a constant.

This equation effectively takes into account the gradual decrease in the density of an exploited prey population. Its form, however, tempts one into the belief it covers a larger number of components than it does in fact. Consequently, the adequacy of the model has been tested using experimental data that are affected

not only by exploitation but many other components as well (Varley and Edwards 1957; Tinbergen and Klomp 1960). Inevitably, therefore, the model's descriptive powers are shown to be quite inadequate, but this is only because it is incomplete and not necessarily because it is unrealistic. When the adequacy of the model is tested using data more suited to its scope (by holding prey density constant, and varying predator density) it does satisfactorily describe some interactions (Kuno 1962), although even here components other than exploitation do show some effect.

The next model listed in Fig. 1 was originally developed by Gause (1934) and later used extensively by Ivlev (1945, 1961). This model extends the greatly simplified model of Lotka and Volterra to include the hunger component. Gause assumed that a predator can generate a certain maximum number of attacks, K , and that the rate of attack is proportional "to still unutilized opportunity" for attack. That is,

$$\frac{dN_A}{dN_0} = a''(K - N_A),$$

which integrates to

$$N_A = K(1 - e^{-a''N_0}),$$

where a'' = a constant, and K = maximum number of attacks that can be generated. In experiments in which predator density was held constant the model has been shown to describe adequately the effect of prey density on attack by a number of different species of predator and parasitoid (Ivlev 1945, 1961; Watt 1959). The adequacy of the explanation incorporated in the model is more suspect however (Holling 1959b) and it ignores many components that are obviously important. In an important paper, Rashevsky (1959) has carefully analyzed the structure of this model to show the precise biological meaning of its parameters. He points out that the predator is assumed in the model to have a continual input of energy and no output. Since food is actually continually being removed from the gut for energy consumption and fecal production, Rashevsky modified the model to account for these changes (his equation (15), *op. cit.*), and thereby expressed the hunger component in a more realistic way. The effectiveness of this revision in improving explanatory and descriptive powers has not yet been assessed experimentally.

Finally, Watt (1959) developed the most complete model to date. He incorporated the effects of hunger in the same way Gause did but added to this the effects of exploitation and interference. The specific way these latter components were added was dictated more by the demands of the mathematical language chosen (calculus), however, than by real animals, so that it is unlikely that this portion of his model provides much more than a very approximate explanation. Nevertheless the model describes very well the effects of prey and predator density on attack by a variety of parasitoids in the laboratory (Watt 1959) and in nature (Miller 1959, 1960). Because it includes more components than any other model and because it describes many interactions so well, this model can be a very useful tool whenever a simple description of attack, as distinct from an explanation, is required.

All these published models share three drawbacks. First, since so few components are considered, the models are extremely restrictive. While no model should be so complete that it is mired in superficial detail, it should be sufficiently complete to suggest at least some of the diversity that can occur. The various combinations of basic with subsidiary components shown in the top row of Fig. 1 suggest 32 different kinds of predation and yet each of these models suggests only one. Secondly, the choice of calculus as the language of expression imposes

major limitations. The more components included, the more obvious this becomes, since it becomes progressively more difficult to include new components in a differential equation and even more difficult to integrate it. The models therefore tend to be dead ends, preventing future revision and expansion. Thirdly, the assumptions upon which the models are based have not been accepted on the basis of specific experiments designed for that purpose. The choice has been largely intuitive, supported by general observation and indirect evidence. Although such a technique has proved to be very profitable when applied to simple processes of classical physics, it can be grossly misleading when applied to more complex biological processes. When so many components operate, their mode of action and interaction is not intuitively obvious so that the analysis must be given detailed direction through an intimate wedging of theory and experiment. The present analysis of predation, of which this paper is a part, has been designed to avoid these three limitations.

Because of the gradual, step-like progression of this analysis, it is important for the reader to be aware precisely where the present paper fits into the overall research program. The components that have been included in the analysis to date are also shown in Fig. 1. The first step in the analysis of the functional responses employed an artificial system in which a blindfolded subject — the "predator" — searched for sandpaper discs — the "prey" — tacked to a table at different densities (Holling 1959b). The only components affecting the response were the rate of search, the time "predator" and "prey" were exposed and the time spent handling discs after they were located, features common to every attack situation. The example therefore represented the basically simple type required in the first step of the components analysis and its analysis led to the development of the "disc" equation (Fig. 1) which accurately described and explained the observed response to disc density.

This equation can be developed from one of the simplest expressions of the effects of prey density on attack:

$$N_A = aT_T N_0, \quad (1)$$

where

N_A = number of prey attacked,

a = rate of successful search,

T_T = time the prey are exposed to the predator,

and

N_0 = prey density.

Equation (1) states that the number of prey attacked rises indefinitely as a linear function of prey density. The observed response to disc density was quite different, however, for the number of discs picked up increased at a progressively decreasing rate to a sustained maximum. The departure from the prediction of equation (1) was caused by the time spent handling discs — time that was removed from the total time available. Therefore the time prey are exposed to predators should be reduced by the time required to handle prey in order to yield the actual time spent searching. If

T_H = the time spent handling each prey (time to pursue, capture, kill and eat), then equation (1) can be rewritten as

$$N_A = a(T_T - T_H N_A)N_0, \quad (2a)$$

or, transposing,

$$N_A = aT_T N_0 / (1 + aT_H N_0) \quad (2b)$$

In the next step of the analysis the basic explanation embodied in equation (2a) was extended to include the effects of hunger. This is the step reported in this paper and the resulting model is labelled the "invertebrate" functional response model in Fig. 1, since it will be shown in a later section that it describes the form of all the responses that have been obtained using invertebrate predators (11 different species).

A further step beyond this has been taken and this is labelled in the figure as the "vertebrate" functional response model (Holling 1965). It extends the explanation to include learning and prey inhibition components. The addition of the learning component produced a model that reproduces the salient features of the responses of vertebrates, which in all the cases studied so far are distinctively different from those of invertebrates. It is likely, however, that future studies will show that some invertebrates with highly developed learning ability (e.g. Hymenoptera and cephalopods) have responses similar to those of vertebrates. Thus the labelling of the response models as invertebrate or vertebrate should be considered only as a convenience.

THE ANALYSIS

The Experimental Animals

The predator chosen for most of this analysis was the praying mantid *Hierodula crassa* Giglio-Tos. The original colony was established in the laboratory from stocks provided by Dr. H. Mittelstaedt, who has used the species extensively in his intriguing analyses of orientation to prey, using systems control theory (Mittelstaedt 1954, 1957). The animal is not greatly disturbed by handling and is readily reared in the laboratory at 27° C. and 60 to 70% R.H. First-instar nymphs were fed wingless *Drosophila melanogaster*, second to third instars were fed *Drosophila virilis*, and the remaining instars were provided with houseflies, *Musca domestica*.

H. crassa, like many insect predators, waits in ambush for its prey. It hangs upside down from any convenient surface and rarely moves except to stalk or strike at prey. Other locomotor movements seem to be exclusively restricted to mating or egg-laying behaviours (Roeder *et al.* 1960). The attack behaviour itself has been frequently described (Mittelstaedt 1957; Rilling *et al.* 1959). The mantid locates prey with its well-developed compound eyes, and when a fly moves into the visual field it is fixated by a movement of the mantid's head. If the fly moves still closer the mantid may begin stalking or pursuing it—a very slow, deliberate movement often accompanied by a distinctive swaying motion of the whole body. The mantid finally may strike at the fly if it comes in reach of the grasping forelegs, which are well suited to capture objects of certain sizes efficiently (Holling 1964). The release of these various behaviours of course depends on the internal state of the animal and to a large extent the experiments reported here were designed to show how one kind of internal motivation, hunger, affected attack behaviours.

Since the mantid was chosen simply as a "hunger" analogue of all invertebrate predators, I wanted to choose individuals with high food consumption and in as constant and reproducible a condition as possible. Initially I decided to choose adult insects because of their long life (over two months), but it was also important to determine the effects of adult age on consumption of prey. Eight female and 11 male mantids therefore were individually caged in small boxes measuring 19 × 10 × 7 cm. and were provided daily with a surplus of flies (50 per cage) from the first day after adult eclosion. On the fifth day the females

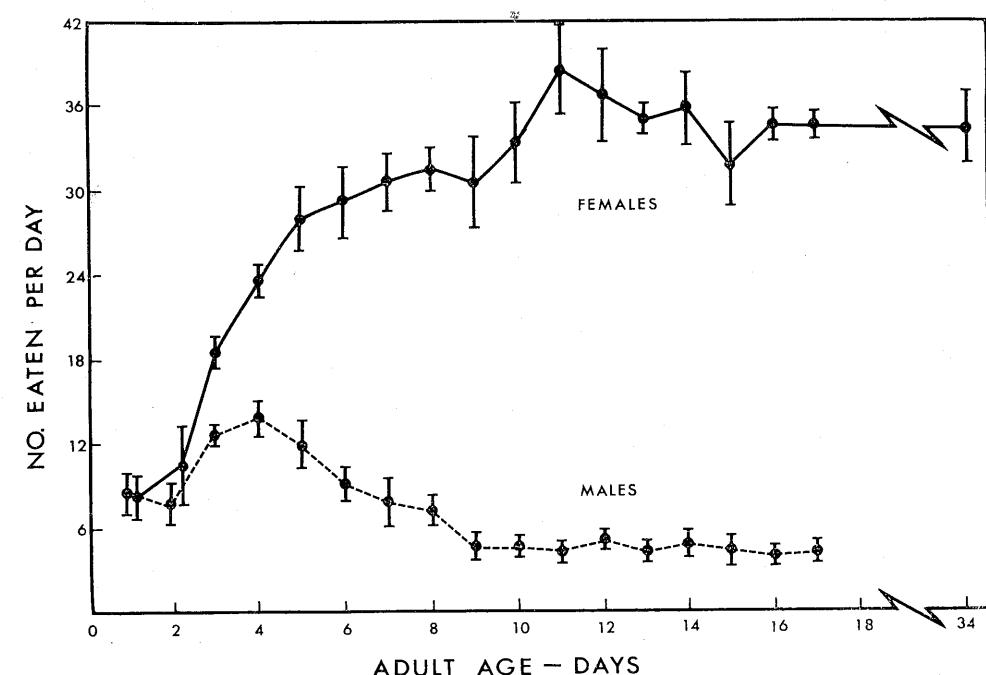


Fig. 2. Effect of age on the number of prey eaten per day per mantid by 11 male and 8 female *H. crassa*.

were mated. Figure 2 records the daily consumption and shows that females ate considerably more than males. The consumption by both sexes initially increased, presumably resulting in a postmoult growth. After the fourth day, however, consumption by males began to decline, and finally stabilized at a very low value after the tenth day. Consumption by females, however, continued to rise, presumably because of the demands of egg production, to finally reach a maximum by the eleventh day. Consumption remained relatively constant thereafter for at least another 23 days, when the experiment was terminated. The only exception occurred when egg cases were laid—usually about a month after adult eclosion. For one day before and one day after egg-laying, consumption often dropped to a very low value. On the basis of these data the standard mantid was chosen as a mated female with an adult age between 11 and 40 days. Whenever one of these "standard mantids" laid eggs during an experiment the data collected on the day before and after were deleted.

The response to prey can change not only between days but within a day as well, because of diurnal or circadian rhythms of feeding activity. All mantids were reared after hatching under controlled light conditions with 16 hours of light (0700–2300 hours E.S.T.) alternating with 8 hours of dark (2300–0700 hours E.S.T.), so that it seemed reasonable that these visually oriented animals would have assumed a light-dominated periodicity. To test this, six standard mantids were placed in individual cages under continuous light for 48 hours. Every two hours during this time each mantid was fed until, for three consecutive times, it refused to eat when the juices of a crushed fly were touched to its mouthparts. It had been found earlier that mantids that were too satiated to strike and capture prey themselves could be induced to eat more food by force-feeding in this manner. The weight of food eaten is shown in Fig. 3. Despite the continuous

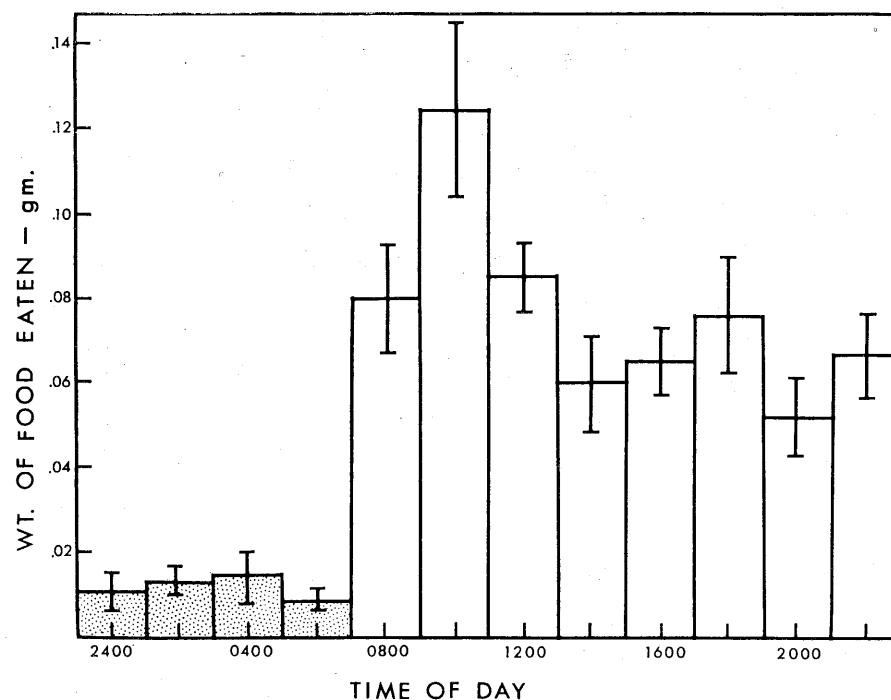


Fig. 3. Diurnal rhythm of feeding activity of standard female *H. crassa* (average of 12 replicates).

light, the mantids still maintained a feeding rhythm identical with the light-dark rhythm to which they had previously been exposed. During the period in which darkness normally occurred, only about 0.01 g. of food was eaten every 2 hours — less than half the weight of a single fly. Once 0700 hours was reached, when the lights normally came on, the consumption increased abruptly and stayed at a high level for 16 hours. There was a distinct tendency for the consumption to be higher at the beginning of the period of high feeding activity, probably in order to make up for the previous 8 hours of low food consumption. Since the mantids showed such a pronounced diurnal rhythm in feeding, all measurements of attack behaviours were confined to the 16 hours between 0700 and 2300 hours.

The prey used in all experiments, except where indicated, were adult female houseflies that had emerged from puparia at least 4 days previously. The flies were reared on an evaporated milk, yeast, water, and cellucotton mixture following the technique of Fisher and Jursic (1958). All the puparia were first screened through a sieve with openings 2.83 mm. wide and then through one with openings of 2.38 mm. Only puparia retained by the smaller meshed screen were retained. When adults emerged they were continually provided with a dry mixture of yeast, milk powder, and sugar (1:3:6), a liquid mixture of evaporated milk and water (1:1), and water. The flies produced in this way were very constant in size; the females used in the experiments averaged 0.0245 ± 0.0003 g. ($N = 325$).

General Form of Functional Response to Prey Density

The "disc" equation provides a useful start for the analysis. Rather than considering it as a specific model of a basic functional response, it can usefully be considered simply as a generalized statement of fact in which the parameters a ,

T_T and T_H are not presumed to be constants but to be components with unspecified values. Thus equation (2a), which reads:

$$N_A = a(T_T - T_H N_A) N_0,$$

states that at any one density of prey the number of prey attacked by one predator depends only on the predator's rate of successful search (a), on the time the predator and prey are exposed (T_T) to each other and upon the time spent handling each prey (T_H), irrespective of the number of components involved in the particular example. The effect of any subsidiary component, like hunger, can then be considered as exerting its effect through any one or all of the three basic components.

Each of these three components can be completely defined in terms of discrete subcomponents as follows (Holling 1963):

- (1) Rate of successful search:
 - (a) the reactive distance of the predator for prey, i.e. the maximum distance at which a predator will react by attacking prey,
 - (b) speed of movement of the predator,
 - (c) speed of movement of the prey,
 - (d) the capture success, i.e. the proportion of prey, coming close enough to be attacked, that are successfully captured.
- (2) The time prey are exposed to predators:
 - (a) the time spent in activities not related to feeding, e.g. non-feeding periods,
 - (b) the time spent in activities related to feeding.
- (3) Time spent handling each prey:
 - (a) time spent pursuing and subduing each prey,
 - (b) time spent eating each prey,
 - (c) time spent in a "digestive pause" after a prey is eaten and during which the predator is not hungry enough to attack.

Hunger, the new component involved, could conceivably affect nearly all of these nine subcomponents. A hungry predator, for example, might move faster, react to more distant prey, capture more successfully, spend more time in a feeding period and spend shorter times in pursuit, eating and the "digestive pause", than a sated predator. Even the speed of movement of the prey might be affected, since some prey might be able to detect and react to predator behaviours that are affected by hunger. It is likely, however, that such a response would be restricted to vertebrate prey only. Before these effects can be examined, however, it is necessary to obtain a measure of hunger itself.

Hunger

Hunger is, of course, an internal motivational state, but it can be defined operationally in terms of its effect on behaviour. There are many behaviours it can affect but it is most useful to select one that closely reflects the internal condition of the animal. A convenient measure is the weight of food necessary to return the animal to a condition of complete satiation, since this weight is a measure of the emptiness of the digestive tract. Hence hunger will be defined here as the number of grams of food required to satiate a mantid. The criterion of satiation was three consecutive refusals to eat crushed flies that were touched

to the mantid's mouthparts. When a mantid is satiated in this way no other method could be discovered to make it eat more. The experiments designed to investigate hunger and all the experiments described in this paper were conducted at $27 \pm 1^\circ \text{C}$. and 50–60% R.H.

In order to determine the effects of food deprivation on hunger, 12 standard mantids were fed to satiation and each was subsequently deprived of food for various intervals of time from $\frac{1}{2}$ to 72 hours. All deprivation times were arranged to end during the normal feeding period of the mantid (at least between 0800 and 2200 hours E.S.T., cf. Fig. 3), and each mantid was tested once at each deprivation time. Otherwise the times were assigned randomly. At the end of each interval of deprivation the mantids were fed flies weighed to the nearest 0.01 mg.

Figure 4A shows how the weight of food required to satiate or hunger (H) changed with time of food deprivation (TF). As the time increased, the hunger also increased, but at a progressively decreasing rate up to a sustained maximum. One of the simplest ways to express these effects would be to assume that the rate at which hunger changed with time was directly proportional to the amount of food in the gut. When the gut was very full the rate of change of hunger would be greater than when the gut was nearly empty. The measure of hunger used here is really a measure of the amount of food that has been assimilated and evacuated from the gut, so that the amount of food left in the gut can be expressed as $(HK - H)$, where $HK =$ maximum amount of food the gut can hold. Hence the assumption above can be written as

$$dH/dTF = AD(HK - H)$$

where $AD =$ a constant, the rate of food disappearance. This integrates to

$$H = HK(1 - e^{-AD(TF)}). \quad (3)$$

This equation can be transformed into a linear form as follows:

$$(HK - H)/HK = e^{-AD(TF)}$$

whence

$$\ln \left(\frac{HK}{HK - H} \right) = AD(TF). \quad (4)$$

Equation (4) provides a way to test the descriptive powers of the original assumption, for if equation (3) does describe the relationship adequately, then a plot of $\ln \left(\frac{HK}{HK - H} \right)$ vs. TF should yield a straight line passing through the origin, with slope AD . If enough values of hunger are obtained well on the plateau, HK can be measured directly as an average of these values. In the present case, however, only the one value of 0.97 at 72 hours could be confidently placed very near the plateau so that HK was selected instead by an iterative technique in which the HK that maximized the correlation coefficient was considered to be the correct one. In this case the HK equalled 1.001 g., very close to the highest hunger observed at 72 hours.

The appropriate transformation using this value for HK is shown in Fig. 4B. Although the relationship is satisfactorily linear, as required by the postulate, the line does not go through the origin but cuts the ordinate above zero. When equation (4) is modified to include an intercept, and the specific values obtained for the slope and intercept are placed in an equation with form similar to equation (3), predicted hungers can be generated to produce the line and equation shown in Fig. 4A. This line describes very satisfactorily the relationship but again the

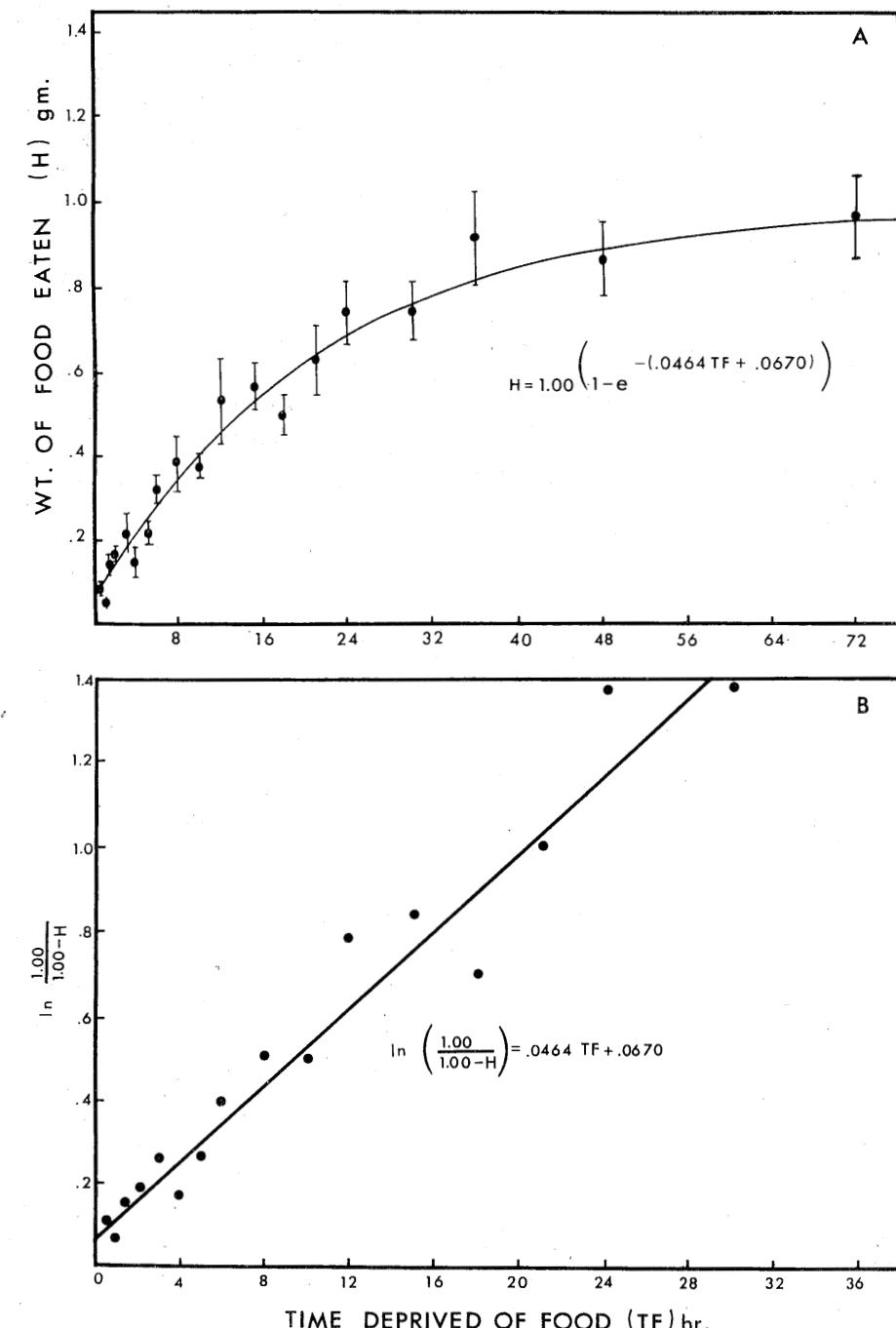


Fig. 4. The effect of time of food deprivation on hunger of *H. crassa*. A: untransformed data (average of 12 replicates \pm 1 S.E.). B: data transformed to test conformity of data to equation (4).

curve does not go through the origin. This obviously is unreasonable, and can be partly attributed to a weighing error. Earlier it was mentioned that the criterion of satiation required that each mantid reject the last three flies offered. As a result, remains of the last three flies were always left and these had to be weighed in order to determine the actual amount eaten. Because of the demands of the experiment this weighing could only be done some hours later and it was discovered that there was a significant weight loss during this period that averaged 0.00583 g. per fly (approximately 25%). Thus each measure of hunger should actually be reduced by 0.01749 g. (3×0.00583) to compensate for this weighing error. This correction would affect the low hungers proportionately more than the high ones and therefore tend to make the curve run closer to the origin. When this correction was made the y-intercept in Fig. 4A was in fact lowered from 0.0650 to 0.0475 g., but since the improvement was relatively minor it was not included. It is likely that this departure from the expected, although barely significant statistically ($P = 0.05$), is biologically real. The most likely cause is a nutritional deficit acquired after long periods of food deprivation, a deficit that cannot be made up at one sustained feeding but shows its effects on subsequent feedings as well. Since long deprivation times tended to be followed by shorter ones, therefore the hunger measured at these shorter intervals tended to be higher than the actual deprivation time would warrant.

Despite the long-term effects of this nutritional deficit, however, the data do not depart greatly from those required in the original, simple assumption. A quite adequate description is still obtained if a line is fitted to the data in Fig. 4B by forcing it through the origin. Thus the intercept becomes zero and the slope (AD) increases to 0.05013. The inherent variability of the data does not justify a more rigorous treatment.

In order to assure that the hunger equation has general application it is essential to test its descriptive power using a variety of species. An adequate test requires so many measurements, however, that it is extremely difficult to find these kinds of data in the literature. In order to provide some basis for accepting the generality of the equation, similar data therefore were also obtained for another species of mantid, *Mantis religiosa*, which is considerably smaller than *H. crassa*. Specimens were collected in nature and 11 females of similar size were selected for testing. The experiments and treatment of the data were identical with those described above, except that the correction for the weighing error, discussed earlier, had to be applied because food consumption of *M. religiosa* was so much lower. The untransformed data are presented in Fig. 5A, and the transformation required to produce linearity in Fig. 5B. In both cases the line is based on the prediction of the hunger equation. Again equation (3) is shown to describe the data very well, although the values for the parameters are naturally different: AD larger at a value of 0.140 and HK much smaller at 0.109. The curve again cuts the ordinate, rather than going through the origin, but the departure is not statistically significant and forcing the line through the origin increases AD only a modest amount to 0.146.

