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Optimal Use of Resources: Classic Foraging Theory, Satisficing and Smart Foraging – Modelling Foraging Behaviors of Elk

by

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Abstract

It is generally accepted that the Marginal Value Theorem (MVT) describes optimal foraging strategies. Some research findings, however, indicate that in natural conditions foragers not always behave according to the MVT. To address this inconsistency, in a series of computer simulations, I examined the behaviour of four types of foragers having specific foraging efficiencies and using the MVT and alternative strategies in 16 simulated landscapes in an ideal environment (no intra- and inter-species interactions). I used data on elk (*Cervus elaphus*) to construct the virtual forager. Contrary to the widely accepted understanding of the MVT, I found that in environments with the same average patch quality and varying average travel times between patches, patch residence times of some foragers were not affected by travel times. I propose a mechanism responsible for this observation and formulate the perfect forager theorem (PFT). I also introduce the concepts of a foraging coefficient (F) and foragers' hub (α), and formulate a model to describe the relationship between the perfect forager and other forager types. I identify situations where a forager aiming to choose an optimal foraging strategy and maximize its cumulative consumption should not follow the MVT. I describe these situations in a form of a mathematical model. I also demonstrate that the lack of biological realism and environmental noise are not required to explain the deviations from the MVT observed in field research, and explain the importance of scale in optimal foraging behaviour. I also demonstrate that smart foraging, which is a set of rules based on key ecological concepts: the functional response curve (FRC), satisficing, the MVT, and incorporates time limitations, should allow for fitness maximization. Thus, it should be an optimal behavior in the context of natural selection. I also demonstrate the importance of the FRC as a driver for foraging behaviors and argue that animals should focus more on increasing the slope of their FRC than on choosing a specific foraging strategy. Natural selection should, therefore, favor foragers with steep FRC. My findings introduce new concepts in behavioural ecology, have implications for animal ecology and inform wildlife management.

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I would like to thank my Parents for their support, without which this project would have never been possible, and even more for giving me the gift of inquisitive mind.

My special thanks go to my wife Malgosia. You joined me on this journey that sometimes led though dark and cold places. You never complained, you endured it all and you always supported me. And you gave me the greatest joy of my life.

Even before I became interested in academic research, I devoted my intellectual journeys to the search for the truth and its small components. *Quaecumque vera* – I strongly believe that it is the journey in the search for the truth, which describes the World, where one finds one's self. I thank God that I had the privilege to go on my own, small journey to search for the truth.

TABLE OF CONTENTS

List of Tables

List of Figures

Chapter 1. General Introduction

1.1. Classical foraging theory

All living beings need energy to survive and reproduce. The process of acquiring energy by mobile organisms is generally termed foraging. Therefore, the theories and models used to explain foraging mechanisms are fundamental to all branches of ecology. Undoubtedly, different foraging patterns have been observed in the animal kingdom by early naturalists who noticed that in most cases animals do not deplete resources completely. After consuming some amount of forage at one location they usually move to a new foraging location. No mechanism had been proposed to describe this pattern and the drivers for this behavior were poorly understood until MacArthur and Pianka (1966) and Emlen (1966) proposed ideas that formed the early foraging theory. They focused on the idea that optimal foraging is crucial for individual's survival and, therefore, it should be possible to predict the behavior of an optimal forager. Emlen (1966) emphasized the relationship between the abundance of food and consumer's food preferences. He noted that foraging behavior of predators could be used to evaluate the role of food in limiting the population of the predator. MacArthur and Pianka (1966) developed a theoretical and empirical model that led to a better understanding of foraging behavior. The authors concentrated on the optimal use of a patchy environment in the context of the forager's cost-benefit ratio and concluded that factors such as patch size and productivity of an environment should have direct impact on the foraging behavior of animals.

Most environments are characterized by some form of patchiness and focusing on foraging in patchy habitats resulted in the next milestone in the development of the classical foraging theory. Formulation of the marginal value theorem (MVT) proposed by Charnov (1976) introduced one of the key concepts in ecology. Charnov (1976) examined foraging behaviors of Great Tits (*Parus major*) and proposed a model that linked the travel time between patches of food and the observed gain from a patch to obtain specific patch residence times. According to Charnov (1976), a forager should stay in a patch longer if the patch had more abundant forage. The forager should also forage longer in the same patch in habitats with sparsely distributed patches when travel between patches is long.

1.2. Need for a new approach

Charnov's model received support from several field studies (Best and Bierzychudek 1982, Bonser et al. 1998, Jiang and Hudson 1993, Laca et al. 1993, Pyke 1978, Wajnberg et al. 2000). Some authors (Carmel and Ben-Haim 2005, Moen et al. 1998, Nonacs 2001), however, argued that foraging strategies other than the MVT could be used by animals to achieve similar or better results. In a simulation modeling study, Moen et al. (1998) showed that moose using the MVT stopping-rule created a landscape that resulted in extinction of the moose population in less than 40 years. Others (Alonso et al. 1995) argued that foragers only use MVT under specific circumstances and attributed the deviations from the MVT to the imperfect knowledge that animals have about their environment and social behavior. The view expressed by Nonacs (2001) that the reason for refuting the MVT by several studies (e.g., Hansen 1987, Hanson and Green 1989, Howell and Hartl 1980, Kamil et al. 1993, Moen et al. 1998, Schluter 1982) is that MVT lacks biological realism, but explains foraging behavior in a perfect world seems to be widely accepted (Alonso et al. 1995, Begon et al. 1990, Nonacs 2001, Searle et al. 2005). Nonacs (2001) argued that it is environmental noise that results in deviations from the predictions of MVT and that this noise needs to be accommodated if one is to precisely describe foraging strategies. Consequently, he proposed that state-dependent strategies describe the actual foraging behavior in real situations more precisely than MVT.

Significant research conducted on foraging behavior observed in the animal kingdom reflects the importance of the foraging theory in ecology. Indeed, as stated by Emlen (1966), the efficient exploitation of food resources is vital for all animals and, therefore, the foraging theory and study of foraging strategies are of critical importance to ecology. Clearly, foraging theory has much broader implications that originally envisioned by Emlen (1996). Recent works in fields such as anthropology, economy and artificial intelligence further emphasize the importance of the foraging theory in disciplines not directly related to biology that use the optimal foraging concept to address complex issues (Arroyo 2009, Quijano et al. 2006, Pavlic 2007).

The controversy around Charnov's model resulted in extensive research that has been conducted with an aim to broaden our understanding of foraging theory, a concept critical to most aspects of ecology. Attempts have been made to develop accurate foraging models for herbivores (Hobbs et al. 2003, Hobbs et al. 1983, Hudson and Watkins 1986, Shipley et al. 1999, Trudell and White 1981, Wickstom et al. 1984). Searle et al. (2005) proposed that MVT does not explain foraging behavior of herbivores sufficiently and that a more adequate model is needed. The apparent discrepancy between the reported deviations from the MVT and studies that supported Charnov's concept triggered this research that aims at addressing the gaps identified in the foraging theory (Moen et al. 1998, Nonacs 2001, Searle et al. 2005, Spalinger and Hobbs 1992).

The process of model building allows for identification of knowledge gaps and the outputs of simulation experiments allow for revealing patterns that could not be observed in field studies where a researcher is limited by a number of constraints. Therefore, computer models are excellent tools to examine concepts. In a series of computer simulation experiments, I explored in detail the topic of foraging in a patchy habitat using elk (*Cervus elaphus*) as a case species. Elk is a well-studied species and its food requirements, habitat use and foraging behavior are well understood (Baker and Hobbs 1987, Clutton-Brock et al. 1982, Hartley et al. 1997, Hudson and Watkins 1986, Hudson and White 1985, Hudson and Nietfeld 1985, Jiang and Hudson 1993, Wickstom et al. 1984), which makes this species an ideal subject for development of a computer simulation model.

In simulation experiments I examined the MVT and alternative foraging models such as satisficing (Carmen and Ben Haim 2005, Ward 1992). I was interested in examining the consequences of employing various foraging strategies by foragers of different foraging efficiencies across a spectrum of landscapes of varying productivity in situations where a foraging animal is not involved in any activities that could distract it from foraging (no inter or intra-species interactions). The ultimate question that I wanted to address was whether an animal aiming at optimizing resource use should use MVT at all times, what are the consequences of employing alternative strategies and when it may be better to abandon the MVT as a foraging staregy. I initially concentrated on a forager's behavior within short temporal and small spatial scales limited to foraging in an average patch and average travel time within a given landscape required to reach that patch. Next, I scaled up my focus and examined different foraging behaviors at a landscape scale within a daily foraging cycle. This enabled me to identify new patterns and propose new concepts in foraging theory.

