

# A mathematical framework for optimal foraging of herbivores

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Received 6 April 1994; received in revised form 20 June 1994

**Abstract.** The aim of this paper is to study a model of optimal foraging of herbivores (with special reference to ungulates) assuming that food distribution is arbitrary. Usually the analysis of foraging of herbivores in the framework of optimal foraging theory is based on the assumption of a patchy food distribution. We relax this assumption and we construct more realistic models. The main constraint of our model is the total amount of food which the animal may eat and the currency is the total foraging time. We represent total foraging time as a variational expression depending on food eaten and the length of the path. We prove that there exists a threshold  $\lambda$  for food acquisition. More explicitly, it exists a positive real number  $\lambda$  such that, at any point  $x$  of the path, the animal either eats till the density of food is decreased to the value  $\lambda$  or, if the density of food at  $x$  is less than  $\lambda$ , there it does not eat. We discuss the results and emphasize some biologically important relationships among model parameters and variables. Finally, we try to give a sound biological interpretation of our results.

**Key words:** Mathematical model – Optimal foraging – Herbivores – Ungulates – Calculus of variations

## 1 Introduction

The observation that often predators do not consume all of the prey has been clearly explained, in the framework of optimal foraging theory, by Charnov's [10] marginal value theorem (MVT). When food is patchy distributed, then a rate-maximizing forager should leave the food patch when the derivative of the net gain is equal to the long-term average rate of food intake in the environment. MVT has had a deep influence on the theory of foraging and finds widespread application in behavioural ecology; Stephens and Krebs

[35] listed several experiments where both qualitative and quantitative predictions of MVT were confirmed.

However there are many biological situations where the assumption of a patchy food distribution is violated. In a series of articles, Arditi and Dacorogna [3, 4, 5]; Botteron and Dacorogna [7] and Botteron and Marcellini [8] have developed a theoretical framework for the study of optimal foraging on arbitrary food distributions.

Non-patchy food distributions characterize the ecology of ungulates (e.g. cattle, sheep, horse, antelope, deer). As clearly stated by Illius and Gordon [23] "herbivores inhabit a world in which food plants are more or less continuously distributed in space and time. By comparison with a carnivorous predator, whose food is patchy distributed, highly nutritious and mobile, the herbivore confronts food plants where the nutrient are more evenly distributed". Under natural conditions, we have no proof that any definition of food patch may correspond to the way an animal perceives its habitat.

In some experimental studies the distribution of food has been altered in order to get artificial grass or tree patches (Allden and Whittaker [1]; Vivås and Saether [38]; Gillingham and Bunnell [15]; Danell et al. [11]; Illius et al. [22]; Langvatn and Hanley [25]). In such conditions Åström et al. [6] and Jiang and Hudson [24] were able to apply the MVT to ungulates. However Langvatn and Hanley [25] have noted that the experimental procedure used to obtain artificial patches is unable to remove completely the within-patch variations. Moreover a similar approach cannot be used to study the behaviour of animals under natural conditions.

Åström et al. [6] and Saether [31] showed that moose (*Alces alces*), foraging on trees, does not consume all available food; Focardi et al. [13] described a similar process in fallow deer (*Dama dama*): the deer ignore a part of the food available in most of foraging stations and do not exploit some of the potential foraging stations. The question arises whether partial food consumption is due only to differences in palatability of different parts of the plant, or among plants within a foraging station (*hedyphagia*, Provenza and Balph [28]), or it is also present when food is qualitatively homogeneous.

The aim of this paper is to understand why animals do not eat all available food. One of our main results is that there exists a critical value of food density below which the animal does not eat, i.e. a "clever" ungulate should stop foraging when the food density falls below a critical threshold.

We discuss a model of optimal allocation of the foraging effort in herbivores, with special reference to the biology of ungulates, where (i) the food distribution is arbitrary, (ii) the constraints are pertinent to physiology and behaviour of herbivores and (iii) the currency used for the optimization should be relevant for these animals. The approach of Arditi and Dacorogna ([5] and related papers) is to assume that the forager has to maximize its energy intake in a fixed time. The foraging activity of ungulates, especially ruminants, is organized in meals (Bunnell and Gillingham [9]): the animal moves around and forages until satiation, after that it begins to ruminate or rest. The ability of ungulates to process food is limited by gut size and, in most

environments, the available plant biomass is large enough to fill the animal's gut. In this paper we assume gut size as a constraint and time as currency. Because ungulates devote a large part of the day to foraging (from 30% in small species to 70% in large ones) time minimization is important, because the extra time saved by a time-minimizer may be allocated to other fitness-related activities such as predator avoidance, patrolling the territory, mate search and so on. Therefore our model is based on the study of a time-minimizing forager, given a fixed amount of food which can be processed.

Mathematically speaking the quantity to minimize, i.e. the total foraging time  $T(v, l)$ , results to be an integral of the form

$$T(v, l) = \int_0^l f(x, v'(x)) dx, \quad (1.1)$$

(related to a function of two real variables  $f = f(x, \xi)$  which will be described later, cf. (3.2)) where  $l$  is the length of the one-dimensional path  $[0, l]$  physically described by the animal,  $v = v(x)$  ( $\geq 0$ ) is the amount of food gained by the animal until the point  $x$  and  $v' = \frac{dv}{dx}$  (density of acquisition of food) is the derivative of  $v$  with respect to  $x$ .

We minimize  $T(v, l)$ , both with respect to  $l \in I$  ( $I$  is an interval in  $\mathbb{R}$ , bounded below; see (3.4)) and with respect to  $v \in W$  ( $W$  is a class of functions defined in the interval  $[0, l]$ , with pointwise constraints in the gradient  $v'$ ; see (3.5)). Note that  $W$  depends on  $l$ . Moreover  $v$  and  $l$  satisfy the *a-priori* constraint that, at the end of the excursion, the animal has filled his gut.

The mathematical model is based on a detailed description of the mechanism by which animals gather their food. The intake rate of animals is a function of the forage biomass at the foraging station (*functional response*). Arditi and Dacorogna [3] have shown that the functional response has quantitative, but not qualitative, influence on model predictions; for mathematical convenience these authors used a linear Lotka-Volterra function, but non-linear terms are more suitable to study the foraging behaviour of ungulates at least in the few species for which the functional response has been experimentally evaluated (Allden and Whittaker [1]; Trudell and White [36]; Wickstrom et al. [39]; Short [33]; Hudson and Frank [20]; Spalinger et al. [34]; Andersen and Saether [2]).

Real [29, 30] presented the following form of the functional response

$$\Phi(\xi) = k \cdot \frac{\xi^\alpha}{b + \xi^\alpha}, \quad (1.2)$$

where  $\Phi$  is the intake rate per unit length,  $\xi$  the food density,  $k$  and  $b$  are constants and  $\alpha$  is a positive parameter which determinates the shape of the functional response mainly for small values of  $\xi$ . Some of the experimental data collected on ungulates have been fitted with accuracy to (1.2) with  $\alpha = 1$ .

In this paper we develop a model based on a *general* functional response  $\Phi(\xi)$ , with  $\Phi: [0, +\infty) \rightarrow [0, +\infty)$  strictly increasing and  $\Phi(0) = 0$ . This monotonicity assumption is consistent with the variational problem we study;

in fact the *increasing monotonicity* of  $\Phi$  corresponds, in (1.1), to the *convexity* of the function  $f(x, \xi)$  with respect to the gradient variable  $\xi = v'$ . Then, in the discussion of Sect. 5, we specify the functional response  $\Phi(\xi)$  as in (1.2) and we study the dependence of the solution on the relevant parameters of our problem.