The only other available data that were sufficiently detailed to permit an adequate test of the descriptive power of the hunger equation were obtained by Green (in press) in a study of the effect of hunger on activity of the blowfly, *Phormia regina*. Dr. Green kindly provided me with his original data, which were replotted to conform with the graphs presented above. Hunger was determined in two ways: by measuring the volume of a 0.5 M sucrose solution imbibed by the flies (Figs. 5C and D) and by measuring the change in volume of the crops

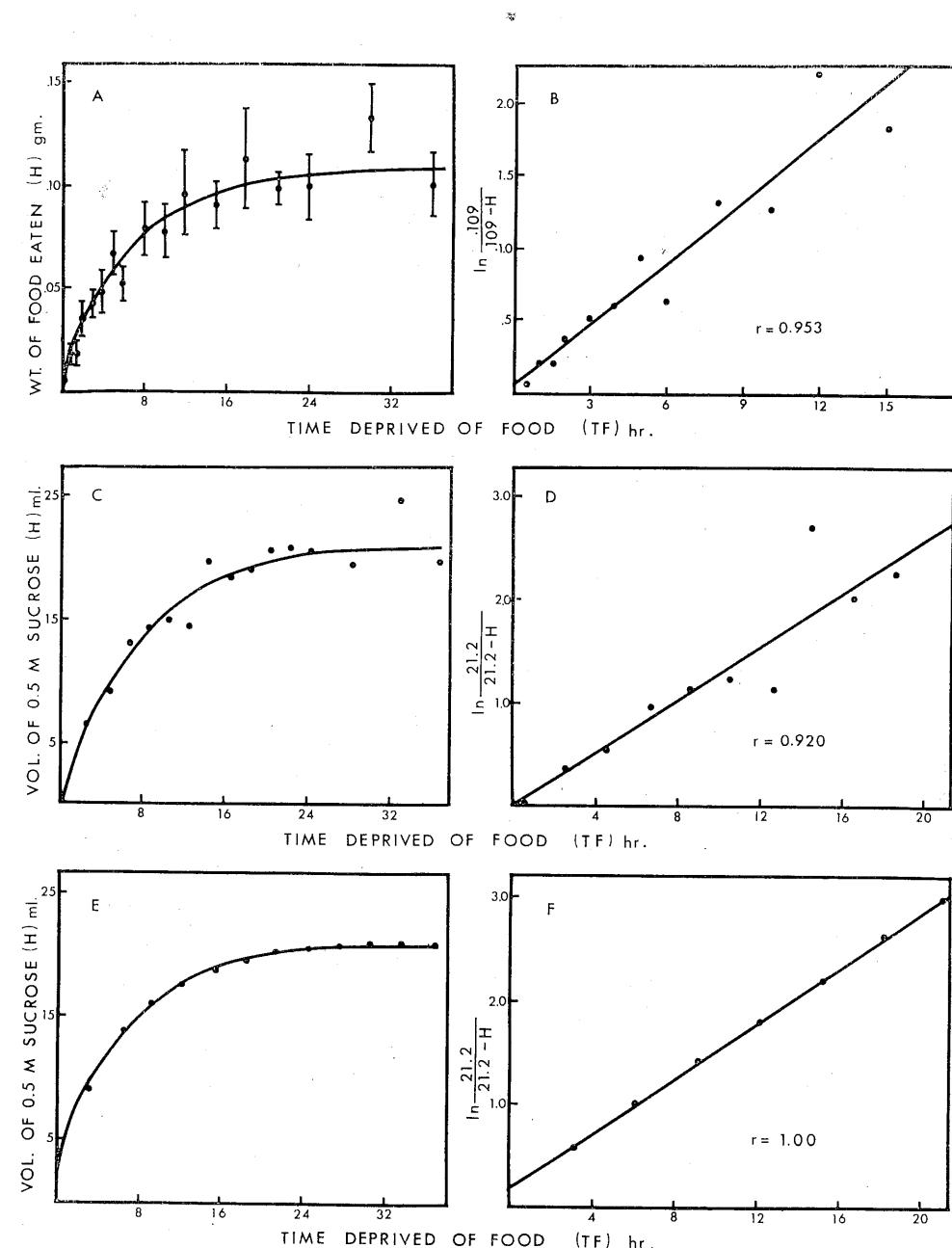


Fig. 5. Effect of time of food deprivation on hunger. A and B: untransformed and transformed data (average of 11 replicates ± 1 S.E.) for *Mantis religiosa* eating houseflies. $H = 0.109 (1 - e^{-0.140TF + 0.0588})$. C and D: untransformed and transformed data (average of 5 replicates) for *Phormia regina* consuming a sugar solution (Green 1965), with hunger measured by the volume of solution imbibed, $H = 21.2 (1 - e^{-0.129TF + 0.0009})$. E. and F: untransformed and transformed data (average of 9 replicates) for *Phormia regina* consuming a sugar solution (Green 1965), with hunger measured by the volume of solution disappeared from the crop. $H = 21.2 (1 - e^{-0.134TF + 0.188})$.

of flies using an X-ray technique (Figs. 5E and F). As the graphs show, the postulate embodied in the hunger equation seems to apply as well to blowflies as to mantids. The closeness of the fit to the data obtained from direct measurements of crop volume is particularly convincing, since the variability is so small. In this case, however, the intersection of the line with the ordinate is probably the result of an error in estimating the starting volume of the crop. It was not practically feasible to measure directly the volume at the point of satiation so Green derived a value by visually extrapolating the curve. Any error in this estimate would affect the Y-intercept. With the exception of the differences between Y-intercepts, the data obtained using the two methods are practically identical. In each case $HK = 21.2$ and the values for AD are very similar (0.129 for the data in Figs. 5C and D, and 0.134 for the data in Figs. 5E and F). Thus, as assumed earlier, the amount of food consumed closely approximates the amount of food removed from the digestive tract through assimilation and evacuation.

Although the data in the literature concerning hunger curves of other species do not justify a test of the goodness-of-fit of the hunger equation, the curves obtained for locusts (Edney 1937), a salamander (Goldstein 1960) and the rat (Siegel and Steinberg 1949; Cotton 1953) have the same general form as the hunger curve of mantids — i.e. a negatively accelerated rise to a plateau. Tentatively, therefore, equation (3) will be accepted as a generalized equation that describes the way hunger changes with time. Later, when the generality of the model is discussed, ways will be suggested to incorporate modifications that might be significant for some predators. Now that an accurate description of hunger is available, it is next necessary to determine how the nine subcomponents listed earlier are affected by food deprivation, and, ultimately, by hunger.

Interaction of Hunger With Other Components

Rate of Successful Search

Size of the Area of Reaction of Predator for Prey

Mantids are visual predators and will stalk and strike at a fly behind a glass barrier or at model prey constructed from paper (Rilling *et al.* 1959). A specific kind of movement seems to be the critical stimulus that releases attack, since potential prey, whether real or artificial, are ignored until they move with the distinctive jerky movements characterized by many insects. Rilling *et al.* (*op. cit.*) found that they could duplicate this movement by attaching the prey to a thread, and twisting it irregularly, first in one direction and then another, so that the prey twirled at about 18 cycles per second. This technique provided a convenient method to measure the maximum distance of reaction of *H. crassa* at various levels of hunger.

The detection of a prey by a mantid can release three kinds of reaction: awareness, as indicated by a movement of the head, stalking or pursuit, and striking. Since awareness could be triggered without subsequent stalking or striking, most of the experiments concerned the stalk and strike response.

The maximum distance of pursuit or strike was measured by dangling a fly on a thread some distance in front of a mantid, and, as it was twirled, gradually moving it closer. When any one of the four walking legs moved or when the mantid struck, the distance between the prey and the mantid was then noted as the maximum distance of stalking or striking. Each mantid was tested in a cage $35 \times 12 \times 12$ cm. made from translucent white plastic and illuminated by two daylight fluorescent tubes running the length of each cage and placed 40 cm. from the back. Flies were dangled through a slot on the top, 1 cm. wide, that ran the

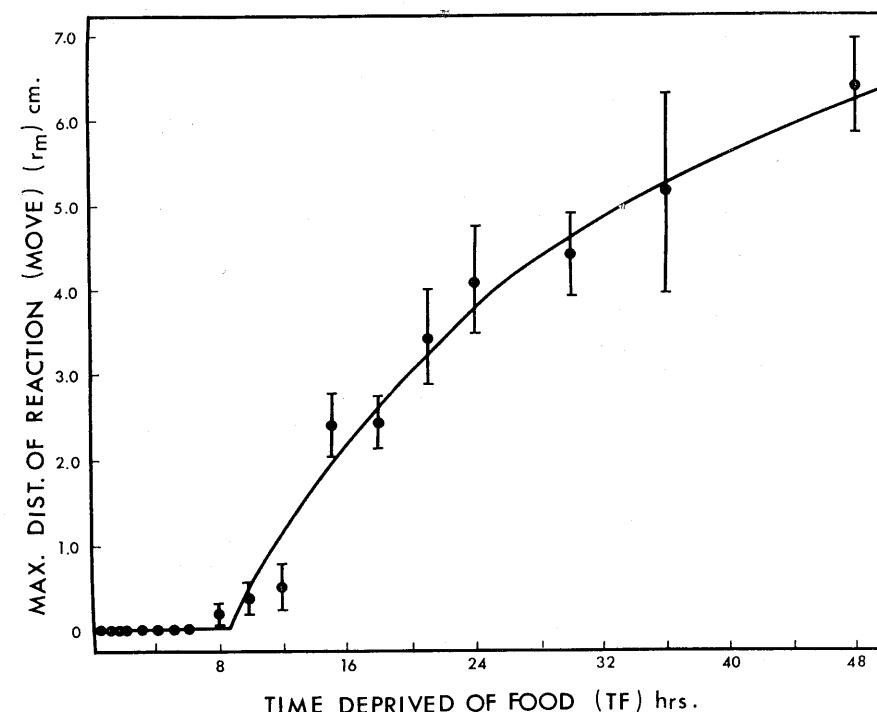


Fig. 6. Effect of time of food deprivation on the maximum distance that *H. crassa* stalked or struck at flies (average of 12 replicates \pm 1 S.E.).

length of the cage. The data were collected from the same 12 standard *H. crassa* used in the hunger experiments described in the previous section.

The effect of duration of food deprivation on the maximum distance of pursuit or strike, r_m , is shown in Fig. 6. No response, either stalking or striking, could be elicited less than 8 hours after satiation. Thereafter, the maximum distance of reaction increased in a curvilinear fashion as the time of food deprivation increased. When the same measurements of pursuit or strike distance are plotted against hunger level, rather than time of food deprivation, a straight line describes the relationship very well (Fig. 7). Again a threshold emerges as a significant feature, for below a hunger level of 0.369, no stalking or striking occurs and above it the maximum distance of reaction becomes progressively greater.

Recently, additional experiments have been conducted using model prey of different sizes and these data show that the hunger level that triggers attack changes with prey size. But more important for the present purpose, these data suggest that the relation between r_m and H is actually curvilinear such that a plot of r_m^2 vs. H yields a straight line. Moreover, an analysis of the mechanics of binocular vision has suggested that the accuracy of distance perception is also a linear function of the square of the distance between the viewer and the object. If different levels of hunger simply require different degrees of accuracy in the estimate of distance before an attack is initiated, and if this relation is linear, it follows therefore that r_m^2 , rather than r_m , should be a linear function of hunger. However, since additional data are still being collected in order to satisfactorily support this relation, for the purpose of the present paper it will be assumed that there is a linear relation between r_m and H . If this assumption is grossly in error

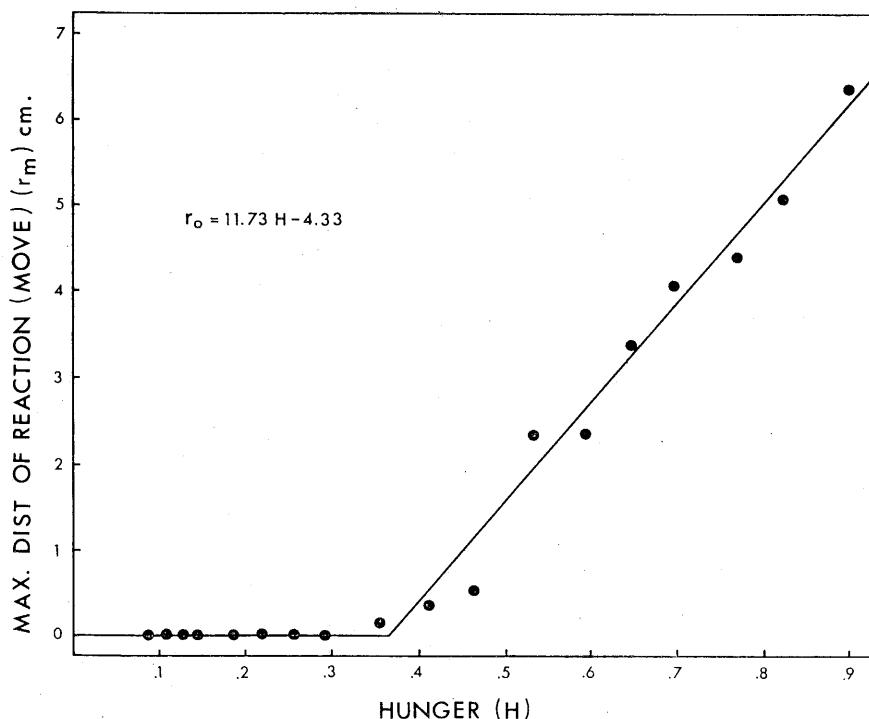


Fig. 7. Effect of hunger on the maximum distance that *H. crassa* stalked or struck at flies (average of 12 replicates).

it should become apparent when the predictive powers of the final model are tested.

Since a straight line does satisfactorily describe the relation in Fig. 7 we may write

$$r_m = GM(H - HT), \quad H > HT \quad (5)$$

and

$$r_m = 0, \quad H \leq HT \quad (6)$$

where

r_m = maximum distance of stalk or strike,

GM = the slope, a constant,

and

HT = the attack threshold.

In the present case $GM = 11.73$ and $HT = 0.369$. Moreover, since the relation between H and TF is provided by the hunger equation (equation 3) the maximum distance of stalk or strike can be expressed in terms of time of food deprivation by substituting (3) in (5). Thus

$$r_m = GM(HK - HT - (HK)e^{-AD(TF)}), \quad TF > TFT \quad (7)$$

and

$$r_m = 0, \quad TF \leq TFT \quad (8)$$

where

TFT = the TF when $H = HT$. This can be derived from equation (4):

$$TFT = \frac{1}{AD} \ln \left(\frac{HK}{HK - HT} \right).$$

The line drawn in Fig. 6 was derived from equations (7) and (8).

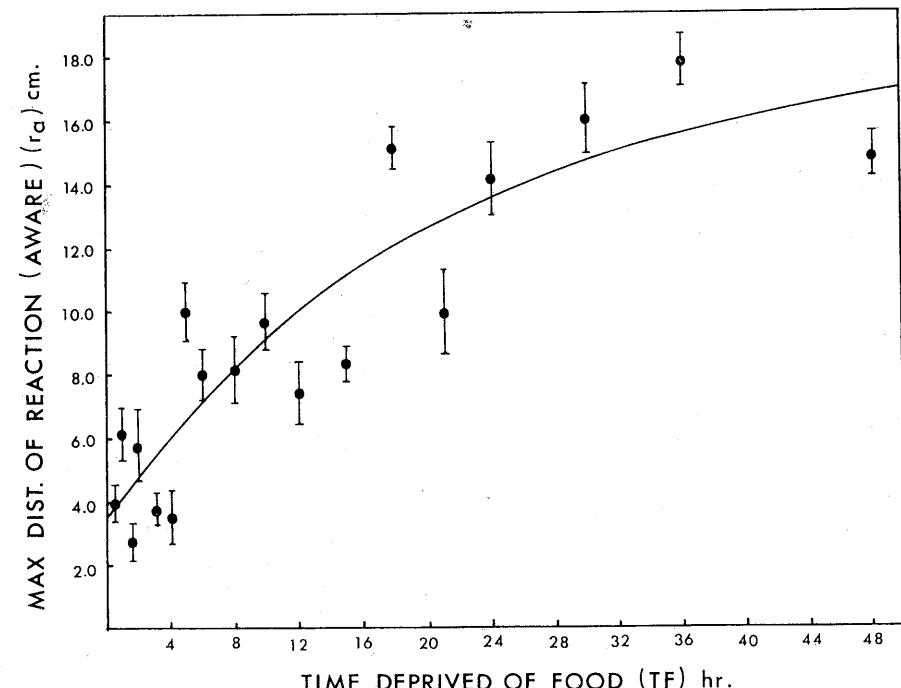


Fig. 8. Effect of time of food deprivation on the maximum distance that *H. crassa* became aware of prey (average of 12 replicates ± 1 S.E.).

While the distances of stalk and strike are the main determinants of the distance of attack by mantids, data were also collected concerning the maximum distance of awareness, r_a . These were obtained in the same experiments used to measure pursuit distances, but the criterion of reaction was the head movement made to fixate the fly. The data are plotted in Fig. 8, and show a curvilinear relation to TF, similar to that obtained for pursuit. When the maximum distance of awareness was plotted against hunger, a straight line again described the relation very well. The values for slopes and intercepts obtained from this transformation were placed in an equation with the same form as (7) to generate the line in Fig. 8. While the form of the relation between r_a and T_F seems to be the same as that between r_m and T_F , its magnitude is quite different. The mantids were always aware of the prey at much greater distances than they would stalk them. Moreover, no hunger threshold for awareness existed, since the mantids showed awareness of prey even when completely sated. This clearly has survival value, for while it is only necessary that hungry predators be aware of prey, it is extremely important that both hungry and sated predators be aware of potentially dangerous objects.

So far only the effects of hunger on the distance of reaction have been considered. As far as the number of prey attacked is concerned, however, it is the size of the whole reactive field that is important. The size of the field of a predator that searches in a three-dimensional manner — in water or air, for example — would be measured in terms of volume. The mantids in the experiments, however, confined their attack to those prey that appeared on a two-dimensional surface. In this case the effective field of reaction is a two-dimensional area. In order to obtain a measure of the area of this field it is necessary to measure not only the maximum distance of reaction directly in front of the mantid, as de-

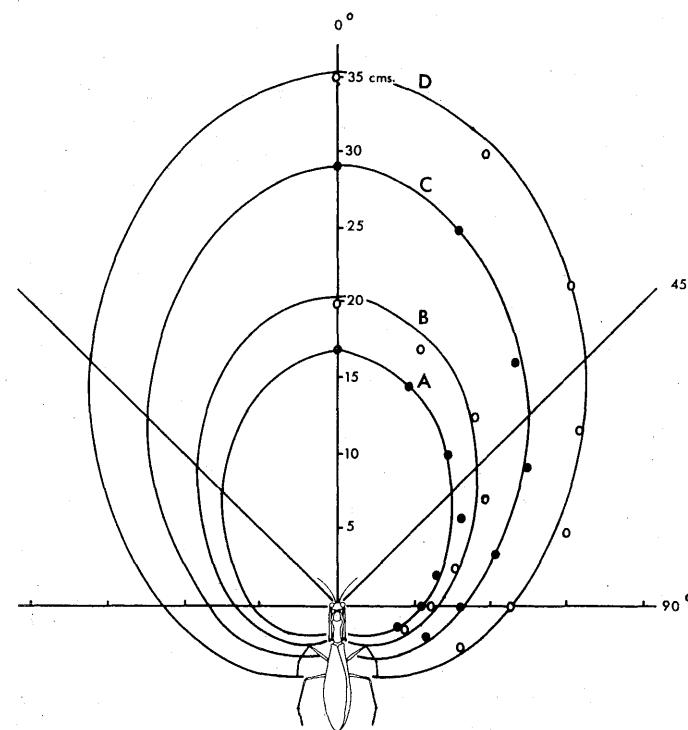


Fig. 9. Shape of reactive field of awareness of *H. crassa* at four different levels of hunger from low (A) to high (D) (average of 8 replicates).

scribed above, but at the side and rear, as well. Eight standard mantids were chosen for the experiments and initially each was kept for over 48 hours in the presence of an abundance of flies. Thereafter they were deprived of food for various intervals of time so that four levels of hunger were produced, with two mantids representing each level. The shape of the reactive field was determined by moving a fly, dangled on a thread, towards the mantid along radii set at angles to the body axis. When the mantid's head moved to fixate the fly, the distance was noted. Distances were measured along seven radii from 0° (directly in front of the mantid) to 108° , and, for each mantid, four replicates were made of the measurement on each radius (two on the right side, and two on the left). Since two mantids were tested at each hunger level there were therefore eight replicates of each measurement.

Figure 9 shows the shape of the four reactive fields of *H. crassa* as plotted using polar coordinates. As is expected from the previous discussion, the reactive fields at the lower levels of hunger are smaller than at the higher. Their shapes seem to be essentially the same, however, irrespective of size. In each case the maximum distance of reaction was greatest directly in front of the mantid (0°) and decreased towards its back. Although quantitatively accurate measures beyond 108° were difficult to obtain, enough additional tests were made to show that the mantid's visual field covers almost a full 360° . Sightings made of the pseudopupil (see example in Fig. 10) showed that binocular vision was restricted to part of this field — between approximately 310° and 50° .

If the same data are plotted using Cartesian coordinates, the maximum distance of reaction declines in an S-shaped manner as the angle to the body axis

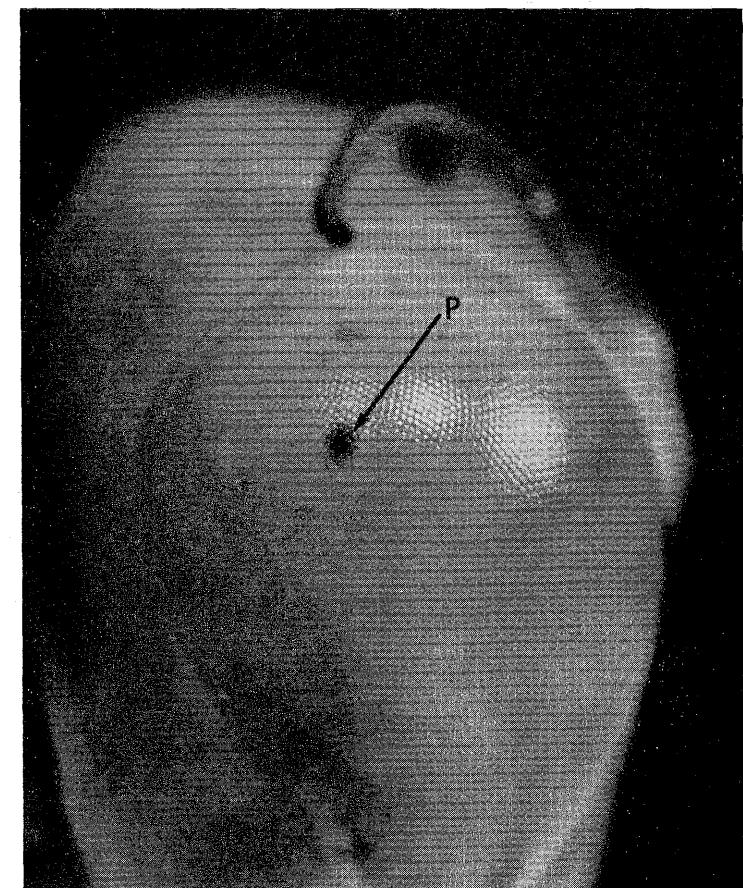


Fig. 10. Photograph of right eye of *H. crassa* to show the pseudopupil (P).

increases (Fig. 11). A curve of this shape is often produced when two components interact in opposite ways, so that a double transformation is often necessary to produce linearity. The first transformation that comes to mind concerns the distance of reaction itself. This distance must in part be a function of the size of the object viewed, since a larger object presumably could be noticed at a greater distance than a smaller one. The important determinant of awareness is likely to be angle subtended by the object, since this angle is a measure of the number of photoreceptors or ommatidia that are stimulated. This angle can be termed the angle of vision, and the minimum angle of vision for awareness would represent the angle subtending an object at the extreme boundary of the visual field (Fig. 12). If the size and maximum reactive distance are known, the minimum visual angle for awareness can be calculated from the expression

$$\tan \alpha/2 = L/2r_a,$$

whence

$$\alpha = 2 \arctan L/2r_a, \quad (9)$$

where

α = minimum visual angle for awareness,

L = length of prey,

and

r_a = maximum distance of awareness.

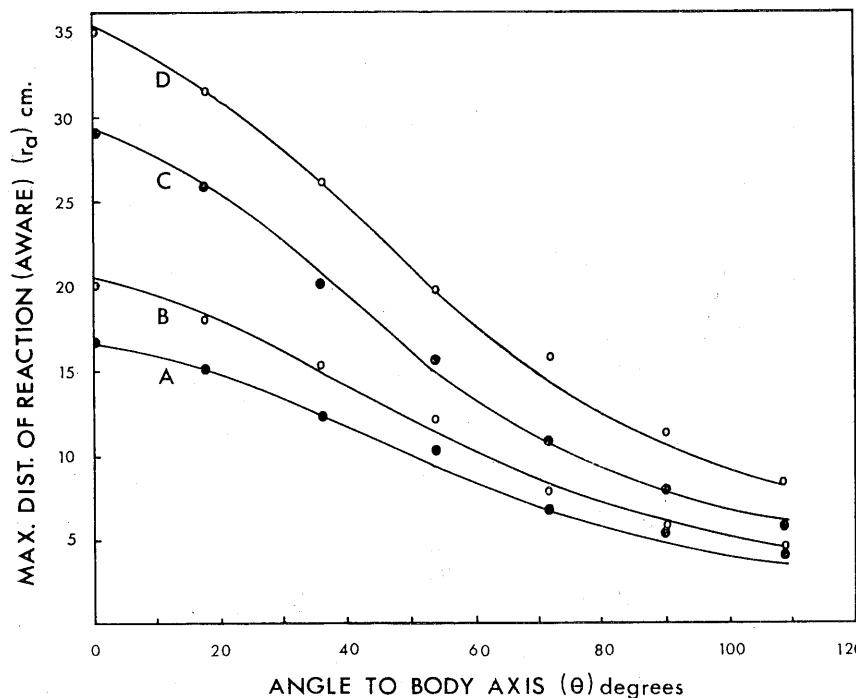


Fig. 11. Maximum distances of awareness of *H. crassa* for houseflies at four hunger levels in relation to the angle to the body axis (averages of 8 replicates).

In the present case the average length of the flies was 0.85 cm. so that the measurement of r_a can be transformed into α , the minimum visual angle, by using equation (9).

This transformation successfully changes the S-shaped curves of Fig. 11 to curves with slopes that change continually in one direction (Fig. 13). Since this graph depicts angles of vision rather than distances, the relations are reversed so that the minimum angle of vision increases as the angle to the body axis increases. This suggests that the effective size of the ommatidial angle may change in the same way from the front to the back of the eye, although the situation is complicated in the region of binocular vision where ommatidia from both eyes are stimulated. No sections of mantids' eyes were made to confirm this, since it would

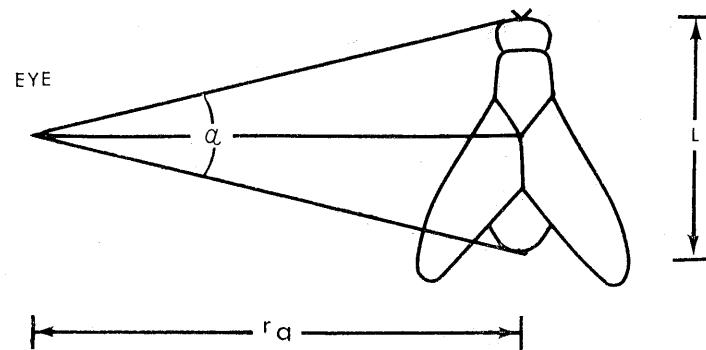


Fig. 12. Diagram to show the relation between the minimum angle of vision (α), and the size (L) and distance (r_a) of prey.

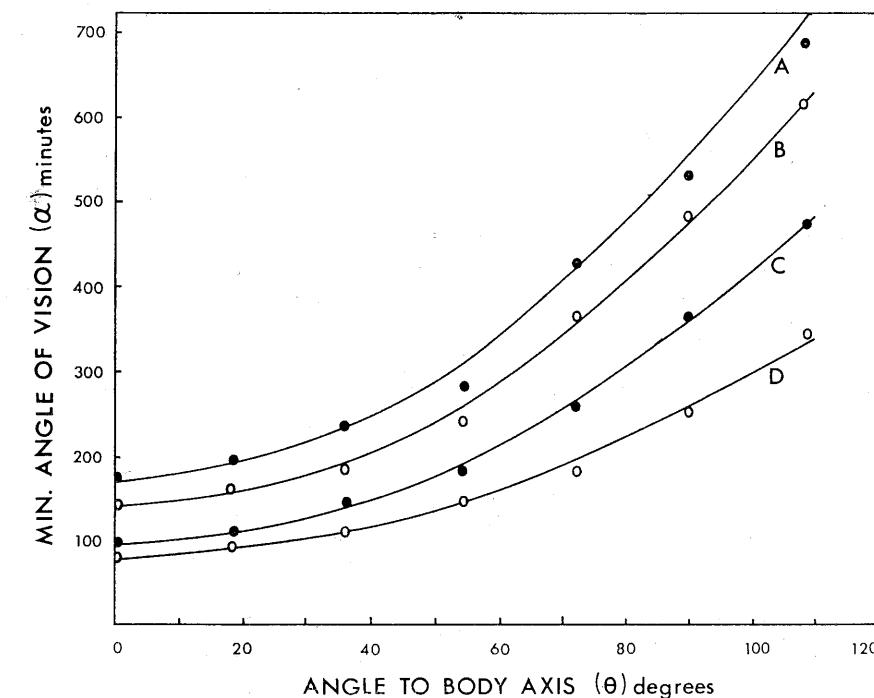


Fig. 13. Minimum angles of vision of *H. crassa* at four hunger levels in relation to the angle to the body axis (averages of 8 replicates).

represent an unnecessary diversion from the main purpose, but the ommatidial angles in eyes of other insects (e.g. the honeybee, Baumgärtner, in Roeder 1953, p. 510) have been shown to vary from 4° at the periphery to 1° at the centre. The curvilinear form of the relation shown in Fig. 13 therefore probably results from the specific architecture of the mantid eye, and a second transformation is necessary to produce linearity.