1.3. Thesis structure

This thesis follows a paper format and is composed of five chapters, three of which constitute individual manuscripts (Chapters 2, 3 and 4). Chapter 1 (this chapter) provides the rationale for this research, states its goals and introduces the main concepts.

In Chapter 2, I first examine the behavior of different foragers (having specific foraging efficiency) across a spectrum of habitats with varying average patch quality and average travel time on a short temporal and small spatial scale. I expected that each forager, as predicted by the MVT, depending on the shape of its functional response curve (FRC) should behave differently when foraging according to the MVT and that this should be reflected in behavioral differences associated with a specific forager using the MVT. Based on my findings, I describe, in a form of a mathematical model, potential relationships between the observed behaviors and formulate the perfect forager theorem (PFT) that defines a forager not affected by the distribution of patches across the landscape. I also propose a relationship that exists between the perfect forager and all other forager types. To describe the perfect forager, I introduce concepts of a foraging coefficient F and foragers' hub α.

In the next chapter (Chapter 3), I assess if there are any specific reasons for foragers to deviate from MVT in the absence of environmental noise (no inter- and intra-species interactions). A close examination of how a forager feeding in a landscape consisting of a number of patches distributed over a specific area should behave depending on its foraging strategy (MVT versus alternatives) and what the consequences (cumulative gains and the cost-benefit ratio) of these strategies are allowed me to assess the consequences of using strategies different than MVT. I was able to determine if it is possible for foragers to meet or exceed their dietary requirements using a foraging strategy different than the MVT. My important finding is that depending on time limitations, strategies other than MVT may provide advantage to foragers not using MVT. I also argue that the widely assumed advantage of MVT over other foraging strategies applies only under specific circumstances and depends on the time scale. In this process I describe the relationship between the total time, foraging time and search time that is responsible for strategies other than MVT being more profitable. To illustrate this relationship I define a concept of a foraging cycle, explain its importance for foragers and discuss how it relates to the proposed model of an alternative foraging strategy that accounts for time limitation.

Chapter 4 considers foraging strategies alternative to MVT with emphasis on statisficing (Carmel and Ben-Haim 2005, Simon 1955, 1956, Ward 1992). Based on this analysis, I propose a concept of smart foraging and define its rules. I also demonstrate that smart foraging, which is a set of rules based on key ecological concepts: the functional response curve (FRC), satisficing, MVT, and time limitations, should allow for fitness maximization. Thus, it should be considered as an optimal behavior in the context of natural selection. I also demonstrate the importance of the shape of the FRC as a driver for foraging behaviors and argue that animals should focus more on increasing the slope of their FRC than on choosing a specific foraging strategy. Natural selection should, therefore, favor foragers with steep FRC.

I argue that to be more successful (than competition) in dispersing its genes, an animal does not have to perform at its best. It is enough to be better than competitors. Therefore, there is no real need for animals to maximize their consumption and optimize their cost-benefit ratio. If, using a specific foraging strategy, the animal is able to pass to the next generation more genes than competing individuals, this particular strategy should be good enough and there is no real motivation for the individual to employ other strategies (especially if they incur additional costs that cannot be transformed into higher fitness).

Chapter 5 synthesizes the work and reinforces the main findings in the context of their importance to ecology. In this chapter I also identify future research needs in the field of behavioral ecology related to foraging theory and other disciplines that incorporate foraging theory as a functional concept.

My findings and concepts that I propose deepen the current understanding of foraging behaviors and thus are important contributions to the science of ecology. Although my work is not directly related to the management of wild populations, enhanced understanding of wildlife behavioral responses to resources should inform and improve wildlife management. The concepts that I propose can be used as important ecological indicators. I believe that my main contribution is in proposing the perfect forager theorem and the notion of the foragers' hub, as well as in quantifying the importance of the FRC to foraging behavior. I believe that these concepts are fundamental in understanding foraging behaviors and the theory of resource optimization. My another important contribution is the explanation I provided for the discrepancy between research that support and counter the marginal value theorem and in clarifying some common misinterpretations of the MVT, which over time became widely accepted as directly derived from the Charnov's (1976) model. My work also illustrates the importance of the interdisciplinary transfer of ideas and significance of individual based models in behavioral ecology and in understanding animal behavior.

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Chapter 2. What elk, wolves and caterpillars have in common - the Perfect Forager Theorem

2.1. Introduction

Nutritional status and energy budgets are the key factors that determine survival and reproductive success of animals. A variety of parameters affects the availability and accessibility of food for wildlife and, to utilize forage resources, each individual needs to respond to these environmental factors. Individual animals have specific abilities to exploit available resources and may use different foraging strategies to satisfy their basic food requirements for survival. These are known for most of the common herbivores (Burness et al. 2001, Nagy 2001). It is widely accepted that the Marginal Value Theorem (MVT) proposed by Charnov (1976) explains the foraging behavior and describes the optimal foraging strategy. Therefore, the MVT forms the foundation of the classical foraging theory. Charnov's model, derived from observations of foraging behavior of Great Tits (*Parus major*), received support from several field studies (Best and Bierzychudek 1982, Bonser et al. 1998, Jiang and Hudson 1993, Laca et al. 1994, Pyke 1978, Wajnberg et al. 2000) including research on herbivores (Jiang and Hudson 1993, Laca et al. 1994). Some authors (Carmel and Ben-Haim 2005, Moen et al. 1998, Nonacs 2001), however, argued that foraging strategies other than the MVT could be used by herbivores. In a simulation modeling study, Moen et al. (1998) showed that moose using the MVT stopping rule created a landscape that resulted in extinction of the moose population in less than 40 years.

In another study, Alonso et al. (1995) illustrated that foragers use MVT strategies only under specific circumstances and attributed the deviations from the MVT to the imperfect knowledge that animals have about their environment and social behavior. Recently, Nonacs (2001) argued that the reason for refuting the MVT by several studies (e.g., Hansen 1987, Hanson and Green 1989, Howell and Hartl 1980, Kamil et al. 1993, Moen et al. 1998, Schluter 1982) is that MVT lacks biological realism. Whereas Alonso et al. (1995) concentrated on how habitat productivity and social behavior affects the applicability of the MVT, Nonacs (2001) argued that animals are simultaneously doing more than just searching for food. For example, most individuals need to be vigilant to avoid predation. Mating opportunities are another factor that significantly affects foraging strategies and results in deviations from the predictions of the classic MVT. Nonacs (2001) argued that strategies that maximize long-term survival trade-off between foraging gain and exposure to risk, predict animal behavior better. In other words, Nonacs (2001) argued, that it is the environmental noise that results in deviations from the predictions of the MVT and that this noise needs to be accounted for if one is to precisely describe foraging strategies. Consequently, he proposed that state-dependent strategies describe the actual foraging behavior in real situations more precisely than the MVT. Similar to Nonacs (2001), Fortin et al. (2004a) argued that even though mammalian herbivores are able to carry out many tasks without interrupting food processing, this multitasking (vigilance) has a negative impact on bite rate that affects food consumption. In a different study Fortin et al. (2004b) concluded that mammalian herbivores can carry out multiple tasks without interrupting food processing, but this possibility is not considered in existing foraging models. Clearly, the ideas presented by Fortin et al. (2004a, 2004b) focused on the fact that the classic MVT lacks biological realism (an animal actually does more than just looking for food), which is similar to the proposal suggested by Nonacs (2001). On the other hand, the idea that multitasking allows for cost-free vigilance (Fortin et al. 2004b) implies that 'biological realism' should not result in major deviations from the MVT. This contradicts the views of Nonacs (2001).