Our model is specific for time-minimizing foragers, with a limited gut size, on arbitrary food distribution. Such model may be suitable to study many species of herbivores assuming that they are not central place foragers, i.e. they are not constrained to return to a home or nest at the end of the foraging excursion (Arditi and Dacorogna [4]), and that their movement is continuous on the surface, i.e. they do not fly or jump. Moreover we attempt to discuss in more detail the interspecific variations of the foraging behaviour of wild ungulates in relation to body mass. The effect of body mass on foraging behaviour has been extensively discussed: in an influential paper Demmet and Van Soest [12] showed that large species should be characterized by a diet composed by low-quality items (grass/roughage feeders), while small ones by rich food items (concentrate selectors); in particular ungulates body mass is linearly scaled to the mass of gut contents. However other factors modify this simple "size rule". Hofmann [18] showed that both groups of foragers include large as well as small species and that many difference between grass feeders and concentrate selectors depend on the anatomy of the digestive system; here we wish to analyze how the foraging strategy varies without assuming qualitative differences among feed.

This paper is organized as follows: in Sect. 2 we introduce the mathematical model. In Sect. 3 we study the general setting with a bounded, possibly discontinuous, distribution of food, while in the following section we consider the special, but relevant, case of uniform (i.e. constant) food distribution. Sections 3 and 4 can be skipped, at a first reading, by non-mathematicians. In Sect. 5 we show some biologically interesting relations among variables and parameters. Finally, in Sect. 6, we try to give a biological interpretation of the model.

## 2 Mathematical model

In this section we introduce a mathematical model to explain the foraging behaviour of herbivores. Specifically, with this study we wish to give an adaptationist explanation of the foraging behaviour. In particular we wish to answer questions such as: why does the animal forage only in some of the available sites it has found during its movement? Why does it leave a selected foraging location before the food is exhausted? We do not attempt to explain why an animal has followed a specific foraging path; we assume that such a path is determined by other factors than foraging, such as species-specific search behaviour. Moreover, the resultant direction of animal motion may be determined by the necessity to move between two different habitats, to avoid predators or to reduce competition with conspecifics. Random movements

may occur, for instance, when deer wander in a clearing with the only purpose of foraging. There is some experimental evidence that the structure of the foraging paths is quite homogeneous within a population and even among different populations of the same species (Focardi et al. [13]; Focardi et al. *in prep.*); this may suggest that the path itself is not determined by the foraging process.

We study the animal behaviour during one foraging excursion. In ungulates we can observe that foraging is concentrated in certain parts of the day (in many species around twilight) and that periods of intense foraging are interrupted by time intervals devoted to resting and rumination. More specifically we assume:

- (i) the animals are not limited by the available food. This assumption is correct for most ungulate populations (with the exception of very unfavorable season such as winter) if the population is not too dense: this is the case of populations limited by predation or harvesting;
- (ii) the amount of food (say  $A$ ) which can be processed by the animal is limited; this condition is general among herbivores but it is very strong for ruminants which have to stop foraging when about  $4/5$  of the rumen is filled with food;
- (iii) we assume that the animal speed is bounded;
- (iv) the food search is a sequential short-range process without jumps; in other word the detection range is small compared to the length of the foraging excursions and, at each step, the moving animal is able to estimate the edible biomass at that point. The assessment of the standing biomass at the foraging point is continuous during the foraging process;
- (v) the animal is informed about the food distribution in its environment. This assumption is typical of many models of optimal foraging (cf. Stephens and Krebs [35]). In this context it means that the animals assess mean and variance of the distribution of food density (many species are able to estimate such parameters, provided that the environment is familiar to them); this does not mean that they know the spatial distribution of food.

In this model we have not a clear distinction between searching and handling time. At each location of the excursion the animal first evaluates the available biomass, then it decides to accept or to reject the location. If the location is accepted, then the animal takes a bite, chews and swallows the food; after that it evaluates again the biomass and decides whether or not to continue grazing at that location. Clearly all these processes are in part overlapping. In the following we will refer to this process simply as eating.

The mathematical model is based on the minimization of the total time used to search and handle food along a given path. Mathematically speaking, we minimize a functional with respect to variables describing the *amount of food gathered* at a generic point of the excursion (a real function) and the *length of the path* of the excursion (a real number).

To introduce the mathematical model, let us consider a curve (the path performed by the animal) in a two-dimensional domain, parametrized by a variable  $x \in [0, l]$ .

It should be noted that the length of the foraging excursion is variable and its actual value depends in a complex way on the interplay of food density and distribution with the foraging physiology of animals.

The food distribution along the *one-dimensional* curve, in general, is not uniform. We denote by  $\rho = \rho(x)$  the *density* of food at a generic point  $x \in [0, l]$ . The function  $\rho(x)$  is nonnegative, bounded and measurable in  $[0, l]$ ; however, not necessarily it is continuous and, in applications, usually it has jump discontinuities in the interior of  $[0, l]$ . The assumption that, during its excursion, the animal is able to find all the food it needs can be expressed by the condition

$$\int_0^l \rho(x) dx \geq A, \quad (2.1)$$

where  $A$  is the total amount of food gathered by the animal, or, equivalently,  $A$  is the mass of gut contents.

How long does an animal remain to eat at a point  $x$ ? To answer this question we study the dynamics of food consumption at  $x$  in dependence of the *functional response* of the animal: the *velocity* of food acquisition is given as a function  $\Phi$  of the density of remaining food.

To write down a precise formula, let us denote by  $\tau = \tau(x)$  the foraging time per unit length, i.e. the time that the animal spends at a point  $x$  to acquire food; moreover, let us denote by  $\delta = \delta(\tau) = \delta(\tau(x))$  the density of food eaten at  $x$ . Then the velocity of food acquisition at  $x$  is  $\frac{d\delta}{d\tau}$ ; therefore we have

$$\frac{d\delta}{d\tau} = \Phi(\rho - \delta), \quad (2.2)$$

where  $\rho - \delta$  is the density of remaining food and the *functional response*  $\Phi: [0, +\infty) \rightarrow [0, +\infty)$  is a strictly increasing function, with  $\Phi(0) = 0$ .

As references and examples, let us mention the classical model of Lotka and Volterra, with a linear *functional response* (here  $\xi = \rho - \delta$ )

$$\Phi(\xi) = k \cdot \xi, \quad (2.3)$$

where  $k$  is a positive constant; or the models of *functional responses* proposed for sheep, rabbits and kangaroos by Short [33], and for *Peromyscus maniculatus* by Real [30], given (for some constants  $k, \alpha, b > 0$ ) respectively by

$$\Phi(\xi) = k \cdot (1 - e^{-\alpha\xi}), \quad (2.4)$$

$$\Phi(\xi) = k \cdot \frac{\xi^\alpha}{b + \xi^\alpha}. \quad (2.5)$$

We can integrate the ordinary differential equation (2.2) and we obtain the time (per unit length)  $\tau = \tau(x)$  that the animal spends at the point  $x$

$$\int \frac{d\delta}{\Phi(\rho - \delta)} = \int d\tau ,$$

i.e., more precisely, since  $d\delta = -d(\rho - \delta)$ , we obtain the time  $\tau$ , up to an additive constant  $\tau_0$  (constant with respect to  $\tau$ , but generally depending on  $x$ ),

$$\tau = \tau_0 + G(\rho - \delta) , \tag{2.6}$$

where the derivative with respect to  $\xi$  of  $G(\xi)$  is equal to

$$G'(\xi) = \frac{dG}{d\xi} = -\frac{1}{\Phi(\xi)} ; \tag{2.7}$$

$\tau_0 = \tau_0(x)$  can be determined by the condition that, if the animal does not eat at the point  $x$  (i.e.  $\delta(\tau(x)) = 0$ ), then at  $x$  it does not spend time to acquire food (i.e.  $\tau(x) = 0$ ). We obtain  $0 = \tau_0 + G(\rho)$  and thus  $\tau = G(\rho - u') - G(\rho)$ . Hence, by denoting explicitly the dependence on  $x$ , we have

$$\tau(x) = G(\rho(x) - \delta(\tau(x))) - G(\rho(x)) .$$

Therefore the *total time to acquire food* is given by

$$\int_0^l \tau(x) dx = \int_0^l G(\rho(x) - \delta(\tau(x))) dx - \int_0^l G(\rho(x)) dx . \tag{2.8}$$

