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OPTIMAL FORAGING: ATTACK STRATEGY OF A MANTID

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Much recent theoretical work in foraging theory derives hypotheses from the general assumption that animals are "efficient" in their foraging activities. Useful reviews may be found in Krebs (1973), Schoener (1971), MacArthur (1972), and Charnov (1973). The problems considered usually relate to breadth of diet (Schoener 1969, 1971; Emlen 1966; MacArthur 1972; Marten 1973; Pulliam 1973; Werner and Hall 1974; Timin 1973; MacArthur and Pianka 1966; Pearson 1974; Rapport 1971), strategies of movement (Cody 1971; Pyke 1974*a*, 1974*b*; Smith 1974*a*, 1974*b*), or use of a patchy environment (Royama 1970; MacArthur and Pianka 1966; Pulliam 1973; Krebs et al. 1974; Smith 1974*a*, 1974*b*; Tullock 1970; Emlen 1973; Charnov, Orians, and Hyatt 1975). This list includes only the more theoretical contributions and is far from exhaustive. Several studies test the predictions of these formal models (Krebs et al. 1974; Pyke 1974*a*; Werner and Hall 1974; Smith 1974*a*, 1974*b*).

In this paper I develop a simple model of breadth of diet for a random-encounter situation. Predictions made by the model will then be compared to the behavior of a real predator, the mantid, *Hierodula crassa*. I show that this mantid supports the predicted behavior. The final section argues that, even though the behavior is as predicted, several alternative explanations are not excluded. In fact, at least with this type of predator, the foraging behavior may reflect several ultimate factors, with energetic efficiency being only one.

THE MODEL

The predator to be modeled has the following characteristics: (1) It encounters individual prey items. The food value (Rapport 1971) of a prey item is measured in calories or grams. (2) The prey items are handled one at a time, and this handling time is unavailable for searching; no new prey may be encountered during the handling of a prey item. The handling time is assumed to begin when the predator gives its attention to a single prey item (decides to go after it). (3) The predator takes no time to recognize a prey "type." After recognition, the predator has the choice of going after the item or not. (4) The prey are not

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so large as to be dangerous to the predator. (5) The particular components of the foraging process (search, pursuit, eating) are not differential with respect to mortality risk to the predator. (6) During a foraging period, the predator is only engaged in searching and handling prey items. The goal of the predator is to maximize the net rate of caloric intake during a foraging period. (7) In order to keep the mathematics simple, one final assumption will be made: the energetic cost to the animal is the same over all components of the foraging process. Readers desiring a more general argument should see Charnov (1973).

An equation giving the rate of energy intake in a random encounter (non-patchy) situation may be derived as follows. Let E be the energy taken in during a feeding period of length T , which is made up of T_s (time searching) and T_h (time handling all prey items). A net rate of energy intake (En/T) is

$$\frac{En}{T} = \frac{E}{T_h + T_s}.$$

Let there be k prey types, each type (i) having the following four characteristics: λ_i = number of prey type i encountered in one unit of search time, E_i^* = expected net energy from one item of type i , h_i^* = expected handling time for an item of prey type i , and P_i = probability that the predator goes after an item of type i when one is encountered. This parameter is controlled by the predator. It follows directly that

$$\begin{aligned} E &= \sum \lambda_i E_i^* T_s P_i, \\ T_h &= \sum \lambda_i h_i^* T_s P_i, \\ \frac{En}{T} &= \frac{\sum \lambda_i E_i^* T_s P_i}{T_s + \sum \lambda_i h_i^* T_s P_i}, \text{ or} \\ \frac{En}{T} &= \frac{\sum \lambda_i E_i^* P_i}{1 + \sum \lambda_i h_i^* P_i}. \end{aligned} \quad (1)$$