If Nonacs's (2001) predictions were true, then a healthy animal secure from predation and not exposed to competition for forage resources or other intra and inter-species interactions, occurring outside the breeding season, should always follow the MVT while foraging. The research that contradicts the MVT (including simulation studies), suggests that arguments provided by authors such as Nonacs (2001), Alonso et al. (1995) and Fortin et al. (2004), although important, may not account for all factors responsible for the observed deviations from the MVT. It is logical to assume that the intrinsic ability of the foragers to utilize forage resources could have consequences for the foraging strategies that animals employ. However, many papers that assess foraging strategies in the context of the MVT do not consider the forager's functional response and its consequences for an animal's selection of a foraging strategy (e.g., Alonso et al. 1995, Laca et al. 1994, Nonacs 2001). Holling (1959) described three types of functional responses. Type I functional response can be illustrated by a linear increase in intake rate with increasing forage biomass up to a plateau caused by satiation. In type II functional response intake rate increases asymptotically with increasing forage biomass. A sigmoid relationship describes type III functional response. It is widely accepted that type II functional response is the most commonly observed functional response in nature and has been reported by several studies on a wide range of species including herbivores and predators (Fryxell et al. 2004, Hudson and Watkins 1986, Messier 1995, Wickstrom et al. 1984). Although type II functional response is the most widespread relationship between consumption rate and the availability of resources, the functional response curve (FRC) may have different slopes depending on how efficient the animal is in utilizing resources.

The first goal of this research was to examine the behavior of different foragers (having specific foraging efficiency defined by the slope of the functional response curve) using MVT strategies across a spectrum of habitats with varying average patch quality and average travel time. I expected that each forager, as predicted by the MVT, depending on the shape of its type II functional response curve, should behave differently when using the MVT as its foraging strategy. Therefore, there should be a behavioral difference associated with a specific forager if it is using the MVT. My second and main goal was to describe, in a form of a mathematical model, the potential relationships between the observed behaviors (patch residence times, Tr) of foragers of different foraging efficiencies feeding in different landscapes.

Based on a series of simulation experiments, I propose a mathematical model that describes the behavior of different foragers in response to specific landscape characteristics when maximizing their forage consumption even if environmental noise is not present. By doing this, I formulate the perfect forager theorem that defines a forager not affected by the distribution of patches across the landscape and propose a relationship that exists between the perfect forager and all other forager types. To describe the perfect forager I introduce the concepts of a foraging coefficient F and foragers' hub α.

2.2. Methods

2.2.1. Model structure

The first goal of this simulation research was to examine how the foraging behaviors of different foragers (medium, high or low efficiency) are affected by the characteristics of the landscape (quality and distribution of forage patches) at short temporal scales (within a patch) based on the combination of the shape of the functional response curve, patch quality and travel time required to reach the patch. The second goal was to determine if there is a specific relationship between the behaviors displayed by different types of foragers feeding in landscapes of differing productivity.

To achieve these goals, using STELLA Research (isee systems, 2008) modeling software, I built a computer simulation model called SeekSMART. It allows the examination of forage consumption by a forager having its own intrinsic characteristics and feeding in different landscapes by using different foraging strategies (such as the MVT, satisficing and alternatives). SeekSMART is a mechanistic and deterministic model that has a fine temporal and spatial resolution and the ability to inspect the foraging behavior across multiple spatial and temporal scales. SeekSMART has a user-friendly interface that allows the user to control several characteristics of both the forager and the landscape. The model allows for examination of different foragers by defining their intrinsic foraging efficiency responsible for a given functional response type II curve, i.e., the *maximum intake* rate (M) and the slope of the functional response curve (defined by a foraging biomass at which intake rate is equal to half of the maximum intake rate, called the *efficiency* (E)). By adjusting the *maximum intake* (M) rate and the *efficiency* (E) of the forager, any shape of type II functional response curve can be assigned to the forager. Another set of parameters that define the forager is the *digestion time* (DT), *digestion rate* (DR) and *full stomach* (FS). The DT is the time required by a satiated forager to digest a specific proportion of the current stomach content that would allow the forager to resume foraging. *Full stomach* is a parameter that specifies the amount of forage consumed (grams of dry matter (DM)) at which the forager's stomach is full and the forager is satiated. The model assumes that the forager will pause its foraging if its stomach is full. The *digestion rate* (DR) is the proportion of consumed forage that the forager is able to digest within one hour. The model assumes that the forager is not ruminating (digesting) while foraging and rumination and digestion occur only when the forager moves from one patch to another patch (according to the multitasking principle proposed by Fortin et al. 2004b) or when the animal pauses its foraging bout due to a full stomach. Table 2.1 outlines all user-defined parameters of the forager.

By allowing assigning specific characteristics of the forager and the landscape, my model enabled me to examine the constraints of a forager as proposed by two schools of thought. The first one focuses mainly on the ecological framework and proposes that it is the characteristics of the landscape (i.e., the distribution and abundance of resources) and other ecological factors such as interactions with other individuals of the same or other species, in other words on intra (e.g., mating, herding behaviour, biosociological interactions) and inter (e.g., predation) specific interactions that determine the foraging behavior. The classic example of this approach is the MVT (Charnov 1976). The second school of thought focuses mostly on physiological constraints and proposes that it is the morphological and digestive mechanism that is responsible for a specific foraging behavior (Baker and Hobbs 1987, Hudson and White 1985, Illius et al. 2002, Shipley et al. 1999, Spalinger and Hobbs 1992). According to this physiological framework, it is mostly the gut processes, rumen kinetics and handling time that define the constraints for the forager and are responsible for the harvest rate.

In my model, by incorporating a detailed description of both the forager and the landscape in which the forager uses different strategies to access and consume the resources existing in a specific landscape, I am able to examine both approaches (ecological versus physiological frameworks) and to see how they interact and how all of the above constraints influence the intake rate of forage across multiple temporal and spatial scales. In this sense SeekSMART is similar to the model proposed by Whelan and Brown (2005). In contrast to the work by Whelan and Brown (2005) who proposed a model to describe a hypothetical forager feeding on two types of resources, SeekSMART is based on empirical field estimates and calibrated for a real biological species. As such it can be validated using specific field based scenarios.

In addition to the characteristics of the forager described above, SeekSMART allows modification of the decision-making processes that the forager uses on when to leave a patch. The following four rules can be examined in the model. The forager leaves the current patch (N) and moves to the next patch (N+1) when:

1) the density of forage available in the current patch drops to an arbitrary assigned value (the forager may or may not know the landscape);
2) the density of forage available in the current patch drops to the average of forage density in all patches (assumes that the forager knows the landscape);

3) the forager follows the Marginal Value Theorem (MVT). In this case the average travel time between patches and the forager's gain curve determine when the forager leaves the current patch (N) and moves to the next patch (N+1), (assumes the forager knows the landscape); and

4) the forager feeds in a patch for an arbitrary assigned patch residence time (the forager may or may not know the landscape).

The set of traits that can be assigned to the forager and its decision making process when choosing its foraging strategy makes the model capable of examining all kinds of foragers (highly efficient vs. low efficiency foragers, having a wide spectrum of digestive capabilities) in a variety of landscapes.

SeekSMART describes an animal feeding in a landscape consisting of a series of forage patches (Figure 2.1). Depending on the type of the landscape, forage patches have a specific distribution and forage biomass (quality). In a very productive habitat, patches of forage form a continuum and the availability of forage varies slightly between patches. Under less favorable conditions, patches of forage are scattered in a forage deficient space and the variability among forage patches is greater. A poor quality habitat is characterized by few, low-quality patches remotely dispersed across barren land. A continuum of different states between the above three states exists (Figure 2.2). The forager feeding in a landscape enters a patch (N) and after feeding in the patch N, moves to the next patch (N+1). The time that the animal spends feeding within one patch can be arbitrary assigned or is determined by the foraging strategy that the forager chooses as per the above description.

The total number of patches that the animal feeds in during a specific time interval is determined by the combination of the simulation length (total time), travel times between patches and total residence time (in all patches). For example, if the average travel time is long and the residence time is long, the forager will use a smaller number of patches than an animal grazing in a landscape characterized by short distances between patches and employing a foraging strategy that results in short residence time.

Selection of patches of forage is linked to foraging behavior and variety of approaches has been proposed to describe selection of forage patches by animals (Barton et al. 2009, Fortin et al. 2005, Fryxell et al. 2008). In this work, I was not interested in examining the process that foragers use to decide on which patch to forage. Rather, I focused on strategies that animals use to optimally utilize resources in a patchy environment once the decision on patch selection has been made by the foraging animal. Excluding the selection process was critical to examine the consequences (cumulative consumption) of variety of foraging strategies (defined by the giving-up density (GUD) and related patch residence time (Tr), as well as travel times (Tt) between patches). I also believe that including patch selection mechanism would not inform the discussion on the differences between foraging strategies (the selection has been already made) and would only confound the analysis of foraging behavior as defined above.

