

Optimal Foraging in Nonpatchy Habitats. I. Bounded One-Dimensional Resource

ROGER ARDITI

*Institut de Zoologie et d'Écologie Animale,
Université de Lausanne, CH-1015 Lausanne, Switzerland*

AND

BERNARD DACOROGNA

*Département de Mathématiques, Ecole Polytechnique Fédérale, CH-1015 Lausanne,
Switzerland*

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ABSTRACT

We present a model of optimal foraging in habitats where the food has an arbitrary density distribution (continuous or not). The classical models of foraging strategies assume that the food is distributed in patches and that the animal divides its time between the two distinct behaviors of patch exploitation and interpatch travel. This assumption is hard to accept in instances where the food distribution is continuous in space, and where travel and feeding cannot be sharply distinguished. In this paper, the habitat is assumed to be one-dimensional and bounded, and the animal is assumed to have a limited foraging time available. The problem is treated mathematically in the context of the calculus of variations. The optimal solution is to divide the habitat in two subsets according to the food density. In the richer subset, the animal equalizes the density distribution; in the poorer subset, it travels as fast as possible.

1. INTRODUCTION

Since the first papers of Emlen [8,9] and MacArthur and Pianka [16], classical optimal-foraging theory has mostly dealt with the two problems of estimating the "best" diet (i.e. choice between different prey types) and the "best" exploitation of prey patches (i.e. choice between places with different prey densities).

Patch models assume that the food is distributed among discrete, sharply delimited areas, each with a uniform food density distribution. As a consequence, the animal is assumed to present the two distinct, noninterfering behaviors of interpatch travel and intrapatch foraging. The classical patch

model is the “marginal-value theorem” [6], which predicts the length of time the animal should stay in each patch in order to maximize the overall average energy intake rate. Some of the assumptions of this model are (1) diminishing returns in each patch, (2) equally spaced patches, (3) unlimited number of patches, (4) unlimited foraging time.

The assumption of patchy distribution of the food has proved fruitful and many important results have been obtained (see e.g. [14,17] for reviews). However, it is not always a good description of the space distribution of the food. As has recently been pointed out [13,15], the delimitation of patches may be difficult. For example, an antelope grazing in the savanna exploits a food with a continuous distribution in space. In such a case, traveling and feeding cannot be easily distinguished. It is therefore necessary to study foraging models in which the food is not assumed to be patchily distributed.

The most elaborate treatment of a nonpatchy food resource has been done by Andersson [2] for a habitat with *uniform* food density, with return of the animal to a central place. He showed that energy maximization is obtained if the animal equalizes the “marginal cost” of additional food. Bond [5] suggested approaching the case of continuous distributions by studying patch models with patches of variable size and uncertain location. We prefer to tackle the general problem directly by considering habitats where the food can present an *arbitrary* distribution in space. Continuous distributions (including the uniform distribution) and patchy distributions can then be studied as special cases. The classical calculus of variations offers powerful mathematical tools to deal with this problem.

Dropping the assumption of patchy distribution, we also drop the assumption of unlimited foraging time. Instead, it is generally agreed that the animal has a foraging period T available [17]. This period can be thought of as the “time horizon” [12] or available “search effort” [2] over which the energy gain should be maximized [19].

In the present paper, we consider a simple but plausible situation: a one-dimensional food resource with fixed boundaries. Such a situation can apply, for example, to animals living in hedges or along rivers, like many birds and small mammals. We also assume that any time needed to travel between the animal’s nest and the food resource is fixed. Therefore, the problem is to find how the animal must allocate its total foraging time T to the different points of the habitat in order to maximize the energy intake. In these conditions, it will be shown that, in general, the animal should only exploit the part of the habitat where the food density is higher than some threshold. In this part, the food should be exploited so as to equalize the remaining density.

The assumptions of this model are more fully discussed in Section 6, where possible applications are also considered. The assumptions are rather restrictive, but they will be useful in setting the modeling framework and

explaining the mathematical methods. Further articles will deal with more general situations.

2. THE MODEL

We assume that the food resource is distributed on the bounded interval $[0,1]$. The animal starts the exploitation at $x=0$ at time $t=0$ and has a limited foraging time T to reach the end of the interval:

$$x(0) = 0 \quad \text{and} \quad x(T) = 1. \quad (2.1)$$

This implies that the average velocity is $1/T$.

It will also be assumed that the velocity of the animal is bounded by an upper physiological limit, and that it only moves in the positive direction:

$$0 < \frac{dx}{dt} \leq \beta. \quad (2.2)$$

Let $q(x)$ be the food density at point x . At a given position x , the food is exploited according to the presence of the animal. It will be assumed that, during the time the animal is at position x , the food density follows the classical Lotka-Volterra consumption equation

$$\frac{dq}{dt} = -aq. \quad (2.3)$$

The assumption that the quantity consumed is strictly proportional to the food density may in some circumstances be grossly unrealistic. More generally, Equation (2.3) can be replaced by

$$\frac{dq}{dt} = -\varphi(q), \quad (2.4)$$

where $\varphi(q)$ is the so-called "functional response" [11]. Typically, functional responses increase (in various ways) with the food density and tend to some upper asymptote due to the saturation of the predator. For the sake of simplicity, the Lotka-Volterra functional response (2.3) will be assumed in the following theorem, but it will be shown in Section 5 that all results remain qualitatively valid for any strictly increasing function φ .