Equation (1) is a multispecies version of the Holling disk equation (Holling 1959) and is identical to that which results from the corresponding stochastic argument (Charnov 1973). In equation (1) the only things that the predator can control are the values of the P_i —whether or not it will go after an item of prey type i . The basic disk model has been derived independently by several people, all of whom proved the theorem (Pulliam 1973; Werner and Hall 1974; Charnov 1973; Timin 1973; Pearson 1974; Schoener 1969, 1971; Maynard Smith 1974). The theorem is a generalization of a result which first appeared in MacArthur and Pianka (1966) and which was also generalized (although not with the disk model) by MacArthur (1972). The theorem is as follows. Relating to (1), En/T is maximized when: (1) $P_i = 0$ or 1 ($i = 1, 2, \dots, k$). (2) If the prey types are ranked by the ratio E_i^*/h_i^* , then whether or not a prey type i should be eaten is (i) independent of the abundance of type i (independent of λ_i) and (ii) dependent only on the abundances of those prey types with rank higher than i . For convenience, when En/T is the maximum value, I shall write it as En^*/T^* . (3) The

set of prey types to be eaten (the *optimal set*) are those of rank such that

$$E_j^*/h_j^* > En^*/T^*. \quad (2)$$

These assertions can be proved as follows:

For some prey type c assumed not to be in the optimal set, the following inequality must hold, since adding c to the diet must cause En/T to decrease:

$$\frac{En^*}{T^*} > \frac{En^* + \lambda_c E_c^* P_c}{T^* + \lambda_c h_c^* P_c},$$

which implies that type c has the characteristic that

$$\frac{En^*}{T^*} > \frac{E_c^*}{h_c^*}. \quad (3)$$

It is also easy to show that the inequality in (3) is the condition for $(\partial En/T)/\partial P_c$ to be negative, so that no prey type in the optimal set makes (3) true. This means that a prey type (j) in the optimal set has the characteristic that

$$\frac{E_j^*}{h_j^*} > \frac{En^*}{T^*},$$

which proves statement 3.

Statement 1 is true because 2 is either true or false, independent of the value of P_j . If true, P_j should = 1; if false, it should = 0. Statement 2 is true because λ_c cancels out in the derivation of equation (3). Only those prey types in the optimal set determine En^*/T^* , so that type c cannot get itself added to the optimal set by being very abundant (e.g., λ_c large). As the abundance of some type in the optimal set gets large ($\lambda_j \rightarrow \infty$), $En^*/T^* \rightarrow E_j^*/h_j^*$, which results in all prey of lower rank being dropped out of the optimal set. Prey type j should be dropped from the optimal set if still higher ranked prey become abundant enough.

Figure 1 is one useful way of showing these relations. Prey types are accumulated in En/T in rank order. In figure 1 for some set of λ_i , the optimal set includes prey types of rank greater than the rank of type 9. Figure 2 is a general graphical solution for this problem. Individual prey items have associated with them an E_i^* and h_i^* and so may be plotted as points on a graph with coordinates E_i^* and h_i^* . If the ray from the origin with slope En^*/T^* is plotted, the optimal set includes all prey items above the ray. In figure 2, ab is meant to represent some prey species. Those individuals close to a are in the optimal set; those close to b are not. A decrease in abundance of a prey above the line causes En^*/T^* to decrease; an increase in abundance causes it to increase.

A TEST OF THE THEOREM

In order to test the hypothesis against the behavior of a real predator, we need first to choose an animal which meets the background assumptions in the model. The mantid studied by Holling (1966) comes close, since it is nonmobile

