OPTIMALITY, CONSTRAINTS, AND HIERARCHIES IN THE ANALYSIS OF FORAGING STRATEGIES

BY

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Three phases of foraging behavior were analyzed: (1) the preparation for prey (specifically trap construction by antlions), (2) diet choice, and (3) consumption of prey. Optimal foraging models were formulated for each phase. Results suggest that behavioral modeling should be constructed in a hierarchical framework. (1) Antlion larvae were shown to line their pitfall traps with fine sand, which significantly increases capture efficiency. This fine-sand layer is caused by physical properties of sand (angle of repose and sand trajectory), and by three components of pit-construction behavior: regulation of trajectory angle and initial velocity, and pre-sorting of thrown sand. (2) Two general models were derived that predict diet choice when foraging time is unconstrained and when external factors constrain foraging-bout length. For a two-prey system, the forager should specialize when $M_{ij} > E_j h_j / (E_i h_j - E_j h_i)$, where i,j=high and low quality prey (respectively), E=energy, h=handling time. M_{ij} is the number of i missed while handling j and is shown to correlate with relative cost of eating i. When foraging-bout length is constrained such that one prey is taken per bout, M_{ij} no longer measures the cost of eating i. Here the predator should specialize when $P(Y_j<Z_i<t)>E_jP(Y_j)/E_i$ where $P(Y_j)$=probability that j arrives in a foraging bout and $P(Y_j<Z_i<t)$=probability that j comes before i in time t. This model predicts that as foraging time decreases, the diet should expand. Published data on three predators (salamanders, intertidal gastropods, and house wrens) support the prediction. (3) Partial prey consumption by ambush predators was modeled. Assuming a Michaelis-Menten uptake curve, at high densities optimal handling time was found to be $t_{oph}=(-D_{pe}t_pC-(g_{max}t_pC(D_{pe}C+g_{max}-D_{pe}t_p))^{0.5}$, where g_{max} and C are coefficients from the uptake curve, t_p is pursuit time, and D_{pe} is pursuit minus eating costs. At low prey densities, t_{op} is $t_{opl}=(CD_{we}-(D_{we}g_{max}C)^{0.5})/(-D_{we})$, where D_{we} is waiting minus eating costs. At medium densities, t_{op} will always be less than t_{opl}, and varies with prey encounter rate. Each model generates different predictions. The low-density model was tested on antlion larvae. I calculated t_{op} from empirical estimates. Antlions extracted the optimal proportion of each prey, but handling time was shorter than expected. Results suggest that antlion prey-handling behavior is adapted to stochastic prey-arrival conditions.

INTRODUCTION

The number of papers dealing with the use of optimality models has grown rapidly since the study of optimal foraging was first introduced in 1966 (MacArthur and Pianka 1966; Emlen 1966). Many studies in this field have been strongly influenced by a few, elegant models. Two of these models are the marginal value theorem (Charnov 1976a) and variations of MacArthur and Pianka's (1966) optimal diet choice model (Werner and Hall 1974; Schoener 1971; Charnov 1976b; Pulliam 1974; Hughes 1979). In some cases, the models have been modified by various authors to fit specific situations, but the underlying assumptions were not challenged.

At the onset of my research for this dissertation, I used these elegant models as a tool in the study of the foraging behavior of antlion larvae (a description of this behavior is found in Chapter I). These models provided specific predictions about the foraging behavior of antlions. In addition, like any type of model, these also provided a specific intellectual framework within which questions could be addressed. During the initial phase of my study, it became clear that the predictions generated from these models were inappropriate for the system I was examining. This meant that a number of other studies had also used these models inappropriately. As a result, the focus of the work changed from the application of existing models to an evaluation of the models themselves.

The first four chapters of this dissertation are results of this evaluation. The first chapter, which discusses the biophysics of pit construction by antlion larvae, is an illustration of a system in which the original predictions were upheld. The next three chapters discuss systems in which the original predictions were rejected. Normally in studies of optimality, the specific details of the model would be altered to generate a new model that more closely fit the observed responses of the organism (Maynard Smith 1978). However, I show that the restrictive nature of the framework defined by the models may be the primary cause for the lack of their predictive value in these and other studies. For example, optimal diet choice models have assumed that decisions about diet choice concern the addition or deletion of prey types from the diet. The researcher's perception of how the animal makes diet-choice decisions will be profoundly influenced by this assumption. In chapter IV, I show that by focusing on a different decision, and thereby changing our perception of the system, optimality models become more realistic and also better predictors of foraging behavior.

In Chapter V I discuss general features of optimality models, both my own and those derived by other authors. I come to the conclusion that generalities about foraging decisions should be derived from studying the framework of the systems under which foraging behavior evolves, and not from models which address single aspects of an animal's behavior. Hierarchical design may be the simplest and best method to use in studying this framework. The organization of the dissertation follows the hierarchical framework.

An optimality model, like other models, can be thought of as a story, or a conceptualization of a particular system. The system can be anything from diet choice to an ecosystem. The story has two major parts: a list of factors that are important in the expression of the trait that is being modeled, and the specific structure or relationship among those factors. The variables in the model include some of the factors, but other factors may be implicit in the structure of the model, such as the underlying distribution of prey in a foraging model. The mathematical model provides a structure within which specific predictions can be made.

In testing the model, the condition of optimality is assumed. In fact, optimality is more of a paradigm than an assumption. The test of the model is simply a test of the list of factors and the structure of those factors in the model. As Maynard Smith (1978) pointed out, much of the confusion about optimality theory has arisen from a misunderstanding of the exact features that are being examined. The conclusion that the animal is not foraging optimally if it does not fit the model is not appropriate for this type of research. If the model fails, we conclude that the model is either incomplete or incorrect, not that the animal is non-optimal (Maynard Smith 1978). Thus the model helps us understand the nature of foraging adaptations and is not used to determine if the animal is foraging optimally.

Optimality modeling is a technique that can be used to understand a system. In this dissertation I use optimality theory as a tool for examining the salient features of foraging behavior. If we were to conclude that an animal was foraging non-optimally because it did not fit an optimality model, we would be implying that we were omniscient in our perception of the system. Clearly this is not the case. If the model failed to predict the response of an animal, we are always left with two alternatives: (1) the animal is behaving non-optimally, or (2) our perception was incorrect. The first alternative is counter productive, since it yields no further predictions, nor does it provide any further insight into the behavior of the animal. Since it is very unlikely that our perception of animal behavior is perfect, then by taking the second alternative we may learn more about the system than we already know. This approach is no different than the standard scientific method. Chapters I-IV all use this approach. Where the models did not work, I re-evaluated the list of factors I thought might be important. In each case, either the list proved to be incomplete or the structure incorrect, and a new testable hypothesis was generated by expanding the list or changing the model. Thus, the technique is useful in the study of behavior, but only if optimality is implicity assumed.

CHAPTER I
THE BIOPHYSICS OF PIT CONSTRUCTION

Introduction

Several groups of animals build devices to capture prey. Among these, spiders are perhaps the best known, but various other arthropods, such as the larvae of antlions (Neuroptera), wormlions (Diptera), some caddisflies (Trichoptera) (Wheeler 1930; von Frisch 1974) and fungus gnats (Diptera) (Eberhard 1980), also use some form of trap to capture prey. The trap often represents a major investment, both in terms of time and energy (Ford 1977; Prestwich 1977; Griffiths 1980), which is expended before any return is realized. Thus, the predator incurs an initial cost weighed against some later expected gain. Based on the predictions of optimal foraging theory (Schoener 1971; Pyke et al. 1977), trap construction should reflect a maximum return rate from prey per unit cost. Natural selection should act to minimize the cost of the trap per prey item by optimizing trap design, by using available materials to their greatest effectiveness, and by minimizing trap construction costs.

Antlions construct conical pitfalls in sand or loose soil. When prey organisms fall into these pits, their escape is impeded by loose sand on the high-sloped walls. The pit serves several functions: it funnels prey to the antlion, increasing the "striking distance" over which the predator can capture prey, and it increases prey escape time and, therefore, the probability of capture. Pit efficiency depends strongly on the physical properties of the materials with which it is built. This study is an analysis of some of the physical principles that govern the construction and use of the antlion pitfall trap as well as the behavior of the antlion during pit construction.

All the experiments reported here used one species of antlion, *Myrmeleon crudelis*, but I have observed three other species (*M. carolinus*, *M. mobilis*, and *M. immaculatus*) in which pit construction appears to be virtually identical.

General Methods

All observations and experiments reported in this paper were conducted in the laboratory (Gainesville, Florida) during spring and summer, 1980. I collected antlion larvae at the University of Florida Marine Laboratory, Sea Horse Key (Levy County), Florida, and transported them individually in sand to the laboratory. Here they were kept in 10x10 cm containers filled to about 6 cm depth with sand of mixed grain sizes (0.1 to 1 mm diameter). Each antlion was kept at 24° C for about two weeks before the experiments were run and fed two dumpy-winged *Drosophila melanogaster* per day. Live antlion larvae were weighed with a Mettler analytical balance. Ants were collected on the University of Florida campus and held no longer than one day before they were used in the experiment. The light-colored sand used throughout the study was obtained commercially as children's sterilized play sand. Dark-colored sand was mixed with light-colored sand to illustrate the distribution of sand grain size in the pit. This sand was also purchased commercially and was sold as "terrarium sand." Sand grains of different sizes were obtained by sifting through a series of U.S.A. Standard Testing Sieves.

Pit-Construction Behavior

Pit construction consists of several stages. (1) The antlion moves just under the surface of the sand, crawling backwards in what appear to be random directions (Fig. 1.1a). It uses two means of propulsion: the hind legs are used to pull the antlion through the sand, and contractions of the wedge-shaped abdomen are also used to plough backwards through the sand. (2) The antlion then moves in a circular path during which it flicks sand to the outside of the circle (Fig. 1.1b). (3) By spiralling inward, the antlion deepens and expands the furrow it creates (Fig. 1.1c), until a conical pit is formed (Fig. 1.1d) (Turner 1915; Youthed and Moran 1969; Tusculescu et al. 1975; Topoff 1977).

Sand particle size affects the sand throwing behavior. For small particles, the head and mandibles are loaded with sand which is then tossed in a clump. This is accomplished when the antlion walks backwards into the furrow wall causing sand to fall onto its head from the sloped wall. Larger particles are isolated by sifting away all smaller particles and then individually tossing them out, either to the side or directly behind the antlion. Particles too large to toss are carried out of the pit on the antlion's back (Topoff 1977; personal observation). My paper deals only with the behavior of the antlion while constructing pits with small particles. This behavior is most

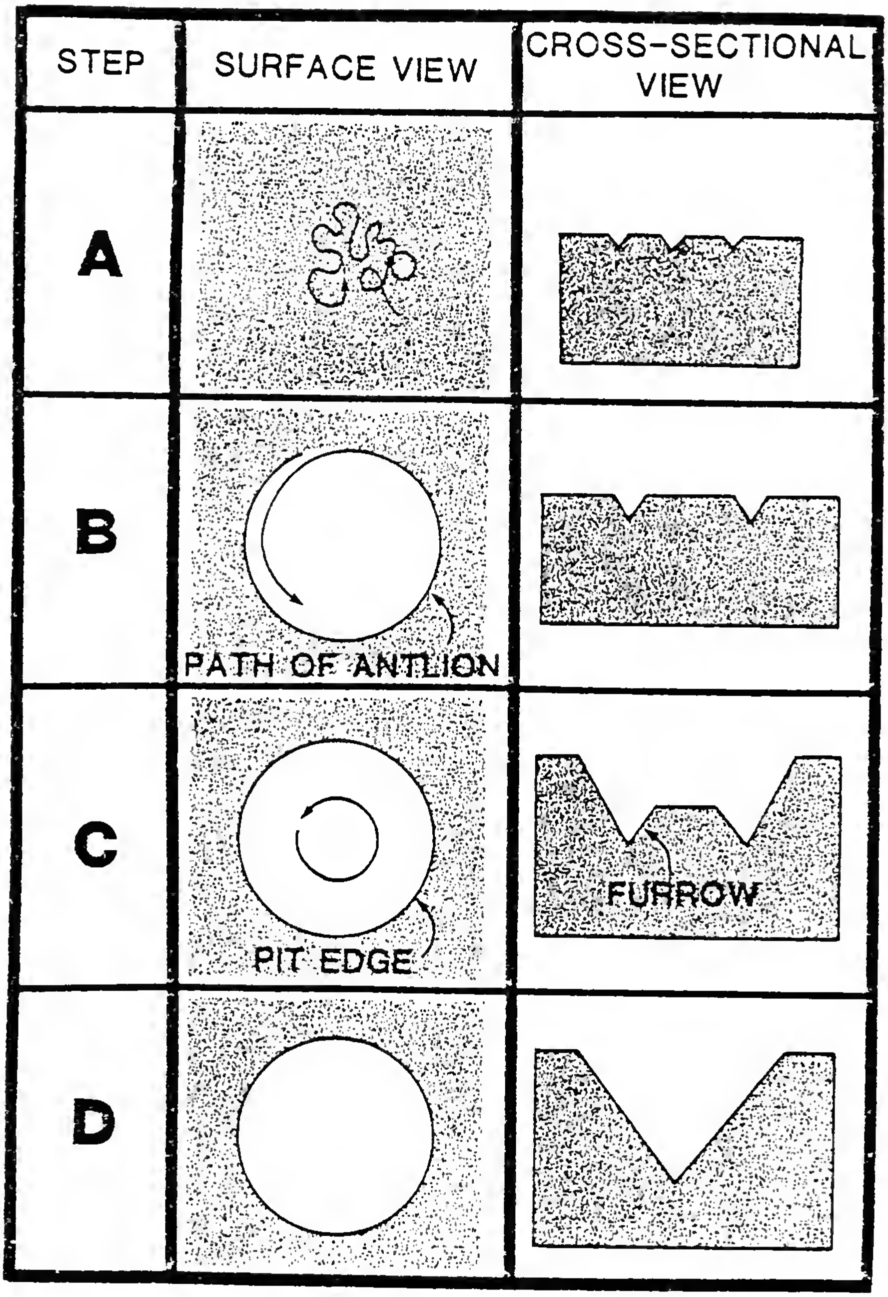


Figure 1.1. Steps of pit construction by antlion larvae. (A) Random movement. (B) Beginning of circular movement; sand thrown to outside of circle. (C) Antlion continues to circle inward in a spiralling path, creating a furrow. (D) Finished pit.

common in sandy areas, but is utilized to some degree in any habitat type.

Pit Morphology and Prey Behavior

If an antlion constructs a pit in sand consisting of several grain sizes (which is the usual case in nature), the completed pit is generally lined with the finest sand available (Fig. 1.2). To test whether this feature functions to increase the efficiency of the pit, I constructed artificial pits by pressing conical molds into sand of different grain sizes. Escape time from these pits was measured for two species of ants, the carpenter ant (*Camponotus floridanus*) and the smaller fire ant (*Solenopsis invicta*).

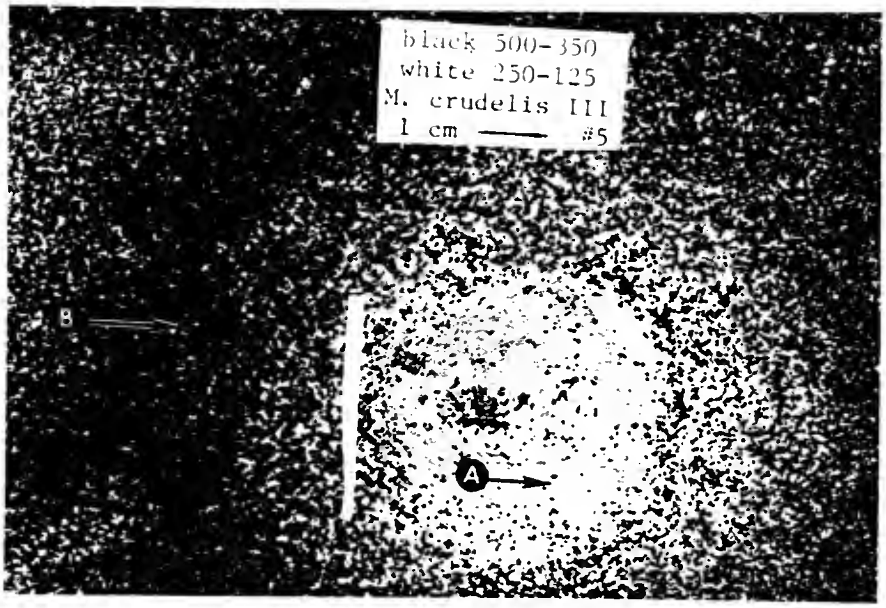
Ant escape time increased significantly with decreasing sand grain size for both ant species (Table 1.1, Figs 1.3 and 1.4). Therefore an antlion pit lined with the finest sand available should serve as a more efficient trap than a pit lined with the unsorted spectrum of available sand. Two other variables also significantly affected ant escape time: pit diameter and slope (Table 1.1).

Two components may affect the distribution of sand in the pit: (1) the physical properties of sand as they apply to pit morphology, and (2) the behavioral aspects of pit construction. These components are examined separately in the following sections.

Physical Components of Pit Construction

Pit morphology is affected by two different physical processes. The first determines the "behavior" of sand on the furrow walls during

Figure 1.2. Photograph of a completed antlion pit showing the distribution of fine (white) and coarse (black) sand grains. (A) Pit wall lined with white sand. (B) Position of black sand 'ring'. The white line marks the pit edge.


black 500-350
white 250-125
M. crudelis III
1 cm #5
B
A

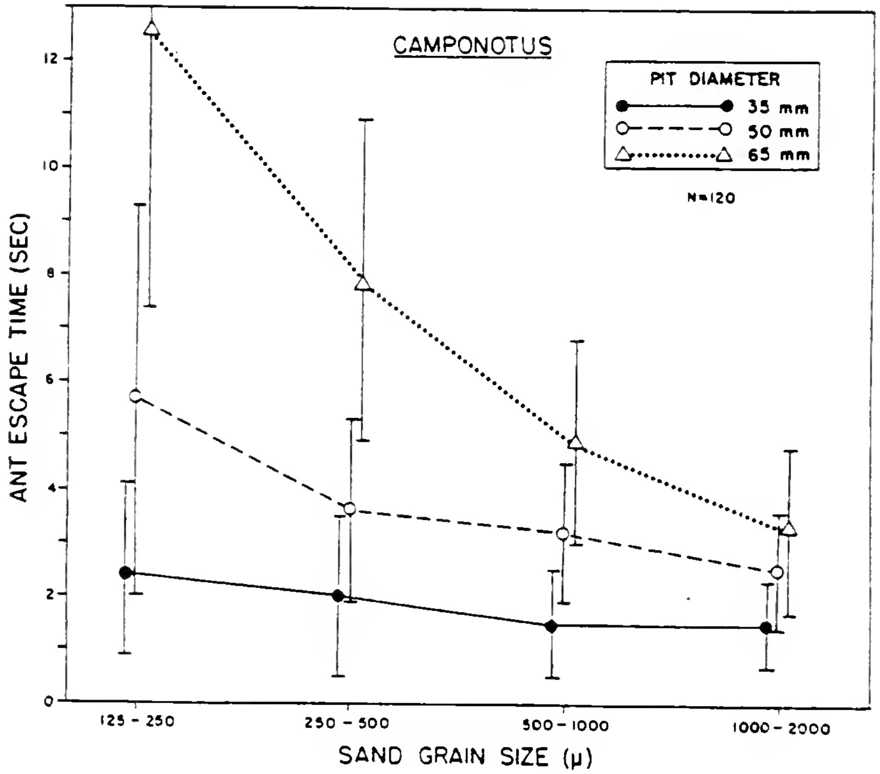


Figure 1.3. Escape time of the carpenter ant (Camponotus floridanus) from artificially constructed pits. Slope of pit walls was 40 degrees.

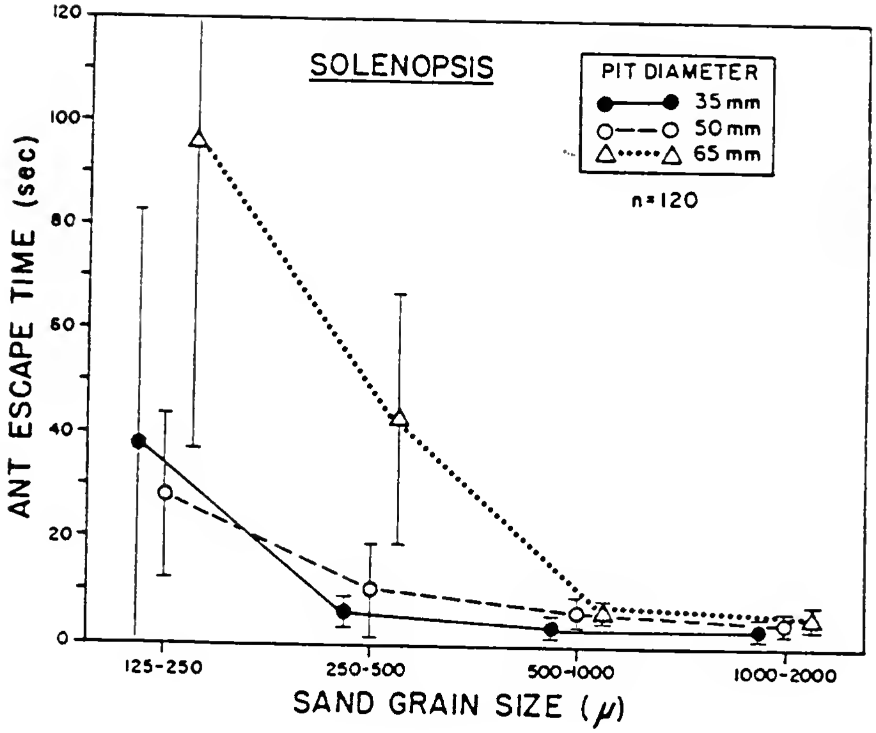


Figure 1.4. Escape time of the fire ant (Solenopsis invicta) from artificially constructed pits. Slope of pit walls was 40 degrees.

Table 1.1. Multiple Regression Analysis for Ant Escape Times from Artificially Constructed Pits Differing in Pit Diameter, Slope and Sand Size*

Solenopsis invicta

Independent variables **	degrees of freedom	F value	Prob.>F
1. Pit diameter	1	34.35	0.0001
2. Slope	1	102.60	0.0001
3. Sand size ***	3	51.04	0.0001
4. Regression model including all variables	5	58.06	0.0001
5. Error	475		

Camponotus floridanus

Independent variables	degrees of freedom	F value	Prob.>F
1. Pit diameter	1	127.88	0.0001
2. Slope	1	20.72	0.0001
3. Sand size ***	3	25.61	0.0001
4. Regression model including all variables	5	45.08	0.0001
5. Error	235		

* All regression analyses were run on SAS computer program GLM (Barr et al. 1979). Each data point represents a different individual.

** The following values of the independent variables were used: _Solenopsis_ and _Camponotus_: pit diameter: 35, 50 and 65 mm; sand grain size: 125-250, 250-500, 500-1000 and 1000-2000 um; _Solenopsis_ slope: 30, 35, 40 and 45°; _Camponotus_ slope: 35 and 40°.

*** Sand size was entered as a class variable and therefore is treated as a non-continuous variable with four levels.

construction. This process will directly affect the morphology of the pit and is closely related to the angle of repose (as discussed below). The second process governs the trajectory of thrown particles. Particle trajectory indirectly influences pit morphology in that it will determine what types of sand particles leave the pit after being thrown.

Slope: Angle of Repose

The antlion pit is lined with fine sand even before it is completed (Fig. 1.5). During construction the larger particles tend to fall to the bottom of the furrow where the animal is digging, leaving the furrow walls lined with finer sand. The differential response of particles of different sizes on the furrow walls suggests that particle size may in itself affect the distribution of sand on the slope. To test this, I constructed artificial pits of different grain sizes. This was done by drawing sand through a hole in the bottom of a tray filled with sorted sand. The slope of the pit walls constructed in this way reflects the angle of repose of the sand. The angle of repose ($\emptyset'$) is the maximum slope that sand will attain without collapsing.

A significant negative correlation was obtained between sand grain size and slope ($r_s=-0.771$, $N=34$, $P<0.01$). Thus, for the sand in which the antlion was making a pit, larger particles had a lower $\emptyset'$ and therefore were more likely to fall off a slope than smaller ones.

Although a significant correlation was demonstrated, this correlation may reflect differences in particle angularity, roughness, or water content which can covary with particle size. All these factors will affect the angle of internal friction ($\emptyset$, the minimal angle of

Figure 1.5. Photograph of an antlion pit in construction showing the distribution of fine (white) and coarse (black) sand grains. (A) Position of antlion in trough of pit. The white line marks the pit edge.


A
red 500-250
white 250-125
M. crudelis III
1 cm =6

stress where a mass is in equilibrium)(Singh 1976), and therefore will affect the angle of repose. Marachi et al. (1972) have shown that Ø decreases with increasing particle size, but they note that other studies suggest either no relationship or an opposite one. However, the actual physical factors that create the negative correlation between slope and particle size are unimportant. I have observed antlions constructing pits in several types of soil and this correlation held in each case. Thus, a pit will tend to be lined with fine sand through the differential response of particle size and Ø' alone.

Particle Trajectory: Stoke's Law

If an antlion constructs a pit in sand consisting of a variety of particle sizes, rings are formed around the pit in order of increasing particle diameter (Fig. 1.2). This indicates that larger particles are thrown farther during pit construction than smaller particles. Thus, in addition to a differential sand sorting on the furrow walls due to the angle of repose of sand (Ø'), there appears to be sorting according to the size of the thrown sand. To understand the basis of the latter sorting, the physical processes affecting sand particle trajectory must be understood.

The trajectory of a particle with a given initial velocity is affected by the drag force imparted on it by friction due to air. As derived below, the drag force on a particle will vary with particle radius. The smaller the particle, the higher the drag force due to air relative to its momentum and the shorter the distance it will travel. At Reynolds numbers below 0.1, Stoke's Law defines this force (F_k)

(Bird et al. 1960):

$$F_k = \pi R^2(0.5pV^2)(24/Re)=6\pi uRV, \qquad (1)$$

where

Re=Reynolds number=$(2RVp)/u$,

R=particle radius,

p=fluid density=0.00123 g/cm^3 for air at about 25°C and 66°/o relative humidity,

V=particle velocity,

u=fluid viscosity=0.000184 g/cm s.

The relationship between particle trajectory and the characteristics of particles can be more easily analyzed if Stoke's Law is expressed in terms of its effect on the distance a particle travels. Here distance ($D(x)$) is defined as the total horizontal distance a particle travels (see Lucas 1982 for the derivation):

$$D(x)= \frac{V_o^2\sin 2\theta}{g}\left[1-(4/3)\frac{K'V_o\sin\theta}{gR^2}\right] \qquad (2)$$

where

$K'=(7.16\text{x}10^{-5})c$,

θ=initial trajectory angle,

g=acceleration due to gravity=980 cm/s^2,

V_o=initial particle velocity,

c=dimensionless coefficient=4.5 for a sphere (Bird et al. 1960).

Equation (2) is a standard Newtonian ballistics equation which incorporates momentum loss due to drag. According to Stoke's Law, the variables that affect the distance a particle travels are initial velocity, trajectory angle, and particle radius. This equation predicts the following relationships: (1) Distance (D(x)) will increase monotonically with increasing initial velocity (V_o). (2) The effect of trajectory angle (Θ) on D(x) will vary with sand particle size (R). The trajectory angle at which distance is maximized will decrease from 45^o as particles become smaller. As sand particle size increases, D(x) is maximal at $\Theta=45^o$. (3) As sand particle size increases, distance should increase monotonically.

At intermediate Reynold's numbers ($2<Re<500$), Stoke's drag force is underestimated and must be modified as follows (Bird et al. 1960):

$$F_k= R^2(0.5pV^2)(18.5/Re^{0.6}), \quad (3)$$

which changes the derived Stoke's equation (equation 2) to (see Lucas 1982 for the derivation)

$$D(x)= \frac{V_o^2\sin2\Theta}{g}\left[1 - \frac{K''V_o^{1.4}c(\Theta)}{gR^{1.6}}\right], \qquad (4)$$

where

$$K''=(7.79x10^{-5})c.$$

The relationships between particle size, trajectory angle, and distance listed above for equation (2) are the same for equation (4).

A sand particle with a diameter of 200um would have a Reynolds number of 2 if it travelled only 15 cm/s. Although I did not directly measure particle speed, a rough estimate suggested that the antlion threw sand at a much greater velocity than this. Therefore, the Reynolds number was thought to be greater than 2.

I measured the distances over which antlions threw sand of different sizes (different R) during pit construction. With empirical measurements of trajectory angle (θ)(see Behavioral Components Section), thrown distance ($D(x)$), and particle radius (R), the observed data were best fit to the modified Stoke's equation (4) using the least squares method. To measure the distances that particles were thrown, I placed a card covered with double-sided tape along the edge of the pit and behind the antlion. I measured the distance thrown for each sand grain on the tape. The sand grain diameter was measured under a microscope.

With equation (4), the c value that produced the best fit to the data was 16.4 (Fig. 1.6). This value is a higher c value than the c of a sphere (4.5), which suggests that the irregularities of the sand particle surface increase the drag on the particle. With a c value of 16.4, equation (4) generally produced predicted distances close to the mean distances that antlions threw particles. When equation (2) was best fit to the data, a c value of approximately 70 was obtained. This corroborates the fact that the unmodified Stoke's Law (equation 1) underestimates the friction force in this system. Thus, it appears that the presence of sorted sand rings around the antlion's pit is due to the effect of sand particle radius on the drag (F_k) to momentum ratio. This ratio is lower for larger particles. This means that when an antlion throws mixed sizes of sand, the finest particles fall out first and the largest particles travel farthest.

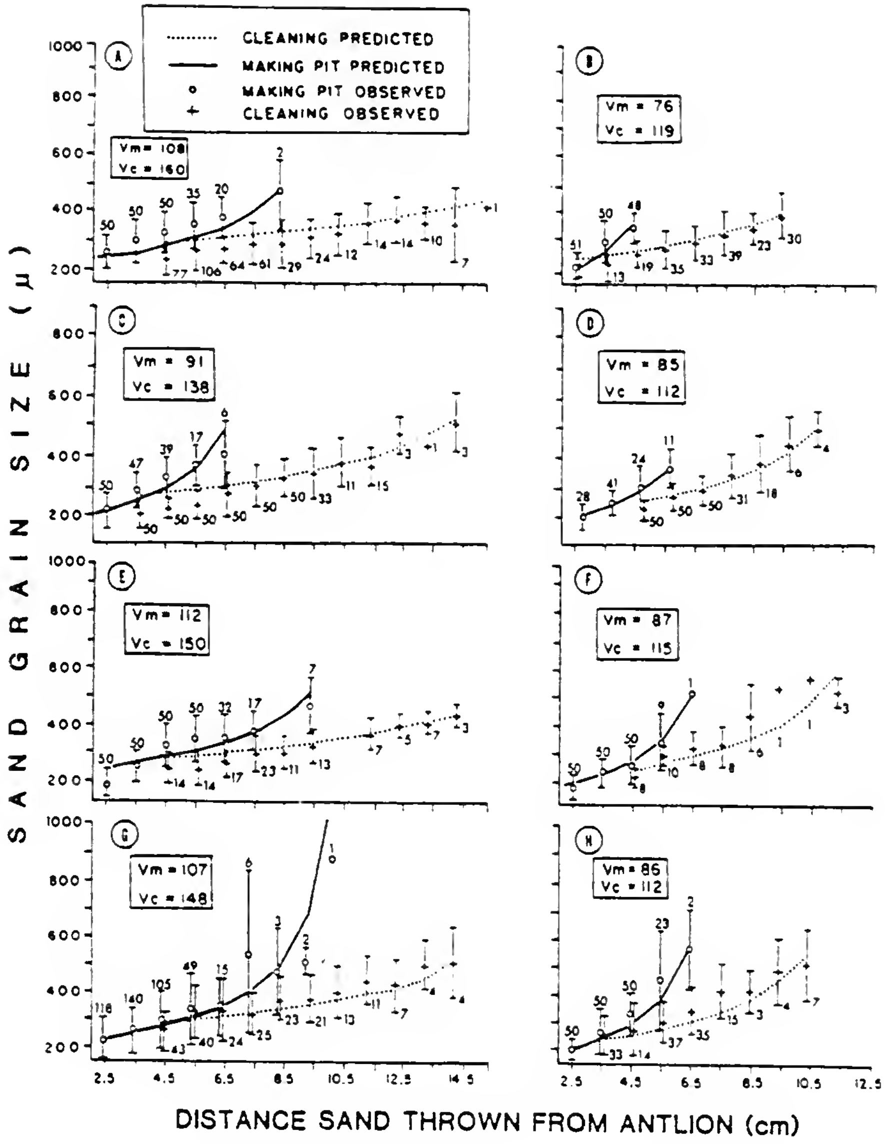


Figure 1.6. Observed and predicted values of diameters of sand grains thrown during pit construction and cleaning. Bars represent mean observed values +/- 1 SD. Curves represent values predicted by equation (4) (see text). V_c=best fit value for particle velocity during initial cleaning phase. V_m=best fit value for particle velocity during pit construction. Velocities listed are cm/s.