Some strictly empirical transformations were attempted and it was finally found that squaring the angle to the body axis successfully produced linearity for all field sizes (Fig. 14). As a result, the relation between α and the angle to the body axis can be expressed by

$$\alpha = \alpha_0 + m\theta^2$$

where

θ = angle to the body axis

α_0 = minimum angle of vision directly in front of the mantid ($\theta = 0^\circ$)

and

m = the slope, a function of field size, or hunger.

This equation can be made more useful, however, if m , the slope, is expanded. Since the relation between α and θ is a function of the structure of the mantid eye, and this structure is not subject to changes induced by hunger, it is likely that the minimum angle of vision at any angle θ bears a constant relation to α_0 , irrespective of hunger. That is,

$$\alpha_i/\alpha_0 = k$$

where

α_i = minimum angle of vision at $\theta = i$

and

k = a constant.

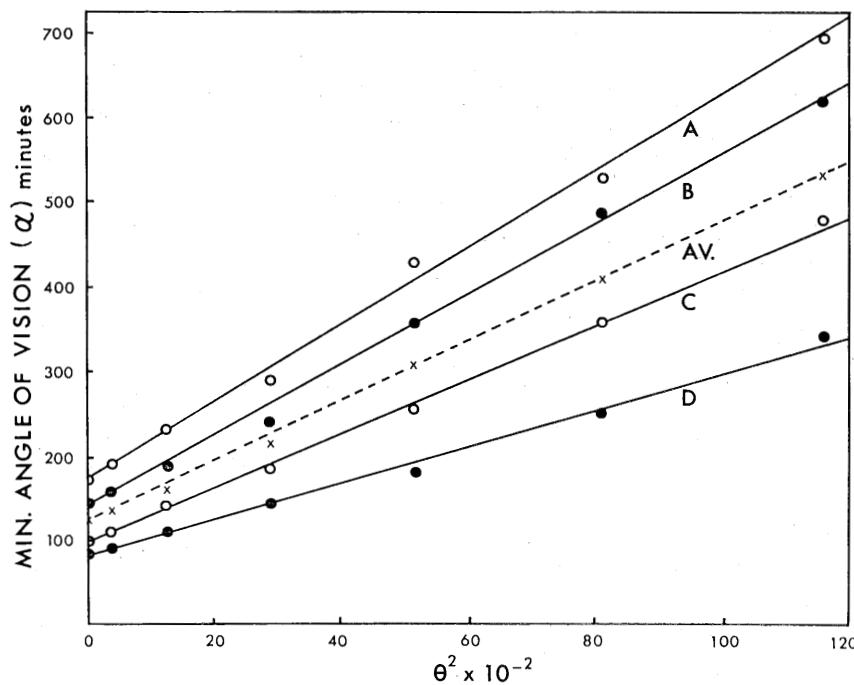


Fig. 14. Transformation of the relation between minimum angle of vision of *H. crassa* (α) and angle to the body axis (θ) to produce linearity (averages of 8 replicates).

In order to fulfill this condition, the slope m , in equation (10), must be a function of α_0 , such that

$$m = \alpha_0 C,$$

where C = a constant, independent of hunger, that describes the way effective ommatidial angles change from the front to the back of the mantid.

When C is calculated by dividing α_0 into m , using values obtained by regression analysis of the data in Fig. 14, the values obtained for C are reasonably constant (Table I) and show no consistent trend with field size. Therefore equation (10) can be rewritten in a more useful form as

$$\alpha = \alpha_0 + \alpha_0 C \theta^2. \quad (11)$$

Since this equation describes the relationship consistently and well, it is now possible to express the shape of the mantids' reactive field in a realistic way. It has already been shown in deriving equation (9) that

$$\tan \alpha/2 = L/2r_a$$

TABLE I
Summary of parameter values calculated from regression in Fig. 14

Reactive field	X-intercept α_0	slope m	$m/\alpha_0 = C$
A	174.60	0.0446	0.000256
B	141.00	0.0415	0.000294
C	98.95	0.0323	0.000327
D	82.14	0.0219	0.000266
Av.	124.45	0.03500	0.000281

whence

$$r_a = L/[2 \tan(\alpha/2)]. \quad (12)$$

If α is small, equation (12) can be greatly simplified, for then $\tan \alpha = \alpha$, expressed in radians. That is, equation (12) can be written

$$r_a = L/\alpha. \quad (13)$$

This simplification will lead to error only when α becomes quite large. Under these conditions, however, the field would be so small it would be effectively zero and the error would not be felt. This equation probably has general application to any visual predator, since it simply involves the geometry of vision. Equation (11), which describes the specific way in which the minimum visual angle of mantids changes at various angles to the body axis, can now be substituted in (13). That is,

$$r_a = L/(\alpha_0 + \alpha_0 C \theta^2)$$

or

$$r_a = L/\alpha_0 [1/(1 + C \theta^2)].$$

Since, from equation (13)

$$r_o = L/\alpha_0,$$

where r_o = the maximum distance of reaction directly in front of the mantid when $\theta = 0$,

therefore

$$r_a = r_o/(1 + C \theta^2). \quad (14)$$

Equation (14) provides a description of the shape of the reactive field, independent of hunger, if r_o and C are known. The lines drawn in Fig. 9 are based on this equation, using the empirically determined values for r_o and C shown in Table I and the shape of each field size clearly is very well described by the lines. Since area, rather than shape, is the important determinant of number of prey discovered, however, it is necessary now to determine the area embraced by a field whose radii are given by (14). This can be done by integrating equation (14) for area around polar coordinates. If A = the area of the field then

$$A = \int_{\theta=0}^{\theta=\pi} r_a^2 \cdot d\theta,$$

where θ is measured in radians.

Substituting (14) in this expression

$$A = r_o^2 \int_0^\pi \frac{d\theta}{(1 + C \theta^2)^2}.$$

This can be integrated through rationalization by trigonometric substitution into the following equation:

$$A = \frac{r_o^2}{4\sqrt{C}} \left(\frac{\pi\sqrt{C}}{1 + C\pi^2} + \text{Arctan } \pi\sqrt{C} \right). \quad (15)$$

A value for the area of the field can be computed from (15) if r_o and C are known. For *H. crassa*, an average value for C was earlier presented in Table I. This value, however, was computed with θ in degrees, but since (15) expresses θ in radians, this computed value of C has to be changed by multiplying by $(180/\pi)^2$, to produce an average value of C equal to 0.9231. When this is substituted in (15),

$$A = 0.8064 r_o^2. \quad (16)$$

The areal expression in equation (15) is highly specific to the mantid, since its form reflects the specific structure of the mantid's eye. And yet one of the aims of this study is to produce a general model that has wide application. When the specific value for C is assigned in the equation, however, it becomes obvious (equation 16) that the area of the field is equal to a constant times r_o^2 . The specific and characteristic shape of the mantid's reactive field is simply represented by the specific value assigned to this constant. If the field was circular with the predator in the centre, as is likely for predators that locate prey by touch or odour, the value of this constant would be π . If, on the other hand, the field was more elongate than that of the mantid's, the value of the constant would be less than 0.8064. Thus the generalized expression for the area of reaction of any predator would simply be

$$A = (KA)r_o^2, \quad (17)$$

where

KA = an areal constant, which has a value of 0.8064 for *H. crassa*.

Equation (17) therefore expresses area in terms of the distance of reaction directly in front of the mantid. This, in fact, is precisely the measure that was used to determine the effects of hunger on field size shown earlier in Figs. 6, 7 and 8. Since the data in these figures provided the information to express r_o as a function of hunger (in equations 5 and 6) area therefore can also be expressed as a function of the same variable by substituting (5) and (6), in equation (17). Thus,

$$A = KA[GM(H - HT)]^2, \quad H > HT \quad (18)$$

and

$$A = 0, \quad H \leq HT. \quad (19)$$

Equations (18) and (19) fulfill the aim of this section; i.e. to develop expressions that accurately and consistently describe the effects of hunger on the size of the area of reaction of a predator for prey. This, however, represents only one of the four subcomponents of the rate of successful search, so that it is now necessary to examine the remaining three: speed of movement of predator and prey, and capture success.

Speed of Movement of Predator and Prey

Although many predators, like the mantid, are ambush types that wait for prey to come within reach, they still move, and it is possible that the speed and frequency of this movement is a significant feature that affects the number of prey attacked. In order to measure speed of movement as well as other behaviours of *H. crassa*, standard mantids starved for 36 hours from satiation were placed individually in large screen-topped cages, 1.19×0.58 m. together with flies at various densities. Each cage was illuminated from above by two fluorescent tubes one foot above and running the length of the cage. A reflecting box around the lights and a light diffuser made from translucent paper diffused the light more evenly in the cage. Each cage had a glass bottom and was suspended in a frame above a mirror placed at a 45° angle. In this way the observer could sit, in darkness, some distance from the cage and record various activities without disturbing mantids or flies. Activities were recorded with an Esterline Angus event recorder, and, in addition, each movement was filmed at eight frames per second with a 16-mm. Bell and Howell movie camera. By using the event record to determine the time spent moving, and the film record to determine the distance moved, the rate and frequency of movement could be calculated. Each experiment was conducted for 16 hours between 0700 and 2300 hours E.S.T.

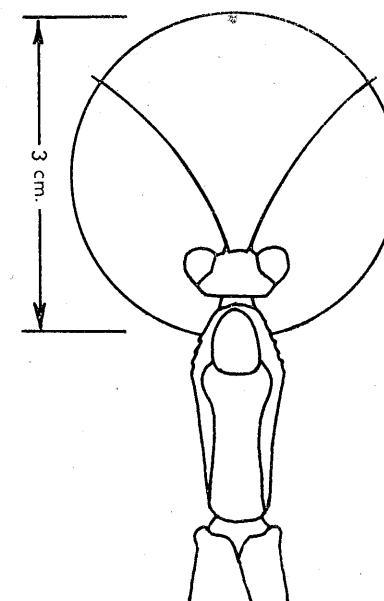


Fig. 15. Drawing of dorsal view of anterior portion of an adult *H. crassa* to show the area of the strike zone.

Two distinct kinds of walking movement were recorded. The first and most common was the stalk, or pursuit, which could be readily identified because of its slow deliberate nature and because it was always directed towards flies. This kind of movement is involved as part of a subcomponent of handling time so that it will be considered later. In this section we are interested only in the second kind of walking movement, which was faster and clearly not directed towards flies. In a total of 464 mantid-hours of observation only eight such movements were recorded, comprising less than 1% of the total time. Moreover, four of these movements were recorded on 1 day from one mantid that laid eggs the following day. Since these movements were recorded at both low and high prey densities and were so rare, it was concluded that predation by standard adult *H. crassa* effectively represents a limiting condition in which the speed of movement, VD, is zero at all prey densities and hunger levels.

Contact between mantid and fly is therefore a property of fly movement alone. Although it is highly unlikely that the level of a mantid's hunger can directly affect the activity of flies, it is very likely that prey density will affect prey activity and, independently, the predator's hunger, and so give a spurious correlation between the two. It is therefore essential to examine the effects of prey density on prey activity.

The speed of prey movement was measured in the same experiments described above by recording the number of contacts of flies with a 3-cm. diameter contact area at the front of the mantid that represents the striking zone (Fig. 15). Since the main aim of this paper was to study predator and not prey behaviour, the flies used in the experiments were treated in a very artificial way in order to assure that their speed of movement was low and constant throughout the 16 hours. This was done by using well-fed female flies 11 ± 1 days old that had been kept, as adults, under an 8-hour light (2300-0700 hours E.S.T.) — 16 hour dark regime (0700-2300 hours E.S.T.), the reverse of the diurnal pattern experienced by the

TABLE II
Number of walking and flying flies contacted, struck at and captured by *H. crassa*

	Flies walking	Flies flying	Total	% Flying
No. contacts	1279	339	1618	21
No. strikes	898	112	1010	11
No. captures	566	15	581	2.6
Strikes/contacts	0.702	0.331		
Captures/strikes	0.630	0.134		

mantid. In this way the 16-hour period of the experiment coincided with the 16-hour period of darkness that the flies normally experienced. During the experiment food (1:1 mixture of evaporated milk and water in cellucotton) and water was always present in excess. Fly activity was recorded at eight different densities with three replicates at each.

Contacts were made with flies that were both walking and flying. As can be seen in Table II, however, only 21% of the contacts were with flying flies and many fewer prey were struck at when flying than walking (33.1% compared with 70.2%). As a result, only 11% of all strikes were directed at flies in the air. Moreover, the mantids were very unsuccessful in capturing flying prey, since only 13.4% that were struck at were captured, compared to 63.0% success in capturing walking flies. Therefore the total proportion of flying prey captured is very small (2.6%) and little error results if we assume that *H. crassa* effectively confines its attack to walking houseflies.

The average cumulative number of contacts with walking houseflies throughout the 16 hours are shown in Fig. 16 for each density. Since the data are quite well described by straight lines, fly activity was reasonably constant for the full 16 hours. All the lines cut the ordinate above zero, however, as the result of a slight increase in activity in the first hour of the experiment. This is so slight that it can be ignored.

Since fly activity is constant throughout the whole period, the same data can be used to compute the average velocity of each fly (VY). The number of contacts made is a function of velocity, time, and fly density, and if everything but velocity is measured, VY can be calculated using the expression derived in Appendix I:

$$VY = (N_c - 7.069 N_o)/3 N_o$$

where

VY = speed of movement in centimeters per hour,

N_c = number of contacts per hour,

N_o = fly density in number per square centimeter.

The speed of movement of flies was computed using the same data shown in Fig. 16, and the changes in the values in response to changing fly density are shown in Fig. 17. Density clearly had a marked effect, for the average velocity of flies decreased sharply at first and then more gradually as fly density increased. These figures actually represent the apparent velocity of flies, since they are averages that include periods of immobility as well as mobility. Although no careful measurements were made of actual velocity it seemed that when flies were moving they moved at about the same speed irrespective of their density. Therefore the apparent decrease in velocity shown in Fig. 17 probably occurs because the flies spent less time moving at high than at low densities. This assumption is all the more likely, since it was observed that moving flies often ceased to move, upon

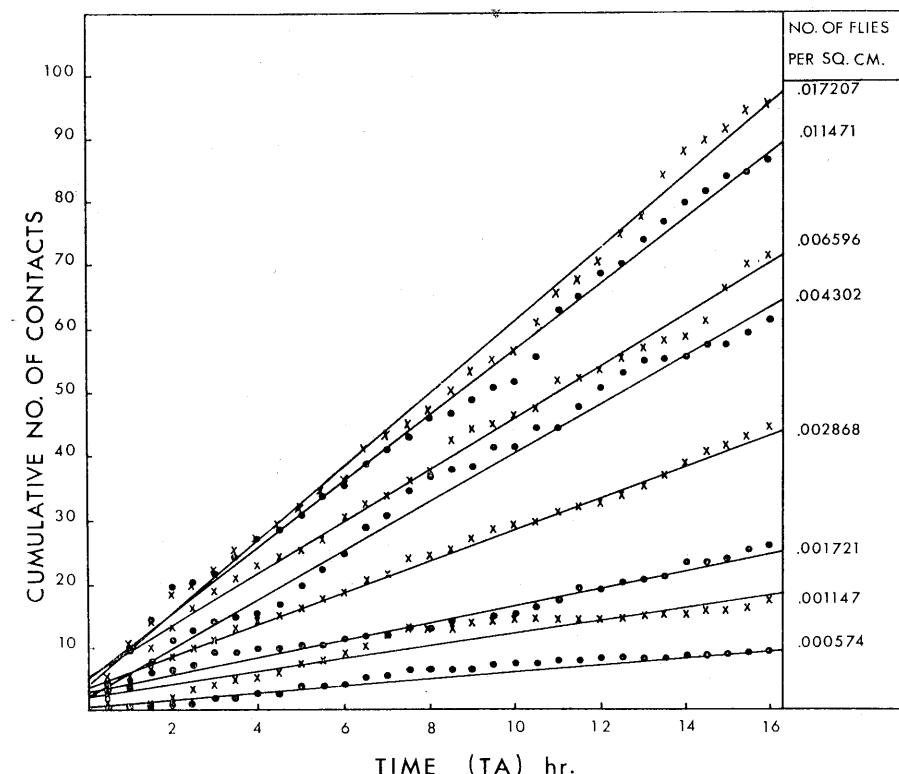


Fig. 16. Effects of time of day and fly density on fly activity (averages of 3 replicates).

contact with others, for a sufficient time that small clusters of immobile flies tended to accumulate. Since the chances for contact increased with density, therefore the periods of immobility and the size and number of fly clusters also increased. Although postulates could be readily devised to express these effects, it is unlikely that the resulting equation would be very general, since the flies were treated in such a highly selective manner. Flies treated differently, or other species of prey, might well behave quite differently and it is even reasonable to expect that some prey would become more active at higher densities because of mutual disturbance. This condition has, in fact, been observed with *Drosophila melanogaster* by Haynes and Sisojevic (1964). The whole process of animal activity should therefore be investigated using the same kind of component analysis used here for predation. Until this is done it is sufficient for the present purpose to derive an expression that accurately describes the specific activity of flies observed in this study. Such an expression was devised from some simple assumptions and this led to the equation

$$VY = (V_{\max} - V_{\min}) e^{-a_v N_o} + V_{\min}$$

where

V_{max} = maximum velocity of flies at N_o = 0

V_{min} = minimum velocity of flies at N_o = ∞

a_v = a constant.

This equation can be transformed to

$$\ln(VY - V_{\min}) = \ln(V_{\max} - V_{\min}) - a_v N_o,$$

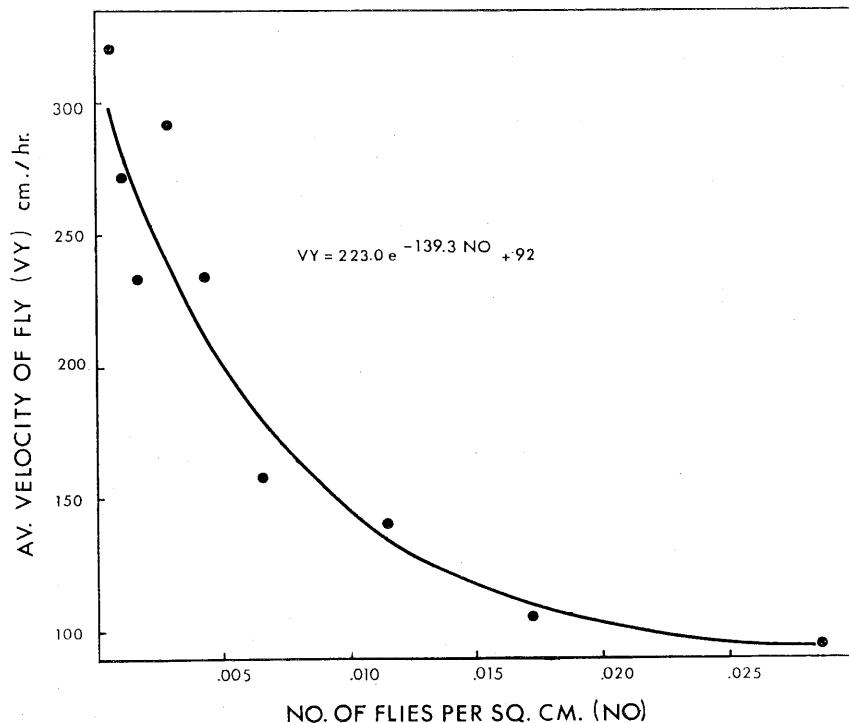


Fig. 17. Effects of fly density on the average velocity of each fly.

so that a plot of $\ln(VY - V_{\min})$ vs. N_o should yield a straight line. The parameter V_{\min} is determined by choosing trial values and selecting the one that maximizes the arithmetic value of the correlation coefficient. As shown in Fig. 18, the above equation does permit adequate rectilineation from which slopes, a_v , and Y-intercept, $\ln(V_{\max} - V_{\min})$, can be calculated. The line drawn in Fig. 17 represents the velocity predicted by this equation.

Capture Success

The last subcomponent of the rate of successful search is the success the predator has in capturing prey that enter its perceptual field. It is convenient to break this success into three stages as follows:

1. SR: Recognition success, i.e. success of recognizing a prey that enters the predator's perceptual field, expressed as the ratio (number of recognized encounters)/(total number of encounters). This parameter reflects the acuity of perception of the predator, the effectiveness of the prey's camouflage, and the clarity of the environment.

2. SP: Pursuit success, i.e. success of pursuing a prey that is recognized. A pursuit is considered as successful if the predator gets close enough to the prey to strike at it, and is expressed as the ratio (number of strikes made)/(number of pursuits initiated).

3. SS: Strike success, i.e. success of capturing a prey once a strike is made, expressed as the ratio (number of successful captures)/(number of strikes initiated).

The total capture success, SC, is given by the product of the above success ratios. That is

$$SC = (SR)(SP)(SS). \quad (20)$$

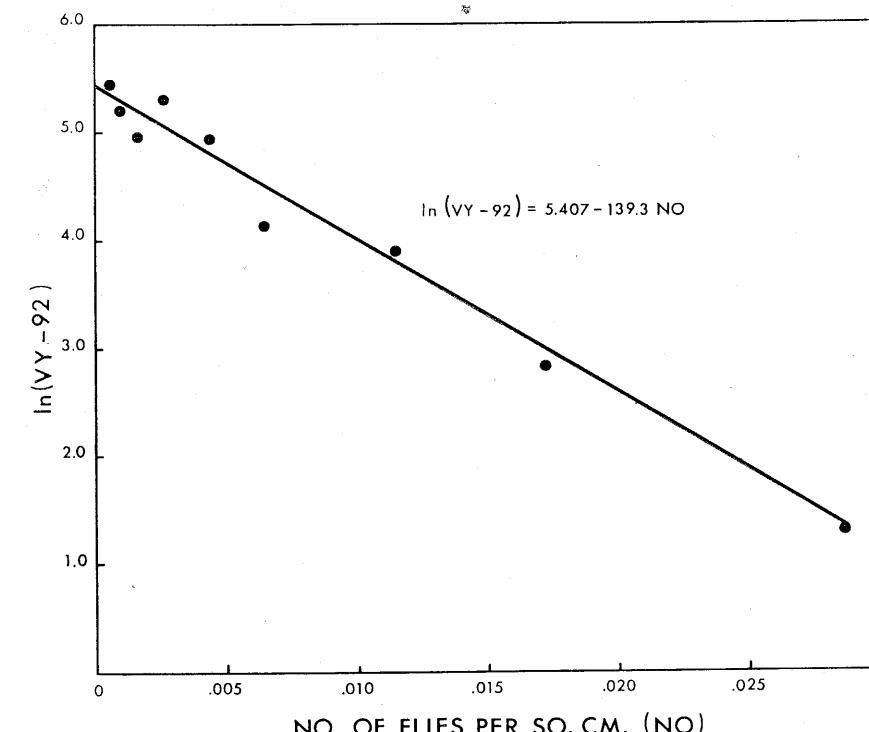


Fig. 18. Transformation of fly velocity to produce a linear relation with fly density.

Each of the three success ratios will be considered in turn, starting, for convenience, with the strike success, SS.

It is conceivable that strike success could be affected by hunger. A mantid, for example, might be very successful in capturing prey within striking distance when it is hungry (a high SS) and less successful when it is less hungry. The effects of hunger on the strike success were determined in the same experiments described earlier to demonstrate the effects of time of food deprivation on hunger (cf. Fig. 4). In these experiments, flies dangled on threads were offered to mantids deprived of food for various intervals of time, until they refused to eat more. Since the number of strikes directed at each fly was recorded, it was therefore possible to compute the strike success as each fly was eaten. Moreover, the weight of each fly was known so that it was possible to determine the hunger level at the time of capture of any one fly. The data for each mantid, at each food deprivation time, were therefore arranged in order from the last fly eaten ($H = 0$) to the first fly eaten ($H = \text{total weight eaten in the feeding period}$) and the strike success and hunger level were determined at each capture (see Fig. 19). This meant that the low hungers had many more replicates than the high, since the mantids' hunger at all deprivation times ultimately reached 0, while only at the long deprivation times was the hunger level at first high. A total of 3321 flies were struck at and captured, to give an average number of replicates of 83 (range from 163 at the lowest hunger level to 12 at the highest).

As shown by Fig. 19, hunger level had little effect on the strike success. When a line was fitted to these data a slight positive value for the slope was obtained (0.0939). This did not differ significantly from zero ($t = 0.327$; degrees of freedom = 40, $P = 0.7 - 0.8$). Therefore the success of striking flies dangled

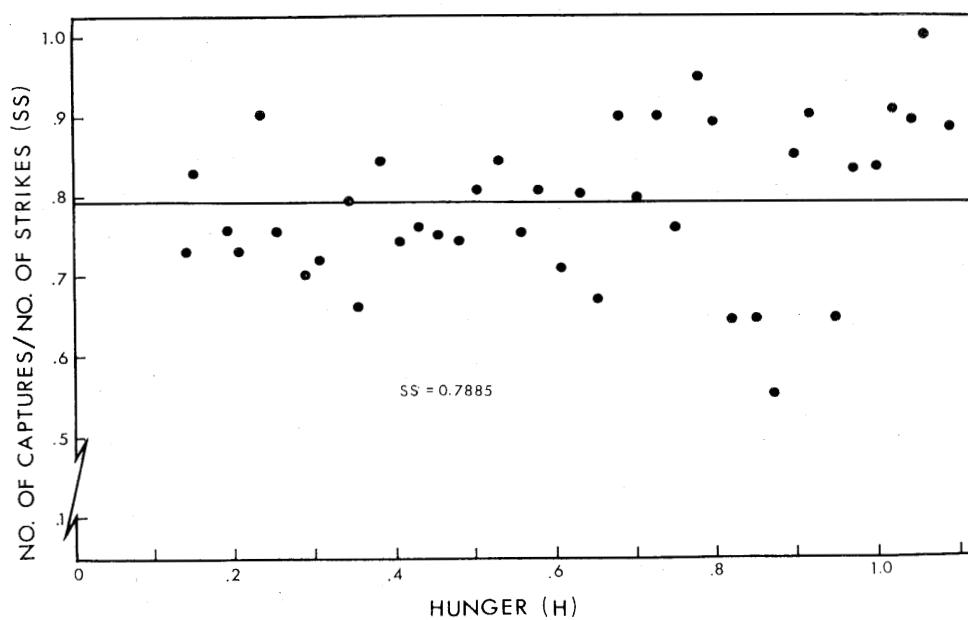


Fig. 19. Relation between strike success of *H. crassa* and hunger (see text).

on threads could be determined by averaging all data. This gave a value of 0.7885 ± 0.0654 . Although these data show the form of the relation to hunger, they do not provide an accurate quantitative measure of the success of striking freely moving flies. Earlier, in Table II, data showing the strike success of mantids exposed to freely moving flies were presented, and the strike success computed as 0.630. As expected, therefore, the success of capturing freely moving flies is less than that of capturing flies on threads, although it must be equally independent of hunger.

Although the strike success is unaffected by hunger, it is highly likely that the pursuit success, SP, will change with increasing hunger. Earlier it was shown that the distance of reaction increased with increasing hunger so that the pursuit time must similarly increase. Since it seems reasonable that the longer the mantid spends pursuing a fly the more likely it will be that the fly escapes, pursuit success must decrease with increasing hunger.