The following landscape characteristics can be defined in the model by adjusting the main attributes of the patches:

1) *Initial patch biomass density* (DM kg/ha) – IPBD;
2) *Patch size* (m^2)- PS;
3) *Initial patch biomass* (DM g) - IPB. This value is calculated by the model based on the values provided for PS and IPBD according to the following equation:

   $$IPB = IPBD*(0.0001*(PS^2)))*1000$$
4) Distances between patches expressed as travel time (hr) - TravelT.

Additionally, the following settings of the landscape can be specified in the model allowing examination of the effects of distribution of patches, their initial biomass densities, and overall landscape productivity:

1) all forage patches are equal (they have the same initial forage biomass density);
2) patches are different, i.e. every patch has a unique initial forage biomass density;
3) travel time between patches is the same and can have any value including zero;

4) travel time between patches is not equal. Travel time between any consecutive patches can be arbitrary assigned and can have any value including zero.

SeekSMART's design allows for examination of patches of any size. However, to limit the number of factors potentially affecting foraging behavior, in all simulations described in this thesis the simulated Patch Size (PS) was 9 m^2. I assigned this value arbitrarily based on data reported from field research (Gedir and Hudson 1999, Hartley et al. 1997, Jiang and Hudson 1993, WallisDeVries et al. 1999).

A combination of the above parameters (summarized in Table 2.2) describes the landscape for the forager in a simulation run. The combination of travel time and biomass of patches determines the overall landscape productivity. Therefore, SeekSMART defines the patch based on the density of forage per unit of area and its size (that can be arbitrarily assigned) and is independent of the animal size or behaviour. A patch reflects the geographical characteristics of the landscape defined in the model.

The model also allows for setting the following global parameters:

1) Total simulation time, which is the period of time over which the total consumption and the landscape level intake rate are measured;

2) Number of patches that the forager feeds in. This can also be determined by a combination of the total simulation time, travel time and residence time.

2.2.2. Mechanism of the model

SeekSMART is a mechanistic and deterministic model (Figure 2.3) that describes foraging by a virtual animal in a simulated landscape (Figure 2.4). It assumes that at the start of a simulation run the animal is located at point A in a predefined landscape consisting of patches of specific biomasses and distributed according to the assigned travel times (TravelT) among the patches. From point A the animal has to travel to patch N for specified units of time (TravelT). Upon entering patch N, the forager has to decide whether to stay within this patch and start foraging or whether to skip the patch and start traveling to patch N +1. This decision, as well as the forager's next decision on how long to feed in a patch, are made by the animal based on the foraging strategy that the forager uses according to the parameters specified in the model (Tables 2.1 and 2.2) and described above as the four rules for when to leave a patch. While feeding within a patch, the forager's consumption rate is driven by the functional response curve described by the following Michaelis-Menten equation that is generally accepted as a formula explaining type II functional response curve (FRC) for foraging ungulates (Fryxell 2004, Hudson and Watkins 1986, Wickstrom et al. 1984):

$$\mathbf{IIR = M\,(\,F/\,(E+F)\,)}$$

Where:

IIR – instantaneous intake rate (g/hr);

M – asymptotic (or maximum) intake (g/hr);

F – density of available forage biomass (kg/ha);

E – the forage biomass density (kg/ha) at which the instantaneous intake rate equals half of the maximum intake rate (IIR = 0.5 x M);

Therefore, the *instantaneous intake rate* (IIR) is determined by the two parameters described earlier: the *maximum intake* (M) and *efficiency* (E). Based on the IIR, actual forage biomass density (AFBD), and patch residence time (Tr), consumption from the patch is calculated.

The forager continues to feed within the patch until either its gut is full (*gut fill* (GF) reaches the value specified by *full stomach* (FS)) or if the time to leave the patch, based on the foraging strategy (as per the four rules described earlier) has elapsed. After leaving patch N the forager travels to patch N +1 and the process described above starts again. A forager may use the same foraging strategy defined at the onset of the simulation run for the entire total time of the run or it can change its strategy, as defined by the settings, at any given time by adjusting the parameters of the model that define the forager and the landscape.

During a simulation run all variables in the model are being calculated and monitored by SeekSMART. This allows for a very close examination of the changes to the landscape such as depletion of particular forage patches, consumption from each patch, and the number of forage patches fed on until a given time. It also allows the examination, in detail, of the behavior of the forager. Variables such as total time spent on foraging and traveling, time spent feeding in each patch, time required to reach a patch, average residence time within a patch and average travel time between patches, gut fill, cumulative consumption, consumption rate, provide valuable outputs that can be used to describe the consequences of a specific foraging strategy. Among all variables tracked by the model of particular interest are: Cumulative Forage Eaten (CFE) that is the amount of forage consumed from the start of the simulation time. It allows for calculating the value of the Landscape Intake Rate (LIR). LIR is calculated by dividing the CFE by time according to the following equation:

LIR = CFE / TIME

Where:

LIR – Landscape Intake Rate (g/hr);

CFE - Cumulative Forage Eaten (g);

TIME – total time from the start of the simulation run (hr)

LIR provides an average rate at which forage is being consumed by the forager over the entire foraging path within the landscape and over a long period of time (relative to the instantaneous intake rate (IRR) calculated from one patch and over a short time interval). The importance of LIR stems from the fact that in any given landscape an animal foraging within a single patch may have relatively high instantaneous intake rate within that patch, but still be malnutrished. This may occur if the landscape consists of very few good quality patches dispersed over a vast area devoid of forage. If this is the case, the animal may still be malnourished even if its instantaneous forage intake rates (IRR) remain high. Therefore, only the Landscape Intake Rate (LIR) allows for detecting this nutritional stress on the animal in a low productivity landscape consisting of few rich patches. Figures 2.3 and 2.4 provide a simplified overview of the mechanism used in the model to calculate LIR.

One of the key components of SeekSMART is the mechanism that allows for scaling up the Instantaneous Intake Rate (IIR) to the Landscape Intake Rate (LIR) as shown in Figure 2.4. In this mechanism the *initial patch biomass* (IPB) in a patch is calculated based on the *initial patch biomass density* (IPBD) and *patch size* (PS). Both these components are the parameters in the simulator and their values can be arbitrarily assigned. The IPB is the initial value for the *actual patch biomass* (APB) that is tracked by the model according to the *consumption* (C) of forage from the patch. This *consumption* (C) depends on IIR that is driven by the *maximum intake* rate (M), *efficiency* (E) and the *actual patch biomass density* (APBD) in a patch (calculated based on PS and IPBD and C). This approach ensures that consumption rate reflects the IIR as measured within a patch in response to a specific forage biomass density expressed in kilograms per hectare (kg/ha), a component of the model based on field data (as opposed to *actual patch biomass* (APB)). For example, a 10 m^2 patch with the density of 2000 kg/ha has 2000 g of forage, but a 3 m^2 patch with the same forage density (2000 kg/ha) would have only 600 g of forage. However, the initial consumption rate due to IIR should be the same for both patches and the mechanism in SeekSMART reflects that relationship.

2.2.3. Model settings

The main purpose of this modeling experiment was to assess the behavior of different foragers (efficiency) following the MVT in landscapes of different productivity; examine the potential differences in the resulting foraging behaviors, and to identify if any specific relationships between these different foragers exist. To set the discussion in a specific context, I chose elk as an experimental subject. I decided to use this species because its ecology, including diet composition and foraging behavior, is well known and documented (Baker and Hobbs 1987; Clutton-Brock et al. 1982; Hartley et al. 1997; Hobbs et al. 1983, Hobbs et al. 2003, Jiang and Hudson 1993; Hudson and Watkins 1986; Hudson and White 1985; Hudson and Nietfeld 1985; Wickstom et al. 1984), thus allowing to populate SeekSMART with real field data and test the outputs of the model against actual field measurements.

SeekSMART comprises of a large number of parameters and variables. Of the key importance are two groups: one that defines the forager and the second one that describes the landscape.