Behavioral Components of Pit Construction

Clearly, the structure of a pit is influenced by the physics of sand, but does the antlion exhibit any behavioral patterns that tend to increase its efficiency at constructing the pit in terms of these physical laws?

Trajectory Angle During Pit Construction

Based on equation (4), two variables that the antlion can potentially regulate are trajectory angle (θ) and particle velocity (V_o). At $\theta=45^{\circ}$, large particles will travel a maximum distance. Small particles, on the other hand, will travel increasingly longer distances as θ is reduced from 45 to 0°. This suggests that there will be a particle size crossover point. At particle sizes below this point, particles will travel farther as θ is decreased from 45°, and above this size particles will travel farther when the trajectory angle is 45°. At an initial velocity of 100 cm/s (approximately the velocity used during construction; see Fig. 1.6), this crossover occurs within the range of sand grain sizes used in this study (300-400 um; see Fig. 1.7). Therefore, the predictions derived from equation (4) will affect the importance of regulating θ for the antlion. Thus θ will affect not only the distribution of sand particle sizes in the final pit but also the cost of removing these particles. We expect natural selection to act on antlion behavior in such a way that antlions utilize θ to enhance pit structure while keeping construction costs at a minimum.

To measure θ, a cardboard covered with two-sided sticky tape was placed over a pit during construction. Sand thrown by the antlion stuck

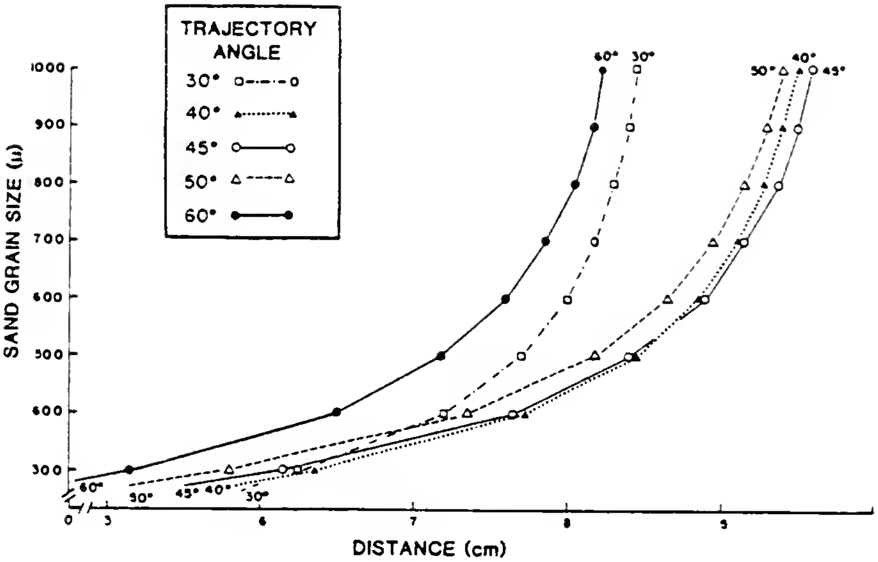


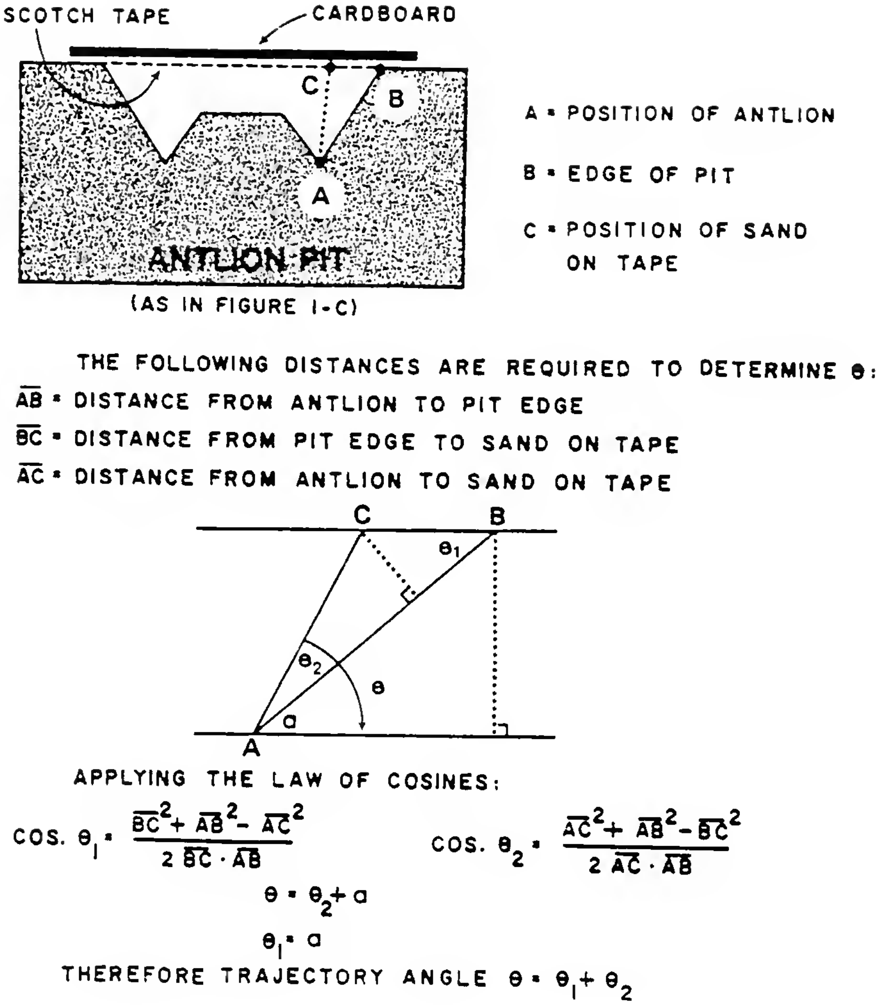
Figure 1.7. Distances sand grains of different radii travel under varying trajectory angles as predicted by equation (4) (see text). V_o was 100 cm/s.

to the tape, leaving a record of the dispersion of sand as it was thrown out of the pit. Thus θ was estimated by measuring (1) the pit angle, (2) the distance from the antlion's mandible (visible at the bottom of the pit) to the pit edge, and (3) the distance from the pit edge to the sand on the tape (Fig. 1.8). Trajectory angle and dispersion of sand during pit cleaning (described below) were also measured in this manner. This method tends to underestimate θ slightly, if sand particle trajectory is not linear between the release point and the point where it attaches to the tape. However, since this distance was never more than 2 cm, the underestimation, if any, would be slight.

The mean θ was 47° with about a 12° scatter (Table 1.2). Judging from these data, the antlion appears to be tossing particles so as to maximize the distance larger particles travel and to maximize particle dispersion. Particles above 400um will travel farthest at $\theta=45^{\circ}$. However, to show that the antlion can truly regulate θ behaviorally, it is important to show that an antlion is capable of altering θ. To demonstrate this, another behavior was analyzed, namely cleaning the pit after prey handling.

Trajectory Angle During "Pit Cleaning"

When an antlion captures an arthropod prey, it punctures the prey with its sharp mandibles and injects enzymes that externally digest the prey. Then it ingests the soft tissues and discards the exoskeleton (Wheeler 1930). During prey capture and handling, the pit walls are usually disturbed, causing the bottom of the pit to be partially filled with sand.



THE FOLLOWING DISTANCES ARE REQUIRED TO DETERMINE θ:

$\overline{AB}$ = DISTANCE FROM ANTLION TO PIT EDGE

$\overline{BC}$ = DISTANCE FROM PIT EDGE TO SAND ON TAPE

$\overline{AC}$ = DISTANCE FROM ANTLION TO SAND ON TAPE

APPLYING THE LAW OF COSINES:

$$\cos.\ \theta_1 = \frac{\overline{BC}^2 + \overline{AB}^2 - \overline{AC}^2}{2\,\overline{BC}\cdot\overline{AB}} \qquad \cos.\ \theta_2 = \frac{\overline{AC}^2 + \overline{AB}^2 - \overline{BC}^2}{2\,\overline{AC}\cdot\overline{AB}}$$

$$\theta = \theta_2 + a$$

$$\theta_1 = a$$

THEREFORE TRAJECTORY ANGLE $\theta = \theta_1 + \theta_2$

Figure 1.8. Diagram of method used to estimate trajectory angle (θ). A-position of antlion; B-edge of pit; C-position of sand on tape. The following distances are required to determine θ: AB-from antlion to pit edge; BC-from pit edge to sand on tape; AC-from antlion to sand on tape.

Table 1.2. Particle Trajectory Angle (θ) for PIt Construction and Both Phases of Pit Cleaning; Numbers in Parentheses are Standard Deviation (SD).

	Pit construction	Pit cleaning, initial phase	Pit cleaning, final phase
Mean θ	47.0° (0.7)	46.4° (2.3)	60.0° (4.5)
Range of θ for each antlion	12.2° (2.3)	16.0° (2.8)	43.7° (8.6)
N*	10	10	10

* Each data point represents one throw from a separate individual.

There are two different phases in pit cleaning used in removing the prey and the excess sand. Initially the antlion throws the prey carcass and some sand particles from the pit at an angle of approximately 46°. Finally the antlion cleans the pit by increasing Θ to about 60° (Table 1.2). At this time, the antlion also alternately throws sand to either side, creating a heart-shaped distribution on the tape (Fig. 1.9). The sand thrown during the first phase has a significantly greater particle size than during the final phase (Table 1.3). Thus, the antlion initially clears the pit of the prey carcass and the larger particles that have fallen into the pit during prey capture. The trajectory angle used in this phase (46°) tends to maximize the distance thrown for these larger particles. The antlion then increases the trajectory angle and throws finer sand onto the walls to re-establish the slope of the walls at the bottom. By increasing Θ, the antlion keeps the smaller particles inside the pit, thus increasing the number of fine particles lining the pit. As was mentioned at the outset, this directly relates to the ability of these pits to catch prey (Figs. 1.2 and 1.3). This final phase of pit cleaning is similar to the final phase of pit construction.

Particle Velocity

The function of the initial cleaning sequence is to clear the pit of the prey carcass and any large particles of debris that have fallen into it. The antlion should use a high V_o during this phase to decrease the probability of debris or the carcass blowing back into the pit. Continually removing these objects would increase the cost of pit

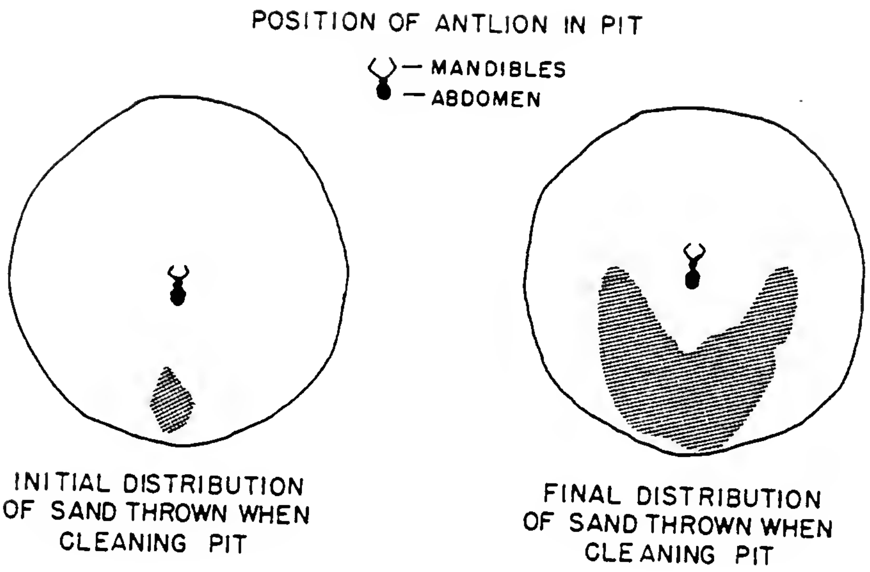


Figure 1.9. Distribution of sand tossed by antlion during the initial and final phases of pit cleaning.

Table 1.3. Sand Grain Sizes (in µm) for Initial and Final Phases of Pit Cleaning.

Antlion number	mean grain size (standard deviation)				
	Initial phase	N	Final phase	N	Z^*
1	303 (83)	50	206 (71)	50	5.40^{**}
2	334 (102)	50	236 (64)	50	4.80^{**}
3	355 (97)	50	251 (73)	50	5.19^{**}
4	323 (107)	50	226 (76)	50	5.05^{**}
5	324 (80)	50	238 (41)	50	5.65^{**}

* Mann-Whitney U-test for large sample size.
** Significant at the $P<0.001$ level.

maintenance. Also, by clearing debris from the pit periphery, there will be a low chance of the debris falling back into the pit when the antlion reshapes or enlarges the pit (which they sometimes do once or more per day; personal observations). Conversely, the function of tossing sand during pit construction is to empty the pit in order to construct a funnel. During pit construction, then, the antlion need only throw sand at a velocity high enough for sand to land outside the pit. A high V_o during pit construction would increase the cost of the pit, with no concurrent benefit. A reduction in V_o during construction would both decrease pit construction costs and tend to retain small particles within the pit, enhancing the pit efficiency. Thus, if the antlion could regulate V_o, it would be advantageous to keep V_o low during pit construction and increase V_o during cleaning. Do antlions regulate particle velocity?

The V_o can be estimated using equation (4) and the following parameters: trajectory angle (Θ), particle radius (R), particle density (p_p), and the particle coefficient. Methods for estimating Θ, R and c have been described previously. Particle density was obtained by determining volume displacement of a known weight of sand. With these parameters, an estimate of V_o could be obtained by best fitting particle distance and particle diameter distributions for V_o. I estimated the velocity that eight antlions used for pit construction and for cleaning (Fig. 1.6).

The particle velocity during pit construction was approximately 72 percent (+/-5) of that used during cleaning. Thus, it is clear that the antlions are able to regulate particle velocity. The consequence of this regulation is that small particle dispersion is reduced during construction, enhancing the differential sorting on the walls due to the angle of repose. By using a 46° trajectory angle the antlion is maximizing the dispersion of sand grain sizes. By reducing particle velocity, the antlion enhances pit efficiency by reducing the number of finer particles that leave the pit and also reduces pit construction costs. Are there any other behavioral components that may be important?

Foreleg Vibration

An antlion moves backwards under the sand during pit construction. Sand that falls onto the antlion's head from the furrow walls is tossed out of the pit. Individuals of all antlion species hold their forelegs along the sides of their heads. The legs are vibrated while the pit is constructed and this appears to aid in the movement of sand onto the head. The antlion can scoop sand up with its mandibles, but it does this only in the last stage of pit construction (which resembles the final phase of cleaning). Turner (1915) showed that the loss of forelegs did not eliminate the antlion's ability to construct a pit and he therefore suggested that the forelegs did not function at all in pit construction. Although forelegs may not be required to construct a pit, they appear to provide some finer behavioral regulation during pit construction. The foreleg movement is clearly a vibration and not a shovelling movement. The function of these vibrations may be to sort sand, although I have no direct evidence for this. Preliminary observations of sand mixtures show that smaller particles tend to sink when vibrated. The antlion may be sorting out the larger particles, preferentially moving these onto its head by sifting out the finest particles with its legs. Since the retention of fine particles in the pit has been shown to be advantageous, the function of this behavior would be to selectively remove the larger particles. The finest particles would then tend to stay in the pit and would be used during the last stage of construction when fine particles are thrown onto the walls.

Spiralling

Tusculescu et al. (1975) have published the only study to date on the physics of pit construction. They suggested that the inward spiralling of the antlion (Fig. 1.1) could be explained solely by physical factors. They assumed that the slope of the furrow walls was equal to the angle of repose, and that the area of sand removed by the shovelling action of the antlion's head and mandibles was equal on both the interior and exterior furrow walls. Under these assumptions, the volume of sand that falls from the walls will be unequal, with more sand falling off the exterior wall than the interior wall. As a result of this inequality, the bottom of the furrow would tend to shift inward. Thus, the antlion need only follow the furrow bottom to spiral inward without behaviorally modifying the path it takes. Unfortunately, the assumptions on which Tusculescu et al. (1975) rest their model are untested. It is extremely difficult to assess the amount of sand removed from either wall of the furrow. Also, the antlion could easily regulate the differential flow of sand through the use of the front legs, mandibles, or head angle. The ability to spiral inward is certainly exhibited in the earliest pit construction stages before there is a furrow. Even if these assumptions are correct, the difference in the shape for the interior and exterior wall would be negligible during these initial stages. During this phase, it seems very unlikely that the furrow bottom would shift inward. Thus during this stage, the antlion must be choosing the path that it takes.

The assumption that all sand above that removed at the bottom will collapse is also unrealistic. Removing a portion of a body of sand at the angle of repose will cause that body to shift as Tusculescu et al. (1975) suggest only if the sand is cohesionless (Krynine 1941). Particle friction would tend to reduce the impact of sand removal on sand located above the removal site. I examined Tusculescu and other's assumptions as follows.

I allowed last instar antlions to construct pits in different sand grain sizes. The assumption that the pit is always constructed at the angle of repose is not supported by my data. Multiple regression analysis showed that a significant proportion of the variation in pit slope is accounted for by sand grain size with no significant variation attributable to pit diameter. In addition to sand grain size, the effect of antlion weight on slope was highly significant (for grain size $F=4.27$ and $P=0.020$, $N=24$; for weight $F=24.01$ and $P<0.001$, $N=24$). These data indicate that the slope of the antlion pit is not at the angle of repose, although sand size does affect the slope. This suggests that the antlion may possess some as yet unknown mechanism for regulating pit slope. For a given volume of sand removed, a reduction in slope will increase pit diameter. Thus, the optimal slope will not necessarily be the angle of repose, but may be at some angle that is less than this, where the benefits of increased diameter equal the costs of a reduction in slope.

General Discussion

Studies on trap construction and use by animals have, with very few exceptions, dealt with ecological questions such as energetics (Ford 1977; Prestwich 1977), trap-building behavior (Witt et al. 1968; Youthed and Moran 1969; Witt et al. 1972; Topoff 1977), orientation (Wilson 1974; McClure 1976; Uetz et al. 1978; Hieber 1979), capture rates and trapping success (Turnbull 1973; Griffiths 1980; Hildrew and Townsend 1980). With the notable exception of Denny's (1976) work, the biomechanical aspects of trap construction and the interface between biomechanics and trap-constructing behavior have been neglected. Trap efficiency is strongly affected by trap design and by the materials from which it is built. Thus, the study of trap biomechanics will increase our understanding of the advantages and constraints of traps on the foraging capabilities of the predator. It will also enhance our ability to evaluate the evolutionary adaptations that the organism exhibits in the mechanics of trap-constructing behavior.

Trap biomechanics have been studied in only two groups of organisms, the orb-weaving spiders (Denny 1976) and antlions (this study). Denny (1976) showed that the spider web conforms to the principle of least-weight structures, known as Maxwell's lemma. A trap built with this design will minimize the amount of material needed to function as a prey-catching device. Thus the spider maximizes the efficiency of the web per unit silk, which reduces both material and energy expenditure. Denny (1976) also showed that orb-weaving spiders construct their webs so that very large and potentially harmful prey fly through the web. Griffiths (1980) suggested that antlion pits may function similarly through changes in pit diameter with antlion size: prey that are too large or dangerous to handle can escape easily. The potential for damage to antlions due to larger or dangerous prey has been demonstrated by Lucas and Brockmann (1981). The present study shows that in addition to pit diameter regulation, antlions are able to regulate the mechanics of pit construction. This is done through the manipulation of sand particle velocity and trajectory angle in addition to an initial sorting through foreleg vibration. In so doing, they enhance the efficiency of the pit in capturing prey by maximizing the proportion of fine sand on the pit walls.

One prediction of optimal foraging theory states that an animal should forage so as to maximize its net rate of return from prey (Schoener 1971; Pyke et al. 1977). Both this study on antlions and Denny's (1976) study on orb-weaving spiders suggest that trap-constructing behavior supports this prediction. However, the methods with which they follow this prediction differ due to differences in the nature of the traps. Spiders exhibit much more control than do antlions over trap material composition and, in fact, utilize at least four different silk types in the construction of the orb web (Work 1981). At least two of these silks differ significantly in their physical properties (Denny 1976). Therefore spiders are able to manipulate the properties of the trap by using different silk types and by varying the number of fibers in each web element. They can also regulate overall trap design to maximize net capture rate (Denny 1976).

Antlions, on the other hand, are constrained by the properties of the material with which they construct their traps. The physical properties of the sand in which they build their pit will strongly affect the properties and design of the trap. The angle of repose and Stoke's drag force complement each other to produce a pit with enhanced capturing efficiency regardless of antlion behavior. [Thus, adaptations in trap-constructing behavior in antlions will consist primarily of minimizing energetic requirements of construction, although some control over the trap design is exhibited. Energy is saved through a reduction of particle velocity and in the utilization of a trajectory angle that maximizes the distance that larger particles are thrown. Pit design is modified by the identical final phases of construction and pit cleaning, which result in a additional fine-sand layer on the pit walls. Antlions may also regulate pit diameter and the slope of the pit walls.]

Several distinct taxonomic groups utilize similar trap types. These include spiders and fungus gnat larvae (Eberhard 1980) (silk webs and silk thread traps), and antlions and rhagionid wormlions (Wheeler 1930) (sand pitfall traps). Since these groups are morphologically distinct, it would be interesting to compare their behaviors to see if the similarity in trap physics has caused a convergence in trap-constructing behavior. For example, wormlions use the anterior portion of the thorax to throw sand (Wheeler 1930), while antlions use only their heads. Yet both groups should use similar trajectory angles and velocities in order for them to forage optimally.

CHAPTER II
MODELS OF PARTIAL PREY CONSUMPTION

Introduction

Predators are generally thought to consume their prey whole. This conception is reflected in the optimal diet choice models developed by Charnov (1976a), Pulliam (1974, 1975), Rapport (1971, 1980), Werner and Hall (1974), and others. Each of these authors treats the energy derived from a single prey item as a constant. However, many predators either occasionally or predominantly consume only a portion of their prey. In this case, the energy derived from a single prey will be a function of the handling time invested in that prey. A number of models have been proposed that directly address partial prey consumption (Cook and Cockrell 1978; Griffiths 1982; Holling 1966; Johnson, Akre and Crowley 1975; Sih 1980a). These models generally fall into two categories: (1) models of proximate mechanisms that refer to physiological constraints on foraging, and (2) optimal foraging models. In this paper I review these models and their predictions. I then derive a new optimal foraging model that predicts partial prey consumption by ambush predators. The model illustrates that no global foraging model can generate predictions for a wide variety of predators. The models also show that even small changes in predator behavior or prey conditions may change the expected predatory response to prey.

Proximate Models

Models concerning the physiological constraints on foraging have focused on two aspects of the predator, (1) gut size (The Gut-Limitation Model) and (2) the maximal rate of ingestion (Digestion-Rate-Limitation Model).

Gut-Limitation Model

The Gut-Limitation Model (GLM) was first proposed by Holling (1965, 1966). He suggested that predatory behavior could be thought of as a number of separate phases, each of which is driven by its own controlling mechanism. Thus, the behaviors of search, pursuit, strike and eat are each independently controlled, and each is triggered by a given threshold of hunger. Holling suggested that hunger thresholds are determined by the amount of food in the gut and are therefore gut limited. If the threshold for eating is greater than that for capture, then the predator may kill prey without eating anything. Eating is terminated when the predator is satiated, or when the hunger threshold drops to zero. If the threshold for eating is low, then the predator may only eat a small portion of the prey before it is satiated and will only partially consume its prey.

Johnson et al. (1975) proposed modifications of Holling's model for insect systems. They suggested that there are essentially two levels of satiation, one involving the filling of the foregut (which affects eating and striking) and the second involving the filling of the midgut (which affects striking). Thus, this model differs from that of Holling (1966) in that two separate compartments (foregut and midgut) each affect some portion of predatory behavior, whereas the original model only assumed one compartment.

Both of these models assume that the degree of satiation directly controls predatory behavior. In terms of partial prey consumption, the models predict that partial consumption occurs only when the predator does not have enough room in its gut to eat an entire prey. As prey density increases, there is an increasing probability that a predator is nearly full at the time of prey capture. Thus, there should be a negative correlation between prey density and percent consumption of prey. There should also be a concomitant decrease in handling time per prey item with increasing prey density, since it should take less time to eat a smaller proportion of a prey item.

The assumption that predators are often satiated appears to be valid in laboratory studies conducted by Holling (1966), Johnson et al. (1975), and Nakamura (1977) on mantids, damselfly larvae, and wolf spiders (respectively). However, a number of predators that partially consume prey are clearly not constrained by satiation (ex. Cook and Cockrell 1978; DeBenedictis et al. 1978; Sih 1980a). In fact, the predatory mite (*Amblyseius largoensis*) has been shown to feed to satiation then return to the same prey after a "digestive pause" (Sandness and McMurtry 1970). In this case, satiation occurs regularly, but does not entirely affect prey-consumption behavior. A second prediction from this model is that there should be a correlation between inter-capture interval and percent consumption. The importance of this prediction is discussed in a later section.

Digestion Rate Limitation Model

Many predators externally digest their prey and then ingest the pre-digested material. Spiders, antlions, and hemipterans include many species that utilize prey in this manner. When feeding on insects, this type of predator is generally unable to ingest the exoskeleton and therefore always consumes only a portion of each prey item. Griffiths (1982) suggested that the rate of digestive-enzyme production increased with an increase in the rate at which prey were captured and eaten. This means that the rate of ingestion should increase with increasing feeding rate (or increased prey density) and the amount of time spent per prey item should decrease as a result. Thus, handling time is constrained by the rate of extra-intestinal digestion. Griffiths (1982) provided data on one species of antlion that supported the model and suggested that the data from Giller (1980) on backswimmer (Notonectidae) feeding behavior also could be interpreted in this way. Mayzaud and Poulet (1978) demonstrated empirically that enzyme production increases with feeding rate in a number of species of copepods. Thus, this model may be appropriate for particle feeders as well as the fluid feeders referred to by Griffiths (1982). Griffiths showed that antlions (which normally feed at low prey densities) extract the same proportion of each prey. Thus antlions exhibit no change in partial consumption with increasing prey density even though there is a decrease in handling time. So in contrast to the Gut-Limitation Model, the Digestion-Rate-Limitation Model predicts no change in percent consumption (for predators that feed at low rates), but a decrease in handling time with increasing feeding rate.

Optimal Foraging Models

Charnov (1976a; also see Parker and Stuart 1976) proposed a model to predict the behavior of predators foraging at a series of patches. This model, the Marginal Value Theorem, predicted the amount of time the predator should stay in a patch, given three sets of information: (1) the search time required to find the next patch, (2) the average net rate of benefit accumulated for all patches, and (3) the instantaneous rate of benefit accumulate for the present patch. Cook and Cockrell (1978) and Sih (1980a) independently proposed that in many cases, a single prey item could be treated as a patch with a given search time required to find the next patch (prey item). They used this analogy to adapt the Marginal Value Theorem to the study of partial prey consumption.

In this section, I will review the Marginal Value Theorem as it applies to partial prey consumption. I then show that this model is inappropriate for ambush predators (for which it has been used in the past) and develop an analogous model for this type of predator.

Searching Predators

All optimal foraging models assume that the predator chooses (or is programmed to select) the sequence of behaviors that maximizes the net rate of benefit per unit foraging time (Pyke et al. 1977; Schoener 1971). In many cases, benefit has been expressed in terms of energy (Jaeger and Barnard 1981; DeBenedicts et al. 1978; Hughes 1979; Pyke 1978; Krebs et al. 1977). In terms of the predator that consumes only a proportion of its prey, optimal foraging theory would predict that the predator should eat only the proportion of each prey that would yield a maximal net rate of benefit.

The solution for the optimal percent consumption can be expressed as follows: Let the behavior of the predator consist of three phases, search, pursuit and capture, and ingestion. The times associated with these phases are

t_p=pursuit and capture,

t_s=search time,

t_e=ingestion or feeding time,

T_T=total foraging time=$t_p+t_s+t_e$,

where t_p and t_s are constants and T_T is a function of t_e. Let the gross benefit extracted from the prey ($g(t_e)$) be a Michaelis-Menten function (e.g. Shoemaker 1977; as in Sih 1980a):

$$g(t_e) = \frac{g_{max}\, t_e}{C + t_e}, \qquad (1)$$

where g_{max} is the maximal benefit that can be extracted from the prey and C is a constant that affects the rate of extraction. The Michaelis-Menten function will be used in all further derivations. This function, which was originally used by Sih (1980a) in his analysis of partial prey consumption, gives an asymptotic curve and should generally resemble the extraction rate curves exhibited by foragers. There should be little qualitative difference between similar asymptotic functions (e.g. Michaelis-Menten, exponential, etc.) in the predictions generated from these models. I will assume that each prey is similar in that $g(t_e)$ is equivalent between prey. I also assume that capture probability is unity, although this assumption will be relaxed later in this paper. I define the costs of foraging as

C_p=cost of pursuit and capture per unit time,

C_s=cost of search per unit time.

Therefore,

$C_p t_p$=total cost of pursuit and capture,

$C_s t_s$= total cost of search.

The total benefit (E) per unit foraging time (T_T) is (Sih 1980a)

$$\frac{E}{T_T} = \frac{g(t_e)-C_p t_p - C_s t_s}{t_e+t_p+t_s} = \frac{g_{max} t_e}{(C+t_e)T_T} - \frac{C_p t_p}{T_T} - \frac{C_s t_s}{T_T} . \qquad (2)$$

The optimal solution is obtained when

$$\frac{\partial\ (E/T_T)}{\partial\ \ t_e} = 0. \qquad (3)$$

From equation 2

$$t_{eop}=[(g_{max}C(t_p+t_s)+C_p t_p+C_s t_s)/g_{max}]^{0.5} \qquad (4)$$

(see Fig. 2.1 for the graphical solution to t_{eop}).