Let $\tau(x)$ designate the "presence" of the animal at position x , i.e., the length of time it spends at this point. From Equation (2.3), the quantity of food remaining at point x after a presence $\tau(x)$ of the animal is

$$\sigma(x) = q(x) e^{-a\tau(x)}. \quad (2.5)$$

On the whole habitat, the energy acquired will be

$$\int_0^1 \varrho(x) [1 - e^{-a\tau(x)}] dx. \quad (2.6)$$

Since the objective is to maximize the net gain of energy, costs must still be subtracted from (2.6). We can assume that energy expenses are attached to the time spent (basal metabolism)

$$c_m dt, \quad (2.7)$$

the distance traveled (cost of searching)

$$c_s dx, \quad (2.8)$$

the velocity (cost of locomotion)

$$c_l \frac{dx}{dt} dt, \quad (2.9)$$

and the food consumed (cost of handling)

$$c_h d\varrho. \quad (2.10)$$

The net energy gain is then

$$\int_0^1 (1 - c_h) \varrho(x) [1 - e^{-a\tau(x)}] dx - c_m T - c_s - c_l. \quad (2.11)$$

Eliminating all constants, the problem reduces to calculating the following minimum:

$$\min_{\tau} \int_0^1 \varrho(x) e^{-a\tau(x)} dx, \quad (2.12)$$

under the constraints (2.1) and (2.2).

Naturally, the function $\tau(x)$, describing the duration of the presence of the animal at position x , is related to the trajectory $x(t)$. We assume that the animal has a finite "section" r in which it detects food. (This is the one-dimensional analog of Andersson's "detection area" [2].) This section is assumed to be much smaller than the whole habitat, and the velocity is assumed to be approximately constant while the animal travels the distance r . The time during which the point x is within this section is inversely proportional to the velocity:

$$\tau(x) = \frac{r}{dx/dt}. \quad (2.13)$$

Let $s(x)$ be the inverse function of the trajectory $x(t)$ (the "schedule" of the animal). Equation (2.13) means then that

$$\tau(x) = r \frac{ds}{dx}. \quad (2.14)$$

We now define new variables and parameters:

$$w(x) = ars(x), \quad (2.15a)$$

$$\alpha = \frac{ar}{\beta} \quad \text{and} \quad S = arT. \quad (2.15b)$$

With this notation, the problem is finally to find the function w which minimizes the integral

$$\int_0^1 \varrho(x) e^{-w'(x)} dx, \quad (2.16)$$

with the conditions

$$w(0) = 0, \quad w(1) = S, \quad \text{and} \quad w'(x) \geq \alpha. \quad (2.17)$$

Since the average value of w' is S , it must obviously be assumed that $S \geq \alpha$; otherwise the problem would be meaningless.

With the notation (2.15), the density distribution of the food remaining after the passage of the animal (2.5) is

$$\sigma(x) = \varrho(x) e^{-w'(x)}. \quad (2.18)$$

3. THE MAIN THEOREM AND SOME EXAMPLES

We first introduce the set of admissible functions w :

$$\mathcal{W} = \{ w \in \text{Lip}(0,1) : w(0) = 0, \quad w(1) = S, \quad \text{and} \quad w'(x) \geq \alpha \text{ a.e.} \},$$

where $\text{Lip}(0,1)$ stands for the set of locally Lipschitz functions w , i.e., for every $x, y \in [0,1]$, there exists $K \geq 0$ such that

$$|w(x) - w(y)| \leq K|x - y|.$$

In particular, a locally Lipschitz function is everywhere continuous and has a derivative, which is uniformly bounded, at almost all points.

Thus, our problem is to find $\tilde{w} \in \mathcal{W}$ satisfying

$$(P) \quad \min_{w \in \mathcal{W}} \int_0^1 \varrho(x) e^{-w'(x)} dx.$$

We shall assume that the food density $\varrho: [0,1] \rightarrow [0,\infty)$ is a piecewise continuous function, i.e. continuous except on a finite number of points d_1, \dots, d_N . We denote

$$I \equiv [0,1] \setminus \{d_1, \dots, d_N\},$$

and for $x \in I$, we define

$$A_x = \{z \in I: \varrho(z) \geq \varrho(x)\} \quad (3.1)$$

and

$$\Omega = \left\{ x \in I: \log \varrho(x) \geq \frac{1}{|A_x|} \left[\int_{A_x} \log \varrho(z) dz - (S - \alpha) \right] \right\}, \quad (3.2)$$

where $|A_x|$ denotes the measure of the set A_x .

Remarks.

(i) Ω is the set where the Euler equation associated to (P) without the constraint $w' \geq \alpha$ is satisfied.

(ii) Roughly speaking, the set Ω^C ($\equiv I \setminus \Omega$) represents a set where there is "little" food.