Forager: Feeding behavior

Travel times between patches and the length of a foraging bout are the key factors that define a foraging strategy. In a recent study of elk foraging bouts, Didkowsky (2006) assumed that a foraging bout is terminated when the animal ceases cropping bites for a minimum of 3 minutes. Didkowsky 2006 also used the general approach described by Sibly et al. (1990) to determine a "breakpoint" value in steps/bite at which an individual was considered to have stopped feeding in a patch. Didkowsky (2006) observed that animals can be standing and chewing, without actually leaving the spatial extent of a patch, even though they have stopped cropping bites. She concurred with Jiang and Hudson (1993) that the interaction between movement and the cropping of bites is a better definition of when the animal actually decides to stop eating and move to a new patch. In other words, an animal must stop cropping bites and step away from its location in order to have left a foraging patch. In their study on the foraging behavior of reproductive female elk, Gedir and Hudson (1999) recorded animal behaviors at 10 minute intervals and categorized the behaviors into four classes (foraging, bedding, standing, other) if the behavior was demonstrated by the observed animal for at least 5 consecutive minutes. Gillingham et al. (1997) used similar methods for examining behavior of black-tailed deer (*Odocoileus hemionus*) and considered active bouts that lasted more than 5 min. Because my research is focused on foraging in a series of forage patches across multiple temporal and spatial scales, and SeekSMART defines the behavior of the forager (foraging and non-foraging are mutually exclusive events that do not overlap) and the characteristics of the landscape, then, based on the above data, to clearly define foraging within a patch and travel between patches, I assumed that travel between patches is defined as at least a 6 minute period of non foraging (the above mentioned calculation based on field research suggests that movement between two distinct patches should be defined as at least 5 minute activity). Therefore, to ensure that short interruptions in foraging within the patch are not included as travel time between patches, and to represent realistically foraging behavior by elk, I added one minute to the time interval used by Gedir and Hudson (1999) and assigned this value as the smallest time step in the model (0.1 h = 6 minutes). Consequently, all travels that are 6 or more minutes in duration are considered travel between patches and all movements shorter than 6 minutes are categorized as movements between feeding stations. The decision to use 6 minutes as a threshold value was also helpful in establishing SeekSMART as a simulator capable of examining multiple temporal and spatial scales.

Forager: Digestion mechanism

One of the unique features of SeekSMART is its ability to look at two groups of factors that determine, limit or constrain forage intake by herbivores. The first is the ecological framework that looks at landscape characteristics and the behavior of the animal in relation to this landscape and other animals present around. The second approach, called the physiological framework, describes the internal, intrinsic characteristics of the forager and how it influences forage intake. According to the physiological framework, gut fill and the process of rumination are the main drivers responsible for a specific foraging behavior and intake rates. Hudson and White (1985) provide an in-depth discussion on bioenergetics of wild herbivores including a conceptual framework for the computational blocks and the sequences that could be used to simulate the bioenergetics of a female elk. In their work, Hudson and White (1985) calculated that rumination times in elk range from 3 h in summer to 9 h in winter and that this difference is mostly due to different types of forage consumed depending on the season. Therefore, the parameter in the model called *digestion time* (DT) can have assigned any value from the above range. Hudson and White (1985) also estimated digestion rates to have values ranging from 0.06 per hour to the upper limit of 0.15 per hour. The lower value represents digestion rate for graminoid plants and the higher value is the digestion rate for browse, forbes, and foliage. In their model, Hudson and White (1985) used a value of 0.12 for the digestion rate to represent elk's diet composition. To be consistent with the values reported from the prior field research that reflect elk's diet composition, I decided to construct the model in a way that allows the use of any value from the range of 0.06 to 0.15 for DR and assign 0.12 as the default value for DR in SeekSMART.

Forager: Maximum intake (M)

Available data on the *maximum intake* (M) provide a range of values. Wickstrom et al. (1984) observed the asymptotic grass consumption rate to be 14.04 g per minute (842.4 g/h). Hudson and Nietfield (1985) provided the asymptotic value to be 17 g/minute (1020 g/h) and Hudson and Watkins (1986) reported the maximum intake at 11g/minute (660 g/h) in summer, but also obtained the asymptotic intake rate at 22g/minute (1320 g/h) during autumn. They pointed out that the intake rate varied depending on the season and the seasonal content of moisture in forage. Based on the research on elk foraging and consumption rates (Gedir and Hudson 1999, Gedir and Hudson 2000, Hartley et al. 1997, Hudson and Watkins 1986, Jiang and Hudson 1993, Spalinger and Hobbs 1992, Westra and Hudson 1981, Wickstrom et al. 1984), it is apparent that many factors (biomass of available forage, plant structure, diet composition, forage moisture content, bite size) are responsible for the observed intake rates. Because the purpose of SeekSMART is to examine different characteristics of foragers and their habitats, any value can be applied to the parameter describing the *maximum intake rate* (M). For a default value, based on the above discussion and field observations I calculated the mean asymptotic intake rate to be 960.6 g/h and used that as the default value for the maximum efficiency parameter in SeekSMART.

Forager: Efficiency (E)

I used a similar approach to estimate the *efficiency* (E) of the virtual forager. Wickstrom et al. (1984) calculated E to be 541.83 kg/ha for elk feeding on grass. Hudson and Watkins (1986) reported two values of 385 kg/ha and 533 kg/ha for summer and autumn respectively and associated this difference with seasonal variations in elk diet (higher proportion of grass in autumn diet). To calculate a default value of the *efficiency* (E) parameter I used the approach applied when calculating the *maximum intake rate* (M) and set the parameter E at a default value of 486.61 kg/ha (average of the values reported from field experiments) with an option to assign any value to parameter E in the model depending on the purpose of a specific simulation run.

To examine foraging strategies and their consequence in response to specific distributions of resources, I eliminated environmental noise and made important assumptions about the forager that applied to all simulations. First, the forager was free from the risk of predation. Second, there were no other animals in the foraging area, and there were no factors that distracted the forager from choosing the best strategy to maximize its forage intake or to satisfy its forage requirements from the entire foraging area consisting of a series of patches distributed across the landscape. Moreover, the nutritional state of the animal was neutral, which means that the forager was neither satiated nor malnourished but its gut was close to empty at the onset of a simulation run.

Landscape: Forage Biomass

Reported values of available forage biomass in elk habitat give a wide range of biomass with a low of 533 and a high of 4300 kg/ha. Hudson and Watkins (1986) provide forage biomass at values as high as 3200 and 4300 kg/ha depending on the season. In their review of intake and foraging energetics of elk and deer, Wickstrom et al. (1984) provide a range of understory biomass from 533 to 1783 kg/ha. The above differences are likely due to different study locations, associated climatic conditions and resulting habitat productivities (typically higher forage biomass in grassland habitats). SeekSMART's design allows for testing any value of forage biomass. To reflect those wide ranges of forage availability in elk's natural habitat, for the purpose of this discussion, I created three types of landscapes of different productivity as described below.

2.2.4. Scenarios

In most ecological studies, field observations provide a range of values and thus the variations in available forage, intake rates, maximum intake and forager's efficiency are not surprising. Computer simulation models are excellent tools to conduct sensitivity analyses, examine the dynamics of the system across a spectrum of values and explore the consequences of the variability observed in the field.

To assess the consequences of foraging by different foragers in landscapes of different productivity at a small scale, I examined four types of foragers feeding within an average patch in three main types of landscapes defined based on the average patch biomass (Landscape types A, B and C). Each landscape type was further divided based on the average travel times between patches. This created a total of 15 landscapes and resulted in 60 scenarios. I used the following settings for the specific scenarios (Tables 2.3, 2.4 and 2.5).

There are five parameters that define the forager in SeekSMART: *maximum intake* (M), *efficiency* (E), *digestion time* (DGT), *digestion rate* (DGR) and *full stomach* (FS). Because I was interested in testing how foragers of different efficiency (i.e., having different slopes on the functional response curve) perform in specific landscapes, I maintained four of the above parameters the same and only varied the *efficiency* (E). Table 2.6 provides the values used for all the above parameters for the four following types of foragers: extremely efficient forager (EE Forager), efficient forager (E Forager), medium efficiency forager (ME Forager) and low efficiency forager (LE Forager).

