

A Dynamic Habitat Selection Game

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ABSTRACT

A patch selection game is formulated and analyzed. Organisms can forage in one of H patches. Each patch is characterized by the cost of foraging, the density and value of food, the predation risk, and the density of conspecifics. The presence of conspecifics affects the finding and sharing of food, and the predation risk. Optimal foraging theory can be viewed as a "1-person" game against nature in which the optimal patch choice of a specific organism is analyzed assuming that the number of conspecifics in other patches is fixed. In the general game theoretic approach, the behavior of conspecifics is included in the determination of the distinguished organism's strategy. An iterative algorithm is used to compute the solution of the " n -person" game or dynamic ESS, which differs from the optimal foraging theory solution. Experiments to test the proposed theory using rodents and seed trays are briefly discussed.

INTRODUCTION

Two of the fundamental problems in behavioral ecology involve habitat choice (where to live) and group formation (with whom to live). Reviews can be found in [1-3]. In particular [3, 4] contain a general model for patch or habitat choice. This model is based on a premise of maximizing a measure of Darwinian fitness over an interval of length T . Fitness at the end of this interval is given by a function $f[X(T)]$, where $X(T)$ denotes the value of a state variable (e.g., energy reserves) at time T , and where $f(x)$ is the Darwinian fitness from T onwards given that $X(T) = x$. Habitat choices are made for times between t and $T-1$ in order to maximize the expected value of terminal fitness taking into account predation and starvation risks. Clark [5] and Mangel and Clark [3] have also developed models of group foraging in which foraging takes place in a single habitat.

In this paper I combine habitat selection and group formation by developing a theory for the optimal choice of habitat by an organism when conspecifics are present in the patches. The interplay of habitat selection

and the density of organisms can be important as a source of biological diversity [6] and may have crucial effects on population dynamics and evolutionary processes [7]. Morris [8] analyzed the spatial scale and the cost of density-dependent habitat selection. In the absence of conspecifics, optimal foraging theory [2] can be used to compute optimal habitat selection. In this case optimal foraging theory can be viewed as a "1-person" game in which the forager plays against nature and the payoff is an absolute measure of fitness. The presence of conspecifics complicates matters. One could simply treat the number of conspecifics as fixed but alter patch parameters, and still apply optimal foraging theory. The alternative, which is adopted here, is to take a strategic or game theoretical approach (cf. the analysis in [9]) for a full analysis of the problem. In this case, one analyzes an " n -person" game in which the foraging organism optimizes a payoff relative to the other players. In this manner a dynamic ESS [10] is found, and can be compared to the optimal foraging solution. Reecer et al. [11] provide an alternative approach using a "habitat matching rule."

THE MODEL

I model organisms that can forage in one of H discrete patches, for example, rodents foraging in seed trays [12-15]. The i th patch is characterized by the following parameters:

- α_i = energetic costs of foraging in the patch.
- β_i = probability per period of predation while foraging.
- λ_i = probability per period of finding food while foraging.
- Y_i = energetic value of the food found. (1)

The state of the organism is characterized by a single variable $X(t)$ denoting energetic reserves at time t . The model can be extended for more than one state variable. In addition, a distribution of food types can be included without difficulty.

The organism whose decisions are being modeled will be called the "distinguished" individual. Conspecifics affect the predation risk, the probability of finding food, and the amount of food that the foraging organism obtains. If there are n conspecifics present in a patch, the predation risk, the probability of finding food, and the energetic value of food found must be modeled as functions of n . Here I adopt the following computational forms for these functions when there are n conspecifics in a patch in addition to the distinguished individual:

$$\beta_i(n) = \beta_{i0}e^{*n}/(n+1), \quad (2)$$

$$\lambda_i(n) = \min\{1, \lambda_{i0}e^{\gamma n}\}, \quad (3)$$

$$Y_i(n) = Y_{i0}/(n+1). \quad (4)$$

In these equations, parameters indexed by 0 are values when no conspecifics are present in the i th patch, and κ and γ are parameters.

The justification of the functional forms is as follows: In the absence of conspecifics, each patch is characterized by a fixed predation probability, a probability of encountering food, and a nondepleting food resource. The presence of conspecifics may increase the probability that a predator detects the group, hence the $e^{\kappa n}$ multiplying β_{i0} ; but if a successful predator attack occurs when there are n additional organisms in the patch, then the chance that the distinguished individual is killed is $1/n+1$. Second, the probability of finding food while foraging is increased by conspecifics, hence the $e^{\gamma n}$ multiplying λ_{i0} , but the share of food found is decreased, hence the factor $n+1$ dividing Y_{i0} . The parameter γ measures the enhancement of the rate at which food is found by a group. For rodents foraging for seed in trays [12–15] for example, γ might be 0 if the seeds were dispersed, but greater than 0 if the seeds were clumped. The parametric forms in Equations (2)–(4) are chosen as possible representations of the biological situation and not as a particular model of a particular experiment. The objective here is to illustrate the differences between the “1-person” and “ n -person” games. The specific results will depend to some extent on the choice of functional forms and parameters, but the basic ideas will not change.

First consider the “optimal foraging theory” (OFT) or “1-person” game solution for the optimal behavior of the distinguished individual. In this case the number of conspecifics in each patch is fixed. That is, there is no predation of conspecifics in the OFT solution. Rather, the level of conspecifics is treated as a parameter. In each period t between 1 and $T-1$, the organism must choose which habitat to visit during that period. The basic patch selection model of Mangel and Clark [3, 4] now becomes

$$F(x, t, T) = \max_i \{ [1 - \beta_i(n_i)] [\lambda_i(n_i) F(x'_i, t+1, T) + (1 - \lambda_i(n_i)) F(x''_i, t+1, T)] \}. \quad (5)$$

In this equation, $x'_i = \text{chop}[x - \alpha_i + Y_i(n_i); x_c, x_m]$ and $x''_i = \text{chop}[x - \alpha_i; x_c, x_m]$, where $\text{chop}[x; a, b]$ equals a if $x < a$, b if $x > b$, and x in any other case.

Equation (5) is solved backwards, letting t run from $T-1$ to 1 and using the end condition that $F(x, T, T) = f(x)$. (See [3] for further details and computational algorithms.) As it is solved the optimal decisions are determined. These are denoted by

$$d^*(x, t) = i, \text{ if the optimal decision is to visit patch } i \text{ in period } t \text{ when } X(t) = x. \quad (6)$$

The optimal decisions can be used to divide the (t, x) plane into regions according to which patch should be visited. The line labeled “OFT” in