(iii) If $\varrho(x) = 0$ for some $x \in I$, then, by extension, we will have $x \in \Omega^C$.

(iv) We will assume throughout that $S \geq \alpha$, in order that the set W be nonempty. This will also imply that $\Omega \neq \emptyset$.

We may now state the theorem.

THEOREM

Let ϱ be as above. Then (P) possesses a unique minimum $\tilde{w} \in W$ defined as follows:

$$\tilde{w}'(x) = \begin{cases} \log \varrho(x) + \frac{1}{|\Omega|} \left[S - \alpha |\Omega^C| - \int_{\Omega} \log \varrho(z) dz \right] & \text{if } x \in \Omega, \\ \alpha & \text{if } x \in \Omega^C. \end{cases} \quad (3.3)$$

In particular, if ϱ is differentiable in Ω , then

$$\frac{d}{dz} \left[\varrho(z) e^{-\tilde{w}'(z)} \right] = 0 \quad \text{for every } z \in \Omega. \quad (3.4)$$

Remark. It is not difficult to see that if ϱ is differentiable in $[0,1]$, then \tilde{w} is not only locally Lipschitz but also differentiable everywhere.

We now give some simple examples of food density distributions and of the solutions associated to them.

Example 1 (The uniform distribution). If $\varrho(x) \equiv c$ for every $x \in [0,1]$, then $\Omega = [0,1]$ (since $S \geq \alpha$). Thus $\tilde{w}'(x) \equiv S$ for every $x \in [0,1]$, and hence $\tilde{w}(x) = Sx$, which is the obviously expected result.

Example 2 (The N-patch model). We will suppose that $0 = x_0 < x_1 < \dots < x_N = 1$ and

$$\varrho(x) = c_i \quad \text{if } x_{i-1} < x \leq x_i. \tag{3.5}$$

There is no real loss of generality if we suppose that $c_1 \geq c_2 \geq \dots \geq c_N$, but this simplifies the notation. Let $I = [0,1] \setminus \{x_1, \dots, x_N\}$. Two cases may happen.

Case 1: $S + x_k \log c_k - \sum_{j=0}^{k-1} (x_{j+1} - x_j) \log c_{j+1} \geq \alpha$ for every $k \in \{1, \dots, N\}$. Then $\Omega = I$, and

$$\tilde{w}'(x) = S + x_k \log c_k - \sum_{j=0}^{N-1} (x_{j+1} - x_j) \log c_{j+1} \quad \text{if } x_{k-1} \leq x < x_k. \tag{3.6}$$

The food remaining after the passage of the animal is then

$$\sigma(x) \equiv \exp \left[-S + \sum_{j=0}^{N-1} (x_{j+1} - x_j) \log c_{j+1} \right] \quad \text{for every } x \in [0,1]. \tag{3.7}$$

In this case, the animal has therefore enough time to equalize the food distribution over the whole habitat.

Case 2: There exists $k \in \{1, \dots, N\}$ such that

$$\begin{aligned} S + x_k \log c_k - \sum_{j=0}^{k-1} (x_{j+1} - x_j) \log c_{j+1} &\geq \alpha, \\ S + x_{k+1} \log c_{k+1} - \sum_{j=0}^k (x_{j+1} - x_j) \log c_{j+1} &< \alpha. \end{aligned} \tag{3.8}$$

Then $\Omega = [0, x_k) \cap I$, and $\Omega^C = (x_k, 1] \cap I$, and

$$\tilde{w}'(x) = \begin{cases} \frac{S - \alpha(1 - x_k)}{x_k} + \log a_i & \\ - \sum_{j=0}^{k-1} \frac{x_{j+1} - x_j}{x_k} \log a_{j+1} & \text{if } 0 \leq x_{i-1} < x < x_i \leq x_k, \\ \alpha & \text{if } x_k < x \leq 1. \end{cases}$$

The food distribution remaining after the passage of the animal is then

$$\sigma(x) = \begin{cases} \exp \left[\frac{-S + \alpha(1 - x_k)}{x_k} + \sum_{j=0}^{k-1} \frac{x_{j+1} - x_j}{x_k} \log a_{j+1} \right] & \text{if } 0 \leq x < x_k, \\ a_j e^{-a} & \text{if } x_k \leq x < x_j. \end{cases}$$

Therefore, the animal will in this case equalize the food distribution only in $[0, x_k)$.

Example 3 (A continuous food distribution). Let us take the example $q(x) = e^x$ for $x \in [0, 1]$. Then

$$A_x = \{z \in [0, 1] : q(z) \geq q(x)\} = [x, 1],$$

and

$$\begin{aligned} \Omega &= \{x \in [0, 1] : x^2 + 2x + 1 - 2(S - \alpha) \leq 0\} \\ &= [0, 1] \cap [1 - \sqrt{2S - 2\alpha}, 1 + \sqrt{2S - 2\alpha}]. \end{aligned}$$

So, as before two cases can happen.

Case 1: $1 \leq 2(S - \alpha)$. In this case, $\Omega = [0, 1]$ and

$$\tilde{w}'(x) = x + S - \frac{1}{2} \quad \text{for } x \in [0, 1],$$

and the food distribution after the passage of the animal is

$$\sigma(x) \equiv \exp\left(\frac{1}{2} - S\right) \quad \text{for every } x \in [0, 1].$$

So again the animal equalizes the whole food distribution.

