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BEHAVIORAL ASPECTS OF PREDATION AND RESOURCE ALLOCATION

by

Leslie Allan Real

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
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in The University of Michigan
1977

Doctoral Committee:

Associate Professor John H. Vandermeer, Chairman
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Professor Marc H. Ross

When first I applied my mind to Mathematics I read straight away most of what is usually given by the mathematical writers . . . I was not surprised that many people, even of talent and scholarship, should, after glancing at these sciences, have either given them up as being empty and childish or, taking them to be very difficult and intricate, have been deterred at the very outset from learning them . . . But when I afterwards bethought myself how it could be that the earliest pioneers of Philosophy in bygone ages refused to admit to the study of wisdom any one who was not versed in Mathematics . . . I was confirmed in my suspicion that they had knowledge of a species of Mathematics very different from that which passes current in our time.

Rene Descartes

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INTRODUCTION

Recent years have seen a marked elevation of interest in the quantitative analysis of behavior. As yet, no great body of literature devoted to the more theoretical aspects of animal behavior exists similar to that which is available in the ecological and evolutionary literatures. Especially lacking, surprisingly enough, are investigations concerned with the quantitative relationships between the ecological setting of the organism and the organism's behavioral response to that setting. Any treatment of an organism's behavior must include these inseparable relations, and inclusion of these relations is of primary importance in any theoretical structure postulated as a behavioral description. With this in mind, the chapters that follow represent the writer's theoretical and empirical formulations on certain of these aspects of animal behavior.

This discussion is concerned with one basic behavioral question, namely, given a set of resources, distributed within a particular ecological setting, how does the organism utilize the resources over a short interval of time? Although the basic question is the same throughout the text, the analytical approach presented in chapters one and two is different from that in chapters three and four. They are different in both method and intent. Before describing the exact differences between these two approaches, I would like to discuss the reasons for choosing these different perspectives in analyzing behavioral questions.

In any analysis of a particular phenomenon or natural action, one can basically ask two questions. First, <u>how</u> does this phenomenon occur? This question usually results in a description of the system under investigation and may include a description of the various forces acting upon the system, causing or controlling the actions of the system at any moment in time. The best example of this approach is Newton's analysis of the motion of a particle given certain forces acting upon the particle in space.

Secondly, one can ask the question, <u>why</u> does this phenomenon occur? At this point, we must look at the phenomenon from a completely different perspective. Simple descriptions of the phenomena are no

longer adequate, and we are forced to look at underlying reasons for the existence of the phenomena themselves. Asking the question "why?" generally leads to the formulation of a principle or rule which will govern the behavior of the system. For instance, Newton's laws of motion are excellent descriptions of how a particle will move in space, but they do not address themselves to the question of "why" the particle moves in a prescribed fashion. It was not until the late 18th century, with the introduction of Lagrange's method, that the "why" of particle motion was understood. It was understood in the following way. Lagrange showed that the Newtonian laws of motion were reducible to one unifying principle, the principle of least action, which stated that a particle would travel that path which minimizes the potential energy within the system. We now see "why" the apple falls from the tree in a straight line, since it is that path that minimizes the potential energy.

Frequently, the difference in these two approaches is typified by whether the system is represented by a set of differential equations describing the system or whether the system is represented as having some objective or goal. This objective is usually represented by some characteristic of the system either being maximized or minimized. It is not coincidence that the unifying principle of evolutionary biology is usually expressed in terms of a mixiмization principle, i.e., maximizing the genetic representation in future generations or maximizing fitness (Wright, 1937). This tells us the "why" of evolutionary patterns. It is ironic that evolutionary biology may have found its unifying principle before developing its descriptive methodology.

I have purposefully used these examples from physics to illustrate the differences between chapters one and two and chapters three and four; for the differences between these chapters are the differences between the "how" and the "why" of behavioral ecology.

The analysis presented in chapter one is constructed to determine the pattern of resource allocations among competing individuals of the same and/or different species in some habitat. It is not a descriptive analysis of resource allocation, but considers the organism to be allocating resources according to some objective or

maximizing principle. It is postulated that competing individuals have at their disposal various activities which can be carried out at different intensities and consume or produce resources in the habitat linearly. The linearity of resource utilization restricts the analysis to cases of exploitative competition. Each resource is assigned values representing the reproductive gain and cost to the organism incurred while using the resource. The individuals attempt to choose the amounts and kinds of resources which maximize the net reproductive gain. Resource utilization is restricted by the availability of resources in the habitat, the patterns of consumption associated with the activities of the individuals, and the demand for the individual resources (fixed through competition pressure) in the habitat. It is proved that under these restrictions, a competitive equilibrium exists where resources are utilized so as to maximize individual reproductive gain and that this equilibrium generates the most efficient utilization of the resources in that habitat.

Chapter two generalizes the optimization approach to any kind of objective function and any number of constraining relations. It is demonstrated that any such system when maximized must satisfy the Lagrange equations. A biological interpretation of the Lagrange multipliers is given, showing that the multipliers are measures of the relative importances of the associated constraints in determining the organism's behavior.

With chapter three, we change from the optimization approach to a description of a particular animal behavior. A discussion of Holling's hyperbolic functional response relationship is presented and the formulations expressing the underlying organismal interactions which might generate such relationships are generalized to the sigmoidal functional response exhibited by learning predators. An equation derived through an analogy with allosteric enzyme kinetics is given which will account for both the hyperbolic and sigmoidal responses.

Chapter four uses the mathematical formulas developed in chapter three in the analysis of experimental results from some examples of functional response. The analysis concerns Peromyscus maniculatus predation upon insect larval forms and seeds under varying ecological situations. The analysis indicates that similar changes in an

organism's functional response can result from very different underlying behavioral mechanisms.

I feel inclined at this point to include a brief note on the utility of these two approaches. Albert Einstein once stated that there are basically two kinds of theory. One he called constructive, the other analytic. A constructive theory proceeds from little data and tries to encompass a large realm of phenomena. Although it has a high probability of being inadequate for explaining any particular case, it has the advantage of being very general and providing a framework in which many different kinds of questions may be asked. An analytic theory, on the other hand, proceeds from a greater store of fact. However, although it has a high probability of representing a realistic interpretation of a given phenomenon, it lacks generalizability and scope. For the case in hand - or the thesis in hand - chapters one and two may be regarded as constructive, while the remainder are analytic. Both types of theory are necessary. Both lead to important conclusions about the nature of reality. Holding to Richard Levin's statement that the "truth" is the intersection of independent "lies," the writer hopes that somewhere within this set of independent lies there exists a kernel of truth.

CHAPTER I

A GENERAL MODEL OF RESOURCE ALLOCATION AMONG COMPETING INDIVIDUALS

Within recent years many ecologists have become interested in the analysis of resource allocation by individuals of a particular species and by sets of species co-occurring in a defined habitat. Concurrently, the problem of optimal food choice by animals has been a theme of major interest in the ecological and behavioral literature (e.g. Emlen, 1966, 1968; Fretwell, 1972; Marten, 1973; Schoener, 1971). Proposed models of optimal food choice have been concerned with the maximization of energy (caloric) input to the organism, but have neglected general constraints operating on the individual, e.g., nutritional requirements. On the other hand, models of resource allocation among species have been limited to small numbers of species competing for a few resources. This chapter is intended to present a general model of the allocation of large numbers of resources between several individuals of the same and/or different species subject to defined constraining conditions.

Individuals associated with a particular habitat have at their disposal a number of ecological activities which they can operate at various levels or intensities. Individuals may be involved with such diverse activities as hunting, food storage, establishment of territory, nest building, etc. Suppose that the reproductive gain from operating an activity at unit level can be determined, and suppose that the individual seeks to maximize its total reproductive gain subject to certain limitations on the amounts of supplies available as inputs to the activities. In a more formal sense, suppose that an individual performs n activities $G_1,\ldots,G_n$ and has at its disposal m resources $R_1,\ldots,R_m$. The activity matrix, A, for the individual is given by the n x m matrix:

$$\begin{array}{c} \\ G_1 \\ \vdots \\ G_n \end{array} \begin{array}{c} \begin{array}{ccc} R_1 & \cdots & R_m \end{array} \\ \begin{bmatrix} a_{11} & \cdots & a_{1m} \\ \vdots & & \vdots \\ a_{n1} & \cdots & a_{nm} \end{bmatrix} \end{array} = A,$$

where a_{ij} is the amount of R_j consumed when G_i is operated at unit intensity. An activity G_i is being operated at intensity x_i if the total consumption of resources is given by the numbers $x_i a_{i1}$, $x_i a_{i2}$, $\ldots, x_i a_{in}$. For this discussion we define the supply vector, S, as the vector of amounts of resources available for consumption in the habitat.

Assume there are q individuals in the habitat, where the kth individual can be represented by an activity matrix A_k. Our main problem will be to determine how the resources of the habitat are distributed among the component individuals. We will show that this problem is solved through the interactions of individuals in competition for resources in limited supply.

It is convenient to subdivide what we have loosely called resources into two categories: resources such as raw materials which the individuals compete for, and co-resources such as the available equipment which is rigidly attached to a given individual. For Escherichia coli glucose belongs to the first category while the enzymes of the glycolytic pathway belong to the second. In the establishment of territory in birds, space and nesting materials would be resources and associated visual and vocal displays would be co-resources. The category to which an item belongs may depend upon the particular application. For instance, for some purposes one may wish to think of mycorrhizal fungi as being rigidly attached to certain plants and carrying out fixed activities; for others one may assume that plants are competing for the symbiotic relation afforded by the fungi, or visa versa.

It is easy to introduce this distinction between supply types into the model. One method of doing this would be to divide the supply vector into those elements indicating resources and those indicating co-resources. An equivalent and notationally more convenient method is to split the activity matrix as well as the supply vector into two parts. Let us first consider the case of co-resources.

Let $X_k = (x_{1k}, x_{2k}, \ldots, x_{nk})$ be the intensity vector for the kth individual. This vector is limited by the available co-resources according to the inequality:

$$X_k B_k \leq b_k, \tag{1.1}$$

where b_k is a vector giving the amounts of various sorts of co-resources available to the kth individual. The ijth element of the matrix B_k gives the amount of the jth co-resource used to operate the ith activity at unit level. Note, both B_k and b_k are nonnegative.

Subject to condition (1.1) above the kth individual consumes or produces resources in a linear manner. That is to say, there is a matrix A_k such that at intensities X_k the individual consumes (or produces) the vector of resources X_kA_k. The matrix A_k need not be nonnegative and we shall choose our signs so that a positive coordinate of X_kA_k corresponds to an amount consumed; a negative coordinate to an amount produced. It is easy to see how individuals may be actively producing resources if we consider symbiotic relationships occurring in the biotic community.

There is now the important further constraint which states that the aggregate of all the individuals must not use up more resources than the habitat can provide. Let $S = (\sigma_1,\sigma_2,\ldots,\sigma_m)$ be the vector such that σ_j is the maximum amount of the jth resource which is available in the habitat. Then the desired condition takes the form:

$$\sum_{k=1}^{q} X_kA_k \leq S. \tag{1.2}$$

Returning now to the resource allocation problem we see that we are looking for a set of vectors X_k which satisfy the inequalities (1.1) and (1.2). As yet no objective function has been introduced, and, in general, there will be an infinite number of solutions to these inequalities. We shall now describe how competition could act to determine such a solution.

In any community, organisms will be limited in one form or another by some primary factor (or the interaction of factors) of production (Liebig's Law of the Minimum). Suppose that an arbitrary nonnegative set of values $P = (\pi_1,\pi_2,\ldots,\pi_m)$ has been assigned to the various resources of the habitat indicating the reproductive cost (i.e., the amount to which reproductive success is reduced) by utilizing one unit of resource j, π_j. Let Ψ_i^k be the reproductive gain to the kth individual from operating the ith activity at unit level. Then the

gross reproductive gain from operating all activities at levels given by the vectors X_k is X_kC_k where $C_k = (\psi_1^k, \psi_2^k, \ldots, \psi_n^k)$. The reproductive cost of this operation is given by X_kA_kP. The individual will try to act so as to maximize its reproductive gain given by the expression $X_k(C_k - A_kP)$. In other words, given the value vector P the kth individual acts so as to solve the maximum problem of finding a nonnegative vector X_k such that

$$X_k(C_k - A_kP) \tag{1.3}$$

is a maximum subject to condition (1.1).

However, if each of the q individuals acts so as to solve the above maximization problem the vectors X_kA_k obtained will in general not satisfy condition (1.2), that is, the utilization of resources demanded by the various individuals may not be compatible with the available resources. Classical ecological theory asserts, according to Liebig's Law, that the reproductive costs of the limiting factors will increase as these factors become more limiting. These changes will result in a shift in the intensity vector X_k and the value vector P. Hopefully after a series of such adjustments equilibrium values for reproductive costs will be found such that there is no excess demand for any resource. An example might be in order at this moment.

Consider an organism or group of organisms in some habitat limited by some nutritional requirement, say water requiring rodents in a desert environment. We can see that the organisms expend a certain amount of energy in finding and utilizing foods so as to maintain water balance. This energy cost will be a function of the availability of water in the habitat. This availability will be related to the abundance of water containing foods and the magnitude of competition between individuals over these foods. It is well known that rodents show diet shifts in areas of species overlap (Alcoze and Zimmerman, 1973; Drickamer, 1970; Reichman, 1973). We can imagine that even if the resource is more abundant than some other resources in the habitat (within some definite range), if those other resources are under less demand (the magnitude of competition thereby being lowered) their availability to individuals in the habitat will be greater and we can expect to see a greater representation of those foods in the diets of the animals.

Assume also that there is a very large quantity of magnesium salts in the foods of the habitat. In this case, little if any energy will be expended in utilizing magnesium in the diet. Thus, the value for π water will be very high; while π magnesium will be comparatively low.

Organisms are well known to exhibit sampling programs and shifts in diet associated with shifts in availability of food items (Allen and Clark, 1962; Gibb, 1962; Goss-Custard, 1970; Moment, 1962; Popham, 1941, 1942; Royama, 1970; Tinbergen, 1960; Whitaker, 1966). We expect these shifts in resource utilization after sampling to be sensitive to the magnitude of competition with high-cost, low-gain resources being phased out of use. The vector X_k indicating the intensity at which the various activities use the resources is sensitive to the values of vector P using high-cost, low-gain resources less often. Since these items will be used less often there will be a decrease of competition over these resources, thus causing shifts in the values of P. As was already pointed out, after a series of such adjustments equilibrium values for reproductive costs can be found. The distribution of resources induced by these equilibrium values is the solution of the allocation problem. We can use linear programming theory to prove the existence of such values; whether they are ever reached in nature remains to be tested.

There is one additional requirement to be made on the equilibrium values. We have remarked that by Liebig's Law the value or reproductive cost of limiting resources will increase. We can use the same law to state that if a resource is over-abundant, then its reproductive cost will drop and approach zero. We can now say that a set of m + 1 vectors $(X_1, X_2, \ldots, X_m, P)$ is said to yield a competitive equilibrium if they satisfy conditions (1.1), (1.2), and (1.3) and in addition

$$\sum_{k=1}^{a} X_k A_k v_j \leq \sigma_j$$

implies $\pi_j = 0$, where v_j is the unit vector for the jth coordinate.

Before proving the existence of a competitive equilibrium we make the important ecological observation that if an equilibrium exists, resources will be distributed in such a way as to maximize the total

gross reproductive input to the community. Formally we have the following.

THEOREM 1. If $(X_1, X_2, \ldots, X_m, P)$ yields a competitive equilibrium the vectors X_k maximize the function $\sum_{k=1}^{q} X_k C_k$ subject to conditions (1.1) and (1.2).