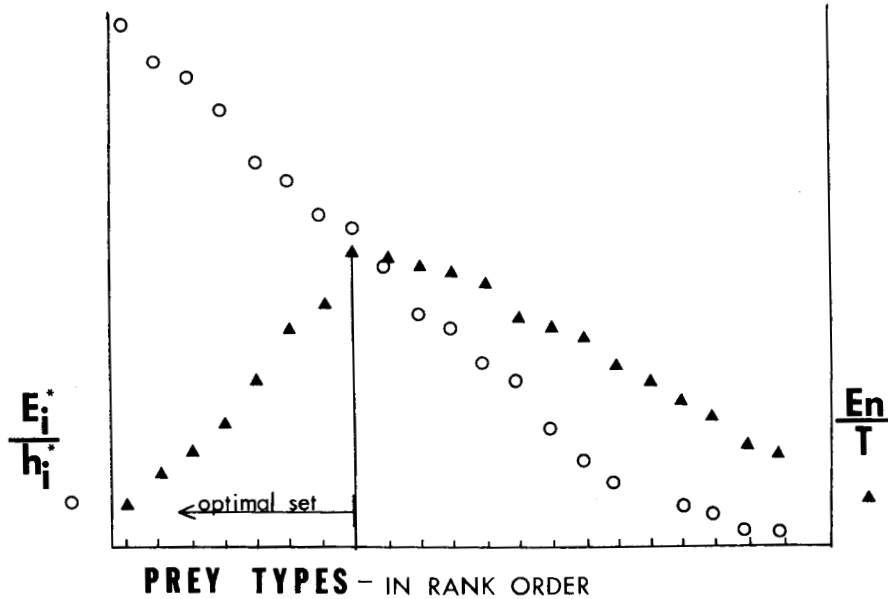


FIG. 1.—Choice of an optimal set of prey types. Prey types are first ranked by the E_i^*/h_i^* ratio, and then the cumulative En/T is calculated by adding prey types to En/T in rank order. En/T is maximized for a set of prey types of rank above the prey type (m) where En/T first becomes $> E_m^*/h_m^*$.

(spends a foraging period in one place), was studied feeding on nondangerous prey, and is occupied while handling individual items. Characteristic 5, relating to risk and foraging components, may not be met. I shall discuss this further after the basic analysis.

If the behavior of the mantid fits the theorem, the following predictions should hold: (1) The mantid has some estimate of the rate of food intake, or, rather, its prey choice behavior is related to this rate. This corresponds to knowledge about En/T . (2) Prey types are added to or dropped from the diet as the rate of food intake changes. The adding or dropping should be in rank order as given by the E^*/h^* variable. (3) A prey type that is not being eaten cannot get itself added to the diet by being very abundant. (4) A prey type that is being eaten cannot get itself dropped from the diet by decreasing in abundance but can cause the mantid to drop prey of lower rank from the diet by increasing in abundance (thus increasing the rate of food intake). Predictions (3) and (4) are not really independent of (1) and (2), so I shall concentrate on the first two in the test of my hypothesis.

Dr. C. S. Holling has kindly provided me with data from his laboratory experiments of predation by the mantid, *Hierodula crassa*, on houseflies, *Musca domestica*. Since his 1966 monograph is readily available, only certain data will be reproduced here. The work to be described was done under very controlled laboratory conditions with a single prey species. Nevertheless, it is the most complete set of data available. The discussion will take the form of questions.