Moreover, we have to take into account the time used by the animal to move and to search for food. We assume that it moves at a point  $x$  with velocity  $V_0(x)$ , so that the *total time to move* in the path of length  $l$  is given by ( $dx = V_0(x) \cdot dt$ )

$$\int_0^l \frac{1}{V_0(x)} dx . \tag{2.9}$$

As we already said, our mathematical model is based on the minimization of the total time used by the animal to search and to gather food. Therefore we add (2.8), (2.9) and we obtain the *total time to acquire food and to move*:

$$T = \int_0^l \left\{ \frac{1}{V_0(x)} + G(\rho(x) - \delta(\tau(x))) - G(\rho(x)) \right\} dx . \tag{2.10}$$

Let us denote by  $v(x)$  the amount of food gathered by the animal until the point  $x$ . Then, in particular, we have  $v(0) = 0$  and  $v(l) = A$  (recall that we denote by  $A$  the maximum amount of food which can be eaten by the animal). Then  $v$  is related to  $\delta$  (density of consumed food) by the condition

$$v(x) = \int_0^x \delta(\tau(y)) dy , \quad \forall x \in [0, l] ,$$

i.e.,

$$v'(x) = \frac{dv}{dx} = \delta(\tau(x)) . \tag{2.11}$$

By (2.10) and (2.11) we are led to *minimize*, with respect to the variables  $v$  and  $l$ , the functional (*total time to acquire food and to move*)

$$T(v, l) = \int_0^l \left\{ \frac{1}{V_0(x)} + G(\rho(x) - v'(x)) - G(\rho(x)) \right\} dx. \quad (2.12)$$

Since  $0 \leq \delta(\tau(x)) \leq \rho(x)$  and  $\delta(\tau(x)) = v'(x)$ , the *class of feasible functions*  $v$  is given by

$$W = \{v = v(x); v(0) = 0, v(l) = A; 0 \leq v'(x) \leq \rho(x), \forall x \in [0, l]\}, \quad (2.13)$$

while the real variable  $l$  is bounded from below so that condition (2.1) is satisfied.

In the next section we will state assumptions in order to handle the problem and we will be more precise on the functional class where to look for the minimum.

### 3 Main mathematical results

Let  $\rho = \rho(x)$  (*density of food*) be a nonnegative, bounded and measurable function in  $[0, l]$ . Let  $\Phi = \Phi(\xi)$  (*functional response*) be a nonnegative, strictly increasing function, with  $\Phi(0) = 0$ . Let  $G = G(\xi)$  be a primitive of the function  $\xi: \rightarrow -1/\Phi(\xi)$ , i.e. such that

$$\frac{d}{d\xi} G = \frac{-1}{\Phi(\xi)}. \quad (3.1)$$

Let  $V_0 = V_0(x)$  be a positive bounded function such that  $1/V_0(x)$  is summable. We consider the minimization of the integral functional (*total time*)

$$T(v, l) = \int_0^l \left\{ \frac{1}{V_0(x)} + G(\rho(x) - v'(x)) - G(\rho(x)) \right\} dx. \quad (3.2)$$

We assume that the total amount of food present in the habitat is sufficient for the animal; i.e.

$$\int_0^{+\infty} \rho(x) dx > A \quad (3.3)$$

for some fixed  $A \in \mathbb{R}$ . This condition guarantees that  $T(v, l)$  in (3.2) is finite for some  $(v, l)$ . We define the set  $I$  of possible  $l$  values

$$I = \left\{ l \in \mathbb{R}: \int_0^l \rho(x) dx \geq A \right\}. \quad (3.4)$$

Since the integral in (3.4) depends continuously on  $l$ , the interval  $I$  is closed. Finally we define the class  $W$  of functions

$$W = \{v \in Lip([0, l]): v(0) = 0, v(l) = A; 0 \leq v'(x) \leq \rho(x), \forall \text{a.e. } x \in [0, l]\} \quad (3.5)$$

(as usual, we use denote by  $Lip([0, l])$  the class of Lipschitz continuous functions in  $[0, l]$ . For completeness, we recall that  $v \in Lip([0, l])$  if there exists a constant  $L$  (= Lipschitz constant) with the property that  $|v(x) - v(y)| \leq L|x - y|$  for every  $x, y \in [0, l]$ . Each function  $v$  of this class is continuous and admits derivative  $v'$  almost everywhere. This  $v'$  is a measurable function, bounded by  $|v'(x)| \leq L$ .

**Theorem 3.1** *Let us consider the functional  $T(v, l)$  in (3.2) in the class of functions  $W \times I$ . Let the assumption (3.1) (where  $\Phi$  is a nonnegative, strictly increasing function, with  $\Phi(0) = 0$ ) be satisfied. Then  $T$  has a minimizer  $(u, l) \in W \times I$ . Moreover there exists a real positive number  $\lambda$  such that, for almost every  $x \in [0, 1]$ , either  $u'(x) = 0$  (if  $\rho(x) \leq \lambda$ ), or  $u'(x) = \rho(x) - \lambda$  (if  $\rho(x) > \lambda$ ).*

*Remark 3.2.* The number  $\lambda$  is the *critical density* of food: if  $\rho(x)$  is below  $\lambda$ , then the animal does not eat at the point  $x$ ; vice-versa, if  $\rho(x)$  is greater than  $\lambda$ , then the animal eats with *density of acquisition of food*  $u'(x) = \rho(x) - \lambda$ .

In the proof of Theorem 3.1 we will make use of the following Lemmas 3.3 and 3.4.

**Lemma 3.3** *Let us define the function of two real variables  $B: [0, +\infty) \times I \rightarrow \mathbb{R}$  by the integral*

$$B(\lambda, l) = \int_0^l [\max\{\rho(x), \lambda\} - \lambda] dx, \quad (\lambda, l) \in [0, +\infty) \times I. \quad (3.6)$$

*Then, for every  $l \in I$ , there exists a unique  $\lambda \geq 0$  such that*

$$B(\lambda, l) = A; \quad (3.7)$$

*the corresponding function  $\lambda = \lambda(l)$ , defined implicitly by (3.7), is continuous for every  $l \in I$ .*

*Proof.* For every  $\lambda \geq 0$  let us define in  $[0, l]$  the function

$$\varphi_\lambda(x) = \max\{\rho(x), \lambda\} - \lambda.$$

Let us first prove that, for every  $x \in [0, l]$ , we have

$$0 \leq \varphi_{\lambda_1}(x) - \varphi_{\lambda_2}(x) \leq \lambda_2 - \lambda_1, \quad \forall \lambda_2 \geq \lambda_1 \geq 0. \quad (3.8)$$