The predictions from equation 4 are as follows (Sih 1980a):

1) there should be a positive correlation between feeding time (and percent consumption) and the following parameters
   - a) pursuit time,
   - b) search time,

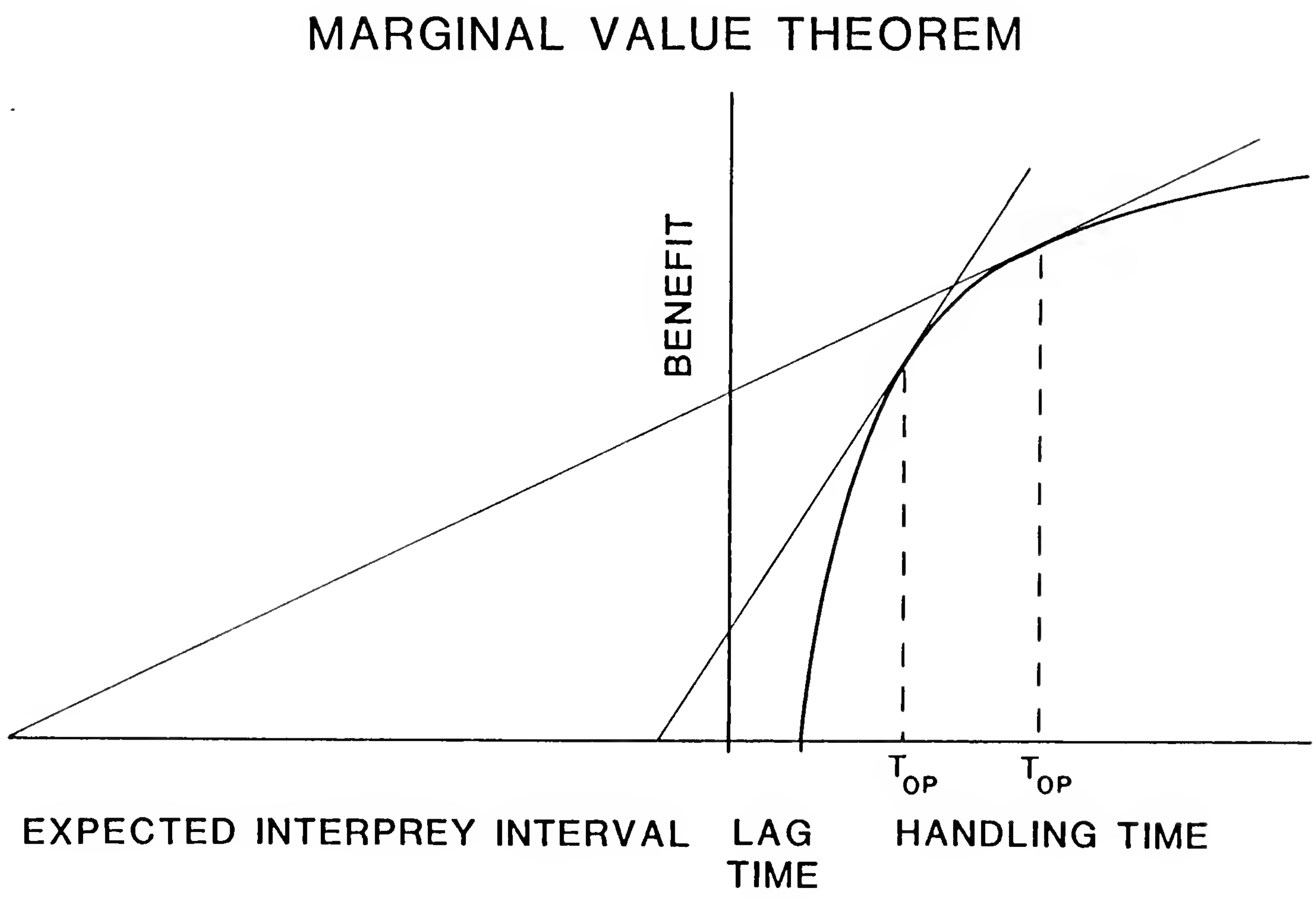


Figure 2.1. Graphic method for solving the Marginal Value Theorem (see Sih 1980a).

c) pursuit cost,

d) search cost;

2) since prey density should be negatively correlated with search time, feeding time and percent consumption should decrease with increasing prey density;

3) there should be a negative correlation between feeding time (and percent consumption) and the extraction rate, since the extraction rate is inversely proportional to C.

Cook and Cockrell (1978; also see Parker and Stuart 1976) also suggested that the predator should respond to the mean encounter rate and not to each individual inter-arrival interval. This implies that there should be no correlation between inter-prey interval and feeding time if the overall rate of prey encounter remains constant.

These predictions are based on the fact that the predator should weigh any benefit derived from ingestion against the benefit associated with dropping the prey and searching for another. As the rate of extraction decreases, there should be a point where searching for the next prey will be more beneficial than continuing to feed on the present prey. The optimal solution to this tradeoff between ingestion and search is expressed in equation 4.

Ambush Predators

For a searching predator, the inter-arrival interval is dependent on search time, and therefore, the forager has some control over prey encounter rate. For an ambush predator, prey arrive independently of the behavior of the ambusher. This means that prey inter-arrival intervals for ambush predators are not the same as those for searching predators. As a result, there is no tradeoff between search time and feeding time for ambush predators, and therefore, the Marginal Value Theorem (MVT) is not an appropriate model for this mode of predation. Inter-prey interval may affect prey consumption, but for reasons unrelated to the MVT. This is demonstrated by the models listed below.

For the first set of models, I assume that each prey encountered is captured, and that the gross benefit derived from each prey per unit feeding time can be expressed as in equation 1. The model for ambush predators generates different predictions at different prey densities. I will address each of these prey density regions (high, medium and low prey density) separately.

Ambush model -- high density

At high prey densities I assume that prey are continuously available to the predator, such that as soon as the predator drops one prey, it can immediately begin pursuit of a second prey. At these densities, the predator will always be in either the pursuit or feeding phase of predation. At satiation, the predator may also exhibit some digestive pause (see Johnson et al. 1975; Sandness and McMurtry 1970). If the predator is not yet satiated, then the optimal feeding time will be similar to that predicted by the Marginal Value Theorem, except there is no search. Thus the net rate of benefit accumulation is

$$\frac{E}{T_T} = \frac{g(t_e) - C_p t_p - C_e t_e}{t_e + t_p}$$

$$= \frac{g_{max} t_e}{(C + t_e)(t_e + t_p)} - \frac{C_p t_p}{(t_e + t_p)} - \frac{C_e t_e}{(t_e + t_p)}, \quad (5)$$

where C_e is the cost of feeding per unit feeding time (t_e) and the total cost of eating is a linear function of eating time. The optimal feeding time is (see Fig. 2.2)

$$t_{eop} = \frac{-Dt_p C - [g_{max} t_p C(DC + g_{max} - Dt_p)]^{0.5}}{Dt_p - g_{max}}, \quad (6)$$

where

$$D = C_p - C_e .$$

The predictions from equation 6 are as follows:

1) there should be a positive correlation between feeding time (and percent consumption) and the following parameters:
   a) pursuit time,
   b) pursuit cost;
2) prey density should have no effect on either handling time or percent consumption, unless the time or cost of pursuit is affected by prey density (for example see Treherne and Foster 1981);
3) there should be a negative correlation between feeding

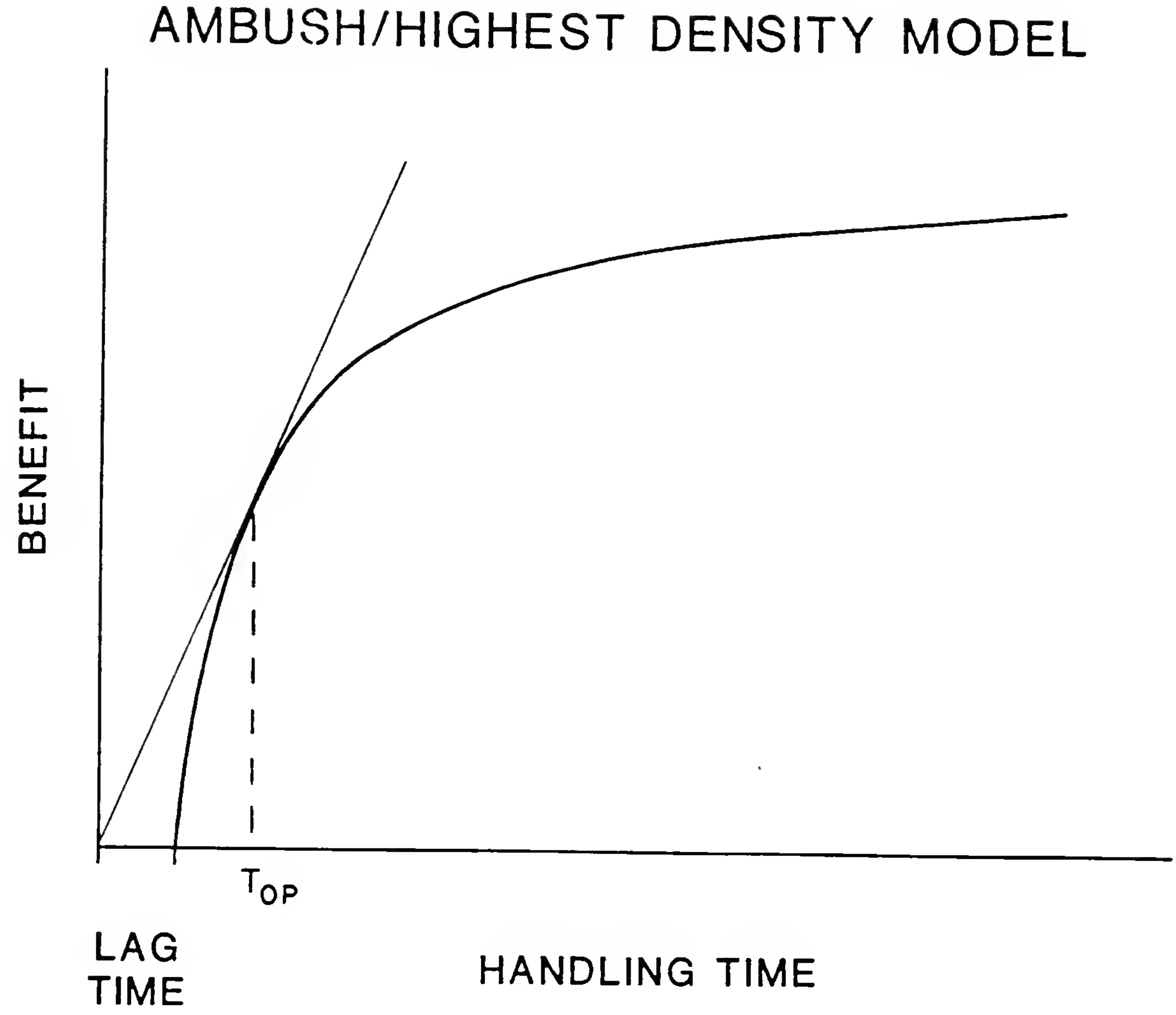


Figure 2.2. Graphic method for solving the Ambush-Predator Model with high prey density. C_e=0 and C_p=0 for this graph.

time (and percent consumption) and the following parameters:

a) extraction rate (see predictions from eq. 4),

b) cost of eating.

The digestive pause may have a variety of effects on foraging, depending on how the pause constrains foraging. For example, the predator may not return to the prey after satiation, in which case the gut clearance rate and gut size will set an upper bound on feeding time and percent consumption (as shown by Holling 1966 and Johnson et al. 1975). I will model the simplest case here, where the predator can return to the prey (as shown in mites by Sandness and McMurtry 1970). In this case, equation 5 is expanded to include the cost of the digestive pause (C_d) and the time required for the pause (t_d)

$$\frac{E}{T_T} = \frac{g(t_e) - C_p t_p - C_d t_d - C_e t_e}{t_e + t_p + t_d} . \qquad (7)$$

The optimal feeding time is

$$t_{eop} = [(g_{max}(t_p + t_d) + C_d t_d + C_p t_p)/g_{max}]^{0.5} . \qquad (8)$$

The predictions from eq. 8 are the same as those from eq. 6. In addition, increases in t_d and C_d should increase te_{op}.

Ambush model -- low density

I define low prey density as densities at which the probability of encountering a prey during either the lag or ingestive phases is essentially zero. Here the inter-prey interval is long, but this interval cannot be treated as it was with the MVT. Prey arrive at given intervals of time, regardless of how the predator uses that time. With the MVT, prey arrive at given intervals of search time only. Thus, the inter-prey interval is influenced by the amount of time the predator invests in each phase of predation. For ambush predators, prey arrive at given intervals of total time.

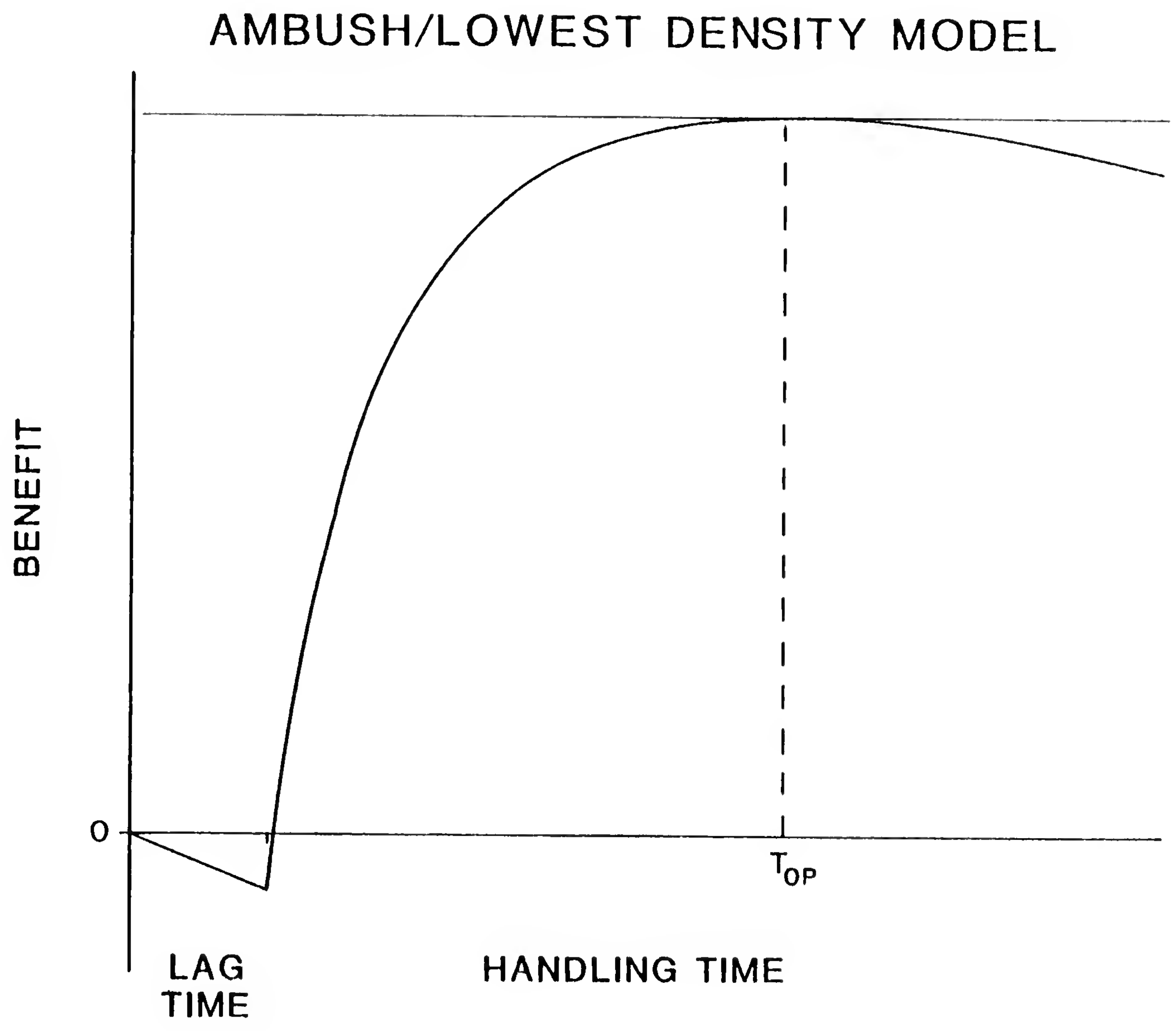
At low densities, the sum of the pursuit time (t_p), feeding time (t_e) and waiting time (t_w=time from the end of feeding until the next prey encounter) is constant (T) and not a function of t_e. Here

$$T=t_p+t_e+t_w \ .$$

I will also treat pursuit time as a constant.

If waiting costs (C_w) and feeding costs (C_e) are negligable, then the predator should hold on to its prey until it is entirely consumed. Unfortunately, the Michaelis-Menten function asymptotes to g_{max} at infinity, thus assuming that the predator can always extract more from the prey. If feeding costs are non-negligible, then the predator should retain the prey approximately until the net rate of benefit accumulation drops to zero (Fig. 2.3). If feeding cost is a linear function of handling time, then the total benefit accumulated per unit foraging time is

Figure 2.3. Graphic method for solution of the Ambush-Predator Model with low prey density. C_e is a constant and the total ingestion cost is a linear function of t_e.


AMBUSH/LOWEST DENSITY MODEL
BENEFIT
0
T_{OP}
LAG TIME
HANDLING TIME

$$\frac{E}{T_T} = \frac{g(t_e)-C_e t_e-C_p t_p-C_w(T-t_e-t_p)}{T} .$$

Thus,

$$\frac{E}{T_T} = \frac{g_{max} t_e}{T\ (C + t_e)} - \frac{C_e t_e}{T} - \frac{C_p t_p}{T} - \frac{C_w(T-t_e-t_p)}{T} . \qquad (9)$$

Here

$$t_{eop} = \frac{C(C_e-C_w)-[(C_e-C_w)g_{max}C]^{0.5}}{-\ (C_e-C_w)} . \qquad (10)$$

Equation 10 predicts that the predator should handle the prey until its rate of net benefit accumulation drops to C_w. At handling times greater than this, it will be more costly to feed on the prey than it would be to drop it and wait for the next prey to come along. Further predictions from equation 10 are as follows:

1) feeding time and percent consumption should be positively correlated with g_{max} and C_w;
2) feeding time and percent consumption should be negatively correlated with C and C_e;
3) prey density should have no effect on either feeding time or percent consumption;
4) neither pursuit time nor pursuit costs should have any effect on feeding time or percent consumption.

Ambush model -- medium density

At densities intermediate to the low and high density cases, prey arrive at intervals short enough to overlap with the pursuit or feeding phases. At medium densities, when a prey arrives, the predator can either drop the prey item it is currently eating and pursue the second prey, or ignore the second prey and continue eating the first (Fig. 2.4). We should expect the decision made by the predator to reflect the maximal net rate of benefit accumulation.

At these densities, the inter-prey interval sets the feeding times. In fact, the pursuit time (t_p) plus the feeding time (t_e) are equal to the inter-capture interval. However, the predator should never hold on to a prey longer than the time predicted by the ambush/low-density model (once inter-prey interval drops below this threshold, the ambush/low-density model predicts predatory behavior). A few new terms must be defined:

T_{IP}=inter-prey interval=t_p+t_e,

X=the number of intervals before the xth prey is encountered,

Y=the number of intervals before the yth prey is encountered,

G(X)=benefit per unit foraging time derived from eating every xth prey,

G(Y)=benefit per unit foraging time derived from eating every yth prey.

The net benefit of foraging (E_{net}) is

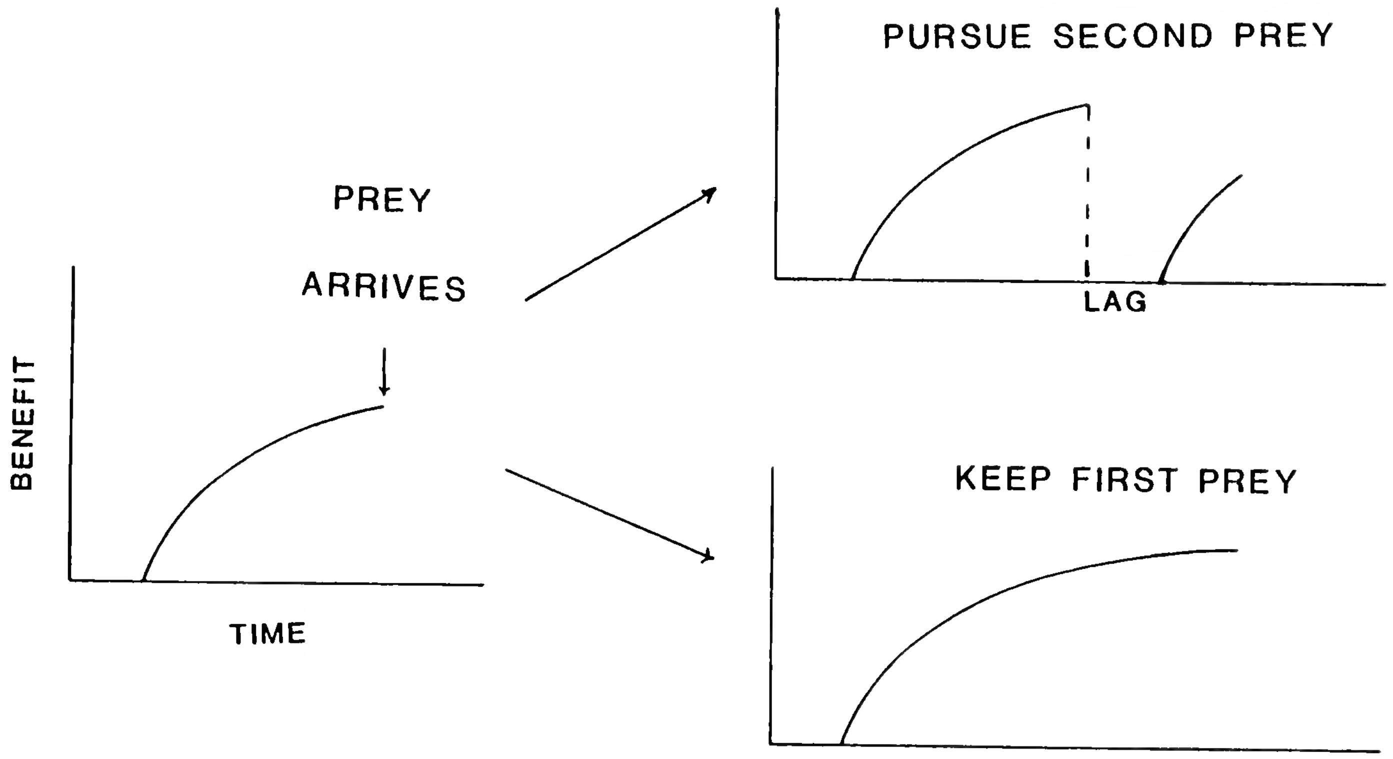


Figure 2.4. The choices available to the ambush predator feeding at intermediate prey densities.

$$E_{net} = \frac{g_{max} t_e}{C + t_e} - C_p t_p - C_e t_e \, . \qquad (11)$$

The net benefit per unit foraging time will be

$$G(X) = \frac{g_{max}(XT_{IP} - t_p)}{(C + XT - t_p)(XT_{IP})} - \frac{C_p t_p}{XT_{IP}} - \frac{C_e t_e}{XT_{IP}} \, . \qquad (12)$$

If X<Y, then the predator should choose the xth prey when

$$\frac{(XT_{IP} - t_p) g_{max}}{(C + XT_{IP} - t_p)(XT_{IP})} - \frac{C_p t_p}{XT_{IP}} - \frac{C_e t_e}{XT_{IP}} >$$

$$\frac{(YT_{IP} - t_p) g_{max}}{(C + YT_{IP} - t_p)(YT_{IP})} - \frac{C_p t_p}{YT_{IP}} - \frac{C_e t_e}{YT_{IP}} \, . \qquad (12)$$

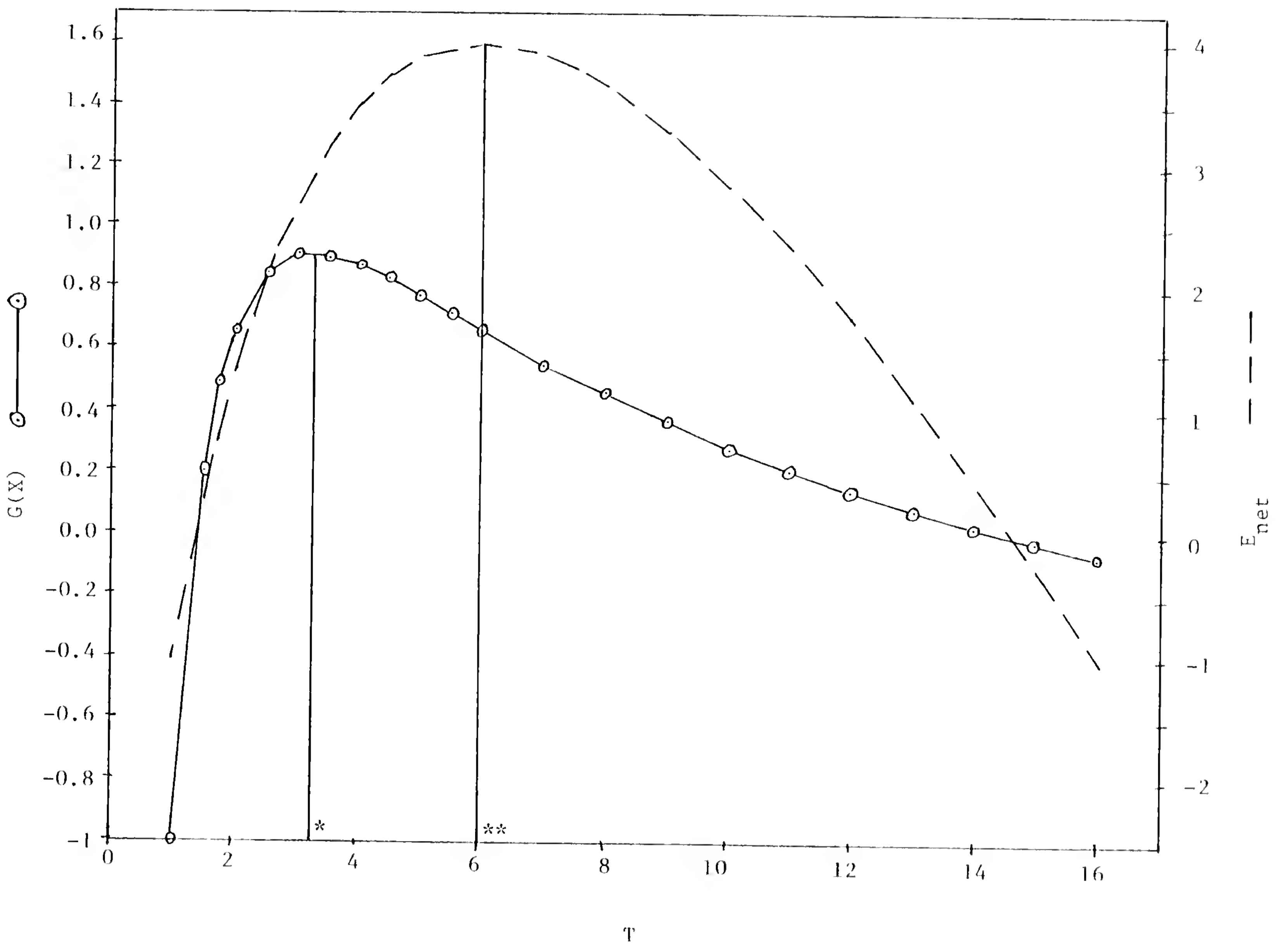
Equation 6 generates the optimal feeding time for an ambush predator at high densities. This optimal feeding time will also correspond to the "optimal" inter-prey interval. Since G(X) decreases monotonically as the inter-prey interval increases above this optimum (see Fig. 2.5), the following predictions can be made:

1) at intervals larger than the "optimal" inter-prey interval, each prey encountered should be pursued;
2) at intervals less than the optimal, the best interval will depend on the characteristics of the curve from eq. 11.

Prediction 1 generates two other predictions that are relevant:

3) as prey density increases, handling time and percent consumption will decrease until the "optimal" prey

Figure 2.5. Net rate of benefit accumulation (G(X)) and total benefit accumulated (E_{net}) for a predator foraging at intermediate prey densities. T=pursuit time+handling time. *=handling time predicted by Ambush/High Density Model. **=handling time predicted by Ambush/Low Density Model. If T>** then the Ambush/Low Density Model predicts foraging behavior. C_w=0 for this simulation.


G(X)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1
0
2
4
6
8
10
12
14
16
T
*
**
E_{net}
4
3
2
1
0
-1
-2

interval is reached;

4) since each prey item is pursued in this region, variation in prey encounter should be correlated with variation in handling time and percent consumption.

Prediction 3 is identical to the predictions from the MVT; thus at medium densities the ambush predators should treat prey similar to searching predators. However, prediction 4 is different than the analogous prediction for searching predators and is identical to one of the predictions from the GLM.

Capture Probability and Ambush Predation

The models listed above illustrate that many factors will affect the predictions from optimal foraging. I have focused on two factors, the mode of predation (searching vs. ambush) and the effect of density on the predicted predatory behavior.

In this section I develop a model for ambush predators which incorporates capture probability. Griffiths (1982) suggested that there should be selection for reduced handling time if the capture probability is lower when the predator is handling a prey than when it is "empty handed". The model presented below explicitly demonstrates this relationship. Another important factor is whether or not the predator returns to a prey item once it is dropped. For example, damselfly larvae apparently do not return to prey (Johnson et al. 1975), whereas antlion larvae may cache partially utilized prey on the pit wall, capture the second prey, then return to the first (pers. observation). I will assume that the predator can return to the first prey, so that if a prey comes before the predator is finished with a previously captured prey, it will cache the first prey until it can go back to it and finish it. Let

λ =encounter rate of prey,

P_w=probability of capture while handling a prey,

P_o=probability of capture while empty handed,

$P_d=P_o-P_w$,

N=total number of prey handled in a foraging bout lasting a given length of time, T_T,

T_d=total time predator devotes to a given prey=t_p+t_e.

To simplify the model, I will also assume that the cost of eating and pursuit are negligible. This assumption will not affect the qualitative predictions of the model.

First the number of prey eaten while handling a prey (N_w) and the number eaten while empty handed (N_o) must be calculated:

$$N_w = \lambda NTP_w , \qquad (13)$$

$$N_o = \lambda (T_T - NT)P_o . \qquad (14)$$

The total number of prey eaten (N) is therefore

$$N=N_w+N_o = \lambda NTP_w + \lambda (T_T-NT)P_o . \qquad (15)$$

Solving for N,

$$N = \frac{\lambda T_T P_o}{1+ \lambda T_d(P_o-P_w)} = \frac{\lambda T_T P_o}{1+ \lambda T_d P_d} . \qquad (16)$$

The benefit associated from each prey,

$$g(t_e) = \frac{Kt_e}{C+t_e} , \qquad (17)$$

times the number of prey yields the gross benefit for the foraging bout:

$$B = g(t_e)N = \frac{(Kt_e)(\lambda T_T P_o)}{(C+t_e)(1+\lambda T_d P_d)} . \qquad (18)$$

The benefit gained per unit foraging time is

$$\frac{B}{T_T} = \frac{(Kt_e)(\lambda P_o)}{(C+t_e)(1+\lambda T_d P_d)} . \qquad (19)$$

The optimal solution to equation 19 is

$$t_{eop} = \left(Ct_p + \frac{C}{\lambda P_d}\right)^{0.5} . \qquad (20)$$

From equation 20, a predator should decrease handling time as the difference in capture probability ($P_o - P_w$) increases. This is because there is an added cost to holding onto a prey that must be weighed against the diminishing return from that prey. Equation 20 is unique among the ambush models presented here because it is the only model that requires that the predator "anticipate" the next prey, or at least modify its behavior before the next prey arrives. Thus, differences in capture probability should affect how the predator treats variation in the inter-prey interval.

Discussion

Different predators appear to exhibit a wide diversity in their responses to prey. Also, as conditions change, the behavior of a single predator may be predicted to change considerably. Many predators (for example *Plethodon*; Jaeger and Barnard 1981) may switch from ambush to searching predators as prey density fluctuates. Some predators may continuously reach satiation (ex. mantids in Holling 1966, damselfly larvae in Johnson et al. 1975), while others may rarely if ever be satiated (ex. hummingbirds in DeBenedictis et al. 1978; antlions in Griffiths 1982). This diversity is an important consideration in using an optimal foraging approach to partial prey consumption, since predictions change both quantitatively and qualitatively with changes in predator or prey conditions (see Table 2.1).

One primary focus of a number of papers to date has been the evaluation of proximate vs. optimal foraging models. The Marginal Value Theorem (Cook and Cockrell 1978; see also Sih 1980a) was originally used to show that the Gut Limitation Model was inadequate. Cook and Cockrell (1978) showed that for a cocinellid and a notonectid, percent consumption and handling time both decreased with increasing prey density (predicted by the MVT and GLM) and that individual feeding times were independent of the previous inter-catch interval (predicted by the MVT, but not by the GLM). Giller (1980) repeated the experiment on notonectids and found that individual feeding times were not independent of the previous inter-catch interval (predicted by the GLM). Giller (1980) also found that handling time per item decreased through the foraging bout independent of prey density, suggesting that the predator may be forming a search image through some optimal feeding mechanism. Griffiths (1982) proposed the Digestion-Rate-Limitation (DRL) model to explain this decrease in handling time in notonectids and showed that the DRL Model applied to antlion larvae as well. He also showed that antlion larvae fed at low feeding rates do not change the percent consumption with changing feeding rates, as predicted by the GLM.

Table 2.1. The effect of predator and prey characteristics on predictions from partial prey consumption models. '+' = positive correlation, '-' = negative correlation, '0' = no correlation expected, 'N/A' = not applicable.

	handling time/percent consumption						
variable	GLM	DRL	MVT	A/H	A/L	A/M*	A/CP
prey density							
a) near satiation	-/-	-/-	-/-	0/0	0/0	-/-	-/-
b) no satiation	0/0	-/0	-/-	0/0	0/0	-/-	-/-
intercapture interval							
a) near satiation	+/+		0/0	N/A	0/0	+/+	0/0
b) no satiation	0/0		0/0	N/A	0/0	+/+	0/0
cost of pursuit (C_p)	0/0	0/0	+/+	+/+	0/0	0/0	
cost of search (C_s)	0/0	0/0	-/-	N/A	N/A	N/A	N/A
cost of eating (C_e)	0/0	0/0	-/-	-/-	-/-	0/0	
cost of waiting (C_w)	N/A	N/A	N/A	N/A	-/-	N/A	
pursuit time (t_p)							
a) near satiation	+/+	+/+	+/+	+/+	0/0	0/0	+/+
b) no satiation	0/0	0/0	+/+	+/+	0/0	0/0	+/+
extraction coefficient (C)							
a) near satiation	-/-	-/-	-/-	-/-	-/-	0/0	-/-
b) no satiation	0/0	0/0	-/-	-/-	-/-	0/0	-/-

* predictions for interprey intervals greater than the 'optimal' inter-prey interval only. The predictions for no correlations are due to the fact that all prey should be pursued (see text).