Proof. Let X_k' be any vector satisfying (1.1) and (1.2). Then from (1.3) we have

$$X_k(C_k - A_k P) \geq X_k'(C_k - A_k P), \quad \text{for all } k.$$

Summing these inequalities over k gives

$$\sum_{k=1}^{q} X_k C_k - \sum_{k=1}^{q} X_k' C_k \geq \sum_{k=1}^{q} X_k A_k P - \sum_{k=1}^{q} X_k' A_k P. \tag{1.5}$$

From (1.2) we know that $\sum_{k=1}^{q} X_k' A_k \leq S$ so $\sum_{k=1}^{q} X_k' A_k P \leq SP$. But from (1.2) and (1.4) it easily follows that $\sum_{k=1}^{q} X_k A_k P = SP$. Therefore, the right-hand side of (1.5) is nonnegative and hence:

$$\sum_{k=1}^{q} X_k C_k \geq \sum_{k=1}^{q} X_k' C_k.$$

This result is quite similar to MacArthur (1972) and Gill's (1972) conclusions on exploitative competition. That is, under exploitative competition, utilization of resources within the community will be maximally efficient. The assumptions of linear resource utilization make the present model similarly one of exploitative rather than interference competition. We shall now prove the existence of a competitive equilibrium.

THEOREM 2. If the total gross reproductive input to the community is bounded above, then there exists a competitive equilibrium. (Note that this condition is always satisfied since a perfectly reproducing system is bounded by the total energy entering the system).

Proof. Consider the maximum problem of finding nonnegative vectors such that

$$\sum_{k=1}^{q} X_k C_k \tag{1.6}$$

is a maximum subject to conditions (1.1) and (1.2). Since (1.6) is bounded above it attains its maximum for some sets of vectors $\overline{X}_k$, and therefore from the duality theorem of linear programming (see Karlin, 1959) there exists nonnegative vectors $\overline{Y}_1,\ldots,\overline{Y}_m$ and P such that

$$B_k \overline{Y}_k + A_k P \geq C_k, \quad \text{for all } k, \tag{1.7}$$

and

$$\sum_{k=1}^{q} \overline{Y}_k b_k + PS = \sum_{k=1}^{q} \overline{X}_k C_k. \tag{1.8}$$

We assert that the vectors $\overline{X}_k$ and P give the desired equilibrium. To show this we must verify that $\overline{X}_k$ satisfies (1.3). That is, each $\overline{X}_k$ maximizes $X_k(C_k - A_k P)$ subject to (1.1) above. The dual of this problem is that of finding a nonnegative vector Y_k such that $Y_k b_k$ is a minimum subject to

$$B_k Y_k \geq C_k - A_k P. \tag{1.9}$$

Now the vector $\overline{X}_k$ is clearly feasible for this problem, and from (1.7) we see that $\overline{Y}_k$ satisfies (1.9) and is therefore feasible for the dual problem. By the optimality criterion $\overline{X}_k$ will be optimal if

$$\overline{Y}_k b_k = \overline{X}_k(C_k - A_k P). \tag{1.10}$$

To prove (1.10) note that $\overline{Y}_k b_k \geq \overline{X}_k(C_k - A_k P)$ or

$$0 \leq \overline{Y}_k b_k + \overline{X}_k A_k P - \overline{X}_k C_k, \quad \text{for all } k. \tag{1.11}$$

Summing (1.11) over all k gives

$$0 \leq \sum_{k=1}^{q} \overline{Y}_k b_k + \sum_{k=1}^{q} \overline{X}_k A_k P - \sum_{k=1}^{q} \overline{Y}_k C_k. \tag{1.12}$$

Now from (1.2) the right-hand side above is at most $\sum_{k=1}^{q} \overline{Y}_k B_k + PS - \sum_{k=1}^{q} \overline{X}_k C_k$, but from (1.8) this expression is zero. It follows that equality holds in (1.12). But the right-hand side of (1.12) is the sum of the nonnegative terms on the right-hand side of

(1.11). Therefore, each such term is zero, which gives the desired equation (1.10). Finally, we note that the vectors $\bar{X}_k$ and P satisfy condition (1.4), for this condition is precisely the statement of the equilibrium theorem applied to constraints (1.2).

In summary, under the assumption of linear resource utilization (valid under the restriction to exploitative competition) and subject to the limitations of resource availability within the habitat, an equilibrium point exists which results in maximal resource utilization within the habitat. This equilibrium point is reached through competition for limiting resources and each individual in the habitat trying to maximize its own reproductive gain.

As the simplest example of the biological applications of this approach, let us examine the selection of a diet by an organism not in competition with other organisms for food items (i.e., the magnitude of competition is zero and all foods are available according to their absolute abundance).

Many behavioral ecologists have speculated on mechanisms of optimal food choice in animals (Emlen, 1966, 1968; MacArthur and Pianka, 1966; Marten, 1973, Rapport, 1971; Westboy, 1974). Suppose our animal under investigation is presented with n different foods in the wild. Call these n foods $F_1, F_2, \ldots, F_n$. From these n foods the animal must choose a diet subject to satisfying the conditions of the general allocation of resource problem. In general, organisms have a certain set of nutrient requirements which must be incorporated into the diet. Let the nutrients be denoted by $N_1, N_2, \ldots, N_m$. Suppose that our animal is required to consume at least λ_1 units of F_1, λ_2 units of $F_2, \ldots, \lambda_m$ units of F_m, per day. Let β_{ij} denote the amount of the ith nutrient contained in one unit of the jth food. Then we see that the diet must satisfy the nutritional requirements

$$\sum_{j=1}^{n} x_j \beta_{ij} \geq \lambda_i, \quad \text{for all} \quad i = 1,2,\ldots,m.$$

Remember that $X = (x_i)$ represents the intensity vector of resource utilization.

Let us assume that associated with each food F_i there is a fixed

reproductive cost. This cost may entail the energy expended during hunting, preparation, digestion, etc. Let π_j be the total reproductive cost of one unit of food F_j. The total reproductive cost of the diet is then given by the expression $\sum_{j=1}^{n} x_j \pi_j$ which we require to be a minimum. In addition, let us assume that we can determine the amount of reproductive gain by utilizing one unit of F_j. Let ψ_j denote this amount. The total reproductive gain of the diet is the $\sum_{j=1}^{n} x_j \psi_j$ which we require to be a maximum. We see that the objective of the optimal food choice problem is to maximize the linear function

$$f(x) = \sum_{j=1}^{n} (\psi_j - \pi_j) x_j .$$

In some cases the nutritional requirements of the organism may be satisfied by any collection of foods and any number of diets are feasible. In this case we may be able to drop the constraints entirely. More realistically we can delimit the number of constraints to only a small collection of inequalities and deal only with them as constraints. For instance, in most animals it may be supposed that the only nutritional constraints are for the B vitamins and a small number of amino acids. Under these circunstances, all other nutritional constraints can be dropped.

Since it is very difficult to determine the reproductive gains associated with running any particular activity, many authors have analyzed diet problems (as well as other ecological problems) in terms of energetic gains and losses. Although this is mechanistically easier to handle, we must not forget that energetic relationships may not be directly related (or analogous) to reproductive relationships.

However, the present model could certainly be tested by looking at energetic costs and gains in organisms for which we have some knowledge of their nutritional requirements. This diet problem also is extendable into the general competition model by making π_j variable with competition pressure and by incorporating other activities beside choice of diet. The form of the model would remain the same. Thus, the model is testable in the general case with the kinds of experiments which are beginning to appear in the ecological literature.

Concluding Remarks

Three rather striking assumptions are implicit in any linear programming model: (1) the assumption of linearity, (2) the assumption of an equilibrium system, and (3) the assumption of a deterministic system.

Linearity. In all the models we have examined we assumed that the system can be described by annumerating the effects of all the independent components of the system and summing up effects over all the components. In this way we ignore all higher-order interactional effects. We are quite certain, however, that no natural system is completely devoid of higher-order phenomena. Therefore in order to be realistic we must introduce the added complication of nonlinear terms (which show up mathematically as multiplicatives of the various state variables). We now have two alternatives: (1) We assume that all nonlinear terms are small (i.e., all higher-order effects are negligible) and can be ignored, giving us a quite adequate linear approximation to the nonlinear system; or (2) we introduce the nonlinear terms and keep them there.

In many natural situations, linear approximations may prove to be quite adequate for our analysis. By keeping to a linear model we have the strong advantage of being able to find analytic solutions to the problems, an occurrence only rarely found in nonlinear systems. Linear models may be useful for heuristic reasons. Since a linear approximation lends itself to easy mathematical analysis, many interesting and important conclusions can be seen that would otherwise be missed in the fog precipitated by the inclusion of nonlinear factors. We may also use the theorems derived from linear approximations as hints to what analogous theorems may be deduced from the nonlinear sister system. Within this framework, I think that linear analysis should not be considered as trivial or uninteresting, but, on the contrary, as a fundamental step in the analysis of more complicated systems.

Alternatively, we stick to analyzing the nonlinear system as best we can. We could do this for a variety of reasons, e.g., the system under examination may have no good linear approximation which at all resembles the nonlinear system, or we may wish to develop and facilitate

the use of non-linear mathematical theory, or we may have exhausted the supply of information which we can get out of the linear approximation and wish to move on to more complicated analyses. Whatever the reasons, we can expand our preexisting linear programming theory into the theory of nonlinear programming, a mathematical programming theory designed specifically to handle higher-order interactions. Unfortunately, nonlinear programming has no general theory, and, much like the theory of nonlinear differential equations, can only handle special cases. This being the case we are severely restricted in choosing the form of our nonlinear model. A recent school of mathematicians, the "global analysts," believe they are on the verge of formulating a general theory of nonlinear programs. If the global analysts succeed, we will be in a position to analyze biological interactions that would otherwise be intractable.

Equilibrium assumption. In biological systems, the parameters which describe the system are in a continual state of change with respect to time; while in our models we have assumed that these variables attain constant values and remain constant regardless of time. We can, and many have, described biological systems as a set of differential equations. However, we are no longer interested in merely describing the system through time, but in analyzing the system as it changes through time toward some desired end. We immediately see that we may be in trouble. For if the system changes objectives from one time interval to the next, almost no mathematical analysis can be used and the analysis becomes hopelessly complicated. This exact situation exists in economic systems, and the failure of our present mathematical knowledge to handle this economic situation was first pointed out by Russell (Scott Gordan, personal communication). As a result of this dilemma, economists may only be able to analyze their systems over short intervals of time, and then the assumption of equilibrium is of no real consequence. Hopefully, biological systems do not operate in a similar fashion, and optimal dynamic strategies can be derived.

Determinism assumption. If we are lucky enough to come up with dynamical systems which adequately describe biological systems, these dynamical systems may be stochastic, i.e., where the state variables become probability functions of time, rather than deterministic, i.e.,

where the state variables have a fixed value at any instant in time. Our present models are all deterministic. If the probability distributions of the present state variables are dependent upon the probability distributions of the past state variables, that is, where the system "learns" from its past history, then the system is called adaptive. Biological systems seem to be of the adaptive type and are additionally under some forms of regulatory control. It is my belief that biological systems analysis will gain much by applying adaptive control processes with optimality criteria.

CHAPTER II

A LAGRANGEAN APPROACH TO OPTIMAL DECISION-MAKING IN ORGANISMS

Many authors have discussed optimal forms of decision-making by organisms. Usually the concern is either with predator preference behavior (e.g. Rapport, 1971; Tullock, 1971), diet selection (e.g. Pulliam, 1974; Westoby, 1974) or general resource allocation (chapter one). In general, these behaviors can be summarized by the following: given a limited set of available resources (prey), organisms choose resource combinations in such a way as to maximize their preference/benefit derivable from the resource (prey) while satisfying the constraints of the environment expressible in time/energy budgets, nutritional demands, competitive pressures, etc.

For example, in Westoby's paper, the organism must choose from some set of foods a diet which will satisfy the organism's minimal nutritional requirements and maximize the net energy gain derivable from using the food resources. The function to be maximized - the objective function - in this case is a single-valued function representing net energy gain whereas the nutritional requirements can be expressed as a system of (in)equality constraints, each constraint representing the demand for each of the nutrients necessary for survival.

In a more formal way, assume there are n different foods available to the organism. From these n foods the organism must choose a diet. Let the required nutrients be denoted by $R_1, R_2, \ldots, R_m$. Suppose that the animal is required to consume at least α_1 units of R_1, α_2 units of $R_2, \ldots, \alpha_m$ units of R_m, per day. Also let β_{ij} denote the amount of the ith nutrient contained in one unit of the jth food. Then the diet must satisfy the nutritional requirements:

$$\sum_{j=1}^{n} x_j \beta_{ij} \geq \alpha_i, \quad \text{for all } i = 1,2,\ldots,m \tag{2.1}$$

where $X = (x_i)$ represents the intensity vector of food utilization.

We assume that associated with each food F_i there is a fixed time/energy cost. This cost may entail the energy expended during hunting, handling, digestion, etc. Let π_j be the total cost of one unit of food F_j. The total cost of the diet is then given by the expression:

$$\sum_{j=1}^{n} x_j \pi_j$$

which we require to be a minimum. In addition let us assume that ψ_j represents the amount of energy gained in one unit of food F_j. Then the total gain of the diet is

$$\sum_{j=1}^{n} x_j \psi_j$$

which we require to be a maximum. We can see that the objective of the optimal diet problem is to maximize the linear function:

$$f(X) = \sum_{j=1}^{n} (\psi_j - \pi_j) x_j \qquad (2.2)$$

subject to the system of inequality constraints (2.1).

The intent of this section is to generalize the mathematical form of these problems involving maximization subject to a set of constraining relations by using the Lagrange method and to generate a biological interpretation of the Lagrange multiplier.

The following problem will be considered the general Lagrange problem: given some function $f(X)$, where X is a vector of resources of nth order, and a system of m equalities $g^i(X) = 0$, $i=1,2,\ldots,m$, $m<n$, find a maximum for $f(X)$ subject to the constraints $g^i(X)$. The method is to form the Lagrangean function

$$L(X,\lambda) = f(X) - \sum_{i=1}^{m} \lambda_i g^i(X)$$

where the λ's are the undetermined Lagrange multipliers. If we take the derivatives of $L(X,)$ with respect to the λ's we have:

$$\frac{\partial L}{\partial \lambda} = -g^i(X)$$
$$= 0 \quad , \quad \text{for all } X \text{ in } S$$

where S is the set of all feasible or attainable resource combinations as defined by the constraints. Also, for all X in S, $L(X,\lambda) = f(X)$. Thus if $L(X,\lambda)$ has a maximum at the point (X^*,λ^*), then since it is unconstrained it has a critical point there with all partial derivatives equal to zero. Since all the partial derivatives with respect to L are zero, we have X^* in S and $L(X^*,\lambda^*) = f(X^*)$, so that X^* gives a maximum for $f(X)$ over X in S and is thus the solution to the constrained maximum problem.

To use the Lagrange technique, we set the partials of the Langrangean equal to zero obtaining n equations of the form:

$$\frac{\partial f(X)}{\partial x_j} - \sum_{i=1}^{m} \lambda_i \frac{\partial g^i(X)}{\partial x_j} = 0, \quad j = 1,2,\ldots,n.$$

If for a suitable choice of λ's and X's we can find a solution to the above system of equations, then the vector of resources, X, which satisfies the system (with associated λ's) will maximize the constrained problem as well. In other words, for a vector X to be an optimal solution of the original constrained problem, X must satisfy the above system of equations for some suitable choice of Lagrange multipliers. We will now turn to an interpretation of the Lagrange multiplier.

Consider an optimization problem solved by the Lagrange method to give some solution (X^*,λ^*). Let the ith constraint be of the form $g^i(X) = b_i$.

Originally b_i was zero, but we wish to examine the consequences of relaxing one of the constraints. This would be equivalent to saying, for example, the organism now only reauires four liters of water a day as opposed to six.

