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Marc Mangel, Colin W. Clark

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## TOWARDS A UNIFIED FORAGING THEORY<sup>1</sup>

MARC MANGEL

*Departments of Mathematics, Agricultural Economics, and Entomology,  
University of California, Davis, California 95616 USA<sup>2</sup>*

AND

COLIN W. CLARK

*Institute of Applied Mathematics, University of British Columbia, Vancouver,  
British Columbia V6T 1W5, Canada*

**Abstract.** In the broadest sense, foraging adaptations can include problems of finding food, avoiding predation while looking for food, and reproducing. In this paper, a theory that treats these three behaviors in a consistent, unified manner, with one common currency, is presented. The theory is called unified foraging theory, although it actually pertains to a wider class of behavioral problems. The theory is based on models using Markovian decision processes and leads to quantitatively testable predictions about behavioral strategies.

**Key words:** animal behavior; foraging; Markov decision processes; modeling; patch selection; resource allocation.

### INTRODUCTION

In recent years the theoretical basis of behavioral ecology has developed in many directions, including for example: optimal foraging theory (Schoener 1971, Charnov 1976, Krebs and Davies 1978, 1984, Cowie and Krebs 1979, Stephens and Charnov 1982, Krebs et al. 1983, Clark and Mangel 1985); life history theories (Cody 1966, Stearns 1976, Grafen 1984); theories of territorial behavior (Krebs and Davies 1978, 1984, Schoener 1983, Stamps and Buechner 1985); theories of anti-predator and competitive behavior (Krebs and Davies 1978, 1984, Caraco 1981, Clark and Mangel 1985); and theories of reproductive strategies (Cody 1966, Schaffer 1974, Krebs and Davies 1978, 1984, Dingle 1984, Grafen 1984) (additional references can be found in Krebs and Davies 1978, 1984).

The approach of studying one aspect of animal behavior at a time has the usual advantages of reductionist science, which is particularly useful in controlled laboratory situations. That is, the experimenter is able to isolate the one particular behavioral aspect that is of interest and apply the appropriate theory. On the other hand, this reductionist approach is of more limited value in the analysis of field data, since under natural conditions animals are continually subject to multiple decisions concerning which of several activities to adopt at any time, as well as how best to undertake the chosen activity.

The need for more general, unified behavioral theory has been recognized by a number of authors in widely varying contexts (Pianka 1976). For example, Lima et al. (1985) studied the trade-off between foraging efficiency and risk of predation in grey squirrels. They also

cite a number of cases in which there is need for a theory that allows one to assess such trade-offs in an easily measurable currency. They state: "As we mentioned earlier, deriving such predictions concerning trade-offs of this sort is likely to be an elusive goal in the study of animal behavior . . . . Although the theoretical problem may be formidable, the empirical evidence presented here and elsewhere suggests that such a task may well be worth the effort." (Lima et al. 1985: 163). Rodman and Cant (1984), in a discussion of foraging adaptations of nonhuman primates, describe three comprehensive adaptations of animals: avoiding predation, acquiring food, and reproducing. A unified theory of foraging or animal behavior should allow one to treat these three adaptations in a consistent theoretical manner. Roitberg et al. (1982), in a study of the foraging behavior of a tephritid fruit fly, stress that data generated from simple laboratory experiments (i.e., under reductionist conditions) may be misleading for interpretations of behavior in nature. Finally, Zach and Smith (1981) in a review entitled "Optimal Foraging in Wild Birds?" question the usefulness of the optimal foraging reductionist paradigm in understanding adaptations in the wild. They argue that most field situations are too complex to allow meaningful predictions of optimal foraging performance, that optimal solutions are very difficult to define (and thus to test), and that there is a need for the ability to apply optimality thinking to problems in the complex situations that arise in the wild.

Reductionist models of animal behavior have commonly employed some simple proxy for fitness (Grafen 1984). In optimal foraging theory, for example, fitness has often been equated to the average long-term rate of food or energy intake (the energy maximization hypothesis), or to the reciprocal of the average time required to obtain a specified amount of food (the time minimization hypothesis). The restrictive nature of

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<sup>2</sup> Address correspondence to M. Mangel, Department of Mathematics.

these assumptions was demonstrated by recent studies in which fitness was defined instead in terms of the probability of survival (Caraco 1981, Houston and McNamara 1985). A further shift in outlook would occur if reproductive success were taken into consideration. Similar problems related to the choice of fitness currency are encountered in studying other types of behavior. Thus, in addition to the need for a class of models that allows for the simultaneous consideration of alternative behavioral choices, there is a need to incorporate a unified concept of fitness.

It is clear that an animal's choice of behavioral activity at any time will normally depend on the current state of the animal, on the current state of its environment, and possibly also on past and expected future states (Cheverton et al. 1985). Any unified behavior theory should incorporate such state variables and their dynamics, preferably in a stochastic framework. (In fact, the inclusion of state variables is highly desirable for isolated behavior theories as well, since the state variable paradigm provides insights into problems that might not be gained in other ways. Clark [1986] discusses the case of group formation, and Mangel [1986] discusses the case of oviposition decisions in which the state variable approach provides key new insights.)

In this paper we develop such a class of unified behavioral models, which we call unified Foraging Theory (UFT). We choose this term rather than Unified Theory of Animal Behavior or Mathematical Ethology because foraging behavior must always be taken into consideration by an animal, unless it is sleeping or hibernating. UFT is based on three main concepts:

- 1) a state variable (or set of variables)  $X$  that characterizes the current physiological state of the forager (McFarland and Houston 1981) and that changes in a stochastic fashion, depending upon the state of the environment, the state of the forager, and its decisions;
- 2) a concept of fitness that is directly related to the long-term contribution to the gene pool;
- 3) a methodology for determining the behavioral strategy (as a function of the state variable) that optimizes fitness over a long time interval, using stochastic dynamic programming (SDP) and Markov decision processes (Aoki 1967, Ross 1983, Heyman and Sobel 1984, Mangel 1985).

A state variable paradigm has been used by other authors (e.g., Cane 1959, Katz 1974, McCleery 1977, Metz 1977, Craig et al. 1979, Putters et al. 1984, Root and Kareiva 1984) but not as extensively as we do in this paper. More recently, the techniques of Markovian modeling were applied by Houston and McNamara (1985), Iwasa et al. (1984), and Sibly and McCleery (1985) to cases of isolated foraging theory. It is our view, however, that the full potential and generality of Markovian modeling of animal behavior has not yet been realized.

Our main purpose is to introduce (by way of examples) the paradigm of UFT and show how simple

it is to use. For this reason, we present situations that are, to some extent, caricatures of the real biological world. It will be clear, however, that various modifications can easily be made to render our models "more realistic." We have recently applied UFT to the study of group size in social carnivores (Clark 1986) and to the study of host selection and clutch size in parasitic insects (Mangel 1986). In both cases, UFT is much more successful than classical foraging theory at explaining the observed data; UFT also leads to additional predictions that are experimentally testable.

The UFT models that we discuss all have a common framework, namely that of discrete-time Markov decision processes. Such models are easy to formulate, and the resulting optimization problem is easily expressed as a dynamic programming problem, which itself is readily programmable for numerical iteration. (All of our numerical results were obtained quickly on IBM PC/AT desktop microcomputers.) These UFT models have the additional advantage that their parameters have obvious biological meaning. The parameters can be estimated from field or laboratory data, but in this paper we rely on artificial data for our numerical illustrations. (See Clark 1986 and Mangel 1986 for UFT models based on actual data.) We do not assume that the reader is familiar with MDP models or stochastic dynamic programming; the paper is completely self-contained.