Case 2: $1 \geq 2(S - \alpha)$. In this case,

$$\Omega = [1 - \sqrt{2S - 2\alpha}, 1],$$

and thus

$$\tilde{w}'(x) = \begin{cases} \alpha & \text{if } 0 \leq x \leq 1 - \sqrt{2S - 2\alpha}, \\ x + \alpha - 1 + \sqrt{2S - 2\alpha} & \text{if } 1 - \sqrt{2S - 2\alpha} \leq x \leq 1. \end{cases}$$

The remaining food density is then

$$\sigma(x) = \begin{cases} \exp(x - \alpha) & \text{if } 0 \leq x \leq 1 - \sqrt{2S - 2\alpha}, \\ \exp[1 - \alpha - \sqrt{2S - 2\alpha}] & \text{if } 1 - \sqrt{2S - 2\alpha} \leq x \leq 1. \end{cases}$$

As before, food equalization occurs only in Ω .

4. PROOF OF THE THEOREM

We first start with two lemmas which give a characterization of Ω .

LEMMA 1

For $x \in I$, let

$$g(x) \equiv S + |A_x| \log \varrho(x) + \int_{A_x} \log \varrho(z) dz. \quad (4.1)$$

Then

$$g(x) \geq g(y) \iff \varrho(x) \geq \varrho(y). \quad (4.2)$$

Proof. From the definition of Ω , one has

$$x \in \Omega \iff g(x) \geq \alpha. \quad (4.3)$$

Observe that

$$g(x) - g(y) = \int_{A_y} [\log \varrho(z) - \log \varrho(y)] dz - \int_{A_x} [\log \varrho(z) - \log \varrho(x)] dz. \quad (4.4)$$

Direction \Leftarrow : If $\varrho(x) \geq \varrho(y)$, then $A_x \subset A_y$, and thus

$$\begin{aligned} \int_{A_y} [\log \varrho(z) - \log \varrho(y)] dz &\geq \int_{A_x} [\log \varrho(z) - \log \varrho(y)] dz \\ &\geq \int_{A_x} [\log \varrho(z) - \log \varrho(x)] dz, \end{aligned}$$

and therefore $g(x) \geq g(y)$.

Direction \Rightarrow : Let now $\varrho(x) < \varrho(y)$. Then $A_y \subset A_x$ and

$$\begin{aligned} \int_{A_y} [\log \varrho(z) - \log \varrho(y)] dz &< \int_{A_y} [\log \varrho(z) - \log \varrho(x)] dz \\ &\leq \int_{A_x} [\log \varrho(z) - \log \varrho(x)] dz, \end{aligned}$$

and thus $g(x) < g(y)$. ■

LEMMA 2

Let

$$\beta = \sup \{ \varrho(x) : x \in \Omega^C \}. \quad (4.5)$$

Then

$$S + |\Omega| \log \beta - \int_{\Omega} \log \varrho(z) dz \leq \alpha. \quad (4.6)$$

Proof. Let $x \in \Omega^C$. Then $A_x \supset \Omega$ [since if $y \in \Omega$, then from (4.3) $g(y) \geq \alpha > g(x)$, and from (4.2) we deduce $\varrho(y) \geq \varrho(x)$, i.e. $y \in A_x$]. Let

$$B = \bigcap_{x \in \Omega^C} A_x. \quad (4.7)$$

Then $B \supset \Omega$.

Let $\varepsilon > 0$ be fixed. Then, from the definition of β , there exists $x_\varepsilon \in \Omega^C$ such that

$$\log \beta \geq \log \varrho(x_\varepsilon) \geq \log \beta - \varepsilon, \quad (4.8a)$$

$$\text{meas}[A_{x_\varepsilon} \setminus B] \leq \varepsilon. \quad (4.8b)$$

Note that

$$\begin{aligned} \lambda &\equiv S + |\Omega| \log \beta - \int_{\Omega} \log \varrho(z) dz \\ &= g(x_\varepsilon) + |\Omega| \log \beta - |A_{x_\varepsilon}| \log \varrho(x_\varepsilon) + \int_{A_{x_\varepsilon} \setminus \Omega} \log \varrho(z) dz. \end{aligned}$$

Since $x_\varepsilon \in \Omega^C$ and satisfies (4.8a), we have with (4.3)

$$\begin{aligned} \lambda &< \alpha + \varepsilon |A_{x_\varepsilon}| + \int_{A_{x_\varepsilon} \setminus \Omega} (\log \varrho(z) - \log \beta) dz \\ &= \alpha + \varepsilon |A_{x_\varepsilon}| + \int_{A_{x_\varepsilon} \setminus B} (\log \varrho(z) - \log \beta) dz \\ &\quad + \int_{B \setminus \Omega} (\log \varrho(z) - \log \beta) dz. \end{aligned} \quad (4.9)$$