We denote the optimal solution of $f(X)$ as V^*. V^* would correspond to something like the optimal vector of foods selected by the

organism in the diet example. Now a small relaxation in the ith constraint will permit small changes in the solution, but assume that the optimum conditions remain satisfied so that the new vector of resources is also optimal. The effect on the optimal value of the objective function, f(X), will be given by:

$$\frac{\partial V^*}{\partial b_i} = \sum_j \frac{\partial f(X)}{\partial x_j} \frac{\partial x_j}{\partial b_i} \quad . \tag{i}$$

From the constraints we have:

$$\sum_j \frac{\partial g^k(X^*)}{\partial x_j} \frac{\partial x_j}{\partial b_i} = 0, \quad \text{for } k \neq i$$

$$= 1, \quad \text{for } k = i \quad . \tag{ii}$$

If we multiply the kth equation in (ii) by λ^*_k and sum over k, we have:

$$\sum_k \sum_j \lambda^*_k \frac{\partial g^k(X^*)}{\partial x_j} \frac{\partial x_j}{\partial b_i} = \lambda^*_i \quad .$$

Subtracting this from the right-hand side of (i) gives:

$$\frac{\partial v^*}{\partial b_i} = \lambda^*_i + \sum_j \left[\frac{\partial f(X^*)}{\partial x_j} - \sum_k \lambda^*_k \frac{\partial g^k(X^*)}{\partial x_j} \right] \frac{\partial x_j}{\partial b_i} \quad .$$

The bracketed expressions on the right are the optimum conditions and are zero, so

$$\frac{\partial v^*}{\partial b_i} = \lambda^*_i \quad .$$

Thus λ^*_i corresponds to the rate of change of the optimal resource combination of the objective function, f(X), with respect to a slight relaxation of the ith constraint, other constraints remaining unchanged. In other words, the Lagrange multiplier is a measure of how fast an organism will change its optimal behavior if there is a slight relaxation of one of the constraints, for instance, the relaxation of competitive pressures or resource scarcity. The multiplier may be likened to a force being exerted on the organism's behavior associated with meeting the requirements of the constraining relationship; slight changes in a strong force resulting in rapid movements away from the original optimal solution. Given this interpretaion we can arrive at

some estimate of the relative importances of the different constraints in determining the organism's behavior. Those constraints which correspond to greater multiplier values will be more influential in determining an organism's pattern of behavior than those with lesser multiplier values.

CHAPTER III

THE KINETICS OF FUNCTIONAL RESPONSE

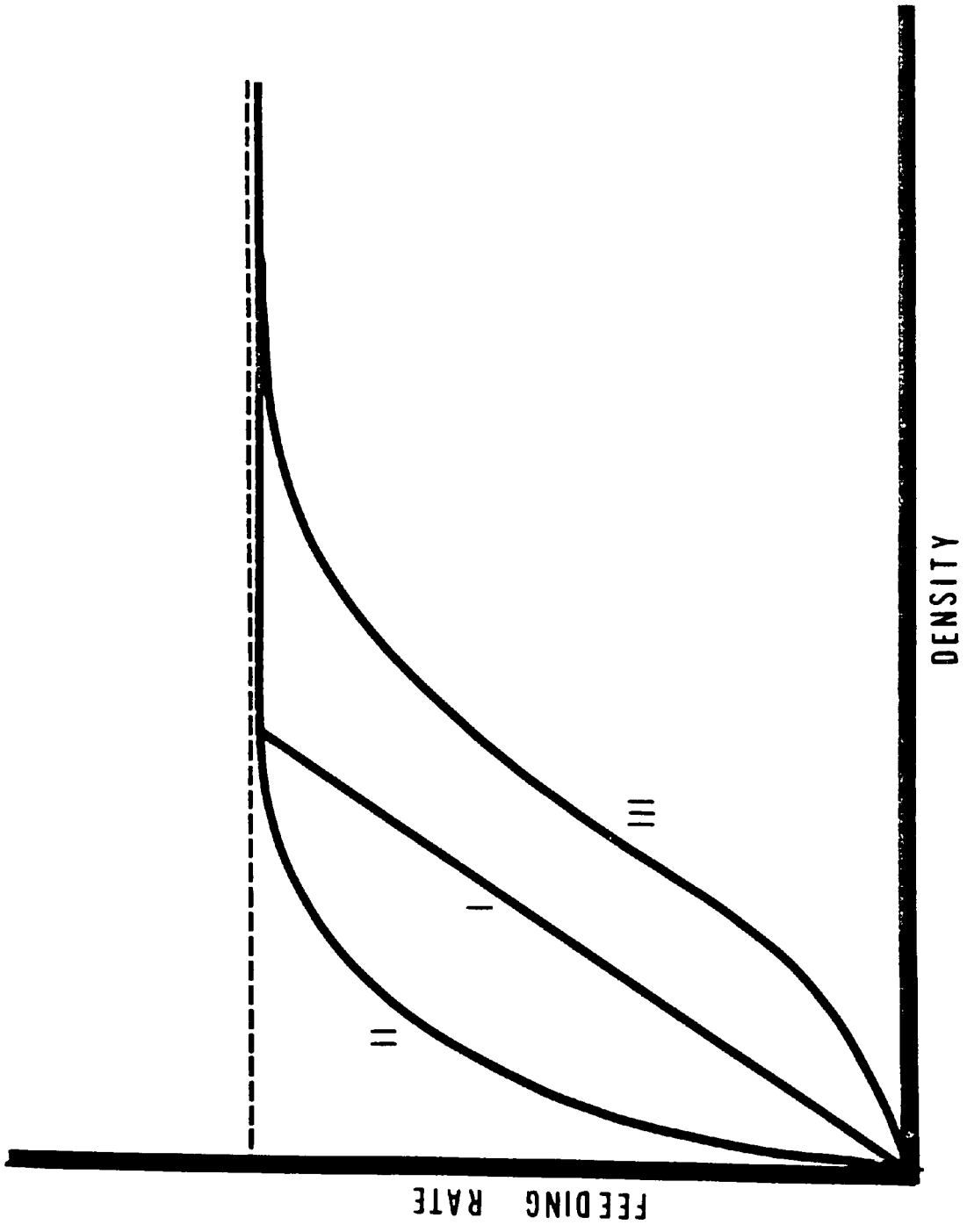
To date, C. S. Holling's studies (1959, 1965, 1966) stand out as the most comprehensive analysis of the factors influencing rates of resource utilization by predators. His research describes changes in a predator's feeding rate as a function of changes in the density of food items in the habitat. Holling calls these changes in feeding rate the organism's "functional response." In general, organisms show one of three types of functional response (Fig. 1). These response curves seem to correspond to three different kinds of foraging strategy: Type I curves are characteristic of animals who consume food at a rate proportional to their rate of encounter with food items (e.g. filter feeders) up to a saturation level where there is no longer any change in feeding rate with increased food density. Type II curves are characteristic of most organisms which take a certain amount of time to ingest and capture their foods. Many insect parasitoids follow this kind of functional response and the curve has been called the "invertebrate curve." The Type III curves are indicative of organisms which show some form of learning behavior, where below a certain level of threshold density the organism will not utilize the prey for food at any great intensity. However, above that density the organisms increase their feeding rates until some saturation level is reached. Holling reasoned that these animals tend both to learn slowly and forget the value of a food unless they encounter it fairly often. Thus, when a usual food item is scarce, it will be eaten proportionatly less often and a lag will appear in the functional response.

The first mathematical descriptions of functional response date from Holling (1965). He suggested the following derivation. Let N_A be the amount of food consumed, N_0 the amount offered, T_t the total time the animal has to feed, and T_h the time required to handle one food item, then

$$N_A \propto (T_t - N_A T_h)N_0 \text{ . so that } N_A = \frac{aT_t N_0}{1 + aT_h N_0} \qquad (3.1)$$

Figure 1. The three types of functional response (after Holling, 1959).

Figure 1



where a is a proportionality constant related to attack rate. A plot of N_A against N_O generates a Type II curve.

Emlen (1973) gives an alternative derivation using two food species i and j. If P_{is} and P_{js} represent the proportion of encountered food items of i and j that are eaten, then

$$\frac{N_{Ai}}{N_{Ai} + N_{Aj}} = \frac{N_{Oi}P_{is}}{N_{Oi}P_{is} + N_{Oj}P_{js}} = \frac{N_{Oi}}{N_{Oi} + (P_{js}/P_{is})N_{Oj}}$$

Since the total amount of food eaten, $N_{Ai} + N_{Aj}$, should be roughly proportional to the total amount of time feeding takes place, T_t, we can write:

$$N_{Ai} = \frac{N_{Oi}(N_{Ai} + N_{Aj})}{N_{Oi} + (P_{js}/P_{is})N_{Oj}} = \frac{N_{Oi}bT_t}{N_{Oi} + (P_{js}/P_{is})N_{Oj}}$$

If one defines

$$a = \frac{P_{is}b}{N_{Oj}P_{js}}, \text{ so that } N_{Oj}\frac{P_{js}}{P_{is}} = \frac{b}{a}, \text{ then}$$

$$N_{Ai} = \frac{N_{Oi}bT_t}{N_{Oi} + (b/a)} = \frac{aT_tN_{Oi}}{1 + (a/b)N_{Oi}} \qquad (3.2)$$

This is equivalent to an expression given by Tinbergen (1960), and is identical with equation (3.1) when (a/b) is constant.

Although these equations are adequate in describing the Type II functional response, they are not easily generalized, as formulated, into the Type III functional response. Holling (1965) does present a computer simulation model for the Type III curve. However, he uses approximately 53 parameters in his description (thereby losing generality) and does not relate the Type III curve to the Type II formulation in any clear way. The Type II functional response can be derived from first order kinetic interactions, however, and this analysis can be extended to Type III curves as follows.

An Enzyme-Predator Analogy: This derivation is based upon the analogy between organismal feeding and enzyme kinetics of non-allosteric enzyme reactions for Type II foragers and allosteric enzyme reactions for Type III foragers. The analogy can be made very strong by thinking

of enzymes as predators specialized on a particular prey item - their substrates - and noting that allosteric enzymes are essentially "learning" predators that become more efficient at utilizing substrate as substrate density increases.

The Type II organism's feeding interactions can be described by the equation:

$$A + C \underset{k_2}{\overset{k_1}{\rightleftarrows}} X \xrightarrow{k_3} P + C$$

where A represents some quantity of prey, say biomass; C biomass of predator; P the biomass incorporated toward the production of new predators; and X an intermediate form associated with handling, capture, etc. k_1, k_2, k_3 are the various rate constants associated with transformations into the designated states. The kinetic equations for the interaction are:

$$(3.3) \qquad -\frac{dA}{dt} = k_1AC - k_2X$$

$$(3.4) \qquad \frac{dX}{dt} = k_1AC - (k_2 + k_3)X$$

$$(3.5) \qquad \frac{dC}{dt} = (k_2 + k_3)X - k_1AC$$

$$(3.6) \qquad \frac{dp}{dt} = k_3X \text{ , plus the conservation constraint}$$

$$(3.7) \qquad C_0 = C+X \text{ , where } C_0 \text{ is a constant.}$$

The solution to these equations can be generated only numerically, and are graphed in Fig. 2. From the figure we note that a numerical solution shows that dX/dt and dC/dt become zero after a short interval of time. Steady-state approximations are then in order. Thus:

$$\frac{dX}{dt} \cong 0 \cong k_1AC - (k_2 + k_3)X \quad \text{or}$$

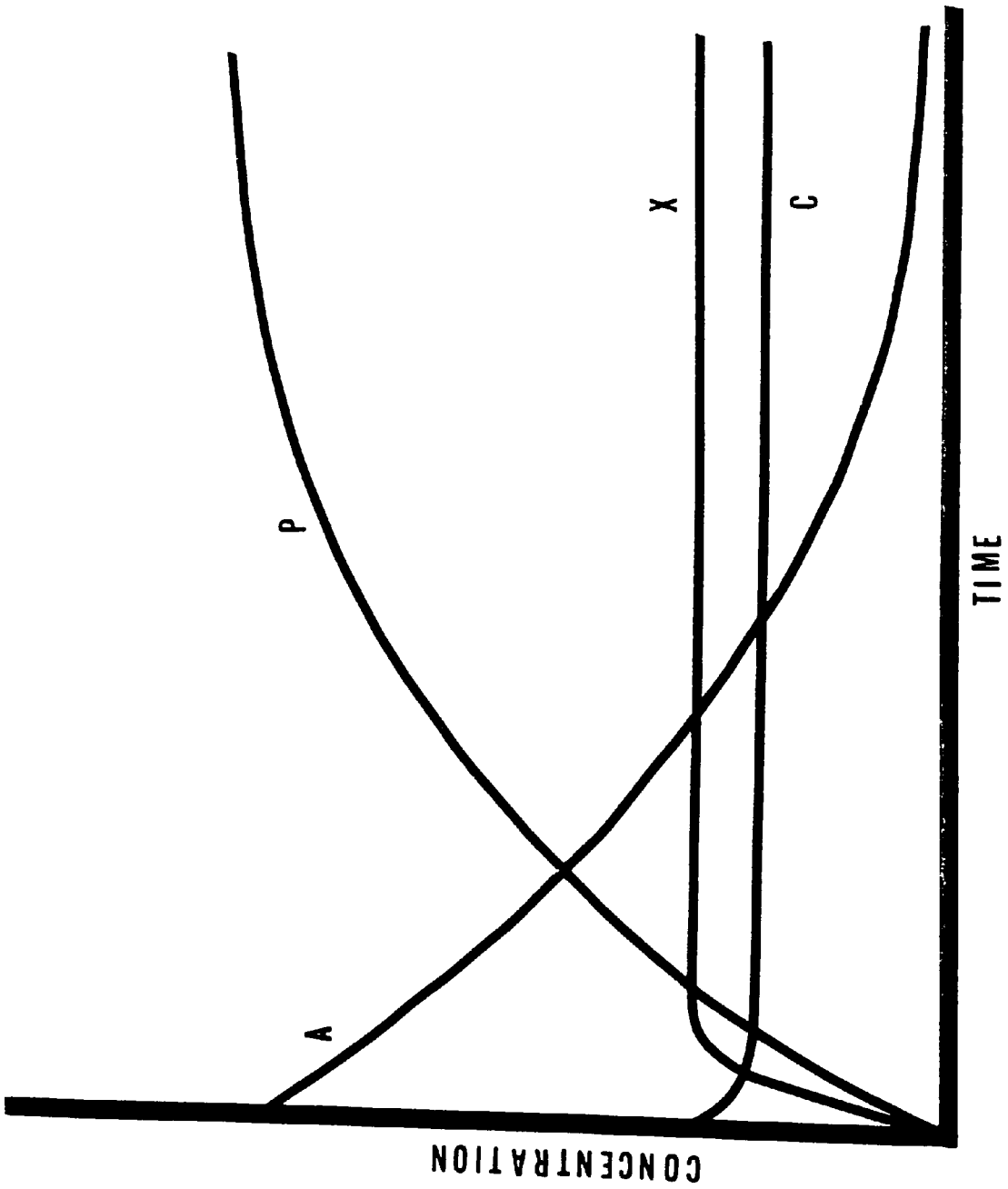
$$k_1AC = (k_2 + k_3)X \ .$$

Substituting this into equation (3.7) gives:

$$X = \frac{k_1AC_0}{k_1A + k_2 + k_3}$$

Figure 2. Numerical solutions to the dynamical system describing Type II feeding interactions.