For ME Forager, I used the default value of 486.61 kg/ha as calculated above. To test a wide spectrum of foragers I next increased the value of *efficiency* (E) by 80% to 875.88 kg/ha and decreased it by 80% to 97.32 kg/ha to simulate LE and E Forgers respectively. To examine very efficient foragers reported in literature (Owen-Smith 2002) and a potential relationship between the *maximum intake rate* (M) and *efficiency* (E) (9.6 = 960.6/100), I also tested EE Forager (E = 9.6

kg/ha). Figure 2.5 illustrates the shapes of the functional response curves associated with the above four types of foragers.

To simulate three different types of landscapes, I arbitrarily set three different ranges of the *Initial Patch Biomass Density* (IPBD). Landscapes of type A were poor landscapes with low resources. The range of the initial forage densities across all patches was 1000 kg/ha ± 30% (850 - 1150 kg/ha). Landscapes of type B were medium productivity landscapes with the initial patch biomass density (IPBD) within the range of 2000 kg/ha ± 30% (1700 - 2300 kg/ha). Landscapes of type C were the most productive habitats and the IPBD was within the range of 3000 kg/ha ± 30% (2550 - 3450). To avoid bias, instead of arbitrarily assigning IPBD for each individual patch, I used STELLA Research (ieee systems 2008) to randomly generate these values within each of the three landscape types. Landscapes of type A had a mean IPBD of 1008.8 kg/ha (range: 852 - 1150, SD = 89.67), IPBD was 2035 (range: 1702 – 2299, SD = 192.62) and 3011.3 kg/ha (range 2564 – 3448, SD = 275.84) for Landscapes of type B and C respectively (Figure 2.6).

I focused on the short-term forage consumption by an animal feeding in a patch that was the average patch (IPBD, TravelT, and PS) for a given landscape. Because patch biomass assigned to Landscapes type C seemed most realistic, I started with Landscapes C and used five average travel times: 0.1h, 0.5h, 1h, 2h and 4 h. The above average TravelT values were assigned arbitrarily with a range of ±0.1 h. STELLA Research's random number generator was used to assign a specific TravelT for each patch within the above ranges. This resulted in five landscapes of type C: CT1, CT2, CT3, CT4 and CT5. Although the patches (and the average IPBD) were the same for all five landscapes, landscape CT1 was most productive (the average TravelT was 0.1 h) and the overall productivity of the landscape was lower for the consecutive landscape types and lowest for landscape CT5 where the average TravelT was 4 h. I used the same approach for landscapes of type B and A to vary their forage productivity while keeping the same average IPBD for all four landscape sub-types.

To obtain gain functions (forage consumed as a function of time) that could be next used in calculating the residence times (Tr) for the MVT foragers, I performed initial runs with foragers feeding in the average patch until forage biomass in the patch was completely depleted (dropped to 0 g). Initial runs generated curves that described gains from average patches (Figure 2.6) and allowed for assessing the residence times (Tr) of animals following the MVT. These were used next for further analysis and model validation.

Validation run

To validate the model and test the daily (24 h) behavior of the virtual elk in SeekSMART, I used the values listed in Tables 2.1 and 2.2, which are the default values for the key parameters in the model. Table 2.7 provides the individual characteristics of each patch for the first 20 patches in the feeding sequence (according to Jiang and Hudson 1993; and Gedir and Hudson 1999, an elk should forage in about 9 patches during the 24 h period). Patches were unequal (each patch had a unique IPBD) and travel time was also unique for each patch with an average of 0.1 h (6 minutes). In other words, the virtual elk in the validation run was a ME forager that foraged in landscape CT1. When foraging, the virtual elk applied the MVT (Jiang and Hudson 1993), which means that the animal stayed and fed in the patch until the giving-up-density (GUD) in the patch was equal to the GUD obtained at the end of the residence time (Tr) in the initial runs examining foraging within the average patch in landscape CT1.

2.3. Results

2.3.1. Scenarios

As predicted by the MVT travel time (TravelT) and patch biomass affected patch residence time (Tr) of some foragers. However, contrary to MVT predictions, travel time (TravelT) did not affect patch residence time (Tr) of all foragers (Tables 2.8, 2.9 and 2.10).

In landscapes of type C, the longest Tr was 4.2 h resulting from a combination of long average travel time (4 h), high average patch biomass (initial average patch biomass = 2710 g) and low efficiency of the forager (E = 875.88). The shortest Tr for Landscapes of type C was 1.3 h and was associated with the low efficiency of the forager (E=875.88) feeding in a landscape with shortest travel times (TravelT

= 0.1 h). The amount of forage consumed from the average patch in landscapes of type C varied from 992 to 2710 g. It was the extremely efficient (EE) forager (E=9.60) that was able to achieve the highest consumption from the average patch in four scenarios within the following four landscapes: CT2, CT3, CT4 and CT5. In these landscapes, the maximum amount of forage consumed by the extremely efficient forager was the same as the initial amount of forage in the patch (2710g) indicating that the animal was able to deplete the patch completely. The EE forager was not able to deplete the average patch only in one scenario with the shortest average travel time (Tt = 0.1 h, landscape CT1) when its total consumption at the end of the residence time (2.60 h) was 2570 g leaving 140 g of forage in the patch. In the same landscape, with the same shortest travel time (0.1 h), the LE forager left the patch at Tr = 1.30 h (note 50% shorter Tr than for the EE forager) consuming only 992 g (the lowest consumption in all types of Landscape C for all foragers). An interesting trend can be noted in outputs presented in Table 2.8. The EE forager had the longest residence time of all foragers feeding in a landscape with the shortest average travel time (Tr = 2.60, Tt = 0.1 h). However, in the landscape with the longest average travel time (Tt = 4 h) the same forager had the shortest residence time (Tr = 2.85 h) of all foragers. Increasing the average travel time by 4000% resulted in an increase of the residence time of the EE forager by 9.62% and by 323.08% for the LE forager.

Foraging in Landscapes of type B by all four foragers resulted in shorter Tr (range of 0.8 to 3. 2 h) which is the outcome of a lower quality of patches (lower average IPBD) as compared to landscapes C. It is interesting to note that, similarly to Landscapes C, both the longest and the shortest Tr were associated with the LE forger. The shortest residence time (0.8 h) that resulted from the LE forager feeding in landscape BT1 (Tt = 0.1 h) allowed the animal to consume 574 g from the average patch. The same forager attained consumption of 1598 g from the average patch when feeding in landscape BT5 (Tt = 4.0 h). The highest consumption was achieved by the EE forager that consumed 1832 g by staying for 1.9 h in the average patch of habitats BT2 (Tt= 0.5 h) and BT5 (Tt = 4.0 h). In both these scenarios the forager was able to completely deplete the average patches (average initial patch biomass for all scenarios in Landscapes B was 1832 g). The EE forager had similar gains in Landscapes BT3 and BT4 (1815 g) and only in Landscape BT1 its forage consumption was considerably lower (1662 g after leaving the patch at Tr = 1.65 h). It is interesting to note in Landscape B the same trend that was observed in Landscape C: the EE forager had the longest Tr (1.65 h) of all foragers in landscape with the shortest travel time (BT1, TravelT = 0.1 h) and the same forager had the shortest Tr (1.9 h) in the landscape with the longest travel time (Tt = 4 h at BT5). Increasing the average travel time by 4000% resulted in an increase of the residence time of the EE forager by 15.15% and by 400% for the LE forager.

As expected, residence times in Landscapes of type A were shortest and had smaller range than in more productive landscapes. The shortest Tr was 0.55 h and was associated with the ME forager feeding in a landscape with shortest travel times (average TravelT = 0.1 h). The LE forager had very similar Tr (0.6 h) in the same landscape (AT1). In landscape AT1 the ME forager and the LE forager consumed 389 and 329 g respectively from the average patch. Similarly to Landscapes of type C and B, the longest residence time (Tr = 2.45 h) was associated with the LE forager feeding in the landscape with longest travel times (AT5, Tt = 4.0 h). The highest consumption (908 g) was achieved by the EE forager feeding in three landscapes: AT3 (Tt = 0.5 h), AT4 (Tt = 2.0 h), AT5 (Tt = 4.0 h) for a residence time (Tr) of 0.95 (AT3) and 1.00 h (AT4 and AT5). This highest consumption was equal to the initial biomass of forage in the average patch. Because the smallest time unit in SeekSMART was 0.1 h, the patch residence time (0.95) for the EE forager in landscape AT3 should be rounded to 1:00 h. It can be then calculated that the EE forager required 1:00 h to completely deplete the patch in 3 scenarios with the longest, second longest the third longest average travel times (initial average patch biomass was 908 g in all scenarios in landscapes of type A). It was the LE forager that had the lowest consumption from the average patch at 329 g when feeding for 0.6 h in the average patch of landscape AT1 (Tt = 0.1 h).