In fact, if  $\rho(x) \leq \lambda_1 \leq \lambda_2$ , then  $\varphi_{\lambda_1}(x) = \varphi_{\lambda_2}(x) = 0$  and (3.8) holds. If  $\lambda_1 < \rho(x) \leq \lambda_2$ , then  $\varphi_{\lambda_1}(x) = \rho(x) - \lambda_1$  and  $\varphi_{\lambda_2}(x) = 0$ ; thus  $\varphi_{\lambda_1}(x) - \varphi_{\lambda_2}(x) \geq 0$  and

$$\varphi_{\lambda_1}(x) - \varphi_{\lambda_2}(x) = \rho(x) - \lambda_1 \leq \lambda_2 - \lambda_1;$$

again (3.8) holds. Finally, if  $\lambda_1 \leq \lambda_2 < \rho(x)$ , then

$$\varphi_{\lambda_1}(x) - \varphi_{\lambda_2}(x) = \rho(x) - \lambda_1 - (\rho(x) - \lambda_2) = \lambda_2 - \lambda_1, \quad (3.9)$$

which concludes the proof of (3.8). Since we will use it later, we note that, by (3.9),

$$0 \leq \lambda_1 < \lambda_2 < \rho(x) \Rightarrow \varphi_{\lambda_1}(x) > \varphi_{\lambda_2}(x). \quad (3.10)$$

Let us consider the function  $B: [0, +\infty) \times I \rightarrow \mathbb{R}$  defined in (3.6). Then, by (3.8),  $B$  is Lipschitz continuous with respect to  $\lambda$ , according to the inequality

$$|B(\lambda_1, l) - B(\lambda_2, l)| \leq \int_0^l |\varphi_{\lambda_1}(x) - \varphi_{\lambda_2}(x)| dx \leq l \cdot |\lambda_1 - \lambda_2|, \\ \forall \lambda_1, \lambda_2 \geq 0. \quad (3.11)$$

For future use let us notice that  $B$  is Lipschitz continuous with respect to  $l$ , too. In fact, since  $\rho(x)$  is bounded, there exists a constant  $M$  such that  $0 \leq \rho(x) \leq M$ ; then we have also  $0 \leq \varphi_\lambda(x) \leq M$  and thus

$$|B(\lambda, l_1) - B(\lambda, l_2)| \leq M \cdot |l_1 - l_2|, \quad \forall l_1, l_2 \in I. \quad (3.12)$$

When  $\lambda \geq M$  then  $\varphi_\lambda(x) = 0$  for every  $x$ ; therefore  $B(M, l) = 0$ ; moreover

$$B(0, l) = \int_0^l \varphi_0(x) dx = \int_0^l \rho(x) dx \geq A;$$

therefore, for every fixed  $l$ , there exists  $\lambda \in [0, M)$  such that  $B(\lambda, l) = A$ . Such number  $\lambda$  is unique, since, for  $\lambda_1, \lambda_2 \in [0, M)$ , (3.10) holds on a subset of positive measure of  $[0, l]$  and thus  $B(\lambda, l)$  is strictly decreasing with respect to  $\lambda \in [0, M)$ .

It remains to prove that the function  $\lambda = \lambda(l)$  is continuous on  $I$ . To this aim, let us consider in  $I$  a generic sequence  $l_k$  converging to  $l$  (we denote by  $L < +\infty$  an upper bound for  $l_k$ ); the corresponding sequence of values  $\lambda(l_k)$  is bounded too (recall that  $\lambda(l) \in [0, M)$  for every  $l \in I$ ). We will prove that  $\lambda(l_k)$  converges to  $\lambda(l)$  by showing that from every subsequence, that we still denote by  $\lambda(l_k)$ , we can extract a further subsequence that converges to  $\lambda(l)$ . In fact, let  $\lambda(l_{k_h})$  be a subsequence that converges to a real number  $\lambda_0 \in [0, M]$ . Since  $B(\lambda(l_{k_h}), l_{k_h}) = A$ , by (3.11), (3.12) we obtain

$$|A - B(\lambda_0, l)| = |B(\lambda(l_{k_h}), l_{k_h}) - B(\lambda_0, l)| \leq |B(\lambda(l_{k_h}), l_{k_h}) - B(\lambda_0, l_{k_h})| \\ + |B(\lambda_0, l_{k_h}) - B(\lambda_0, l)| \leq L \cdot |\lambda(l_{k_h}) - \lambda_0| + M \cdot |l_{k_h} - l|,$$

and as  $h \rightarrow +\infty$

$$B(\lambda_0, l) = A. \quad (3.13)$$

Since (3.7) has a unique solution, then (3.13) implies that  $\lambda_0 = \lambda(l)$ , which concludes the proof of Lemma 3.3.

**Lemma 3.4** *Let  $l \in I$  be a fixed real number. Under the previous assumptions, the functional  $T_1(v) = T(v, l)$  has a minimum in the class  $W$ . The minimizer  $u = u_l$  is unique and there exists a real positive number  $\lambda = \lambda(l)$  such that, for almost every  $x \in [0, 1]$ , either  $u'(x) = 0$  or  $u'(x) = \rho(x) - \lambda$ .*

*Proof.* Fix  $l \in I$ , let  $\lambda = \lambda(l)$  be the real number satisfying the equation (3.7)  $B(\lambda, l) = A$ . Let  $u = u(x)$  be the function of  $W^{1, \infty}([0, l])$ , such that

$$u(0) = 0 \quad \text{and} \quad u'(x) = \max\{\rho(x), \lambda\} - \lambda \quad (3.14)$$

(here  $l$  is fixed and we do not denote explicitly the dependence of  $u$  on  $l$ ; later, when necessary, we will use also the notation  $u = u(x) = u_l(x)$ ). We will prove that  $u$  is the minimizer of  $T_1(v) = T(v, l)$  in the class  $W$ .

First we observe that  $u$  satisfies the boundary conditions  $u(0) = 0$ ,

$$u(l) = \int_0^l u'(x) dx = \int_0^l [\max\{\rho(x), \lambda\} - \lambda] dx = B(\lambda, l) = A$$

and the constraints  $0 \leq u'(x) \leq \rho(x)$  (in fact, by its definition, either  $u'(x) = 0$ , or  $u'(x) = \rho(x) - \lambda$ ). Secondly, we will show that

$$T_1(v) \geq T_1(u), \quad \forall v \in W; \quad (3.15)$$

to this aim we observe that  $G(\xi)$ , having first derivative increasing by (3.1), is a convex function and thus it satisfies the inequality  $G(\eta) \geq G(\xi) + G'(\xi) \cdot (\eta - \xi)$ , for every  $\xi, \eta > 0$ . By this convexity condition, we get

$$\begin{aligned} \int_0^l G(\rho - v) dx &\geq \int_0^l \{G(\rho - u') + G'(\rho - u') \cdot (u' - v')\} dx \\ &= \int_0^l G(\rho - u') dx + \int_0^l G'(\lambda) \cdot (u' - v') dx \\ &\quad + \int_0^l \{G'(\rho - u') - G'(\lambda)\} \cdot (u' - v') dx. \end{aligned} \quad (3.16)$$

Moreover, since the difference  $u - v$  vanishes at  $x = 0$  and  $x = l$ , we have

$$\int_0^l G'(\lambda) \cdot (u' - v') dx = G'(\lambda) \cdot \int_0^l (u' - v') dx = 0; \quad (3.17)$$

finally, the quantity  $G'(\rho - u') - G'(\lambda)$  is different from zero only if  $u' = 0$  (otherwise  $\rho(x) - u'(x) = \lambda$ ) and in that case

$$\{G'(\rho - u') - G'(\lambda)\} \cdot (u' - v') = \{G'(\rho(x)) - G'(\lambda)\} \cdot (u' - v') \geq 0 \quad (3.18)$$

for all  $x$ , since, being  $\rho(x) \leq \lambda$  then  $G'(\rho(x)) - G'(\lambda) \leq 0$  (in fact  $G'$  is increasing, by (3.7)), while  $u' - v' = -v' \leq 0$  (because  $v \in W$ ).