By definition, the pursuit success represents the success the predator has of coming within striking distance of the prey, and this will depend on how long a fly stays in one spot. If the time spent stalking is 10 minutes, for example, and only 40% of the flies stay in one spot for that period of time, then SP will be 0.40. That is, SP = the probability of a fly not moving away during the time of a pursuit. The movement of a fly away from a spot can either be the result of a fly's inherent pattern of activity or can be caused by the fly being startled by the approach of a mantid. Although some prey can certainly be startled by the pursuit of a predator, the whole behaviour pattern of the stalk of the mantid has evolved to minimize this effect. The mantid's stalk is an extremely gradual process and is often accompanied by a distinctive swaying motion that might well mask the gradual increase in the mantid's silhouette as it approaches. Certainly when flies did move away from a stalking mantid there was no indication they were startled into the move except when a strike occurred. In the present

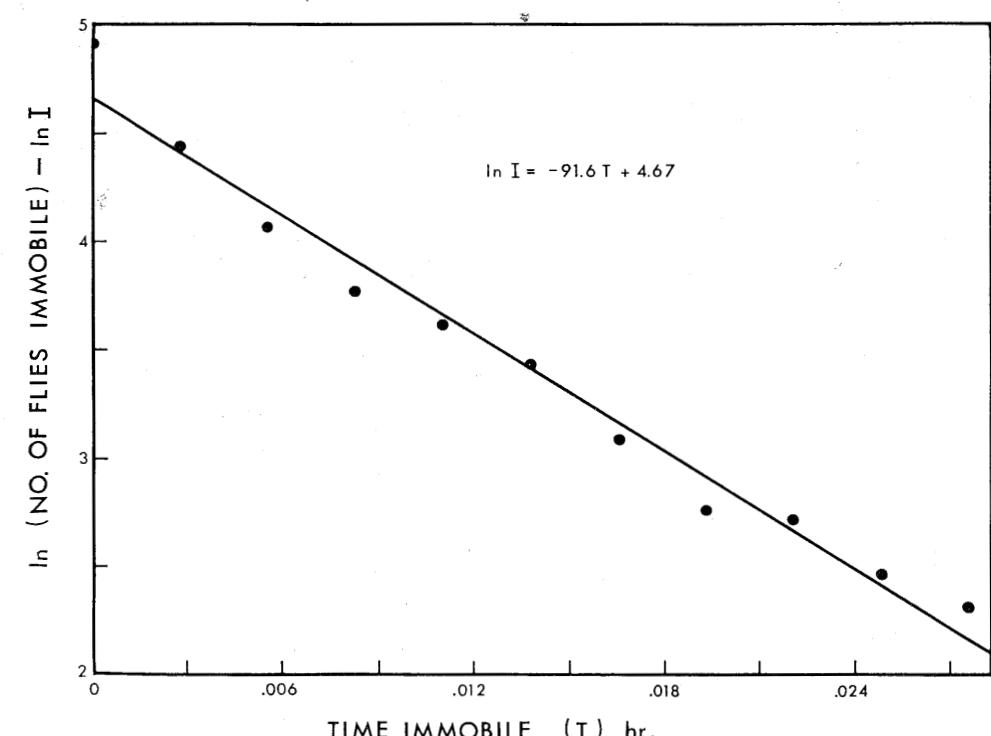


Fig. 20. Relation between number of flies immobile and the duration of the period of immobility.

case, therefore, the escape of a fly from pursuit is related to the inherent pattern of activity of flies.

Assuming that duration of movements of flies are randomly distributed, the probability of a fly not moving is given by e^{-mt} , where m is a constant and t is time, i.e. by the zero frequency class of a Poisson distribution. If this assumption is correct, then

$$I = ne^{-mt}, \quad (21)$$

where

I = the number of periods of immobility lasting t units of time,

and

n = total number of periods of immobility.

If equation (21) is transformed into

$$\ln I = -mt + \ln n,$$

it immediately becomes possible to test the assumption, for periods of immobility can be timed and if $\ln I$ is plotted against t, a straight line should result.

The necessary data were obtained by placing 20 flies individually in small cages, $19 \times 10 \times 7$ cm., and timing the duration of each period of immobility. In order to accelerate the collection of data very active flies were used by selecting females 6 ± 1 days old and testing them during the normal period of activity that coincided with the diurnal period of light. The duration of 137 periods of immobility was measured and grouped into 10 classes of 9 seconds duration. The number occurring in each class provided the information for Fig. 20. Although the relationship between $\ln I$ and t is adequately described by a straight line, the

points actually seem to form a shallow curve, suggesting some degree of contagion. Nevertheless, this departure from the expected is so modest, that equation (21) can be accepted as a satisfactory expression.

These data were collected using flies at only one density — one per cage. Earlier, however, it was shown that the change in the velocity of flies in response to changes of fly density most likely was caused by changes in the duration of the periods of immobility. Therefore, the constant m , in equation (21), is actually a function of fly density, so that m would become smaller as density and duration of immobile periods increased. The actual change in the duration of immobile periods can be readily derived from the equation developed earlier to express the effects of density on the apparent velocity of flies, if it is assumed that the actual velocity, during movement, is constant, irrespective of density. We are not interested here, however, in fly activity per se but only in its involvement in determining pursuit success. Since pursuits are largely confined to a restricted range of low densities where the predator is hungry enough to react to prey at some distance, it hardly seems necessary to express SP as a function of prey density. It should be quite satisfactory to consider m as a constant.

If these arguments hold true, then the pursuit success can be derived from equation (21). Since $SP =$ the proportion of flies not moving away during the time of a pursuit, then

$$SP = I/n. \quad (22)$$

Substituting (21) in (22), and placing $t = TP$

$$SP = e^{-m(TP)}. \quad (23)$$

The descriptive powers of this equation can be tested by measuring success and duration of pursuits and by determining if there is a linear relation between $\ln SP$ and TP . It proved to be particularly difficult to collect enough data to test this relationship, since the success of a single pursuit is an all-or-none event and it was not feasible to control the distance of pursuit by manipulating flies or mantids. Some information was finally obtained from the experiments described in the last section in which hungry mantids were placed individually in large cages together with flies for 16 hours. Whenever a pursuit was started it was timed and recorded as successful or not. Seventy-two pursuits were observed and these were grouped into five approximately equal-sized groups ($n = 13$ to 15), each covering a different range of pursuit times. The ratios of successful pursuits to total number are shown in Fig. 21. The relation between $\ln SP$ vs. TP seems to be reasonably linear, so that the effect of pursuit time on pursuit success can be adequately described by equation (23) and the chain of arguments leading to the equation is supported. In this instance the slope, m , was calculated as 8.17 so that

$$SP = e^{-8.17TP}. \quad (24)$$

Later, when the effects of hunger on TP are demonstrated, equation (23) can be transformed to express SP as a function of hunger.

Now that the strike and pursuit success have been considered above, only the recognition success has to be analyzed in order to express the total capture success. The success a predator has in recognizing prey depends on the perceptual acuity of the predator, the camouflage of the prey and on the clarity of the environment. In the present experiments the flies showed up so distinctly against the white background of the cages, that the mantids had little difficulty in recognizing their appearance even at the outer limits of the field of reaction. As a result, the recognition success was always so close to 1.0 that it was not feasible

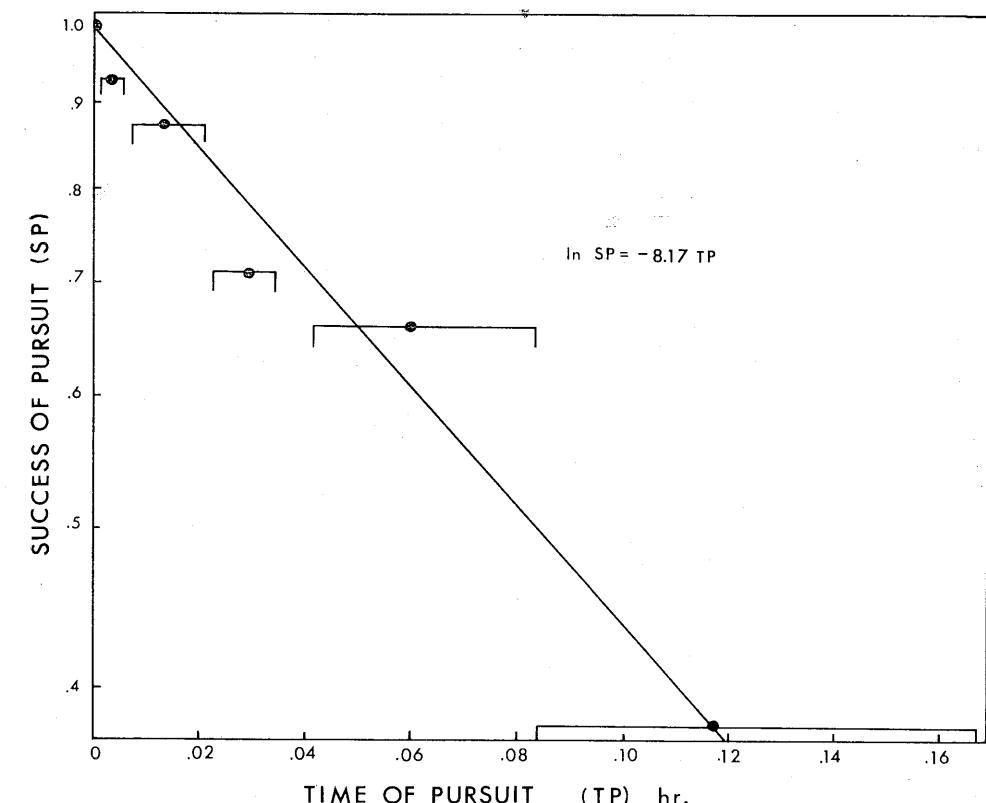


Fig. 21. Relation between the pursuit success of *H. crassa* and the duration of pursuit (averages of 13 to 15 replicates). The abscissa is in logarithmic units.

to determine how it was affected by hunger or distance of perception, as it presumably must be. This portion of the model, therefore, must be explored using other predators and for present purposes it will be presumed that SR is a constant equal to 1.0.

Since total capture success, SC, is a product of the three success ratios, it can now be expressed as

$$SC = (SR)(SS)e^{-m(TP)}. \quad (25)$$

For standard *H. crassa* attacking the selected houseflies

$$SC = 0.630 e^{-8.17(TP)}.$$

At this point all the subcomponents of the rate of successful search have been analyzed, and by way of a summary the final expressions devised for each are shown below:

Area of reaction, A:

$$A = KA[GM(H - HT)]^2, \quad H > HT$$

and

$$A = 0, \quad H \leq HT$$

Speed of movement of predator, VD:

$$VD = 0.$$

Speed of movement of prey, VY:

$$VY = (V_{\max} - V_{\min}) e^{-avN_0} + V_{\min}$$

Capture success, SC:

$$SC = (SR)(SS) e^{-m(TP)}$$

Now it is necessary to explore the characteristics of the subcomponents of the time predator and prey are exposed, TT.

Time Predator and Prey Are Exposed

The total time predator and prey are exposed to each other can be conveniently divided into the time associated with non-attack activities (TN), like mating or egg-laying for example, and the time associated with all attack activities (TA), including the "digestive" pause. However, since only mated female mantids were used in the experiments and since data collected during egg-laying were deleted, few of the expected non-attack activities had to be considered. The period of attack was essentially confined to the 16-hour period of light and the time of non-attack activities to the 8-hour period of dark (cf. Fig. 3). Although the maximum duration of the feeding period of a visual predator, like the mantid, must be set by the diurnal changes in light, it is still possible that within these limits, decreasing hunger could shorten the period devoted to feeding behaviours. If this is the case, then the feeding period of the standard *H. crassa* should be reduced to less than 16 hours when the mantids are provided with abundant food. This is exactly the condition maintained in the experiments that provided the data for Fig. 3, since all mantids were force-fed to satiation every 2 hours for 48 hours. And yet this figure clearly demonstrates that a full 16 hours was still utilized for feeding. Therefore the duration of the feeding period, TA, and its opposite, the non-feeding period, TN, are determined by factors other than hunger. Hunger exerts its effect by modifying the rate of attack during the feeding period but not the feeding period itself. TA and TN are constants.

Time Spent Handling Prey

The time spent handling prey is comprised of three subcomponents in mantids — time spent in pursuing or stalking prey, time spent eating prey, and time spent in a digestive pause. These time-consuming activities are important because once initiated they preclude further search. Thus when a fly is fixed and pursued, only rarely will a mantid attack another fly that might be closer. Similarly, the external stimuli received when a mantid is holding or eating a fly effectively inhibits further attack as do the internal stimuli received during the "digestive" pause when the hunger is below the attack threshold.

Time Spent Pursuing or Stalking Prey

The time spent pursuing a prey (TP) depends on both the speed and the distance of the pursuit and it is necessary here to determine if hunger can affect either. Mantids share with many animals a particular kind of pursuit in which the predator slowly stalks the prey. The characteristics of this stalk, particularly its velocity, have clearly evolved to minimize the chance of a prey becoming startled before the mantid comes within striking distance. Since the success of capture is dependent on the velocity of the stalk, it seems highly unlikely that it would be affected by hunger. If it was, a hungry mantid presumably would stalk faster than a more sated one, but in so doing it would increase the chance of startling the prey and thereby jeopardize, rather than enhance, its

chances of eating. The behaviour would have a marked selective disadvantage. Therefore I shall assume that the velocity of pursuit, VP, is a constant at all hungers. Data were obtained to show specifically how fast *H. crassa* stalked prey in the earlier experiments in which individual mantids and flies at various densities were placed together in large cages and observed continuously for 16 hours. Both the duration and distance of each stalk were recorded using an event recorder and movie camera. Adequate records were obtained for 51 stalks involving 13 different mantids and these gave an average velocity of pursuit of 210.6 ± 14.8 cm. per hour. That is, for *H. crassa*

$$VP = 210.6 \text{ cm. per hour.} \quad (26)$$

Although it is unlikely that the velocity of pursuit is affected by hunger, the distance of pursuit very definitely is affected, as was shown earlier in Fig. 7. Below the hunger threshold for attack, no pursuit occurs, and above it, the maximum distance a mantid will pursue prey increases. The measure of pursuit distance used in this figure was the maximum distance directly in front of the mantid. Flies, however, can approach the mantid from any direction so that it is necessary to compute an average pursuit distance. Since I have shown earlier that the shape of the reactive field of *H. crassa* is accurately described by equation (14), it should be a simple matter to integrate this expression to express the average distance from the mantid to the outer contour of its reactive field. Because equation (14) is specific to *H. crassa*, however, I felt a cruder but more general approach was better. The general expression for the area of the reactive field of any predator is given by equation (17), $A = (KA)r_o^2$, and if we assume that the average distance to the outer contour of the reactive field equals the radius of a circle with the same area, it is possible to develop a general expression for the average pursuit distance. If \bar{r}_m is the average distance to the outer contour, then

$$\pi\bar{r}_m^2 = (KA)r_o^2$$

and

$$\bar{r}_m = r_o \sqrt{(KA/\pi)}$$

or

$$\bar{r}_m = (KR)r_o \quad (27)$$

where

$$KR = KA/\pi.$$

Although \bar{r}_m represents the average distance between a mantid and the outer contour of its reactive field, the actual distance the mantid has to walk to capture a fly that has crossed the contour is somewhat less, since a mantid can strike and capture a fly when it approaches within the strike area shown in Fig. 15. If the average strike distance is represented by DS, and the pursuit distance by DP, then

$$DP = \bar{r}_m - DS. \quad (28)$$

Substituting equation (27) in (28),

$$DP = (KR)r_o - DS. \quad (29)$$

In addition, since equations (5) and (6) express r_o as a function of hunger, DP can be expressed in terms of the same variable by substituting (5) and (6) in (29):

$$DP = (KR)(GM)(H - HTP) - DS, \quad H > HTP \quad (30)$$

and

$$DP = 0, \quad H \leq HTP \quad (31)$$

where

HTP = the hunger level at which actual pursuit starts, i.e. where $r_o = DS$.

By substituting DS for r_m and HTP for H in equation (5), HTP can be expressed as the following function of HT:

$$HTP = [DS + GM(HT)]/GM.$$

Specific values for the constants GM and HT appropriate for *H. crassa* have already been presented. KR, however, has not yet been considered, but since it equals $\sqrt{KA/\pi}$ and since KA was earlier shown to be 0.8064, its value for *H. crassa* is as follows:

$$KR = \sqrt{(0.8064/3.1416)} = 0.5066.$$

The strike distance for *H. crassa* is shown in Fig. 15, and amounts to 2.5 cm. directly in front of the mantid. This represents the extreme strike distance, however, for in practice it was usually less. In moving picture records of 51 stalks that ended in a strike, the average strike distance, DS, was 1.54 ± 0.21 cm.

Equations (30) and (31) provide general expressions for the distance of pursuit. Since the velocity of pursuit, VP, is a constant, it now is possible to fulfill the aim of this section by developing a general expression for the effect of hunger on the time spent in pursuit. Since

$$TP = (DP)/(VP), \quad (32)$$

TP can be expressed as a function of H by substituting (30) and (31) in (32):

$$TP = [KR(GM)(H - HT) - DS]/VP, \quad H > HTP \quad (33)$$

and

$$TP = 0. \quad H \leq HTP \quad (34)$$

Time Spent Eating Each Prey

The time required for *H. crassa* to eat prey was determined using data obtained from the experiment, described earlier, designed to determine how the weight of food required to satiate (H) was affected by time of food deprivation. Each fly offered to the mantids in these experiments was not only weighed but the time taken to eat it was also measured with a stop watch. It was therefore possible to estimate the hunger just before eating any one fly and to relate it to the time required to eat that fly in a manner identical with that used earlier to show the effects of hunger on strike success (see Fig. 19). Somewhat more data could be used, however, since consumption of prey could be induced when the mantids were too satiated to strike at prey. The data are presented in Fig. 22, where each point of the upper line represents the average time to eat one fly and the corresponding points on the lower line represent the average weight of each fly that was eaten. A total of 4152 measurements was obtained so that the average number of replicates was 92 (range from 168 at the lowest hunger level to 12 at the highest). With the exception of the first three points both the time taken to eat each prey and the weight of each prey eaten were constant and unaffected by hunger. In each case there was a slight positive slope, but this did not differ significantly from zero ($t = 1.62, P = 0.1-0.2$ for the TE vs. H regression and $t = 0.162, P = 0.8-0.9$ for the W vs. H regression). The first three points are an exception only because of the way the satiated condition was determined. Since the criterion of satiation was the refusal to consume three consecutive flies completely, it is inevitable that the first three points are low.

The same data can be plotted somewhat differently, as in Fig. 23, where the total time spent eating to satiation is plotted against the weight of food eaten, or hunger at the start of eating. The data are well described by a straight line, which indicates again that the rate of eating is unaffected by hunger. The line

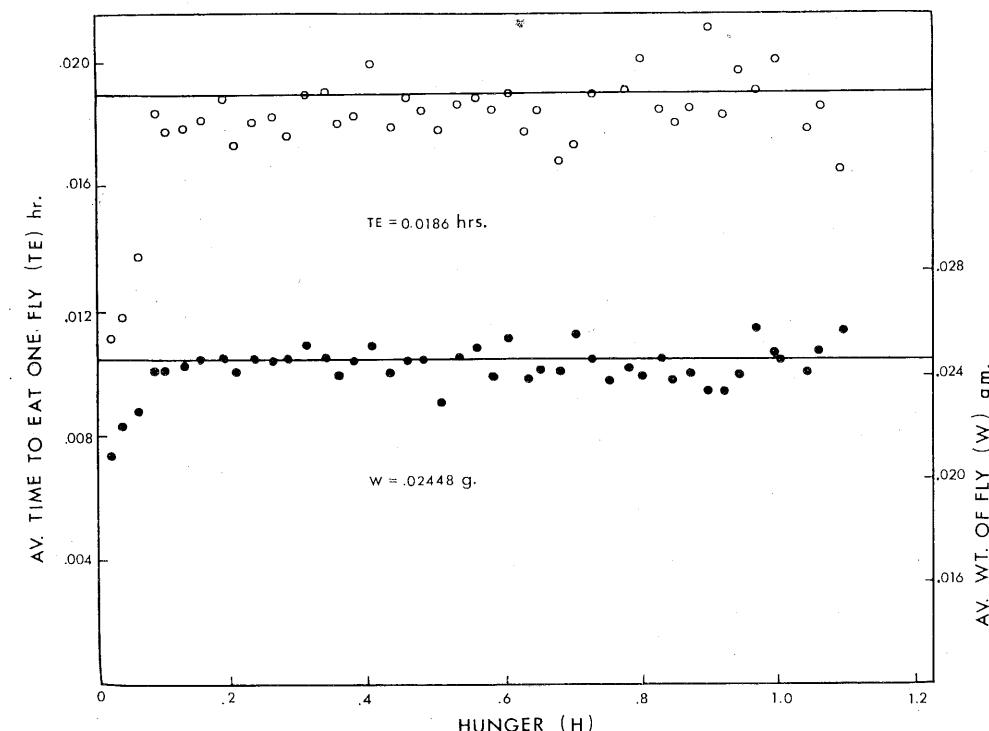


Fig. 22. Relation between time spent eating one fly and hunger of *H. crassa* (see text).

cuts the X-axis because of the constant weighing error described earlier. Similar data were obtained for *Mantis religiosa* (Fig. 24), and since this relation is also linear, this species' rate of consumption is similarly unaffected by hunger. The slopes of these two lines represent the number of hours required to consume 1 g. of food (termed KE), and as might be expected, the larger *H. crassa* eats much faster than its smaller relative *M. religiosa* (0.811 hour per gram as compared to 2.96 hours per gram). A more accurate measure of KE for *H. crassa*, unaffected by the weighing error associated with the last three flies eaten, can be obtained from the data in Fig. 22, however, if the first three points are deleted, and the remaining ones averaged. This gave a value for KE of 0.7600 ± 0.0008 hour per gram ($n = 3468$).

Since the rate of food consumption is unaffected by hunger we may write

$$TE = KE(WE), \quad (35)$$

where

TE = time spent eating each prey,

KE = feeding rate in time per unit weight,

and

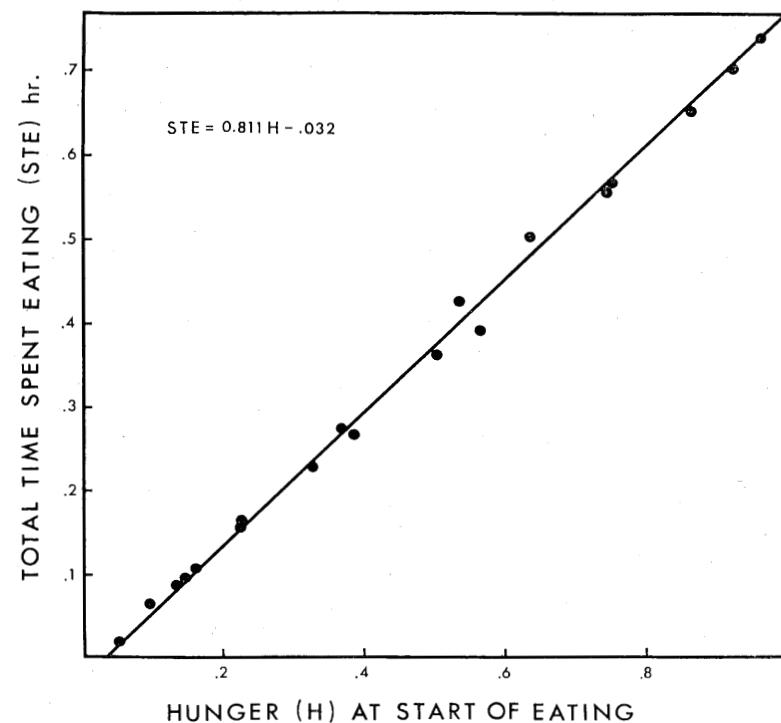
WE = weight of each prey eaten.

For *H. crassa* attacking houseflies

$$TE = 0.760(0.0245) = 0.0186.$$

Time Spent in a "Digestive" Pause

The "digestive" pause after a prey is eaten represents a refractory period during which the predator is not hungry enough to search for or attack prey.



HUNGER (H) AT START OF EATING

Fig. 23. Relation between the total time spent eating by *H. crassa* and the hunger at the start of eating (averages of 12 replicates).

By definition, it is therefore affected by hunger and the exact relation can be derived from data that already have been presented. Earlier it was shown in Fig. 7 that the mantid would attack prey only when its hunger exceeded a certain value, termed the hunger threshold for attack, HT. Whenever the hunger drops below this threshold because a prey has been consumed, a digestive pause follows and lasts until the hunger again reaches HT. If HO is the hunger when a prey has just been consumed, then the "digestive" pause, TD, is the time required for the hunger to rise from HO to HT, and this time can be derived from the equation (3), the hunger equation. It is simpler, however, to use a version of this equation that expresses hunger in terms of unspecified time, T, rather than time from a condition of satiation when H = 0. The derivation of this modification is presented in Appendix II. In this modified form the hunger equation is

$$H = HK + (HO - HK) e^{-AD(T)}, \quad (36)$$

where HO = the hunger at T = 0, in this case just after a prey is eaten. It can also be transformed into

$$T = \frac{1}{AD} \left(\ln \frac{HK - HO}{HK - H} \right), \quad (37)$$

which expresses the time required for the hunger to rise from HO to H. Since the digestive pause represents the time taken for the hunger to rise from HO to HT, equation (37) can express TD as a function of hunger if H is replaced by HT under the condition HO < HT. That is

$$TD = \frac{1}{AD} \left(\ln \frac{HK - HO}{HK - HT} \right), \quad HO < HT. \quad (38)$$

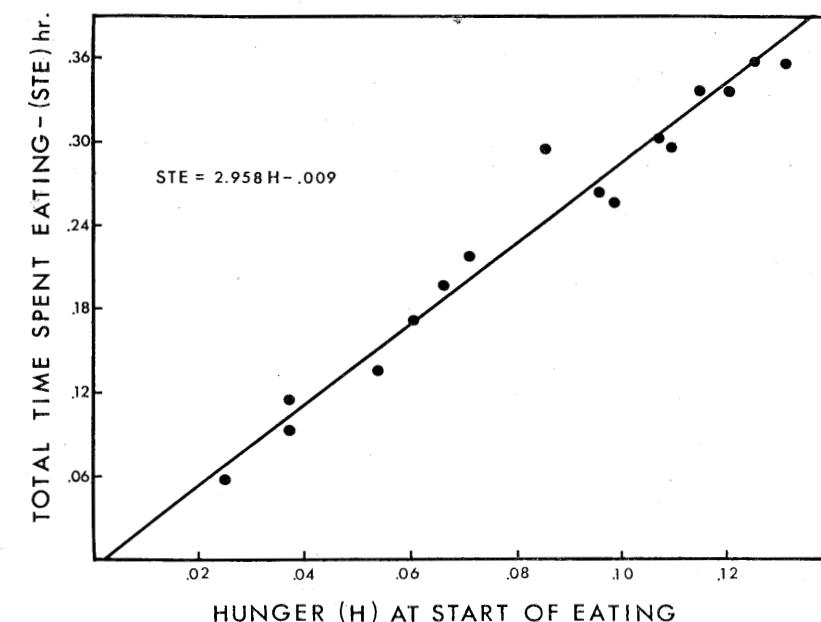


Fig. 24. Relation between the total time spent eating by *M. religiosa* and the hunger at the start of eating (averages of 11 replicates).

If HO is greater than HT, then TD is of course zero:

$$TD = 0, \quad HO \geq HT \quad (39)$$

Equations (38) and (39) therefore provide expressions for the "digestive" pause, the final subcomponent of handling time.

Since all the subcomponents of handling time have now been considered in this section the final equations developed are listed below as a summary.

Time spent pursuing each prey:

$$TP = [KR(GM)(H - HT) - DS]/VP, \quad H > HTP \quad (33)$$

and

$$TP = 0, \quad H \leq HTP \quad (34)$$

Time spent eating each prey:

$$TE = KE(WE). \quad (35)$$

Time spent in a "digestive" pause after eating each prey:

$$TD = \frac{1}{AD} \left(\ln \frac{HK - HO}{HK - HT} \right), \quad HO < HT \quad (38)$$

and

$$TD = 0, \quad HO \geq HT \quad (39)$$

Other Components Affecting the Functional Response of *H. crassa*

Very early in this paper I discussed 10 different components that could affect the functional responses of predators. Four of these, the rate of successful search, the time predator and prey are exposed, handling time, and hunger, have been dealt with in this paper. Since the first three have been considered before (Holling 1959b), the analysis to this point therefore provides the experimental informa-

tion needed to expand our knowledge of the functional response to include one more component — hunger. As the aim of this paper was limited to this one step, it would seem that there is no necessity for more analytical data. There is no reason to believe, however, that attack by *H. crassa*, the animal used in these experiments, is affected only by the four components listed above. If other components are involved they might interact with hunger to distort its exact role. It is essential, therefore, to determine whether other components could affect the functional response of *H. crassa*.

Of the ten components listed in Fig. 1 the last four are largely effects of predator density. As all experiments were conducted with isolated individuals, predator density was essentially constant at a low value, and most of the possible effects of these components could be safely ignored. The one exception concerns exploitation, for even a single predator reduces the density of its prey whenever it eats one. Only those experiments in which individual mantids and various numbers of houseflies were kept together in large cages could be affected by this problem, and it was circumvented by simply adding another fly to the cage whenever one was eaten. The complications introduced by the exploitation component were therefore circumvented by this "Lazarus" ploy.