The simplicity of our approach is obtained with some sacrifice of generality. We ignore, in this paper, learning and population genetics. UFT can, however, be extended to cover these as well. Events are constrained to occur on a suitably specified discrete-time scale. Continuous-time dynamic programming models can also be used in behavioral studies (see Iwasa et al. 1984, for example), but even with many simplifications they usually involve somewhat complicated solution techniques. We believe that, with appropriate discretization, UFT models will prove to be adequate for most applications.

It is well known that dynamic programming problems become computationally infeasible as their dimension increases. However, this is an inevitable feature of dynamic optimization problems, not just a limitation of dynamic programming. Simple UFT models are already much more "realistic" than classical foraging models, and we have reason to be confident that numerically feasible UFT models will provide new insights into behavioral phenomena. Faster algorithms for dynamic programming are continually being developed (Larsen and Casti 1978), and the advent of parallel processors should further expand the range of applicability of UFT models.

#### THE STATE CONCEPT IN FORAGING THEORY

The key to the unification of foraging theory is the introduction of a state variable,  $X(t)$ , which characterizes the condition of the forager at time  $t$ . (See Table

1 for definitions of key variables and parameters.) In general, we will interpret  $X(t)$  as a level of stored energy, but the specific interpretation of  $X(t)$  depends (to some extent) upon the particular problem. The state variable should be measurable and should be connected to the fitness of the individual. Some other examples of state variables are gut content or body mass (Katz 1974, Craig et al. 1979, Mittelbach 1981, DeAngelis et al. 1984, Anderson and Fedak 1985), territory size (Myers et al. 1979, Kacelnik et al. 1981, Stamps 1984, Harvey and Corbet 1985), number of eggs that a parasitic insect has left to lay (Roitberg and Prokopy 1983, 1984, Charnov and Skinner 1984, Skinner 1985), body length (McClaren 1963, Lawlor 1976, Stamps and Tanaka 1981), or deficits such as food, water, or oxygen deficits (McFarland 1977, Krebs and McCleery 1984).

The state variable is assumed to have the following properties (1)  $X(t)$  decreases due to metabolism and increases due to the (usually random) results of foraging. (2)  $X(t)$  can never exceed some fixed value  $C$  which is the forager's energy capacity. (3) Death by starvation corresponds to  $X(t)$  falling below a critical value,  $x_c$ , which we can usually normalize to be 0. Death may also result from other causes, particularly predation on the forager.

The forager's behavior at time  $t$  is assumed to depend upon the current value of the state variable  $X(t)$  and on environmental conditions. For example, whenever  $X(t)$  is at or near capacity  $C$ , it is reasonable to believe that fitness will be maximized by nonforaging behavior: defending a territory, hiding from predators, etc. Isolated behavioral models do not allow for such "feedback" strategies, which follow automatically from UFT. In addition to allowing for the consideration of alternative strategies, UFT also produces feedback decision rules. In particular the well-known principle of risk-averse vs. risk-prone foraging (Oster and Wilson 1978, Caraco 1981, Real et al. 1982) arises also in UFT models, but in a more realistic setting that allows for finite capacity, and without the restrictive assumption of normality.

For computational simplicity, we will henceforth assume that decision periods are discrete time units, e.g., days. In order to introduce the simplest case of UFT, assume that the change in the energy reserves of the forager from time  $t$  to time  $t + 1$  can be expressed by the equation

$$X(t + 1) = X(t) - \text{energy loss} + \text{energy increase} \\ \text{due to food discoveries and consumption,} \quad (1)$$

subject to the constraint that

$$x_c < X(t + 1) \leq C. \quad (2)$$

In the event that the forager is killed by a predator, or that  $X(t + 1)$  falls to or below  $x_c$ , the process is terminated (by death).

We intentionally leave the choice of the units of  $t$

TABLE 1. Definitions of parameters and variables used in tables and figures.

Symbol	Meaning
$x$	current value of the state variable $X$
$p(x, s)$	maximum probability of surviving to time $s$ starting with a state variable at value $x$
$i^*$	optimal patch choice among patches $i$
$m$	clutch size
$p(x_1, x_2, T, t)$	maximum probability that a nestling survives to time $T$ given that the value of the parental state variable at time $t$ is $x_1$ and that the value of the nestling state variable is $x_2$
$\phi^*(x_1, x_2)$	optimal fraction of forage for parent to allocate to nestlings when current value of the parental and nestling state variables are $x_1$ and $x_2$ , respectively
$\alpha$	forager's energy cost of activity, per unit time
$\beta$	probability that the forager suffers death by predation, per unit time
$Y$	energy value of foraged food items
$\lambda$	forager's probability of finding food, per unit time
$C$	food (energy) capacity of the forager
$W$	number of intruders in the forager's territory
$k$	fraction of intruders expelled from the territory by the forager
$b$	intrusion rate into a territory, per unit time
$\bar{W}$	equilibrium number of intruders in a forager's territory

unspecified, since they may change with each problem. For example, if one is considering the patterns of meals in small birds, the interval might be 5 min (S. Lima, *personal communication*), whereas for large carnivores the interval might be 1 d (Clark 1986).

Suppose that at any time  $t$  the forager has a choice of strategies  $s_i$ ,  $i = 1, 2, \dots, S$ . The particular strategy chosen may affect energy loss, the probability of discovering food, and the probability of being killed by a predator. If strategy  $s_i$  is used in period  $t$ , Eq. 1 becomes

$$X(t + 1) = X(t) - \alpha_i + Z_i \quad (3)$$

(subject to the constraints of inequality 2), where  $\alpha_i$  is energy loss and  $Z_i$  is the energy value of food discovered. Both  $\alpha_i$  and  $Z_i$  may be random variables. The probability of predation corresponding to  $s_i$  is denoted by  $\beta_i$ . Examples of situations in which the  $\alpha_i$  and  $Z_i$  have been computed or measured are found in the papers by Alkon and Saltz (1985) on porcupines, DeAngelis et al. (1984) on bass, Grahame (1973) on the intertidal prosobranch *Littorina littorea* (L.), McClaren (1963) on marine zooplankton, Pyke (1981) on honeyeaters and hummingbirds, Pyke (1980) on bumble bees, Pough and Andrews (1985) on a lizard, Roitberg and Prokopy (1984) on fruit flies, Sibily and McCleery (1985) on herring gulls, and Stamps and Tanaka (1981) on lizards. The point of giving this list is to convince the reader that the state variable paradigm is a biologically reasonable and feasible one.

Both the results of foraging and the possibility of predation are assumed to be chance variables, so that

TABLE 2. Parameters for five hypothetical food patches  $i$  among which a foraging animal can choose (see Examples: Patch Selection). Parameter definitions are given in Table 1.

$i$	$\alpha_i$	$\beta_i$	$Y_i$	$\lambda_i$
1	1	0	0	0
2	1	0.05	2	0.20
3	1	0.15	2	0.35
4	1	0.25	2	0.35
5	1	0.40	2	0.50

even if  $X(t)$  is known with certainty,  $X(t + 1)$  will not be. The probability distribution of  $X(t + 1)$  will depend upon the actions of the forager at time  $t$ . To show how these probability distributions are computed and used, we begin by ignoring reproduction and consider a non-breeding period consisting of  $T$  days. We then identify evolutionary fitness over this period with the forager's probability of survival (Caraco 1981, McNamara and Houston 1982). While the conceptual basis of this assumption is clear, it should be noted that at least two important factors are omitted: (1) possible effects of strategy on kin, and (2) the need to build up an energy reserve for subsequent breeding activities (both of these can be included in a consistent manner, however; see Examples: Further Developments). The probability of survival is an example of a fitness function  $f(x)$  that relates the value of the state variable to a level of fitness (more general functions are discussed in Conclusions and Discussion).