From (4.8b), we deduce that there exists $K > 0$ such that

$$\int_{A_{x_r} \setminus B} (\log \varrho(z) - \log \beta) dz \leq K\varepsilon.$$

Thus, returning to (4.9), we get

$$\lambda < \alpha + \varepsilon(K + |A_{x_r}|) + \int_{B \setminus \Omega} [\log \varrho(z) - \log \beta] dz. \tag{4.10}$$

Observe finally that from the definition of β we have, for all $z \in \Omega$, $\varrho(z) > \beta$. Therefore $\varrho(z) \leq \beta$ for all $z \in B \setminus \Omega$, and hence

$$\int_{B \setminus \Omega} [\log \varrho(z) - \log \beta] dz \leq 0.$$

Returning to (4.10), we deduce that

$$\lambda < \alpha + \varepsilon(K + |A_{x_r}|).$$

ε being arbitrary, we have indeed obtained the result $\lambda \leq \alpha$. ■

In order to prove the theorem, the main tool will be the classical Jensen's inequality (see e.g. [4]), which we recall here:

JENSEN'S INEQUALITY

Let $f: R \rightarrow R$ be convex, and let u be an integrable function in Ω (a bounded open set). Then

$$\frac{1}{|\Omega|} \int_{\Omega} f(u(x)) dx \geq f\left(\frac{1}{|\Omega|} \int_{\Omega} u(x) dx\right). \tag{4.11}$$

We are now in a position to prove the theorem.

Proof of the theorem. We want to show that for every $v \in W$,

$$E(v) \equiv \int_0^1 \varrho(z) e^{-v'(z)} dz \geq E(\tilde{w}) = \int_0^1 \varrho(z) e^{-\tilde{w}'(z)} dz, \tag{4.12}$$

where \tilde{w} is the solution defined in (3.3) of the theorem.

The proof will be divided in three steps.

Step 1. We first show that if

$$W_1 = \left\{ w \in \text{Lip}(0,1) : w(0) = 0, w(1) = S, \right. \\ \left. w'(z) \geq \alpha \text{ a.e., and } \int_{\Omega} w'(z) dz = S - \alpha|\Omega^C| \right\}, \tag{4.13}$$

then \tilde{w} , defined in (3.3), belongs to W_1 and realizes the minimum of

$$(P_1) \quad \inf \left\{ \int_{\Omega} \varrho(z) e^{-v'(z)} dz : v \in W_1 \right\}. \quad (4.14)$$

Observe first that $\tilde{w} \in W_1$, since $\tilde{w}'(z) = \alpha$ in Ω^C and

$$S = \int_0^1 \tilde{w}'(z) dz = \int_{\Omega} \tilde{w}'(z) dz + \int_{\Omega^C} \alpha dz.$$

Using now Jensen's inequality,

$$\begin{aligned} \int_{\Omega} \varrho(z) e^{-v'(z)} dz &= \int_{\Omega} e^{\log \varrho(z) - v'(z)} dz \\ &\geq |\Omega| \exp \left[\frac{1}{|\Omega|} \int_{\Omega} [\log \varrho(z) - v'(z)] dz \right]. \end{aligned} \quad (4.15)$$

Since $v \in W_1$, then (4.15) implies

$$\begin{aligned} \int_{\Omega} \varrho(z) e^{-v'(z)} dz &\geq |\Omega| \exp \left[\frac{-1}{|\Omega|} \left[S - \alpha |\Omega^C| - \int_{\Omega} \log \varrho(z) dz \right] \right] \\ &\equiv \int_{\Omega} \varrho(z) e^{-\tilde{w}'(z)} dz, \end{aligned}$$

and this concludes step 1.

Step 2. We now return to (4.12) and show that this inequality reduces to a one-dimensional minimization problem, which we shall study in step 3. Observe that, trivially,

$$\begin{aligned} E(v) &= \int_0^1 \varrho(z) e^{-v'(z)} dz \\ &= \int_{\Omega^C} \varrho(z) e^{-v'(z)} dz + \int_{\Omega} \varrho(z) e^{-v'(z)} dz \\ &= \int_{\Omega^C} \varrho(z) e^{-v'(z)} dz \\ &\quad + \exp \left[\frac{1}{|\Omega|} \int_{\Omega^C} (v'(y) - \alpha) dy \right] \\ &\quad \times \int_{\Omega} \varrho(z) \exp \left[-v'(z) - \frac{1}{|\Omega|} \int_{\Omega^C} (v'(y) - \alpha) dy \right] dz. \end{aligned} \quad (4.16)$$

We now see that if we let

$$u'(z) = v'(z) + \frac{1}{|\Omega|} \int_{\Omega^c} (v'(y) - \alpha) dy \quad \text{if } z \in \Omega, \quad (4.17)$$

and $u(0) = 0$, $u(1) = S$, and $u'(z) \geq \alpha$ a.e. in Ω^c , then $u \in W_1$, since trivially $u' \geq \alpha$ a.e. in Ω and

$$\int_{\Omega} u'(z) dz = \int_{\Omega} v'(z) dz - \alpha |\Omega^c| = S - \alpha |\Omega^c|. \quad (4.18)$$