1. Does the mantid have a measure of the average rate of food intake?

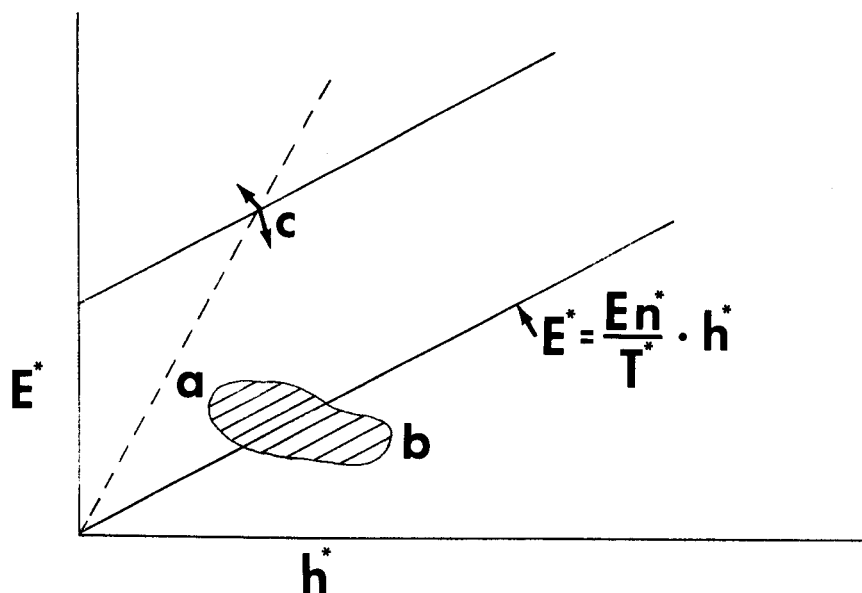


FIG. 2.—Choice of an optimal set of prey types. Prey types are points on the (h^*, E^*) plane. The optimal set includes all prey types above the ray from the origin with slope En^*/T^* . A single prey species may contain many prey types. The area ab represents a single species. Those individuals near a are in this optimal set; those near b are not. Point c is a prey type in this optimal set. If we shift c along a line with slope En^*/T^* , En^*/T^* does not change in value. If c is moved to above this line, En^*/T^* increases; if it is moved to below the line, En^*/T^* decreases. If $\lambda_c \rightarrow \infty$, En^*/T^* increases until finally it equals E_c^*/h_c^* and can be represented as a ray from the origin passing through c .

As a measure of hunger, Holling used the amount of food (grams of fly) needed to satiate the animal after a fixed time interval from a previous satiation feeding. Adult female mantids were fed until they would not even accept crushed houseflies presented at the mouth parts; they were fed again at a specified time interval. If the food eaten at the second feeding reflects the amount of food removed from the gut during the interval, it provides the basis for a model of how fast food is removed from the gut. Holling made 228 such measurements, 12 replicates at 19 time intervals. Figure 3 is reproduced from his paper. The data are well described by an exponential decline for the food present in the gut. He estimated the average gut capacity to be 1 g. The rate at which food is leaving the gut is $AD \times G$, where G is the amount of food in the gut and AD is a proportionality constant estimated to be 0.05 g/hour.

If we assume that the mantid is in equilibrium with its food supply (i.e., during a feeding period), the average amount of food in the gut is constant and the rate of food intake is equal to the rate at which food is leaving the gut. The simulation model constructed from his data showed that at a constant housefly density the animal rapidly reaches an equilibrium where the average amount of food in the gut is constant, so that this assumption is valid. Animals coming into equilibrium with fuller guts thus have a higher rate of food intake than those

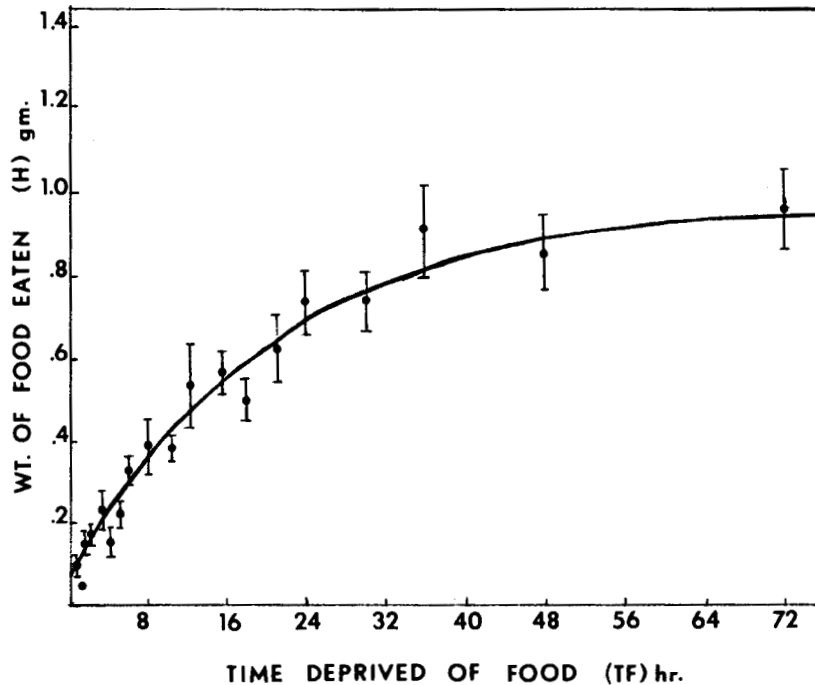


FIG. 3.—The effect of time of food deprivation on hunger of *H. crassa*. Untransformed data (average of 12 replicates ± 1 SE) from Holling (1966).

in equilibrium with more empty guts. Under this model, the mantid can indeed measure the rate of food intake.