Define  $p(x, T)$  as the *maximum* probability of surviving for  $T$  time units, given that  $X(0) = x$ . The problem of determining the foraging strategy  $s = s(x, T)$  that achieves this maximum probability is known as a Markov decision process (MDP) (Aoki 1967, Ross 1983, Heyman and Sobel 1984, Mangel 1985). The solution is easily obtained numerically by iteration of the corresponding dynamic programming equation. The process of deriving and solving the dynamic programming equation will be illustrated by a number of examples, pertaining to: foraging behavior (patch selection), reproductive behavior, allocation of parental effort to offspring, and territorial defense.

#### EXAMPLES

##### Patch selection

Consider a forager that must forage in one of  $S$  distinct patches on each day. The  $i^{\text{th}}$  patch is characterized by the parameter values

- $\alpha_i$  = energy cost (per period),
- $\beta_i$  = probability of death by predation (per period),
- $Y_i$  = energy value of food items,
- $\lambda_i$  = probability of discovering one item (per period).

For simplicity all food items in the  $i^{\text{th}}$  patch are assumed to have the same energy content, but this could easily be relaxed to make  $Y_i$  a random variable as well (that is,  $Y_{ij}$  is the size of the  $j^{\text{th}}$  food item in patch  $i$ ,

and now  $\lambda_{ij}$  is the probability of finding it). These parameters often might be estimable from field observations, although  $\beta_i$  might be difficult to estimate in practice. With this formulation, the patch selection problem is quite general but it should be clear that it applies to many kinds of foraging situations (cf. Cowie and Krebs 1979, Magurran and Pitcher 1983, Hoffman and Turelli 1985). With the general patch selection formulation, one can use UFT to study the trade-off, in a common currency (cf. McNamara and Houston 1986a), between the risk of predation and the risk of starvation. The problem of finding a theoretical framework in which to consider this trade-off has been important for experimental scientists (e.g., Stein and Magnuson 1976, Milinski and Heller 1978, Heinrich 1979, Fraser and Cerri 1982, Sih 1982, Magurran and Pitcher 1983, Lima 1985, Lima et al. 1985, Caldwell 1986). Also see McNamara and Houston (1986b) for a theoretical discussion of this trade-off.

The dynamic programming algorithm for this example proceeds as follow. First we have

$$p(x, 0) = \begin{cases} 1 & \text{for } x > x_c \\ 0 & \text{for } x \leq x_c \end{cases} \quad (4)$$

i.e., with no periods left, the forager is alive if and only if its energy reserves exceed  $x_c$ . Next, if  $T + 1$  periods remain and strategy (patch)  $i$  is selected in the first period, then we have, for  $x > x_c$ ,

$$\begin{aligned} \Pr(\text{survive } T + 1 \text{ periods} | X(0) = x) \\ = \Pr(\text{survive first period}) \\ \times \Pr(\text{survive remaining } T \text{ periods}) \\ = (1 - \beta_i)[\lambda_i p(x'_i, T) \\ + (1 - \lambda_i)p(x - \alpha_i, T)], \end{aligned} \quad (5)$$

where

$$x'_i = \min(x - \alpha_i + Y_i, C) \quad (6)$$

unless  $x'_i \leq x_c$ , in which case  $x'_i = x_c$ . Since by definition  $p(x, T + 1)$  is the maximum probability of survival, we have, for  $x > x_c$ ,

$$\begin{aligned} p(x, T + 1) = \max_i [ & (1 - \beta_i) \\ & \cdot [\lambda_i p(x'_i, T) \\ & + (1 - \lambda_i)p(x - \alpha_i, T)] \end{aligned} \quad (7)$$

and of course  $p(x, T + 1) = 0$  for  $x \leq x_c$ .

Eq. 7, the basic dynamic programming equation, and Condition 4 provide an iterative algorithm for determining  $p(x, T)$ , as well as the optimal strategy  $s(x, T)$ , for all  $x, T$ . As a technical point, note that if  $\alpha_i, Y_i$ , and  $C$  are restricted to integer values, then we can also restrict  $x$  to integer values  $0, 1, \dots, C$ . In this case we obtain a finite-state MDP, which further simplifies the computations. As a second technical point, note that if the time interval is sufficiently small, one can avoid problems of finding food "late" versus "early," since a small time interval corresponds to a basically instantaneous process.

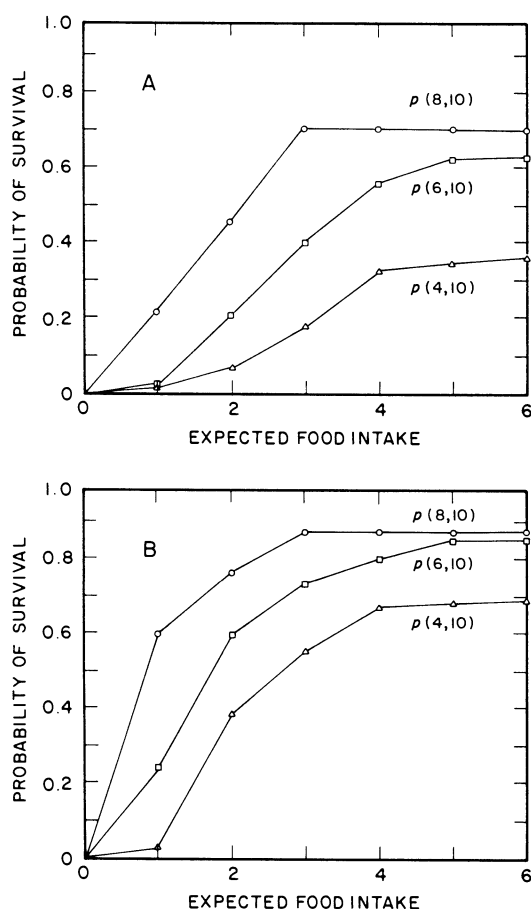


FIG. 1. Probability of survival for a hypothetical foraging animal, as a function of food intake. It is assumed that the only alternative to hiding is to forage in a food patch where  $\alpha$  (=energy cost per unit time) = 1,  $\beta$  (=probability of death by predation, per unit time) = 0.05, and (A)  $\lambda$  (=probability of discovering one food item) = 0.2 or (B)  $\lambda$  = 0.3. The capacity of the forager is  $C = 10$ . Variables and parameters are defined in Table 1.

As an example we consider the following parameter values:  $C = 10$ ,  $x_c = 0$ , and patch parameters given in Table 2. Patch 1 corresponds to "hiding" ( $\beta_1 = \lambda_1 = 0$  in Table 2), while patches 2–5 involve increasingly hazardous foraging in increasingly productive patches. Note that patch 4 is comparable to patch 3 in terms of probability of finding food, but riskier in terms of probability of predation. For this reason, one expects that patch 3 will always be chosen over patch 4. The resulting maximum survival probabilities  $p(x, T)$  and optimal strategies  $i^*$  are given in Table 3, for  $T = 10$  and 20. Not surprisingly, a low-risk strategy is optimal when the forager's metabolic state is at a high level, while increasingly risky strategies become optimal as the state decreases. In other words, the more "desperate" the forager's food requirements, the more risky the foraging behavior that should be adopted (Caraco 1981, Stephens and Charnov 1982, Clark and Mangel

1985). Note, too, that for fixed  $x$ , as the time horizon increases, the forager may adopt a more hazardous strategy (e.g., compare the optimal strategies for  $x = 6$  in Table 3), but this appears to be a relatively minor effect.

The probability of survival  $p(x, T)$  is also a function of the parameters  $C$ ,  $\alpha_i$ ,  $\beta_i$ ,  $\lambda_i$ , and  $Y_i$ . For example, the dependence of  $p(x, T)$  on expected food intake per period,  $\lambda Y$ , may be important for the analysis of foraging experiments (J. R. Krebs, *personal communication*). Fig. 1 shows this dependence for the case of two patches:  $s_1$  (hiding), with  $\lambda_1 = Y_1 = \beta_1 = 0$ , and  $s_2$  (foraging), with  $\lambda_2 = 0.2$  or  $0.3$ ,  $Y_2$  variable,  $\beta_2 = 0.05$  (and  $\alpha_i = 1$  for  $i = 1$  or  $2$ ). Similar calculations are easily performed on the basis of Eq. 7 for other parameter combinations.