In Landscapes A, I observed the same trend that was prevalent in Landscapes C and B: the EE forager had the longest residence time of all four types of foragers in a landscape with the shortest average travel time (0.85 h in AT1). It also had the shortest (1.00 h) residence time of all four foragers in a landscape with the longest average travel time (AT5, Tt = 4.00 h). Increasing the average travel time by 4000% resulted in an increase of the residence time of the EE forager by 17.6% and by 408.33% for the LE forager (Table 2.10).

2.3.2. Model validation

As pointed by Hudson and White (1985) models are not right or wrong, they are simply more or less useful in ordering current information, identifying patterns and guiding future research inquires. To assess the accuracy of my model I compared SeekSMART outputs with data obtained from field studies.

In their research on estimating dry matter digestibility and intake in elk using the double n-alkane ratio technique, Gedir and Hudson (2000) obtained the mean measured intake rate of 9.18 ± 1.56 kg of dry matter per day (range: 6.99 - 12.53 kg of dry matter per day). In another study on seasonal foraging behavioral compensation in reproductive elk hinds, Gedir and Hudson (1999), found that females grazed longest in late lactation (12.8 h per day), when they spent 94% of their active time foraging and that the animals forage fewer hours (8.2 h per day) and less intensively (66% of active time) during an early gestation. In a discussion on foraging time of elk, Gates and Hudson (1983) suggest that fatigue and demand for alternative activities place an upper limit on daily foraging time and that this is believed to be around 12 h. Other research supports this observation (Clutton-Brock et al. 1982, Heydon et al. 1992) and similar findings were reported for other ungulates (Gillingham et al. 1997 found that black tailed deer (*Odocoileus hemionus*) spent 92% of active time foraging). A review of published data suggests that typically the length of the foraging bout increases in summer with a decrease in their frequency (Jiang and Hudson 1993: 70 minutes per bout, 9.2 bouts per day; Gedir and Hudson 1999: 64 minutes per bout, 9.7 bouts per day).

Overall the above data suggest that an average female elk during its 24 h activity should forage for 8 to 12 h (depending on its reproductive condition). This total foraging time should be divided between 9.2 to 9.7 foraging bouts and result in cumulative consumption of dry matter in the range of 6.99 to 12.53 kg of forage (on average 9.18 kg).

From simulations in scenario CT1, the ME forager fed in the average patch for 1.5 h and consumed 1267 g of forage. In other words, a forager following MVT should leave the patch when 1443 g (or the density of 1,604 kg/ha) of forage remained in the patch.

In SeekSMART's validation run the lower limit of the consumption range (6.99 kg) was reached by the virtual elk using an MVT foraging strategy at 9.1 h of the simulation. The animal needed exactly 12 h to consume 9.18 kg of forage (Figure 2.9A). At Total time = 19.6 h the virtual animal consumed 12.53 kg reaching the upper limit of daily consumption according to Gedir and Hudson (2000). Assuming that the animal's gut is full at 9.18 kg, the forager reached this condition at 12.9 h and required a period of rest to be able to continue foraging. As illustrated in Figures 2.8 and 2.9, due to a digestion and rumination processes that occur when not grazing, cumulative consumption of the virtual elk was different from gut fill and reached the value of 9.18 kg at 12 h. In validating the model, I assumed that the forager can multitask (Fryxel et al. 2004) and digest the consumed food when traveling from one patch to another. Consequently I assigned a value of 0.12 for DR (Hudson and White 1985). With these settings, the feeding elk was constrained again by gut fill at 21.2 h and required another foraging pause. The total consumption at 24 h was 13.64 kg. This value is higher than the upper limit of the range calculated by Gedir and Hudson (12.53 kg), however, the value of the DT parameter (3.0 h) in the model was assigned arbitrarily as the lowest value of the range reported by Hudson and White (1985). Increasing this value would result in lower total daily consumption that would be in the range reported by Gedir and Hudson (2000). The same applies to the total foraging time that was 18.0 h in the simulation. Increasing DT (time required to ruminate after the animal is fully satiated to resume foraging) or DR would result in lower total foraging time and cumulative consumption. The virtual animal was not involved in activities other then foraging and resting (ruminating) when its gut was full. Introducing foraging pauses for other activities such as bedding if not hungry, would result in lower total daily consumption and lower total foraging time.

The forager in the validation run visited 11 patches (Figure 2.8), however, travel times to reach patches 1, 2, 5, 6, 7 were 0.0 h. Therefore, foraging in patches 1 and 2, as well as in 5, 6 and 7 could be interpreted as foraging within one patch because the forager did not interrupt its foraging bouts. The number of foraging bouts during the 24 h period for the virtual elk was 9.1 (as shown in Figure 2.8, the forager started its 10th foraging bout at time 23.9 h) in the validation run.

Therefore, in the validation run the forager performed within the range of values obtained in field research. When the default settings were used to describe the forager and the landscape, SeekSMART produced very realistic results that closely reflected actual field observations.

2.4. Discussion

My results indicate that for animals using the MVT as a foraging strategy, patch residence time depends on the distribution of patches of resources, their quality and foraging efficiency of the forager. The outputs also indicate that the efficiency of the forager in combination with travel times and quality of patches produces specific patterns of behavior (Figure 2.7).

An interesting finding is that some foragers are immune to changes in travel times. In other words, changing travel times do not affect the patch residence times of these foragers. One would assume that in hypothetical habitat 1 with sparsely distributed patches, foragers would stay longer within an average patch than in habitat 2 characterized by the same patches (the same forage biomass in any given patch) where the average travel time between patches is shorter. This is the common interpretation of the MVT. My findings show that while this is true for most foragers, it does not apply to very efficient foragers. My results indicate that with the increasing efficiency of foragers, their residence times are less affected by travel times between patches.

There are several factors that may affect foraging efficiency. It may be the type of forage (for example graminoids versus foliage) and seasonal changes in its structure and composition; it may be the age of the forager (e.g., mouth size, neck length, muscle weight, etc.). All these factors affect the efficiency and thus indirectly affect patch residence time. Therefore, an elk using the MVT foraging strategy and feeding on patches of grass in spring will most likely have ‘spring’ residence times different than ‘fall’ residence times in the same habitat (the same distribution and biomass of patches). The same principle would apply to other species feeding in their habitats.

If travel between patches is short, then very efficient foragers should stay in the patch longer then medium efficiency foragers, and the low efficiency foragers should stay in the patch for the shortest time. These results are in agreement with the common understanding of the consequences of the MVT: the intake rates of very efficient foragers at low biomass of forage are not much lower then their intake rates at a higher amount of forage. This allows the efficient foragers to exploit patches at a rate not much lower than the maximum intake rate even if patch biomass density is low. Therefore, it is a good idea for a very efficient forager (i.e., having a very steep functional response curve) to stay in a patch for a longer time than for a forager of a lower efficiency. On the contrary, the intake rate of a low efficiency forager, (i.e., those having a gentle slope of the functional response curve) is affected by the decreasing biomass in a patch soon after initiating the foraging bout within a patch. Therefore, it is more beneficial for this forager to move to a new patch if travel between patches is short.

This situation is reversed in a landscape where travel between patches requires more time. Although most foragers in this case should stay longer in an average patch than in a landscape with shorter travel times, this change is most pronounced for low efficiency foragers. When travel time becomes significant, low efficiency foragers should stay longer in a patch and continue to exploit the current patch, whereas a highly efficient forager should leave the patch earlier and use its high potential in exploiting resources at a new patch.

It is apparent that highly efficient foragers are more immune to changing travel times. For a very efficient forager, travel time had little effect on patch residence time. For example, the EE Forager ($E = 9.60$) in Landscape CT1 according to the MVT, should stay within the patch for 2.6 h and this increased to 2.85 h in Landscape CT5. This is a 9.6 % increase in Tr with a 40 fold increase in travel time. For the same increase in travel time the increase in residence time for a low efficiency (LE) forager was 323% (from 1.3 h to 4.2 h). It can be shown that for most extremely efficient foragers, applying the MVT , travel time should not affect patch residence time. In the simulations, extremely efficient foragers (E = 9.60) had almost the same patch residence times for each landscape type (Landscape C: 2.6 – 2.85, mean 2.77 h; Landscape B: 1.65-1.9, mean 1.84 h; Landscape A: 0.85 – 1.00, mean 0.94 h).