Only two of the remaining six components have not been considered as yet — learning by predators and inhibition by prey. Learning of some kind is a pervasive feature of life from amoeba to man (Thorpe 1963). Nevertheless, associative learning, whereby an act released by a particular stimulus is more efficiently performed with practice, is not a universal feature of all behaviours, particularly among invertebrates. Fortunately, Rilling *et al.* (1959) have carefully explored the possible effects of learning on attack by the same species of mantid, *H. crassa*, used in these experiments. Moreover, the individual mantids used by Rilling *et al.* were closely related to those used in my own studies, since both were provided from the colony established by Dr. H. Mittelstaedt. By hand-rearing isolated mantids from the time the egg hatched to the adult stage, adults that had never seen a living fly or other mantid were obtained. These individuals therefore had never struck at or caught a living insect. Nevertheless, when actively moving prey were finally provided, the inexperienced mantids proved to be as reactive to the stimulus as experienced ones. The strike-releasing qualities of the prey therefore are not learned through experience. Rilling *et al.* were able to show, however, that the subsequent acts of catching and bringing the prey to the mouth were improved by experience. Since all the animals used in the experiments discussed in this paper had been continually exposed to active flies it is extremely unlikely that this effect of learning would have any detectable effect on the results presented so far. The effect of learning on the functional response of mantids therefore can be ignored.

Inhibition of attack by contact with prey is the only component that might modify results presented to this point. The attack behaviours could be inhibited because of distasteful or threatening qualities of the prey (Morris 1963), or simply because the act of attacking caused a change in the neural network mediating the behaviours, a change that lowered responsiveness to subsequent stimuli from prey. The latter effect would be completely in agreement with neurophysiological data involving many species of animal and many behaviours. Again the paper by Rilling *et al.* (1959) shows that such inhibition does occur in *H. crassa*. Whenever they offered real prey behind a glass window, or model prey to a mantid, it initially struck readily. The strike-frequency decreased rapidly after about a minute, however, until the animal ceased to show any response after about 5

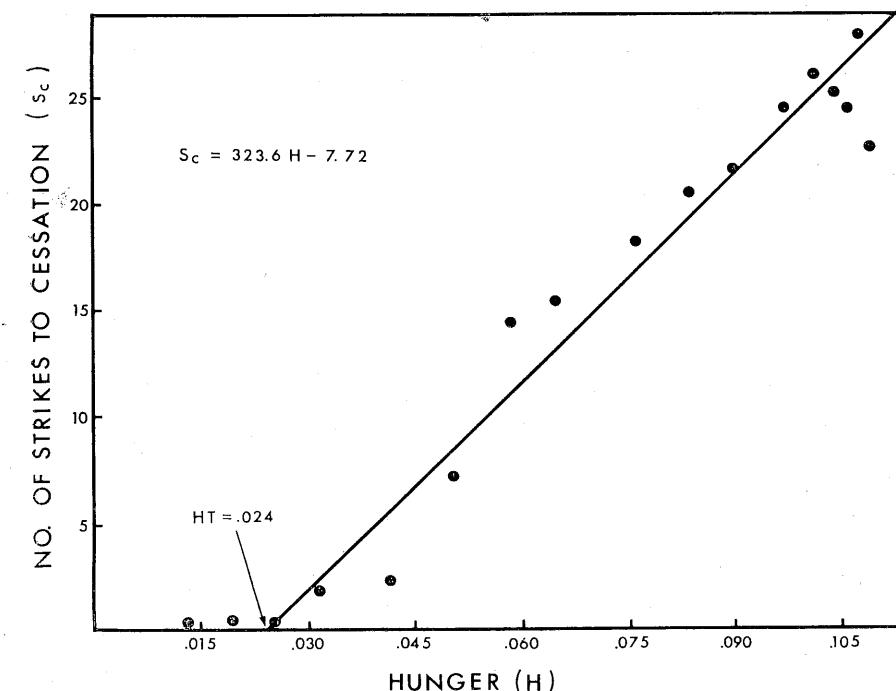


Fig. 25. The effect of hunger on the number of strikes that can be elicited from *M. religiosa* by a fly dangled behind a glass barrier.

minutes at the most. They termed this "stimulus satiation" after Thorpe (1963) and the same behaviour has been reported for other predators (e.g. the backswimmer, *Notonecta glauca*, Wolda 1961).

Inhibition of attack by contact with prey therefore is probably a common feature of many attack systems, and the effect could confuse the data presented earlier. Its effect was explored in more detail using the *Mantis religiosa* individuals that provided the data for the hunger curve in Fig. 5A. As described before, the 11 mantids used in these experiments were satiated and then deprived of food for various intervals of time, after which the amount of food required to return the animal to a fully satiated condition was measured. Immediately before the animals were fed, however, a fly was dangled behind a glass window within striking distance of the mantid. The mantids struck readily but could not, of course, capture the fly. The number of strikes were counted until they refused to strike for 30 seconds. This number is termed the number of strikes to cessation (s.) and its relation with hunger level is shown in Fig. 25. The form of this relation is very similar to that shown for the effects of hunger on distance of reaction (Fig. 7). The relation is at least approximately linear and very rarely is a response elicited below an attack threshold. Once the hunger rises above this threshold the mantid will strike, and the hungrier it is the more it will strike. Ultimately, however, the response stops, presumably because each strike inhibits a small amount and these inhibitions accumulate until the animal becomes completely unresponsive.

If we assume that each strike inhibits by a constant amount, then the amount of inhibition, I, can be given by

$$I = I_0 s,$$

where

I_o = the amount of inhibition caused by one strike

and

s = the number of consecutive strikes.

As argued in another paper (Holling 1965), it is likely that this inhibition will be manifested as a change in the attack threshold, HT , for the higher this threshold the lower the responsiveness of the predator for prey. Thus each strike would raise the threshold a small amount, and all strikes would cease when the attack threshold reached or exceeded the hunger level. Therefore the amount of inhibition required to cut off all strikes, I_c , is the amount required to raise HT to H . That is,

$$I_c = H - HT. \quad (41)$$

We also know from (40), however, that if the number of strikes causing complete inhibition is written as s_c , then we may write

$$I_c = I_o s_c. \quad (42)$$

Substituting (42) in (41)

$$I_o s_c = H - HT$$

and

$$s_c = (1/I_o) H - (HT/I_o). \quad (43)$$

Therefore, if the above arguments are correct, the number of strikes to cessation should form a linear relation with hunger. As shown in Fig. 25 the relation is, in fact, roughly described by a straight line. The data really are not adequate to proceed much further, but it does seem that the linearity is only approximate and that the relation is more likely to be curvilinear. This suggests that the inhibition caused by one strike, I_o , is not a constant. In fact, as discussed elsewhere (Holling 1965), it is more likely that I_o is a function of both the hunger and the attack threshold at the moment of strike. Moreover, there must be some recovery from inhibition between strikes. Since the inhibiting effect of prey contact and the recovery from this inhibition is explored in detail in the paper cited, and a model devised to include the effect, it is unnecessary here to explore the qualitative relation between inhibition and hunger any further.

It is necessary, however, to comment on the quantitative effect of this inhibition, since it might affect previous conclusions. According to equation (43), the amount of inhibition caused by one strike should be the reciprocal of the slope of the regression between s_c and H ; i.e. $1/323.6$ or 0.0031 . This is such a very small amount (only about 3% of the highest hunger) that it would only assume importance if several strikes occurred consecutively. Since this condition did not hold for any experiments described before this section, the effects of inhibition can be safely ignored in the mantid-housefly system.

THE SYNTHESIS

The preceding analysis provides a number of expressions that realistically describe various parts of the attack system. These are summarized in Appendix III. Each, however, represents only a very small fragment, and if the aim of this paper is to be achieved fully, the fragmental equations must be integrated into one model of the whole system.

General Form of the Synthesis

It was first thought that all the effects described here could be incorporated into a differential equation which could be integrated to yield an expression for

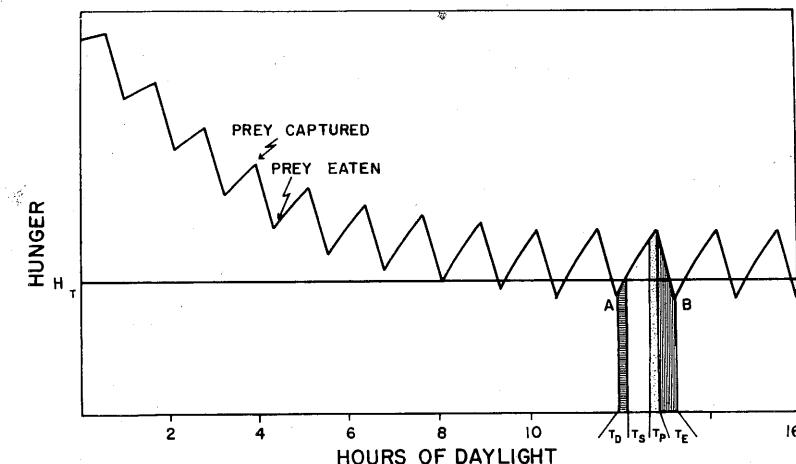


Fig. 26. Diagram to show the hypothetical changes in hunger of a predator during a 16-hour feeding period.

the number of prey attacked at different prey densities. It quickly became evident, however, that the inclusion of each fragment became progressively more difficult as the model was expanded. In fact, the point was quickly reached where the partially synthesized equation became intractable. There is clearly a relation, therefore, between the complexity of a process and the complexity of the model designed to simulate it realistically. If calculus is the sole language of expression then, beyond a certain point, each unit increase in the complexity of the process is accompanied by a progressively greater increase in the complexity of the model. This relation itself could be modelled and might well be approximated by an exponential form. The insistence on calculus therefore threatens one of the prime aims of this program of research: that is, to assure that the analysis and synthesis remain open-ended and amenable to addition and further expansion. Such an insistence would lead to a model that would quickly become so mired in complexity as to be intractable.

In searching for a more flexible language that could handle complexity, it became obvious that the difficulty arose not only because of the number of fragments involved, but also because of certain distinctive features that characterized the attack system. These can be best appreciated from Fig. 26 which shows the hypothetical changes in the hunger of a predator during a day of attack. At the beginning of the day the hunger is high because it is presumed that no attacks were made during the preceding night. The hunger continues to rise until the first prey is caught. It is eaten and the hunger is thereby abruptly lowered to a new level. Again the hunger rises until the second prey is attacked whereupon the hunger drops for the second time. Similarly, the third, fourth, and subsequent attacks are generated successively until the feeding period comes to an end (in this case after 16 hours of daylight). Thereafter the hunger rises until the next feeding period. In the example shown in Fig. 26 the density of prey is high enough that hunger gradually declines to a stable level near the end of the day, where it fluctuates between two fixed points occurring just before and just after capture. If the density was very low, however, the hunger could rise during the day, depending on the hunger level at the start.

Three prime features characterize this system. First, it is basically discontinuous, for there are relatively few contacts between predator and prey, and

every prey consumed abruptly changes the condition of the predator. Secondly, there is a strong historical element, for what happens at any moment depends not only on the conditions at that moment, but in the past as well. Finally, thresholds and limits are extremely important features of attack. One threshold, the attack threshold, HT, is shown in Fig. 26, and it assumes importance because no attack occurs if the hunger is less than HT. There are, in addition, a number of other thresholds and these, together with limits, like the one set by the maximum capacity of the gut, HK, give a distinctive character to predation.

These prime features of predation can be preserved if the model is built around the individual attack cycle. The total number of prey attacked during the feeding period equals the number of attack cycles that are generated and the number generated in turn depends on the duration of each cycle. Referring to the cycle between A and B in Fig. 26, the time taken to generate it is the sum of four distinct time-consuming activities. At A, just after a prey has been eaten, the hunger is below the attack threshold so the predator will not search for or attack prey. The time taken for the hunger to reach the threshold therefore is the "digestive" pause, TD. Once the threshold is reached the predator is responsive to prey and as it becomes still hungrier it searches at a faster rate because of the influence of hunger on the distance of reaction. Depending on the concentration of prey, a time is finally reached where a prey is located and recognized, and this represents the time spent searching, TS. Once the prey is located, a certain time, TP, is then taken to pursue it, and a further increment of time, TE, to eat it. The total time taken for the cycle, TI, is the sum of these four times:

$$TI = TD + TS + TP + TE. \quad (44)$$

Each of the four elements in this equation can be expressed in terms of hunger level using the fragmental equations presented earlier. Therefore, if a starting level of hunger is chosen, the time taken for the first cycle can be calculated as well as the new hunger level at the end of the cycle. The second cycle can then be generated and each successive one thereafter. To make the model more versatile a second, larger cycle can be superimposed on the attack cycles, so that attack can be divided into consecutive one-day intervals. This is simply done by keeping track of the total attack time that has elapsed, so that the generation of attack cycles can stop when the feeding period ends. The hunger can then be predicted for the beginning of the next day and another series of attack cycles generated. In this way it is possible to devise a very flexible model in which the number of attacks and hunger level can be computed for any interval of time and any density of prey. The model basically takes the form of a complex difference equation (Goldberg 1961).

Detailed Structure of the Attack Cycle

To begin each cycle the starting level of hunger, just after the last prey has been consumed, must be known. This can be designated as HO.

Time Taken in a Digestive Pause, TD

The expressions for TD have already been developed earlier (equations 38 and 39) and require no further modification here. That is,

$$TD = \frac{1}{AD} \ln \left(\frac{HK - HO}{HK - HT} \right), \quad HO < HT$$

and

$$TD = 0, \quad HO \geq HT.$$

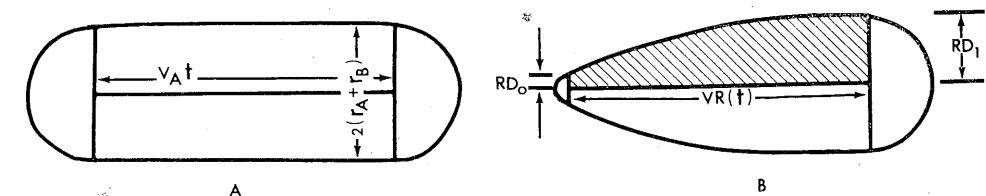


Fig. 27. Diagram of encounter paths swept out by a predator. A: distance of reaction remains constant with time. B: distance of reaction increases with time.

Time Spent Searching, TS

The expression for TS is the most complex and significant one of all the four, and it can be developed from the existing fragmental equations. In order to derive a general expression, it is most convenient to start by considering a population of moving particles of two types, A and B, moving at a velocity of v_A and v_B respectively. Each particle has an effective radius (r_A and r_B respectively) which determines how close the particles can approach before a collision or encounter results. First consider one of the A particles. As it moves it sweeps out a path $2r_A$ wide. When any part of a B particle is swept by this path an encounter results. Hence the maximum encounter distance from the centre of the A particle to the centre of any B particle is $r_A + r_B$. The "encounter path" swept out by the moving A particle therefore has a width of $2(r_A + r_B)$, so that during time t the area swept out by the moving A particle is (see Fig. 27A),

$$2v_A t(r_A + r_B) + \pi(r_A + r_B)^2.$$

If the B particles are stationary and present at a density of n_B , then the number of times the A particle will encounter B particles is

$$[2v_A t(r_A + r_B) + \pi(r_A + r_B)^2] n_B \quad (45)$$

The B particles are not stationary, however, but move at a velocity v_B . The velocity appearing in the above expression therefore should be the velocity of A particles relative to that of B particles, or v_R . At times, A and B particles will move directly towards each other at a combined velocity of $v_R = v_A + v_B$, and at times they will move towards each other at some angle less than 180° , at a velocity $v_R < (v_A + v_B)$. The magnitude of the relative velocity, v_R , when the objects converge at the angle θ , can be derived by forming the triangle of velocities and using the Law of Cosines, i.e.

$$v_R^2 = v_A^2 + v_B^2 - 2v_A v_B \cos \theta.$$

When θ can assume any value, the average relative velocity, VR , is given by

$$VR = \frac{1}{2\pi} \int_0^{2\pi} v_R \cdot d\theta. \quad (46)$$

Skellam (1958) developed a similar expression for a related problem and was able to show that equation (46) could be approximated by

$$VR = (v_A^2 + v_B^2)^{\frac{1}{2}}. \quad (47)$$

He also showed that the error introduced by this approximation was modest, being greatest when $v_A = v_B$ (under this condition amounting to 10%) and decreasing to zero when either v_A or v_B decreased to zero. As a result, equation (47) can be accepted as a satisfactory estimate of VR.

Thus when both A and B particles are moving, the number of B particles encountered by one A particle in time t will be, from (45)

$$N_E = [2(VR)t(r_A + r_B) + \pi(r_A + r_B)^2] n_B, \quad (48)$$

where N_E = the number of B particles encountered by one A particle, and VR = the average relative velocity as expressed by equation (47).

To this point I have attempted to assure some measure of generality by talking about A and B particles, rather than about predator and prey. Now, however, we can specify that the A particle is a predator and the B particles are prey so that the symbols in equations (47) and (48) can be changed as follows:

$VD = v_A$ = velocity of predator,

$VY = v_B$ = velocity of prey,

$RD = r_A$ = average distance of reaction (i.e., move to attack) of predator for a prey,

$RY = r_B$ = radius of prey,

$NO = n_B$ = density of prey,

t = time spent searching.

Transposing these new symbols into equation (48), and making $RY = 0$, for simplicity, the number of prey encountered by one predator searching for time t , is given by

$$N_E = [2t(VR)(RD) + \pi(RD)^2] NO. \quad (49)$$

Not all of the prey encountered are successfully captured. It was earlier shown that the capture success ratio, SC , was the product of the success of recognition, pursuit and strike ($SR \times SP \times SS$), and if all the time is spent in searching, the number of prey successfully attacked would be $NE \times SC$. Therefore, if NA = the number of prey attacked we may write, from (49)

$$NA = [2t(VR)(RD) + \pi(RD)^2] NO(SR)(SP)(SS) \quad (50)$$

if NA in equation (50) is made equal to 1, then t becomes the time required to search before one prey is successfully captured, i.e. it becomes TS . Thus

$$1/[NO(SR)(SP)(SS)] = 2(TS)(VR)(RD) + \pi(RD)^2 \quad (51)$$

from which

$$TS = [1 - \pi(RD)^2(SR)(SP)(SS)NO]/2(VR)(RD)(SR)(SP)(SS)NO. \quad (52)$$

Equation (52) provides an expression of TS for the simple case where the width of the encounter path, RD , is constant with time. In the case of the mantid, however, the distance of reaction, and hence RD , changes with hunger so that equation (52) must be modified to include this effect. The right-hand side of equation (51) represents the encounter area swept out by a single fly. This path actually increases in width as time passes because the mantid becomes hungrier. If a typical path is drawn as in Fig. 27B, then the "encounter" area swept out during TS is equal to:

2(area of shaded portion) + area of the two semicircles.

If the search starts at $T = 0$, when $H = HO$ and $RD = RD_0$, and stops at $T = TS$, when $H = HI$ and $RD = RD_1$, then this area swept out is given by

$$2(VR) \int_0^{TS} (RD) \cdot dT + \frac{\pi}{2} [(RD_0)^2 + (RD_1)^2]$$

Substituting this expression for the right hand side of equation (51)

$$\frac{1}{NO(SR)(SP)(SS)} = 2(VR) \int_0^{TS} (RD) \cdot dT + \frac{\pi}{2} [(RD_0)^2 + (RD_1)^2] \quad (53)$$

This expression provides the means to compute a realistic value for TS , since the integral expression, RD_0 and RD_1 can be derived from the fragmental equations. To a mathematician, the derivation of equation (53) would not seem particularly rigorous, but I chose the method because it seemed most comprehensible to the biologically oriented reader. The same expression can be derived differently, however, using the elegant and mathematically rigorous treatment that Skellam (1958) devised for a related problem.

Appendix IV presents the precise way that $\int_0^{TS} RD \cdot dT$, RD_0 and RD_1 in equation (53) were derived from the fragmental equations presented earlier. When these expressions are substituted in (53)

$$\frac{1}{(KR)(GM)(SR)(SS)(NO)} = \left(2(VR) \left[(HK - HT)TS + \left(\frac{HO - HK}{AD} \right) (1 - e^{-AD(TS)}) \right] + \frac{\pi(KR)(GM)}{2} [(HO - HT)^2 + (HK - HT + (HO - HK)e^{-AD(TS)})^2] \right) SP, \quad HO \geq HT. \quad (54)$$

If the conditions of this equation are violated by HO being less than HT , then TD is calculated as outlined in the preceding section, and HO is made equal to HT . This equation is tediously cumbersome, particularly when it is realized that SP , in the equation, should actually be expanded according to equations (23) and (33). It can, however, be drastically simplified with little error, by assuming that $RD_1 = RD_0$ (cf. equation 53) and by expanding the exponential terms into portions of a Taylor series, similar to a technique outlined elsewhere (Holling 1965, appendix I). Although these modifications would make the expression considerably more manageable, I felt that simplification, at this stage, should be delayed until the ramifications of any modification were better understood. Since the whole approach used here has been designed to assure realism, if I erred in any direction I preferred it to be toward excessive realism. If the expression later proved to be unnecessarily detailed it could always be simplified. Therefore the methods used to simplify the expression and the effect of these modifications will be left to a later paper (Holling, Brown and Watt 1965).

Since the complex form of the equation was retained it had to be solved to provide a value for TS . This is at least theoretically possible in the mantid-housefly system, since values for all the symbols, except TS , were available. An iterative technique using an I.B.M. 1620 computer was finally developed by Dr. D. M. Brown, Statistical Research Service, Canada Department of Forestry. We found that the solution was more readily obtained, however, by expressing equation (54) in terms of the hunger at the point of pursuit (HI) rather than in terms of TS . Once HI is known, it then is a simple matter to compute TS from the hunger equation (equation 37), since TS is the time required for the hunger to rise from HO to HI . This version reads as follows:

$$\frac{1}{(KR)(GM)(SR)(SS)(NO)} = \left(\frac{2(VR)}{AD} \left[(HK - HT) \ln \left(\frac{HK - HO}{HK - HI} \right) + HO - HI \right] + \frac{\pi(KR)(GM)}{2} [(HO - HT)^2 - (HI - HT)^2] \right) e^{-\frac{m(KR)(GM)(HI-HT)}{VP}}, \quad HO \geq HT. \quad (55)$$

Time Spent Pursuing Each Prey, TP

The fragmental equations for the time spent pursuing each prey (equations 33 and 34) can be accepted here with little modification. At the point of pursuit the

hunger, H_l , is determined from equation (55). This is simply substituted for H in equations (33) and (34) to give the desired expressions:

$$TP = \frac{(KR)(GM)(H_l - HT) - DS}{VP}, \quad H_l > HTP \quad (56)$$

and

$$TP = 0, \quad H_l \leq HTP \quad (57)$$

Time Spent Eating Each Prey, TE

Again little modification of the fragmental equation for eating time (equation 35) is required. It reads

$$TE = KE(WE), \quad (35)$$

but in order to make it more versatile it is better to include the actual weight of the prey (W) instead of the weight of prey eaten. As long as the hunger level is greater than the weight of the prey, then all the prey will be eaten and $WE = W$. If, however, the hunger level is less than the weight of the prey, then only enough of the prey will be eaten to lower the hunger to zero. If H_l is the hunger at the point of capture (approximately true since TP will generally be small), therefore, in this case, $WE = H_l$ and the weight of the prey that is discarded equals $W - H_l$.

These modifications lead to two equations:

$$TE = KE(W), \quad W \leq H_l \quad (58)$$

and

$$TE = KE(H_l), \quad W > H_l, \quad (59)$$

where

W = weight of each prey.

It follows from the same arguments, that the amount of each prey that is eaten and discarded can be computed as follows:

$$WE = W, \quad W \leq H_l, \quad (60)$$

$$WE = H_l, \quad W > H_l, \quad (61)$$

$$WD = 0, \quad W \leq H_l, \quad (62)$$

and

$$WD = W - H_l, \quad W > H_l, \quad (63)$$

where

WD = weight of each prey discarded.

The Complete Attack Cycle

The attack cycle begins when a prey has just been eaten and the hunger lowered to HO . The length of the digestive pause is then calculated from equation (38), if HO is less than HT , or from equation (39) if HO is equal to or greater than HT . The hunger level when the next prey is pursued (H_l) is then calculated from equation (55), making $HO = HT$, if HO is in fact less than HT . H_l is then introduced into a version of the hunger equation (Appendix II, equation 70) to give the time spent searching, TS . The time spent in pursuit of the prey is then obtained from equations (56) and (57) depending on whether H is greater or less than HTP . Finally, the time spent eating is computed from equations (58) or (59) and the weight eaten from equations (60) or (61). The total time required for the full cycle, TI , then is simply

$$TI = TD + TS + TP + TE,$$

and the hunger level for the beginning of the next cycle is given by

$$HO = H_l - WE. \quad (64)$$

This brings the calculations full circle, and with this new value for HO the next attack cycle can be generated.

It should be clear by now that a computer is essential in order to solve, in a reasonable length of time, the equations making up the model. I shall not, however, describe the computer program itself in detail. It was devised by Dr. D. M. Brown, Dr. K. E. F. Watt and the author and its basic form can be inferred from the foregoing. Further details, particularly the way the day cycle was introduced, will be described when the results of a simulation study using the model are presented in another paper (Holling, Brown and Watt 1965).

The move to the computer proved to be particularly fortunate. Before the model was programmed the group of equations seemed to be excessively cumbersome and detailed, and while each fragment of the model could be understood it was difficult to grasp the significance of the whole model. The difficulty arose largely because of the attempt to retain the discontinuities and thresholds that seemed to be so fundamentally characteristic of predation. Once the model was expressed using I.B.M.'s Fortran language, however, the cumbersome quality disappeared and the model could be presented in a succinct and integrated manner. The problem of discontinuities no longer proved troublesome since certain Fortran statements were admirably suited to cycle operations economically through one attack after another. Similarly, other statements directed the flow of computations so as to handle the threshold problem. Digital computers and the languages used to program them seem to be ideally suited to cope with the magnitude and kind of complexity found in biological systems.

OUTPUT FROM THE MODEL

Even though the form of the model has been dictated by extensive experimental data, its predictive powers should be demonstrated before it can be used with complete confidence. This can be done by substituting into the model parameter values measured in a real attack system, so that the events occurring at various times and prey densities can be simulated and compared to the real events. It is not, however, an easy task to obtain accurate quantitative measures for some of the parameters, for the act of measuring them can so disturb the animals that the values are changed. In the mantid-housefly systems, for example, the two parameters that determine the distance of reaction (GM and HT , see Fig. 7) are likely to be sensitive to disturbance, since they are behavioural responses that direct the animal to food. Additional, independent measures of both parameters would therefore be helpful as a check.

HT , the attack threshold, represents not only the hunger at which the distance of reaction becomes zero (cf. Fig. 7), but also the hunger at which the mantid stops striking at flies. All food eaten thereafter must be "force-fed" and the total weight eaten after striking stops, should have the same value as that determined for the threshold in Fig. 7. Two independent measures of HT therefore can be obtained, one from the data in Fig. 7 and one from the data showing the effects of time of food deprivation on hunger (Fig. 4). In the latter case, only data from feedings in which the mantids struck at four or more flies were used in order to ensure that the attack threshold of actively feeding, undisturbed animals was measured. The average weight of food eaten after the last voluntary capture in 115 cases was 0.3131 ± 0.0154 g. The value of the threshold obtained from the data in Fig. 7 is given by the X-intercept of the regression line: $4.33/11.73 = 0.3693$. These two values are reasonably close to each other and their average, 0.341, probably provides as accurate a measure of HT as can be obtained.

TABLE III
Values of attack parameters of standard female mantids attacking houseflies*

Parameter	Dimension	<i>H. crassa</i>		<i>M. religiosa</i>	
		Value	Source	Value	Source
AD	g./hr.	0.0501	Fig. 4 A and B	0.146	Fig. 5 A and B
GM	cm./hr.	24.63	Text	—	Text
HBEG	g.	0.799	Text	0.108	Text
HK	g.	1.000	Fig. 4 A and B	0.109	Fig. 5 A and B
HT	g.	0.341	Fig. 7 and text	0.024	Fig. 25
KE	hr./g.	0.760	Fig. 22	2.96	Fig. 24
KR		0.507	Appendix IV	—	—
M	prop./hr.	8.17	Fig. 21	—	—
SR		0.80	Text	—	—
SS		0.630	Table II	0.656	Text
TA	hr.	16.0	Fig. 3	16.0	Text
VD	cm./hr.	0	Text	0	Text
VP	cm./hr.	210.6	Equation (26)	—	—
W	g.	0.0245	Fig. 22	0.0245	Fig. 22

*VV is computed from the equation $VV = 223e^{-189.8NO} + 92$ (see Fig. 17).