Note that the  $i^*$  shown in Table 3 prescribes the optimal strategy in the first period only. Subsequent decisions depend upon the results of the first period, which involve chance outcomes. Note also that once the forager has accumulated enough reserves to "make it to the end," the optimal strategy is simply to hide. This strategy comes out of the UFT calculation; an explicit calculation is found (for a simpler version of the problem) in Mangel and Clark (1986).

#### Continuous reproduction

Consider next a forager whose strategic choices in any period are to hide, forage, or reproduce (for example, by laying eggs). Insects such as monarch butterflies or milkweed bugs provide an example (Dingle 1984). Note that in this case benefits accrue to the forager over the entire interval between 0 and  $T$ , rather than just at the end as in the patch-selection survival model. Recently, Charnov and Skinner (1984, 1985), Iwasa et al. (1984), Parker and Courtney (1984), and Skinner (1985) have examined theoretical questions associated with viewing oviposition site selection and clutch size as a foraging problem. Mangel (1986) provides a detailed application of UFT to this problem. Here, we show how the basic ideas of UFT are applied.

Assume that the forager will die naturally at the end

TABLE 3. Probability of survival for  $T$  time units ( $P[x, T]$ ), given optimal strategy  $i^*$  (=the choice of patch  $i$ ; patch parameter values are given in Table 2).

Energy reserve, $x$	$i^*$	$p(x, 10)$	$i^*$	$p(x, 20)$
1	5	.023	5	.002
2	3	.045	3	.004
3	3	.109	3	.009
4	3	.137	3	.013
5	3	.257	3	.025
6	2	.286	3	.030
7	2	.479	3	.053
8	2	.506	2	.060
9	2	.746	2	.100
10	2	.757	2	.107

of a single season lasting  $T$  periods. (The case of a random lifetime also can be treated by UFT by assuming a distribution for  $T$  and then averaging over that distribution in each period.) Assume that all eggs have the same probability of hatching, and do so simultaneously. A reasonable formulation of fitness would then be the total expected number of offspring (eggs) produced over the forager's lifetime:

$$J(x, T) = \text{maximum expected progeny (eggs) over periods } 0, \dots, T, \text{ given } X(0) = x. \quad (8)$$

(This simple formulation overlooks such questions as density dependence, dispersal, population growth, etc.; see, for example, Levin et al. 1984.)

The dynamics of the energy state  $X(t)$  are given by Condition 2 and Eq. 3; we will now use subscripts  $h$ ,  $f$ , and  $r$  to designate the mutually exclusive strategies of hiding, foraging, and reproducing in any given period  $t$ , respectively. If the reproductive strategy is used, then we assume that a fixed number ( $R$ ) of progeny (eggs) are produced, provided that (a) the energy state  $X(t) > x_R$ , a critical reproductive level ( $x_R \geq x_c$ ), and (b) the forager is not killed by a predator in period  $t$ . Other formulations of the model are possible, and an example using actual data is treated in Mangel (1986).

It follows immediately that

$$J(x, 1) = \begin{cases} R(1 - \beta_r) & \text{if } x > x_R \\ 0 & \text{if } x \leq x_R \end{cases}. \quad (9)$$

The dynamic programming equation that  $J(x, T)$  satisfies is easily seen to be (for  $x > x_c$ )

$$\begin{aligned} J(x, t+1) &= \text{maximum}\{J(x - \alpha_h, t), \\ &\quad (1 - \beta_f)[\lambda_f J(x', t) \\ &\quad \quad + (1 - \lambda_f)J(x - \alpha_f, t)], \\ &\quad (1 - \beta_r)[RH(x) + J(x - \alpha_r, t)]\}, \end{aligned} \quad (10)$$

where

$$x' = \min(x - \alpha_f + Y_f, C) \quad (11)$$

as long as  $x' > x_c$ , and

$$H(x) = \begin{cases} 1 & \text{if } x > x_R \\ 0 & \text{if } x \leq x_R \end{cases}. \quad (12)$$

The three expressions on the right side of Eq. 10 represent the expected number of progeny for the respective strategies  $h$ ,  $f$ , and  $r$ , given  $X(t+1) = x$ .

With no density dependence in egg survival, it is clear that the hiding strategy will never be used, since it leads to neither egg production nor an increase in food. For the choice between foraging and reproducing, it is clear that reproduction is favored when  $X(t)$  is large and foraging when  $X(t)$  is small. The role of UFT here is to provide predictions about the values of  $x$  and  $t$  at which the strategy switches, as a function of the environmental parameters  $\alpha_i$  and  $Y_i$ . Mangel (1986) provides a numerical example.

### Feeding of offspring

A parent animal faces the choice of foraging for its own needs, or for the purpose of feeding its young. Starlings, for example, must make decisions on the allocation of food to nestlings during the nesting period (Kacelnik 1984). UFT provides a natural theoretical basis for understanding observations of parental behavior, and also allows one to investigate the determinants of clutch size (e.g., Cody 1966, Klomp 1970, Schaffer 1974, Spight and Emlen 1976). Explicitly, consider a parent bird with  $m$  identical nestlings (the model can be modified to allow for dominance effects among nestlings). The parent's strategy choices are to hide or to forage, and, if it forages, to feed some fraction  $\phi$  ( $0 \leq \phi \leq 1$ ) of its food discoveries to its offspring. (Another parental strategy that we will not discuss here is the choice of abandoning a nestling.) The energy states of the parent and a typical nestling,  $X_p(t)$  and  $X_n(t)$ , respectively, satisfy:

$$\begin{aligned} X_p(t+1) &= X_p(t) - \alpha_{pi} + (1 - \phi)Y_i \\ X_n(t+1) &= X_n(t) - \alpha_{ni}(t) + \frac{\phi}{m}Y_i. \end{aligned} \quad (13)$$

Critical levels of the state variables are denoted by  $x_{pc}$  and  $x_{nc}$ , both of which we normalize to be zero, and capacities are  $C_p$  and  $C_n(t)$ . Note that we explicitly allow the metabolic rate and capacity of the nestling to change over time in order to model the growth of nestlings. The metabolic rate of the nestling could also depend upon  $m$ , since the nestlings warm each other when the parent is absent. Such a case can easily be treated by UFT.

Assume that the parental objective is to maximize the probability of survival of the  $m$  (identically treated) offspring over a fixed time horizon  $T$ . That is, we consider parental survival only in the sense that it affects offspring survival. At the end of this section, we consider a combination of parent and offspring survival as the objective functional.

Let  $p(x_1, x_2, T, t)$  denote the maximum survival probability for an offspring from time  $t$  up to time  $T$ , given that  $X_p(t) = x_1$  and  $X_n(t) = x_2$ . (Since identical offspring are considered, one only has to deal with a single function  $p[x_1, x_2, T, t]$ .) We then have

$$p(x_1, 0, T, t) = 0 \quad \text{for all } x_1, T, t \quad (14)$$

$$p(x_1, x_2, T, T) = 1 \quad \text{if } x_2 > 0 \quad (15)$$

$$p(0, x_2, T, t) = \begin{cases} 1 & \text{if } x_2 > \sum_{j=t}^T \alpha_n(j) \\ 0 & \text{if } x_2 \leq \sum_{j=t}^T \alpha_n(j) \end{cases}. \quad (16)$$

Eq. 14 follows from the specification  $x_{nc} = 0$ ; Eq. 15 says that the nestlings have survived if  $x_2 > 0$  at the

end of the nesting period; Eq. 16 asserts that the nestlings will survive following the death of their parent if and only if their current state  $x_2$  is large enough that their state remains positive to the end of the nesting period.