By (3.16), (3.17), (3.18) we obtain (3.15) and  $u$  is a minimizer for  $T_1$  on  $W$ . That  $u$  is the unique minimizer follows from the strict convexity of the function  $G(\xi)$ , consequence of (3.1) and of the assumption that  $\Phi(\xi)$  is strictly increasing. This completes the proof of Lemma 3.4.

*Proof of Theorem 3.1.* First, with the notations  $T_1(v) = T(v, l)$  and  $u = u_l$  of the previous Lemma 3.4, we observe that

$$\inf_{(v, l) \in W \times I} \{T(v, l)\} = \inf_{l \in I} \left\{ \inf_{v \in W} T(v, l) \right\} = \inf_{l \in I} \{T(u_l, l)\} = \inf_{l \in I} T_1(u_l) .$$

We define

$$T_2(l) = \inf_{v \in W} T(v, l) = T(u_l, l) = T_1(u_l) .$$

It remains to prove that  $T_2(l)$  has minimum in  $I$ . Since for  $u = u_l$  in (3.14) we have

$$\begin{aligned} \rho - u' &= \rho - \max\{\rho, \lambda\} + \lambda = \rho + \lambda + \min\{-\rho, -\lambda\} \\ &= \min\{\rho + \lambda - \rho, \rho + \lambda - \lambda\} = \min\{\lambda, \rho\} , \end{aligned} \tag{3.19}$$

then  $\rho(x) - u'(x) = \min\{\lambda, \rho(x)\}$  and

$$T_2(l) = T_1(u_l) = \int_0^l \left\{ \frac{1}{V_0(x)} + G(\min\{\lambda, \rho(x)\}) - G(\rho(x)) \right\} dx . \tag{3.20}$$

The function  $T_2$  depends on  $l$  not only through the right endpoint of the interval  $[0, l]$  used in the integration, but also through  $\lambda = \lambda(l)$ . We can use Lemma 3.3 to infer the continuity of  $\lambda(l)$  and, as a consequence, the continuity of  $T_2(l)$  in (3.20) for every  $l \in I$ .

Recall that the set  $I$  is a *closed* interval (of the form  $[l_0, +\infty)$ , for some  $l_0 > 0$ ); moreover, since  $V_0(x)$  is a positive bounded function, then

$$\lim_{l \rightarrow +\infty} T_2(l) \geq \lim_{l \rightarrow +\infty} \int_0^l \frac{1}{V_0(x)} dx = +\infty .$$

Therefore  $T_2(l)$  admits a minimizer on  $I = [l_0, +\infty)$ . The proof of Theorem 3.1 is complete.

#### 4 The case of constant density of food

In this section we analyze the result of the previous section in the particular case of *uniform* (i.e. *constant*) density of food (for instance, an artificial meadow). Then it is natural to assume also that the animal moves in the habitat with constant velocity. That is, we assume that  $\rho$  and  $V_0$  are real positive constants. As in (3.2), in our case the functional to minimize is

$$T(v, l) = \left[ \frac{1}{V_0} - G(\rho) \right] \cdot l + \int_0^l G(\rho - v'(x)) dx \tag{4.1}$$

where  $G$  is defined (up to an additive constant) through the functional response  $\Phi$  by the condition

$$\frac{d}{d\xi} G = - \frac{1}{\Phi(\xi)} , \tag{4.2}$$

where  $\Phi$  is a nonnegative, strictly increasing function, with  $\Phi(0) = 0$ . The interval  $I$  defined in (3.4) can be represented in the form

$$I = \{l \in \mathbb{R} : \rho \cdot l \geq A\} = [A/\rho, +\infty) . \tag{4.3}$$

Finally  $W$  is the class of functions

$$W = \{v \in Lip([0, l]): v(0) = 0, v(l) = A; 0 \leq v'(x) \leq \rho(x), \forall \text{a.e. } x \in [0, l]\} . \tag{4.4}$$

**Theorem 4.1** *Let  $\Phi$  be a differentiable nonnegative, strictly increasing function in  $[0 +, \infty)$ , such that  $\Phi(0) = 0$ . Then the functional  $T(v, l)$  in (4.1) has a minimizer in the class  $W \times I$ . The minimizer  $(u, l)$  is unique and is given by the formulas*

$$u(x) = (\rho - \lambda)x \quad \text{and} \quad l = \frac{A}{\rho - \lambda} , \tag{4.5}$$

where  $\lambda$  is the unique solution, in the open interval  $(0, \rho)$ , to the equation

$$\frac{1}{V_0} - \frac{1}{\Phi(\lambda)}(\rho - \lambda) + \int_{\lambda}^{\rho} \frac{1}{\Phi(\xi)} d\xi = 0 . \tag{4.6}$$

*Remark 4.2.* The threshold  $\lambda$ , defined by (4.6), is independent of the mass of gut contents  $A$ . As a consequence, the length of the path (see  $l$  in (4.5)) is proportional to  $A$ . Also the total foraging time, being proportional to  $l$  (see (4.9) below), comes out to be proportional to  $A$ .

*Proof.* Following the notations and the proofs given in the previous section, for every  $l \in I$  (i.e.  $l \geq A/\rho$ ) we define the threshold  $\lambda$  as the solution of (3.7):

$$B(\lambda, l) = \int_0^l [\max\{\rho, \lambda\} - \lambda] dx = A . \tag{4.7}$$

Values of  $\lambda \geq \rho$  do not satisfy (4.7); for  $\lambda < \rho$  we obtain

$$B(\lambda, l) = (\rho - \lambda) \cdot l = A , \quad \text{that is } \lambda = \rho - \frac{A}{l} . \tag{4.8}$$

For  $l \in I$  fixed the minimizer  $u = u(x) = u_l(x)$  is defined in (3.14). It is given by

$$u(x) = (\rho - \lambda)x = \frac{A}{l} x .$$

It remains to minimize the function  $T_2$  (the total foraging time) in (3.20), expressed in our case, since  $\lambda < \rho$ , by

$$T_2(l) = \left( \frac{1}{V_0} + G(\lambda) - G(\rho) \right) \cdot l = \left( \frac{1}{V_0} + G\left(\rho - \frac{A}{l}\right) - G(\rho) \right) \cdot l . \tag{4.9}$$

The first and the second derivatives with respect to  $l$  of  $T_2$  are given by

$$T_2'(l) = \frac{1}{V_0} + G\left(\rho - \frac{A}{l}\right) - G(\rho) + G'\left(\rho - \frac{A}{l}\right) \cdot \frac{A}{l}; \tag{4.10}$$

$$T_2''(l) = G''\left(\rho - \frac{A}{l}\right) \cdot \frac{A^2}{l^3}. \tag{4.11}$$

We can express these derivatives in terms of the functional response, by using (4.2); in particular, for the second derivative we have

$$T_2''(l) = \left[ \Phi\left(\rho - \frac{A}{l}\right) \right]^{-2} \cdot \Phi'\left(\rho - \frac{A}{l}\right) \cdot \frac{A^2}{l^3}$$

and we can see that  $T_2'' \geq 0$  if and only if  $\Phi' \geq 0$ . Since  $\Phi' \geq 0$  by assumption, then  $T_2'' \geq 0$  and  $T_2'$  is increasing on  $I$ . Since, by assumption,  $\Phi$  is strictly increasing, then  $\Phi'$  cannot be identically zero on an interval (with nonempty interior). Therefore  $T_2'$  is strictly increasing too and  $T_2$  is strictly convex on  $I$ . This gives the existence of at most one minimizer  $l$  of the function  $T_2$ , and also the existence of at most one solution in  $I$  to the equation  $T_2'(l) = 0$ .