Once a mantid starts reacting to flies, the distance of reaction increases with hunger at a rate determined by the value of GM. In Fig. 7 this value was calculated as 11.73, but observations of undisturbed mantids in large cages indicated that this value was too low. To check it, the distance of reaction of 12 standard mantids, deprived of food for 24 hours after being satiated, was tested in the same way as before, except that extreme precautions were taken to avoid disturbing the animals. Experiments were performed in a room with flat black walls, lights were shielded so that the operator remained in the dark, and black clothes, mask and gloves were worn. The average distance of reaction was 8.67 ± 0.51 cm., slightly more than twice the value obtained (4.11 ± 0.66) when fewer precautions were taken to avoid disturbing the animal. The value of GM calculated in Fig. 7 is therefore an underestimate. A more accurate measure can be obtained from the knowledge that $HT = 0.341$, and that the distance of perception and hunger when $TF = 24$ hours is 8.67 and 0.693 respectively. Thus $GM = 8.67/(0.693 - 0.341) = 24.63$.

Values for all other parameters of the model that have been presented earlier either were obtained using unrestricted mantids and flies in large cages, or represented morphological and physiological parameters that would probably not be sensitive to minor disturbances of the animals (i.e. AD, HK, KE, KR, TA and W). Their values therefore can be accepted as being reasonably accurate. Only one parameter, the recognition success, SR, was not specifically measured. As mentioned earlier, however, the success a predator has in recognizing a prey depends in large part on its contrast with the background. Since the flies were black and the background white in the final experiments, SR must be close to but probably not identical with 1.0. The value of 0.80 therefore was selected as a reasonable approximation.

The quantitatively accurate values for all the parameters of a *H. crassa*—housefly system are listed in Table III, together with available values for some of the parameters of a *M. religiosa*—housefly system, for comparison. These quantities are all that are required to simulate the functional response of *H. crassa* to various densities of houseflies. A range of densities was therefore chosen to cover completely the rising phase of the functional response curve and the beginning hunger, HBEG, was arbitrarily assigned a value corresponding to 36 hours of food-deprivation after satiation.

In order to compare the simulated with the real system, an experiment was designed in which standard mantids, deprived of food for 36 hours after they were satiated, were placed individually in large cages (1.19×0.58 m.) together with various densities of selected houseflies for 16 hours. Most of the details of the apparatus and experiments have already been described in the section concerning speeds of movement of predator and prey, but in addition, the mantids were kept under continual observation for the full 16 hours of attack, flies were replaced as they were captured, and three replicates were obtained at each of eight different densities.

The number of flies attacked per hour at different densities are shown by the histograms in Fig. 28. In order to reduce variability, the data were pooled and averaged in the following groups: the three lowest densities, 0.000574, 0.001147 and 0.001721 flies per sq. cm. to provide nine replicates, the three next highest densities 0.002868, 0.004302 and 0.006596 flies per sq. cm. to provide nine replicates and the two highest densities 0.011471 and 0.017207 flies per sq. cm. to provide six replicates. Therefore the three divisions of Fig. 28 represent three different prey density ranges from the lowest in Fig. 28A to the highest in Fig. 28C. In every case the attack rate at the beginning of the feeding period was high because the mantids' hunger and therefore distances of reaction were high. As prey were captured, however, the resulting decrease in hunger caused a decline of the number attacked per hour. Towards the end of the period the hunger stabilized, as suggested in Fig. 26, so that the attack rate remained constant. The decline in number of flies attacked per hour was most pronounced at the highest density because the higher consumption of food caused the hunger to range over greater extremes.

The lines in Fig. 28 represent the independent prediction of the model. In view of the difficulty in obtaining quantitatively accurate values for the parameters, the agreement between the simulated and real attack is remarkable. Both the form and the magnitude of the relations are very well predicted by the model.

In Fig. 29 the same data are presented in more detail to show how prey density and duration of attack affect the number of prey killed. The points represent data from the actual experiments (averages of three replicates) and the lines represent the prediction of the model. Again the model provides a very satisfactory prediction of the amount of attack that occurred in the real situation. Only at the two lowest densities at times greater than 10 hr. does the observed depart consistently from the predicted. If the departure from predicted is real, it probably results from the assumption that the distance of reaction is linearly related to hunger. As mentioned in the relevant section, it is more likely that the square of this distance is a linear function of hunger, so that distances of reaction, and hence attack rate, would tend to be overestimated at low densities when the hunger is high. Nevertheless, so few points are involved that the departure from predicted is not greatly disturbing and might well simply reflect the inevitable variability that arises when only a few replicates can be obtained.

One further test of the predictive power of the model can be made. At the end of each 16-hour experiment the mantids were removed from the cage and fed to satiation with weighed flies. The weight of food eaten represents the hunger level at the end of the experiment and this can be compared to the level predicted by the model. The comparison is shown in Fig. 30. The 45° line running through the origin connects identical values of observed and predicted. The actual data are distributed around quite a different line, suggesting that the model considerably overestimates the actual hunger at the end of the experiment. This

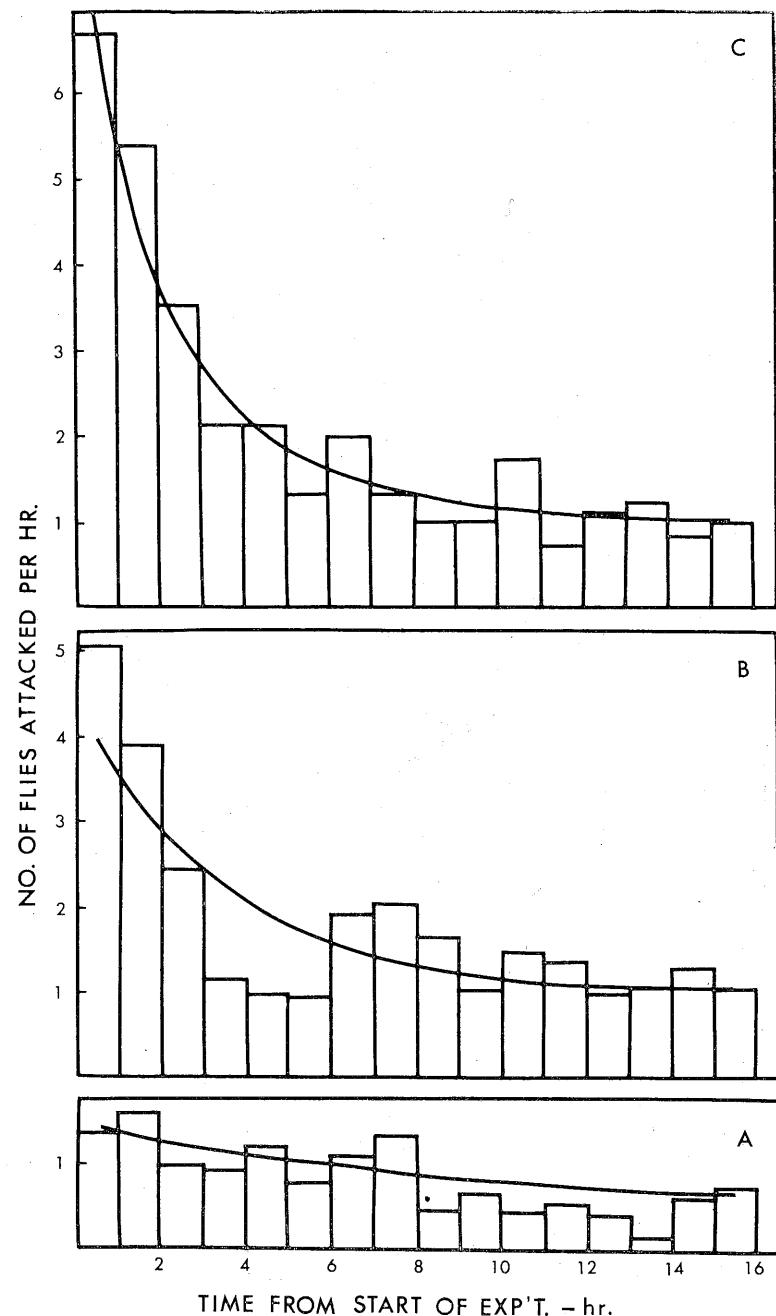


Fig. 28. The rate of attack of *H. crassa* predicted by the model (the lines) at various times during the feeding period compared with the observed data (the histograms). A: low prey densities, averages of 9 replicates. B: intermediate prey densities, averages of 9 replicates. C: high prey densities, averages of 6 replicates.

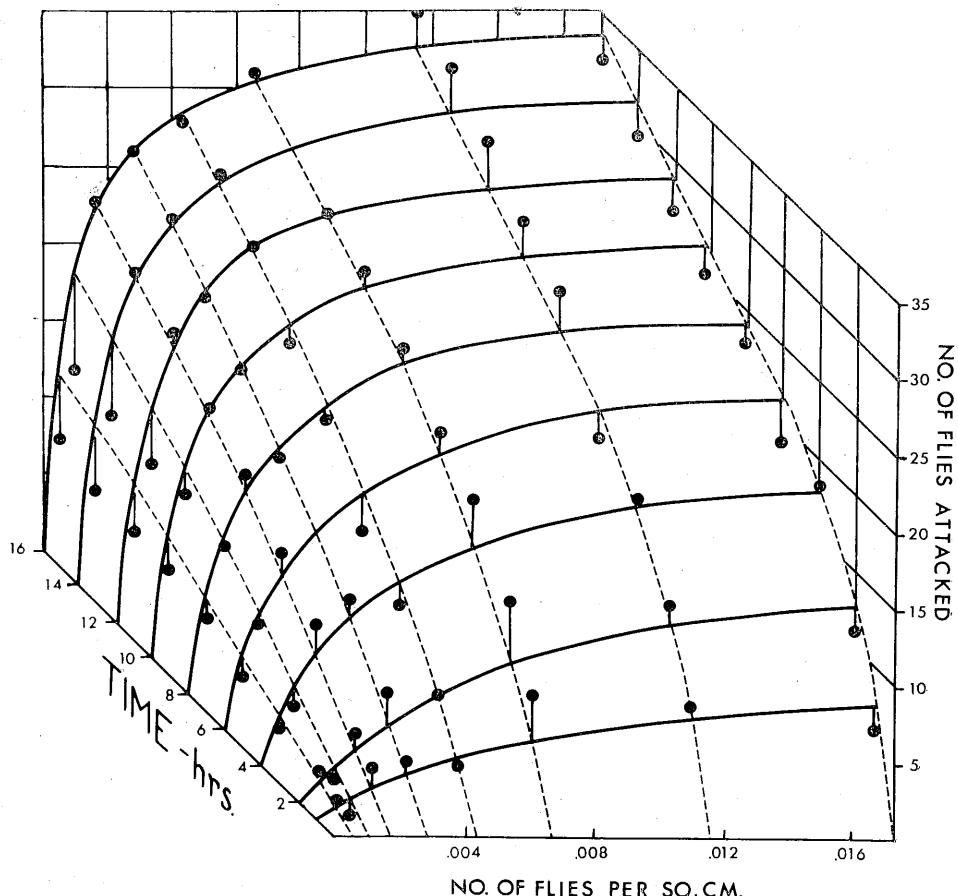


Fig. 29. Number of flies attacked by *H. crassa* at various prey densities and times. The points are actual data (averages of 3 replicates) and the lines are generated by the model.

hunger was measured, however, between 2300 and 2345 hours after the full 16-hour feeding period. It was shown earlier in Fig. 3 that consumption drops suddenly at this point as part of a diurnal rhythm of feeding that is independent of hunger. Therefore it is perfectly reasonable that the level of hunger measured at this time would be lower than expected. If the lowered consumption triggered by the diurnal rhythm is caused by a "stop-eating" hunger threshold being raised a constant amount, independent of hunger, then the plot of observed against predicted should yield a straight line parallel to the 45° line (slope = 1.0) in Fig. 30, but displaced to the right. This is exactly what occurs and the slope of the regression line, 1.07, is not significantly different from 1.00 ($t = 0.638$, $P = 0.5$ to 0.6). If the slope is then fixed at 1.00, the line of best fit runs 0.222 hunger units below the expected prediction. That is, irrespective of the hunger level, after the normal feeding period the mantids can be satiated with 0.222 g. less food than is required during the normal feeding period. This strongly suggests that the diurnal changes in rate of feeding are caused by changes in a "stop-eating" threshold. During the normal feeding period the mantids stop eating force-fed flies when $H = 0$, and during the non-feeding period stop when $H = 0.222$.

The foregoing comparisons between a simulated and a real system show that the model has good predictive powers. It accurately predicted, both qualitatively

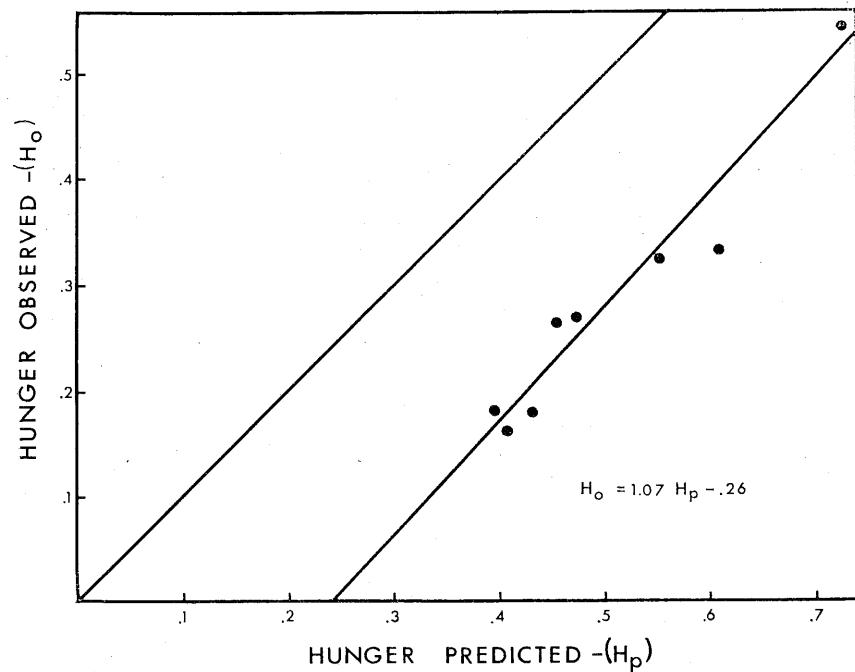


Fig. 30. Comparison of the observed hunger of *H. crassa* after 16 hours of attack with the hunger predicted by the model (averages of 3 replicates). Upper line represents perfect agreement between observed and predicted. Lower line represents the observed agreement.

and quantitatively, the effect of duration of feeding on the number of flies attacked by *H. crassa*, the effect of fly density on the amount of attack, and the level of hunger after a day of attack. Since the structure of the model was dictated by an intimate feedback between experiments and theory, the additional demonstration of its high predictive accuracy provides convincing evidence that the model is realistic.

A realistic, precise model that accurately predicts events in a system as complex as predation can be an extremely powerful tool. First, it can be used to analyze the structure of predation by showing how density, time and hunger affect components that can be measured only with great difficulty in real situations. Secondly, the logical consequences of evolutionary hypotheses can be inferred from the model by determining the effects of such hypotheses on the specific values of the parameters. If, for example, predators have evolved so as to maximize energy input, and minimize energy output, the range of parameter values that achieves this end can be determined. Thirdly, a large number of different examples of predation can be simulated quickly and efficiently by arbitrarily assigning various values to each parameter. In this way the spectrum of attack types that could occur in nature can be determined. Fourthly, the same simulation studies can be used to assess the exact importance of each parameter. Does a high rate of digestion, for example, confer an advantage to a predator as a control agent? Is speed of movement of predator and prey important? What influence does size of predator and prey have on predation? These, and similar questions can be answered from the simulation studies, thereby providing not only a theoretical benefit but, if the answers prove helpful in selecting efficient biological control agents, a practical benefit as well. Finally, the model can be used to devise simplified versions that can be used more easily in specific situations. It

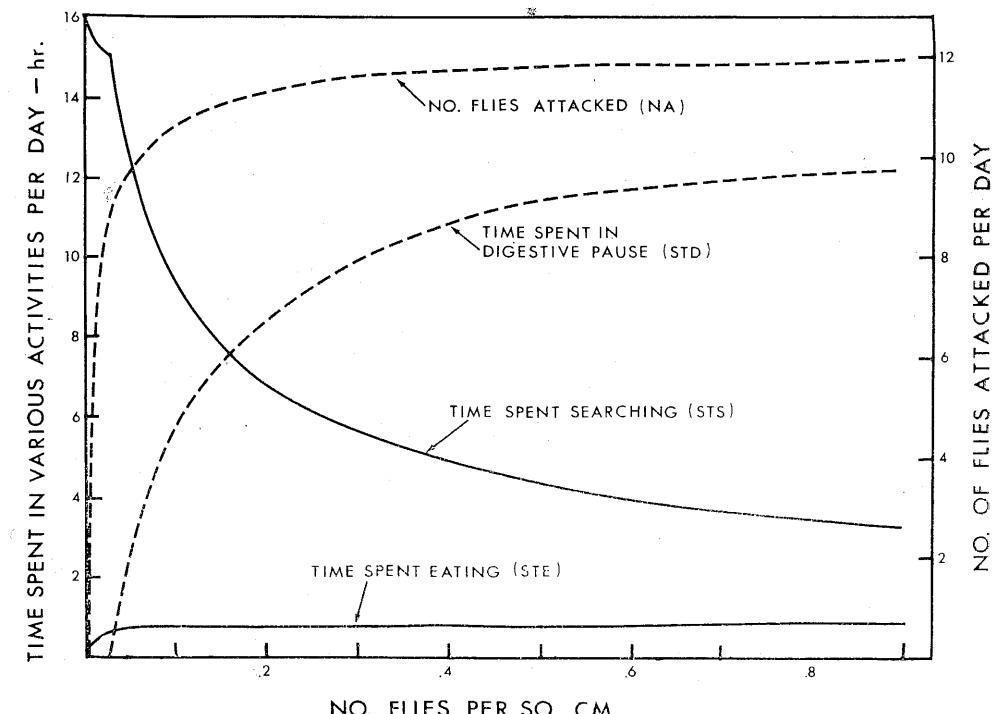


Fig. 31. Simulated output of a *M. religiosa*-housefly system showing the effects of fly density on attack and on a number of time-consuming activities.

is unlikely, for example, that the unmodified complex model could be used directly in a field study designed simply to describe the effects of predation by a specific predator. Too many parameters would have to be measured to make its use feasible. The model's complexity for this purpose is a drawback but one that can be easily rectified by using output to test the predictive powers of existing models (like those listed in Fig. 1), or more directly by introducing simplifying assumptions that seem reasonable in the light of the simulation studies and additional biological information. These steps were not taken earlier in the belief that it would be easier to make an overly complex, but realistic, model more simple, than to make an overly simple one more realistic.

A major simulation study is required to fulfill these five objectives. Such a study will be presented in another paper (Holling, Brown and Watt 1965), but to complete this section I shall introduce output from one more case in order to suggest more specifically some of the potential uses of the model.

Various parts of the analytical section were supported by data collected using *M. religiosa*. Enough of these data are available to provide specific quantitative values for many of the parameters of the model (Table III), so that it seemed logical to generate output that would approximately simulate a *M. religiosa*-housefly system. Those parameters not measured were assigned values they assume in an *H. crassa*-housefly system. Some of the output from the simulation are presented in Fig. 31, which shows the effect of fly density on the number of flies attacked per day (NA) and on the total time spent in various activities during a day. The functional response to prey density (NA vs. NO) curve has the same form as in the *H. crassa*-housefly system—a negatively accelerated rise to a plateau. The amount of attack is considerably smaller,

however, reflecting the smaller size of *M. religiosa*. No experimental data were obtained to confirm completely the shape and magnitude of this predicted response. In any case, since some of the parameters were arbitrarily assigned the values they assumed in the *H. crassa*-housefly system, complete congruence between observed and predicted is hardly expected. Nevertheless, some data were obtained to check the predicted maximum consumption at high densities. These data were collected by daily counting the number of flies eaten by nine *M. religiosa* placed in small cages ($13 \times 7 \times 7$ cm.) and provided with a surplus of flies (30 per day). Each mantid was tested for 4 days and the average daily consumption was 10.81 ± 0.68 flies per day ($N = 36$), not very different from the 12 per day predicted by the simulated case.

The amount of attack is directly influenced by the time spent in four activities: the "digestive" pause, searching, pursuing, and eating (cf. equation 44). The total time that the simulated *M. religiosa* spent pursuing, however, was so small (never greater than 0.02 hour) that only the time spent in the remaining three activities are shown in Fig. 31. Each of these times changes as prey density changes. Since there is a direct linear relation between the total time spent eating (STE) and the weight or number of prey eaten (cf. equation 35), the curve showing the effect of prey density on total eating time is identical in form with the functional response curve (NA vs. NO). The duration of the remaining two activities, the digestive pause and searching, are not so simply related to the number of prey eaten. At the lower prey densities, from zero to about 0.03 flies per sq. cm., too few flies are consumed to lower the hunger below the attack threshold and so produce a "digestive" pause. All the time is therefore spent either searching or eating, and the relevant portion of the curve of time spent searching is simply equal to the length of the feeding period minus the time spent eating. At a density of about 0.03 flies per sq. cm., however, enough food is consumed to produce a "digestive" pause, and as prey density increases further, the length of the pause increases at first rapidly and then progressively less rapidly to a plateau. Above 0.03 flies per sq. cm., therefore, the time spent searching is given by the length of the feeding period minus both the feeding time and "digestive" pause. The magnitude of these various curves is very sensitive to changes of some of the parameters. 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* system than the *M. religiosa* one.

Data of the type shown in Fig. 31 can be used to suggest other points as well. One of the important components of predation, for example, concerns the way prey density affects the production of predator progeny for the next generation (the numerical response). This production is affected by the amount of energy that is available to maintain the life of the parent predator and the amount that can be spared for other uses. If the energy content of prey is known, then the energy input can be determined from functional response curves similar to that in Fig. 31 (NA vs. NO). If the energy expended during various activities can also be measured, then the total energy expenditure can be calculated from time curves similar to the remaining three curves of Fig. 31. The difference between energy input and energy output provides a measure of net energy gain. At low prey densities this value will be negative, indicating that the predator could not survive in its given state. At some higher density, however, the net energy gain would be zero so that the predator could just maintain its given state. At still higher densities more and more energy would become available, energy that

could be turned to progeny production.* It should therefore be possible, with only a little more information, to generate a numerical response using data simulated by the functional response model.

The model can also provide solutions to practical, as well as theoretical, problems. One of the most persistent of these problems is one that faces the field ecologist who must determine the number of prey killed by predators in a specific situation. In a few cases the problem is avoided because the predator leaves a sign behind it when it kills a prey — e.g. small mammals attacking sawfly prepupae within cocoons (Holling 1959a). In most cases, however, no sign is left behind when a prey is killed, and the amount of predation often has to be determined through less satisfactory, indirect methods. Most ecologists who have grappled with this problem have felt that a universal key could lie in determining the amount of predation from the amount of prey found within the bodies of samples of predators. This can be determined by measuring the quantity of prey remains in the gut of a predator (e.g. Korschgen 1957) or by using a serological technique to measure the amount of some species-specific prey material within a predator's body (e.g. Loughton *et al.* 1963). But even if it is feasible to obtain an accurate quantitative measure of the amount of prey material within the predator, it is still necessary to convert this measure into the number of prey killed per unit time. In rare cases it can be presumed that the presence of prey within a predator indicates one prey has been eaten in the previous 24 hours (e.g. Dempster 1960). This can hardly be true in many cases, however, and to my knowledge no one has devised a general method to translate the quantity of prey found in a predator to the number killed per unit time. To do so requires information concerning rates of attack and rates of digestion. Since these features form an integral part of the functional response model described here, it should be possible to use the model to determine whether it is feasible to obtain accurate estimates of the amount of predation from stomach or serological analyses.

One of the quantities predicted by the model is the hunger level at any moment. By definition, this hunger level is the quantity of food required to completely satiate the predator, and therefore can be considered as a measure of the emptiness of gut. The difference between the maximum capacity of the gut and hunger ($HK - H$) therefore represents the quantity of prey material within the predator, and it should be possible to use the output from the two simulated cases to show how $HK - H$ is correlated with the number of prey attacked in a day, NA. The output discussed so far, however, is not quite comparable to a natural situation, since the hunger at the beginning of the day of attack was arbitrarily set at a level equal to the level produced by 36 hours of food deprivation after satiation. If several successive days of attack are generated, however, eventually the hunger at the beginning of the day stabilizes and is repeated indefinitely. At this point the hunger totally reflects the conditions of the situation and not the level of some arbitrarily assigned starting level of hunger. Since we are interested here in describing a natural situation, only data generated after the beginning hunger had stabilized will be considered.

The relation between the number of prey attacked per day and the amount of food in the gut is shown in Fig. 32, at the beginning and at the end of the feeding period. In both cases there is a strong correlation, and while the relationship is slightly curvilinear, it can be described adequately with a straight line:

$$NA = c'G,$$

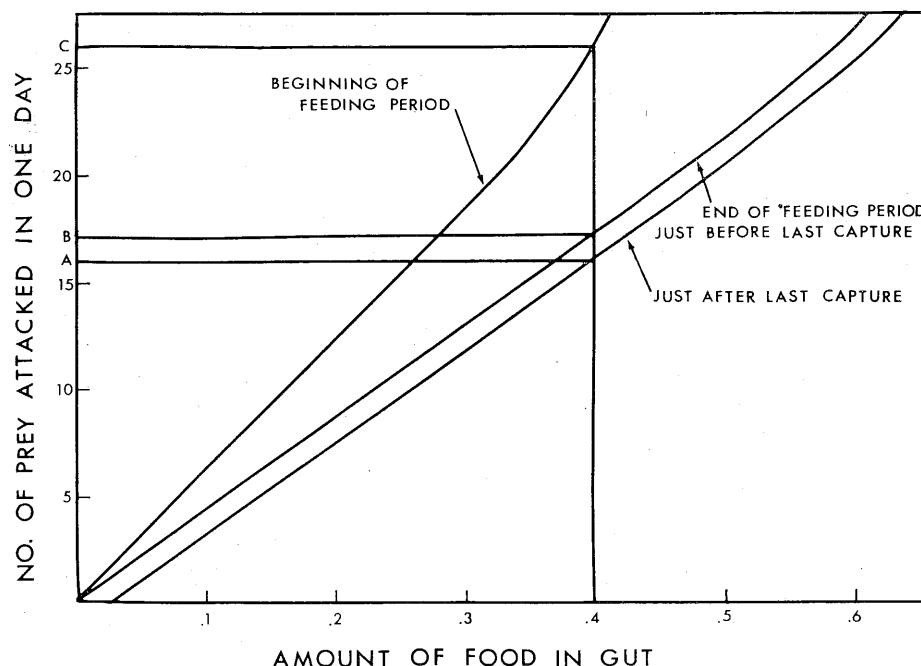


Fig. 32. Simulated output of a *H. crassa* - housefly system to show the relation between number of prey attacked per day and the amount of food in the gut.

where

$$c' = \text{a constant,}$$

and

$$G = \text{the amount of food in the gut (HK} - H).$$

Although the form of the relationship is unaffected by the time of day the sample is taken, the magnitude changes from the beginning to the end of the feeding period. This is to be expected, since the beginning of the feeding period was preceded by an 8-hour period in which no feeding took place. The correlation at this time is the result of the historical character of attack, for it reflects events that occurred in the previous feeding periods. If the amount of food in the gut is ever to be used as a measure of the number of prey killed, it is therefore very important to collect predators at one time of day. In Fig. 32, for example, a predator with 0.4 g. of food in the gut could indicate that 16 prey were killed per day (A), if the predator was sampled at the end of the feeding period, or 26 (C), if it was killed at the beginning of the feeding period. Variability is also introduced by the time elapsed since the last prey was eaten, as indicated by the two lines based on data collected at the end of the feeding period, one just before and one just after the last capture. The line obtained just after the last capture is displaced 0.0245 g., the weight of one prey, to the right of the line obtained just before the last capture. Because the prey is small relative to the size of the predator, in this case, the variability introduced is not excessive, and it should be possible to devise a simple and reliable field method to determine the number of flies attacked by *H. crassa* per day from stomach or serological analyses. Equation (65) would form the basis of the calculation, and the constant c' would be determined empirically using predators caged under approximately natural conditions and fed known quantities of prey. The best prediction would be obtained

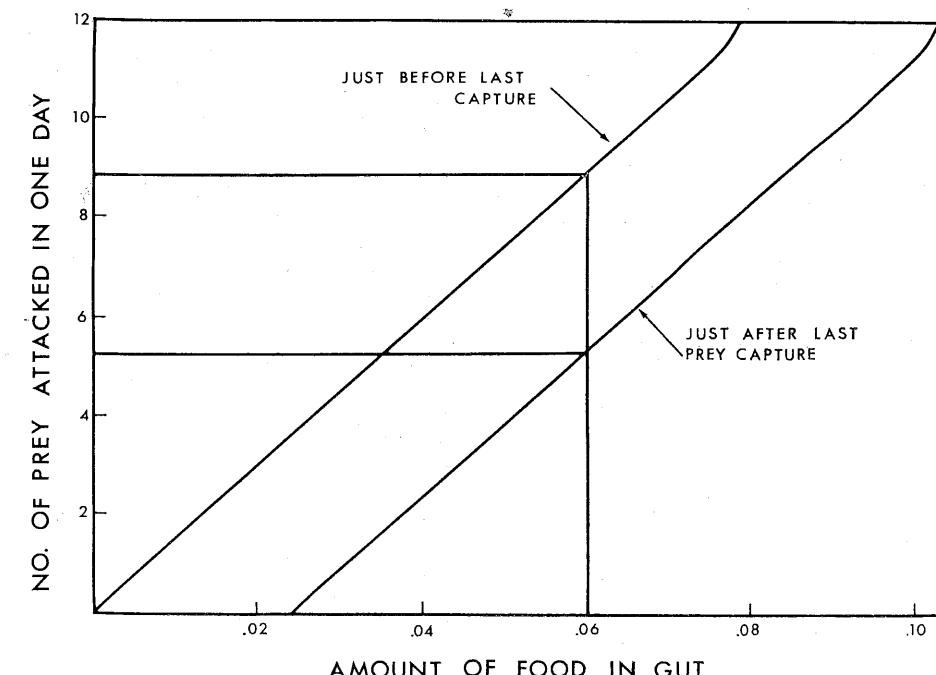


Fig. 33. Simulated output of a *M. religiosa* - housefly system to show the relation between number of prey attacked per day and the amount of food in the gut.

if predators were sampled at the end of the feeding period, since the lower the value of the slope c' , the more accurate the prediction of NA. Moreover, the influence of time becomes less critical as the feeding period progresses, since the hunger changes most rapidly at first and tends to stabilize towards the end of the period (cf. Fig. 26). At the highest prey density, for example, the amount of food in the gut increased by 0.184 g. (from 0.386 to 0.570) in the first 8 hours and by only 0.001 g. in the last 8 hours.