2. Is there a prey ranking that may correspond to an E_i^*/h_i^* ranking?

The houseflies were chosen for uniformity of size (0.0245 ± 0.003 g [1 SE], $N = 325$) and age, so they appear at first to be a single-prey type. Since the mantid is a sit-and-wait predator, its choice is whether or not it will stalk a fly that has appeared a certain distance away. This allows us to ask, What are the E_i^* and h_i^* associated with a housefly X cm from the mantid? The data allow for the calculation of some of the necessary quantities. I will establish that the ratio E_i^*/h_i^* (for houseflies) is decreasing with increasing pursuit distance from the mantid. While this result is not surprising, it seems important to establish the fact using data, rather than merely assume it. This method of defining prey types is identical to Schoener (1969). To be valid in the present context, one other assumption follows. This is that, by being willing to attack a housefly $X + K$ cm away, the mantid does not change the encounter rate with flies X cm away. If this does not hold, then the λ_i are not independent of the optimal set and the problem becomes much more complex. Since there are no data bearing on this, it will have to stand as an unproven assumption.

h_i^* assumption.—Define the following: h_1 = time for the predator to get close enough to the item to try to kill it, h_2 = time spent in pursuit if pursuit is not successful, and h_3 = time to eat the item plus any digestive pause. After Holling (1966), I assume the following conditional capture probabilities for type i :

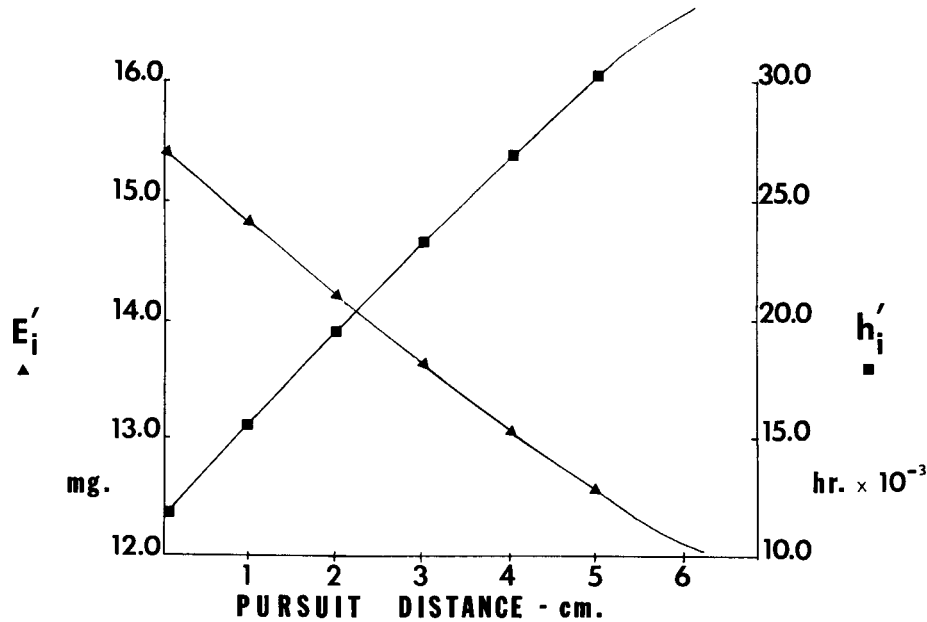


FIG. 4.—The energy gain (E_i^*) and handling time (h_i^*) values as a function of pursuit distance for the mantid *H. crassa* attacking house flies, *M. domestica*. The final result is that the ratio E_i^*/h_i^* decreases with distances from the mantid. Data from Holling (1966).