To show that in fact the equation  $T_2'(l) = 0$  has a solution in  $I$  (which, by its convexity, will be also the minimizer of  $T_2$ ), it is enough to observe that

$$\lim_{l \rightarrow (A/\rho)^+} T_2'(l) = -\infty \quad (\text{see Lemma 4.3 below});$$

$$\begin{aligned} \lim_{l \rightarrow +\infty} T_2' &= \frac{1}{V_0} + \lim_{l \rightarrow +\infty} G'\left(\rho - \frac{A}{l}\right) \cdot \frac{A}{l} \\ &= \frac{1}{V_0} - \lim_{l \rightarrow +\infty} \left[ \Phi\left(\rho - \frac{A}{l}\right) \right]^{-1} \cdot \frac{A}{l} = \frac{1}{V_0}. \end{aligned}$$

With the position  $\lambda = \rho - (A/l)$  we then obtain that  $\lambda$  is the unique solution in the interval  $(0, \rho)$  to the equation

$$\frac{1}{V_0} + G(\lambda) - G(\rho) + G'(\lambda) \cdot (\rho - \lambda) = 0,$$

which corresponds to (4.6).

**Lemma 4.3** *The function  $T_2'$  in (4.10) satisfies the limit condition*

$$\lim_{l \rightarrow (A/\rho)^+} T_2'(l) = -\infty. \tag{4.12}$$

*Proof.* Since  $T_2'$  is increasing in  $I = [A/\rho, +\infty)$ , then the limit in (4.12) exists and either is finite, or it is equal to  $-\infty$ . We split the proof into two parts, according either if

$$\lim_{l \rightarrow (A/\rho)^+} G\left(\rho - \frac{A}{l}\right) = +\infty \tag{4.13}$$

or not. If (4.13) holds, then

$$\lim_{l \rightarrow (A/\rho)^+} T_2(l) = \lim_{l \rightarrow (A/\rho)^+} \left( \frac{1}{V_0} + G\left(\rho - \frac{A}{l}\right) - G(\rho) \right) \cdot l = +\infty$$

and this implies that (4.12) holds. In fact, if  $T_2'(l)$  would stay bounded as  $l \rightarrow (A/\rho)^+$ , then  $T_2(l)$  should be Lipschitz continuous in a neighborhood of  $l = A/\rho$  and thus  $T_2(l)$  should remain bounded too.

In the second case, i.e. if (4.13) does not hold, then (recall that  $G$  has a limit, being convex)  $G(\rho - A/l)$  converges to a finite limit as  $l \rightarrow (A/\rho)^+$  and

$$\lim_{l \rightarrow (A/\rho)^+} T_2'(l) = \lim_{l \rightarrow (A/\rho)^+} \frac{1}{V_0} + G\left(\rho - \frac{A}{l}\right) - G(\rho) + G'\left(\rho - \frac{A}{l}\right) \cdot \frac{A}{l} = -\infty,$$

since  $G'(\rho - A/l) = -[\Phi(\rho - A/l)]^{-1} \rightarrow -\infty$  as  $l \rightarrow (A/\rho)^+$ .

### 5 Results

The results obtained for the mathematical model allow us to study many aspects and relations among the most relevant parameters that characterize our problem. In particular, in the case of uniform density of food  $\rho$ , we have an explicit representation formula for the threshold  $\lambda$  in terms of the functional response  $\Phi$ , the velocity  $V_0$  and the food density  $\rho$ .

Since in the Introduction we proposed to non-mathematicians to skip, at a first reading, Sects. 3 and 4, we briefly summarize here what we proved in the case of uniform density of food: we considered the minimization of the total time  $T(v, l)$  in (2.12). Since the density of food  $\rho$  and the velocity of the animal  $V_0$  are constant, the total time  $T(v, l)$  takes the form

$$T(v, l) = \left[ \frac{1}{V_0} - G(\rho) \right] \cdot l + \int_0^l G(\rho - v'(x)) dx \tag{5.1}$$

Under some natural assumptions on the functional response  $\Phi = \Phi(\xi)$  we proved that the total time  $T(v, l)$  in (5.1) has a unique minimum which is realized by

$$v(x) = (\rho - \lambda)x \quad \text{and} \quad l = \frac{A}{\rho - \lambda}, \tag{5.2}$$

where the food which remains, i.e. the *threshold*  $\lambda$ , is the unique solution to the equation

$$\frac{1}{V_0} - \frac{1}{\Phi(\lambda)}(\rho - \lambda) + \int_\lambda^\rho \frac{1}{\Phi(\xi)} d\xi = 0 \tag{5.3}$$

in the open interval  $(0, \rho)$ . Note that the food eaten at each foraging site is constant and equal to  $v' = \frac{dv}{dx} = \rho - \lambda$ .

Adopting the form of the functional response given by Real [29, 30]

$$\Phi(\xi) = k \cdot \frac{\xi^\alpha}{b + \xi^\alpha}, \quad (5.4)$$

for  $\alpha \neq 1$  the threshold  $\lambda$  is the real solution to the equation

$$\lambda \in (0, \rho): \quad \frac{1}{V_0} - \frac{b}{k\lambda^\alpha}(\rho - \lambda) + \frac{b}{k(1-\alpha)} \cdot (\rho^{1-\alpha} - \lambda^{1-\alpha}) = 0, \quad (5.5)$$

while, for  $\alpha = 1$ , the equation is

$$\lambda \in (0, \rho): \quad \frac{1}{V_0} - \frac{b}{k\lambda}(\rho - \lambda) + \frac{b}{k} \cdot (\log \rho - \log \lambda) = 0. \quad (5.6)$$

After some simplification, these can be written equivalently in the form

$$(\alpha \neq 1) \quad \lambda \in (0, \rho): \quad \frac{\rho}{\lambda} - \frac{1}{1-\alpha} \cdot \left[ \left( \frac{\rho}{\lambda} \right)^{1-\alpha} - 1 \right] = 1 + \frac{k}{bV_0} \cdot \lambda^{1-\alpha}, \quad (5.7)$$

$$(\alpha = 1) \quad \frac{\rho}{\lambda} > 1: \quad \frac{\rho}{\lambda} - \log \frac{\rho}{\lambda} = 1 + \frac{k}{bV_0}. \quad (5.8)$$

Note that we can obtain (5.8) directly from (5.7) as the limit for  $\alpha \rightarrow 1$ .

By means of (5.5) and (5.6) (or (5.7) and (5.8)) we can make numerical experiments to analyze the relations between the main parameters. Note that (as we already said in Remark 4.2) some of these relations are now easy to describe; for example the threshold  $\lambda$  is independent of the mass of gut contents  $A$  (while the length  $l$  of the path as well as the total foraging time are proportional to  $A$ ). By (5.7), (5.8) we see that  $\lambda$  depends on the parameters  $V_0, k, b$ , through the ratio  $k/(bV_0)$ ; by (5.8) we find also that, for  $\alpha = 1$ , the threshold  $\lambda$  is proportional to  $\rho$  (i.e. the ratio  $\rho/\lambda$  is constant when  $k/(bV_0)$  is fixed).