Therefore, by step 1, we deduce from (4.16) that for every $v \in W$

$$\begin{aligned} E(v) &\geq \int_{\Omega^c} \varrho(z) e^{-v'(z)} dz \\ &\quad + \exp \left[\frac{1}{|\Omega|} \int_{\Omega^c} (v'(z) - \alpha) dz \right] \cdot \int_{\Omega} \varrho(z) e^{-\tilde{w}'(z)} dz. \end{aligned}$$

Therefore

$$\begin{aligned} E(v) - E(\tilde{w}) &\geq \int_{\Omega^c} \varrho(z) \left[e^{-v'(z)} - e^{-\alpha} \right] dz \\ &\quad + \left[\exp \left(\frac{1}{|\Omega|} \int_{\Omega^c} [v'(z) - \alpha] dz \right) - 1 \right] \cdot \int_{\Omega} \varrho(z) e^{-\tilde{w}'(z)} dz \\ &\equiv F. \end{aligned} \quad (4.19)$$

So if we prove that the right-hand side of the inequality (4.19), F , is positive, we shall obtain (4.12) immediately. Let, as in Lemma 2,

$$\beta = \sup \{ \varrho(z) : z \in \Omega^c \}.$$

Then one has, since $v'(z) \geq \alpha$ (a.e.),

$$\int_{\Omega^c} \varrho(z) \left[e^{-v'(z)} - e^{-\alpha} \right] dz \geq \beta \int_{\Omega^c} \left[e^{-v'(z)} - e^{-\alpha} \right] dz. \quad (4.20)$$

And using again Jensen's inequality, we obtain

$$\int_{\Omega^c} \varrho(z) \left[e^{-v'(z)} - e^{-\alpha} \right] dz \geq \beta |\Omega^c| \left[\exp \left[\frac{-1}{|\Omega^c|} \int_{\Omega^c} v'(z) dz \right] - e^{-\alpha} \right]. \quad (4.21)$$

Therefore, returning to (4.19), we get

$$E(v) - E(\tilde{w}) \geq F \geq \beta |\Omega^C| \left[\exp\left(\frac{-1}{|\Omega^C|} \cdot \int_{\Omega^C} v'(z) dz\right) - e^{-\alpha} \right] \\ + \left[\exp\left(\frac{1}{|\Omega|} \int_{\Omega^C} [v'(z) - \alpha] dz\right) - 1 \right] \int_{\Omega} \varrho(z) e^{-\tilde{w}'(z)} dz. \quad (4.22)$$

So if we let

$$\mu = \int_{\Omega^C} v'(z) dz \quad (\geq \alpha |\Omega^C|), \quad (4.23)$$

(4.22) becomes

$$E(v) - E(\tilde{w}) \geq \beta |\Omega^C| \left[\exp\left(\frac{-\mu}{|\Omega^C|}\right) - e^{-\alpha} \right] \\ + \left[\exp\left(\frac{\mu - \alpha |\Omega^C|}{|\Omega|}\right) - 1 \right] \int_{\Omega} \varrho(z) e^{-\tilde{w}'(z)} dz \\ \equiv J(\mu). \quad (4.24)$$

Hence if we show that

$$J(\mu) \geq 0 \quad \text{for every } \mu \geq \alpha |\Omega^C|, \quad (4.25)$$

we shall have (4.12) and thus the theorem. Note however that in (4.25) J is a real function and not a functional like $E(v)$.

Step 3. We now show (4.25). Observe that

$$J(\alpha |\Omega^C|) = 0. \quad (4.26)$$

Therefore, if we can show

$$J'(\mu) \geq 0 \quad \text{for every } \mu \geq \alpha |\Omega^C|, \quad (4.27)$$

then we shall have (4.25). It thus remains to show (4.27). We have

$$J'(\mu) = -\beta \exp\left[\frac{-\mu}{|\Omega^C|}\right] + \frac{1}{|\Omega|} \exp\left[\frac{\mu - \alpha |\Omega^C|}{|\Omega|}\right] \cdot \int_{\Omega} \varrho(z) e^{-\tilde{w}'(z)} dz. \quad (4.28)$$

Therefore, $J'(\mu) \geq 0$ is equivalent to

$$\exp\left[\frac{\mu - \alpha |\Omega^C|}{|\Omega|}\right] \cdot \int_{\Omega} \varrho(z) e^{-\tilde{w}'(z)} dz \geq \beta |\Omega| \exp\left[\frac{-\mu}{|\Omega^C|}\right] \quad (4.29)$$

for every $\mu \geq \alpha|\Omega^C|$, i.e.,

$$\exp\left[\frac{\mu - \alpha|\Omega^C|}{|\Omega|} + \frac{\mu}{|\Omega^C|}\right] \cdot \int_{\Omega} \varrho(z) e^{-\tilde{w}'(z)} dz \geq \beta|\Omega| \quad (4.30)$$

for every $\mu \geq \alpha|\Omega^C|$. Since the exponential is an increasing function and $\mu \geq \alpha|\Omega^C|$, it is sufficient, in order to prove (4.30), to have

$$e^{\alpha} \int_{\Omega} \varrho(z) e^{-\tilde{w}'(z)} dz \geq \beta|\Omega|. \quad (4.31)$$