From the models presented in this paper, it appears that the arguments over proximate and optimal foraging mechanisms in notonectids addressed the wrong optimal foraging models, since *Notonecta* is an ambush predator (Gittelman 1974). Giller's (1980) results are predicted by both the optimal foraging model for ambush predators and the GLM. The lack of change in percent consumption for antlions (Griffiths 1982) is also predicted by the ambush optimality model. Thus, the differences between proximate models and the correct optimal foraging models are non-existent for the parameters addressed in the literature cited above. Griffiths (1982) also suggested that in many cases proximate and optimal models will generate similar predictions, though he incorrectly equated the predictions from the MVT (which was the incorrect model anyway) and the proximate models (DRL and GLM) at low prey densities. However, it seems counterproductive to compare the two sets of models in the first place, since the goals of the different approaches are dissimilar. Holling's (1966) goal in modeling proximate mechanisms of predation was to generate a realistic model that could be used in a number of theoretical studies. These studies include an analysis of functional and numerical responses, and the relative advantages of digestion rate, prey size or predator size. He also suggested that his model could be used to test whether the mode of predation exhibited by a predator maximized energy input or minimized energy output. Thus, his proximate models required a complete knowledge of predatory behavior, but could then be used to test other aspects of predation. On the other hand, optimal foraging models attempt to predict the behavior that should be expected from an organism based on our knowledge of the factors (or currencies, Pyke et al. 1977) that may be important in the life of that organism. The output of these models says nothing about the proximate mechanisms that drive these behaviors. It is implied that the evolution of proximate mechanisms should proceed in such a manner as to approximate the optimal behavior patterns. The models are used to test how well our understanding of the important factors account for the evolution of the behavior (Maynard Smith 1978), irrespective of the exact evolutionary pathway that culminated in the behavior.

All optimal foraging models rely on a set of assumptions. For example, optimal foraging models have all assumed that the extraction rate curve is constant. However, the DRL model proposes that the curve may change with feeding rate. This change does not refute the optimality approach, it simply requires a change in the assumptions about the rate curves. In fact, an increase in extraction rate with increasing prey densities undoubtedly will increase the net rate of ingestion over the entire foraging bout. Thus predators that can increase extraction rates will probably do better than predators whose rates remain constant.

In a review of optimization theory, Maynard Smith (1978) said that biologists need simple biological models that hold qualitatively in a number of cases, even if they are contradicted in detail in all cases. He implied that a qualitative fit to predictions will generally bring the researcher closer to an understanding of the problem in question. Unfortunately, generalizations can lead us to accepting models prematurely. This problem is aptly demonstrated by this review of models about partial prey consumption. In a sense, part of the question concerns the definition of detail. For example, one could argue that the expected correlation between intercapture interval (given a constant density) and handling time is irrelevant detail, in which case the difference between some of the models presented here is unimportant. However, I would argue that one of the strengths of optimization theory is that a quantitative prediction can be explicitly generated and tested. A number of factors can contribute to the lack of quantitative fit to a model. Three of the most important of these are constraints on foraging behavior (including both physiological constraints and ecological constraints), the failure to include important parameters into the optimization model and the divergence from an optimal solution using a satisficing criterion (see Simon 1956). The lack of fit to an optimization model is bound to yield a greater understanding of the system when these alternative factors are pursued. But this is a reasonable pursuit only if models specifically suited to the system are tested.

CHAPTER III
PARTIAL PREY CONSUMPTION BY ANTLION LARVAE

Introduction

In chapter 2 I addressed existing models of partial prey consumption and compared two different types, mechanistic and optimality models. The models were found to generate different predictions under different conditions. Thus, although some generalizations may be made concerning partial prey consumption, even qualitative predictions cannot be formulated without restricting them to a specific system. This chapter is a test of Griffith's (1982) "digestion rate limitation" model and the optimality models from chapter 2, using antlion larvae as predators. Antlions are particularly appropriate for testing the models since Griffith's mechanistic model was derived with antlions in mind.

I will first present the predictions and tests of Griffith's model. I then derive and test predictions of an optimality model appropriate for the antlion system. Antlions construct conical pitfall traps in sand that aid in the capture of arthropod prey. Once a prey item is captured, the antlion injects digestive enzymes into the prey and ingests the predigested material (Wheeler 1930). The exoskeleton is never eaten, and therefore the antlion never consumes the entire prey. As I show below, an antlion may also discard a prey before all of the extractable prey biomass is ingested.

Digestion Rate Limitation (DRL) Model: Predictions

Predictions

Griffiths (1982) showed that the rate at which an antlion ingests prey increases as prey-capture rate increases. This is presumably due to the fact that antlions produce digestive enzymes at a higher rate when prey capture rate increases. Handling time was shown to decrease with increasing capture rate (Griffiths 1982), which is consistent with this model. Griffiths also suggested that the proportion of each prey extracted should not change if prey are not simultaneously encountered. He predicts that at relatively low feeding rates, antlions should simply extract all they can from their prey irrespective of encounter rate. The prediction, which originated from the work of Holling (1966), is that partial prey consumption is caused by the filling of the gut. At low prey densities, the gut of the antlion will never be full (if the prey is small enough, as will be true in this experiment). Thus partial prey consumption should be independent of prey density at low feeding rates.

Methods

To see whether antlions followed the two simple predictions generated by Griffith's model, we fed fruit flies (*Drosophila melanogaster*, vestigial winged) to antlions (third instar *Myrmeleon mobilis*; identified according to Lucas and Stange 1981) at four different feeding rates. Antlions were kept in the lab at 24°C for at least seven days prior to feeding and fed one fruit fly per day during this acclimation period. The larvae were then fed one pre-weighed (to +/- 0.00001 gm) fly per day (FS-1) for 3 to 5 days. For each fly, total handling time was measured and the carcass was weighed immediately after it was discarded by the antlion. The difference between the initial weight and final weight was calculated as the extracted wet weight. Percent wet weight extracted (predicted to be constant) was calculated by dividing the extracted wet weight by the intial wet weight. Antlions were then divided into one of three groups corresponding to the remaining three feeding categories: FS-8 (1 fly per 3 hr), FS-24 (1 fly per hr), or FS-48 (1 fly per 0.5 hr). For FS-8, antlions were fed from 4 to 7 fruit flies in a row; for FS-24 they were fed from 6 to 17, and for FS-48 they were fed from 5 to 12 in a row. Each run (FS-1 then FS-8, FS-24, or FS-48) was made with a different antlion. A pilot study suggested that antlions take, on average, less than 30 min to handle a fruit fly. Thus, the maximal feeding rate (FS-48) was set at a rate just low enough to ensure that an antlion never encountered a fly before it had finished the fly it was handling. Thus, by definition (see Chapter 2), the antlion was feeding under low density conditions.

Multiple linear regression (GLM procedure in Barr et al. 1979) was used to test the predictions of the DRL-model. Since handling time decreases with increasing encounter rate (Griffiths 1982), this should result in a negative regression coefficient on handling time when regressed against feeding rate. This was tested to determine whether our species forages in the same manner as Macroleon quiquemaculatus, the species studied by Griffiths (1982). We were unable to control for variance in two factors: initial fly weight and individual variation among antlions. The antlion effect is also compounded by the unequal number of flies given to each antlion. In an attempt to account for variance associated with initial fly weight and inter-individual effects, these two factors were added to the regression model. Thus the regression model used to test the hypotheses was

$$T_h = b_o + b_1 FS + b_2 I + b_3 AN + e ,$$

where T_h = handling time,

FS= feeding schedule,

I = initial fly weight,

AN = antlion "name",

e = error term,

b_o-b_3 = regression coefficients.

This model allowed us to test for the effects of feeding schedule on handling time, independent of the initial fly weight and antlion differences. This same model was used to test for the effects of FS on percent of each fly consumed (predicted to be constant) and total extraction rate (predicted to increase with increasing feeding rate). Percent consumption was transformed using the arcsin square root transform (Sokal and Rohlf 1969). Antlion name was treated as a class variable (see Barr et al. 1979), because it was nominal scale data.

Antlion weight was substituted for antlion number in the above regression equation to determine if larger antlions could handle flies more efficiently. This information was used to build the models listed below under Optimality Model.

Results

As predicted, handling time decreased with an increase in feeding rate (Table 3.1). Contrary to predictions, the percent of each fly consumed dropped significantly with an increase in feeding rate (Table 3.1). Thus, antlions discard prey before they are totally empty even under low density conditions. As prey capture rate increases, the antlion extracts less from the fly, even though it never encounters two at the same time. Thus, the predictions of Griffith's model are not supported. Antlions appear to be regulating prey handling behavior at a finer level than that predicted by the mechanistic models listed in Chapter II. Below I test an optimality model that I derived to test whether antlion feeding behavior was consistent with the prediction that they were maximizing net energy during handling time. The optimality model should not be treated as an alternative to a mechanistic model, since they address different aspects of the same behavior. They appear as alternatives here because they have (unfortunately) been treated as such in the literature.

Deterministic Optimality Model

In chapter 2, I derived an optimality model of partial prey consumption under low prey density conditions. The model predicted that

Table 3.1. Linear Regression statistics for handling time and extraction of biomass from fruit flies. Table A includes antlion name as an independent variable. In Table B, antlion weight was substituted for name (see text). Each number is the probability that the regression coefficient associated with the independent variable is zero. The sign on the probability is the sign of the regression coefficient. AS % ext = arcsin square root transform of percent wet weight extracted from fruit fly. FS = feeding rate, initwt = initial fruit fly weight, lionnm = antlion 'name', lionwt = antlion wet weight, extrate = extraction rate.

A)

dependent variable	FS	initwt	lionnm*	r^2	model df	total df	F	P>F for model
	INDEPENDENT VARIABLES							
AS % ext	-.0051	+.0254	.0001	0.26	79	552	2.1	.0001
T_h	-.0001	+.0001	.0001	0.74	79	552	17.2	.0001
extrate	+.0001	+.0001	.0001	0.64	79	552	10.7	.0001

* Class variable, no slope estimatable

B)

dependant variable	FS	initwt	lionwt	r^2	model df	total df	F	P>F for model
	INDEPENDENT VARIABLES							
AS % ext	-.0234	+.0020	-.2898	.03	3	552	6.0	.0006
T_h	-.0001	+.0001	-.0015	.46	3	552	156.3	.0001
extrate	+.0001	+.0001	+.0020	.30	3	552	80.1	.0001

percent consumption should not vary with prey density. However, the model assumed that the extraction rate curve (ie. extraction rate as a function of handling time) remained constant with changes in prey capture rate; this assumption is clearly violated here. Thus, predictions concerning optimal prey utilization can only be generated after the prey extraction rate curves are constructed.

All optimality models are couched in terms of a currency or currencies (Pyke et al. 1977). Energy is by far the most common currency, although others have been used (see Pulliam 1975; Rapport 1980; Greenstone 1979; Belovsky 1981; Westoby 1978; Owen-Smith and Novellie 1982). I use energy as a currency here for two reasons: (1) It is the most likely currency with which to estimate foraging costs to the predator. Of course, if there is no cost to the animal in terms of any currency, the forager should simply eat the whole prey or extract as much biomass as it is capable of extracting. (2) At eclosion, antlion adults weigh 50 percent of their pre-pupal weight (Lucas, unpubl. data). Thus the weight of the larva at pupation will determine the weight of the adult. If adult weight correlates with fitness in antlions (as it does in many other insects, see Schoener 1971), an increase in the net rate of energy intake as a larvae should increase the fitness of the adult.

There are a number of variables that must be incorporated into a model used to predict optimal prey utilization. These include: (1) an extraction rate curve (here expressed as wet weight per min handling time), (2) the conversion of extracted weight to calories, and (3) an expression of the energetic cost of foraging. The extraction rate curve must predict the biomass extracted at any given time during the handling of a prey. From these three variables, the net energy intake (gross energy minus the cost of extraction) can be calculated as a function of handling time. From this function, the handling time that maximizes net energy can be calculated. This optimal handling time can be compared to the observed handling time to determine whether the criteria on which the model is based, are good predictors of the foraging behavior. Thus, the three variables above are descriptive models of foraging. These models are then combined into a predictive model of optimal behavior.

Methods

(1) Extraction rate curves

Wet weight extraction curves were constructed for each feeding schedule. Antlions were fed flies that were then taken from the antlion after 2, 5, 10 or 15 minutes. These data were combined with extraction data for uninterrupted feeding times (Figs. 3.1-3.4) to generate the extraction rate curves.

From Table 3.1 we know that antlion weight and initial fly weight affect the extraction rate. Initial fly weight additionally will influence the percent of each fly consumed. The construction of the extraction rate model was based on these relationships. I fit the data to three types of curves: (1) a Michaelis-Menten function, (2) an exponential function, and (3) the power function listed below. The third model proved to be the best predictor of the data, and was therefore chosen as the extraction rate curve for the optimality model:

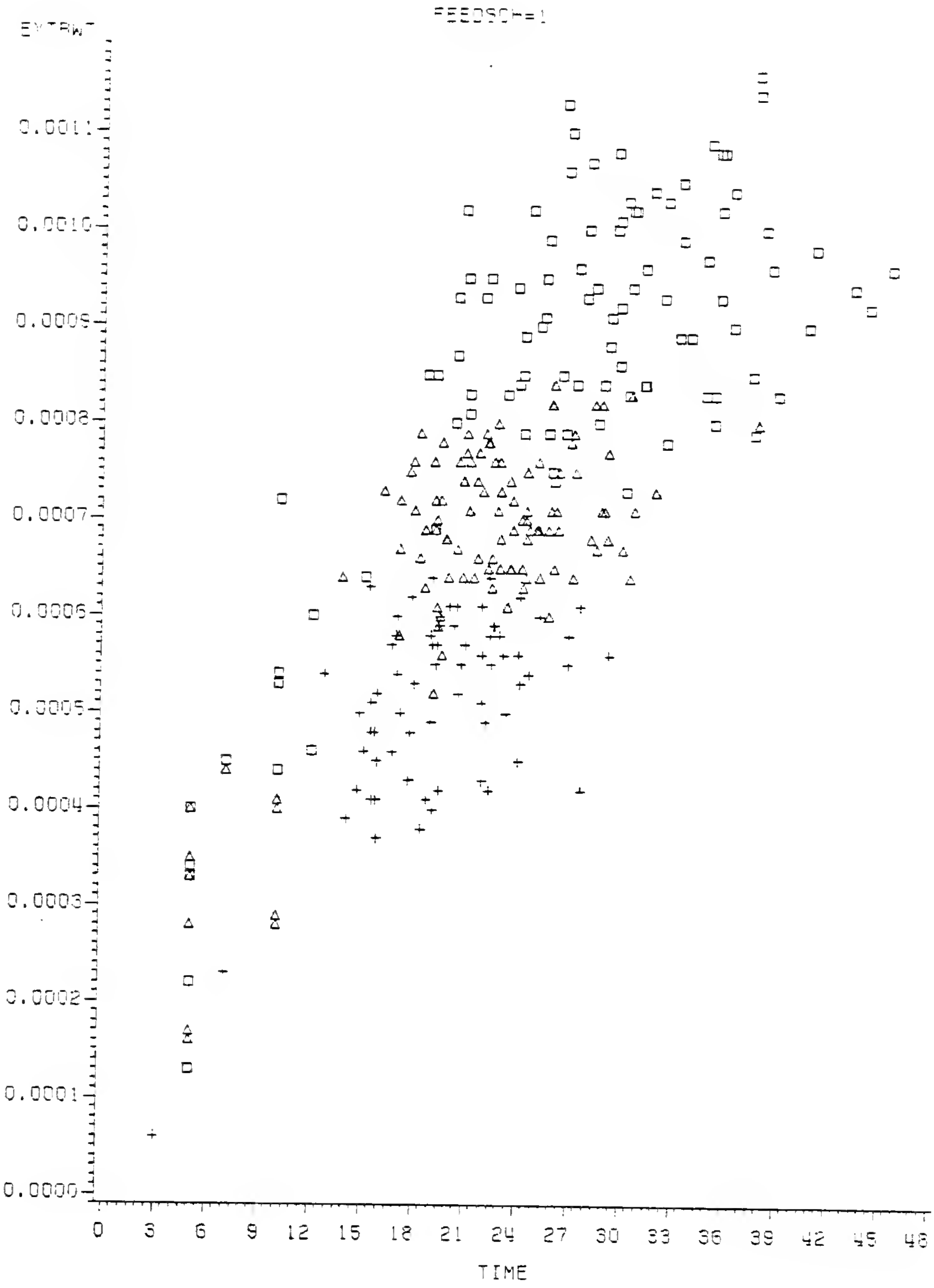


Figure 3.1. Biomass extracted from fruit flies (extrwt) at various handling times (time) when the feeding rate was one fly per day. Extracted weight is expressed in grams wet weight, time in minutes. The symbols represent different initial fly weights: cross: initial weight < 0.0007 gm; triangle: 0.0007 gm < initial weight < 0.0009 gm; square: initial weight > 0.0009 gm.

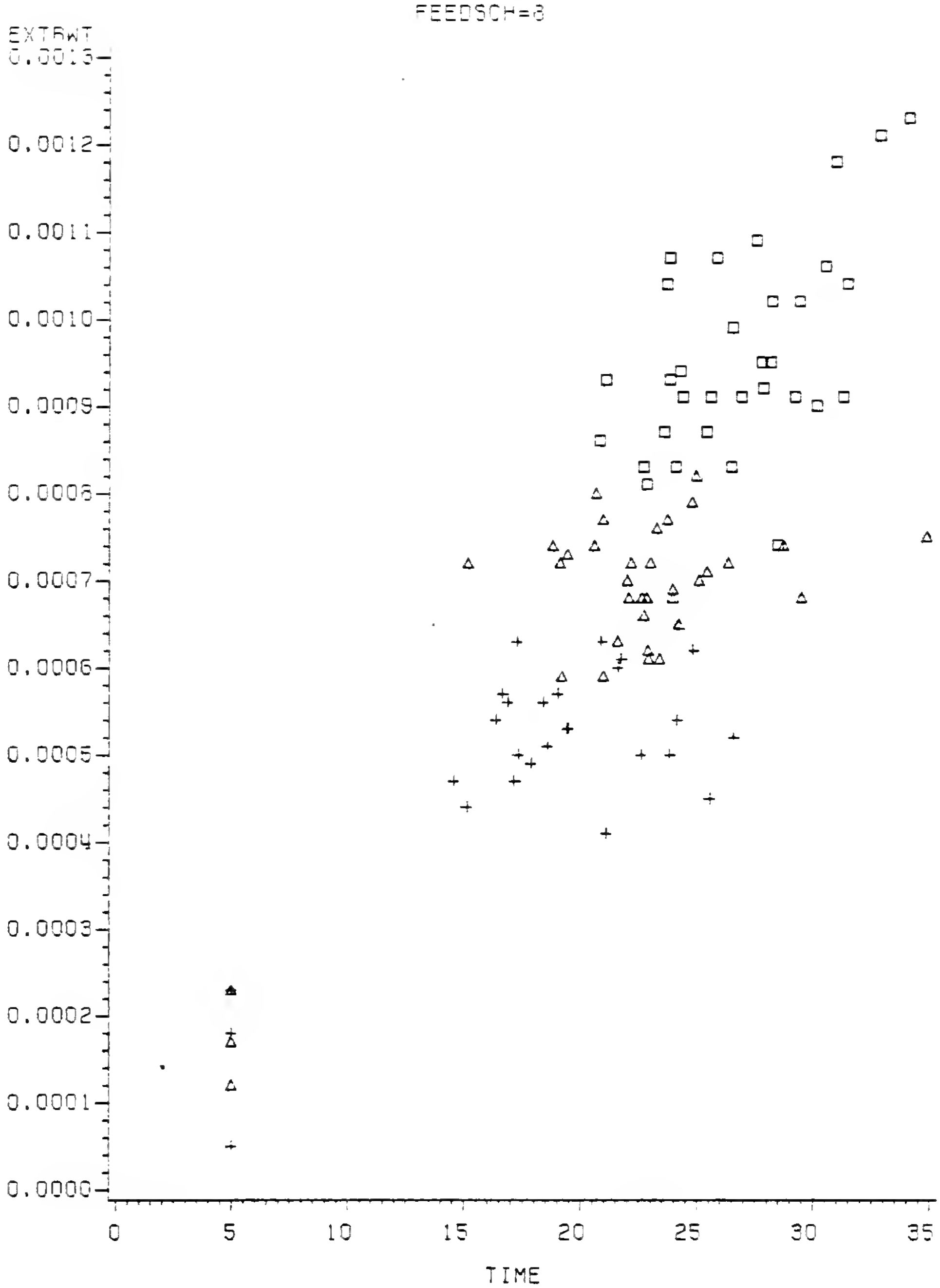


Figure 3.2. Biomass extracted from fruit flies (extrwt) at various handling times (time) when the feeding rate was eight flies per day. Symbols as in Fig. 3.1.

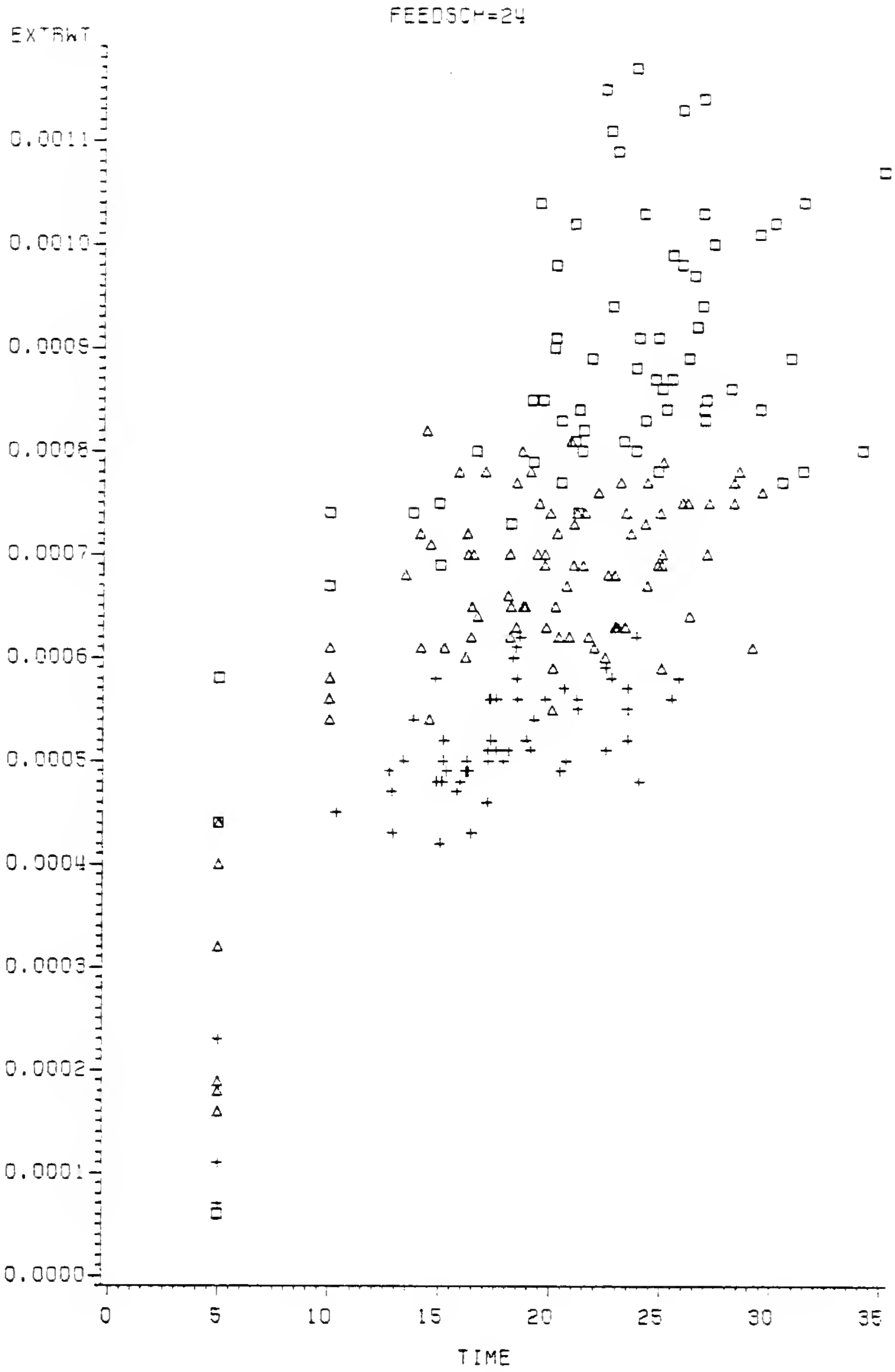


Figure 3.3. Biomass extracted from fruit flies (extrwt) at various handling times (time) when the feeding rate was 24 flies per day. Symbols as in Fig. 3.1.

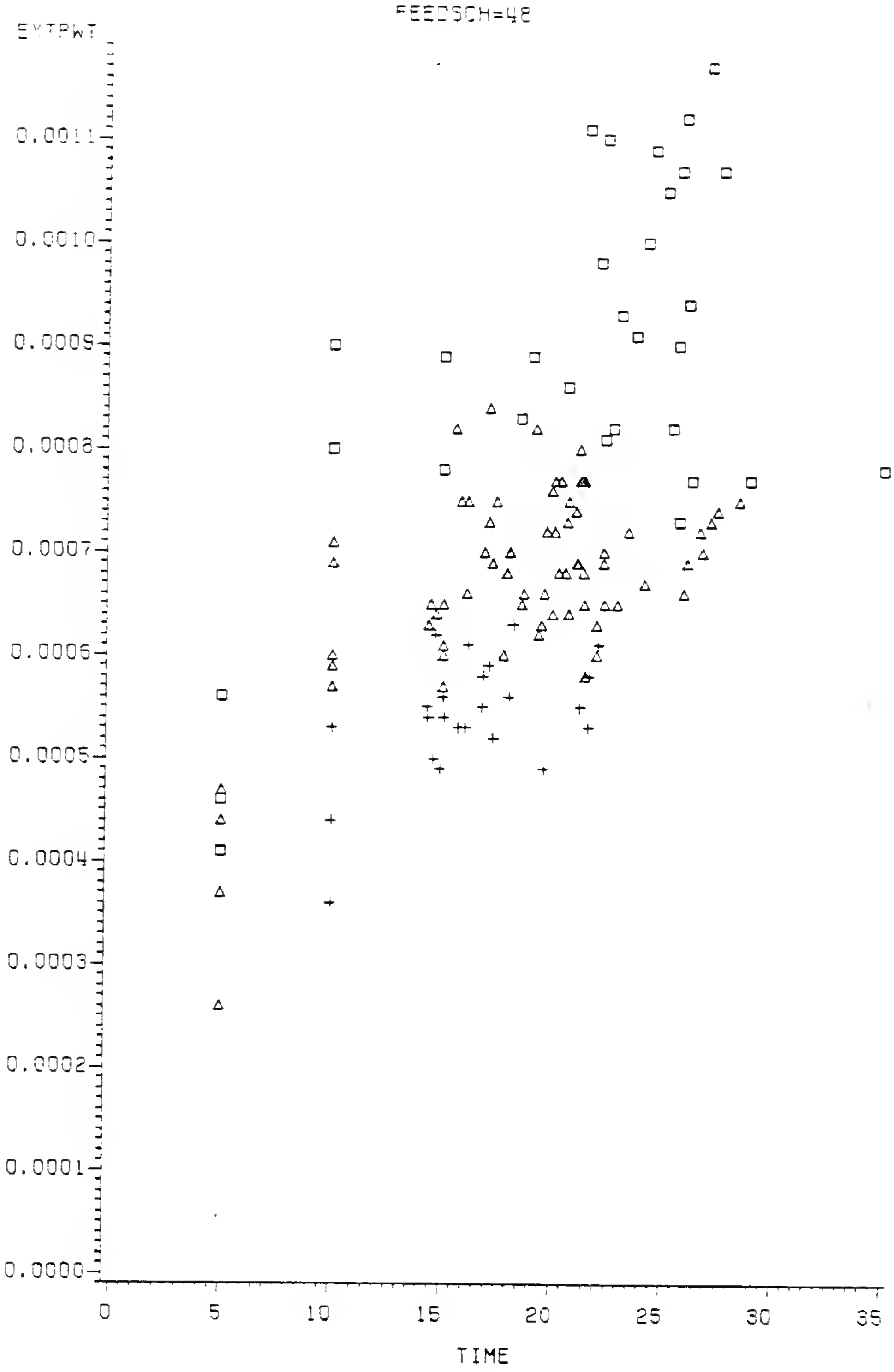


Figure 3.4. Biomass extracted from fruit flies (extrwt) at various handling times (time) when the feeding rate was 48 flies per day. Symbols as in Fig. 3.1.

$$G_g(T) = XI(k_1+k_2I^{k_3})(1-(k_4+k_5I^{k_6}+k_7W^{k_8})^{-c(T-L)}) , \qquad (1)$$

where $G_g(T)$ = the gross gain, in terms of wet weight, extracted from the fly after time T,

T = time starting from introduction of fly and ending at the release of the fly,

I = fly initial wet weight,

W = antlion wet weight,

L = lag time from time of introduction of fly to time when the antlion first begins to extract biomass from the fly,

c, k_1-k_8 = constants,

X = conversion from wet weight to calories, see below.

The coefficients were estimated using a non-linear least squares method (program NLIN in Barr et al. 1979).

(2) Wet weight to calorie conversion

Dry weight was measured on 25 fruit flies that had been weighed wet then dried for 5 days at 60° C. The regression equation fit to these data was used to convert wet weight to dry weight in the extraction rate curves. Dry weight was converted to calories using the following conversion for fruit flies (Cummins 1967; Jaeger and Barnard 1981):

1 gm dry weight = 5797 cal.

(3) Metabolic cost

Both eating costs and waiting costs were measured as rate of oxygen consumption using a Gilson respirometer. All measurements were made at a temperature of 24° C. The respirometer was allowed to equilibrate for one hr before readings were taken. Two cm of sterile sand was placed at the bottom of 15 ml Gilson flasks into which antlions were introduced. Waiting costs were measured after antlions constructed pits in the flasks. Readings were taken every 30 min for 2 hr for each antlion. The mean oxygen consumption rate from these data was used as the waiting cost for the antlion. Measurements were used only if the antlion did not move during the 2 hr measurement period. Eating costs were measured by placing a live fly in a small open-topped vial glued to the inside of the Gilson flask. The vial was sealed on top with a steel ball then the sand and antlion were placed in the flask. When the respirometer had equilibrated, the steel ball was lifted up with a magnet. The fly would then jump out of the vial and fall into the pit. Readings were begun after 2 min, which was enough time for the fly to be killed by the antlion. I was unable to measure pursuit+pre-ingestion costs. This cost was assumed to approximate C_e, since the level of activity was similar for the two behaviors. Errors in making this assumption will not be very major since the calculation of the optimal handling time is independent of C_p (see below). All antlions were kept in the lab for two weeks and fed two flies per day before calculating metabolic rates. Each value represented a single individual.

To calculate an analytical expression of metabolic rate for the two behaviors, the classic metabolic rate equation (cf. Hemmingsen 1960):

$$MR = aW^b ,$$

where W = weight, and

a,b = constants,

was expanded to include a covariance term between waiting and eating. By adding both terms to a single model, I am assuming that there is a linear relationship between the log transformed metabolic rates for activity (eating) and waiting. This is true of two other species of antlions (M. crudelis and M. carolinus) for which I have a large data set of metabolic rates (unpubl. data). The addition of both eating and waiting costs increased the degrees of freedom of the model, which should decrease the error in the estimates of each coefficient. The expression is given here in the linear form used to fit the regression coefficients:

$$\ln(MR) = \ln(a) + b \ln(w) + cE + dE \ln(w) , \qquad (3)$$

where E = 1 for an antlion eating and 0 if the antlion was "waiting" and

a,b,c,d = constants.