Let us consider first the case  $\alpha = 1$ . The threshold value  $\lambda$  and the excursion length  $l$  exhibit a different behaviour when plotted as functions of the food density  $\rho$ ;  $l$  shows a decay while  $\lambda$  shows a linear increase, so that the amount of food  $\rho - \lambda$  consumed at each foraging station increases with  $\rho$  (Fig. 1). Let us denote by  $\beta$  the relative threshold  $\lambda/\rho$ ; then by (5.8) we have that  $\beta \in (0, 1)$  is the solution to the equation

$$\frac{1}{\beta} + \log \beta = 1 + \frac{k}{bV_0}.$$

It is interesting to note that the relative threshold  $\beta$  is independent of  $\rho$  and  $\lambda$ . From (5.2) we obtain

$$l = \frac{A}{1-\beta} \cdot \frac{1}{\rho} = \text{constant} \cdot \frac{1}{\rho}$$

and

$$\rho - \lambda = (1 - \beta) \cdot \rho = \text{constant} \cdot \rho.$$

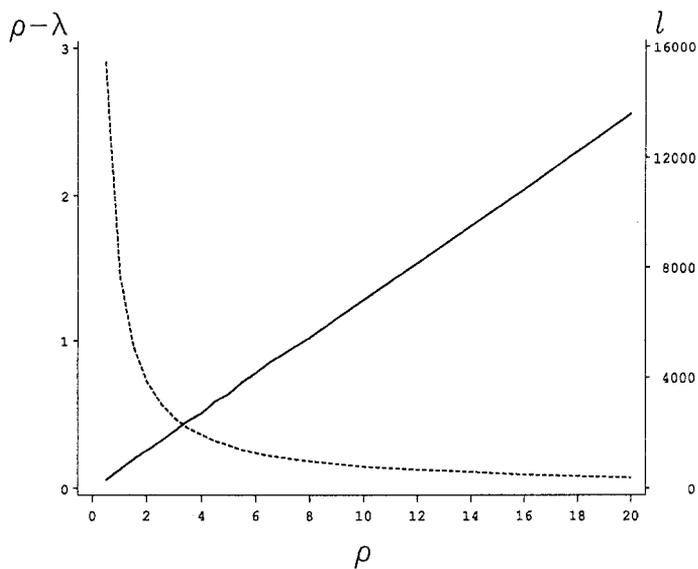


Fig. 1. The food eaten at each foraging station,  $\rho - \lambda$  (continuous line), and the length of the foraging excursion,  $l$  (broken line) are plotted as functions of food density  $\rho$ .  $\alpha = 1$ ,  $A = 1000$ ,  $k/(bV_0) = 0.01$

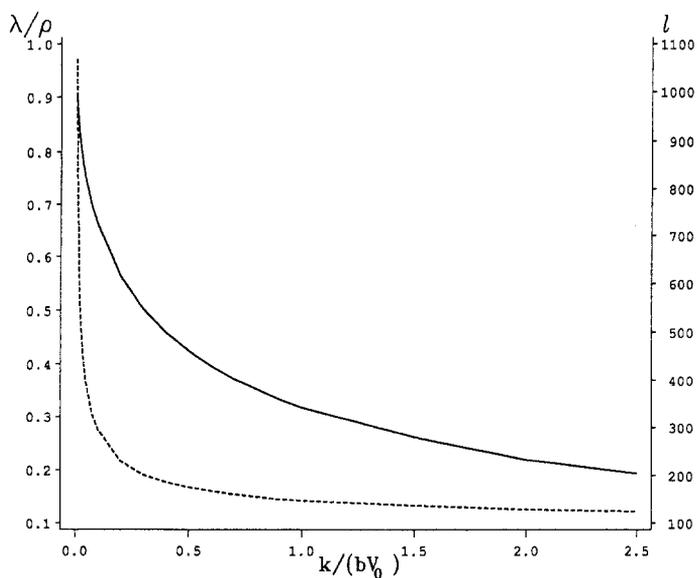
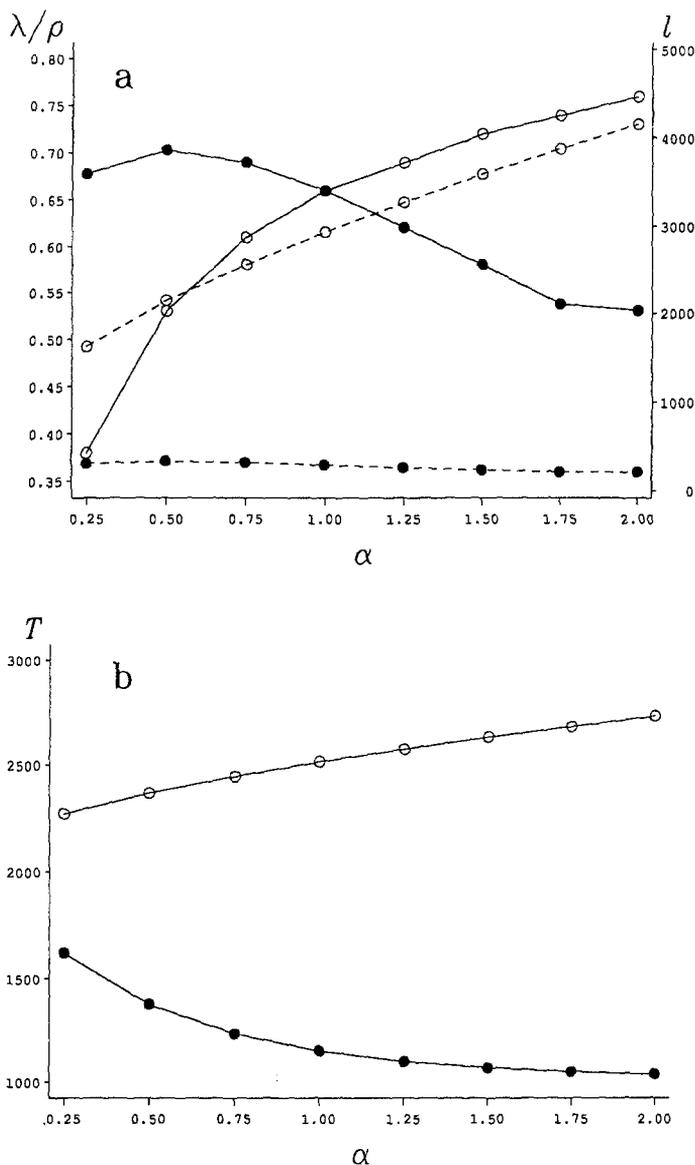


Fig. 2. The relative threshold  $\lambda/\rho$  (continuous line) and the length of the foraging excursion,  $l$  (broken line) are plotted as functions of  $k/(bV_0)$ .  $\alpha = 1$ ,  $A = 1000$ ,  $\rho = 10$



**Fig. 3.** **a** The relative threshold  $\lambda/\rho$  (continuous line) and the length of the foraging excursion,  $l$  (broken line) are plotted as functions of  $\alpha$ , for two  $\rho$  values ( $\rho = 1$ , open circles and  $\rho = 10$ , black circles). **b** The total foraging time,  $T$ , is plotted as function of  $\alpha$  for two values of  $\rho$  ( $\rho = 1$ , open circles and  $\rho = 10$ , black circles).  $A = 1000$ ,  $k/(bV_0) = 0.1$

The relative threshold  $\lambda/\rho$  and the excursion length  $l$  decrease as functions of  $k/(bV_0)$ : when the mobility of the animal in the environment is reduced (for example in case of snow) both variables decrease, the latter at a faster rate than the former (Fig. 2).