The dynamic programming algorithm is now (for  $x_1, x_2 > 0$ )

$$p(x_1, x_2, T, t) = \max \left( \begin{aligned} &p[x_1 - \alpha_p, x_2 - \alpha_n(t), T, t + 1], \\ &\max_{\phi} (1 - \beta_p)(1 - \beta_n) \\ &\quad \{ \lambda_p p(x_1', x_2', T, t + 1) \\ &\quad + (1 - \lambda_p) p[x_1 - \alpha_{pf}, x_2 - \alpha_n(t), \\ &\quad \quad T, t + 1] \} \\ &+ \beta_p(1 - \beta_n) p[0, x_2 - \alpha_n(t), T, t + 1] \end{aligned} \right) \quad (17)$$

where  $\beta_p$  is the probability that the parent dies while foraging,  $\beta_n$  is the probability that the nestlings are lost to a predator while the parent is foraging, and

$$\begin{aligned} x_1' &= \min[x_1 - \alpha_{pf} + (1 - \phi)Y_f, C_p] \\ x_2' &= \min[x_2 - \alpha_n(t) + \frac{\phi}{m} Y_f, C_n(t)], \end{aligned} \quad (18)$$

subject also to  $x_1' \geq x_{pc}$  and  $x_2' \geq x_{nc}$ .

The first expression in Eq. 17 is the nestling's survival probability when the parent does not forage, and the second expression is the survival probability if the parent forages and dispenses a fraction  $\phi$  of its food discovery (if any) to the nestlings.

The qualitative predictions of this model are clear: the parent should forage and feed its nestlings if they are hungry ( $x_2$  near zero) and it is not ( $x_1$  near  $C_p$ ), and the parent should forage and feed itself if it is hungry and its nestlings are not. When parent and nestlings are both hungry the parent faces a trade-off between feeding itself and feeding its offspring. From Eqs. 17 and 18 we see that this trade-off is characterized by the condition

$$\frac{d}{d\phi} p(x_1', x_2', T, t) = 0,$$

which can be written in the form

$$\frac{\partial p}{\partial x_1} = \frac{1}{m} \frac{\partial p}{\partial x_2} \quad (19)$$

(provided this yields an interior solution  $0 < \phi < 1$ ). The intuitive content of Eq. 19 is obvious; it is an operational decision rule provided the marginal benefits  $\partial p / \partial x_i$  are known as functions of  $x_1, x_2$ , and  $\phi$ .

This model is considerably more complicated than the previous examples, in that it involves two state variables, two time variables, and an additional continuous decision variable  $\phi$ . Also, since the decision variable is continuous, the state variables  $x_1$  and  $x_2$  no longer take only integer values. Thus, computing the value function  $p(x_1, x_2, T, t)$  is a little harder in that

either some discrete approximation must be used, or interpolations must be employed; our choice was numerical interpolations.

As an example, consider the following parameter values:  $C_p = 10, \alpha_p = 2, \alpha_f = 3, Y = 12, \beta_n = .05, \beta_p = .025, \lambda = .85$  and  $C_n(t), \alpha_n(t)$  growing according to:  $\alpha_n(t) = 0.1 + \alpha_p(1 - e^{-0.3t}), C_n(t) = 0.1 + C_p(1 - e^{-0.3t})$ . Table 4 shows  $p(5, 1, 10, 0), p(5, 2, 10, 0)$ , and the expected number of surviving offspring as a function of clutch size. In terms of the expected number of surviving offspring, the optimal clutch size is  $m = 5$ .

The optimal allocation  $\phi^*(x_1, x_2)$  is shown in Table 5 for  $x_1 = 5, x_2 = 2$ . These results are in accordance with life history theory (cf. Stearns 1976), which indicates that parental allocation should increase as the future value of the offspring increases (that is,  $p[x_1, x_2, T, t]$  increases as  $T - t$  decreases for fixed  $x_1, x_2$ ).

Other objective functionals can be treated as well. For example, consider (cf. Schaffer 1974, Grafen 1984)

$$\begin{aligned} F(x_1, x_2, T, t) &= \Pr\{\text{parent survives to } T | X_1(t) = x_1, \\ &\quad X_2(t) = x_2\} \\ &+ m \Pr\{\text{nestling survives to } T | X_1(t) \\ &\quad = x_1, X_2(t) = x_2\}. \end{aligned}$$

This objective, and the resulting optimal decisions, can be treated in a manner similar to the handling of Eq. 17.

One can envision numerous extensions of the basic model presented here. One of the most interesting would be an analysis of the experiments of Townshend and Wootton (1985) on the adjustment of parental investment to changing environmental conditions.

### Territorial defense

As the last example, consider a territorial animal that, during any time period, can either forage on its territory or attempt to expel intruders (Gass et al. 1976, Gass 1979, Myers et al. 1979, Schoener 1983, Stamps and Buechner 1985, Ydenberg and Houston 1986). The relationship between territory size and fitness is a thorny one (see, e.g., Fretwell and Lucas 1969, Brooke 1981, Kacelnik et al. 1981, or Stamps and Tollestrup 1984), so that here we will again use Condition 2 and Eq. 3 to model the energetic state of the forager. We introduce an additional state variable  $W(t)$ , the number of intruders on the territory at time  $t$ . The dynamics of  $W(t)$  are given by

$$W(t + 1) = S(t) + b[\bar{W} - S(t)], \quad (20)$$

where  $S(t)$  denotes the number of intruders left after any have been expelled in period  $t$ :

$$S(t) = (1 - k)W(t), \quad (21)$$

with  $k$  = the fraction of intruders expelled. If intruders are never expelled then  $W(t)$  approaches an equilibrium value denoted by  $\bar{W}$  in Eq. 20; we assume that



TABLE 4. Results of clutch size computations. Variables and parameters are defined in Table 1.

Clutch size, $m$	$p(5, 1, 10, 0)$	Expected number of offspring surviving	$p(5, 2, 10, 0)$	Expected number of offspring surviving
1	.63	0.63	.68	0.68
3	.55	1.65	.60	1.80
5	.34	1.70	.42	2.10
7	.05	0.35	.10	0.70
9	.001	0.009	.006	0.054

$0 < b < 1$ , so that this equilibrium is stable. Note that  $b\bar{W}$  can be considered as the basic intrusion rate. (One could also treat the size of the territory as a state variable. This presents no difficulty for UFT.)

The intruders reduce the amount of food available to the territory owner. In particular, we assume that the rate of finding forage by the owner of the territory is decreased by the presence of intruders:

$$\lambda[W(t)] = \frac{\lambda_0}{W(t) + 1}, \quad (22)$$

where  $\lambda(w)$  is the probability that forage is found with  $w$  intruders in the territory, and  $\lambda_0$  is the value if the forager is alone. An alternative is that intruders reduce food quality (consider nectarivores), so that the amount of forage found with  $w$  intruders present is  $Y(w) = Y_0/(w + 1)$ , where  $Y_0$  is the size of forage found when there are no intruders in the territory. Let  $\alpha_e$  be the energy cost of expelling intruders and  $\alpha_f$  the energy cost of foraging.

Let  $p(x, w, T)$  denote the maximum probability of survival to time  $T$ , given that  $X(0) = x$  and  $W(0) = w$ . We have

$$p(x, w, 0) = \begin{cases} 1 & \text{if } x > 0 \\ 0 & \text{if } x = 0 \end{cases} \quad (23)$$

and, by the (we hope) now familiar argument,

$$p(x, w, T + 1) = \max \left( p[x - \alpha_e, (1 - k)w + b[\bar{W} - (1 - k)w], T], \frac{\lambda_0}{w + 1} p[x', w + b(\bar{W} - w), T] + (1 - \frac{\lambda_0}{w + 1}) p[x - \alpha_f, w + b(\bar{W} - w), T] \right). \quad (24)$$

The first expression on the right side of Eq. 24 is the survival probability using the expulsion strategy, while the second expression corresponds to foraging.