The constants were fitted using the least squares technique (program GLM in Barr et al. 1979). Metabolic rate was converted to calories by assuming an R.Q. of 0.8 (which is the most reasonable R.Q. for an insect of this type; K. Prestwich, pers. comm. 1982). Thus one ul O_2 is equivalent to 0.0048 cal (DeJours 1975).

(4) Net extraction rate curve

Net energetic gain was derived by subtracting the energetic cost of eating, pursuit + pre-ingestion, and 'waiting' (the non-foraging time spent between prey handling and pursuit times). Thus net gain, $G_n(T)$, is

$$G_n(T) = G_g(T)-C_pL-C_e(T-L)-C_w(T_T-T) \ , \qquad (2)$$

where C_p = energetic cost of pursuit + pre-ingestion behavior,
C_e = energetic cost of eating,
C_w = cost of waiting, and
T_T = total time = T + waiting time.

(5) Derivation of Optimal Handling Time

Here I derive the optimal handling time predicted from equation 2. The derivation assumes that prey arrive at fixed intervals and that the extraction rate curves can be approximated by the deterministic model given by equation 1.

The constants from equation 1 can be combined as a shorthand:

$$G_g(T) = I(k_1+k2I^{k_3})(1-(k_4+k_5I^{k_6}+k_7W^{k_8})^{-c(T-L)})$$

$$= k_a(1-k_b^{-c(T-L)}). \qquad (4)$$

Thus

$$G_n(T) = k_a(1-k_b^{-c(T-L)}) - C_d(T-L) - C_w(T_T-L) - C_pL ,$$

where $C_d = C_e - C_w$.

The optimal handling time is defined as the point where the partial rate of change of $G_n(T)/T_T$ as a function of handling time is zero (cf. Charnov 1976). Thus the optimal handling time is where

$$\frac{\partial \; G(T)/T_T}{\partial \quad (T-L)} = \frac{-k_a k_b^{-c(T-L)}(\ln(k_b))(-c)}{T_T} - \frac{C_d}{T_T} = 0 . \qquad (5)$$

Replacing the left hand side of equation 5 with zero and rearranging we get

$$\frac{C_d}{Ck_a} = k^{-c(T-L)} \ln(k_b) .$$

Rearranging and taking the natural log of both sides

$$\ln\left(\frac{C_d}{ck_a\ln(k_b)}\right) = -c(T-L)\ln(k_b).$$

From the above equation, the optimal handling time (pursuit + eating time = T_{op}) is

$$T_{op} = \frac{-\ln\left(\dfrac{C_d}{ck_a\ln(k_b)}\right)}{\ln(k_b)c} + L . \qquad (6)$$

The optimal extraction weight and optimal percent extraction can be estimated by replacing T with T_{op} in the equation for gross extraction weight, $G_g(T)$ (equation 1). Thus both the optimal (predicted) handling time and the optimal (predicted) percent prey consumption can be found using equation 1 and 6. Once the variables listed in equation 2 are measured, the foraging response of the antlion in terms of handling time and percent utilization can be compared to the predictions from the models.

Results

1) Extraction Rate Equations

The gross gain model, $G_g(T)$, produced a good fit to the data when initial fly weight and antlion weight were included as variables in the model. For all feeding schedules, over 99 percent of the variance was accounted for by the model (Table 3.2). As Griffiths (1982) had found, extraction rate generally increased with increasing feeding rate (Fig. 3.5).

There was a simple linear relationship between fly wet weight and fly dry weight. Therefore wet weight can be multiplied by a constant to convert to calories (Table 3.3). Estimates for eating and waiting costs are also listed in Table 3.3.

Figure 3.5. Predicted extraction rate curves (calories per minute). Curves predicted by equation 1 (see text). Antlion weight was 0.04 gm; fly wet weight was 0.0009 gm. Other parameters listed in text.

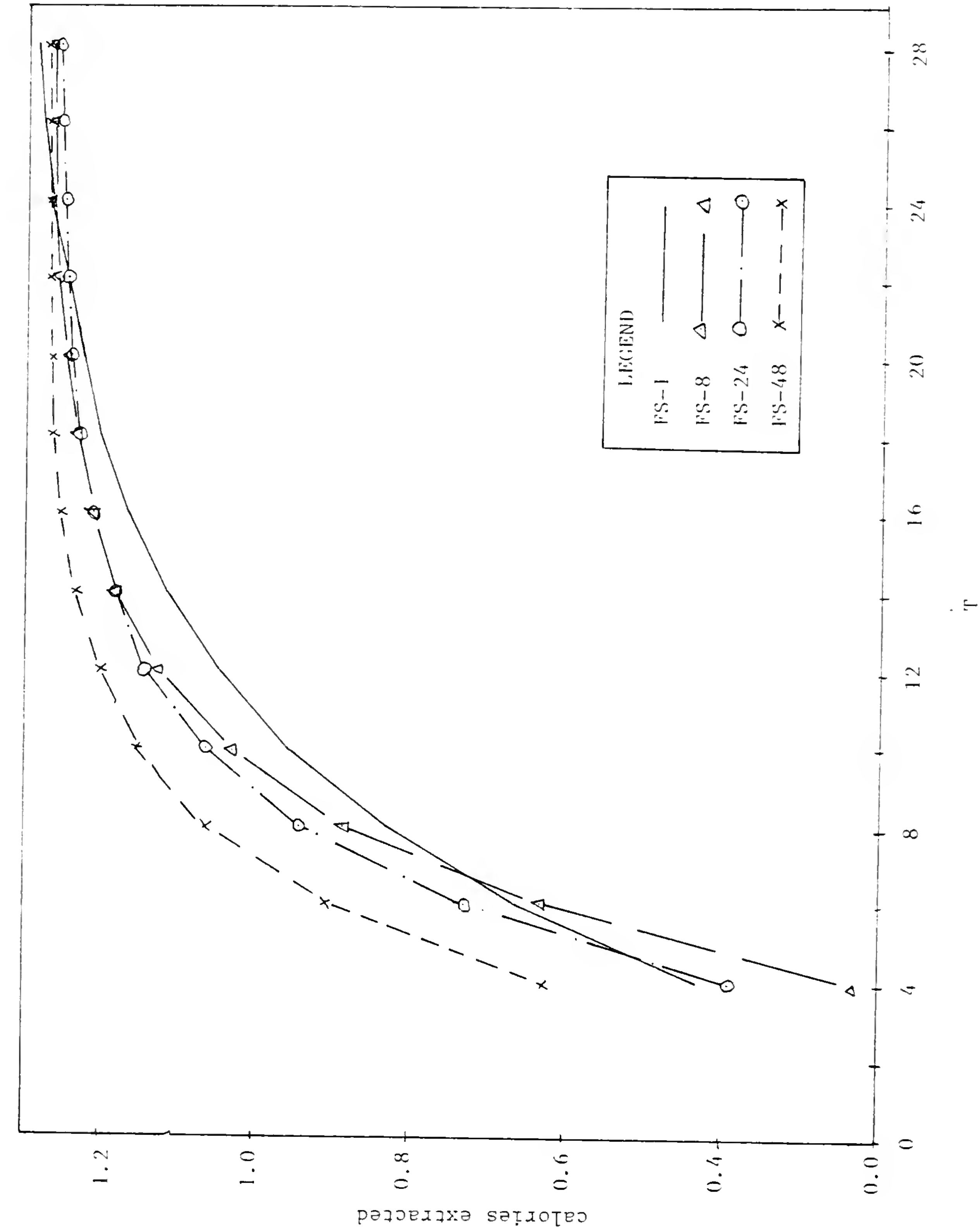

LEGEND
FS-1
FS-8
FS-24
FS-48
calories extracted
0.0
0.4
0.6
0.8
1.0
1.2
T
0
4
8
12
16
20
24
28

Table 3.2. Non-linear models fit through extraction weight data. See equation 1 in text.

FS	k_1	k_2	k_3	k_4	k_5	k_6	k_7	k_8	c	L	N	r^2
1	.9221	10^5	$6.8x10^7$	1.372	-7.961	.4981	.1095	.3303	.9601	2.454	280	.995
8	.8741	$6.37x10^{10}$	4.228	1111.5	$-6.941x10^5$	1.012	-3291.8	.7196	.0463	3.882	97	.998
24	.8662	$1.48x10^{11}$	4.379	1152.5	$-1.898x10^5$	1.034	-4516.3	.5713	.0446	3.217	174	.994
48	.8820	$9.99x10^{10}$	4.263	2250.3	$-1.207x10^6$	.9466	108.3	1.479	.0417	2.122	94	.997

Table 3.3. Fruit fly wet-weight/dry-weight regression equation and metabolic cost equations for eating and waiting behavior in antlion larvae.

Wet weight-dry weight regression

$\ln(\text{dry weight}) = -0.63 + 1.00 \ln(\text{wet weight})$

$\text{dry weight} = 0.23 \ (\text{wet weight}).$

$N=25,\ F=35,\ P<.0001,\ r^2 = 0.602.$

Metabolic Rate Equations

$\ln(MR) = 1.983 + .910 \ln(W) - .255 E - .499 (E \ln(W)).$

metabolism measured as $\mu l\ O_2/hr$

$N=28$ (16 eating, 12 waiting), $F=144,\ P<0.0001,\ r^2=.947$

Caloric Cost of Eating* (assuming R.Q.=.8)

eating $C_e = 0.0043\ W^{.411}$

waiting $C_w = 0.0077\ W^{.910}$

* cost calculated as cal/min

2) Verification of the extraction rate curves

Before using the optimality model to predict optimal handling time, I first tested to see whether the extraction rate curves would predict observed values. If the descriptive rate curves failed to reproduce the data, the predictions from the optimality model would obviously be irrelevant. I tested this by comparing predicted values from the extraction rate curves against observed values from antlions that were allowed to feed until they discarded the carcass. This was done by comparing the percent wet weight extracted by the antlion to the percent wet weight predicted by the model for the time required to handle the fly. This difference was tested statistically by arcsin-square-root transforming the percents then subtracting the transformed values. A one-sample t-test was used to test whether this difference was significantly different from zero. Data from each feeding category were divided into four fly weight categories, since percent weight extracted is influenced by fly initial weight. In 16 comparisons (4 FS x 4 weight categories), only 2 differences were significantly different at $P=0.05$ level (Table 3.4). In fact, with 16 simultaneous tests, this probability level is an over-estimation of the true alpha level. This is because, by chance, one in 20 comparisons may be expected to be significantly different using this test even if the two variables are drawn from populations that are statistically indistinguishable. Thus, the model can be treated as a fair estimator of the data.

Table 3.4. Optimal and observed values for handling time and percent prey consumption by antlion larvae. T_{op} = optimal handling time. T_h = observed handling time. OAS %ext = observed mean arcsin square root of percent extraction. PAS %ext = predicted optimal arcsin square root of percent extraction. %extop = optimal percent extraction (from PAS %ext). %extob = observed percent extraction (from OAS %ext). M-OAS%ext = difference between the observed percent extraction (transformed) and the percent extraction predicted from the model for the observed T_h. Mean fly initial weights (initwt) and antlion wet weights (lionwt) are also given. Fruit fly weight categories (WC) are as follows: 5= less than 0.0006 gm; 7=.0006-.0008 gm; 9= .0008-.0010 gm; 11= greater than .0010 gm. Std=standard deviation.

FS/WC	T_{op}	T_h	PAS%ext	OAS%ext	%extop	%extob	M-OAS%ext	N	initwt	lionwt
1/5	29.7	18.9***	1.279	1.224***	.917	.884	-.015ns	31	.00052	.0278
std	1.5	4.1	.001	.053			.072		.00005	.0094
1/7	34.4	21.9***	1.280	1.231***	.918	.889	-.010ns	93	.00070	.0303
std	1.7	3.4	.001	.052			.054		.00005	.0118
1/9	39.3	25.6***	1.281	1.233***	.918	.890	-.007ns	85	.00088	.0343
std	2.2	5.1	.0004	.064			.075		.00006	.0139
1/11	46.2	31.4***	1.281	1.251***	.918	.901	-.015*	48	.00110	.0357
std	3.2	5.8	.0002	.043			.049		.00008	.0108
8/5	23.5	18.4**	1.205	1.156ns	.872	.838	.026ns	8	.00056	.0303
std	0.3	3.5	.001	.070			.076		.00002	.0096
8/7	24.7	21.7***	1.209	1.216ns	.875	.879	-.015ns	33	.00070	.0293
std	0.6	2.7	.002	.058			.060		.00007	.0064
8/9	26.7	23.7**	1.216	1.217ns	.879	.880	-.009ns	24	.00088	.0292
std	0.7	4.3	.003	.050			.050		.00005	.0064
8/11	33.8	27.4**	1.242	1.218ns	.896	.881	.005ns	25	.00113	.0301
std	7.4	3.3	.015	.066			.052		.00010	.0066
24/5	24.1	15.3***	1.192	1.189ns	.863	.861	-.052*	12	.00055	.0350
std	1.3	2.3	.001	.064			.079		.00003	.0145
24/7	25.3	19.2***	1.195	1.168**	.865	.846	.003ns	61	.00069	.0355
std	2.0	3.4	.001	.072			.068		.00005	.0143
24/9	27.0	21.5***	1.202	1.197ns	.870	.867	-.016ns	51	.00089	.0390
std	2.7	4.5	.003	.076			.072		.00005	.0151
24/11	29.4	24.2***	1.220	1.188*	.882	.860	.012ns	30	.00111	.0389
std	5.7	4.4	.011	.085			.066		.00009	.0133

Table 3.4---Continued.

48/5	21.0	16.7ns	1.217	1.267ns	.880	.911	-.067ns	4	.00058	.0486
std	0.1	3.3	.0003	.055			.061		.00001	.0093
48/7	22.2	18.3***	1.222	1.228ns	.883	.887	-.019ns	32	.00070	.0405
std	0.6	3.0	.002	.066			.068		.00006	.0139
48/9	23.9	21.1***	1.231	1.226ns	.889	.886	-.003ns	30	.00037	.0396
std	0.6	3.8	.004	.055			.060		.00005	.0132
48/11	30.5	24.6ns	1.263	1.246ns	.908	.898	.001ns	9	.00112	.0368
std	8.5	1.6	.019	.062			.056		.00010	.0090

ns - difference not significant at P>0.05
* - difference significant at 0.05<P<0.01
** - difference significant at 0.01<P<.001
***- difference significant at P<.001.

3) Tests of the optimality model

Using equations 1 and 6, the optimal handling time, and optimal percent extracted were calculated for each fruit fly fed to the antlions. These values were then tested against the observed values for both parameters. As shown above, the percent utilization of each fly decreased significantly with increasing feeding rate. Handling time also decreased significantly. How do these changes in foraging behavior compare to the calculated optimal behavior?

With the exception of FS-1, the optimal percent extraction was generally statistically indistinguishable from the observed percent extraction. I should point out again that the true alpha level of 0.05 is at a P value less than 0.05 due to the use of simultaneous tests. Only for FS-24 weight category 7 was there a highly significant difference between predicted and observed values.

Observed values for FS-1 deviated significantly from predicted. Antlions appeared to extract less than they should have at this feeding rate. However, we should expect antlions fed at the lowest rate to extract more from their prey, not less. This underscores one drawback of using the exponential model. The model assumes that the antlion can never fully drain its prey.

If the model was modified to reach an upper limit, how would this affect the predictions? The most parsimonious threshold to set is the percent consumption exhibited by antlions fed at FS-1. Antlions fed one fly a day should be closer to this threshold than any antlion on the other feeding schedules. This is because the antlion should extract more when fed at the lowest feeding rate than when feed at higher feeding rates. Thus if there is an upper limit to the amount of extractable biomass taken from a prey, this limit should be reflected in percent utilization at the lowest feeding rate. If the percent extraction shown at FS-1 is used as the threshold value, the predictions from the other feeding rates are unchanged. Percent extraction was lower in the weight categories of the three remaining FS than it was in FS-1. The only exception was weight category 5 for FS-48, for which there are only four data points. More importantly, the predicted percent extractions were all either similar to or less than the observed data from FS-1. Thus even if there is a threshold percent utilization, which is set at the FS-1 levels, this threshold will not affect the predictions from the other feeding schedules. The reduction in percent consumption noted in Table 3.1 meets a predicted reduction assuming antlions forage so as to optimize net rate of energy intake. At the lowest feeding rate, antlions are either under-utilizing their prey, or they are simply extracting as much biomass as they can from the prey.

A comparison of optimal versus observed handling time shows a different relationship (Table 3.4). Antlions generally threw their prey away a few minutes earlier than predicted. This seems to contradict the percent consumption comparisons discussed above, since discarding a prey item early should result in a lower percent extraction from that prey. Obviously, there was enough variance in percent consumption to offset this potential reduction in optimal prey utilization. Antlions appear to discard their prey earlier than might be expected from the deterministic conditions to which they were subjected. We might expect handling time to affect the energetics of foraging in a number of ways. Handling time obviously influences the energetics of foraging on a single prey, as shown above. However, there may be other effects of handling time on foraging energetics that may select for a reduction in the time spent eating a prey.

Stochastic Optimality Model

In chapter 2, I analyzed a situation where prey show a Poisson distribution. In this case, there is always a chance that prey arrival overlaps with handling time, even at low prey densities. If the forager can return to a prey after dropping it to capture another prey (as is true of antlions), then the forager may do better, in terms of net energetic yield from the diet, if it discards its prey earlier than predicted by the low density model. This statement is true even if the mean encounter rate falls in the low prey density category (as defined in Chapter 2). This tactic is essentially bet-hedging, since the forager should discard its prey in anticipation of the arrival of the next prey. The reduction in handling time is generally adaptive only if there is a difference in the capture probability while handling a prey (P_w) compared to the capture probability while empty handed (P_o). Given this fact, it is possible that the reduction in handling time exhibited by antlions may be attributed to a bet-hedging tactic due to the stochastic distribution of inter-arrival times. Here I show that capture probability does change depending on whether or not the antlion is handling a prey. I then derive a model that incorporates a stochastic prey distribution. This model illustrates that a reduction in handling time can be attributed to the bet-hedging tactic.

Prey Capture Probability

(1) Methods

To test whether antlions are more efficient at prey capture when empty handed than when eating a prey, I fed carpenter ants (*Camponotus floridanus*) to third instar *M. mobilis*. Antlions were given either one soldier or one worker ant, and then given the same type of ant 10 min later. Time to capture or time to escape were recorded for most feedings. Insufficient dexterity on my part accounts for feedings in which no times were recorded. All ants were caught at Gold Head Branch State Park and fed to antlions less than 30 hr after capture.

(2) Results

Antlions are more efficient in prey capture if they are empty handed than when they are eating prey (Table 3.5). This is undoubtedly due to an increase in the time required to catch a prey when the antlion is eating. It may also be due to a decrease in ant escape time due to a difference in pit structure. The pits of antlions that are eating prey have less fine sand on the walls and will also have a lower slope than pits of antlions awaiting prey. Both these features affect prey escape time (Lucas 1982).

Thus, the antlion will gain on average less energy from a prey organism that arrives when the forager is eating than from a prey that arrives when the antlion is empty handed. This can be explained as follows: The benefit associated with increasing handling time is due to

Table 3.5. Predator-prey interactions between carpenter ants and antlions. C=capture; E=escape; ND=no data; sec=seconds to capture or second to escape. The second ant was given to the antlion 10 min after the first.

SOLDIER

	first ant		second ant	
pit size	C/E	sec	C/E	sec
78	C	ND	C	11.1
90	C	9.5	E	52.6
72	C	1.1	E	8.5
80	C	6.1	E	3.4
91	C	4.5	E	3.5
78	C	0.9	E	4.6
84	E	17.0	E	10.6
73	C	1.1	C	ND
84	C	2.1	E	6.1
87	C	1.8	C	30.7
65	E	4.3	C	ND
75	C	1.0	E	18.4

WORKER

	first ant		second ant	
pit size	C/E	sec	C/E	sec
70	C	ND	C	ND
67	C	ND	E	8.0
78	C	0.4	C	15.4
78	C	4.0	C	63.0
82	C	0.8	E	4.1
66	C	0.8	E	10.8
72	C	10.6	C	12.0
84	C	1.8	E	14.0
85	C	2.2	ND	
74	C	ND	ND	
67	C	0.5	ND	
65	C	0.3	ND	
77	C	0.5	ND	
81	C	1.6	ND	

	P_o	P_w	x time to capture w/o prey (N)	x time to capture w/ prey (N)	x escape time without prey (N)	x escape time with prey (N)
soldier	0.83	0.33*	3.1+/- 3.0(9)	20.9+/- 13.9(2)	10.7+/- 9.0(2)	13.5+/-16.6(8)
worker	1.00	0.50	2.1+/- 3.0(11)	30.1+/- 28.5(3)	-	9.1+/- 4.1(4)

* P_o significantly different than P_w, Binomial Test (Siegel 1956), p=0.035

an increase in biomass extracted. However, the costs of increasing handling time are twofold. There is an energetic cost of eating. There is also the cost associated with the potential loss of an encountered prey which would otherwise be available if the antlion were empty handed. This latter cost may influence antlion behavior even if the energetic costs associated with increased handling time are negligible. This is demonstrated in the model derived below.

I should point out that different prey types exhibit different efficiencies in terms of escape capabilities. This is demonstrated in the differences in capture probability between worker and soldier carpenter ants (Table 3.5). Vestigial winged fruit flies never escape. Thus, the type of prey that antlions forage on influences the relative cost of increased handling time.

Derivation of Stochastic Optimality Model

For the following derivation, I assume: (1) that prey show a Poisson distribution, (2) handling time is constant, (3) the forager always pursues prey that come within striking distance (antlions pursue all prey dropping into the pit), (4) when a prey arrives while the forager is eating, the forager drops the prey it is eating and pursues the live prey, (5) the forager returns to all prey that are dropped before it has extracted the optimal amount, and (6) the forager has enough time to extract the optimal amount from all captured prey. I also assume that the cost of returning to any stored prey is negligible. The model is set up this way because antlions will discard prey they are eating, to capture another prey. After the second prey is discarded, the antlion will return to the first prey (personal observation).

The model will be developed in several stages. The purpose of the model is to calculate the relative effect of the overall capture probability and the difference in this probability between prey-handling and empty-handedness. This will tell us how much of an effect prey capture probability should have on the optimal handling time. First, I calculate for a given prey encounter rate how many prey are captured while the forager is eating and how many are captured while it is empty handed. These values will vary with the capture probabilities while empty handed and while prey-handling. The difference between the values, when converted to energy, will be used to predict the effect of capture probability on handling time. From these equations, the energy derived from the prey and time spent pursuing and eating can be determined. The net energetic return from the diet is calculated as the difference between the energy extracted from the prey minus the energy spent during the entire foraging bout. From these equations, the optimal handling time can be derived. These stages are similar to the stages used to derive the deterministic model.

Let

N = total number of prey handled in time T_T,

N_w = number of prey eaten while handling prey,

N_o = number of prey eaten while empty handed,

T = time spent with a single prey = $t_p + t_e$,

P_w = probability of capture while eating,

P_o = probability of capture while empty handed, and

λ = encounter rate.

N_o and N_w can be estimated by calculating the time spent with each prey and the time spent empty handed (waiting). The expected number of prey arriving in these time periods is the arrival rate times the length of the time intervals. For prey arriving while the forager is eating, this yields

TN = time spent with all captured prey,

λTN = number of prey arriving while handling prey,

$N_w = P_w \lambda TN$.

The time spent empty handed will be the total foraging time (T_T) minus the time spent eating minus the time spent pursuing prey that are ultimately missed:

$(1-P_w) \lambda TN$ = number of prey missed while handling prey,

$(1-P_w) \lambda TNt_p$ = time spent pursuing missed prey,

$T_T-NT-(1-P_w) \lambda TNt_p$ = time spent empty handed.

N_o is calculated in the same way:

$\lambda (T_T-NT-(1-P_w) \lambda TNt_p)$ = number of prey arriving while empty handed,

$N_o = P_o \lambda (T_T-NT-(1-P_w) \lambda TNt_p)$.

So .

$$N = N_o T N_w = P_w \lambda TN + P_o \lambda (T_T - TN - (1-P_w) \lambda TNt_p) .$$

Solving for N

$$N = NP_w \lambda T + P_o \lambda T - NP_o \lambda T - NP_o \lambda (1-P_w) \lambda T t_p \ ,$$

$$N = \frac{P_o \lambda T_T}{1-P_w \lambda T+P_o \lambda T+P_o \lambda^2 T t_p (1-P_w)} = \frac{P_o \lambda T_T}{1+P_d \lambda T+P_o \lambda^2 T t_p (1-P_w)} \ ,$$

where

$$P_d = P_o - P_w \ .$$

The gross benefit from the diet ($B_g(T)$) is the benefit derived from each prey (see eq. 4) times the number of prey eaten:

$$B_g(T) = G_g(T) \cdot N = \frac{G_g(T) P_o \lambda T_T}{1+P_d \lambda T+P_o \lambda^2 T t_p (1-P_w)} \ .$$

Foraging costs are the energetic cost spent on each captured prey plus the cost spent in pursuit of missed prey. I will assume that the metabolic rate during eating (C_e) equals the metabolic rate during pursuit (C_p) and that both are linear functions of time:

NT = time spent on captured prey,

$C_e NT$ = energy spent on captured prey.

$M_w = (1-P_w) \lambda TN$ = number prey missed while handling,

$M_o = (1-P_o) \lambda (T_T - NT - (1-P_w) \lambda TN t_p)$ = number of prey missed while empty handed,

$T_m = t_p M_w + t_p M_o$ = time spent on missed prey,

$C_e T_m$ = energy spent on missed prey.

The net foraging benefit will be the gross benefit minus the energy spent on prey minus the energy spent waiting for prey. This waiting cost is

$T_T - T_m - TN = T_T - NT - (1-P_w) \lambda TNt_p$ = waiting time,

C_w = metabolic rate while waiting,

$C_w(T_T - T_m - NT)$ = waiting cost.

Total energy spent in foraging (E_f) is therefore

$$E_f = C_e T_m + C_e TN + C_w(T_T - T_m - TN) = (C_e - C_w)(T_m + TN) + C_w T_T .$$

The net benefit per unit foraging time ($B_n(T)$) is

$$\frac{B_n(T)}{T_T} = \frac{B_g(T) - E_f}{T_T} . \qquad (7)$$

The optimal time spent per prey item (T_{op}) is generated by taking the partial differential of equation 7 with respect to handling time (T-L) and setting this partial differential to zero. After some manipulation, the partial differential of equation 7 becomes

$$0 = k_b^{-c(T-L)}(k_aZ_1+Z_2+Z_2Z_1T) - k_aZ_1 - Z_3 ,$$

where

$$Z_1 = P_d \lambda + P_o \lambda^2 t_p(1-P_w) ,$$
$$Z_2 = ck_a \ln(k_b) ,$$
$$Z_3 = C_d(1+t_pP_d \lambda) - C_dt_p^2 \lambda^2(1-P_w)(1-P_o) .$$

Rearranging

$$0 = k_b^{-c(T-L)} - \frac{k_aZ_1 + Z_3}{k_aZ_1 + Z_2 + Z_2Z_1T} . \qquad (8)$$

The reader should instantly recognize the fact that this is a transcendental function, for which no algebraic solution for T can be found. However, T can be estimated using Newton's Method of approximation (cf. Kaplan and Lewis 1971):

$$x_{n+1} = x_n - \frac{f(x_n)}{f'(x_n)} , \qquad (9)$$

where

x_n = nth estimate of the variable (here variable is handling time),

x_{n+1} = improved estimate of variable,

$f(x_n)$ = value of function at x_n (here this is the right side of eq. 8),

$f'(x_n)$ = derivative of $f(x_n)$.

I iterated equation 9 ten times for each combination of P_o, P_w and FS. This number of iterations gave an estimate of the optimal handling time correct to within at least .001 min. The optimal handling time was derived with the coefficients used in equation 6. The encounter rate was set to the rate at which fruit flies were fed to the antlions (λ = 1/24, 1/8, 1 and 2 flies/hr).

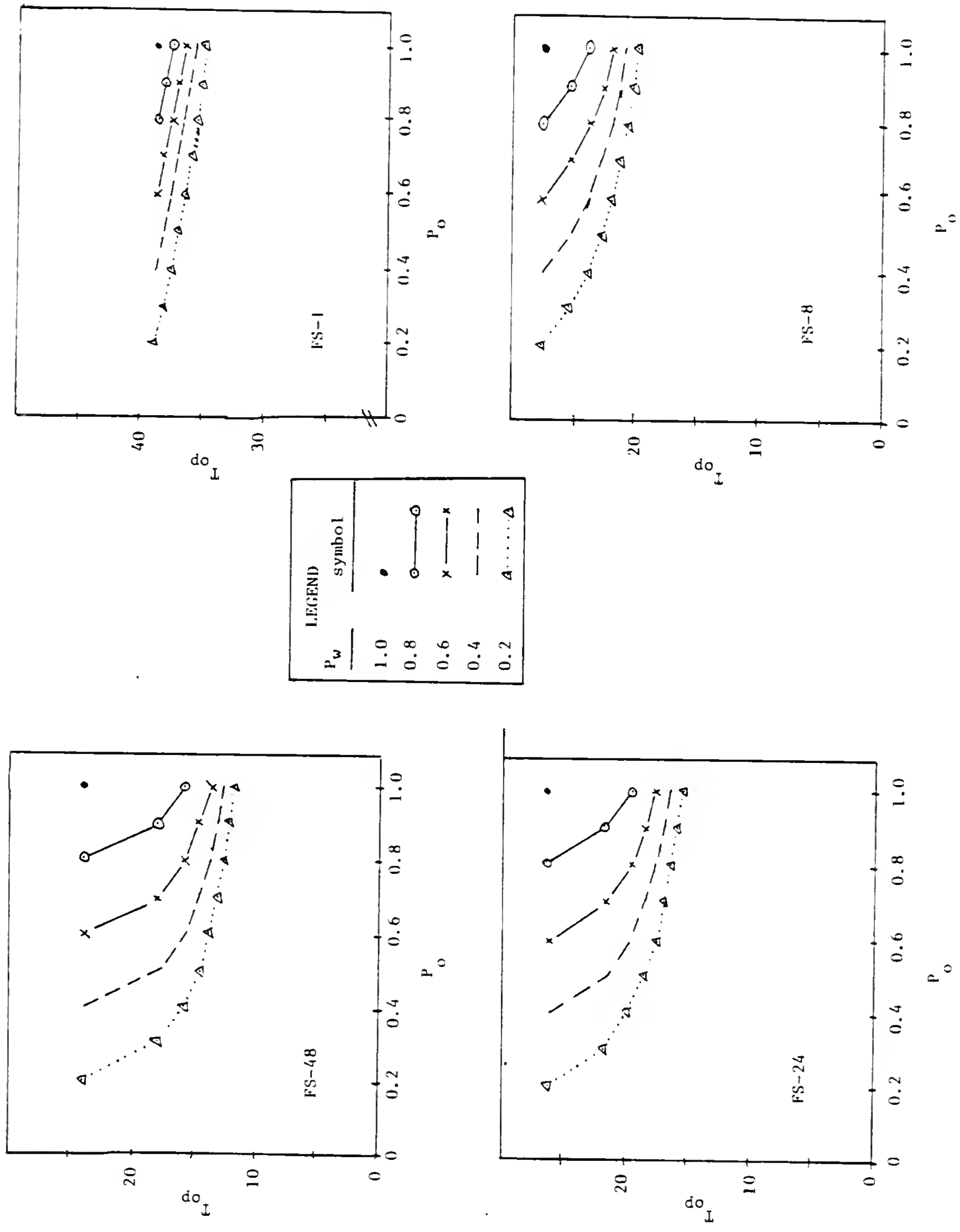
Results

As shown in chapter 2, the optimal handling time is influenced by capture probability. However, when P_o equals P_w, the optimal handling time is relatively independent of the value of the capture probability.

The model predicts that as P_o diverges from P_w, the optimal handling time should decrease (Fig. 3.6). This means that the relative cost of holding on to the prey increases as the probability of missing a prey while eating increases. This effect is highest when prey encounter rate is large.

A reduction in handling time below the level predicted by the deterministic model is predicted if antlions normally forage on prey that are able to escape occasionally. Unfortunately, I have no information on the overall probability of escape for the prey of *M. mobilis* in the wild. Based on a comparison of the mean handling time exhibited by antlions and the predicted values from equation 8, the difference in mean capture probability (P_o-P_w) should be small if the antlions are foraging optimally.

Figure 3.6. Optimal handling time for fruit flies when prey are distributed Poisson. P_o=capture probability while empty handed; P_W=capture probability while eating prey. Fly wet weight was 0.0009 gm, antlion weight was 0.04 gm, and pursuit time was 0.2 min.