S_p = probability that the predator gets close enough to try to kill an item if the item is recognized and the predator chooses to go after it, and S_a = probability that the predator kills and eats an item (the predator gets close enough to try to kill). With these assumptions,

$$h_i^* = S_p S_a h_3 + S_p h_1 + (1 - S_p) h_2.$$

Holling's data allow us to estimate a modified version of h_i^* , defined as follows:

$$h_i^* = S_p S_a h_3 + S_p h_1.$$

E_i^* assumption.—Noting characteristic 7, that energy costs are not differential with respect to attack components, we have an estimate of E_i^* :

$$E_i^* = (S_p S_a W),$$

where W = weight of one housefly (0.0245 g).

From Holling's experiments come the following relationships: (1) S_p was found to be an exponential decreasing function of the stalking time. The mantid stalked at a constant velocity (= 210 cm/hour) and struck at the fly when it got to within 1.5 cm, so $S_p = \exp(-ah_1)$, where h_1 is related to stalk distance (P) by the relation $h_1 = (P - 1.5)/210$. (2) For nonflying houseflies, S_a was a constant equal to 0.630. (3) The h_3 was a constant equal to the inverse of the eating rate (0.760 h/g) multiplied by the weight of a housefly. These three relations are adequate to calculate h_i^* and E_i^* as a function of pursuit distance from the mantid. This is done in figure 4. The h_i^* is an increasing function of

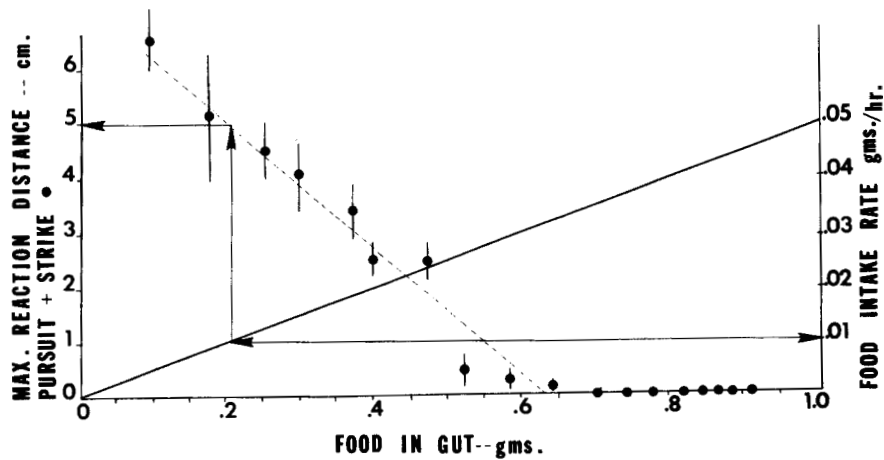


FIG. 5.—Attack strategy of a mantid. The rate of food intake is proportional to the amount of food in the gut, so that mantids in equilibrium with fuller guts are maintaining a higher rate of food intake. The circles represent the average maximum distance that the animal stalked (pursued) or struck at houseflies. Distances up to 1.5 cm are strike distances. The vertical bars are 1 SE with 12 replicates. A decrease in *rank* for a prey type is equivalent to a greater pursuit distance. E.g., at a rate of food intake of 0.01, the animal is only willing to react to prey that are within 5 cm. Data from Holling (1966).

pursuit distance, and E_i^* is a decreasing function. Thus, the ratio E_i^*/h_i^* is a decreasing function of pursuit distance.

3. Is the mantid willing to pursue or stalk further for houseflies at low levels of food in the gut?

Experiments to answer this question were carried out with houseflies manipulated directly in front of the mantid. The animals were fed to satiation, and then at various time intervals flies were moved toward them until they began a stalk (or a strike if the fly came within 1.5 cm with no stalk). The measurement taken was this maximum pursuit distance for various hunger levels. Figure 5 summarizes the results. Only reaction distances above 1.5 cm represent pursuit distances. The "food in gut" measurement is estimated from the appropriate starvation time. As the food in the gut decreases, the average maximum reaction distance increases. I also plot the least-squares regression line from Holling (1966), but newer data suggest that the relationship is nonlinear (Holling, personal communication). Also plotted is the equilibrium food intake rate ($= 0.05 \times \text{food in gut}$). One equilibrium position is illustrated. At a food intake rate of 0.01 g/hour, the mantid is only willing to pursue flies that appear < 5 cm away.