Whether it is preferable to forage or to expel intruders at any given time  $t$  depends upon the current state variables  $X(t) = x$  and  $W(t) = w$  (and also on the time remaining). Foraging is optimal whenever the forager

is sufficiently hungry and intruders are few, while expelling intruders is optimal in the reverse circumstances. In  $(x, w)$ -space there should thus be a curve separating the region (near the origin) where foraging is optimal from the region where expelling is optimal. This curve (which also depends on the time horizon  $T$ ) is easily computed from Eqs. 23 and 24; an example is shown in Fig. 2. The qualitative implications of Fig. 2 are that more effort should be devoted to expelling intruders when the forager's energy reserves  $x$  are high, especially when intruders are easily expelled ( $k$  near 1.0). The model also predicts that expulsion effort will increase relative to foraging effort if the intruder rate  $b$  increases, whereas foraging effort will increase with increases in foraging efficiency ( $\lambda$  or  $Y_0$ ). An extension of the model here allows  $k$  to be a control variable in which, perhaps, different levels of  $k$  are associated with different energy costs. Such an extension is completely straightforward.

#### Further developments

It is clear that these examples can be elaborated in many ways, and that other aspects of animal behavior can also be modeled. The model parameters can be allowed to depend upon the energy state variable—e.g.,  $\lambda$  (the average rate of food discovery) might decrease at low values of  $X(t)$ . Also, the parameters can be made time-dependent, to reflect seasonal changes in food or predator abundance; the reproduction and nonbreeding models can be combined sequentially; depletion of forage can be modeled by including a state variable representing forage abundance; and so on. Information and updating of parameters can be included as well. Such complications would introduce no new conceptual difficulties, but it should be reiterated that computation time is likely to increase rapidly as the complexity of the model is increased.

#### CONCLUSIONS AND DISCUSSION

The introduction of a state variable representing the energy reserves of a foraging animal leads to a fully dynamic theory of foraging behavior, and also permits a comprehensive unification of foraging theory, allowing for the simultaneous consideration of anti-predatory, territorial, reproductive, and other strategies. Many realistic features, such as constraints on energy capacity, death by deprivation or predation, time-vary-

TABLE 5. Optimal parental allocation for  $x_1 = 5$ ,  $x_2 = 2$ , and  $m = 5$ . Variables and parameters are defined in Table 1.

Number of periods until independence $T - t$	Allocation, $\phi^*(5, 2)$
1	1.0
3	0.85
5	0.85
7	0.80
9	0.55

ing environmental parameters, and so on, can easily be included in such models. Behavioral strategy can be assumed to depend on the current state of the forager, and to track or forecast changes in parameters. Such realistically adaptive behavior can be analyzed by UFT, but not by the methods of classical foraging theory.

Our aim in this paper has been to describe the state variable, or Markovian, approach to behavioral theory in the simplest possible form. Although the state variable approach has been used previously (e.g., McFarland 1981, McNamara and Houston 1982, Iwasa et al. 1984), its full potential does not seem to have been appreciated. The methodology of Unified Foraging Theory (by which we mean MDP models) is extremely simple to learn and to apply to specific situations. Parameters have clear biological interpretation, and are subject to estimation from field or laboratory data.

In order to concentrate on the simplicity and generality of the UFT approach, we have not attempted a full qualitative analysis of any of our example models—a dry exercise for models based on artificial data! However, we present two empirical applications of UFT elsewhere (Clark 1986, Mangel 1986). In both of these papers we treat case studies in which classical foraging theory completely failed to give predictions that were consistent with the reported observations. In both cases, consistent predictions were obtained from UFT models. Moreover, merely thinking about the biological situation in terms of state variables quickly revealed why the classical approach failed. UFT is not merely a mathematically elegant generalization of classical foraging theory, but represents a completely different way of thinking about animal behavior.

The main disadvantage of UFT as delineated in this paper is that all predictions must apparently be obtained from computer iteration of the dynamic programming equation. For simple models these numerical computations present no difficulty, but more complex models can rapidly become computationally unwieldy. However, there is by now a large theoretical literature on MDP problems, which may prove useful for calculating long-term equilibrium strategies and convergence properties (see Ross 1983, Heyman and Sobel 1984). Parallel processor technology should further expand the scope of UFT.

We have concentrated on the probability of survival as our objective functional. UFT allows one to work with much more general objectives with virtually no change in conceptual or computational setting. To do this, one first must know the fitness function  $f(x)$  defined by

$$f(x) = \text{fitness of the level } x \text{ for the state variable.} \quad (25)$$

Once  $f(x)$  is given (perhaps the most difficult part of the extension), one defines

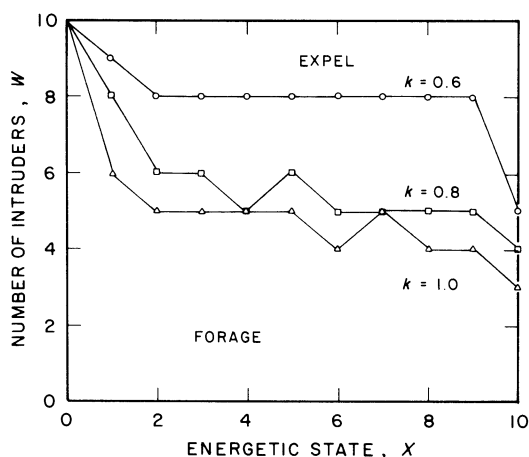


FIG. 2. Feedback control for territorial behavior, for three values of the repulsion factor  $k$ . For a given energy reserve,  $x$ , the territory owner should expel intruders if  $W$  (the number of intruders on the territory) lies above the line shown in the figure. (Other parameter values:  $C = 10$ ,  $\alpha = 1$ ,  $\lambda = 0.5$ ,  $Y = 2$ ,  $\bar{W} = 10$ ,  $b = 0.2$ ,  $T = 15$ .) Variables and parameters are defined in Table 1.

$$F(x, t, T) = \max E\{f[X(T)], \text{ given that } X(t) = x\}, \quad (26)$$

where the maximum is taken over the possible behavioral decisions of the forager and  $E\{\cdot\}$  denotes an expectation over the distribution of  $X(T)$ . The function  $F(x, t, T)$  solves exactly the same kind of iteration equation as the probability of survival  $p(x, T)$  considered in our examples. The only difference is the end condition, which, from Eq. 26, is

$$F(x, T, T) = f(x). \quad (27)$$

Lest we give the reader the (unrealistic) impression that all ethological problems treated by UFT involve the simple iterations shown in our previous examples, we close by describing some examples in which the dynamic programming equations are harder to solve.

The first example involves patch depletion. The difficulty is that the state variable must now include components representing the state of the patches. The major difficulty is not conceptual but computational, since much more information must be carried along in each iteration. Another example in which the major difficulty is computational is the problem of characterizing learning, in which various parameters are unknown to the forager and the forager's actions affect the kind of information obtained. In such a case, entire probability distributions are updated as the foraging process proceeds in time (see, e.g., Mangel and Beder 1985).

We next present two examples in which the difficulty in solving the dynamic programming equation is more conceptual than computational (that is, it involves which kind of algorithm to choose to solve the problem).

First, reconsider the patch selection problem and define  $\bar{T}(x)$  by

$$\bar{T}(x) = \max E[\text{lifetime of the forager} \text{ given that } X(0) = x]. \quad (28)$$

Using the same notation as in the patch selection problem, one sees that  $\bar{T}(x)$  must satisfy

$$\bar{T}(x) = 1 + \max_i (1 - \beta_i) \cdot [(1 - \lambda_i) \bar{T}(x - \alpha_i) + \lambda_i \bar{T}(x_i')], \quad (29)$$

where  $x_i' = \min(x - \alpha_i + Y_i, C)$ . Also

$$\bar{T}(x) = 0 \quad \text{for } x \leq x_c. \quad (30)$$

Eq. 29 constitutes an unconventional system of  $C$  non-linear equations for the unknown values  $T(1), \dots, T(C)$  (assuming  $\alpha_i, Y_i, C$  are all integers).