FS-1
FS-8
FS-24
FS-48
T_{op}
P_o
0
10
20
30
40
0.2
0.4
0.6
0.8
1.0
LEGEND
P_w
symbol
1.0
0.8
0.6
0.4
0.2

General Discussion

Antlions exhibit two responses to changes in prey encounter rate: (1) they reduce handling time, and (2) they decrease the percent extracted from each prey. The second response contradicts the predictions of the DRL model (Griffiths 1982) and the GLM model (Holling 1965; Johnson et al. 1975; also see chapter 2). This reduction in percent extraction was predicted by an optimality model derived for antlion prey utilization. Thus, antlions appear to be making decisions that are intrinsically more complicated than the simple "eat-until-you-are-full" rule posited by Griffiths (1982) and Johnson et al. (1975). A result of these decision rules is that antlions increase the net benefit derived from their diet compared to the mechanistic rules.

The reduction in handling time with an increase in feeding rate is caused by three factors. Two of the factors are predicted by the deterministic model that describes the conditions of the experiment. These are: (1) the increase in extraction rate, and (2) a decrease in the percent extracted as encounter rate increases. However, the decrease in handling time was larger than expected based on just these two factors that were included in the model. One additional factor that may explain this discrepancy is the variance in percent extracted. There may be no energetic difference between handling the optimal amount of time (predicted by equation 6) and handling the amount of time exhibited by antlions. If this is true, then we might expect antlions to lower handling time if factors other than the energetics of eating are influenced by a change in handling time. (3) For antlions, an increase in handling time may decrease the probability of catching the next prey. This potential loss of prey should lower handling. Thus, given a range of handling times over which there is no real difference in net energy derived from eating, the antlion should choose the lowest handling time. Of course, if there is a large difference between capture probability while prey handling and when empty handed, then the antlion may discard the prey much earlier than predicted by the deterministic model (Fig. 3.6). In this case, antlions should reduce the energy derived from any single prey to increase an expected total net energy derived from all prey.

In two similar papers, Sih (1980), and Cook and Cockrell (1978) suggested that partial prey consumption could be studied by the use of optimal foraging theory. More specifically, they suggested that the marginal value theorem (Charnov 1976) could be used as a tool to help understand the specific behaviors exhibited by animals that partially consume prey. The insight in these studies was not that animals may be thought of as optimizers, since by now the idea is a relatively old one (cf. Schoener 1971), but that the techniques developed in other areas of foraging behavior may be useful in understanding partial prey consumption in particular. Unfortunately, the marginal value theorem is not as generally applicable as has been suggested, but this problem is easily, although somewhat tediously, corrected (see chapter 2). On the other hand, the mechanistic models proposed by several authors (chapter 2), failed in my study on antlions, even though the antlion system was the primary focus of one of these models (Griffiths 1982). I do not mean to imply that animals never use simple mechanisms, such as gut filling, as a cue to cease feeding. Predators such as damselfly larvae

(Johnson, et al. 1975) and Rhodnius bugs (van der Kloot 1960) probably do. However, the specific mechanisms that direct foraging behavior in animals should be evolutionarily labile, since different mechanisms will work well under certain conditions and poorly under others. For example, gut filling rules for partial prey consumption may be poorly adapted under conditions where prey density is low, but prey body size is large (Cook and Cockrell 1978). It will also be poorly adapted under conditions where prey encounter rate is relatively high, but prey body size is small. Thus, animals living under different conditions should evolve 'rules-of-thumb' that will optimize prey utilization under those conditions. In other words, we should expect the behavior of an organism to evolve such that the mechanisms underlying foraging maximize the fitness of the organism. In a sense, the mechanisms should to some degree conform to the output of the behavior, since it is the behavioral phenotype on which selection acts. Animals have been consistently shown to exhibit foraging behaviors appropriate to the conditions under which they are tested. This fact suggests that natural selection is a factor in refining the prey utilization of foragers. The technique of developing optimal foraging models to study foraging behavior has been a major contribution in our ability to address this field of study. Animals have also been consistently shown not to conform precisely to the predictions from these models. Partial preference is a perfect example (Krebs et al. 1977). Handling time in antlions is a more specific example. But the optimization technique allows us to set up testable hypotheses to study further refinements of our perception of these systems.

CHAPTER IV
THE ROLE OF FORAGING TIME CONSTRAINTS AND VARIABLE PREY ENCOUNTER IN OPTIMAL DIET CHOICE

Introduction

A variety of optimal foraging models has been proposed within the last decade (see Schoener 1971; Pyke et al. 1977). Many of these models have dealt specifically with diet choice and generate the same general predictions (Charnov 1976b; Pulliam 1974; Werner and Hall 1974): (1) prey types should be ranked according to the ratio E_i/h_i (the energy derived from a prey divided by its handling time), (2) a prey type should be added to the diet solely on the basis of the absolute frequency of encounter with higher ranking prey types, and (3) prey types should either be eaten on every occasion or not at all. However, there are conditions under which these predictions change. For example, prediction 3 may be violated if the diet choice of the forager is limited by nutrient constraints (Pulliam 1975; Rapport 1971, 1980; Westoby 1974). Prediction number 2 is violated when prey recognition time is relatively long or when handling time varies through learning (Elner and Hughes 1978; Estabrook and Dunham 1976; Hughes 1979; Krebs 1978).

The most widely used foraging model is a variation of Holling's disk equation derived by Charnov (1976b). This model has been used to study diet choice in a variety of organisms, including insects, gastropods, birds and mammals (Charnov 1976b; Dunstone and O'Connor 1979; Hughes 1979; Krebs et al. 1977; Palmer 1981). The model is based on the premise that foragers choose prey types that maximize the net rate of return of the limiting currency (or currencies) (see Pyke et al. 1977). For this discussion, I will assume that there is selection on the predator to choose a diet which maximizes the net rate of energy intake. This expected rate of intake is the total net energy gained from foraging (E) divided by the total time spent foraging (T_T):

$$\frac{E}{T_T} = \frac{\sum_i \lambda_i E_i P_i}{1 + \sum_i \lambda_i h_i P_i}, \qquad (1)$$

where E_i = energy derived from prey i,

λ_i = encounter rate of prey i during the search time,

h_i = handling time of prey i,

P_i = probability of attacking i when i is encountered.

From this model, Charnov (1976b) proved that prey i should be added to the diet in order of rank until

$$\frac{E_i}{h_i} < \frac{E_n^*}{T^*}, \qquad (2)$$

where E_n^*/T^* is the maximum net rate of energy intake. Thus, decisions concerning the addition of prey items to the diet should be based on the effect of these decisions on the energetic return from the entire diet.

There is another way of phrasing the decision rule derived from (1). Instead of asking what prey items would increase the rate of energetic return from the diet (as in eq. 2), the effect of each foraging decision can be calculated more directly (see Cost Model below). Although the two methods are mathematically similar, I will show that an emphasis on the costs associated with the foraging decision can lead to two further predictions about diet choice. The first is that the time available for foraging may affect diet choice. The second is that if some of the assumptions of equation (1) are relaxed, then several characteristics of the prey distribution may be exploitable by the forager to increase net benefit from the diet. I show that under these conditions, a forager's perception will affect the predictions generated from an optimization model.

The Cost Model

Assume that a forager feeds on two prey types, one of low quality and the other of high quality. Assume also that the forager encounters prey individually, handles them one at a time and recognizes prey instantly. When both prey types are present at high densities, there should be a high probability of missing the opportunity to capture high quality prey if the predator were to pursue and eat low quality prey. In fact, the "cost" of taking poor quality prey can be evaluated as the potential loss of high quality prey items missed while handling the poor prey. Conversely, the predator should take a poor prey item, regardless of prey density, if it could be assured that no better prey would be missed while handling this poorer prey. Any decision involves the commitment of a given period of time to a particular course of action (Brockmann, et al. 1979). In foraging, a decision is a costly one only if the forager misses a more profitable course of action otherwise available during that period of time.

I will first derive this "cost" for a one-prey situation, then expand it to include a second prey type. Let X_i be the expected harvest rate of prey i over foraging time T_T (when every prey encountered is eaten). I will assume that prey show a Poisson distribution with a mean of $\lambda_i T_T$ (where λ_i is the encounter rate of prey i over T_T). For a diet composed of one prey, the expected number of prey taken in time T_T is

$$X_i T_T = \lambda_i T_T - M_{ii} X_i T_T, \qquad (3)$$

where M_{ii} = the expected number of other prey i missed while handling the captured prey i during h_i (the total amount of time spent capturing and eating i, then resuming search).

The expected harvest rate will be the encounter rate discounted by the rate at which prey are missed while handling captured prey. This will hold for both sit-and-wait predators and active foragers as long as prey show a Poisson distribution throughout the foraging bout. Solving for X_i

$$X_i = \frac{\lambda_i}{1 + M_{ii}} . \qquad (4)$$

Since $M_{ii} = \lambda_i h_i$ for randomly distributed prey, then

$$X_iE_i = \frac{E_i\lambda_i}{1 + \lambda_i h_i} = \frac{E}{T_T}$$

for one prey type. Thus, equation 1 and equation 3 are equivalent even though they address the foraging decision in different ways.

If more prey are added to the diet, then equation 3 expands to

$$X_i = \lambda_i - X_iM_{ii} - \sum_{j \neq i} X_jM_{ij},$$

where M_{ij} = the number of prey i "missed" while feeding on prey j. If prey i is the highest quality prey, then in a two-prey system, M_{ij} is the relative "cost" of adding the low quality prey (j) to the diet, in terms of the alternative decision of specializing on prey i. More specifically, "cost" is a function of the energetic return from the poorer prey item minus the expected return from the higher quality prey that was missed while handling the low quality prey. To simplify the formula, let the handling times and encounter rates of the two prey be equivalent (so that $h_i = h_j = h$ and $\lambda_i = \lambda_j = \lambda$). Therefore $M_{ij} = M_{ji} = M$. Then for a two-prey diet, the expected energetic return from the diet is

$$\frac{E}{T_T} = X_iE_i + X_jE_j = \frac{\lambda(E_i + E_j)}{1 + 2M} .$$

Under these simple conditions, the predator should specialize (eat only prey i) if the energetic return from a single-prey diet is higher than the return from a diet of both prey types:

$$\frac{\lambda_i E_i}{1 + M_{ii}} > \frac{\lambda(E_i + E_j)}{1 + 2M},$$

or

$$M > \frac{E_j}{E_i - E_j} \quad .$$

If we assume that $M_{ij} = \lambda_i h_j$, Charnov's model can be similarly expanded to

$$M_{ij} > \frac{E_j h_j}{E_i h_j - E_j h_i} \quad . \qquad (5)$$

As before, the "cost" of eating prey j is a function of the number of high quality prey missed while handling lower quality prey (M_{ij}). Equation 5 shows that M_{ij} is a function of the relative energetic content and handling times of the two prey types. So if the forager monitors only mean encounter rates and prey are distributed randomly, then the rule on which this cost function is based generates the same three general predictions as those listed above. But under what conditions might this cost function vary? I will focus on two such conditions. (1) If the foraging bout becomes exceedingly short due to constraints on foraging time, the number of higher quality prey otherwise available to the forager while handling a poor prey will decrease (here foraging bout is defined as the amount of uninterrupted time a forager spends searching, pursuing and eating prey). The basis of this statement will be discussed below. (2) If the forager had more information about the distribution of its prey, then it may be able to judge variance in M_{ij}. In this case, partial prey preference is predicted.

(1) Foraging Time Constraints

Total foraging time for a variety of foragers is often broken into relatively short bouts. For example, a bird in an area of high predation risk may often stop foraging to scan for predators (Caraco 1979; Powell 1974). Other foragers, such as some aquatic insects, may often interrupt foraging to flee from predators (Sih 1980b). Also, the foraging of intertidal animals, such as predatory gastropods, will be disrupted by tides (Menge 1974). If these foraging bouts are confined to an interval of time t, the optimal diet may be affected by the magnitude of bout length (contrary to the predictions from equations 1 and 5), as demonstrated below. I am assuming here that the factor(s) that constrains t is extrinsic to decisions about diet choice.

For the following model, I assume that the forager captures only one prey per bout. This may occur either because t is sufficiently short to allow the forager to capture and eat only one prey, or because the forager captures only one prey regardless of the length of t. For example, house wrens and many other birds foraging to feed nestlings might capture only one prey per foraging bout before returning to the nest (Bent, 1964). Here the "cost" associated with foraging on lower ranking prey is not the number of prey missed while handling these prey (as in equation 5), but rather a function of the probability of missing any higher ranking prey within the time left for foraging in the bout, given that a lower ranking prey has been taken.

The length of t can affect foraging in two different ways. If the foraging time available per bout must include handling time, then the time available for searching will include only the interval $[0,t^*]$, where t^* is the end of the foraging bout (t) minus the handling time for prey i (h_i). No prey item should be caught in the interval $[t^*,t]$ since the predator would not have enough time to handle it. Alternatively, if the predator can extend handling time past t, such that it can attend to other requirements while handling the prey, then the time available for searching includes the entire interval $[0,t]$. However, no prey are available after t and the cost of foraging, in terms of handling time, will terminate at t. In either case, the time available for foraging may affect diet choice.

For a two prey system, let g be a higher (good) quality prey and let b be a lower (bad) quality prey. Also let $P(Z_g<t^*)$ be the probability that a g arrives before the end of the searching period t^*. Here Z_g is the first arrival time of a good prey. The expected energy (E(g)) that the forager gains in N number of bouts while foraging only on g is the total number of bouts that yield a prey $(P(Z_g<t^*) \cdot N)$ times the energy derived from one individual prey g (E_g), or

$$E(g) = P(Z_g<t^*) \cdot N \cdot E_g \, .$$

If handling cannot extend beyond t, the total time (T_T) spent foraging is

$$T_T = (t^* + h_g) \cdot N = t \cdot N \ .$$

Thus,

$$\frac{E(g)}{T_T} = \frac{P(Z_g<t^*) \cdot N \cdot E_g}{(t^* + h_g) \cdot N} = \frac{P(Z_g<t^*) \cdot E_g}{t^* + h_g} \ .$$

If prey show a Poisson distribution, then

$$P(Z_g<t^*) = \int_0^{t^*} \lambda_g e^{-\lambda_g z} \, dz \ ,$$

or

$$P(Z_g<t^*) = 1 - e^{-\lambda_g t^*} \ .$$

If a second prey is added to the diet, then the probability of encountering prey g first must be discounted by the probability of first encountering a lower ranking prey (b) within the time available for foraging. This is represented as $P(Y_b<Z_g<t^*)$. Here Y_b is the first arrival time of a bad prey. This probability will be the "cost" of foraging on prey b. Thus, the probability of eating prey g $(P(Z_g))$ in a two-prey diet is

$$P(Z_g) = P(Z_g<t^*) - P(Y_b<Z_g<t^*) \ .$$

The "cost" of foraging on prey b is

$$P(Y_b<Z_g<t^*) = \int_0^{t^*}\int_0^{y} \lambda_g e^{-\lambda_g z} \lambda_b e^{-\lambda_b y}\, dz\,dy$$

$$= (1 - e^{-\lambda_g t^*}) - \left(\frac{\lambda_g}{\lambda_g + \lambda_b}\left(1 - e^{-t^*(\lambda_b+\lambda_g)}\right)\right) .$$

The first part of this expression is the probability that a g will arrive in t^* ($P(Z_g<t^*)$). The second part is the probability that a g arrives first given that an arrival of any prey type has taken place. The difference is the probability of missing g as a result of capturing b. As t^* increases, this probability increases. Thus, as the length of the foraging bout increases, there is an increase in the probability that the forager will miss a high ranking prey if it takes a low ranking prey.

The probability of eating a high ranking prey ($P(Z_g)$) in a two-prey system can now be expressed in terms of t^*:

$$P(Z_g) = \frac{\lambda_g}{\lambda_g + \lambda_b}\left(1 - e^{-t^*(\lambda_g+\lambda_b)}\right) .$$

If t^* is the amount of time available for foraging on b, then the probability of eating b in a two-prey system can be derived similarly:

$$P(Y_b) = \frac{\lambda_b}{\lambda_g + \lambda_b}\left(1 - e^{-t^*(\lambda_g+\lambda_b)}\right) ,$$

so a diet of two prey types would yield

$$\frac{E(g,b)}{T_T} = \frac{P(Z_g) \cdot E_g}{t} + \frac{P(Y_b) \cdot E_b}{t} .$$

The predator should specialize if the net energy derived from eating only g is higher than the energy derived from eating both g and b:

$$E_g \cdot P(Z_g<t^*) > E_g \cdot P(Z_g) + E_b \cdot P(Y_b) \quad .$$

This is also true if handling time can extend beyond t, in which case t is substituted for t^* since the time available for searching is t. Rearranging the above inequality

$$E_g \cdot (P(Z_g<t^*) - P(Z_g)) > E_b \cdot P(Y_b) \quad ,$$

where $P(Z_g<t^*)-P(Z_g)=P(Y_b<Z_g<t^*)$ is the probability of missing a high ranking prey given that a low ranking prey has been caught. This is analogous to M_{ij} from equation 5. So the predator should specialize when

$$P(Y_b<Z_g<t^*) > \frac{E_b \cdot P(Y_b)}{E_g} \quad . \qquad (6)$$

Equation 6 generates two predictions that are different than those of equation 5. (1) Diet choice depends on the amount of time available for foraging (t^*). As available foraging time decreases, diet breadth should increase, because the "cost" of catching low-ranking prey (i.e. the number of high-quality prey missed) decreases as t^* decreases, independent of the encounter rate of either prey type. The "cost" is (in part) weighed against $P(Y_b)$, which also decreases with decreasing t^*. However, $P(Y_b<Z_g<t^*)$ decreases more rapidly than $P(Y_b)$ with changes in t^*. This can be illustrated by analyzing the ratio $P(Y_b<Z_g<t^*)/P(Y_b)$ as a function of t^*. Since the ratio decreases with decreasing t^* (Fig. 4.1), diet breadth should expand as t^* decreases. (2) In this model, diet choice depends on the encounter rates of both low- and high-quality prey (λ_b and λ_g, respectively). In other words, the addition of prey to the diet is affected not only by the encounter rate of higher ranking prey, but of all prey. As the density of low-ranking prey increases, the diet should shift from generalist to specialist. This may seem somewhat counter-intuitive, since the total number of prey available to the predator increases with an increase in the density of low ranking prey. However, the probability of missing a high ranking prey also increases with an increase in the density of low ranking prey. A numerical example illustrates the fact that the "cost" of eating low ranking prey increases more quickly than the benefit associated with eating more low ranking prey (Fig. 4.2). However, changes in λ_g will have a larger effect on diet choice than changes in λ_b (Fig. 4.2).

I have implied here that the beginning of the foraging bout is set. The analysis has addressed changes in the time to the end of the bout. The same predictions hold if the end of the bout is fixed and the forager continually updates the criterion expressed in equation 6 based on the amount of time remaining in the bout. However, bout length in this case would be the interval $[t_o,t^*]$ where t_o is present time. The diet breadth should increase as the length of the interval $[t_o,t^*]$ approaches zero.

Figure 4.1. The effect of time available for searching on the ratio of the probability of missing a high ranking prey ($P(Y_b < Z_g < t^*)$ divided by the probability of encountering a low ranking prey ($P(Y_b)$).

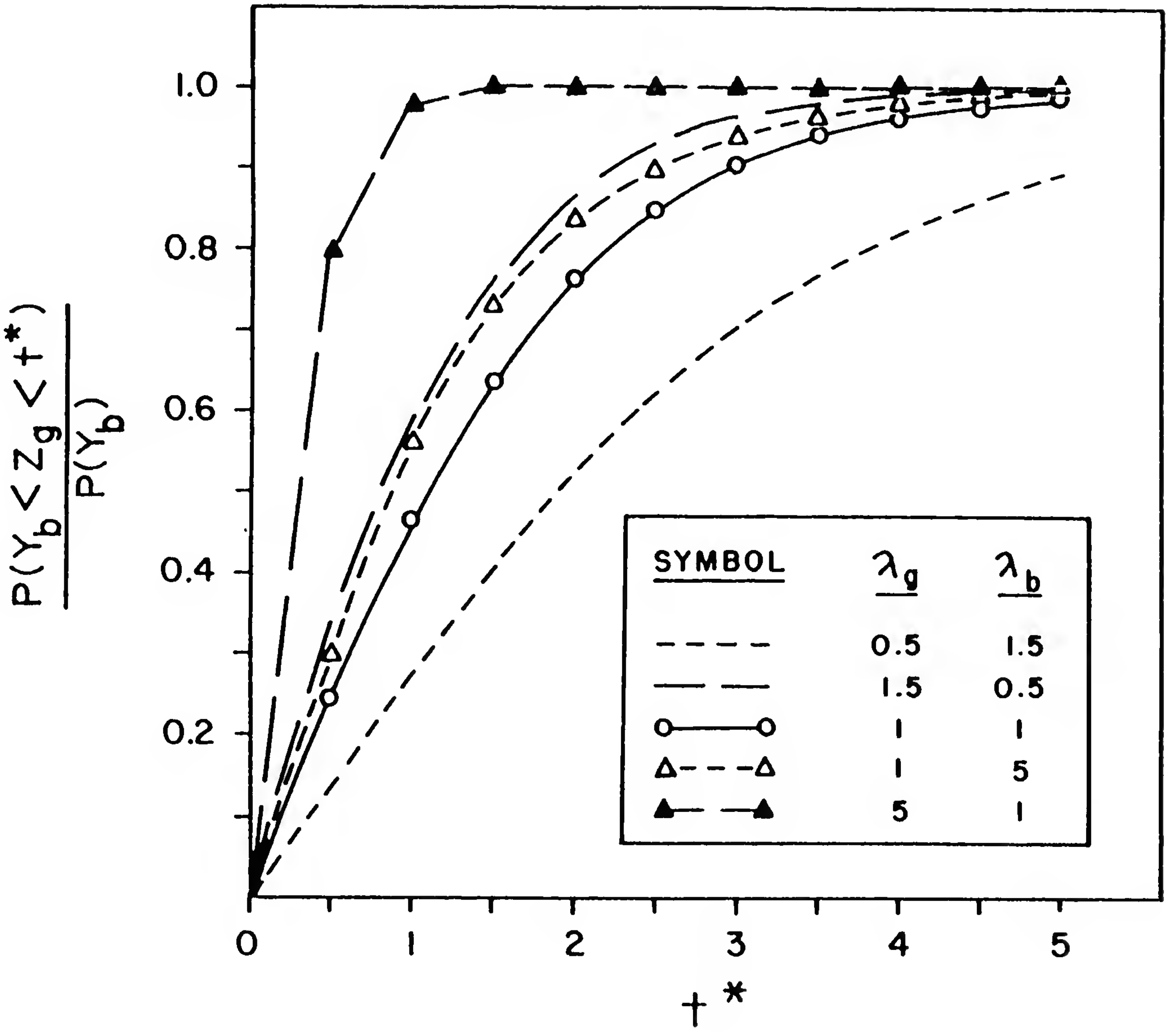
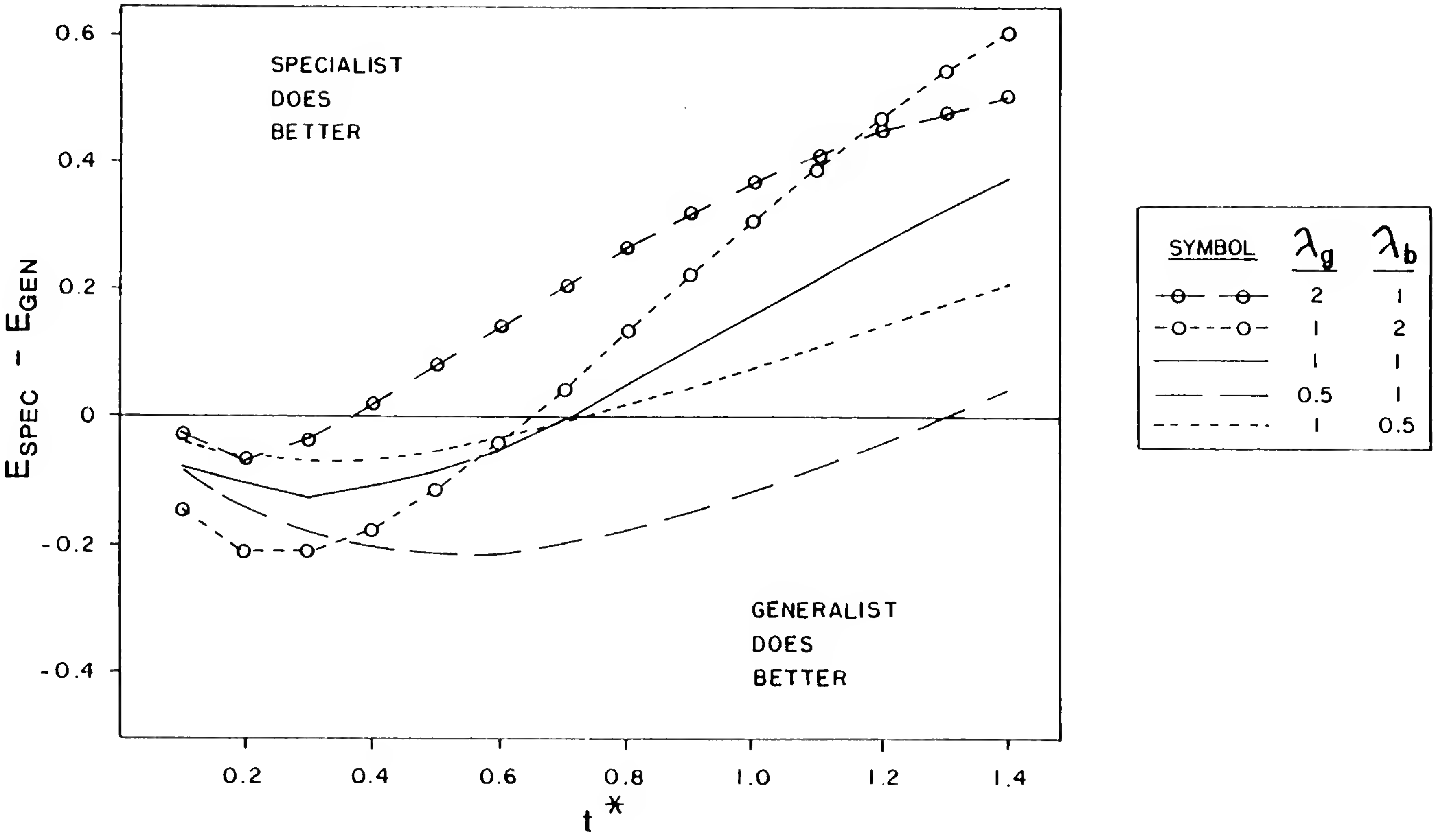

$\frac{P(Y_b < Z_g < t^*)}{P(Y_b)}$
1.0
0.8
0.6
0.4
0.2
0
1
2
3
4
5
t^*
SYMBOL
λ_g
λ_b
0.5 1.5
1.5 0.5
1 1
1 5
5 1

Figure 4.2. Differences between specialist and generalist diets when the forager eats only one prey per foraging bout. E_{spec}=energy from specialist diet; E_{gen}=energy from generalist diet; $E_g=3$; $E_b=1$; $h_g=h_b=1$; λ_g and λ_b are encounter rates for high and low quality prey (respectively); t^*=time available for searching=(foraging bout length)-(handling time). For further definitions of terms see text.

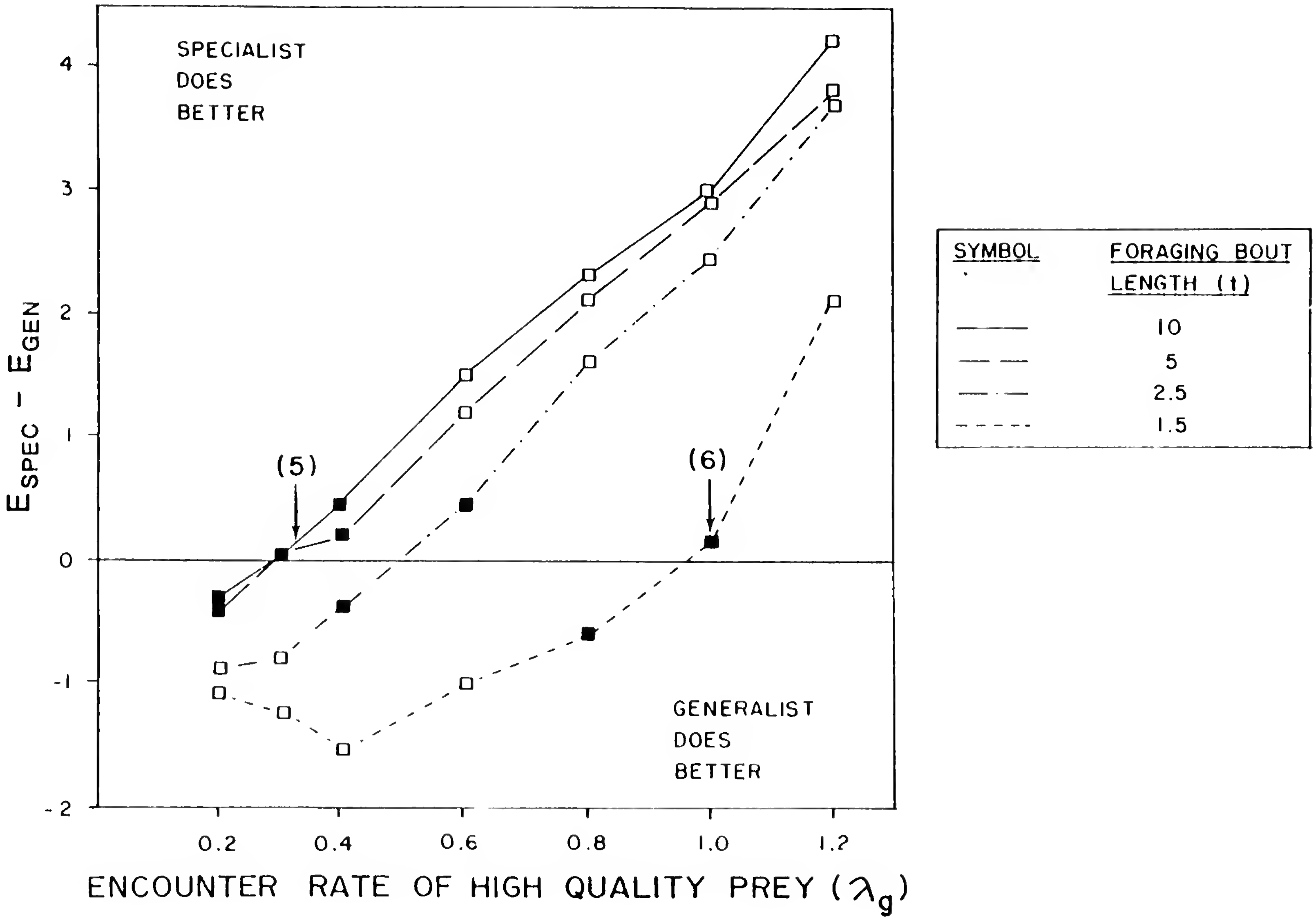

SPECIALIST
DOES
BETTER
GENERALIST
DOES
BETTER
$E_{SPEC} - E_{GEN}$
0.6
0.4
0.2
0
-0.2
-0.4
0.2
0.4
0.6
0.8
1.0
1.2
1.4
t^*
SYMBOL
λ_g
λ_b
2 1
1 2
1 1
0.5 1
1 0.5

Equation 6 explicitly models foragers that eat one prey during the foraging period. However, even if the forager eats a number of prey during a foraging bout and if the length of the bout is set at some time t, then there will be a point at which the time remaining in a foraging bout allows the forager to eat only one prey. Thus, the bout consists of (1) a period in which a multi-prey per bout model expresses the net energetic return from foraging, and (2) an additional period when a single-prey per bout model predicts diet choice. Since the models generate different quantitative predictions, the net rate of energy intake from any one diet will reflect some combination of the two models if the foraging time is long enough for the predator to take more than one prey. If the number of prey types included in the diet does not change within the foraging bout, we can predict that the diet should become broader as t^* becomes smaller. This can be demonstrated by simulating the effect of t^* on the difference between a specialist and generalist diet (Fig. 4.3). If the length of t^* is known by the forager, then we might expect it to exhibit two different choice patterns under the two different conditions of equations 5 and 6.