Figure 2



and substituting this into equation (3.6) gives:

$$f = \frac{dP}{dt} = k_3 X = \frac{k_1 k_3 A C_o}{k_1 A + k_2 + k_3} = \frac{k_3 C_o A}{\left[\frac{(k_2 + k_3)}{k_1}\right] + A}$$

or $f = \frac{FA}{G + A}$, where $F = k_3 C_o$ and $G = (k_2 + k_3)/k_1$. Note this equation is identical to Holling's equation with $T_t = k_3 C_o$ and $T_h = k_1/(k_2 + k_3)$. The graphic representation of the equation is presented in Figure 3, where F is the maximal feeding rate and G is an affinity constant and is equal to the prey density at which feeding rate (f) is half-maximal (i.e. $f = F/2$). This equation is the famous Michaelis-Menton equation of enzyme kinetics, stating that substrate utilization is hyperbolic with change in substrate concentration. Many other authors have used the Michaelis-Menton equation in the analysis of predator-prey interactions (e.g. Canale, 1969, 1970). However, many enzyme reactions do not follow Type II kinetics, but instead show sigmoid behavior similar to the Type III functional response. We now turn to an analysis of such situations.

In 1909, Hill noticed that hemoglobin showed a sigmoid saturation response with changes in the partial pressure of oxygen (Fig. 4). He proposed the following model. Suppose that there were n binding sites for oxygen per hemoglobin molecule, the reaction between hemoglobin and oxygen could be described by the following equation:

$$Hb + nO_2 \longleftrightarrow Hb(O_2)_n$$

for which the binding constant (or equilibrium constant), K_b, was given by

$$K_b = \frac{\left[Hb(O_2)_n\right]}{\left[Hb\right] pO_2{}^n} \qquad (3.8)$$

where pO_2 is the partial pressure of oxygen, or

$$\left[H_b(O_2)_n\right] = K_b pO_2{}^n \left[Hb\right] \qquad (3.9)$$

In equation (3.8) the assumption was made that only two species of hemoglobin exist, Hb and $Hb(O_2)_n$; the possibility of stable

Figure 3. Graphic representation of Type II functional response equation $f = \frac{FA}{G + A}$.

Figure 3

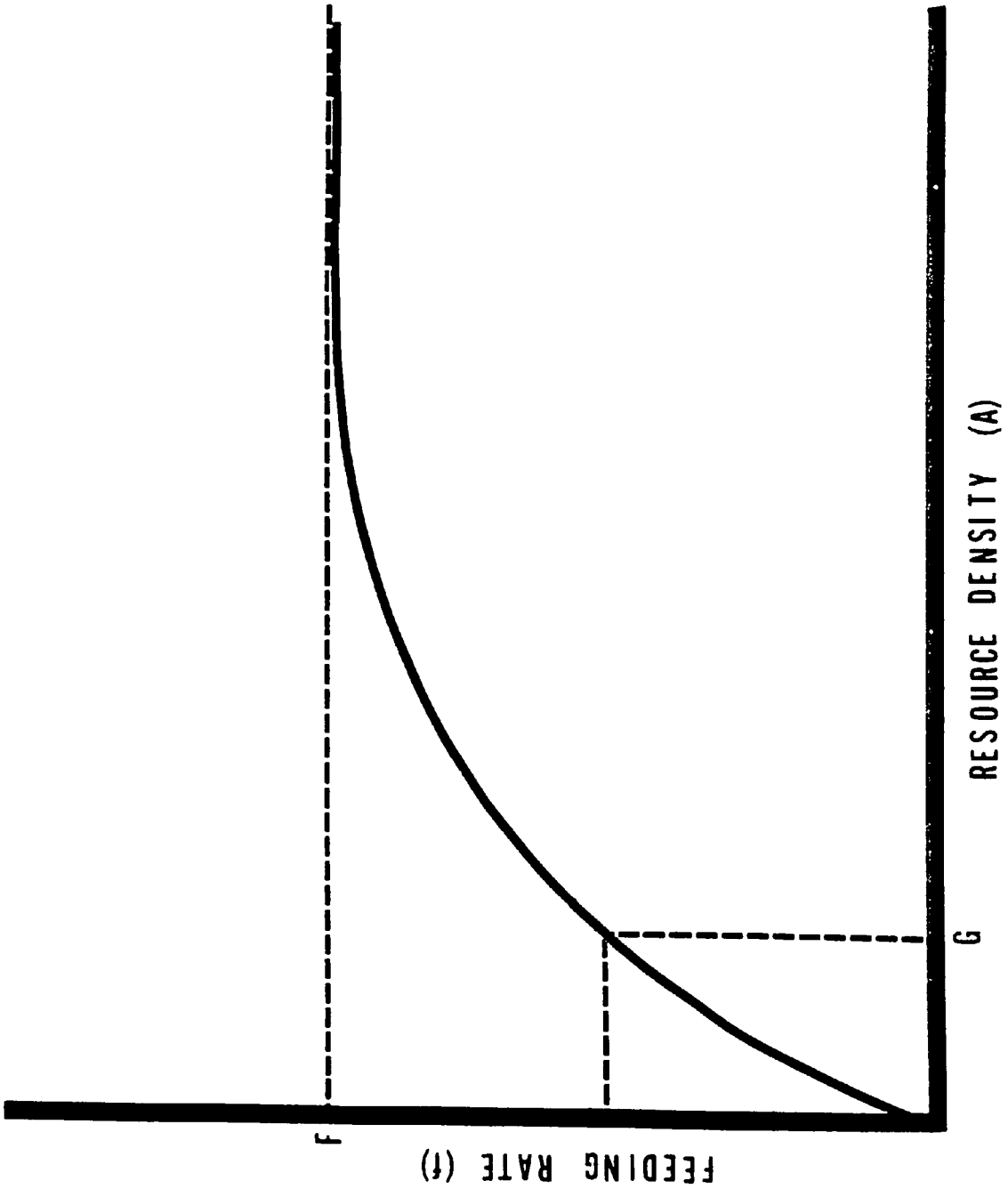
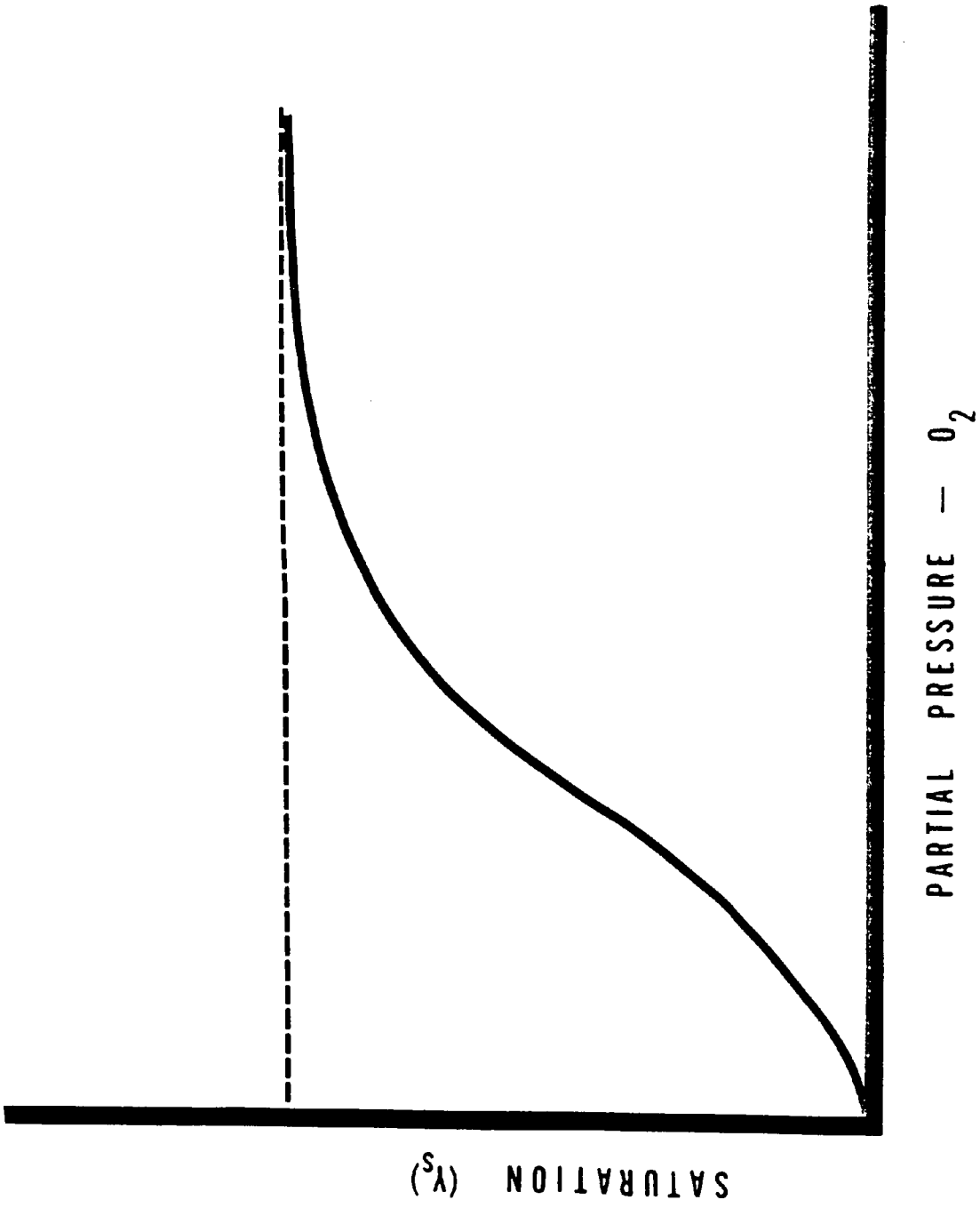


Figure 4. Hill plot of partial saturation of hemoglobin as a function of the partial pressure of oxygen.

Figure 4



intermediates such as $Hb(O_2)_{n-1}$ or $Hb(O_2)_{n-2}$; was not considered. The fractional saturation. Y_s, was derived terms of the binding constant, K_b, and the partial pressure of oxygen. pO_2:

$$Y_s = \frac{[Hb(O_2)_n]}{[Hb] + [Hb(O_2)_n]} \text{ by definition.}$$

substituting for $Hb(O_2)_n$ from equation (3.9), we get

$$Y_s = \frac{K_b pO_2{}^n [Hb]}{[Hb] + K_b pO_2{}^n [Hb]} = \frac{K_b pO_2{}^n}{1 + K_b pO_2{}^n} \qquad (3.10)$$

The situation for an allosteric enzyme with n binding sites is given by:

$$Y_s = \frac{v}{v_{max}} = \frac{A^n}{K_m + A^n} \text{ , where } K_m = \frac{1}{K_b} .$$

Note that if n = 1 (i.e., there is only one binding site) the equation reduces to the Michaelis-Menton equation. A plot of v against A gives a sigmoid response representing cooperativity as the binding sites are filled. For predator-prey systems, we see the analogous situation in feeding response of organisms showing some form of learning behavior, where n becomes the number of encounters a predator must have with its prey before the predator is maximally efficient at feeding on that prey item. As the number of encounters increases the functional response will look like a Hill plot. Thus the equation representing functional response would be:

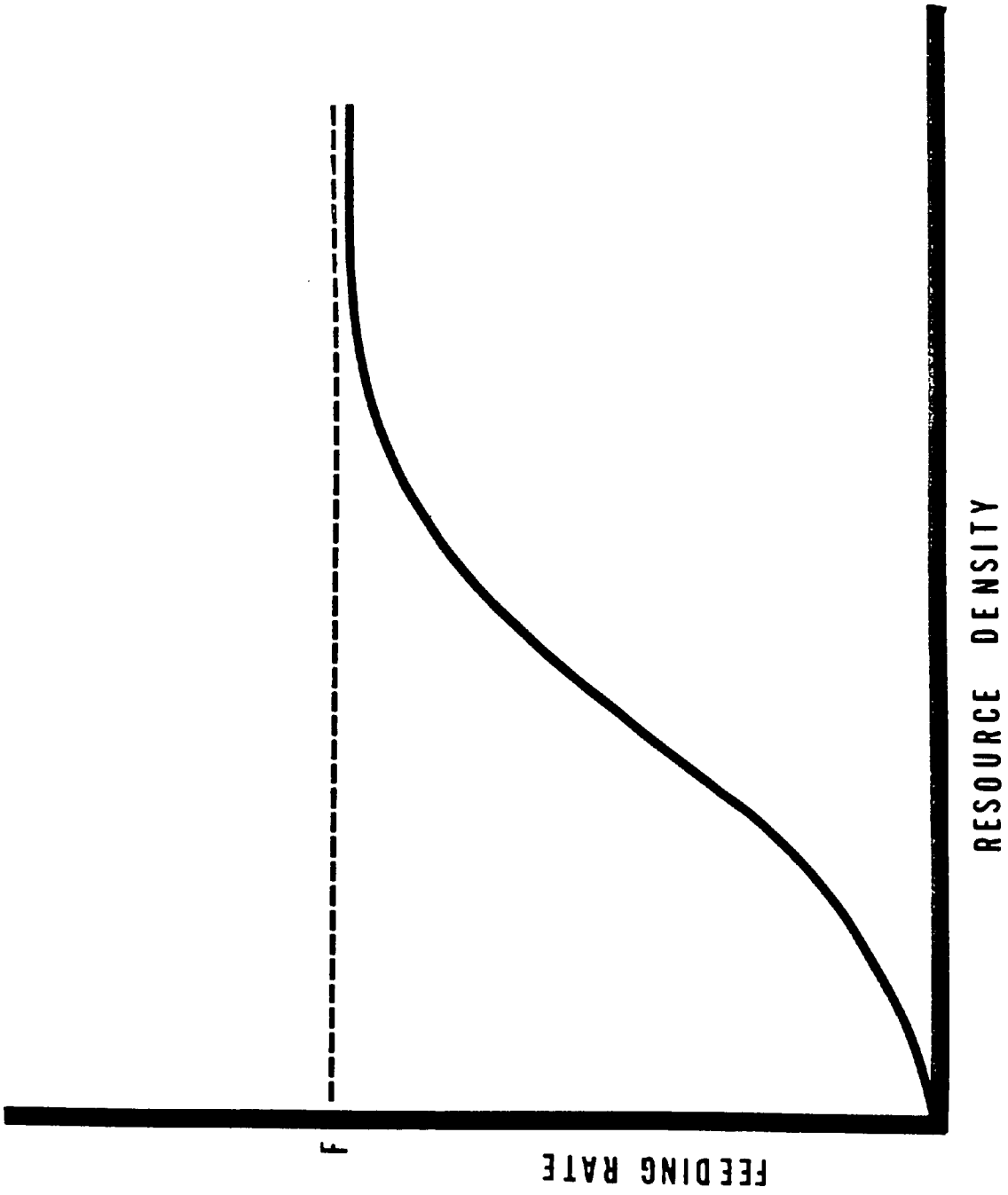
$$f = \frac{FA^n}{G + A^n} \qquad (3.11)$$

and is represented graphically in Figure 5.

We can make this point a little clearer biologically using Holling's notation. The number of encounters represented in the disc equation is directly related to "a" of equation (3.1). Equation (3.1) can be rewritten:

Figure 5. Graphic representation of the Type III functional response relation $f = FA^n/(G + A^n)$.

Figure 5



$$N_A = \frac{T_t}{T_h + \frac{1}{aN_o}}$$

In this form the biological meaning of the terms becomes clear, with the denominator on the right hand side of the equation being the time necessary to search for, pursue, catch, and eat one prey. One part of this denominator is the handling time per prey item, T_h, and the other is the time necessary to locate one prey. Thus the number of encounters is expressed as aT_tN_o. It would be most meaningful biologically to incorporate the effects of learning by expressing a, the rate of potential detection, as a function of number of encounters. From the previous formulations on learning predators, the time for locating one prey item would be:

$$\frac{1}{aN_o^n} = \frac{1}{(aN_o^{n-1})N_o} \quad .$$

Thus the rate of potential detection (or the detection area swept out in one unit of time) is aN_o^{n-1}.