Figure 33 presents similar output generated by the stimulation of the *M. religiosa* - housefly system. Only conditions at the end of the feeding period are considered, and again the line obtained just after the last capture is displaced 0.0245 g., the weight of one prey, to the right of the line obtained just before the last capture. Because the predator is so much smaller, however, the displacement is relatively greater than in Fig. 32, so much so that an unacceptable amount of variability would be introduced. A predator with 0.06 g. of food in the gut, for example, could indicate that between 5.2 flies and 8.9 flies were eaten per day. Since this variability could not be reduced simply by increasing the sample size, under some conditions it is impossible in principle to obtain a satisfactory estimate of the number of prey attacked, knowing the amount of prey material in the stomach.

The conditions under which the technique breaks down depend not only on the size of the prey relative to the predator, but on the value of c' , as well — the lower c' , the more precise the estimate of amount of attack. The value of c' is affected by a number of parameters, particularly the rate of digestion, AD, and considerably more simulation will be required to explore fully the limits of the method. It is sufficient here to conclude that the number of prey attacked in a given period can be described by a linear function of the amount of prey material

in the predator. Consequently, when the prey are small relative to the predators, a simple method can be developed to estimate the amount of predation using data collected from stomach or serological analyses.

The foregoing examples show that the model can be used in a variety of ways to provide fresh insights into theoretical and practical problems. Any one problem might be answered satisfactorily by a considerably simpler model, but to deal adequately with many problems a more realistic and complex model is required. The model devised here fulfills this function admirably, and its full use will be developed later.

DISCUSSION

The Distinctive Features of Predation and Other Biological Processes

The present analysis of predation has been an attempt to apply a systems approach in depth; that is, to develop an integrated explanation for the mode of action of a major part of the predation process that is precise and yet realistic. The joint need for precision and realism led to the development of the experimental components analysis so that the explanation could be built in many small steps, each step being taken only when the explanation posed in previous steps had been experimentally verified. In this way the form of the explanation is dictated not as much by the need for mathematical neatness, but by the process itself. The analysis and the resulting model presented here do not pretend to be complete, however, for the essence of the approach is change and expansion. The model will continually evolve to include more and more of the process. In its present state it represents primarily a functional response to prey density and it does not embrace the functional response to predator density nor the numerical response. Inclusion of these two additional responses is a minimum requirement for a complete model of predation, since the functional responses to prey and predator density and the numerical response are basic features of every predation situation (Holling 1961). Nevertheless, this model of a functional response to prey density includes a major part of the predation process, and enough data have been analyzed to provide insight into the general problem of developing realistic models of complex biological systems.

The complexity of the predation system described here is only partly the outcome of the presence of a large number of components. There are, in addition, qualitative features that give a distinctive character to predation. Three of these features seem particularly important. First, thresholds and limits are extremely common and important. A mantid, for example, will strike at prey only when the hunger exceeds a certain fixed level, and will pursue it only when the hunger rises still further beyond another threshold. These thresholds result in sharp disjunctions in behaviour that are essential features of attack. Limits, like the one imposed by the maximum capacity of the gut (HK), are also common and introduce a fundamentally non-linear character to the components of predation. Thresholds and limits are distinctive features not only of predation but of other biological processes as well. A nerve impulse, for example, is propagated when the intensity of a stimulus exceeds a certain value, and a population of animals persists in an area only when its density attains a certain level. It is true, of course, that thresholds and limits affect non-biological processes as well, but the large number of components affecting biological systems and the commonness of thresholds and limits give a unique character to these systems.

Secondly, time dominates the action of many components of predation, for it takes time for a predator to search for a prey, to pursue, subdue, eat, and digest it. Moreover, these time-consuming activities produce lag effects so that events occurring at any moment depend not only on conditions at that moment but also on conditions in the past. This historical character has long been recognized as an integral part of genetics and evolutionary theory but it is an equally important feature of predation and, indeed, of most biological systems.

Finally, there is an essential discontinuous quality to predation that is imposed by the environment of the predator. This results because there are relatively few contacts between predator and prey, and each prey eaten produces an abrupt change in the predator's hunger. Such extrinsic discontinuities are equally common in other biological processes as well — in parasitism, reproduction and competition, for example, since again there are relatively few contacts between animals. In addition, diurnal rhythms, discrete generation times, and seasonal fluctuations of temperature impose further discontinuities on biological systems.

These three features — the prevalence of thresholds and limits, and the historical and discontinuous features — must be preserved if a model of predation is to be realistic and meaningful. Since these same features seem to pervade all biological systems, the specified way in which they were handled in this paper might apply widely. During analysis, for example, the experimental components approach seems well suited to show which components operate and exactly how they function. During the synthesis, difference equations, and the languages designed for computers are admirably suited to preserve the three prime qualities that characterize biological systems. In fact the predation model can scarcely be presented in a complete form except as a computer program. Control statements in the program direct the flow of computations in such a way that thresholds can be incorporated very readily. Similarly, other statements are so designed that operations can be cycled through one attack after another in an economical way. Finally, because of the computational speed of computers, the significant history can be actually duplicated until a stable condition prevails. Thus the combination of an experimental component analysis, which gives direction to theory, and the digital computer, which effectively copes with the distinctive complexity of biological systems, provides a way to develop precise and realistic models of whole biological systems.

Problem of Achieving Reality and Generality

Reality

It was pointed out early in this paper that the approach was designed to retain four qualities — wholeness, precision, realism, and generality. The wholeness is preserved by proceeding step-by-step in the analysis of a whole system, so that the action and interaction of the individual fragments are discovered.

Precision is assured by expressing conclusions in mathematical forms where they immediately become susceptible to testing. But the attempt to achieve wholeness and precision might have been accomplished only by sacrificing the need for reality. In fact, the specific explanations developed are based upon simple descriptions of events occurring in the variety of components that affect attack. Nor should this be surprising, since the explanation of the action of any process is always based upon descriptions of subordinate processes (Ghent 1963). All that is required for realism is that the equations describe each of the contributing components adequately and consistently. In practise this is most effectively accomplished if the equations are based on at least crude guesses as to the

mode of action of the components. Strictly empirical equations that provide no insight into the operation of components can often be developed to describe adequately one example of the process, but not others. It is not always possible, however, to develop a meaningful set of postulates upon which to base an explanatory equation, and the only alternative is an empirical one. Thus the fragmental equations proposed here are partly explanatory, as in the case of the hunger equation, and partly empirical, as in the case of the relation between minimum angle of vision and angle to the body. In every case, however, the relations were tested against data collected from *Hierodula*, and, where available, from other species, so there is some basis for confidence in the adequacy and consistency of their description power.

Even the explanatory fragmental equations should be considered as having only descriptive utility, since the explanation provides at the best a very crude explanation in terms of further processes underlying their action. As a result, the physiologist interested in hunger, for example, or the biophysicist interested in vision, would probably be deeply unhappy with the formulations proposed for these particular fragments. This is inevitable, for their interests are concentrated on processes that contribute to predation, not on predation itself. For the purpose of explaining a process like attack it is quite unnecessary to insist on explanations so rigorously realistic that they are ultimately based on, say, the kinetics of enzyme action or on electro-chemical events in the nervous system. Such insistence is a road with no end, for enzyme kinetics and neural action can in turn be explained by subordinate processes of biophysics and biochemistry. The striving for excessive realism can lead to a model as mysterious as the process modelled. In Bellman's words (1957, preface), "the Scientist, like the Pilgrim, must wind a straight and narrow path between the Pitfalls of Oversimplification and the Morass of Overcomplication."

Generality

The experimental components analysis and computers make it possible to deal with whole systems precisely and realistically. This gives great depth to the analysis, but it might only be achieved at the expense of generality or great breadth of application. Concern over this possibility perhaps represents the one theme that unifies theoretical ecologists. During an animal's evolutionary history it is confronted with a variety of problems, each of which can be solved in very many ways. A predator confronted with the problem of catching prey, for example, can exploit a wide variety of techniques. A mantid or a hawk exploits the advantages of a grasping structure — the fore-leg and talon, respectively. An ant lion traps prey in a pit dug in sand, the baleen whale sieves out prey using a highly efficient sieving organ, the rattlesnake immobilizes prey with poison, and the spider traps with a web. Natural selection inevitably assures exploitation of as many routes as possible within the limits of an organism's existing organization. The multitude of problems and the variety of solutions therefore produce a diversity that seems overwhelming. Moreover, since the analysis initially has to concentrate on one or a few examples, in the hope that these serve as true analogues of the whole process, there is a very real danger that the explanation and model will become so coloured by the specific and unique features of the example analyzed that it becomes impossible to retain generality. An attempt was made to avoid this by organizing components into basic and subsidiary ones (Fig. 1) and by casting the specific explanations in as general terms as possible. The success of this attempt can be judged only by a broadly comparative study with

direction given by the model. Until this is done, however, we can derive some clue as to the generality of the model from information in the literature.

A given model might incorporate an explanation that applies to only one example and yet still describe a wide variety of examples. This could occur whenever natural selection exploited a number of routes that led to the same end. The first step is therefore to determine if the predation model presented here has descriptive generality. Although the simulation studies are not complete, two different kinds of functional response to prey density have been generated by the model. One represents the general condition in which there is a negatively accelerated rise to a plateau, as in Figs. 29 and 31. This has been termed the Type 2 response elsewhere (Holling 1959a). The other represents a limiting condition where the size of the reactive field does not change with hunger but has a constant positive value whenever the hunger exceeds HT. In this case the time spent searching is computed from equation (52) rather than from equation (54), and the functional response curve rises as a straight line to a plateau as prey density increases. This has been termed a Type 1 response (Holling 1959a). Both Type 1 and 2 responses have been demonstrated experimentally by a number of workers, using a number of different species of predators. Since most of this information has been presented elsewhere (Holling 1965, table I), a brief summary is sufficient here.

At the time that paper was written, information on ten different species of invertebrates was collected from the literature and my own work. Three of these species, two filter-feeding crustacea and one mite, showed a Type 1 response. Since then, another example of this kind of response has been discovered in the attack by a coccinellid, *Coccinella septempunctata*, on the cabbage aphid (Atwal and Sethi 1963). In all these cases there is independent evidence that the size of the reactive fields of these species is in fact constant, as required by the limiting condition of the model. All the remaining seven species of invertebrates (representing Orthoptera, Hemiptera and Coleoptera) showed a Type 2 response with the negatively accelerated rise to a plateau predicted as the general condition by the model. Again one further example has been discovered in the literature, since Reeve (1964) has recently shown that the chaetognath, *Sagitta hispida*, has a Type 2 response when attacking different densities of brine shrimp nauplii. Thus the functional response model presented here can faithfully reproduce the salient features of the responses of all examples of invertebrates for which information could be found.

The functional responses of vertebrates to prey density are fundamentally different in form, however, since the rising phase of the response curves are S-shaped. This Type 3 response cannot be generated by the model presented here. It has already been reported (Holling 1965) that such responses are generated if the model is expanded to include a learning component, so that the lack of generality of the model presented here simply results because it represents a limiting case of a more general condition. Nevertheless, it still adequately describes the responses of all predators in which associative learning plays a negligible role, so that it does have quite a broad application even in this limiting condition.

Although the model does have broad descriptive powers, it is still possible that the explanations incorporated are limited to only a few cases. The degree of structural generality is difficult to assess, however, since appropriate data are not available. The best that can be done for the moment is to obtain a very

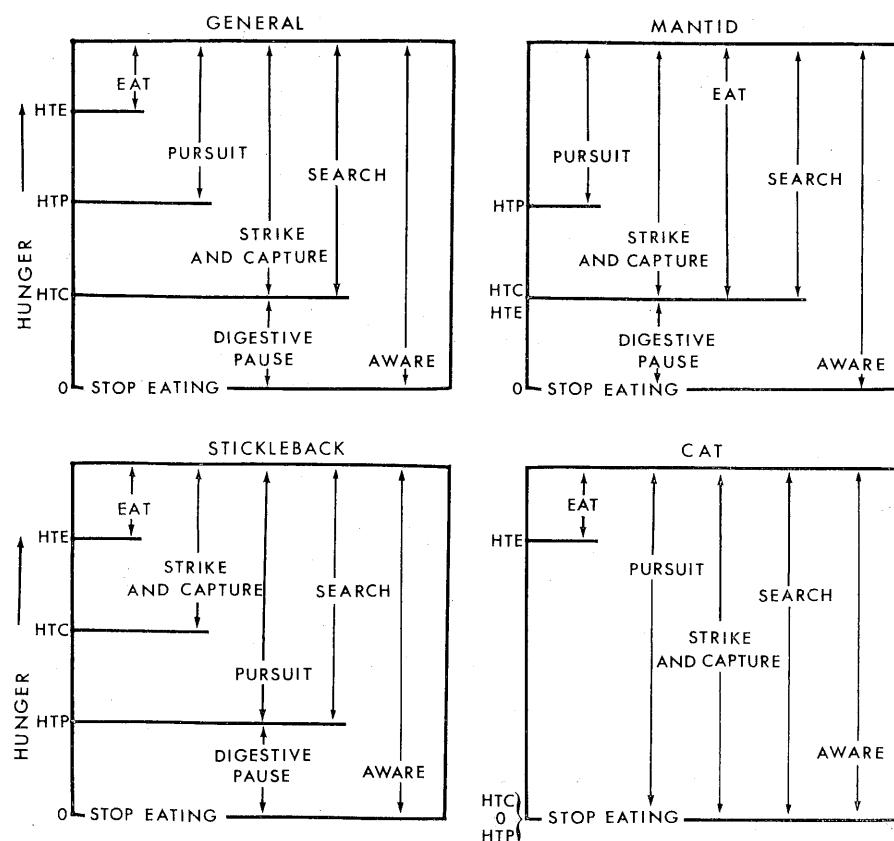


Fig. 34. Relation of the various attack thresholds to each other in four different types of predation.

rough idea of the degree of generality of those parts of the model that are illuminated by at least indirect information.

The model owes its characteristics in part to the interrelationship of the various fragments as well as to the specific way the action of these fragments is described. Moreover, the essential interrelations are concentrated in events occurring in one attack cycle, and are determined in large measure by the relative values of the thresholds. In the mantid there are essentially three attack thresholds. The first can be called a "stop-eating" threshold occurring when the hunger becomes zero. The second is a "capture and eat" threshold, for prey are struck at, captured, and eaten only when the hunger rises to a certain level. The third is a "pursuit" threshold, for the hunger must rise still further before prey are pursued. The various activities initiated when these thresholds are reached are summarized diagrammatically in Fig. 34. The relationship between the thresholds in the mantid is not universal to all species, however. The stickleback, for example, can pursue a prey and yet not be hungry enough to capture it when it comes within reach (Tugendhat 1960). If it is hungry enough to capture the prey then it might not be hungry enough to eat it, and the prey is discarded. The attack thresholds therefore bear quite a different relationship to each other from in the mantid (Fig. 34): the pursuit threshold, HTP, is lowest, the capture threshold, HTC, is next, and the eat threshold, HTE, is highest. In some other predators the relations between the thresholds are still different. A cat, for

example, will continue to search for, pursue, and attack prey even though it will not eat them. As a result, the pursuit and capture thresholds (HTP and HTC) must be zero, and the eat threshold (HTE) some value above zero (cf. Fig. 34). Because the relationship between thresholds is so different, it is difficult to diagram a completely general case, and the best that can be done is shown in the first figure of Fig. 34. Both the mantid and cat represent limiting conditions of this general case where certain thresholds become equal to each other or to zero. The stickleback, however, cannot be derived so simply, since the position of HTP and HTC are completely reversed.

Although it is difficult to diagram a completely general case, it is a straightforward matter to make the model truly general in this respect, since computer programs are ideally suited to handle this kind of switching problem. This revision has, in fact, already been incorporated in the model, and the method used is summarized by the diagram in Fig. 35, which outlines the flow of computations that can take place during one attack cycle. In order to start the attack cycle, input data for the parameters listed in the top box of Fig. 35 must be provided. Since the fragmental equations rely on one threshold, HT, which by definition represents the lowest hunger above which searching occurs, it is necessary to equate HT to either HTC (as in the mantid) or HTP (as in the stickleback) depending on which is lowest. Therefore in step 1, Fig. 35, the question is asked whether the value of HTP or HTC is the lowest. If HTC is the lowest then HT is made equal to HTC (step 2). If HTP is the lowest then HT is made equal to HTP (step 3). In either case the next step (step 4) is needed in order to determine whether the hunger level at the start (HO) is less than or greater than HT. If it is greater than or equal to HT then there is no "digestive" pause (step 5) and searching starts immediately. If HO is less than HT, however, there is a digestive pause that lasts until the hunger rises to HT. This must be computed using equation (38), after which HO is made equal to HT in step 6. Both steps 5 and 6 lead to step 7 where the time spent searching and the new hunger level at the point of pursuit, HI, are computed from equation (55).

Once the simulated predator is ready to pursue a prey it is necessary to determine if it is hungry enough to capture it. This is determined in step 8, and if the predator is not hungry enough to capture the prey ($HI < HTC$), it is ignored, and a new time spent searching and a new value of HI is computed using as a starting hunger the hunger level at the point of the abortive pursuit. Calculations then return to step 7. The loop formed from steps 7 to 8 to 9 and back to 7 continues until the hunger equals or exceeds the capture threshold HTC. At this point a pursued prey will be captured and computations can proceed to step 10 where it is decided if the predator is hungry enough to eat the prey, i.e. if HI is greater than or equal to HTE. If it is less, the prey is simply discarded, and calculations return to step 7. Again a closed loop forms from steps 7 to 8 to 10 to 12 and back to 7, and remains closed until the hunger finally exceeds HTE and a captured prey is eaten (step 11). The amount of this prey eaten depends upon its weight and the predator's hunger, and the relative values of both are tested in step 13. If the predator's hunger is reduced to zero before the prey is consumed, then the amount remaining, WD, is discarded (step 15), and the weight eaten, WE, is simply equal to HI. If, on the other hand, the hunger is greater than W, all the prey will be eaten and none will be discarded (step 14). From steps 14 and 15 computations proceed finally to step 16 where the various time-consuming activities are added to give the length of the attack cycle (TI). In addition, the values of some time-consuming activities are returned to zero and a new hunger level ($HI - WE$) calculated in order to generate another attack cycle at step 4.

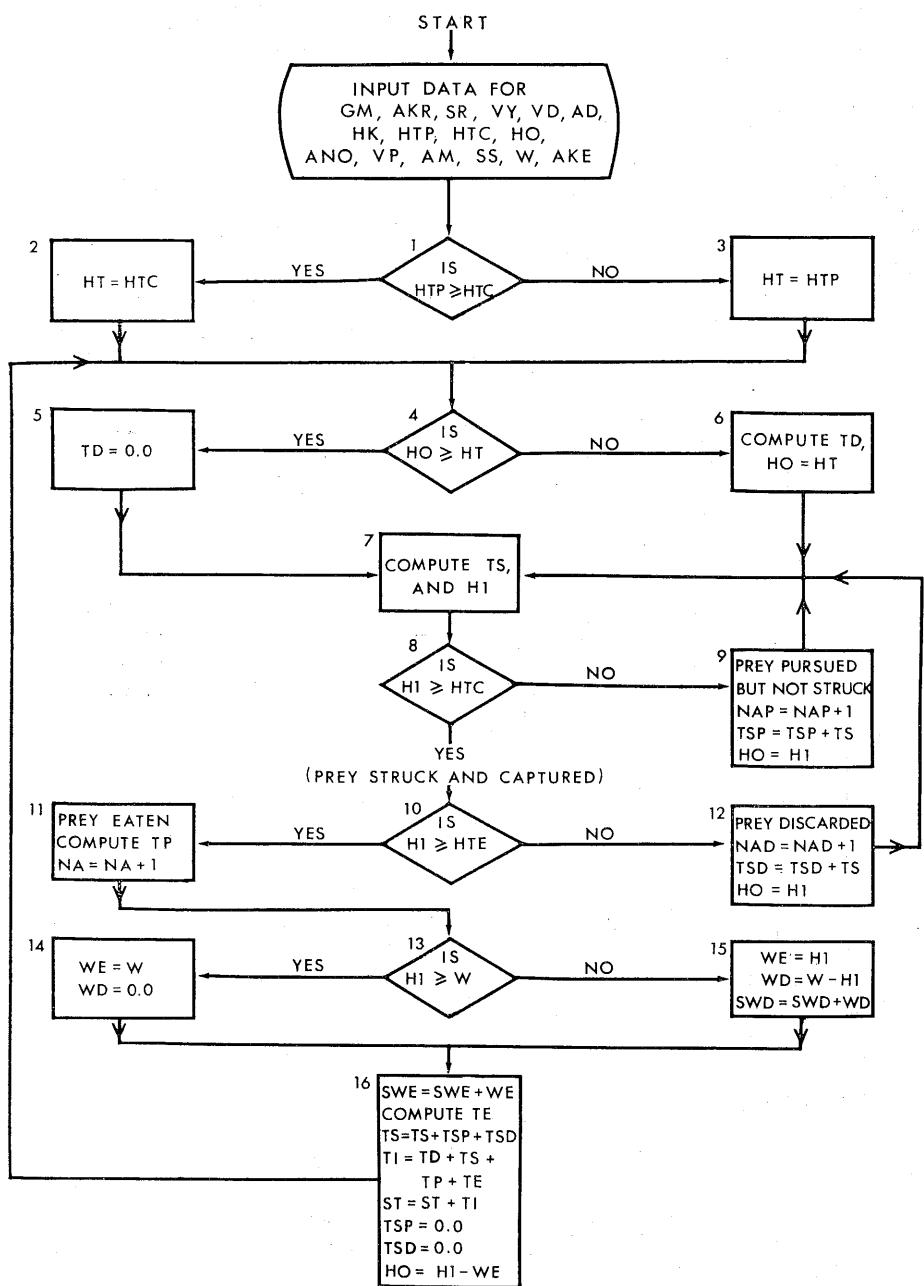


Fig. 35. Flow diagram to show the flow of computations in a generalized attack cycle.

A computer program developed from such a flow chart is sufficiently versatile to handle all the different cases shown in Fig. 34. It represents only a modest increase in complexity from the program designed for the mantid case alone, since only seven additional steps are required (steps 1, 3, 8, 9, 10, 12 and 15). The modest increase in complexity pays off handsomely in a very major increase in the generality of the model.

The degree of generality depends not only on the gross structure discussed above but also on the fine structure, on the specific form of the fragmental equations. Of all these equations the most important and complex is the expression devised to determine the time spent searching (equation 55). Its basic form is not at all unique to this paper, however, since a number of different processes requiring contact between two animals have been treated in fundamentally the same way — cannibalism by Stanley (1932), parasitism by Laing (1938), predation by Fleschner (1950), location of mates by Mosimann (1958), and location of birds for population assessment by Yapp (1955) and Skellam (1958). Although these treatments and that presented here are basically similar they do differ in the generality of the resulting equations. All the expressions except that presented here presume that the distance of perception is constant and does not change with time. In addition the situations examined by Stanley (1932), Laing (1938), and Fleschner (1950) represent conditions that are further limited, since the cannibal, the parasitoid or the predators they were studying searched for immobile prey or hosts ($VY = 0$). In these cases the speed of movement of one particle relative to the other is simply equal to the speed of movement of the attacker, i.e. $VR = VD$. This is similar to the mantid-housefly situation except that here the attacker is immobile ($VD = 0$) and the prey mobile, so that $VR = VY$. Mosimann's intriguing analysis of mating encounters (1958) partially relaxes this limitation, since both particles (males and females) were assumed to move, but at the same speed. Finally, the restrictions placed on speeds of movement were completely relaxed in the papers by Yapp (1955) and Skellam (1958). Skellam showed that equation (46) was the exact solution but that this could be simplified, introducing only a modest error, to the equation used by Yapp (1955) and in this paper (equation 47) i.e. to $VR = \sqrt{(VD^2 + VY^2)}$. Moreover, Skellam was able to demonstrate that equation (46) was not limited to conditions where the organisms moved in straight lines between encounters, but would apply no matter how the organisms moved so long as their path "could be represented to any arbitrary preassigned degree of approximation (no matter how close) by a chain of minute straight links" (*op cit.* p. 389). The present analysis extends the conditions still further in two ways. First, by introducing the parameters SR, SP, and SC, the equation is converted from one that expresses the number of encounters between predator and prey to one that expresses the number of encounters that are successfully recognized, pursued, and captured. Secondly, it was obvious that the distance of perception was not constant but changed with time as the predator's hunger increased. This effect was introduced in the specific way suggested by the experimental data to yield a considerably less restrictive model.

Although this last expansion does increase the generality, it is certainly possible that the specific modification is not truly general. This modification relies initially on the empirically determined relation between hunger and time of food deprivation. Although the equation devised to express this relationship described it well, it is based in part on a postulate that is suspect — that is, that the consumption of a prey immediately affects the behaviour of the predator. It seems more likely, however, that there is at least some delay before the presence of food in the gut changes the internal state of the predator sufficiently to trigger

a change in behaviour. In the mantid, the delay seems to be so slight that it can be ignored. The mantid is certainly not unique in this respect, since Green's (1965) elegant experiments using blowflies show that its activity is immediately affected by the ingestion of a sugar solution. Green was also able to develop a convincing explanation for the effect of food on activity of insects, an explanation that could explain the shortness of the delay. He proposed that when foregut receptors detect the presence of food in the gut, a message is sent to the corpus cardiacum complex stimulating it to release a hormone that inhibits activity. This complex has been shown not only to produce but also to store an activity-inhibiting factor. Since this factor can be stored, no delay is required in order that enough be released to produce an effect. Its release is immediate. The result is a very minor delay between the ingestion of food and the reduction of activity.

Unlike the blowfly, hunger in vertebrates seems to directly involve blood sugar levels (Janowitz and Ivy 1949; Chambers 1956). In such cases blood sugar levels take a significant time to build up after food is ingested, so that the delay between the consumption of food and a change in activity could be long enough to produce important delayed effects. The delay would certainly be enough to explain Brown's (1957) observation that starved fish, suddenly presented with an abundance of food, overeat to the point that the abdomen becomes abnormally swollen. It would also explain Tugendhat's (1960) data, which show that the rate of feeding of starved sticklebacks declines rapidly at first as feeding continues, recovers briefly, and declines again until a constant rate is achieved. This pattern is similar to that presented in Fig. 28 for the mantid, except that the mantid showed no consistent evidence of a brief recovery. Tugendhat proposed quite a different explanation for the phenomenon but, since his explanation requires very restrictive conditions to apply and since it was unsupported by any other evidence, it seems that the effect of a hunger delay is a more likely cause.