From an evolutionary point of view it is interesting to analyze the effect of different functional responses on the foraging strategy and in particular the effect of  $\alpha$ , the parameter determining the shape of the function  $\Phi$  in (5.4). If food density  $\rho$  is small, both  $\lambda/\rho$  and  $l$  increase as functions of  $\alpha$ ; on the contrary, for larger  $\rho$  values we observe that  $\lambda/\rho$  decreases with respect to some  $\alpha$  values and  $l$  remains almost constant (Fig. 3a); note that, for  $\alpha = 1$ ,  $\lambda/\rho$  is independent of  $\rho$ , as previously said. The global foraging time  $T$  depends on  $\alpha$ : if  $\rho$  is small then  $T$  increases, while it quickly decreases if  $\rho$  is large (Fig. 3b).

## 6 Discussion

The existence of partial consumption of food predicted by this model is in agreement both with the conclusions of other theoretical studies (Arditi and Dacorogna [5]) and with the observation of animal behaviour (Åström et al. [6]; Saether [31]; Focardi et al. [13]). The existence of an optimal threshold in the foraging behaviour of wild ungulates is much less evident and to our knowledge there are no studies specifically devoted to this topic. One important difficulty which arises in the experimental detection of the threshold is given by its dependence on the functional response which is known only for few species of ungulates. Since Demmet and Van Soest [12] have shown that there exists a relationship between body mass and gut size and since, for the same functional response, the threshold is independent on gut size, the model predicts that the behaviour of sympatric species should be identical independently of the body mass; only the excursion length should increase proportionally with body mass. Unfortunately, for ungulates there are few detailed studies of short-term movements (e.g. Underwood [37]; Gillingham and Bunnell [15]; Focardi et al. [13]) which are necessary to evaluate the length of the foraging excursion.

Vivås and Saether [38] were able to follow tracks in the snow of moose which foraged upon artificial patches of birch and found that the food intake per plot linearly increased with food density in the way predicted by our model (cf. Fig. 1). The present study shows that foraging behaviour and movement are not independent processes. Previous theoretical analyses failed to stress this link and integrated field studies are not available. Movement patterns are usually studied by long-term radio-tracking in order to evaluate the home range size. Length of the foraging excursion and home range size are not directly comparable measures, however it is probable that they are strongly correlated. The model predicts a linear increase of the foraging excursion with body mass. On the contrary models based on energetic considerations (McNab [26]; Pennycuik [27]) predicts bounded curvilinear relationships and cannot explain the empirical evidence (Hudson [19]; Harvey and Pagel [17]); Harestad and Bunnell [16] showed that, at least in north-American herbivores, the relationship is linear.

The functional response is determined both by the kind of food (Allden and Whittaker [1]; Trudell and White [36]; Spalinger et al. [34]) and by

physical traits of the animals such as teeth size and shape. Many traits which are important for food gathering exhibit strong correlations with body mass (Fortelius [14]). To our knowledge there are no studies specifically devoted to analyze how the functional response change with body mass but Shibly and Spalinger [32] have shown that the maximum feeding rate ( $k$  in our notation) is scaled to body mass. It seems reasonable to us to conjecture that small ungulates are more efficient than large ungulates to handle scattered food items (see Illius and Gordon [21] and references therein) so that  $\alpha$  should increase with respect to body mass.

Thus, under common environmental conditions (abundant food), there is an inverse relationship between threshold and body mass. A lower threshold characterizes the larger species (cf. Fig. 3a), independently by diet choice. This result is interesting because in previous studies between-species differences in selectivity were explained by diet (feed quality) choice. Our study shows that it exists a different kind of selectivity which determines how much food is consumed at each foraging station.

The parameters  $\rho$  and  $V_0$  may changes both among individuals of the same species or even among different periods or habitats experienced by the same animal. On the other side inter- and intra-individual variations of  $\alpha$  values are probably small while is might be important to compare different species. Our results suggest that, for grass/roughage feeders (for which food density is usually high), we should observe an evolutionary trend towards high  $\alpha$  values (which reduce the total foraging time, cf. Fig. 3b), while concentrate selectors should be characterized by lower  $\alpha$  values. This observations stress the importance to develop comparative studies on the functional response of herbivores.

However it has to be noted that the condition of identical food quality is probably not realistic even if animals exploit only one feed, because its quality may depend on biomass. Langvatn and Hanley [25] have showed that dry matter digestibility (i.e. the fraction of plant which can be digested and used by a ruminant) of timothy grass (*Phleum pratensis*) inversely depends on its growth stage; Vivås and Saether [38] have showed that digestibility is inversely related to twig size of birch (*Betula pubescens*) eaten by moose. Thus it might be more convenient for a ruminant to forage on more digestible plants, i.e. where the standing biomass is lower. Therefore a more realistic model should account both for food quality choice and biomass selection. Stephens and Krebs [35] have discussed such a model in the case of patchy food distributions.

Our assumption that there is enough food in the environment to fill the rumen does not mean that animals cannot death of starvation. In fact in unfavorable conditions food quality may be so low that a satiated animal is unable to extract the energy it needs to survive.

The model has been specifically discussed with respect to the foraging behaviour of ungulates; however its formulation is general enough to encompass many species of herbivores. The only constraint we have introduced, limited gut capacity, may be realistic for many other groups such as intertidal

grazers and terrestrial invertebrates.

**Appendix: table of variables** (in parenthesis we denote the dimension of each variable)

- $x$ , position of a generic point of the excursion (*length*)  
 $l$ , position of the final point of the excursion, length of the path of the excursion (*length*)  
 $\rho = \rho(x)$ , density of food at a generic point  $x$  (*mass · length<sup>-1</sup>*)  
 $A$ , total amount of food gathered, i.e. maximum of gut contents (*mass*)  
 $\tau = \tau(x)$ , foraging time per unit length, i.e. time spent at  $x$  to acquire food (*time · length<sup>-1</sup>*)  
 $\delta = \delta(\tau) = \delta(\tau(x))$ , density of acquisition of food at  $x$  (*mass · length<sup>-1</sup>*)  
 $\xi$ , generic variable, usually equal to the density of remaining food  $\rho - \delta$  (*mass · length<sup>-1</sup>*)  
 $\Phi = \Phi(\xi)$ , functional response, equal to the velocity of acquisition of food (*mass · time<sup>-1</sup>*)  
 $k, \alpha, b$ , parameters used with different meanings, whose dimensions depend on the context  
 $G = G(\xi)$ , primitive of  $-1/\Phi(\xi)$  (*time · length<sup>-1</sup>*)  
 $\tau_0 = \tau_0(x)$ , initial foraging time per unit length (*time · length<sup>-1</sup>*)  
 $V_0 = V_0(x)$ , velocity of the animal at  $x$  (*length · time<sup>-1</sup>*)  
 $v = v(x)$ , amount of food gathered till the point  $x$  (*mass*)  
 $T = T(v, l)$ , total time to acquire food and to move (*time*)  
 $u = u(x)$ , same meaning as  $v$ , used to denote a minimizer (*mass*)  
 $\lambda = \lambda(l)$ , the threshold in the acquisition of food, i.e. the critic density of food (*mass · length<sup>-1</sup>*)  
 $B = B(\lambda, l)$ , function of two real variables, used in the mathematical proofs (*mass*)  
 $\varphi_1(x)$ , function of one real variable, used in the mathematical proofs (*mass · length<sup>-1</sup>*)  
 $T_1(v) = T(v, l)$ , time for  $l$  fixed (*time*)  
 $u_1$ , minimizer for  $l$  fixed (*mass*)  
 $T_2(l) = T(u_1, l)$ , optimal time as a function of  $l$  (*time*)  
 $\beta = \lambda/\rho$ , the relative threshold (*adimensional*)

*Acknowledgement.* We are grateful to a reviewer for suggestions which have improved presentation and readability of our paper.

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