This expression increases with N_o for $n > 1$. Thus, the rate of potential detection increases with density until feeding rate is eventually limited by handling time. Formulation in this manner also leads to a sigmoid response. If $n < 1$ then the rate of search or detection would decrease with increasing prey density.

It is important here to note that within this analysis the Type II and Type III functional responses are related to each other very nicely with the Type II response being a special case of the Type III response (i.e., $n = 1$, where a predator is always maximally efficient on the prey item). Thus the two responses can be looked at as one type of behavior; the only difference being in the size of n.

Holling (1959) and Murdoch (1968) have discussed the generation of predator switching behavior associated with the Type III functional response. Any learning process (Type III) which results in predators being able to actively alter their feeding rates and switch from less common to more common prey will generate a high efficiency foraging system; since they will be able to more closely track changes in

fluctuating predator populations and use many alternative resources. The following is a discussion of the kinds of behavior which will result in Type III foraging strategies.

In 1960, L. Tinbergen reported studies on the feeding responses of great tits, Parus major, to changes in insect food abundance and discovered that as abundance of a given insect rose, the birds showed a delayed response, that is, feeding rate on that insect rose with abundance characteristic of a Type III curve. Tinbergen argued that individuals form visual images ("specific-searching-images") of a commonly encountered food type and subsequently feed disproportionately on that food, and that specific-search-images aren't developed until some threshold abundance has been reached.

Since Tinbergen's paper many other behaviors which will shift the functional response curve from Type II to Type III have been described (Dawkins, 1971, and summarized in Krebs, 1974) and can be summarized as:

(1) the predator's learning to go to a particular area to find food (Royama, 1970; Alcock, 1974; Simons and Alcock, 1971; Smith and Dawkins, 1971; Croze, 1970).

(2) the predator's learning to alter its search path so as to increase its probability of encountering prey (Dixon, 1959; Smith, 1971; Croze, 1970; Beukema, 1968; N. Tinbergen, et.al., 1967).

(3) the predator's learning to handle prey more efficiently with increasing experience (Norton Griffiths, 1967; Orians, 1969, Recher and Recher, 1969).

(4) the predator's preferring a particular prey species or avoiding species. For example, avoidance may result from novelty or rarity (Allen and Clark, 1968; Coppinger, 1968; Freeland and Janzen, 1974) or unpalatability or mimicry (Brower, 1963). Preference for a particular food type may result from relatively long-term exposure or exposure during a sensitive period early in life (Rabinowitch, 1968, 1969; Murdoch, 1969; Landenberger, 1968; Mahoud and Lavenda, 1969).

(5) learning of specialized hunting techniques by particular individuals. For example, Tinbergen (1949) found individual Parus major which learned to hunt under leaves and as a result took a large number of arboreal grasshoppers.

(6) learning to look in a particular type of place. Krebs, et. al. (1972) found that if individual Parus major found a meal worm in one of four types of hiding places, they would increase their searching effort in that type of place during the next few minutes.

It is important to note that most of the above learning processes involve predator behavior associated with increasing encounters with prey items. Thus, we see once again that the parameter n in the equation presented becomes the major determinant in shifting responses from Type II to Type III.

Three Hypotheses

Using any number of computer algorithms we can determine the values of the functional response parameters. By looking at different responses under different ecological conditions, we can arrive at the quantitative relationships between the parameters and defined ecological situations. For instance we could determine the way in which changes in food item preferences effect the values of the parameters n, F, and G. Many organisms show food preferences and if, as we suspect, energy requirements and constraints are related to food preferences (Paine and Vadas, 1969; Emlen, 1966, 1968; Schoener, 1971) then we would expect preferences to be reflected in an increase in resource utilization efficiency (F) and affinity (G) and a decrease in values of n (encounters (Figure 6).

Rosenzwieg and Sterner (1970) found that seed-husking-time was inversly proportional to body size. So, we might expect a size ordering of animals to result in shifts-up in the efficiency of resource utilization (F) and affinity (G) (Figure 7). Similarly, as habitat complexity increases organisms will find foraging more difficult and we would expect n, F, and G to follow Figure 8.

Whether the curves for n, F, and G depicted in Figures 6, 7, and 8 take on the suggested forms can be tested experimentally using techniques similar to those first employed by Holling. The writer is in the process of initiating such experiments on seed-eating desert rodents.

Figure 6. Expected values of the parameters n, F, and G given a food preference ordering.

Figure 6

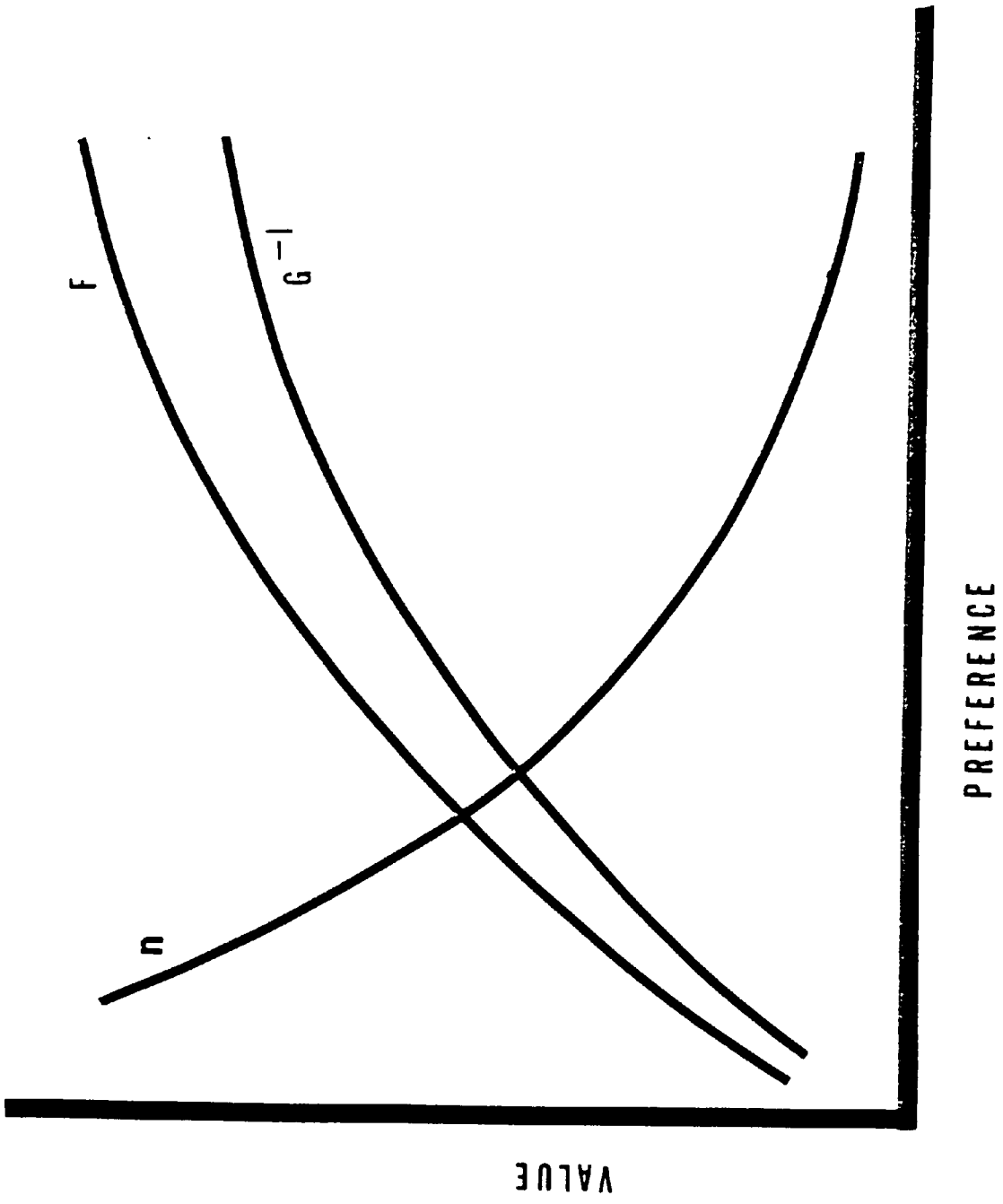


Figure 7. Expected values of the parameters F and G given a food preference and size ordering.

Figure 7

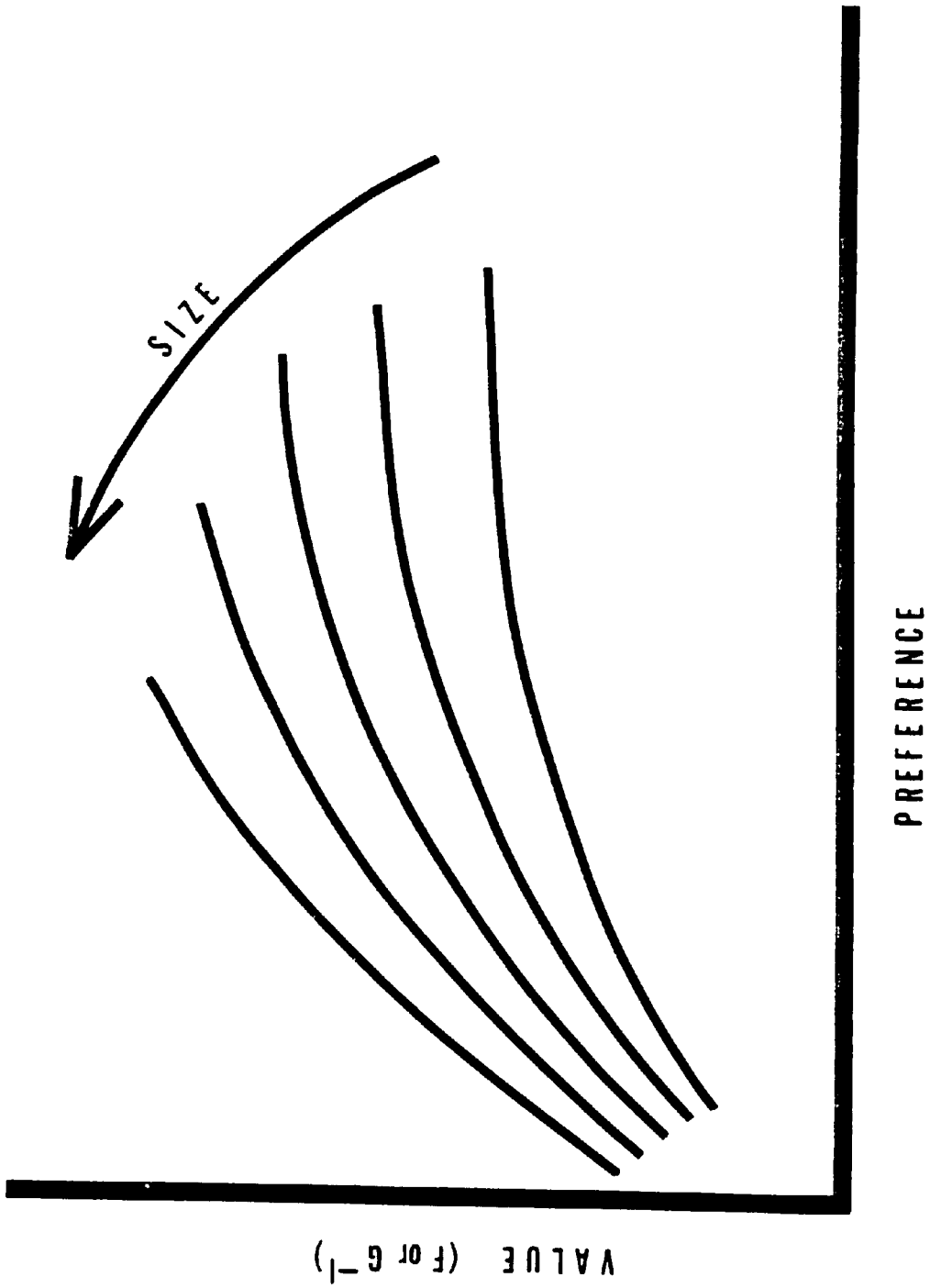
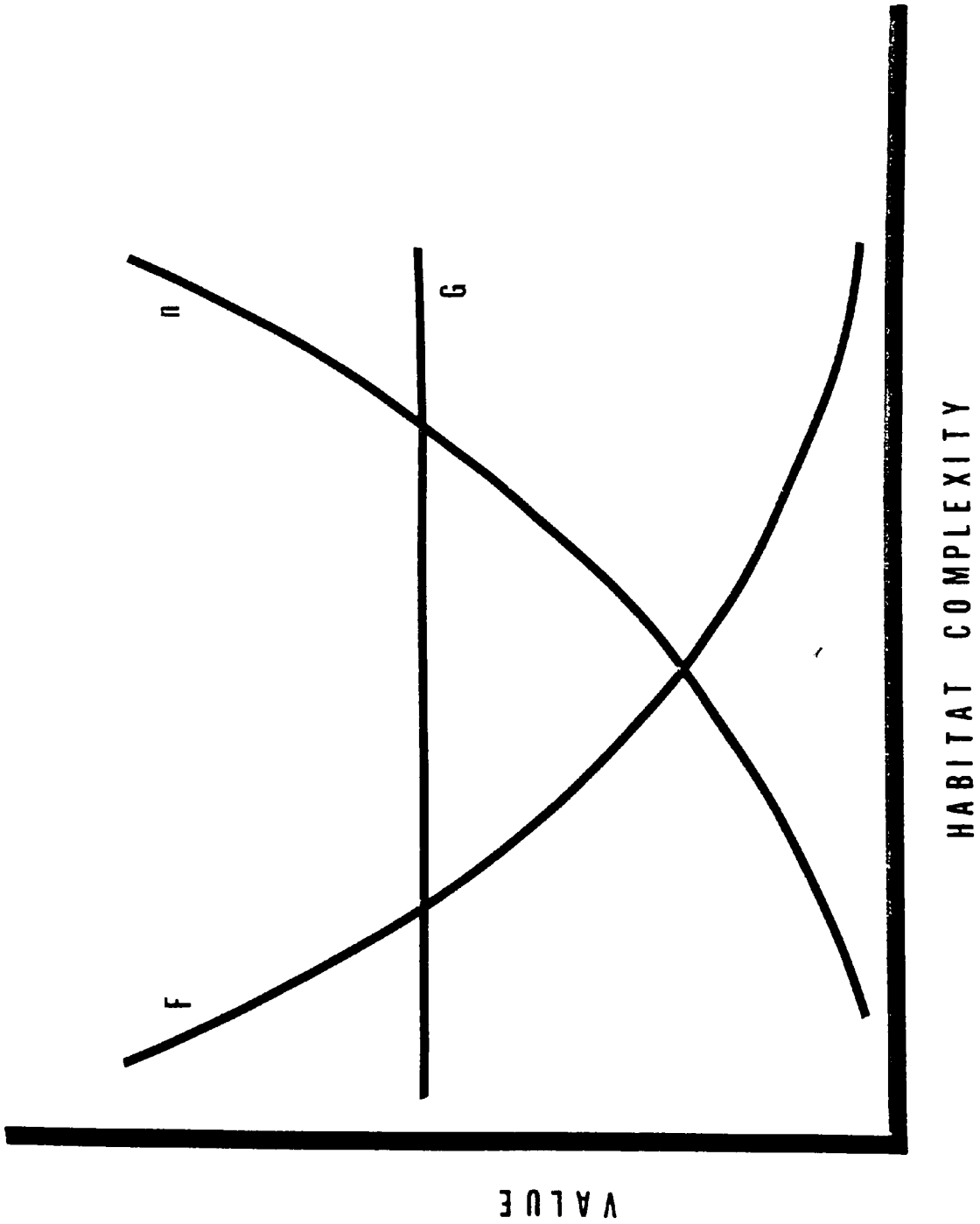


Figure 8. Expected values of n, F, and G as functions of habitat complexity.