Unfortunately, there are insufficient data to justify inclusion of the delayed effects of hunger in the present model, particularly when the effect is probably unimportant among insects. Ultimately, however, such a modification should be made, presumably by expressing hunger as the concentration of some blood constituent which in turn is a function of the amount of food in the gut, metabolic demands, and time. Even without this modification, however, the model still probably applies generally to invertebrates and even describes major parts of the attack of vertebrates.

The specific form of the equation used to determine the time spent searching depends not only on the form of the hunger equation, but also on the specific way hunger and prey density affect the size of the reactive field, the relative speed of movement of predator and prey, and the capture success. The size of the reactive field depends partly on the shape of the field, but, since the shape can be expressed simply by different values of one parameter, KR, this portion of the model is quite general. If the reactive field is circular, as it probably is for predators that locate prey by odour or touch, then KR equals π . If the reactive field is elongate, as it likely is for predators that use binocular vision or echo-location techniques, then KR is less than π . The size of the field is also determined by the way distance of reaction changes with changing hunger. It was shown earlier that the distance of reaction, r, was well described by a straight-line function of hunger. It was also pointed out, however, that recent work has suggested that actually r^2 , rather than r, is linearly related to hunger. This latter function has been partially substantiated by more extensive data than those presented here, and was derived from basic knowledge of the physics of binocular vision. It is therefore probably more generally valid, at least among predators that locate prey visually, but until

its descriptive powers and explanatory content are more fully tested, it would be premature to modify the model. In any case, the relation actually incorporated in the model is sufficiently close to describe adequately the effects of prey density and time on attack.

The relative speed of movement of predator and prey was presumed to be unaffected by hunger. This was the only conclusion that could be drawn from the mantid-housefly system, since it represents a limiting condition where the speed of movement of the predator is always zero. It seems perfectly possible, however, that the average speed of movement of predators that do move could be affected by hunger, with either the frequency of movements or the instantaneous speed of movement, or both, increasing as hunger increased. Turnbull's observations (1964) certainly suggest that this is true of the web-building spider *Achaearanea tepidariorum*, since he observed that the spiders consistently abandoned webs when few or no prey were caught, and then moved to different spots to build new webs. This suggests another kind of threshold of hunger: a movement threshold, such that movement occurs only if the hunger exceeds the threshold. The same argument would also explain Green's data (1965), which show that the activity of blowflies increases with increasing time of food deprivation. He was able to demonstrate that this increase was caused mainly by a decrease in the number and duration of inactive periods, and that when flies did move, they did so at the same rate, irrespective of hunger.

Changing hunger also seems to affect the average speed of movement of at least some vertebrates as well, since a number of authors (Finger 1951; Teitelbaum 1957; Duda and Bolles 1963) have shown that the activity of rats increases as the time of food deprivation increases. There is one apparent exception, however. As part of an exhaustive analysis of predation by fish, Ivlev (1944) showed that their speed of movement was not affected by different densities of prey. Rashevsky (1959), and apparently Ivlev (cf. Rashevsky 1959, p. 163), interpreted this as evidence that hunger did not affect speed of movement, since hunger levels would presumably be different at different prey densities. Ivlev's data, however, were collected using fish that had been deprived of food for a constant interval of time and he measured the speed of movement for a relatively short time thereafter at various prey densities. As a result, it is unlikely that the hunger levels differed very much between experiments at different prey densities and it can only be concluded that density per se does not affect speed.

It seems probable, therefore, that the average speed of movement of many predators is affected by hunger. No data could be collected from the mantid-housefly system to show the form of this relation, so the model is definitely limited in this respect. Nevertheless, speed of movement of the predator is still included as a specific parameter (VD) in the model so that when information is available it should be a fairly straightforward task to expand the model and thereby make it more general.

The final subcomponent involved in determining the time spent searching is the capture success, and it assumes particular importance, since the model is constructed in such a way that the amount of attack is very sensitive to quantitative changes in the capture success. This is only to be expected, since animals clearly have been subject to strong selection pressures that have led to the evolution of behavioural and structural features directed to maximize the capture success in the case of predators, and minimize it in the case of prey.

The capture success is the product of three success ratios—the recognition success, the pursuit success, and the strike success—and each of these three is equally important. The importance of successfully recognizing prey has led

to the evolution of a variety of detection techniques. Prey are recognized with visual, auditory, tactile, infrared sensitive, chemical, and electrical systems that involve highly specialized organs well suited to assure recognition of prey. As a counteraction to the efficiency of these systems, many prey have developed effective camouflage behaviours and colours, like the countershading and posture of some caterpillars (de Ruiter 1956) and the melanism of certain Lepidoptera in industrial areas of England (Kettlewell 1956). Characteristics of the environment also have a profound effect on the recognition success, as shown, for example, by the influence of light intensity and the character and density of cover on fish predation (Steinmetz 1961).

Once a prey is recognized it is necessary for the predator to pursue it successfully. In order to maximize the pursuit success the predator is confronted with two problems: first, how to avoid detection by the prey during the approach, and second, how to cope with the prey's escape responses once the predator is detected. In order for the predator to avoid detection by prey a slow unobstructive approach, the stalk, seems a logical solution. But such a technique does have disadvantages, since the time required for the approach can become so prolonged that the prey could move out of reach as part of its normal pattern of movement. And yet decreasing the time spent pursuing by increasing the speed of pursuit simply would advertise the predator's presence while there was time for the prey to escape. There must be a balance between these two conflicting features, a balance that is a specific attribute of the predator-prey system. When the predator is some distance from the prey the slow stalk typically seems most efficient. As the predator slowly approaches closer and closer, however, a point is reached where even a slowly moving predator becomes very obvious to the prey. The balance then tips in favour of a sudden rapid approach to cope with the prey's escape responses — hence the leap of a cat, the tongue flick of a frog, the strike of a mantid.

Not all predators employ this solution to the twofold problem of avoiding detection and coping with escape responses. Some predators, like the wolf, for example, have such great endurance that it is unimportant if the prey detects its presence, since the predator has an excellent chance of running the prey to exhaustion. In this case the prey's speed of escape cannot be maintained long enough to escape the pursuing predator. In still other examples, the predator is able to slow down the escape responses of prey by artificial means. This is the prime function of the web of the spider or the pit of the ant lion. In these cases the prey are slowed down sufficiently that the predator does not have to resort to a slow, careful stalk in order to increase the pursuit success at the expense of a long pursuit time. With the prey totally, or partially immobilized in a web, it is more important for the predator to reach the prey quickly, for the faster it does, the less the chance of the prey escaping and the greater the pursuit success.

Once a predator reaches a prey it must capture it, and again a variety of techniques have evolved to enhance the probability of capture. The mantid, for example, captures prey with a grasping structure that is admirably suited to hold certain sizes of prey efficiently (Holling 1964). Moreover, the mantid is able to integrate a complex of internal and external stimuli so that the strike is accurately directed (Mittelstaedt 1954, 1957). Other predators increase the probability of capture by injecting poisons that quickly immobilize prey (Edwards 1963). This is such an efficient technique that very often prey considerably larger than the predator can be captured. In the face of these effective capturing techniques, prey have evolved a variety of defences, such as the spines of sticklebacks (Hoog-

land *et al.* 1956) and the vigorous defensive movements of fall webworm larvae (Morris 1963).

The few examples quoted above are enough to demonstrate that a wide variety of methods are used by predators to maximize the capture success. Nevertheless, it is not so much the particular technique that is important, as the resulting value of the capture success. Therefore all these capture systems can be covered by the model, each one simply being represented by specific values of the relevant parameters.

To conclude, the analysis and synthesis presented here have shown that it is possible to develop an integrated model of a complex system that is realistic and precise. Thus the properties promoting great depth — wholeness, realism, and precision — are not mutually exclusive and can be simultaneously retained in a specific model. Great breadth of application is, however, as important to retain as great depth. As yet an insufficient number of different kinds of predator have been examined to provide completely convincing evidence that the highly detailed functional response model has considerable generality. Such a broadly comparative study has just been started and will hopefully survey a variety of invertebrate and vertebrate predators, terrestrial, fresh water, and marine. But even now we know that predators are enormously varied. One predator will grasp prey, for example, while another will filter out prey with a sieve; one will ambush, while another actively moves in its search for prey; one will eat all it kills, while another will eat only some of the prey killed and will hoard or discard the remainder; one will hunt alone, while another will hunt in a pack. This multitude of solutions to specific problems imposes a diversity that seems overwhelming, that seems to obviate any generality in a specific model. But underlying this diversity is a unity, a universality imposed on all matter by the demands of space and time, and on broad taxonomic groups of animals by reason of their common organization. Thus it is not fundamentally important that one predator grasps a prey while another traps prey. What is important is that they both capture prey and that the differences that produce an apparent uniqueness of function simply represent a limiting condition of a general case.

The model presented here therefore seems to have broad application, particularly among invertebrate predators. Further steps in the analysis will increase the generality still further by including new components, such as learning and prey inhibition (as in Holling 1965), or by expressing components already analyzed in more accurate ways. Even in its present state, however, the model promises to provide significant theoretical and practical insights into the operation of predation.

SUMMARY

This paper reports on one of the most recent steps to develop a realistic model of the predation system. An earlier study described a basically simple kind of attack in which rate of searching, time prey are exposed to predators, and handling time were the only relevant components. This paper extends the explanation to include the effects of another important component of attack — hunger. It represents a particularly important step, since it is the first time in this program of research that a process of great complexity has been analyzed to produce a model of a whole system that is realistic, precise and yet general.

In order to make the model realistic, an analytical approach, termed the experimental components analysis, was developed to assure an intimate feedback

between theory and experiment, with theory dictating experiments and experimental results dictating theory in many small steps. The actions and interactions of each subcomponent of the process were analyzed experimentally using a praying mantid - housefly system, and these experiments led to a number of equations that describe adequately each of the relevant fragments of this system. Hunger, for example, exerts its effect largely by affecting the size of the perceptual field of mantids for prey. The exact relation was demonstrated experimentally and an equation devised to express distance of perception as a function of duration of food deprivation. This fragment was then synthesized with others to produce an integrated model of a predation system.

The aim of this synthesis was to preserve three features that imparted a distinctive character to the complexity of the predation process. First, there was a strong historical element such that any event was affected not only by present conditions but by past conditions as well. Secondly, thresholds and limits were extremely common features of predation. Thirdly, there was a basic discontinuous character resulting from the relatively few contacts between predator and prey. These three features were preserved by using difference equations and expressing them in Fortran, a language designed for I.B.M. digital computers. Moreover, this language, and the computer, proved to be ideally suited to handle the complexity arising from these three features. Since the same features characterize many biological systems, the combination of an experimental components analysis with computer languages and techniques could be profitably applied to many biological problems.

The resulting predation model accurately predicted the effects of prey density and time on the amount of attack and hunger level of praying mantids. A preliminary simulation study showed that two types of functional responses to prey density can be generated. In the general case, the functional response curve relating the number of prey attacked to prey density shows a negatively accelerated rise to a plateau. In a limiting case, where the distance of perception is constant, the same kind of curve shows a linear rise to a plateau. One or the other of these two curves describes the responses of all examples of attack by invertebrate predators (12 species) for which information is available. Vertebrate predators, however, generally show a different response to prey density — an S-shaped rise to a plateau. In order to reproduce this response, an additional component, learning, is required and this has already been added elsewhere.

The model is now being used in an extensive simulation study in order to demonstrate the kinds of attack that can occur in nature and the significance of various features of attack with respect to biological control. Simplified versions of the model will also be developed so that it can be readily used in specific situations in the field. One example, discussed here, is a simple equation that relates the amount of prey within the predator to the number of prey attacked per day. Output from the complete predation model shows the precise conditions under which such a relation can be used.

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APPENDIX I

Estimating Fly Velocity Knowing the Number of Contacts of Flies With a 3-cm. Diameter Contact Area

As each fly moves at a velocity of VY it sweeps out a contact zone of width $2r$, where r is the radius of the contact area. That is, if a fly approaches within r units of the centre of the contact area it will be recorded as a contact. Consider now a fly moving during time t . During this time it moves a distance $VY(t)$ and sweeps out an area $2r(VY)t + \pi r^2$.

If

$$N_o = \text{the number of flies per sq. cm. and}$$

$$A_c = \text{the area of the cage,}$$

then the total area swept out by all flies in the cage (i.e. by $N_o A_c$ flies) is

$$[2r(VY)t + \pi r^2] N_o A_c.$$

Since there is only one contact area in the cage, the density of contact areas is $1/A_c$, and N_c , the number of times a fly enters the contact area, is given by

$$N_c = [2r(VY)t + \pi r^2] N_o A_c (1/A_c),$$

or

$$N_c = [2r(VY)t + \pi r^2] N_o,$$

from which

$$VY = (N_c - \pi r^2 N_o)/2rt.$$

In the present case N_c is expressed as the number of contacts per hour so that $t = 1$. Since $r = 1.5$ cm. therefore

$$VY = (N_c - 7.069 N_o)/3N_o.$$

APPENDIX II

Expressing the Hunger Equation in Terms of Unspecified Time

The hunger equation (3) is initially expressed in terms of time of food deprivation, TF , where $H = 0$ and when $TF = 0$. That is,

$$H = HK(1 - e^{-AD(TF)})$$

or, in another form

$$TF = \frac{1}{AD} \ln \left(\frac{HK}{HK - H} \right) \quad (66)$$

It is more convenient, however, to express the equation in terms of unspecified time T , where $H = HO$ at $T = 0$. Thus if $TF = TFO$ when $H = HO$, we want to know the hunger, H , T units of time later when $TF = TFI$. That is,

$$TFI = TFO + T \quad (67)$$

From equation (66) we may write

$$TFI = \frac{1}{AD} \ln \left(\frac{HK}{HK - H} \right) \quad (68)$$

and

$$TFO = \frac{1}{AD} \ln \left(\frac{HK}{HK - HO} \right) \quad (69)$$

Substituting equation (68) and (69) in (67)

$$\frac{1}{AD} \ln \left(\frac{HK}{HK - H} \right) = \frac{1}{AD} \ln \left(\frac{HK}{HK - HO} \right) + T$$

or

$$T = \frac{1}{AD} \left[\ln \left(\frac{HK - HO}{HK - H} \right) \right]. \quad (70)$$

This equation can be transformed into one with the same form as equation (3):

$$H = HK + (HO - HK) e^{-AD(T)} \quad (71)$$

APPENDIX III

Summary of Fragmental Equations

Hunger:

$$H = HK(1 - e^{-AD(TF)}) \quad (3)$$

or

$$H = HK + (HO - HK) e^{-AD(T)} \quad (36) \text{ and } (71)$$

Shape of the reactive field:

$$r_a = r_o / (1 + C\theta^2) \quad (14)$$

Area of reactive field:

$$A = KA[G(M(H - HT))]^2, \quad H > HT \quad (18)$$

$$A = 0, \quad H \leq HT \quad (19)$$

Speed of movement of mantid:

$$VD = 0$$

Speed of movement of prey:

$$VY = (V_{\max} - V_{\min}) e^{-a_v N_o} + V_{\min}$$

Capture success:

$$SC = (SR)(SS) e^{-m(TP)} \quad (25)$$

Time spent pursuing prey:

$$TP = [KR(GM)(H - HT) - DS]/VP, \quad H > HTP \quad (33)$$

$$TP = 0, \quad H \leq HTP \quad (34)$$

Time spent eating each prey:

$$TE = KE(WE) \quad (35)$$

Time spent in a "digestive" pause:

$$TD = \frac{1}{AD} \left(\ln \frac{HK - HO}{HK - HT} \right), \quad H < HT \quad (38)$$

$$TD = 0, \quad H \geq HT \quad (39)$$

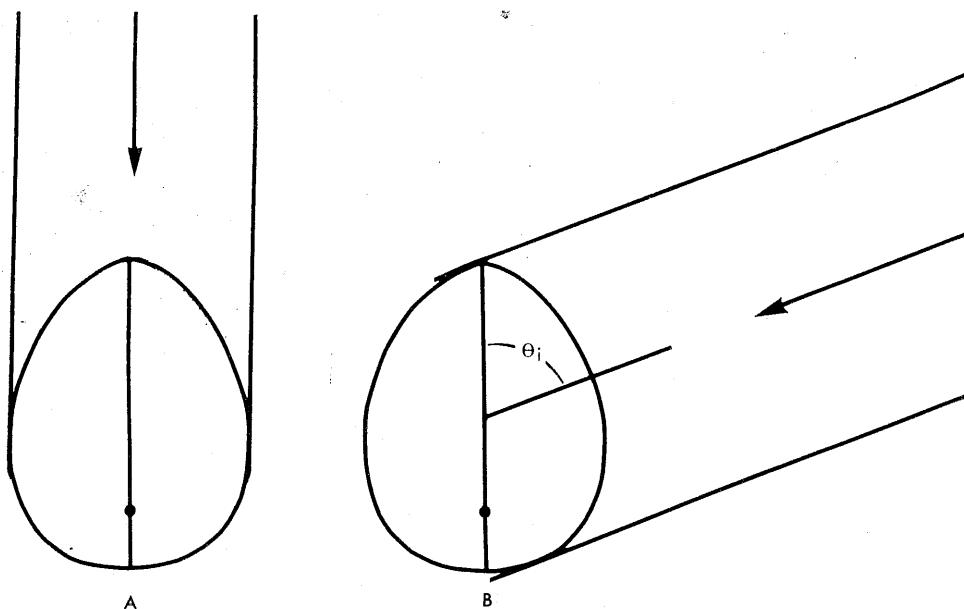


Fig. 36. Diagram to show the effective width of the encounter path of prey travelling at two different angles to the predator's body.

APPENDIX IV

Derivations of Equations Involved in Determining the Area of the Encounter Path

Three functions are required to determine the area of the encounter path (see discussion of Fig. 27B), i.e. $RD_0 = f(H)$, $RD_1 = f'(H)$ and $\int_0^{TS} RD \cdot dt = f(TS)$. The average width of the encounter path is $2RD$ at any moment and this clearly has some relation not only to the size but also the shape of the reactive field of the predator. If the field is a circle with the predator at the centre, then RD is equal to the radius of the circle. In many instances, however, particularly among visual predators, the field is not circular but tends to be elongate with the predator off centre as in Fig. 9. In these cases, if the predator was motionless, whenever a fly approached directly in front, as in Fig. 36A, the width of the encounter path would be the distance between tangents drawn to the contour parallel to $\theta = 0$. But flies could just as easily approach at other angles, and if, for example, one approached from the side at an angle θ_i (Fig. 36B) the width of the encounter path would equal the distance between the two tangents drawn parallel to $\theta = \theta_i$. When flies can approach at any direction with equal probability the average width of the encounter path is therefore the average distance between parallel tangents to the contour drawn at angles from $\theta = 0$ to $\theta = 2\pi$ radians, and RD is equal to one half this average distance. That is,

$$RD = \frac{1}{2\pi} \int_0^{2\pi} r \cdot d\theta$$

Since equation (14) expresses r as a function of θ , the above expression could be integrated to provide an explicit equation for RD . It can be shown, however, as Skellam has (1958, p. 392) that the average distance between parallel tangents

can also be expressed as s/π where s equals the perimeter of the reactive field. Thus RD can also be expressed as

$$RD = s/2\pi.$$

This, however, holds only when the predator, like the mantid, is motionless and no particular direction of motion is favoured. In the extreme condition when the predator moves faster than the prey, all the encounters will be at the front of the contour, and the width of the encounter path will be the distance between tangents drawn parallel to the direction of motion, i.e. to the maximum width of the reactive field. Hence, for the general condition, RD will vary between $s/2\pi$ and the maximum width of the reactive field.

Rather than further develop the above expressions, however, an approximate and general equation for RD can be derived by assuming that RD is the radius of a circle of the same area as the reactive field, A. Thus

$$\pi(RD)^2 = A.$$

From equation (17), $A = (KA)r_o^2$, so that

$$\pi(RD)^2 = (KA)r_o^2$$

and

$$RD = r_o \sqrt{KA/\pi}$$

or, making

$$KR = \sqrt{KA/\pi}$$

$$RD = (KR)r_o. \quad (72)$$

When the actual field is circular and the predator at the centre, as it might be with an olfactory or tactile predator, $KA = \pi$ so that RD equals r_o , the radius of a circle. Visual predators with binocular vision are more likely, however, to have elongate reactive fields with the predator off centre. In these cases $KA < \pi$. In the *H. crassa* - housefly system $KA = 0.8064$ so that

$$KR = \sqrt{0.8064/3.1416} = 0.5066.$$

Since equations (5) and (6) earlier expressed r_o as a function of hunger, equation (72) can be rewritten as

$$RD = (KR)(GM)(H - HT), \quad H \geq HT \quad (73)$$

and

$$RD = 0, \quad H < HT. \quad (74)$$

Moreover, RD can also be expressed as a function of time and hunger at $T = 0$ by substituting the hunger equation (Appendix II equation (71)) into (73) above.

$$RD = (KR)(GM)[HK - HT + (HO - HK)e^{-AD(T)}], \quad HO \geq HT. \quad (75)$$

The average radius of the encounter path at $T = 0$, is RD_0 , one of the three measurements we wish. Substituting $T = 0$ into (75), therefore

$$RD_0 = (KR)(GM)(HO - HT), \quad HO \geq HT. \quad (76)$$

RD_1 , the radius of the encounter path at $T = TS$, can be obtained in a similar manner:

$$RD_1 = (KR)(GM)[HK - HT + (HO - HK)e^{-AD(TS)}], \quad HO \geq HT. \quad (77)$$

The third and final measurement is $\int_0^{TS} RD \cdot dT$, which is required to compute the area swept out from $T = 0$ to $T = TS$. Thus

$$\begin{aligned} \int_0^{TS} RD \cdot dT &= (KR)(GM) \left[\int_0^{TS} (HK - HT) \cdot dT + (HO - HK) \int_0^{TS} e^{-AD(T)} \cdot dT \right] \\ &= (KR)(GM) \left[(HK - HT)T - \frac{(HO - HK)}{AD} e^{-AD(T)} \right]_0^{TS} \\ &= (KR)(GM) \left[(HK - HT)TS + \frac{(HO - HK)}{AD} (1 - e^{-AD(TS)}) \right], \quad HO \geq HT. \end{aligned}$$

APPENDIX V

Table of Symbols

a	— Rate of successful search
α	— Minimum angle of vision
AD	— Rate of food disappearance or rate of digestion
β	— Angle to the body axis
DP	— The pursuit distance
DS	— The strike distance
G	— Amount of food in the gut ($HK - H$)
GM	— A constant relating distance of perception to hunger
H	— Hunger, as measured by the weight of food required to satiate the predator
HBEG	— Hunger level at the beginning of a feeding period
HK	— Maximum capacity of gut
HO	— Hunger level just after a prey is consumed
HI	— Hunger level just at the moment of capture of a prey
HT	— The hunger level at which searching for prey begins
HTP	— The hunger level at which pursuit begins
KA	— An areal constant relating area of the predator's field of reaction to the distance of reaction at $\beta = 0^\circ$
KE	— Feeding rate (time per unit weight of food eaten)
KR	— equals KA/π
m, M	— A constant relating success of pursuit to duration of pursuit
N _A , N _A	— Number of prey attacked
N _o , NO	— Prey density
SC	— The success the predator has in capturing prey that enter its perceptual field
SP	— The pursuit success or the success of pursuing a prey that is recognized
SR	— The recognition success or the success of recognizing a prey that enters the predator's perceptual field
SS	— The strike success or the success of capturing a prey once a strike is made
T	— Time
TA	— Duration of a 24-hour period spent in a feeding condition
TD	— Time taken in a digestive pause after a prey is eaten
TE	— Time spent eating each prey
TF	— Time of food deprivation timed from a condition of complete satiation
T _H	— Time spent handling prey (e.g., time for pursuit, capture, killing, and eating)
TI	— Time taken for one attack cycle from the completion of eating one prey to the completion of eating the next
TP	— Time spent in pursuing each prey
TS	— Time spent searching for each prey
T _T	— Time prey are exposed to predators
VD	— Average velocity of predator during searching
VP	— Average velocity of predator during pursuit
VY	— Average velocity of prey
W	— Weight of one prey
WD	— Weight of each prey discarded, uneaten
WE	— Weight of each prey eaten

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LIST OF THE CANADIAN ENTOMOLOGIST SUPPLEMENTS

Volume	No.	Date Printed in the Issue Itself	Actual Date of Issue	Authority ¹	Author
(87) LXXXVII	Supp. 1	1955	30 Mar. 1955	WRT	Maxwell
(88) LXXXVIII	Supp. 1	Mailed 23 Nov. 1956	10 Dec. 1956	WRT	Becker
(88) LXXXVIII	Supp. 2	1956	16 Jan. 1957	WRT	Beirne
(88) LXXXVIII	Supp. 3	1956	2 Jan. 1957	Lib	Brown

After this issue the "Supplements" became, in fact, a self-contained series with a continuous numbering system independent of The Canadian Entomologist. Nevertheless, they were still issued (with later exceptions) as "Accompanying" volumes of The Canadian Entomologist.

Because 4 Supplements had already been published, the next one was called No. 5. Supplement No. 4 was never published.

No.	"Accompanies Volume"	Date Printed in the Issue Itself	Actual Date of Issue	Authority ¹	Author
5	89	1957	2 Dec. 1957	Lib	Thomas
6	90	1958	8 Apr. 1958	WRT	Hardwick
7	90	1958	28 Apr. 1958	Lib	Freeman
8	90	1958	12 Sep. 1958	Lib	McGuffin
9	90	1958	14 Nov. 1958	EGM	Brooks
10	91	1959	26 Mar. 1959	Lib	MacKay
11	91	1959	26 Mar. 1959	Lib	Kelton
12	91	1959	15 June 1959	Lib	Chant
13	92	1960	14 Nov. 1960	Lib	Richards
14	92	Mailed 17 Feb. 1961	16 Mar. 1961	Lib	Chillcott
15	92	Mailed 27 Jan. 1961	1 Feb. 1961	WM	Heinrich I ²
16	92	Mailed 10 Jan. 1961	11 Jan. 1961	Lib	Freeman
17	no date or volume number		25 Oct. 1961	Lib	Munroe
18	92	Mailed 24 Mar. 1961	4 Apr. 1961	WM	Heinrich II ²
19	93	Mailed 24 Feb. 1961	4 Apr. 1961	Lib	Watt
20	92	Mailed 24 Mar. 1961	6 Apr. 1961	Lib	Brooks
21	93	1961	13 Sep. 1961	Lib, WM	Heinrich III ²
22	93	Mailed 12 Apr. 1961	29 May 1961	Lib	Miller
23	none	1961	21 Dec. 1961	WM	Heinrich IV ²
24	none	1961	27 Dec. 1961	Lib, WM	Munroe
25	none	1961	28 Dec. 1961	Lib, WM	Howden
26	no date or volume number		19 Feb. 1962	WM	Heinrich V ²
27	none	1962	20 Sep. 1962	Lib, WM	Heinrich VI ²
28	none	1962	6 Nov. 1962	WM	MacKay
29	none	1962	27 Nov. 1962	WM	Heinrich VII ²
30	none	1963	1 May 1963	WM	Peck

After Supplement 30, the series continued under the title "Memoirs of the Entomological Society of Canada".

¹The following are the authorities upon which the actual dates of issue are based:

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²The seven parts of Mr. Heinrich's *Revision of Ichneumoninae....* and Part VIII (Indices, addenda and corrigenda) by O. Peck have consecutive pagination and are intended to be bound as a single book.

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No.	"Accompanies Volume"	Date Printed in the Issue Itself	Actual Date of Issue	Authority ¹	Author
31	—	1963	21 May 1963	WM	Morris <i>et al.</i>
32	—	1963	4 June 1963	WM	LeRoux <i>et al.</i>
33	—	1964	19 Mar. 1964	WM	Munroe
34	—	1964	1 Apr. 1964	WM	Peck <i>et al.</i>
35	—	1964	14 May 1964	WM	Peck ²
36	—	1964	21 Oct. 1964	WM	Forbes
37	—	1964	23 Oct. 1964	WM	Fast
38	—	1964	6 Nov. 1964	WM	Arnold
39	—	1964	10 Dec. 1964	WM	Howden
40	—	1965	1 Apr. 1965	MRM	Hardwick
41	—	1965	5 Apr. 1965	MRM	Chant and Baker
42	—	1965	18 June 1965	MRM	Huckett
43	—	1965	23 June 1965	MRM	Paradis et LeRoux
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45	—	1965	7 Dec. 1965	MRM	Holling
46	—	1965	9 Dec. 1965	MRM	Embree
47	—	1965	29 Dec. 1965	MRM	Lindquist and Evans

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