As a second example, consider a forager that must achieve a certain value of  $X$  in order to reproduce. This might pertain, for example, to a spider that needs to make an egg sac. Define  $u(x)$  by

$$u(x) = \max \Pr[X(s) \text{ crosses } x_R \text{ before it crosses } x_c, \text{ given that } X(0) = x]. \quad (31)$$

Then, using the same notation as in the patch selection problem, one shows that  $u(x)$  satisfies

$$u(x) = \max_i (1 - \beta_i) \cdot [(1 - \lambda_i) u(x - \alpha_i) + \lambda_i u(x_i')], \quad (32)$$

with boundary conditions

$$\begin{aligned} u(x) &= 0 & x &\leq x_c \\ u(x) &= 1 & x &\geq x_R. \end{aligned} \quad (33)$$

Eqs. 29 and 32 cannot be iterated over time as the equations in Examples were; new kinds of solution techniques are needed for these equations.

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#### LITERATURE CITED

- Alkon, P. U., and D. Saltz. 1985. Potatoes and the nutritional ecology of crested porcupines in a desert biome. *Journal of Applied Ecology*, *in press*.
- Anderson, S. S., and M. A. Fedak. 1985. Grey seal males: energetic and behavioral links between size and sexual success. *Animal Behaviour* **33**:829-838.
- Aoki, M. 1967. Optimization of stochastic systems. Academic Press, New York, New York, USA.
- Brooke, M. de L. 1981. How an adult wheatear (*Oenanthe oenanthe*) uses its territory when feeding nestlings. *Journal of Animal Ecology* **50**:683-696.
- Caldwell, G. 1986. Predation as a selective force on foraging herons: effects of plumage color and flocking. *Auk*, *in press*.
- Cane, V. R. 1959. Behavior sequences as semi-Markov chains. *Journal of the Royal Statistical Society (London), Series B* **21**:36-58.
- Caraco, T. 1981. Risk sensitivity and foraging groups. *Ecology* **62**:527-531.
- Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* **9**:129-136.
- Charnov, E. L., and S. W. Skinner. 1984. Evolution of host selection and clutch size in parasitoid wasps. *Florida Entomologist* **67**:5-21.
- Charnov, E. L., and S. W. Skinner. 1985. Complementary approaches to the understanding of parasitoid oviposition decisions. *Environmental Entomology*, *in press*.
- Cheverton, J., A. Kacelnik, and J. R. Krebs. 1985. Optimal foraging: constraints and currencies. *Fortschritte der Zoologie* **31**:109-126.
- Clark, C. W. 1986. The lazy adaptive lion: a reconsideration of foraging group size. *Animal Behaviour*, *in press*.
- Clark, C. W., and M. Mangel. 1985. The evolutionary advantages of group foraging. *Theoretical Population Biology*, *in press*.
- Cody, M. L. 1966. A general theory of clutch size. *Evolution* **20**:174-184.
- Cowie, R. J., and J. R. Krebs. 1979. Optimal foraging in patchy environments. Pages 183-205 in R. M. Anderson, B. D. Turner, and L. R. Raylor, editors. *Population dynamics*. Blackwell Scientific, London, England.
- Craig, B. B., D. L. deAngelis, and K. R. Dixon. 1979. Long and short-term dynamic optimization models with application to the feeding strategy of the loggerhead shrike. *American Naturalist* **113**:31-51.
- DeAngelis, D. L., S. M. Adams, J. E. Breck, and L. J. Gross. 1984. A stochastic predation model: application to largemouth bass observations. *Ecological Modelling* **24**:25-41.
- Dingle, H. 1984. Behavior, genes and life histories: complex adaptations in uncertain environments. Pages 169-194 in P. W. Price, C. N. Slobodkinoff, and W. S. Gaud, editors. *A new ecology*. Wiley, New York, New York, USA.
- Fraser, D. F., and R. D. Cerri. 1982. Experimental evaluation of predator-prey relationships in a patchy environment: consequences for habitat use patterns in minnows. *Ecology* **63**:307-313.
- Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**:16-36.
- Gass, C. L. 1979. Territory regulation, tenure, and migration in rufous hummingbirds. *Canadian Journal of Zoology* **57**:914-923.
- Gass, C. L., G. Angehr, and J. Centa. 1976. Regulation of food supply by feeding territoriality in the rufous hummingbird. *Canadian Journal of Zoology* **54**:2046-2054.
- Grafen, A. 1984. Natural selection, kin selection, and group selection. Pages 62-90 in J. R. Krebs and N. B. Davies, editors. *Behavioural ecology*. Blackwell Scientific, Oxford, England.
- Grahame, J. 1973. Breeding energetics of *Littorina littorea* (L.) (Gastropoda: Prosobranchiata). *Journal of Animal Ecology* **42**:391-403.
- Harvey, I. F., and P. S. Corbet. 1985. Territorial behavior of larvae enhances mating success of male dragonflies. *Animal Behaviour* **33**:561-565.
- Heinrich, B. 1979. Foraging strategies of caterpillars. Leaf damage and possible predator avoidance strategies. *Oecologia* (Berlin) **42**:325-337.
- Heyman, D. P., and M. J. Sobel. 1984. Stochastic models in operations research, Volume 2. McGraw-Hill, New York, New York, USA.
- Hoffman, A. A., and M. Turelli. 1985. Resource finding by *Drosophila melanogaster*: effects of experience and starvation. *American Naturalist* **126**:662-679.
- Houston, A., and J. McNamara. 1985. The choice of two prey types that minimizes the probability of starvation. *Behavioral Ecology and Sociobiology* **17**:135-141.