(2) Prey Distributions

Most foraging models presented to date (Charnov 1976b; Pulliam 1974; Werner and Hall 1974) assume that prey are distributed randomly and are encountered one at a time. More importantly, these models implicitly assume that the forager cannot monitor variance in the number of prey i missed while handling prey j (M_{ij}). In this section, I demonstrate that if these two assumptions are relaxed, and if as a result, a forager could monitor this variance, then we should expect

Figure 4.3. Simulated differences in energetic return between a specialist (E_{spec}) and generalist (E_{gen}) diet for different foraging bout lengths (t). Each point is the mean of 150 trials. Open squares represent differences ($E_{spec}-E_{gen}$) significantly different from 0 at $p=0.05$ (t-test). Closed squares represent differences that are not significantly different from 0. Each trial represented the total energetic return from 10 time units (except for $t=1.5$ in which trials were 9 time units long). The forager could not handle prey past t. Encounters were random with means of $\lambda_g = \lambda_b$. $h_g=h_b=1$; $E_g=4$; $E_b=1$. For definitions of terms see text. The arrow marked (5) shows the λ_g where diet should switch as predicted by equation (5). The arrow marked (6) is predicted by equation (6) for $t^*=0.5$.


SPECIALIST
DOES
BETTER
GENERALIST
DOES
BETTER
(5)
(6)
$E_{SPEC} - E_{GEN}$
4
3
2
1
0
-1
-2
0.2
0.4
0.6
0.8
1.0
1.2
ENCOUNTER RATE OF HIGH QUALITY PREY (λ_g)
SYMBOL
FORAGING BOUT LENGTH (t)
10
5
2.5
1.5

some degree of partial preference to be exhibited. In other words, a prey type that is added to the diet will be attacked less than 100 percent of the time when it is encountered. In fact, partial preference is predicted from the models derived above. For foraging bouts during which only one prey is taken, equation 6 predicts that diet choice should change as the time remaining in the foraging bout approaches zero. Over many bouts, a forager will exhibit partial preference due to this change in the optimal diet. In the following discussion, I consider bouts in which more than one prey is taken.

Two important levels of variance may exist in M_{ij}. The first is the variance in expected encounter rates of different prey types. The second is the variance in the actual arrival times of individual prey, in essence, the variation within the expected encounter rates. I will illustrate the importance of these sources of variation to diet choice by using two simple examples.

First let two prey types be distributed in runs of three each where the time between encounters of each prey is equal. In this case, a forager might see the following prey in order of occurrence:

$$g_1 g_2 g_3 b_1 b_2 b_3 g_4 g_5 g_6 b_4 b_5 b_6 \quad ,$$

at times

$$T_1 T_2 T_3 T_4 T_5 T_6 T_7 T_8 T_9 T_{10} T_{11} T_{12} \quad ,$$

where $T_{x+1} - T_x = 1$. Let the benefit from prey g (E_g) be 3 benefit units and $E_b = 1$. The handling times for both prey are equal: $h_g =$

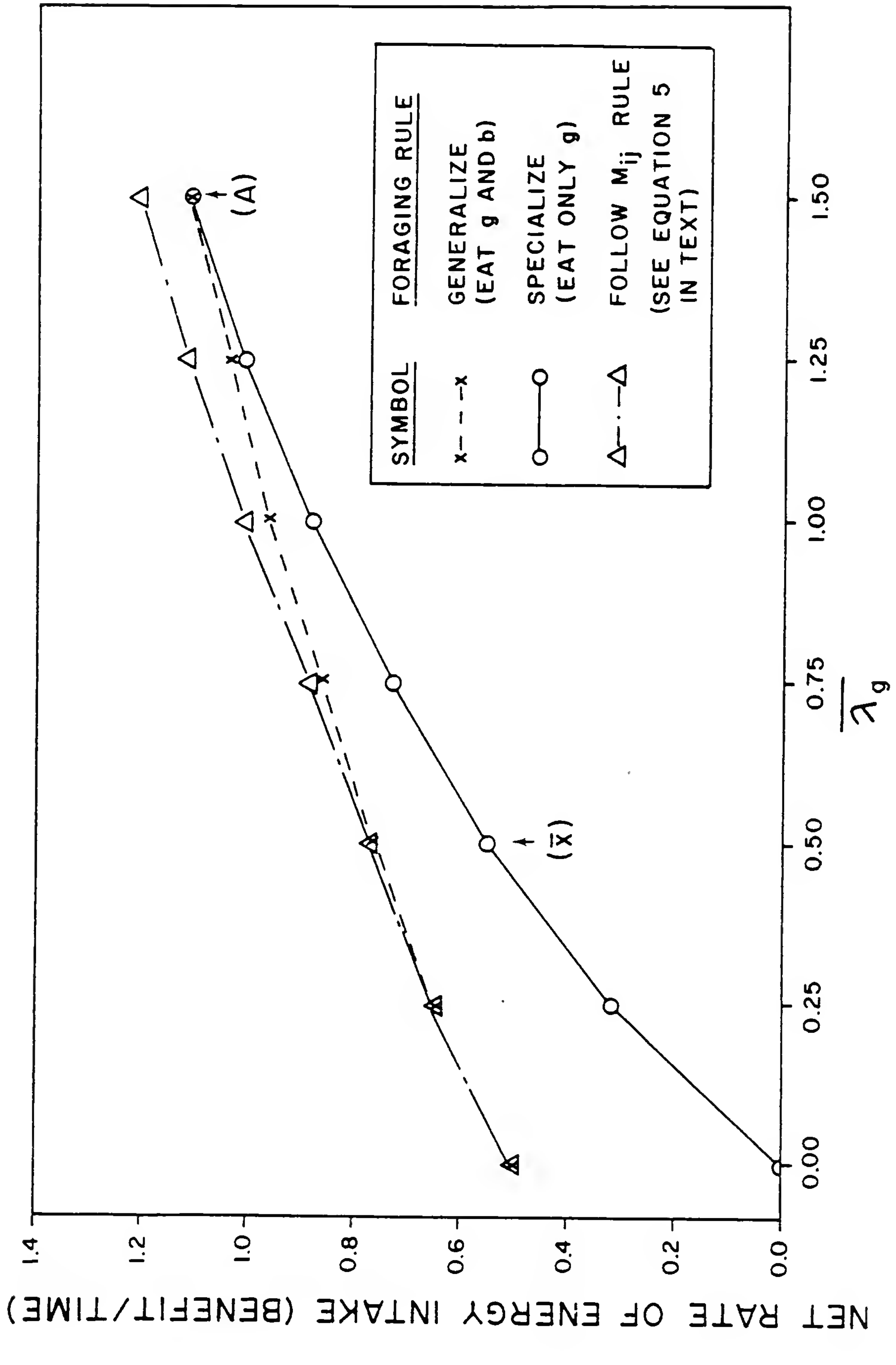
$h_b = 1$. So if the predator captures one prey it will miss the next one. If the forager eats only g, it can start with g_1, then eat g_3, then eat g_4, etc. In the first 6 time units (T_1-T_6) it would collect 6 benefit units. If it started with g_2, it would collect 3 benefit units in the first 5 time units, but thereafter it would collect 6 benefit units for each set of 6 time units (starting with g_4). So as the foraging bout gets infinitely long, the forager will get approximately 6 benefit units in 6 time units. If the forager eats both g and b, it can start with g_1, then eat g_3, b_2, g_3, and so on. With this sequence it gathers 7 benefit units in 6 time units. It can start with g_2, then eat b_1, b_3, g_5, etc. This sequence produces 5 benefit units in 6 time units. So on average, the predator will take in $(7/6 + 5/6)/2=1$ benefit unit per unit time. Now suppose the forager knows the temporal placement of several prey simultaneously. It should eat any g that it encounters since it can do no better, but it should capture b only if no better alternative is available. If the b is followed by another b, it should eat the first prey, because the time spent waiting for the second prey (assuming the predator decides not to take the first prey) should be incorporated into the handling time of the second prey. Here E/h for the first prey is 1 and E/(h + 1) for the second prey is 0.5. On the other hand, if the second prey is a g, then E/(h + 1) for the second prey is 3/2 so the forager should skip the first prey (b) and eat the second prey (g). This means that the relative values of b_1, b_2, and b_3 are different (actually $b_1 = b_2 \neq b_3$). Thus, if the predator could monitor the relative cost of taking each prey, it would take either of the first two of a prey b sequence but never the last. This diet would yield 7 benefit units in 6 time units. Thus, if the animal's foraging decisions were consistent with the Charnov equation then it should on average take in 1 benefit unit per time unit. Under the simple conditions of the example above, if the predator can monitor several prey at a time, it should always do at least as well as Charnov's rule (eq. 2) and may do better when using a decision rule that takes into account the relative temporal position of prey.

If there is any variation in the encounter rate of prey, the effect of averaging on diet choice (as illustrated above) will be important even if the predator can not simultaneously detect a number of prey. This can be demonstrated by simulating the relative effect of the time the animal estimates M_{ij} on the net energetic intake when the mean encounter rate of prey varies. I simulated three different decisions for a two-prey system: (1) take both prey, (2) take only the higher quality prey, and (3) take lower quality prey when

$$M_{ij} < \frac{E_j h_j}{E_i h_j - E_j h_i} \quad .$$

I varied the encounter rate of high ranking prey (λ_g) as a sine function with a range of zero to x (where x varied from 0 to 3.0) (see Fig. 4.4; note that the abscissa is the mean value of the range of λ_g). The simulations illustrate two important properties about decision rules: (1) the forager always does better if it instantaneously monitors M_{ij} than if it follows a rule in which it bases diet choice on the average encounter rate in the foraging bout, and (2) if the encounter rate of high ranking prey varies, we may expect

Figure 4.4. Simulations of net energetic intake from three foraging decision rules. Prey encounter for both high quality and low quality prey was random with a mean encounter rate of λ_g and λ_b (respectively). λ_b was held constant. λ_g varied every 10 time units following the equation: (sin(max. time in interval)+1)$\cdot(\lambda_g)$. $\overline{\lambda}_g$=the mean λ_g over 360 time units. For 360 time units, 36 different levels of λ_g were generated (a new level every 10 time units). The following parameters were used: $E_g=3$; $E_b=1$; $h_g=h_b=1$; $\lambda_b=1.0$. The threshold M_{ij} (see equation 5) for these parameters is 0.5 so the forager should switch from specialist to generalist when $\lambda_g=0.5$. For definitions of terms, see text. Each simulation lasted 720 time units (2 cycles) and each point represents the mean of 10 simulated trials. The arrow marked (X) is the point where the forager should switch from generalist to specialist (as predicted by the Charnov equation) based on the mean λ_g from one full cycle ($\overline{\lambda}_g$). The arrow marked (A) is the point where the forager should actually switch diet assuming diet choice did not change during the foraging bout.


NET RATE OF ENERGY INTAKE (BENEFIT/TIME)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
λ_g
0.00
0.25
0.50
0.75
1.00
1.25
1.50
($\bar{x}$)
(A)
SYMBOL
FORAGING RULE
x– – –x
GENERALIZE (EAT g AND b)
o——o
SPECIALIZE (EAT ONLY g)
Δ–·–Δ
FOLLOW M_{ij} RULE (SEE EQUATION 5 IN TEXT)

to see the diet change through a foraging bout. In other words, the predator may exhibit "runs" of differing diet choice.

These simulations also illustrate that the amount of time the forager takes to estimate λ_g will affect the energetic intake from the diet. For example, if the forager simulated in Fig. 4.4 was to estimate λ_g based on one cycle (360 time units), then it would base diet choice decisions on the mean encounter rate from the cycle. For a range of 0 to 2, the mean would be 1.0. Using the mean encounter rate, Charnov's equation (2) suggests that the simulated animal should switch from generalist to specialist at a mean λ_g of 0.5. Yet the simulations show that this decision underestimates the best switching point. In fact, the switch from generalist to specialist should be closer to a mean λ_g of 1.50 (see Fig. 4.4). The basis of this underestimation can be viewed in terms of M_{ij}. With λ_b constant, most b prey will be taken when the arrival rate of g is low and when M_{ij} is low. When the arrival rate of g is high, the probability of taking b will be small. Thus, summing over all prey b taken, the number of higher ranking prey missed while handling the lower ranking prey will be smaller than expected when the arrival rate of g is constant. In other words, M_{ij} is reduced when variance in prey encounter rate increases. This reduction shifts the optimal switching point to higher levels of $\overline{\lambda_g}$.

A second factor is important when the mean encounter rate varies; the calculation of E/T_T from equation 2 is overestimated for both the generalist and specialist diets. If λ_g is varied as a sine function (as above), then the amplitude of the sine wave can be used to simulate variance in prey encounter rate. As the amplitude increases, the net energy derived from any of the simulated diets decreases (Fig. 4.5). This is because the energetic intake rate (E/T_T) as a function of λ_g changes more rapidly at low values of λ_g than at high values. When the mean value of λ_g is used to calculate E/T_T, this nonlinearlity will cause E/T_T to be overestimated. This can be shown as follows: let E_g, E_b, h_g, and h_b be constants. Also let λ_b be a constant (since the level of λ_b will not affect diet choice anyway under the assumptions of the model). The energetic intake for a two-prey system is

$$\frac{E}{T_T} = \frac{E_g \lambda_g + E_b \lambda_b}{1 + h_g \lambda_g + h_b \lambda_b} .$$

The change in E/T_T with changing levels of λ_g is

$$\frac{\partial}{\partial \lambda_g}\left(\frac{E}{T_T}\right) = \frac{E_g(1 + h_b \lambda_b) - E_b h_g \lambda_b}{(1 + h_b \lambda_b + h_g \lambda_g)^2} . \qquad (7)$$

This function decreases monotonically with increasing λ_g (Fig. 4.6). If Charnov's rule (eq. 2) is considered an estimate of E/T_T, then under most circumstances the forager will overestimate the net energetic return from both the generalist and specialist diets if it requires a relatively long time to estimate λ_g. Thus, the time the forager takes to respond to changes in prey densities should vary inversely with the rate of change in mean prey density. Since a number of predators have been shown to respond to changes in prey density (Elner and Hughes 1978; Giller 1980; Goss-Custard 1981; Jaeger and Barnard 1981; Krebs et al. 1977; Sih 1980a; Werner and Hall 1974), it is not unreasonable to

Figure 4.5. Simulations of net energetic intake from three foraging decision rules when the variance in encounter rate of high ranking prey changes. Prey encounter for both high quality and low quality prey was random with a mean encounter rate of λ_g and λ_b (respectively). λ_g varied every 10 time units following the equation: $(r \cdot \sin(\text{max. time in interval}) + 1) \cdot (\text{mean } {}_g \text{ over 360 time units})$. Thus, r is a function of the variance in λ_g. Mean $\lambda_g = 1.0$ for all simulations. The threshold M_{ij} (see equation 5) for these parameters is 0.5. All other parameters as in Fig. 4.

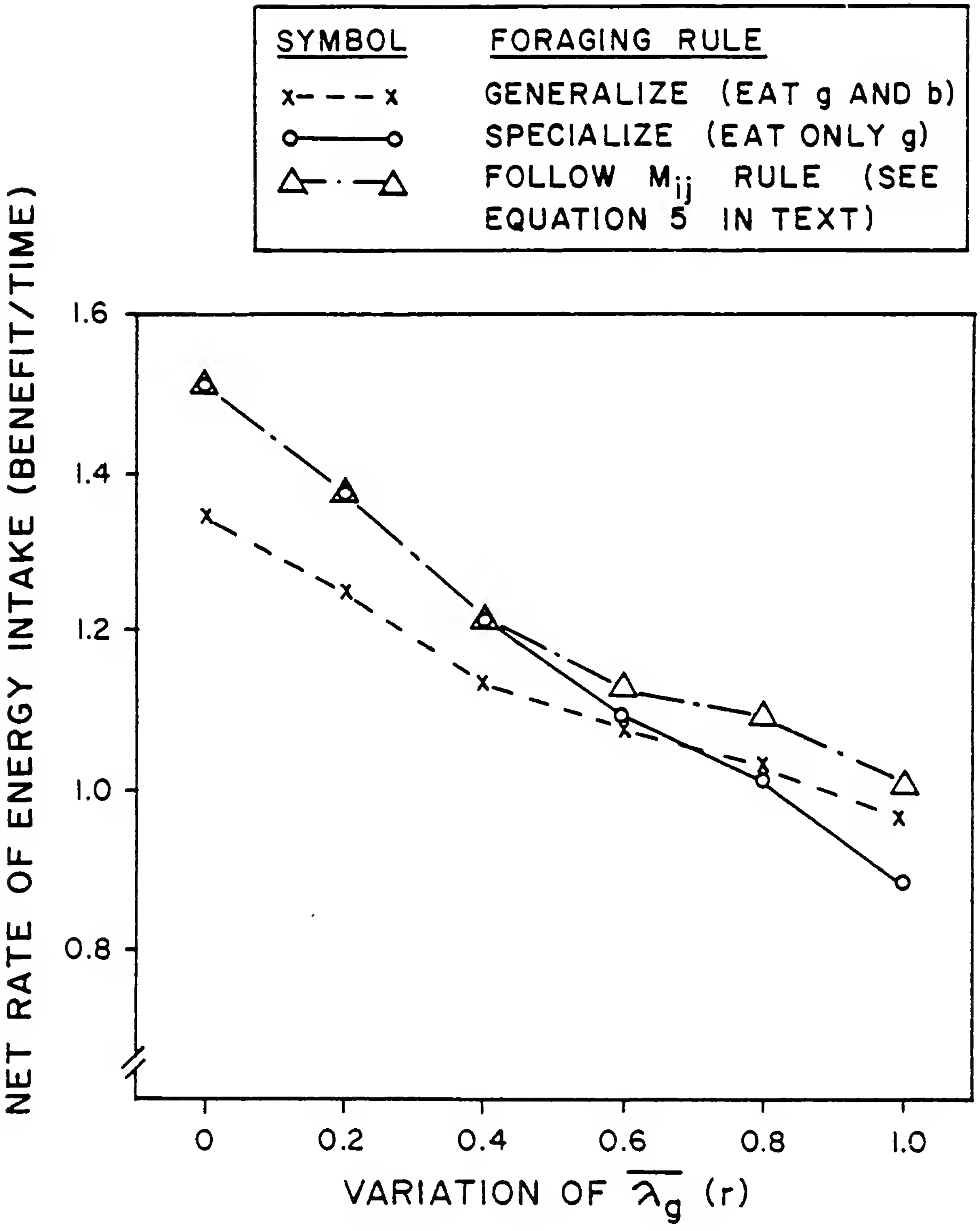
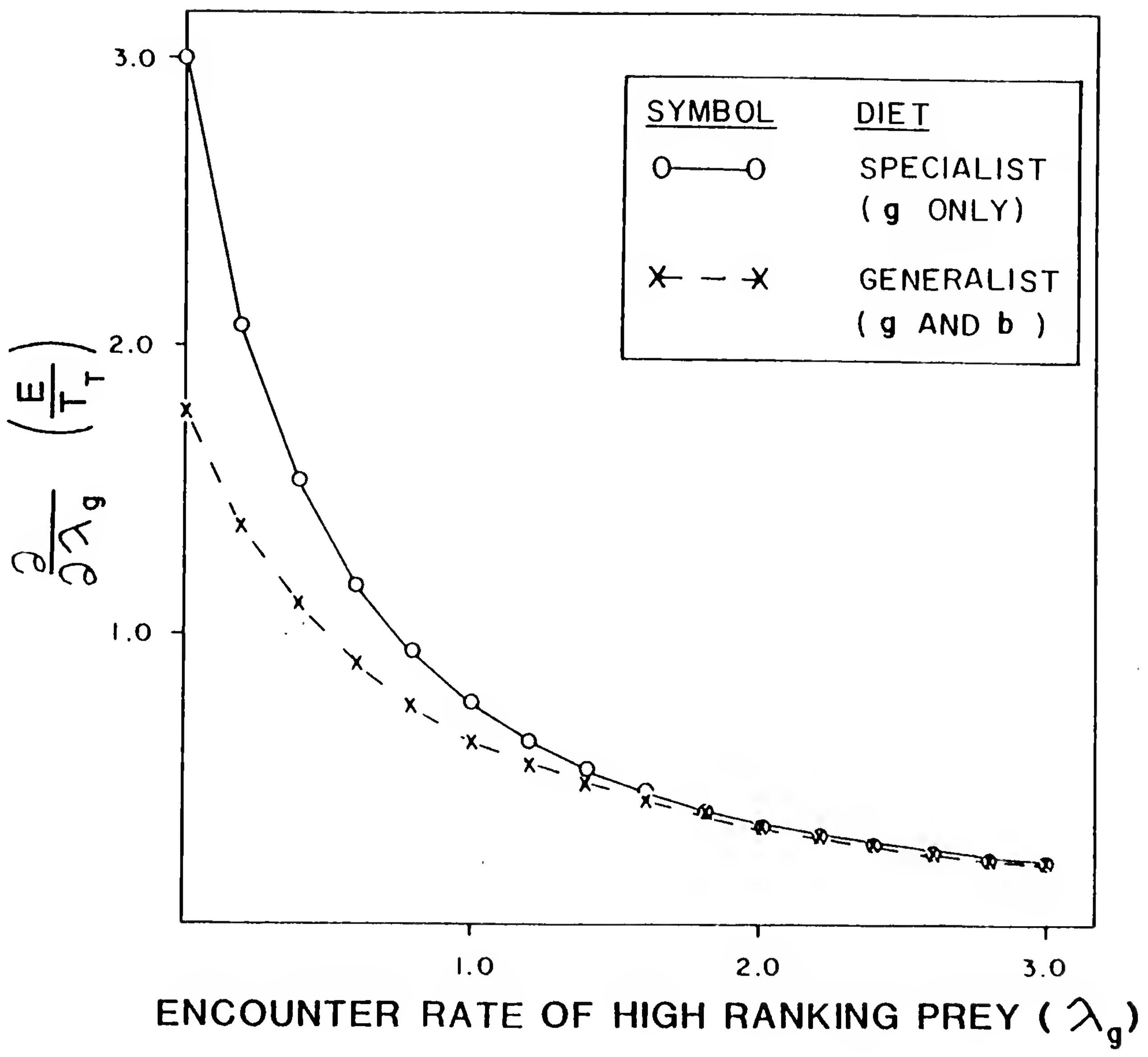

SYMBOL
FORAGING RULE
x- - - -x
GENERALIZE (EAT g AND b)
SPECIALIZE (EAT ONLY g)
FOLLOW M_{ij} RULE (SEE EQUATION 5 IN TEXT)
NET RATE OF ENERGY INTAKE (BENEFIT/TIME)
1.6
1.4
1.2
1.0
0.8
0
0.2
0.4
0.6
0.8
1.0
VARIATION OF $\overline{\lambda_g}$ (r)

Figure 4.6. Predicted change in net energy intake rate (from Charnov's model) with changing encounter rates of high ranking prey (prey g). The predictions are based on the following parameter levels: $E_g=3$; $E_b=1$; $\lambda_b=0.5$; $h_g=h_b=1$. For definitions of terms see text. Rates are predicted by equation (7) from text.


$\frac{\partial}{\partial \lambda_g} \left(\frac{E}{T_T} \right)$
3.0
2.0
1.0
SYMBOL
DIET
SPECIALIST
(g ONLY)
GENERALIST
(g AND b)
1.0
2.0
3.0
ENCOUNTER RATE OF HIGH RANKING PREY (λ_g)

suspect that at least some foragers may be able to monitor M_{ij}. This should hold true especially for predators that hunt by sight for prey which arrive simultaneously (such as planktivorous fish or insects, salamanders, birds foraging in swarms of insects, etc.).

Discussion

The models presented here generate the following predictions: (1) if foraging is confined to a given period of time, t, then as t decreases, diet choice should become less specialized. (2) Diet choice should reflect variance in prey distributions if this variance affects the variation in the relative "cost" of capturing and eating low ranking prey. This cost in a two-prey system, M_{ij}, is the number of higher quality prey missed while handling lower quality prey. Short term changes in prey encounter rates should be incorporated in the decisions the animal makes about diet choice. This is because decisions based on long term averages will yield a lower return than decisions based on short term averages. Thus, variance in the number of prey added to the diet should increase as variance in prey distribution rises. As a result of the variance in diet composition, partial preference should also increase with an increase in the variance in prey distribution. (3) Diet choice will also be strongly affected by the number of prey the predator can monitor at any one time. If several prey can be perceived at once, then the forager should be able to estimate M_{ij} nearly instantaneously. In this case, the optimal diet changes rapidly and as a result, partial preference should be exhibited.

Predictions (2) and (3) above illustrate that how the forager estimates prey distributions will strongly affect the optimal diet. Clumping of prey should select for foraging strategies that restrict the time required to estimate local prey density (e.g. through short term rules of thumb as suggested for granivorous birds by Barnard 1980). Common prey should allow predators to make foraging decisions based on accurate estimates of M_{ij} if more than one prey can be seen during the time of the prey choice decision. The importance of these predictions is illustrated especially in studies on switching in which a predator tends to forage disproportionately on prey that are most abundant (Murdoch 1969; Murdoch et al. 1975). Several authors have shown that switching should occur when some learned foraging response is exhibited by a forager (Hughes 1979; Murdoch 1969; Oaten and Murdoch 1975). But in some cases, switching may be predicted if the forager can quickly monitor changes in prey density, irrespective of any learned behavior. Visual predators such as fish (Bernstein and Jung 1979; Olmstead et al. 1979) and salamanders (Jaeger and Barnard 1981) have been shown to respond quickly to changes in prey density and may therefore be able to monitor M_{ij} closely (equation 5). One prediction that stems from these models is that predators should either use visual estimates of prey density (as shown for salamanders by Jaeger and Barnard 1981), or should restrict the amount of time over which they estimate prey encounter rate if visual estimates are impossible. Thus, the length of the forager's "memory window" (sensu Cowie 1977) should be set small enough to minimize the effect of averaging unless the costs of misjudging encounter rates outweighs the costs of averaging. If foragers are estimating M_{ij} based on short term rules, then as variance in prey encounter rate increases, the number of prey included in the diet will vary. As a result, foragers should exhibit a higher degree of partial preference (see Pulliam 1974). Clearly the foraging decisions exhibited by animals may be much more subtle than foraging theory has allowed. To understand exactly the nature of diet choice decisions, we need much more detailed data on foraging behavior.

Three studies support the first prediction. Jaeger et al. (1981) analyzed feeding selectivity of salamanders foraging on large and small flies. They showed that a salamander on its own territory preferentially fed on large flies, but on unmarked territories or on a conspecific's territory, the salamander exhibited no preference for either fly type. They also showed that a territory owner spends most of its time foraging. A salamander on no territory or one on a conspecific's territory spends a large amount of time either marking or displaying submissive postures, and feeding is interspersed between these two behaviors (R.G. Jaeger, pers. comm.). The conclusion Jaeger et al. (1981; pg. 1100) reached was that salamanders sacrificed "initial caloric yield until they had established marked territories and then (switched) to a higher sustained caloric yield". Jaeger et al. (1981) viewed the foraging bout as the entire time spent in an area. However, the decision of diet choice should not be based on time spent in other activities but solely on time spent foraging. When analyzed in this way, on average only one fly was taken between bouts of marking (when the predator was foraging equally on large and small flies), not including the time spent in a submissive posture. When the predator was foraging selectively, the foraging bout was uninterrupted. The salamander data can be reinterpreted as follows: the length of the foraging bout was long when the salamander foraged on its own territory but extremely short when on another territory or on an unmarked territory. In the latter two cases, foraging bouts were broken up by marking or displaying activities. Thus, if the salamander were to maximize its net rate of energy return while foraging, we would predict that it should increase its degree of specialization with an increase in foraging bout length.

Freed (1981) analyzed diet choice by house wrens foraging for nestlings. When in the presence of a nestling predator (the fox snake), the wrens decreased the amount of time they spent foraging and fed their nestlings smaller prey than when no predator was present in the area. Thus, as foraging bout time decreased, diet selectivity was also reduced. Freed (1981) suggested that, based on these data, the decision rules under which the wrens were choosing their prey changed when a predator entered the area. However, if the rule governing diet choice is to minimize the "cost" of foraging on low ranking prey and thus maximize the net rate at which energy is taken during the foraging bout, then the models presented here suggest that the decision rules with or without predators are identical. The change in the wren's foraging behavior is consistent with the predictions from optimal foraging theory generated from the models presented in this paper.

An exceptionally tractable system for evaluating the effects of foraging time on diet choice is found in the intertidal predators whose foraging bouts are constrained by the tidal period. For example, the predatory intertidal snail, Acanthina, searches only during low tides (Menge 1974). The models I presented above are particularly suited for analyzing this species since only one prey is taken per searching bout. Menge (1974) showed that these snails exhibited strong selection for specific prey early in the tidal phase. As the tide rose and the available searching time decreased, selectivity decreased (less preferred prey were taken when encountered). Here again, the optimal diet changes as foraging time changes . Thus, the relative value of any given prey type also changes as a function of foraging time.

It is often useful to think of foraging behavior (as illustrated by the data from Freed, 1981, Jaeger et al. 1981 and Menge 1974) as hierarchically organized (Dawkins 1976; also see Mesarovic et al. 1970, Hassell and Southwood 1978, and Gass and Montgomerie 1981). In other words, the total set of behaviors that an animal exhibits can be viewed as organized into levels. The decisions made in each level are constrained by information from higher levels. We can dissect foraging behaviors and explicitly model foraging only if we confine the models to work within the constraints imposed by higher order effects. The strength of this organization lies in the fact that foraging models, when viewed as specific levels in a hierarchical design, become more robust than non-hierarchical foraging models. Equation (6) specifies the optimal diet when the foraging bout length is set at some time interval $[0,t]$. This interval may be interpreted as the boundary of the foraging model. Decisions regarding diet choice are based on factors that exist only within these boundaries. At a broader level, the length of the foraging bout is affected by constraints on the total time available for foraging (t). In the above examples, the constraints are predation pressure, intraspecific interactions and environmental effects. Many other studies have pointed to similar factors affecting foraging behavior and foraging time (Baker et al. 1981; Barnard 1980; Caraco 1979, 1980; Hervey 1969; Milinski and Heller 1978; Norberg

1981). The effects of these constraints can themselves be modeled; the output of such time-constraint models would define the boundaries of the foraging models. The foraging model (viewed in terms of one level in a hierarchy) need not be supplanted by another set of models that specifically describe a new set of decision rules for the forager when other factors impinge on foraging. Rather, this hierarchical organization of models generates predictions that should describe foraging behavior under a wide range of conditions and, therefore, may be of more heuristic value than specific models based on unique conditions.

Summary

Predictions generated from optimality models are inescapably based on a number of assumptions. The predictive value of these models is often determined by the degree to which the behavior of an organism fits the underlying assumptions of the model. I analyzed optimal diet choice by relaxing two sets of assumptions made in previous optimality models. (1) Foraging-bout length (the uninterrupted time devoted just to foraging), generally treated as infinitely long, was shown to affect optimal diet choice. For many foragers, foraging-bout length may be considerably shortened by the presence of predators, or by physical or social features of the forager's environment. A model was derived which incorporates a short bout length into the decision of diet choice. The model predicts that animals should become more catholic in their diet choice as the amount of uninterrupted foraging time decreases. This prediction appears to be supported by three studies from the literature.

Jaeger et al. (1981) showed that salamanders incorporated more lower ranked prey (small flies) when they were either on the territory of a conspecific or on no territory as compared with prey choice when they were on their own territory. In this case, foraging time was uninterrupted when the salamanders were feeding selectively, but continuously interrupted by submissive behavior and marking behavior when no diet choice was exhibited. Freed (1981) showed that wrens foraging for nestlings spent less time per foraging bout when a predator was in the nesting area than when no predator was in sight. The reduction in foraging bout time correlated with a reduction in prey size fed to the young. The foraging time of some intertidal snails was shown to be confined by the length of the low tide cycle (Menge 1974). As the end of the low tide drew near, the snails decreased diet selectivity. Thus, as the remaining time available for foraging decreased, the predator exhibited a lower degree of prey selection. (2) Variance in prey encounter interval was shown to affect the utility of classical optimal diet models in predicting the optimal diet. Charnov's (1976b) model is shown to over-estimate the net rate of energy intake when mean encounter rate varies about some fixed level. Predictions from Charnov's model are incorrect over some ranges of prey encounter rates due to this over-estimation. I show that as variance in prey encounter rate increases, the time over which the forager estimates prey encounter rate will have a strong effect on the ability of the forager to maximize the net rate of energy intake. Foragers that forage on patchily distributed prey should use a shorter amount of time to estimate prey density than foragers that prey on evenly dispersed prey. Thus, animals that are capable of reducing the time required to estimate prey density (for example, visually hunting predators in areas of high prey density) should alter their diet in response to local variation in prey density. For this type of forager, as variance in prey encounter rate increases, fluctuations in the number of prey types in the diet will increase. As a result, there should be an increase in the degree of partial prey preference exhibited by the forager with increasing variance in prey encounter rate.