Figure 8



CHAPTER IV

THE ECOLOGICAL DETERMINANTS OF FUNCTIONAL RESPONSE

C. S. Holling first presented his analysis of predator feeding behavior in a series of elegant articles during the late '50s and mid '60s (1959, 1965, 1966). During the succeeding years many authors have examined and expanded upon his approach and upon the biological implications of the functional response. Many investigators have found additional examples of organisms demonstrating a functional response (Murdoch, 1969; Griffiths, 1969; Messenger, 1968), while others have concerned themselves with discussions of the importance of this response in the dynamics of populations (see Murdoch and Oaten, 1975, for a review).

However, one particular facet of the functional response has been greatly ignored. That is, how the functional response curves change, and the associated parameters of the response change, with changes in ecological setting and situation. An understanding of how variation in environmental setting affects the organism's performance within the habitat is of fundamental importance in any attempt at interpreting the organism's behavior or ecology. This chapter is an examination of some of these components of functional response that are related and influenced by variation in environmental pattern.

In a previous chapter, (chap. 3), I presented a general formula accounting for both the hyperbolic (Type II) and sigmoidal (Type III) responses. This formula is derived through an extension of the well-known analogy between predatory functional response and the kinetics of enzyme reactions. Any functional response can be represented in general form by the equation:

$$f = \frac{FA^n}{G + A^n} \qquad (4.1)$$

where f = the feeding rate, F = the maximum feeding rate (saturation), A = the density of the food items, G = the density of food items that

generate half maximal feeding (i.e. that level of A for which f = F/2), and n = the parameter associated with the amount of increase in the potential rate of detection of a food item with an increase in food density. The parameter n is roughly equivalent to the amount of "learning" that is being exhibited by the organism. The parameter G can be viewed as a constant of affinity for resources at low density; the lower the value of G the higher the affinity.

When n = 1, the rate of detection is constant, i.e., there is no learning, and equation (4.1) reduces to

$$f = \frac{FA}{G + A}$$

which generates a Type II hyperbolic functional response. The degree to which n is greater than one is the degree to which the rate of detection is influenced by increasing resource density, and the degree to which the organism is showing increased learning. For n greater than one, equation (4.1) generates a Type III functional response.

What I will be concerned with in this chapter is the manner in which the three determinants of functional response, F, G, and n, are altered by changing the preferabilities of the alternate foods available in the habitat and by varying the spatial distribution of the food items in the habitat.

Methods

Varying preferabilities of alternate prey. Experiments examining the effects of changes in the preferability of alternate foods were performed by Holling (1965) and are analyzed here according to equation (4.1). The general method is described, however. Holling examined the consumption of European pine sawfly cocoons, Neodiprion sertifer (Geoff.) by the deer mouse Peromyscus maniculatis bairdii.

Experiments were conducted at room termperature (ca. 20°c) in a screen-topped cage 10' x 4' x 6'. The cocoons were first buried in sand at the points of intersection of a removable grid. The grid was then removed, and a metal jig was passed over the sand bottom uniformly covering the cocoons to a depth of 12mm. A single deer mouse was then introduced into the cage together with nesting materials, water, and

an alternative food -- either dog biscuits or sunflower seeds. In each experiment the amount of alternate food was kept nearly constant. The mouse was left undisturbed for 24 hours and then removed. The grid was replaced and the number of holes dug and cocoons opened were recorded. Consumption was measured at 6 different densities ranging from 2.25 to 36 cocoons per square foot (approximately 25-325 cocoons per square meter). One set of 22 experiments was performed with the more preferred alternate food source, sunflower seeds; while another set of 19 experiments was performed with the less preferred food alternative, dog biscuits.

Varying spatial distribution. A similar experimental design to that of Holling's was constructed to determine the effects of altering the spatial distribution of the food items. Predator functional response was measured by examining consumption of wheat seeds by the deer mouse Peromyscus maniculatus. Experiments were conducted at room temperature in an aluminum cage 10' x 4' x 30' with a sand substrate floor. A single deer mouse was introduced into the cage and allowed to acclimate over a 24 hour period, with a diurnal cycle of natural light. Nesting materials, water, and alternate food (laboratory rat chow) were in abundance over the 24 hour period. After the acclimation period, the mouse was removed and a 5" x 5" grid was placed on the floor of the cage. Random quadrats were chosen from a list of random numbers, and seeds were placed within the quadrats and tamped down until they were just visible. Random location of quadrats insured the random distribution of seeds over the cage bottom. The grid was then removed and the mouse was introduced and allowed to forage over another 24 hour period. After this period, the mouse was removed, the grid replaced, and the number of seeds eaten recorded. A set of 21 experiments was performed over a range of seven densities from 6 to 210 seeds per 40 square feet (approximately 1.35 to 47.25 seeds per square meter) to determine the functional response when food items are distributed at random. Naive laboratory reared F1 from wild-caught mice were used, and no mouse was used twice for any experiment.

After the functional response for randomly distributed foods was determined, a set of 36 experiments over a range of 12 densities was conducted. In this series, the food items were clumped. All seeds

were deposited in a single 5" x 5" quadrat generating a value of 207 for Morisita's Index (Morisita, 1959). The particular quadrat was chosen randomly from a list of random numbers. All other conditions of the experiment were identical to those for the random distribution of seeds.

Determining the pattern of change under varying spatial distribution becomes important in assaying the degree to which the ecological behavior of the prey (whether they are clumped or hyper-dispersed, for instance) can lessen the degree of predation and/or significantly alter the behavior of the predator. In addition, many of the stabilizing properties of the predatory functional response may be altered or obliterated if changing spatial distribution generates sufficiently different parameter values; for instance, a change from a Type III to a Type II functional response.

Determining the values of F, G, and n. The equation

$$f = \frac{FA^n}{G + A^n}$$

can be transformed under a log-log transformation into the following:

$$\log \frac{f}{F - f} = \log \frac{1}{G} + n \log A. \qquad (4.2)$$

The value of F can be determined by direct inspection of the data graphed on arithmetic axes. A least-squares regression can be performed on the log transformed data generating a value for n, the slope of the least-squares regression. G can be computed by looking at that value of A, the resource density, for which f/(F-f) is equal to one.

Results

The results replotted from Holling's (1965) graph on his experiments are shown in Figure 9. From this figure we estimate the values of F to be 198 cocoons and 136 cocoons for the low palatability and high palatability foods, respectively. Using these values, we transform the graph into its log-log form represented by Figure 10, for which we generate n values of 1.79 and 2.14 and G values of 103.5

Figure 9. Replot of Holling's 1965 data on Peromyscus predation on European pine sawfly cocoons with different palatability alternate foods.

Figure 9

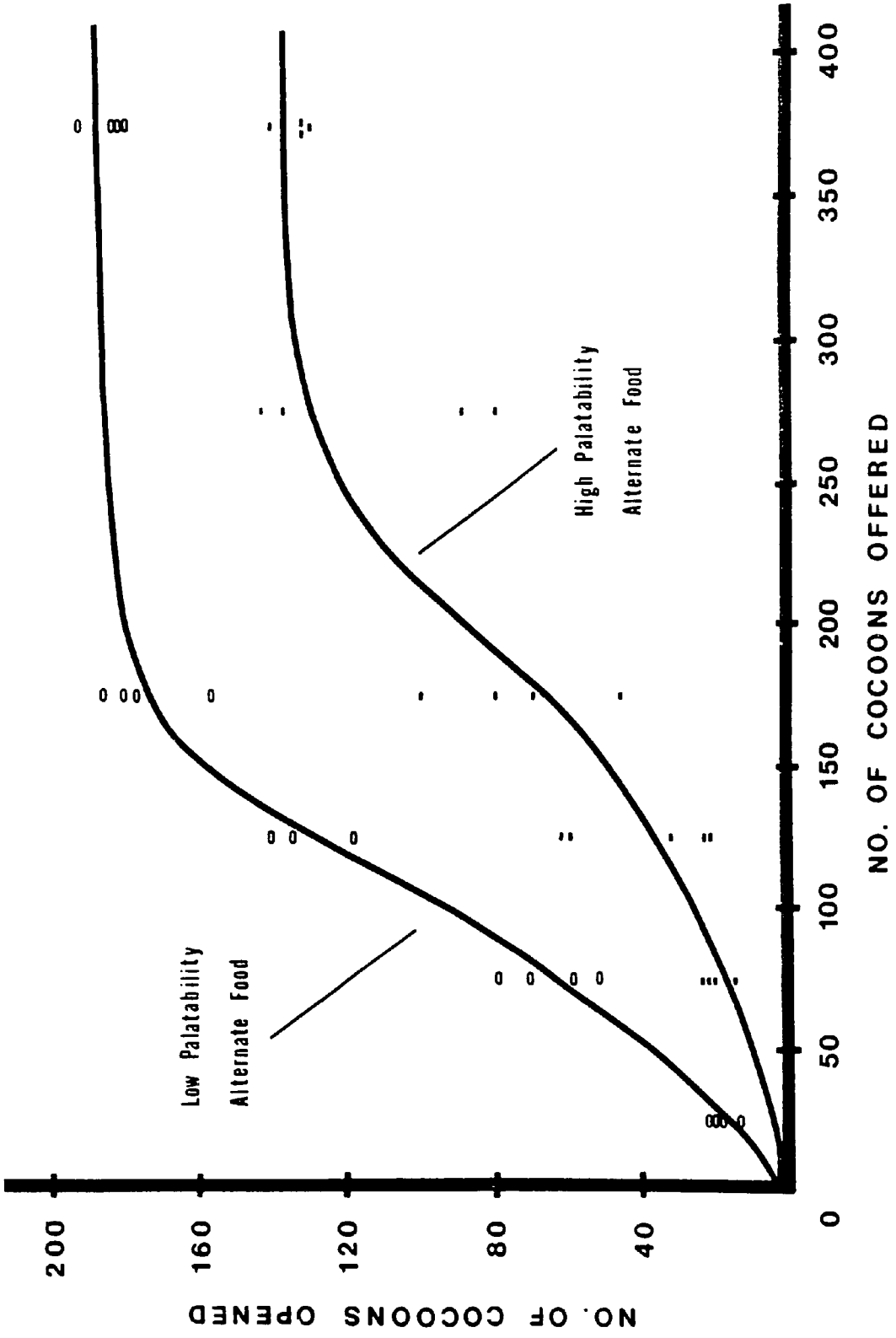
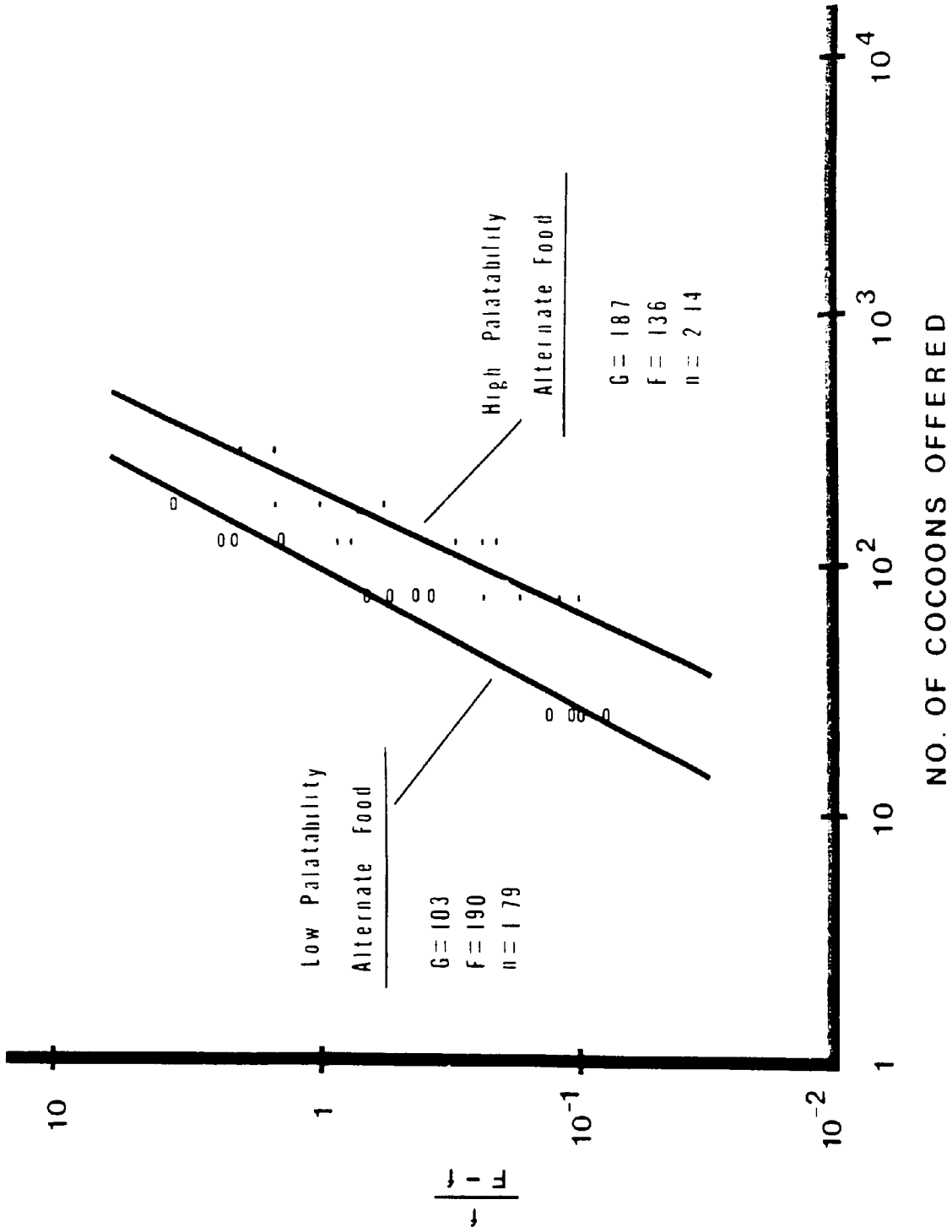

NO. OF COCOONS OFFERED
0
50
100
150
200
250
300
350
400
NO. OF COCOONS OPENED
0
40
80
120
160
200
High Palatability
Alternate Food
Low Palatability
Alternate Food

Figure 10. Log-log transformed data from Holling's 1965 Peromyscus responses with different palatability alternate foods.

Figure 10


10
1
10^{-1}
10^{-2}
1
10
10^2
10^3
10^4
NO. OF COCOONS OFFERED
Low Palatability
Alternate Food
G = 103
F = 190
n = 179
High Palatability
Alternate Food
G = 187
F = 136
n = 214

cocoons and 187 cocoons for the low and high palatability alternatives, respectively.

The results from the experiments on the effect of spatial distribution on functional response are shown in Figures 11 and 12. The values for both sets of experiments are summarized in Table 1.

Discussion

The analysis of Holling's data seems to indicate, firstly, that when a low palatability food item is an alternative in the composition of the predator's diet this will act to increase both the affinity and total utilization of the other foods in the habitat. This is evidenced by a decrease in the value of G from 187 to 103.5 and an increase in F from 136 to 198. This lends some credence to Schoener's (1971) conclusions on optimal foraging, especially that conclusion which states that an organism's diet is determined by the quality of the alternative foods available in the habitat and not by the food items themselves. This certainly seems reasonable in light of the present analysis. If a higher palatability food item becomes abundant in the habitat, then we would expect the predator to spend more time and energy in the utilization of the now more desirable alternative, necessitating a decrease in the utilization of the other foods. However, the second conclusion we can reach from the analysis is quite unexpected. That is, that with a change in the palatability (and concomitant change in preference) very little change in learning is evident. In both cases represented in Figure 10, the slopes are similar, being nearly equal to two: n equal to 2.14 and 1.79. Similar degrees of learning are being exhibited within the system regardless of changes in alternative foods. This could be explained by Peromyscus being equally aware of the cocoons in either the low or the high palatability alternate food situations. When there is a high palatability alternate food available, they act as if they ignore the cocoons, but when a low palatability food is the alternate, Peromyscus switch to eating the cocoons at an increased affinity and utilization

Figure 11. Functional response of Peromyscus on wheat seeds under random and clumped spatial distributions.