The mantid does what the theorem predicts: it adds to or drops from the diet in order of rank based on a measure (food in gut) of the rate of food intake. A prey not in the diet (farther away than the maximum reaction distance) cannot get itself added to the diet because the predator simply does not respond to prey that far away. Likewise, if a prey in the diet should change in abundance,

it would result in one of two things: A decrease in abundance would lower the rate of food intake, resulting in an expansion of the diet. An increase would increase the rate, causing a contraction of the diet. It seems clear that changing the abundance of a single type cannot get that type added to the diet or dropped from it.

DISCUSSION

Since the behavior of the mantid is at least qualitatively as predicted by the theorem, I now discuss certain alternative hypotheses for the behavior observed.

In the test of the hypothesis, an important role was played by the exponential function for food leaving the gut. The evacuation rate has been shown in other animals to be greatly influenced by factors such as food type (protein, fat, carbohydrate) and temperature. At least for some cold-water fish, the gut evacuation rate is better modeled by a constant than an exponential (Ware 1971). Holling (1966) and Jamieson (1973) have shown that the exponential function appears to fit data from some other insects, but this does not appear to be universally true. This is not meant to suggest that the model is not an adequate description for the mantid, only to note that there are a number of complicating factors outside the laboratory. There are other hypotheses which do not require the rate assumption.

If we forget for a moment the E_i^*/h_i^* relation with pursuit distance, several alternative hypotheses may be put forth to explain the observed behavior, namely, that at low levels of food in the gut, the mantid is willing to move farther to get a fly. Is there something associated with the stalk that suggests that hungry mantids should be willing to stalk farther? If there is some *mortality risk* associated with stalking, then well-fed mantids may simply be less willing to face this risk. This risk could be related to the distance moved or the change in position of the animal, or to the time spent moving. Possible candidates for this risk factor include: (1) Risk of detection by predators. Many mantids move little except when stalking and moving prey are much more likely to be detected by predators (Ware 1971). Mantids are generally camouflaged with their surroundings, and there is some evidence that their characteristic rocking movement during the stalk is an antipredator adaptation. Robinson (1969a) found that birds were more likely to respond to objects that moved slowly than when the movement was jerky. There is much evidence supporting the idea that their morphology, postures, and behavior are influenced by predation risk (Crane 1952; Edmunds 1972; Robinson 1969b). (2) Risk of displacement. Is a moving mantid more likely to be knocked off the bush? (3) Risk of an inappropriate response. Holling (1974) put forth the idea that the farther away a prey item is, the more difficult it is for the mantid to estimate the qualities of the item. The accuracy of binocular vision for this estimation falls with distance. It could be that a hungry mantid is more willing to accept a mistake than is a well-fed mantid, the mistake being perhaps a stalk toward a potential predator. His complete hypothesis is rather complicated and will be developed in a forthcoming paper and book.

The above suggestions are put forth in the spirit of open discussion. The data support the optimal foraging interpretation but do not strongly (if at all) exclude the various risk hypotheses. With the exception of Pyke (1974a) and Werner and Hall (1974), few data exist which come anywhere near the completeness of those of Holling (1966). Werner and Hall (1974) tested the same theorem as this paper, using a fish attacking zooplankton of various size. Their data also support the behavior predicted by the theorem.

Optimal foraging is not a theory but a point of view—a way of gaining insight into the behavior of foraging organisms. Like all useful viewpoints, it must help explain existing data, suggest new data to be gathered, and point to new variables that would not have been considered under more traditional viewpoints. Some organisms face considerable risk from their potential prey, while some (many insects) search for both prey and mates simultaneously. Assumptions about energy maximization may provide little or no insight about these animals. This should not deter us from thinking about animals (or plants!) in terms of efficiency in getting resources; in fact, the failure of an “efficiency” model to account for a behavior may well lead to insights as to how other ultimate factors affect behavior.

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