- Iwasa, Y., Y. Suzuki, and H. Matsuda. 1984. Theory of oviposition strategy of parasitoids. 1. Effect of mortality and limited egg number. *Theoretical Population Biology* **26**:205–227.
- Kacelnik, A. 1984. Central place foraging in starlings (*Sturnus vulgaris*). I. Patch residence time. *Journal of Animal Ecology* **53**:283–299.
- Kacelnik, A., A. I. Houston, J. R. Krebs. 1981. Optimal foraging and territorial defense in the Great Tit (*Parus major*). *Behavioral Ecology and Sociobiology* **8**:35–40.
- Katz, P. L. 1974. A long-term approach to foraging optimization. *American Naturalist* **108**:758–782.
- Klomp, H. 1970. The determination of clutch-size in birds. A review. *Ardea* **58**:1–124.
- Krebs, J. R., and N. B. Davies. 1978. *Behavioural ecology*. Blackwell Scientific, Oxford, England.
- Krebs, J. R., and N. B. Davies. 1984. *Behavioural ecology*. Second edition. Blackwell Scientific, Oxford, England.
- Krebs, J. R., and R. H. McCleery. 1984. Optimization in behavioural ecology. Chapter 4 in J. R. Krebs and N. B. Davies. *Behavioural ecology*. Blackwell Scientific, Oxford, England.
- Krebs, J. R., D. W. Stephens, and W. J. Sutherland. 1983. Perspectives in optimal foraging. Pages 165–221 in A. H. Brush and G. A. Clark, editors. *Perspectives in ornithology*. Cambridge University Press, Cambridge, England.
- Larsen, R. E., and J. L. Casti. 1978. *Principles of dynamic programming*. Part II. Marcel Dekker, New York, New York, USA.
- Lawlor, L. R. 1976. Molting, growth and reproductive strategies in the terrestrial isopod, *Armadillidium vulgare*. *Ecology* **57**:1179–1194.
- Levin, S. A., D. Cohen, and A. Hastings. 1984. Dispersal strategies in patchy environments. *Theoretical Population Biology* **26**:165–191.
- Lima, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. *Oecologia (Berlin)* **66**:60–67.
- Lima, S. L., T. J. Valone, and T. Caraco. 1985. Foraging-efficiency-predation-risk trade-off in the grey squirrel. *Animal Behaviour* **33**:155–165.
- Magurran, A. E., and T. J. Pitcher. 1983. Foraging, timidity, and shoal size in minnows and goldfish. *Behavioral Ecology and Sociobiology* **12**:147–152.
- Mangel, M. 1985. *Decision and control in uncertain resource systems*. Academic Press, New York, New York, USA.
- . 1986. Modelling behavioral decisions of insects. In Y. Cohen, editor. *INTECOL Symposium on Control Theory*. Plenum, New York, New York, USA, *in press*.
- Mangel, M., and J. H. Beder. 1985. Search and stock depletion: theory and application. *Canadian Journal of Fisheries and Aquatic Sciences* **42**:150–163.
- Mangel, M., and C. W. Clark. 1983. Uncertainty, search and information in fisheries. *Journal of the International Council for the Exploration of the Sea* **41**:93–103.
- Mangel, M., and C. W. Clark. 1986. Search theory in natural resources modelling. *Natural Resources Modelling*, *in press*.
- McClaren, I. A. 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. *Journal of the Fisheries Research Board of Canada* **20**:685–727.
- McCleery, R. H. 1977. On satiation curves. *Animal Behaviour* **25**:1005–1015.
- McFarland, D. J. 1977. Decision making in animals. *Nature* **269**:15–21.
- McFarland, D. J., and A. I. Houston. 1981. Quantitative ethology: the state space approach. Pitman, London, England.
- McNamara, J. M., and A. I. Houston. 1982. Short term behavior and lifetime fitness. Pages 60–87 in D. J. McFarland, editor. *Functional ontogeny*. Pitman, London, England.
- McNamara, J. M., and A. I. Houston. 1986a. The common currency for behavioral decisions. *American Naturalist* **127**:358–378.
- McNamara, J. M., and A. I. Houston. 1986b. Foraging in patches: there's more to life than the marginal value theorem. In *Quantitative analyses of behavior*, volume 6. Harvard University Press, Cambridge, Massachusetts, *in press*.
- Metz, H. A. 1977. State space models for animal behavior. *Annals of Systems Research* **6**:65–109.
- Milinski, M., and R. Heller. 1978. Influence of a predator on the optimal foraging behavior of sticklebacks (*Gasterosteus aculeatus* L.). *Nature* **275**:642–644.
- Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* **62**:1370–1386.
- Myers, J. P., P. G. Connors, and F. A. Pitelka. 1979. Territoriality in nonbreeding shorebirds. *Studies in Avian Biology* **2**:231–246.
- Oster, G., and E. O. Wilson. 1978. *Caste and ecology in the social insects*. Princeton University Press, Princeton, New Jersey, USA.
- Parker, G. A., and S. P. Courtney. 1984. Models of clutch size in insect oviposition. *Theoretical Population Biology* **26**:27–48.
- Pianka, E. R. 1976. Natural selection of optimal reproductive tactics. *American Zoologist* **16**:775–784.
- Pough, F. H., and R. M. Andrews. 1985. Energy costs of subduing and swallowing prey for a lizard. *Ecology* **66**:1525–1533.
- Putters, F. A., J. A. J. Metz, and S. A. L. M. Koijman. 1984. The identification of a simple function of a Markov chain in a behavioral context: barbs do it (almost) randomly. *Nieuw Archief voor Wiskunde* **2**:110–123.
- Pyke, G. H. 1980. Optimal foraging in bumblebees: calculation of net rate of energy intake and optimal patch choice. *Theoretical Population Biology* **17**:232–246.
- . 1981. Why hummingbirds hover and honeyeaters perch. *Animal Behaviour* **29**:861–867.
- Real, L., J. Ott, and E. Silverfine. 1982. On the tradeoff between the mean and the variance in foraging: effect of spatial distribution and color preference. *Ecology* **63**:1617–1623.
- Rodman, P. S., and J. G. H. Cant. 1984. *Adaptations for foraging in nonhuman primates*. Columbia University Press, New York, New York, USA.
- Roitberg, B. D., and R. J. Prokopy. 1983. Host deprivation influence on response of *Rhagoletis pomonella* to its oviposition deterring pheromone. *Physiological Entomology* **8**:69–72.
- Roitberg, B. D., and R. J. Prokopy. 1984. Host visitation sequence as a determinant of search persistence in fruit parasitic tephritid flies. *Oecologia (Berlin)* **62**:7–12.
- Roitberg, B. D., J. C. van Lenteren, J. J. M. Van Alphen, F. Galis, and R. J. Prokopy. 1982. Foraging behavior of *Rhagoletis pomonella*, a parasite of Hawthorn (*Crataegus viridis*), in nature. *Journal of Animal Ecology* **51**:307–325.
- Root, R. B., and P. M. Kareiva. 1984. The search for resources by cabbage butterflies (*Pieris rapae*): ecological consequences and adaptive significance of Markovian movements in a patchy environment. *Ecology* **65**:147–165.
- Ross, S. 1983. *Introduction to stochastic dynamic programming*. Academic Press, New York, New York, USA.
- Schaffer, W. 1974. Optimal reproductive effort in fluctuating environments. *American Naturalist* **108**:783–790.
- Schoener, T. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* **2**:369–404.

- . 1983. Simple models of optimal-territory size: a reconciliation. *American Naturalist* **121**:608–629.
- Sibly, R., and R. McCleery. 1985. Optimal decision rules for herring gulls. *Animal Behavior* **33**:449–465.
- Sih, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology* **63**:786–796.
- Skinner, S. 1985. Clutch size as an optimal foraging problem for insects. *Behavioral Ecology and Sociobiology*, *in press*.
- Spight, T. M., and J. Emlen. 1976. Clutch sizes of two marine snails with a changing food supply. *Ecology* **57**:1162–1178.
- Stamps, J. A. 1984. Growth costs of territorial overlap: experiments with juvenile lizards (*Anolis aeneus*). *Behavioral Ecology and Sociobiology* **15**:115–119.
- Stamps, J. A., and M. Buechner. 1985. The territorial defense hypothesis and the ecology of insular vertebrates. *Quarterly Review of Biology* **60**:155–181.
- Stamps, J., and S. Tanaka. 1981. The influence of food and water on growth rates in a tropical lizard (*Anolis aeneus*). *Ecology* **62**:33–40.
- Stamps, J. A., and K. Tollestrup. 1984. Prospective resource defense in a territorial species. *American Naturalist* **123**:99–114.
- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* **51**:3–47.
- Stein, R. A., and J. J. Magnuson. 1976. Behavioral response of crayfish to a fish predator. *Ecology* **57**:751–761.
- Stephens, D. W., and E. L. Charnov. 1982. Optimal foraging: some simple stochastic models. *Behavioral Ecology and Sociobiology* **10**:251–263.
- Townshend, T. J., and R. J. Wootton. 1985. Adjusting parental investment to changing environmental conditions: the effect of food ration on parental behavior of the convict cichlid, *Cichlasoma nigrofasciatum*. *Animal Behaviour* **33**:494–501.
- Ydenberg, R. C., and A. I. Houston. 1986. Optimal trade-offs between competing behavioral demands in the Great Tit. *Animal Behaviour*, *in press*.
- Zach, R., and J. N. M. Smith. 1981. Optimal foraging in wild birds? Chapter 5 in A. C. Kamil, and T. D. Sargent, editors. *Foraging behavior*. Garland STPM Press, New York, New York, USA.