Figure 11

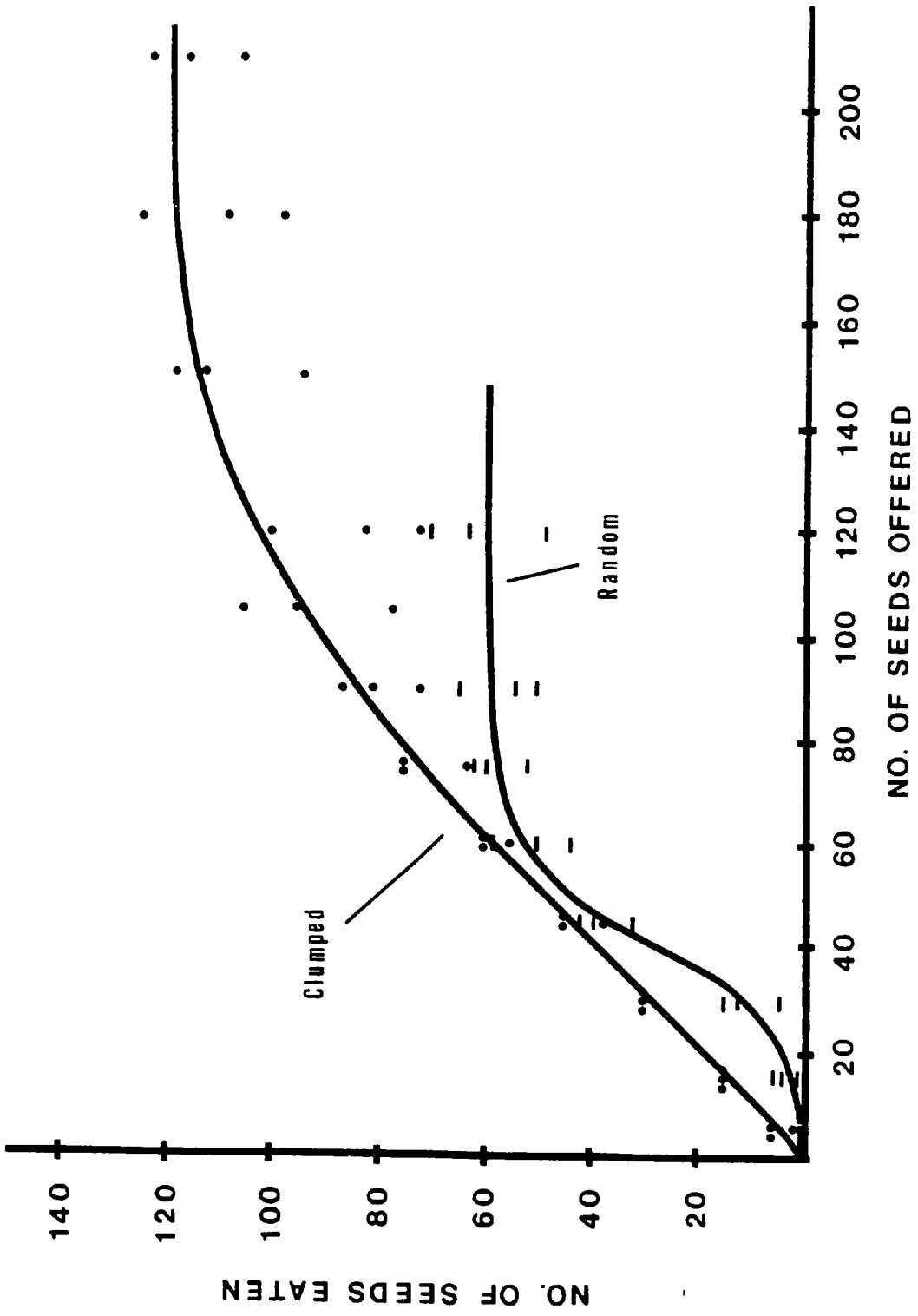

NO. OF SEEDS EATEN
140
120
100
80
60
40
20
NO. OF SEEDS OFFERED
20
40
60
80
100
120
140
160
180
200
Clumped
Random

Figure 12. Log-log transformed functional response curves of Peromyscus predation on wheat seeds under random and clumped distributions.

Figure 12

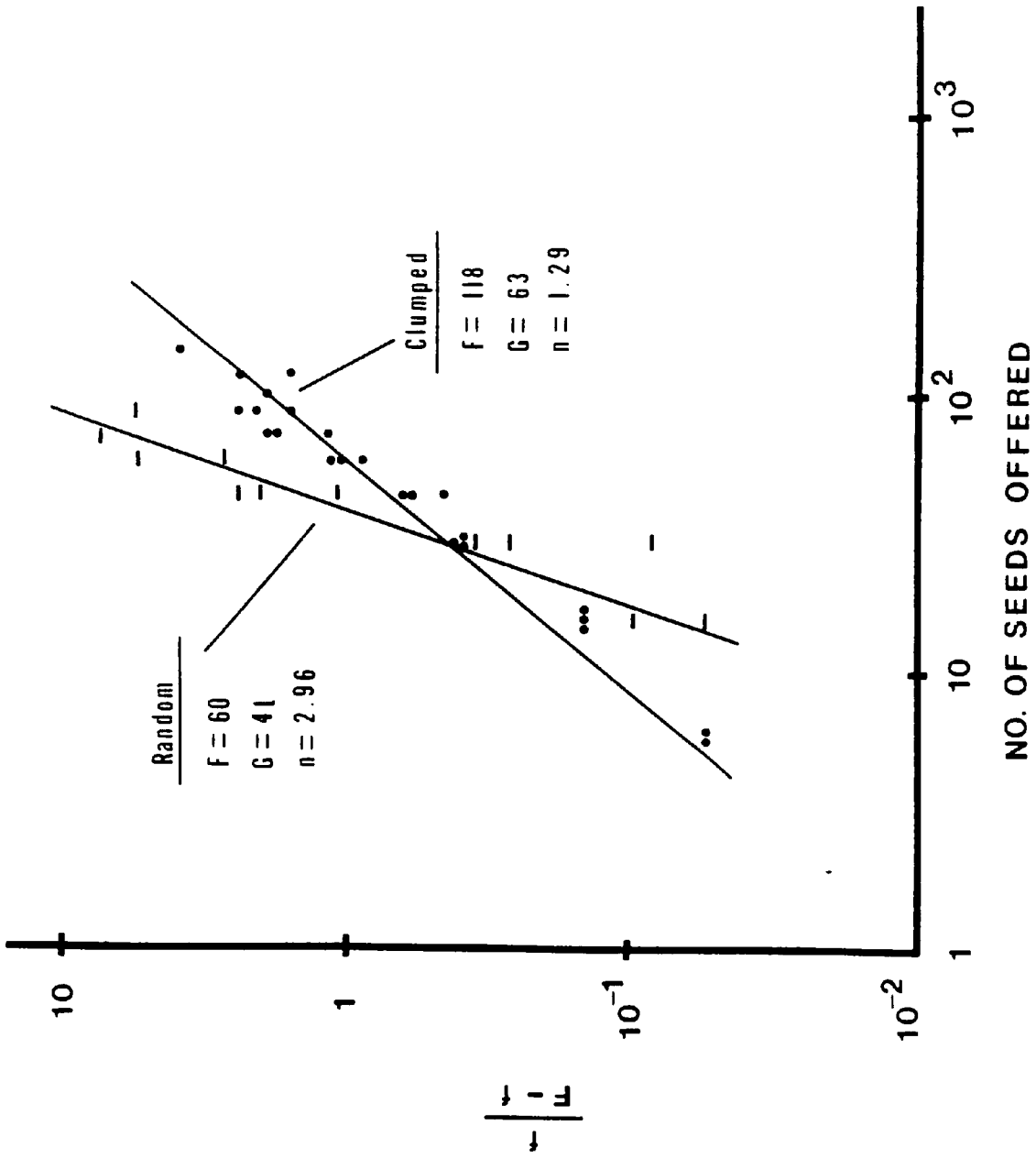

Random
F = 60
G = 41
n = 2.96
Clumped
F = 118
G = 63
n = 1.29
10
1
10^{-1}
10^{-2}
1
10
10^2
10^3
NO. OF SEEDS OFFERED

Table 1. Summary of results from analysis of functional response under varying conditions of alternative prey availability and spatial distribution of prey.

	Parameter Value			Statistics	
Ecological Setting	F	G	n	r^2	STD ERROR
Alternate Foods					
High Palatability	136 ccns	187 ccns	2.14	0.743	0.349
Low Palatability	198 ccns	103.5 ccns	1.79	0.952	0.127
Spatial Distribution					
Random	60 seeds	41 seeds	2.96	0.867	0.364
Clumped	118 seeds	63 seeds	1.29	0.974	0.046

level. There is, however, no increased learning about the cocoons during the switch.

These experiments were designed to ascertain the effects of variable palatability in the alternate foods, but not variation in the palatability of the principle food items being monitored. For instance, if there was variation in the sawfly cocoons themselves it is not certain that the above conclusions would still hold true. If all the alternative food palatabilities were kept constant and the palatabilities of the test food allowed to vary, we might get a very different picture of the organism's learning. The writer is in the process of determining parameter values for cases such as these.

The data from the experiments on spatial distribution paint an entirely different picture. The change from a random to a clumped distribution does increase the total resource utilization (F goes from 60 to 118 seeds), however, the affinity decreases with G increasing from G = 41 to G = 63. Since, in the other experiments, G changed in the opposite direction with increasing maximal resource utilization (F), this shows that there need not be a defined relationship between maximal resource utilization (F) and affinity (G), a fact which has not been recognized by some authors. Dugdale, 1967, for instance, assumes an inverse relationship between F and G with regard to nutrient uptake in diatoms.

We also find that with a change from random to clumped resource distributions the degree of learning being exhibited changes dramatically. It should be recalled that for n = 1, the functional response reduces to the Type II hyperbolic curve characteristic of non-learning interactions between predators and prey. The random resource distribution shows a relatively high degree of learning (n = 1.29). That is to say that the organisms behave, when the resources are clumped, as if they don't have to learn anything about the resource.

These experiments were comparisons between the extremes, from randomness to extreme clumping. By ascertaining parameter values for intermediate degrees of clumping, we could determine whether there might be some kind of critical level of clumping below which the organism must learn a great deal and above which the organism need

learn very little or whether the organism shows some kind of smooth decrease in learning as clumping increases. These differences would be represented graphically by lines A and B in Figure 13, line A representing a critical threshold in learning.

The decrease in the lines A and B to the left of randomness represents an hypothesized decrease in n as one goes from randomness to uniformity in distribution. Under uniform conditions, values for n might lie somewhere between those for random and those for clumped distributions. Intermediate values would indicate that organisms need to learn less about the food items than when the foods are random, but more than when the foods are clumped. It is interesting to observe that Holling's experiments, where foods were distributed more or less uniformly over the cage bottom, do in fact generate intermediate values for n.

I would like to end this discussion with some points of clarification on what I mean by learning or the meaning of learning to which I have attached the parameter n. It is not the kind of learning we associate with changes in an organism's behavior related to the organism's past experiences, but is more akin to the degree to which the organism can and does develop a search image or some other behavioral mechanism (Krebs, 1974; cf. Tinbergen, 1960). We can graphically represent the meaning of n by computing functional response curves where all other parameters, F and G, are kept constant but n is allowed to vary. In Figure 14, I have represented the curves of

$$f = \frac{FA^n}{G + A^n}$$

for F = 60 and G = 41. Parameter n was allowed to take on values of one, two, and three. We can see from the graphs that increasing values of n cause more pronounced lags in response, but once the threshold value of density is reached the organism's approach to saturation is rapid. That is, increasing n makes the response much more attuned to a critical value of density, below which the organism does not utilize prey, above which the organism utilizes the prey close to saturation levels. From a strictly ecological perspective,

Figure 13. Value of the learning parameter as a function of degree of contagion. (A) Smooth decrease in learning with increasing contagion, (B) Threshold decrease in learning with critical level of contagion.