Using now the definition of $\tilde{w}'(z)$ in Ω , we get that (4.31) is equivalent to

$$e^{\alpha} \exp\left[\frac{-1}{|\Omega|} \left[S - \alpha|\Omega^C| - \int_{\Omega} \log \varrho(z) dz\right]\right] \geq \beta, \quad (4.32)$$

i.e.,

$$\exp\left[\frac{1}{|\Omega|} \left[\alpha - S + \int_{\Omega} \log \varrho(z) dz\right]\right] \geq \beta, \quad (4.33)$$

which is precisely Lemma 2; and thus we have step 3 and the existence of the minimum. The uniqueness is trivial, since if $v \neq w$, then at least one of the above inequalities is strict. ■

5. NONLINEAR FUNCTIONAL RESPONSES

The theorem has been developed for the Lotka-Volterra linear functional response, but, as we shall now show, it remains qualitatively valid in the more general case of any strictly increasing functional response. Let us replace Equation (2.3) by

$$\frac{d\varrho}{dt} = -\varphi(\varrho), \quad (5.1)$$

where $\varphi: [0, \infty) \rightarrow [0, \infty)$, $\varphi(\varrho) > 0$, and $\varphi'(\varrho) > 0$ for every ϱ . Let $\phi: [0, \infty) \rightarrow R$ be defined by

$$\phi(\varrho) = \int_1^{\varrho} \frac{dz}{\varphi(z)}. \quad (5.2)$$

This implies that

$$\phi'(\varrho) = \frac{1}{\varphi(\varrho)} > 0, \quad (5.3)$$

and

$$\phi''(\varrho) = -\frac{\varphi'(\varrho)}{\varphi^2(\varrho)} < 0. \quad (5.4)$$

With (5.1),

$$\phi'(\varrho) \frac{d\varrho}{dt} = -1, \quad (5.5)$$

and therefore

$$\phi(\varrho(t)) = \phi(\varrho(0)) - t. \quad (5.6)$$

ϕ is invertible, since $\phi' > 0$ and $(\phi^{-1})'' > 0$, i.e., ϕ^{-1} is strictly convex. Therefore, the law of decrease of ϱ due to consumption is

$$\varrho(t) = \phi^{-1}[\phi(\varrho(0)) - t]. \quad (5.7)$$

The optimization problem (P) becomes

$$(P') \quad \min_{w \in W} \left\{ \int_0^1 \phi^{-1}[\phi(\varrho(z)) - w'(z)] dz \right\}.$$

In the case of the Lotka-Volterra functional response, $\varphi(\varrho) = \varrho$, one has

$$\phi(\varrho) = \log \varrho \quad \text{and} \quad \phi^{-1}(u) = e^u.$$

It can be easily verified that the theorem remains valid in the general case if the log function is replaced by ϕ and the exponential by ϕ^{-1} in (3.2) and (3.3):

$$\Omega = \left\{ x \in I : \phi(\varrho(x)) \geq \frac{1}{|A_x|} \left[\int_{A_x} \phi(\varrho(z)) dz - (S - \alpha) \right] \right\}, \quad (5.8)$$

and

$$\tilde{w}'(x) = \begin{cases} \phi(\varrho(x)) + \frac{1}{|\Omega|} \left[S - \alpha|\Omega^c| - \int_{\Omega} \phi(\varrho(z)) dz \right] & \text{if } x \in \Omega, \\ \alpha & \text{if } x \in \Omega^c. \end{cases} \quad (5.9)$$

If the functional response φ is *not* strictly increasing, as has been observed in a few cases (“dome-shaped” responses), then the problem is

more complicated, since the use of Jensen's inequality or any equivalent technique relying on convexity hypotheses is precluded.

6. DISCUSSION

In summary, the main result is the following. Given any distribution of food on a bounded one-dimensional habitat, the theorem gives explicitly the strategy that the animal should follow in order to maximize the energy gain. Equation (3.3) tells exactly what velocity the animal will take at any point. The habitat is separated into the two parts Ω and Ω^C . The theorem says that the animal will slow down to consume food at any point x where the density is high enough that the condition (3.2) holds, i.e. where $\varrho(x)$ is greater than the critical value ϱ_C defined by

$$\log \varrho_C = \frac{1}{|\Omega|} \left[\int_{\Omega} \log \varrho(z) dz - (S - \alpha) \right]. \quad (6.1)$$

At all these points (i.e. in Ω), the animal adjusts its velocity so as to leave behind a constant food density $\varrho_B = \varrho_C e^{-\alpha}$. In Ω^C , the animal moves as fast as it can, but it also eats a little, since at any given point the duration of presence is not zero (the velocity cannot be infinite). Of course, the model can be modified to assume that no eating is possible when the animal moves at maximum velocity, and no great change should be expected from this.

From the animal's viewpoint, Ω^C is perceived as empty, and Ω as being worth exploiting. Therefore, the habitat can, in some sense, be considered to be patchy *a posteriori*. But this is very different from the classical patch models in which the patches are given *a priori*. For any distribution (say, continuous), our model is able to predict how the *animal* will chop the habitat into patches. The model also gives the strategy that the animal follows *within* each patch.