CHAPTER V
OPTIMALITY, HIERARCHIES, AND FORAGING

Introduction

The conditions under which animals forage are generally complex, even in the laboratory. The animal's perception of its environment, its internal state (sensu Sibly and McFarland 1976), and numerous environmental factors may influence their behavior. This complexity has made some authors doubt the validity of optimality models as a tool in the study of behavior (Simon 1956; Schluter 1981; Zach and Smith 1981). The issue is an important one, since if this complaint is correct, then the approach should be abandoned in favor of a technique (or techniques) that will be more useful in predicting the behavior of animals in nature. At one level the approach is clearly useful, and it has been used successfully in each of the four previous chapters of this dissertation. However, none of the existing optimality models adequately address the complexity of foraging behavior. I think there are two aspects to this problem. First, there is the question of generality: how robust are the predictions generated from optimality models? Second there is the problem of measurability: if foraging decisions are based on environmental conditions, is it possible to measure these conditions adequately? I argue that hierarchical modeling can be used to solve both problems: (1) hierarchies are useful in deriving generalizations about foraging decisions (or any other decisions), and (2) the use of hierarchical models may aid in decreasing the number of variables that need to be measured, and thereby reduce the problem of measurability. I begin this chapter by briefly discussing the major questions that are addressed when using optimality models, and then briefly describe characteristics of hierarchical design. After defining the question and the technique, I can then discuss generality and measurability in foraging studies. The first four chapters of this dissertation will be viewed in light of this discussion.

Optimality

In the introduction I suggested that optimality is a tool that can be used to address specific questions concerning behavior. However, the question is not whether animals are foraging optimally, but whether our perception of the salient features that influence foraging is sufficiently broad to predict an animal's behavior. Maynard Smith (1978) discussed this issue in detail. We can use optimality theory in three ways: (1) to formulate our perception, (2) to generate testable predictions from this formula, and (3) to re-evaluate our perception and add to it where it appears to be inadequate. Step three yields new, testable hypotheses. Where does this fit in the study of behavior?

Tinbergen (1969) has suggested that the complete study of behavior involves four major topics. The first two topics include an analysis of the proximal mechanisms in behavior: (1) the causation or control of behavior, and (2) the development of behavior in the individual. The second two topics deal with ultimate factors in behavior: (3) the adaptive significance of behavior in relation to an animal's environment, and (4) the evolution or phylogenetic origins of behavior. Optimality theory is particularly appropriate to the study of the third topic, the adaptiveness of behavior. Although causal factors are important, I argued in Chapter III that the study of optimal behavior patterns should be made independently of the causal mechanisms, since selection should act at the level of the phenotype (the behavior) and not on its component parts. With optimality we are interested in how the animal adaptively responds to its environment, and the relationship between these adaptations and behavior. Natural selection is assumed. This assumption allows us to compare the response of an animal in a given situation with an expected response based on the selective pressures that we feel are important. A poor fit to predictions suggests that we are either incorrect or incomplete in our evaluation of the selective pressures.

The mechanics of using optimality theory involve the construction and testing of mathematical or graphical models. The model is constructed around a maximization parameter, or currency (Pyke et al. 1977). The use of a given currency assumes that maximizing the net accrual rate of that currency will maximize fitness. Some models have been constructed that address the minimization of a cost function (cf. Sibly and McFarland 1976). However, minimization of net cost can be considered identical to a maximization of net benefit (McCleery 1978). Although most foraging models have used energy as a currency (e.g. Krebs et al. 1977; Goss-Custard 1981; Hughes 1979; Pyke 1978), some studies have shown that energy may not be appropriate for some animals

(Rapport 1981; Westoby 1978; Greenstone 1979). These latter studies also indicate that more than one currency may be necessary to describe the maximization parameters (also see McCleery 1978; Sibly and McFarland 1976).

In this dissertation and in all other studies of optimal foraging behavior, the measurement of the maximization parameter is determined in absolute terms. For example, a joule of energy expended in prey capture is considered to be equivalent to a joule spent traveling to a resource patch or spent during mating behavior. Odum (1982) has suggested that the importance of any absolute unit of currency will correlate with the hierarchical position of the subsystem in which the currency is spent (see "Hierarchy" below). For example, in the ecosystem one joule of puma has a higher "embodied" energy than a joule of grass. This is because the number of joules entering the system (in this case from solar input) required to generate a joule of puma is vastly larger than that required to make a joule of grass. In behavioral systems, a joule spent in early spring searching for mates after a winter hibernation may represent a larger investment than a joule spent searching for food the previous fall. This will be true if the ratio of energy expenditure (or the cost of the behavior) to fitness associated with that expenditure is lower when searching for mates than it is when searching for food. Due to relative differences in currency between subsystems, Odum (1982) suggests that energy should be expressed in terms of embodied energy and not in absolute terms. The use of embodied energy may be critical in comparing costs and benefits of hierarchically distant subsystems, but is less important when the analysis deals with any single level as is the case with most optimality models. This issue is discussed further below (see "Maximum Power and Foraging Hierarchies").

If several maximization parameters are required to describe behavior, two alternatives are available. (1) All parameters can be combined into a single model of behavior. This requires that the costs and benefits associated with all parameters be measured in the same units. For example, the male smooth newt, Triturus vulgaris, performs a long and elaborate courtship on the bottom of a stream (McFarland 1977; Houston et al. 1977). During parts of this courtship sequence he builds up an oxygen debt and must surface to breath. The male must correctly time his courtship and breathing in order to pass his three spermatophores successfully to the female. There are three different behavioral components in the courtship sequence, two of which include different segments of the display, and the third is the rate of spermatophore transfer. These behavioral components were combined into a single model with several parameters that predict oxygen debt at any given time during the courtship. The model was based on the assumption that the newt should maximize the probability of fertilization. Thus each parameter was couched in terms of its effect on the fertilization probability. (2) Instead of a single model, each parameter or set of similar parameters can be treated separately in a series of nested models. Each submodel represents a separate behavioral decision. This is the hierarchical approach. The single model approach can be thought of as a subset of the hierarchical approach, since only one behavior or decision is addressed. In the newt example, the regulation of courtship activity as a whole could be examined with a higher level model that regulated the category of behavior that was exhibited by the animal, such as mating, feeding, or inactivity. One advantage of the hierarchical approach is that each submodel can use a different currency. For example, the influence of predator pressure can be modeled through the use of time budgets. Diet choice can be modeled in terms of calories derived from foraging during the time allotted for foraging behavior. Thus the response to predator pressure can be examined in terms of time, while diet choice can be couched in terms of energy (or nutrients). I used this approach in Chapter IV (also see Lucas 1983), but I only modeled a single hierarchical level (diet choice) by treating decisions concerning time budgets as a simple constraint on diet choice.

Since hierarchies have been used for a wide variety of research fields, including ethology (Dawkins 1976; Tinbergen 1969), ecosystem dynamics (Odum 1983), evolution (Gould 1982; Lewontin 1970), foraging patch utilization (Charnov and Orians 1973; Gass and Montgomerie 1981; Hassel and Southwood 1978), and the expression of sex ratio patterns (Frank 1983), it is important to explain briefly the type of hierarchical design I am using.

Hierarchy

Mesarovic et al. (1970) treated hierarchical systems as a series of input/output subsystems, each at a given level of organization. The input can be thought of as cause, the output as effect. In an optimality model, the inputs are the variables, the subsystem is the model (expressed in the appropriate currency), and the output would be the behavior that resulted from the solution to the model. Mesarovic et al. (1970) suggested that for the hierarchical design to be useful, the functioning on any level must be as independent as possible of the functioning on other levels. Thus each level must be represented by a unique model, although levels will be connected by input constraints or feedback loops (Fig. 5.1). Each subsystem in some way controls or intervenes in the input of the system below it and may receive feedback information from that lower system, although there may be no feedback loops in some subsystems. In foraging, subsystems can use either a maximization parameter or a constraint parameter. Maximization parameters in the wren foraging example include such factors as energy, or the risk of predation. The type of subsystem that represents maximization parameters can be thought of as a specific level of behavior. More than one maximization parameter may be included in a single model, as in the case of energy and nutrient co-requirements from the diet (e.g. Pulliam 1975; Rapport 1971). Constraint parameters include factors that will modify or limit the expression of the behavior associated with lower-level subsystems. Thus, the constraint subsystems will always lie above a subsystem in which maximization parameters are evaluated. Examples of constraint parameters include tidal cycles or daylight cycles that restrict foraging time, and weather patterns that may influence migration or social behavior. Including constraint parameters in subsystems changes the original definition of the hierarchy proposed by Mesarovic et al. (1970), since these subsystems are not input/output systems in the context of behavior. However, this expansion of definition will give a model more flexibility, as I show below.

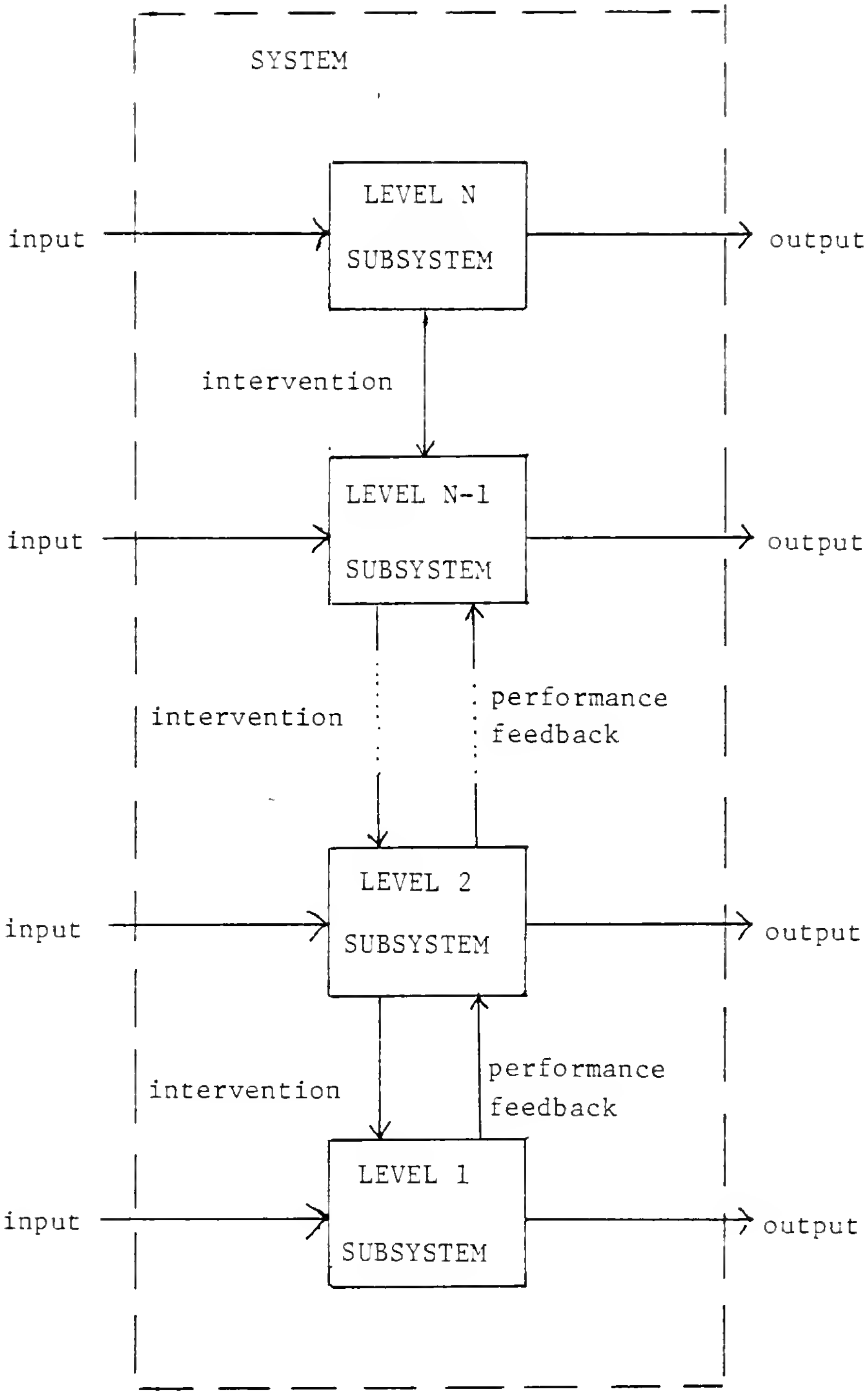


Figure 5.1. A simple hierarchical system (after Mesarovic et al. 1970)

As stated above, adjacent subsystems may or may not include feedback loops. A feedback loop involves the processing of information from lower levels in the formulation of decisions at higher levels. These higher-level decisions will then constrain the lower-level processes. Thus, constraints on lower-level processes will be affected, in part, by the result of previous constraints on those levels. For simplicity, I will call a feedback subsystem a subsystem that receives information feedback from a level below it (as in level 2 in Fig. 5.1), and a non-feedback subsystem is a subsystem that receives no information from the level below it (as in level 1 in Fig 5.1). By this definition, the bottom layer of any hierarchical system will always be a non-feedback subsystem, since it does not receive information from a system below it.

Maximum Power and Foraging Hierarchies

The optimization principles of behavioral systems proposed here assume that the evolution of decision rules will proceed such that animals will maximize the net accrual of limiting resources or currencies. By maximizing the net harvest rate of these resources, an animal should be able to optimize investment in activities that maximize fitness. The decomposability of systems into a hierarchically nested set of subsystems, each of which can be treated as an optimality model, is implicit in the use of hierarchical design in this dissertation. Thus optimization principles apply to the whole as well as to each of the parts. The optimization of time budgeting implies an optimization of behavior within each behavioral bout. The optimization of diet choice implies the optimization of prey utilization. The optimization of patch choice implies the optimization of searching behavior once in the patch. Higher level decisions impose constraints on lower level decisions, and these constraints are to some extent conditional on the behavior exhibited at lower levels. Information ("performance feedback" in Fig. 5.1) is passed from lower levels to higher levels through the behavioral output of the lower levels. The constraints imposed on lower levels can be thought of as feedback from this information flow.

Another type of systems approach has been used in the analysis of ecological and economic systems. Odum (1982, citing Lotka) proposed that the design of systems should follow the maximum power principle. In other words, systems should develop designs that maximize the flow of useful energy. If the maximum power principle is consistent with the optimization principle, then the two fields have developed convergent paradigms, which may lend credence to both. If they are mutually exclusive, then two possibilities exist. One of the paradigms must be incorrect, or there may be no emergent properties that define all systems.

On the surface, the definitions of optimality and maximum power are identical. The maximization of currency intake by an organism is the same as the maximization of the flow of "useful" energy, assuming that any currency can be converted to energy equivalents. However, the two approaches appear to differ over two major issues. The resolution of these differences is a worthwhile goal. One major issue is control. Optimization principles treat control as unidirectional. Higher level subsystems constrain lower level systems. For ecosystems, Odum (1982) states that lower level subsystems (for example producers) will benefit if they increase the feedback from higher-level subsystems (for example consumers). Here feedback is the flow of energy from higher-level to lower-level subsytems which influences the energy accrual properties of the lower-level subsystem. Odum (1982) has shown that this feedback mechanism will generally increase the ability of the lower-level subsystem to draw, or accrue, energy from a source. This viewpoint is reflected in the "maximum power" definition of net energy, which is the productive output (used by higher subsystems) minus the feedback from higher subsystems. The "optimality" definition of net energy would be the intake of energy from lower systems minus the energy spent (or fed back) to acquire that intake.

I define control as the capacity for constraint. In Chapter IV, decisions concerning time allocation set the boundary for, and therefore controlled, diet choice decisions. Here control is based only at the higher level. If control is generally based at all levels of a system, including control of higher-level subsystems by lower-level subsystems as implied above for ecosystems, then the modeling of behavioral decisions would be difficult without knowing the relationship between production and feedback. This relationship requires a model of the higher-level subsystem. Since there will always be a higher-level subsystem, multilevel control is an intractable problem in behavioral systems. On the other hand, if control is mediated through feedback from high-level systems to lower-level systems (as suggested by Mesarovic et al. 1970), then optimality and the maximum power principle may be functionally equivalent. Further work is clearly called for.

A second issue that may differ between the approaches is the issue of embodied energy. Should the energetics of foraging be modeled using absolute or relative measures of currency? The answer lies in the use of the currency. If currency flow is compared between different subsystems, embodied energy may well be the most correct unit of comparison. However, if the flow or accrual rate of currency is to be determined through simulation or model dynamics, then absolute currency measures are required. Here embodied energy is implicit in the dynamics of the model.

Hierarchical models of behavior, as presented here, involve a series of nested decision models about how the animal should behave. Each model is based on the appropriate currency or currencies. Of course, the setting up of a model does not mean that it will be of any use in the study of behavior. Before I discuss the role I think hierarchical models can play in the study of behavior, I will first review the contributions of earlier, non-hierarchical models. This is not intended to be a thorough literature review, since both optimality and optimal foraging have been reviewed elsewhere (Cody 1974; Maynard Smith 1978; Pyke et al. 1977; Schoener 1971). I then discuss these examples in the light of the generalities we are attempting to draw from studies of foraging behavior.

Non-Hierarchical Foraging Models

There are numerous types of non-hierarchical models of foraging behavior, each of which addresses a specific aspect of foraging. Pyke et al. (1977) suggest that most optimal foraging models fall into four major categories: (1) choice of which food types to eat, (2) choice of patch type to forage in, (3) allocation of time to different patches, and (4) patterns and rates of movement while foraging. In their review of optimal foraging studies, Pyke et al. (1977) note that these four decisions are assumed to be independent. However, the categories are not independent since they naturally fall under a hierarchical organization (Gass and Montgomerie 1981; Hassel and Southwood 1978; Charnov and Orians 1973). For example, decisions about patch choice should reflect the type of prey expected to be taken from that patch (diet choice) and the amount of time that will be allocated to the patch. Thus all categories can be treated as a single, hierarchical model.

All four categories listed above have been treated in the literature in a similar manner, so I will focus on one of the four categories, diet choice. The most widely used diet choice model is a variation of MacArthur and Pianka's (1966) original optimal foraging model. As Pyke et al. (1977) note, the same basic model has been (independently) derived by at least nine authors (Schoener 1969, 1971; MacArthur 1972; Charnov 1976b; Charnov and Orians 1973; Timin 1973; Maynard Smith 1974; Pearson 1974; Pulliam 1974; Werner and Hall 1974; Estabrook and Dunham 1976). The diet choice model makes the following predictions (see Chapter IV for a more detailed discussion of Charnov's [1976b] version): (1) prey should be ranked according to the ratio of net energy derived from the prey divided by the time required to handle that prey, (2) the forager should never exhibit partial prey preference (i.e., prey types that are a part of the diet should be taken whenever they are encountered), (3) the inclusion of any given prey type to the diet should be independent of the encounter rate of that prey type.

Prey types should be added to the diet until the net energy per unit handling time from a prey type falls below the net energy per unit foraging time derived from a diet of all higher ranking prey. The models were tested (mostly under laboratory conditions) on a number of different predators (Werner and Hall 1974; Krebs et al. 1977; Charnov 1976b; Zach and Falls 1978; Dunstone and O'Connor 1979; Hughes 1979; Palmer 1981; Goss-Custard 1977) and were found to be generally consistent with the predictions, although partial prey preference appeared to be exhibited more frequently than expected. What do these studies tell us?

The studies cited above illustrate a number of features about foraging behavior. They suggest that the optimality approach can be useful in studying diet choice under simple conditions. Thus foraging behavior can be treated as a selected trait, just as physiological (e.g., see McNab 1980) or morphological (e.g., see Alexander 1982) traits can be. This is an important step because it allows us to use optimality to understand behavioral adaptations. The studies also give us some insight into the decision-making processes of animals, which is a primary focus of this field of research. The fact that the maximization of net energy appears to be a useful maximization parameter is also important because it suggests that energy may be a good parameter to start with in future studies. This by no means implies that it will work in all cases, but the utility of this maximization parameter can be tested.

The fact that so many researchers have come up with the same model independently, and that the model appears to predict, at least qualitatively, the behavior of a variety of foragers, from insects to mammals, suggests that the predictions are robust and have a high degree of generality. However, several studies have shown that the predictions will not hold for certain systems. In the following examples, each factor will change at least one of the predictions: (1) learning will change handling times and capture efficiencies (Murdoch 1969; McNair 1980), (2) foragers may need to test habitats to monitor prey availability (Krebs et al. 1977), (3) foragers often require some finite time to recognize prey (Charnov and Orians 1973; Hughes 1979), (4) a forager's diet choice may be constrained by nutrient requirements or toxicity of food (Pulliam 1975; Rapport 1981; Janzen and Freeland 1974), (5) the presence of predators may influence diet choice (Milinski and Heller 1978; Sih 1980b; Lucas 1983), and (6) foraging decisions may be influenced by variability in prey quality or patch quality (Real 1980; Caraco 1979, 1980). These studies suggest that the list of factors originally included in the first diet choice models must be expanded. I should point out that the optimality approach was used to generate these new factors, and thus provided additional insights into the factors that influence foraging behavior. The studies listed above suggest that the original models are inappropriate under certain circumstances, but not that the foragers are foraging non-optimally. Thus the original formulations will work under some circumstances and not under others. How do we treat these additional factors? They could be treated as special cases, and therefore we might conclude that the original models can produce robust predictions, but that the predictions are invalid in the special cases. On the other hand, we can add the new factors to an overall model for which there are no special cases. I suggest the latter approach. We should be able to generate a model that embodies the essence of foraging behavior under a wide variety of conditions. This model should be far more predictive than any simple model of specific cases of foraging behavior. The best type of model that could be used is a hierarchical one. Hierarchical models will include the generality that is required and the flexibility needed to study foraging behavior in different sorts of animals and under different conditions. The original models were useful in their simplicity; this feature should not be discarded. Using hierarchical models, the simple models can be treated as special cases of the overall model. As a result, simple models can be used under the conditions for which these models are appropriate.

Hierarchy and Optimality Models

The lack of generality in the original diet choice models could have been predicted, given the simplicity of the models. This point brings up a slightly different issue: where should we look for generality in the first place? The approach to all optimality problems is to derive cost/benefit functions that are appropriate to the currency under consideration (Pyke et al. 1977). Thus, one generality of all optimal foraging models is that any given system can be studied using a cost/benefit function. Unfortunately, this generality does not go very far, since it makes no predictions about the type of decisions we should expect to see from a forager. The fact that the diet choice model was used under so many conditions and for so many types of organisms, suggests that researchers can use these models as general predictors of behavior across a diversity of animal groups. The same can be said for the use of the marginal value theorem and its derivatives in the study of patch choice (Charnov 1976a; Parker and Stuart 1976; Parker 1978; Sih 1980a; Cook and Cockrell 1978; Giller 1980; Orians and Pearson 1979; Krebs 1978; Cowie 1977). However, the work presented in Chapters II, III, and IV suggests that the diet choice models and the marginal value theorem may be much less general than was once thought. In some cases, the predictions may have been so general, especially when treated qualitatively, that they were upheld even when the systems were clearly inappropriate for the models. Partial prey consumption is a case in point (see Chapter II). This leads us back to the same question: What models will give predictions that are generally applicable to foraging behavior and that will therefore aid in a broad understanding of this behavior? The generality must enable us to gain insight about behavior, and not lead us to false conclusions. If the predictions generated from a model are so general that they cannot be rejected, even if the model is inappropriate, then the model has no power and should be discarded.

The generalities we seek may be more in the framework or hierarchy than in the specific models. This can be illustrated using an excellent example from sex ratio theory. Sex ratio theory is an attempt to predict the variance in sex ratio patterns seen in nature. In fact, sex ratios have been shown to range from strongly male biased to strongly female biased. Sex ratios should reflect differences in investment pattern required to produce sons and daughters. Fisher (1958) originally proposed that the sex ratio produced by a female should be the inverse of the investment ratio. Sex ratios should be produced such that the female invests equally in both males and females. This theory seems to predict the sex ratio pattern in a number of groups, from insects to mammals (Frank 1983; Charnov 1982). However, under certain demographic conditions, the sex ratio is more female biased than predicted. The fitness of a female within a deme is generally highest if that female invests equally in males and females (assuming no local mate competition; Hamilton 1967). However, the fitness between demes within a population is generally higher if the females in that deme produce mostly females, since demes with a female-biased sex ratio will produce more of the dispersing female offspring than a deme whose sex ratio is 50 percent males. Thus, there is a difference between the sex ratio patterns expected from the two levels of selection, within deme and between demes. If deme size is large enough, the effect of the lowest level will override the effect at the higher level and the sex ratio will be explained by Fisher's equal investment theory (again assuming no local mate competition). When deme size is very small and little breeding occurs between demes, the effect of inter-demic factors becomes more important and the sex ratio becomes more female biased. Conflicts between levels may also arise when subgenomic elements such as mitochondria or viral infections influence sex ratio. Here there may be a conflict between the equilibrium sex ratio at the level of the subgenomic element and the equilibrium sex ratio at the level of the individual. Which model produces the most generality? One could argue that each model (equal investment, group selection, and subgenomic selection) will work under specific conditions, and therefore will be generally applicable under those conditions. On the other hand, if each of the levels of selection is incorporated into a hierarchical framework, then the framework itself will be generally applicable under all conditions. If there are no subgenomic particles and deme size is large, the framework collapses to the original investment ratio theory. If deme size is small and interdemic genetic exchange is low, the framework collapses to the group selection model. This feature of collapsibility is especially compelling, since it may allow us to examine specific levels somewhat independently of other levels.

Collapsibility will be most applicable when the model is collapsed on non-feedback subsystems (see Hierarchy discussion above). This is because the constraints imposed by higher levels on the non-feedback subsystem can be treated as a constant in the model. Also the effect of decisions at lower levels are not incorporated into the decision process, therefore complex time components associated with feedback loops are lacking. Chapter IV is a good example of this. In this chapter I showed that diet choice should reflect the degree to which foraging bout length is constrained. The time constraints model (see Chapter IV) can be used irrespective of the factors that constrain bout length. Thus, the framework could be collapsed and treated as a single constraint within which diet choice decisions must be made. I cited studies where tidal cycle, predator pressure, and intra-specific pressures constrain bout length, yet the influence of each factor on diet choice is identical: as foraging bout length decreases, the diet should become more catholic. The regulation of foraging bout length is a decision about time sharing: how much time should the forager devote to each category of behavior (i.e. foraging, mating, etc.)? A study of this decision would be more complex, because time sharing is a feedback subsystem. To study this behavior properly, the dynamics of at least two levels of decision need to be modeled. For example, with the time-sharing decisions wrens make when foraging for nestlings, the wren must decide to forage or stay and provide predator defense for her young. The two factors are not mutually exclusive, since feeding the young provides a predator deterrent. This level of decision was treated as a "black box" in my study. This decision is a feedback subsystem, because the amount of time required for foraging should be regulated by the net benefit derived from that foraging time. Thus, the study of time sharing in wrens requires at least two submodels to characterize the system. It may need more depending on the structure of the hierarchy.

Most behavioral systems can be characterized by a hierarchy of decisions or effects. If we want to study the system as a whole, then we must study the entire hierarchy if we are to understand the behavior. As illustrated above, if we are interested in specific portions of the hierarchy, then the framework can be collapsed, depending on the type of subsystems characterizing the decision of interest. In chapter I, I showed that the structure of an antlion's pit appears to maximize capture probability. The morphology of the pit included a layer of fine sand on the pit walls, which was shown to retard the escape of prey. Although there are a number of physical characteristics of sand that would tend to generate this type of design, the antlion clearly exhibits a number of behaviors that tend to make use of this particle-size/prey-escape relationship. Antlions regulate both particle velocity and trajectory angle. They also retain small particles inside the pit until the basic shape is attained, after which they line the pit with this fine sand. In addition to particle size distribution, the pit is also characterized by two other features, slope and diameter. Particle size distribution is non-hierarchical in that there are no constraints imposed on this characteristic of pit morphology and the functioning of the pit. The more fine sand on the walls, the better it will function. Pit diameter is quite different. Here the energy invested in enlarging the pit should reflect the expected gain from that investment. The decision is characterized by a feedback subsystem. The decision cannot be addressed without a full knowledge of both the energetics of pit construction and the return from that investment. The same may hold true for pit slope. A simple study of pit morphology is possible due to the non-feedback nature of the decisions associated with that level of organization. A study of the regulation of pit diameter and slope will require a more thorough study to yield the same answer. The decision structure associated with pit-construction behavior would have to address the entire hierarchy, from pit morphology to pit diameter and its relationship with net benefit.

When testing any model, the model gives us a framework within which we can view a system. The model also directs the experimental approach that is taken to study the system. In studies of foraging behavior, the specific models that have been formulated have been useful in some studies, but misleading in others. These mistakes appear to be caused be the restrictive nature of the single model approach. The use of systems-oriented, hierarchical models appears to be a much more powerful method of analysis. Once the system has been characterized, the hierarchy can be collapsed to address specific features of the system. Thus, a systems-level approach will enhance generality, since it can be used to address a broad spectrum of problems. It should increase our ability to understand any system because it forces us to view a number of features of the system under study. It will also allow us to simplify the question. This reduces the complexity of the question and increases our ability to measure the parameters that are important in each subsystem.

CONCLUSIONS

In evaluating the utility of optimality modeling, two issues must be addressed. The first is whether or not the basic assumptions associated with the technique are consistent with observations. Of course, the most basic assumption is that animals are capable of making decisions that approach the theoretical optima. The second issue is a heuristic one. Does the technique provide insight into animal behavior that would otherwise be overlooked using other approaches?

This dissertation covers three different temporal stages of foraging behavior, (1) the preparation for prey capture (specifically trap construction by antlion larvae), (2) the choice of prey, and (3) handling of prey once diet choice decisions have been made (specifically partial prey consumption). Optimal foraging models were used to evaluate each aspect. The results of the study indicate that foraging decisions are invariably constrained by factors that are unique to each stage of foraging. In each case when the constraints were built into foraging decision models, the behavior exhibited by the organisms under study was consistent with the predictions from the models. Trap-constructing behavior is consistent with the prediction that antlions should maximize the net energetic return from foraging through the manipulation of trap design. However, trap design is constrained by the physical properties of the material with which it is built. Thus the study of trap-constructing behavior can only be accomplished through the characterization of physical constraints imposed on this behavior. Diet choice can be similarly constrained by features of the animal's environment. In systems where foraging time is limited through either biotic or abiotic factors, optimal diet choice must be modeled by explicitly including these factors in the model. Predictions from such models agree with the observed diet choice of a variety of animals. Time constraints may also be important in decisions concerning the utilization of prey by foragers that only partially consume prey. Predation modes (e.g. search or ambush methods) will impose unique constraints on the ability of animals to utilize their prey. Here again, if these constraints are included in foraging decision models, the output of the models agrees with the behavior exhibited by foraging animals. From the studies reported in this dissertation, it can be concluded that observations of animal behavior have been consistent with the assumptions and predictions from optimality models, but only if constraints are explicitly included in the models.

Several models were reviewed in this dissertation which failed to incorporate the factors listed above. As a result, the authors of these studies concluded that the animals used in the experiments were not foraging optimally. If we ignore the fact that this conclusion is inappropriate to the technique (see Introduction and Chapter V), the inability of these earlier optimal foraging models to predict behavior suggests that these models were not robust enough to use under a diversity of foraging conditions. Since any given model provides a framework within which the researcher can formulate predictions, these models seem to restrict the perception of behavioral systems as much as they provide insight into behavioral adaptations. The use of optimality models to study animal behavior appears to be valid, but the application of this technique to foraging-behavior studies appears to be limiting our perception of behavioral systems. The non-hierarchical nature of most optimal foraging models is undoubtedly a major contributing factor in this limitation. I propose that models of behavior should be constructed using a hierarchical design. Unlike previous foraging models, hierarchical models require a synoptic perception of behavioral systems, and therefore are not restrictive in their predictive value. The utility of this approach is demonstrated in Chapter IV, where a single model was used to analyze foraging behavior of three taxonomically disparate organisms under extremely different environmental constraints.

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BIOGRAPHICAL SKETCH

Jeffrey Robert Lucas was born in January, 1953. He received his B.S. degree at the Florida Institute of Technology and his M.S. degree at the University of Florida. During his tenure at the University of Florida, Jeff worked on a project funded through the Florida Power Corporation which evaluated the effect of heated effluents on the productivity of estuarine bays. He also worked as a teaching assistant in the Department of Zoology. The fact that he met and married Lynda Peterson should not be overlooked. He has received a NATO Postdoctoral Fellowship to continue his antlion project with Dr. John Krebs at Oxford. Tally ho.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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