Figure 13

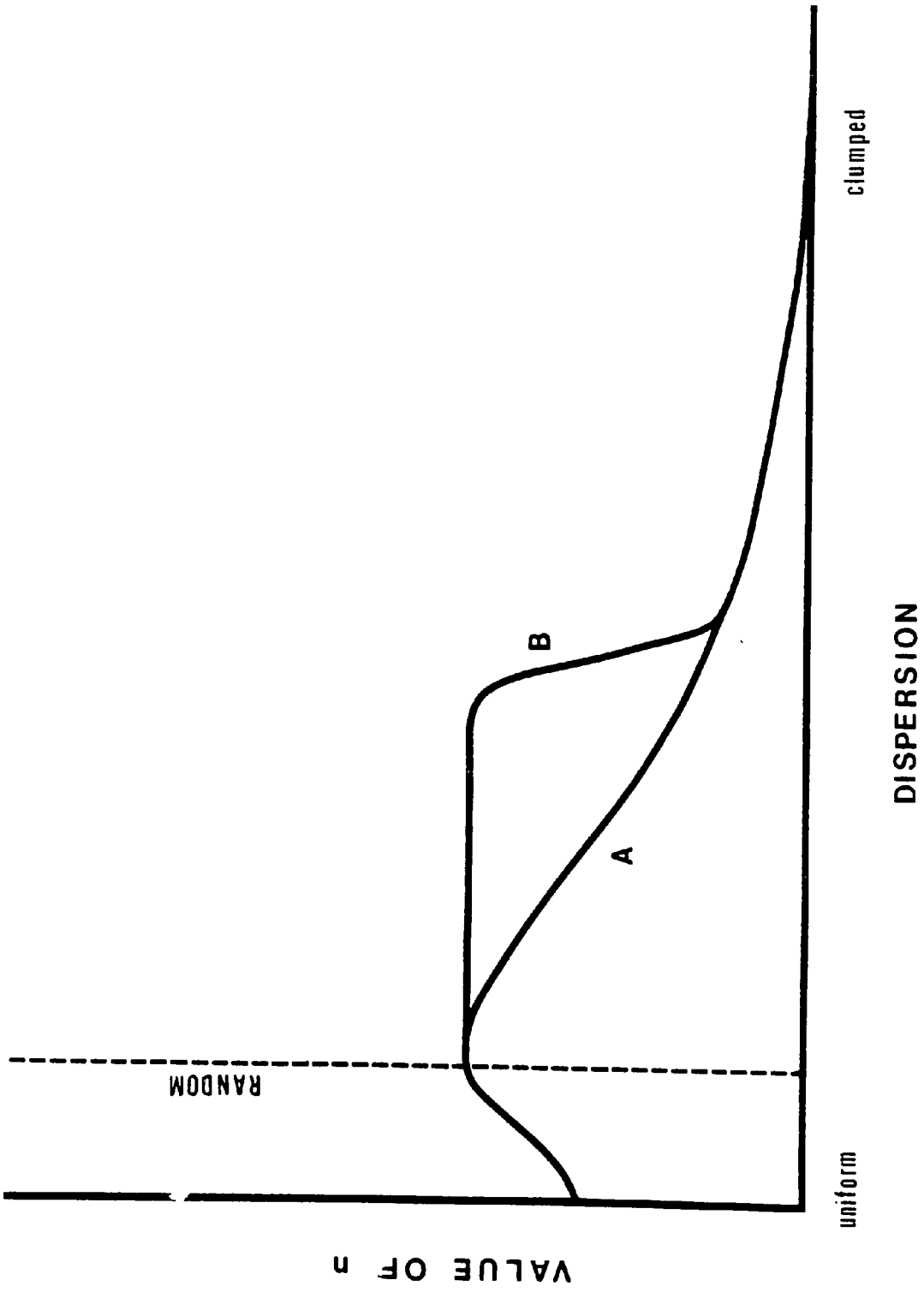
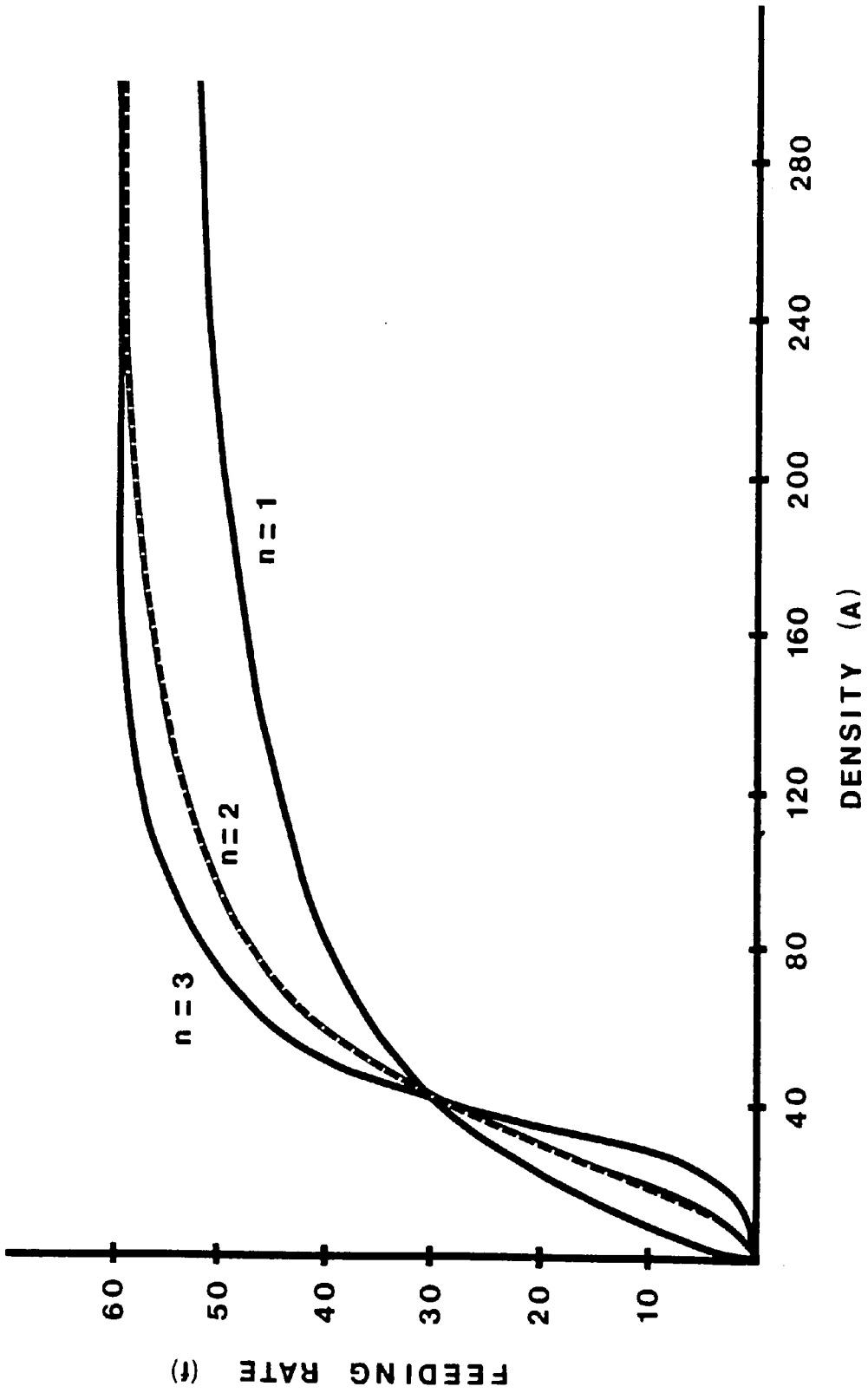


Figure 14. Functional response curves for the relation $f = FA^n/G + A^n$, with F = 60, G = 41, and n assuming values of 1, 2, or 3 in each of the represented curves.

Figure 14


FEEDING RATE (f)
60
50
40
30
20
10
40
80
120
160
200
240
280
DENSITY (A)
n = 1
n = 2
n = 3

n is probably best expressed as the degree to which detection of food items is a function of food density. From a behavioral perspective, we can describe the process as being similar to the organism possessing a jig-saw puzzle search image. As each piece of the puzzle is put in, the potential for incorporating future pieces increases. Parameter n is a measure of the interaction between the pieces of this behavioral puzzle in the formation of a complete search image. Put this way, we can see the behavioral basis for the ecologically defined increase in the rate of potential detection. It would be perfectly feasible to determine the parameter values as functions of experience and the writer is in the process of performing just such experiments.

CHAPTER V

EPILOGUE

Resource Allocation. We are immediately venturing upon thin ice when we postulate a priori that an organism is following some form of maximization principle. There is no reason to assume that an organism is a priori behaving as if maximizing something, and there is little reason to choose one particular objective function over some other objective. What we wish to do is hypothesize that an organism may be performing according to some principle, examine the potential of such a hypothesis, and, if the hypothesis leads to some new insights or methods of analysis, proceed to test whether the organism does, in fact, operate according to the proposed principle.

In order to test the maximization hypothesis, we need to collect two kinds of information sets. The first kind is an exhaustive description of the constraints operating on the organism's behavior. Gathering this information is probably the most critical to any understanding of an optimization approach to behavior. The constraints are those relations that determine from some large set of feasible behaviors that behavior which is actually carried out by the organism. Unfortunately, the constraining relationships are probably the hardest to determine. For instance, how can we hope to determine whether an organism is choosing an optimal diet, if we have no knowledge of the nutritional constraints operating on the organism's choices? But at the same time, the nutritional constraints of an organism are exceedingly difficult to determine. So where does this lead us? One of the values of a theory is to point out areas of needed research and to point out the direction in which our questions should be headed. In this regard, optimization theory has helped to point out the importance of determining the nature of the constraining relationships that a particular organism must meet within a particular habitat. Physiological ecologists have certainly recognized this facet of organismal biology as central to their continued study, but little ecological research has been devoted to determining the nature

of "ecological" constraints of a group of organisms.

The second set of information that we must gather is on the structure of the objective function. Does one really exist? Can we describe it?, etc. This facet may, surprisingly enough, be easier than elucidating the constraints. There are a number of ways we can formulate an objective function, but only one way we can formulate the system of constraints. That is to say that, given a particular system of constraints, we can structure the objective function in many forms, all of which will lead to the same optimal solution. However, we can afford no such luxury with the constraints; different formulations of the constraints will very likely lead to very different optimal solutions. One can try to ascertain the nature of the objective function directly by examining particular objectives and seeing whether organisms seem to follow such a rule, or one can attack the problem axiomatically, i.e., is there a set of behaviors such that when observed in an animal's behavior automatically implies the existence of some kind of objective function? I'll take the already mentioned work of Rapport (1970) and Covich (1972) as an example.

In their analysis of predator choice and decision-making, Rapport and Covich postulate the existence of a set of "indifference curves" which represent an organism's preferences for various items and combinations of items. This set of curves can be represented by some single-valued function, where preferred combinations generate higher values of the function than less preferred combinations and where combinations that are equally preferred generate the same values. They postulate that the organism maximizes its preference thereby maximizing the indifference map function. They have postulated an objective function and it remains to be seen if such a function does exist.

Covich attacks the proof of his assertion by directly trying to construct an indifference map for an organism, using seed selection by Peromyscus under different decision-making regimes, and he has certainly gone a long way in demonstrating the existence of such curves. However, one can take an entirely different line of attack.

Suppose we could demonstrate that given a certain set of observed behaviors we could prove that an indifference map must exist. We no

longer require the direct demonstration of a particular indifference map as proof, we merely show that if the organism behaves according to some set of "axioms" then it must have an indifference map. This axiomatic approach would be much more powerful than a direct observational approach to the proof of the problem, since a demonstration of the axioms requires many fewer experiments and generalizes to any set of resources, whereas the observational approach requires an enormous number of experiments and lacks generalizability. We are fortunate in this particular example, since such a set of axiomatic behaviors can be delineated and can be shown to infer the existence of indifference curves (Real, in prep.).

Functional Response. In the previous section, I have tried to outline some of the aspects of testing and demonstrating the existence of a maximization hypothesis. However, in this section, I would like to talk about methods of extending the functional response relationships put forth in chapters 3 and 4 to the modeling of predator-prey systems. I don't feel the need to discuss the testing of my formulations since they are not really hypotheses, but are more like quantitative tools for describing the system as we observe it. Hopefully we can use some of these tools in building hypotheses which can then be tested, and which will lead to modification of the original equations into better tools to be used in our construction of a concept of nature.

The first observation on the similarities between enzyme kinetics and population dynamics was made by Monod (1950). Monod stated that there exists a relationship between an organism's utilization of limiting resources and the growth of the organism. If the growth is somehow proportional to the organism's ability to sequester resources, then one way we can incorporate resource limitations into the growth equations is to make resource uptake a function of resource density. For Monod, this system of growth could be represented by the following equations:

$$\frac{dN}{dt} = b\left[\frac{R}{G + R}\right] N - aN^2$$

$$\frac{dR}{dt} = C - y\left[\frac{R}{G + R}\right] N - eR$$

where b equals maximal growth rate of the organism, N equals amount of organisms, R equals amount of resource, G equals the organism's affinity for the resource, a equals the death rate of the organism, C = input of the resource, y = yield coefficient of the organism on the resource R, and e = washout rate of the resource.

What Monod did was to interpret resource uptake by the organism as a hyperbolic Michaelis-Menten function of the resource density. These equations have had a wide success in the limnoligical and applied literatures (Titman, 1976; Canale, 1969, 1970), but have received very little attention from most ecologists. They are completely ignored by MacArthur (1972) in his search for a resource-based set of population dynamic equations, and even after MacArthur pointed out the limitations of the Lotka-Volterra system in treating resource-based dynamics, very few authors have sought a new description of population dynamical systems. Koch (1974) uses the Monod equations as a basis for computer simulations of predator-prey systems and reaches some striking conclusions on the role of stochastic effects in the maintainence of stable limit cycles. Titman (1976) has successfully used these equations to predict the outcomes of competition between diatoms limited by silicon and phosphorous.

In a simple way, we can extend Monod's basic equations to the description of organisms showing learning or lags in their resource utilization abilities. The modified equations then become

$$\frac{dN}{dt} = b\left[\frac{R^n}{G + R^n}\right] N - aN^2$$

$$\frac{dR}{dt} = C - y\left[\frac{R^n}{G + R^n}\right] N - eR \qquad (*)$$

where n is the parameter associated with learning. Even for the simplest systems of phytoplankton absorbing inorganic nutrients, there is some evidence that the organism shows a sigmoidal rather than a

hyperbolic uptake of resources as a function of resource concentration (S. Killham, pers. comm.).

The above equations are descriptions of a steady-state resource limitation dynamic. Resources are entering the system at a particular velocity, C, but also leave the system, independent of the predators, at a particular rate e. There is another kind of resource-limited growth which we will call batch dynamics. In this case, resources enter the system at a rate c, but are only removed from the system by predator utilization, i.e., the washout rate of the resource is negligable. Such systems may be described by the equations:

$$\frac{dN}{dt} = b\left[\frac{R^n}{G + R^n}\right] N - aN^2$$

$$\frac{dR}{dt} = C - y\left[\frac{R^n}{G + R^n}\right] N \quad . \qquad (*')$$

It is very important to distinguish between these two types of resource-limited growth. The system of equations (*) will always lead to a stable equilibrium, but (*') is only stable when $c/y<b/a$.

We can easily treat more than one resource in this analysis. For instance, we can model the realistic situation of diatom growth on silicon and phosphorous in lakes, where silicon is following steady-state dynamics while phosphorous is following batch dynamics. This seems to be a realistic interpretation of the inputs of these two nutrients into lakes, for instance into Green Bay (Holland and Claflin, 1975). The equations for such a system would look like the following:

$$\frac{dD}{dt} = b_s\left[\frac{S^n}{G_s + S^n}\right] D + b_p\left[\frac{P^m}{G_p + P^m}\right] D - aD^2$$

$$\frac{dS}{dt} = C_s - \left[\frac{S^n}{G_s + S^n}\right] y_s D - e_s S \qquad (*'')$$

$$\frac{dP}{dt} = C_p - y_p\left[\frac{P^m}{G_p + P^m}\right] D \quad .$$

The writer is modeling the dynamics of the different diatom species in Green Bay, using the above equations.

The relationships between the Type III functional response and apostatic/frequency-dependent selection has also been pointed out by several authors (Emlen, 1973). Given this relationship we can also model apostatic selection using (*''), where instead of resources being absorbed by diatoms, we are looking at predator selection of different characteristics of the prey species. We can ask, what are the parameter values that will generate a stable population polymorphism in the prey species? Are there parameter values that generate stable oscillation in the character pools of the prey species? Are these dynamics generalizable to any number of prey characteristics?

The answers to these questions are not known, but hopefully this discussion has given some idea of the questions these formulations on predatory functional response can generate and have provided an idea of the great applicability of these formulations to a wide range of biological processes and systems.

APPENDIX

LIST OF MATHEMATICAL SYMBOLS

G_i = organism's activity i

R_i = ith resource in the habitat

a_{ij} = amount of R_j consumed when G_i is operational at unit intensity

X_i = intensity of activity i

S = vector of resource supplies; amount of silicon

A_k = activity matrix of the kth individual

B_k = unit utilization matrix of co-resources of the kth individual

b_k = vector of kth individual's co-resources

π_i = reproductive cost of utilizing one unit of resource i

P = (π_i) ; amount of phosphorous

ψ_i^k = reproductive gain to the kth individual from utilizing one unit of resource i

C_k = (ψ_i^k)

v_j = unit vector for the jth resource

σ_j = the amount of resource j in the habitat

Y_k = dual vector to X_k

F_i = ith food in the habitat

N_i = ith nutrient required by the organism

λ_i = minimum requirement for the ith nutrient

β_{ij} = amount of ith nutrient in one unit of food j

$g^i(X)$ = ith constraining relation

$f(X)$ = objective function

λ = Lagrange multiplier

$(X^*; \lambda^*)$ = optimal solution to the Lagrange problem

V^* = $(X^*; \lambda^*)$

N_A = amount of food item taken

T_t = total time available for foraging

T_h = time to handle a single food item

a = attack rate; death rate of predator

P_{is} proportion of encountered food items of food i eaten

K_i = rate constant

A = amount of prey

C = amount of predator; input of resource

X = intermediate complex between predator and prey

P = amount of new predator

C_o = constant equal to C + X

f = feeding rate

F = maximal feeding rate

G = affinity constant of functional response (amount of A such that f = F/2)

k_b = equilibrium constant for hemoglobin

Y_s = saturation of hemoglobin

n = number of binding sites; parameter of learning or sigmoidicity

v = velocity of enzyme reaction

V_{max} = maximal enzyme reaction velocity

K_m = affinity constant for enzyme reaction

R = amount of resource

N = amont of predator

y = yield coefficent of predator on resource R

e = washout rate of resource R

b = maximal birth rate of predator

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