Can this model be applied to real situations, and can its predictions be compared with biological observations? The model makes several assumptions which are probably rarely met in nature: bounded one-dimensional habitat, fixed foraging time, energy maximization, and costs proportional to time, distance, velocity and handling. It is also assumed that the animal knows how the food is distributed before exploiting the habitat. Future work will model more realistic situations by gradually alleviating some of these assumptions. In a second article [3], we have already treated the more general situation in which the food resource is one-dimensional but unbounded, and further articles will consider two-dimensional habitats.

Nevertheless, there are probably some real situations close enough to the assumptions that the present model might be appropriate. The following scenario can be imagined. The animal has a nest and exploits a one-dimen-

sional bounded habitat some distance from the nest. The food is renewed every day with the same distribution; therefore, the animal has learned this distribution. After deduction of all time consuming activities, including travel between the nest and the food resource, the same limited time is available for foraging every day. Then the animal should exploit the habitat as predicted by the model.

Assuming that the above conditions are fulfilled, two sorts of observations are necessary to test the model. First, the food distribution must be measured. This is a difficult task, but certainly possible in some instances. Second, the foraging behavior must be observed; that is, the time spent by the animal at each point of the food resource must be known. Data of this type are not very abundant, but they are available from the more sophisticated studies of home ranges (e.g. [1, 7, 10]), including such one-dimensional habitats as a hedge in the case of the white-toothed shrew [18], or a river in the cases of the Pyrenean desman [20] and the water shrew (J.-P. Lardet, personal communication). Therefore, there is a possibility that the present model can soon be tested with field data.

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REFERENCES

- 1 L. Adams and S. D. Davis, The internal anatomy of home range, *J. Mammal.* 48:529–536 (1967).
- 2 M. Andersson, Optimal foraging area size and allocation of search effort, *Theoret. Population Biol.* 13:397–409 (1978).
- 3 R. Arditi and B. Dacorogna, Optimal foraging in non-patchy habitats. 2: Unbounded one-dimensional resource, submitted for publication.
- 4 G. de Barra, *Introduction to Measure Theory*, Van Nostrand, 1974.
- 5 A. B. Bond, Optimal foraging in a uniform habitat: The search mechanism of the green lacewing (*Chrysopa carnea*), *Anim. Behav.* 28:10–19 (1980).
- 6 E. L. Charnov, Optimal foraging, the marginal value theorem, *Theoret. Population Biol.* 9:129–136 (1976).
- 7 B. A. C. Don and K. Rennolls, A home range model incorporating biological attraction points, *J. Anim. Ecol.* 52:69–81 (1983).
- 8 J. M. Emlen, The role of time and energy in food preference, *Amer. Nat.* 100:611–617 (1966).
- 9 J. M. Emlen, Optimal choice in animals, *Amer. Nat.* 102: 385–389 (1968).
- 10 M. Genoud, Contribution à l'étude de la stratégie énergétique et de la distribution écologique de *Crociodura russula* (Soricidae, Insectivora) en zone tempérée, Doctoral thesis, Univ. of Lausanne, 1981, 167 pp.
- 11 C. S. Holling, The components of predation as revealed by a study of small-mammal predation of the European pine sawfly, *Canad. Entomol.* 91:293–320 (1959).

- 12 J. R. Krebs, A. Kacelnik, and P. Taylor, Test of optimal sampling by foraging great tits, *Nature*, 275:27–31 (1978).
- 13 J. R. Krebs and R. H. McCleery, Optimization in behavioural ecology, in *Behavioural Ecology* (J. R. Krebs and N. B. Davies, Eds), 2nd ed., Blackwell, 1984, pp. 91–121.
- 14 J. R. Krebs, D. W. Stephens, and W. J. Sutherland, Perspectives in optimal foraging, in *Perspectives in Ornithology* (A. H. Brush and G. A. Clark, Jr., eds.), Cambridge U.P., 1983, pp. 165–216.
- 15 C. M. Lessels and D. W. Stephens, Central place foraging. Single prey loaders again, *Anim. Behav.* 31:238–243 (1983).
- 16 R. H. MacArthur and E. R. Pianka, On optimal use of a patchy environment, *Amer. Nat.* 100:603–609 (1966).
- 17 G. H. Pyke, Optimal foraging theory: A critical review, *Ann. Rev. Ecol. Syst.* 15:523–575 (1984).
- 18 J.-C. Ricci and P. Vogel, Nouvelle méthode d'étude en nature des relations spatiales et sociales chez *Crocidura russula* (Mammalia, Soricidae), *Mammalia* 48: 281–286 (1984).
- 19 D. W. Stephens and E. L. Charnov, Optimal foraging: Some simple stochastic models, *Behav. Ecol. Sociobiol.* 10:251–263 (1982).
- 20 R. D. Stone and M. L. Gorman, Social organization of the European mole (*Talpa europea*) and the Pyrenean desman (*Galemys pyrenaicus*), *Mammal Rev.* 15:35–42 (1985).