I argue that if a forager is extremely efficient in consuming resources, its patch residence time should not be affected by the distances between patches. Such a forager can be called a perfect forager. Residence time of the prefect forager is affected by the biomass in the patch and it is the only factor that affects the residence time of the perfect forager. Therefore, if a forager does not adjust its patch residence time across a spectrum of landscapes with different average travel times it does not necessarily mean that the forager is not using the MVT. It simply is a perfect forager. Its main characteristic is its ability to forage with the same rate at most densities of the resource. Therefore, a perfect forager is a forager that stays and feeds in the average patch until all the resources are fully consumed. A caterpillar feeding on a leaf of a plant until the leaf is completely consumed (Heinrich 1979, Karban 1987) is an example of a perfect forager. It feeds on the same leaf with a constant intake rate until the leaf is almost completely consumed or until all edible parts of the leaf are completely consumed. The caterpillar next travels to a new leaf (patch). It is a well known fact that caterpillars would sometimes stop foraging and stay on the same leaf to resume feeding later (Heindrich 1979, 1993). They do not need to move to a new leaf even if a large proportion of the current leaf has been consumed. One can observe a similar pattern in seed eating birds feeding on food provided in feeders. Many non-breeding birds usually perch next to a feeder and continue to feed from the same feeder until all seeds in a given feeder (patch) are fully consumed (*personal observation*). Animals that feed in environments with clumpy distribution of resources, and able to feed within the same patch without reducing their instantaneous intake rate, are examples of perfect foragers.

It is the ratio of the foraging *efficiency* (E) and the *maximum intake* (M) that defines the slope of the functional response curve and the efficiency of the forager. I call this ratio *foraging coefficient* (F) and express it as a quotient of E and M:

$$F = E / M$$

Although my results support the MVT in that with the same travel times, each forager should behave differently in the same patch, my findings show that this difference between the foragers' behaviors are affected by the quotients of the *efficiency* (E) and *maximum intake* (M). Then, a perfect forager is a forager whose foraging coefficient F is close to 0. In other words, if $F \to 0$

then a forager is a perfect forager and its residence time in a patch of resources is not affected by the distances between patches of resources distributed across the landscape.

Figure 2.10 illustrates the functional response curve (FRC), gain curves and patch residence times for a forager that has the characteristics of a perfect forager for all Landscapes of type C. Regardless of travel time, its patch residence time is always 2.80 h. Its *foraging coefficient* F is 0.00104. The foraging coefficient of the hypothetical caterpillar would be similar or smaller.

The forage consumed from an average patch (also called a gain function) as a function of patch residence time of a perfect forager (Figure 2.10B), resulting from a very steep functional response curve, is close to a linear function. Searle et al. (2005) evaluated the strength of evidence in the data for alternative gain functions of mule deer (*Odocoileus hemionus*) and blue duikers (*Cephalophus monticola*) foraging in patches composed of several plant species varying is sizes. They found greatest support for asymptotic and piece-wise linear models and no support for linear gain functions. Contrary to the findings of Searle et al. (2005), Illius et al. (2002) observed linear gain functions for roe deer (*Capreolus capreolus*) feeding in browse patches. Indeed, the idea that linear gain functions could be observed among browsers is further supported by Owen-Smith (2002) who described the functional response curve (FRC) of a browser as having a very steep slope similar to that associated with the perfect forager.

There are other field data obtained in research focused on ungulates that support the perfect forager theorem. Spalinger and Hobbs (1992) in their examination of the mechanisms responsible for forage intake rates of mammalian herbivores noted that intakes of mammalian browsers are often poorly related to food biomass. Based on their own research and studies conducted by Trudell and White (1981) and Risenhoover (1987) they produced a number of graphs illustrating intake rates of caribou (*Rangifer tarandus*), black-tailed deer (*Odocoileus hemionus*) and moose (*Alces alces*). These graphs suggest relatively constant intake rates across a wide range of plant biomass and a sharp drop in these rates when the plant biomass is near 0. This is a pattern exhibited by the perfect forager (Figure 2.10A).

There are examples of field data for carnivores that suggest perfect foragers among large predators. Hayes and Harestad (2000) studied kill rates by wolves (*Canis lupus*) on a rapidly growing moose population in the east-central Yukon. They reported that obtained kill rates were higher than those predicted at low moose densities and described the type II functional response of wolves by the following equation: $y = (2.97x)/(0.03 + x)$. Based on this equation the *foraging coefficient* (F) can be calculated as 0.03/2.97 that gives 0.0101. This indicates a perfect forager. Hayes and Harestad (2000) pointed out that their model suggested that the kill rate (consumption) must increase rapidly from some low moose density and this density would be so low that no data were available for estimating the shape of the functional curve at lower densities.

A careful analysis of the outputs of this research reveals another interesting relationship. Figures 2.11, 2.12 and 2.13, reveal a striking similarity between the initial average patch biomasses and the obtained mean patch residence times for the EE foragers (which are close to perfect foragers). In Landscapes C the initial average patch biomass was 2710 grams or 2.71 kg and the mean patch residence time (Tr) for the EE forager was 2.77 h. In Landscapes B and A these values were 1.83 kg – 1.84 h and 0.91 – 0.94 h respectively. This suggests that for a perfect forager, in the landscapes that I created, the quotient of initial biomass in a patch (B) and residence time (Tr) calculated according to the MVT should be close to or equal 1. This value could be different depending on the species, its habitat, forage type and associated units of measurement. However, it is the relationship between the average patch biomass (B) and the residence time (Tr) that is critical. Assuming that

$$B / Tr = \alpha$$

then, α is a constant value for a perfect forager. Analysis of the research findings presented in this chapter suggest that for a given landscape (average patch biomass B) there is only one average travel time (TravelT) such that for this specific travel time (TravelT) the residence time (Tr) for all types of foragers is the same (Figure 2.7C, Figure 2.14). Therefore, for this specific TravelT, the value of α will be the same for any forager. If for a given average travel time:

$B/Tr > \alpha$

then low efficiency foragers will stay in a patch for a shorter time than efficient foragers (Figure 2.7A-B), and if

$B/Tr < \alpha$

then the low efficiency forager will stay in a patch longer than efficient forager in the same patch (Figure 2.7D-E).

In the landscapes of type C, the travel time for which Tr of all foragers is the same is between 0.5 and 1.0 h and certainly very close to 1.0 h (Figure 2.7C). It can be said that the residence times of different foragers in any given habitat with patches of the same quality, but with variable distances between patches rotate around α that becomes a foragers' hub in a given habitat (Figure 2.14). My findings suggest that each habitat has its foragers' hub (α) and any forager feeding in this habitat can be described in relation to the hub (α). This is supported by field observations of Searle et al. (2005) who examined feeding behaviors of mule deer and blue duikers and observed a pattern that represents a small portion of the relationship described in Figure 2.14. Looking at more foragers with more diverse efficiencies and feeding in habitats described by Searle et al. (2005), but with a wider spectrum of travel times between patches would, according to the principle of the perfect forager and forager's hub, produce the remaining sections of the hub (α) illustrated in Figure 2.14.

The concept of forager's hub could be a useful ecological indicator. The position of a given forager (its α_1) in relation to the hub would indicate the efficiency of the individual forager. Plotting the values of α for the individual animals in a population would illustrate the variability in that population (efficient and less efficient foragers) which could indicate potential competition for resurces, unequal distribution of resources, and therefore, stability of the population (Lomnicki 1978).

2.5. Conclusions

My findings indicate that if a foraging animal does not seem to be following MVT strategies (patch residence time does not change with increasing travel time even though the quality of patches remains constant), it may still use an MVT foraging strategy based on its efficiency in utilizing resources in individual patches. Each perfect forager should stay for the same time in an average patch regardless of travel times. Therefore, patch residence times cannot be used as the only criteria to assess whether the animal is behaving according to the MVT. If a forager's patch residence time does not change with changing travel times, it does not necessarily mean that the animal is forced to abandon the MVT due to its interactions with other individuals of the same or other species (mating season, predation risk, etc.) as proposed by some authors (e.g., Nonacs 2001). I have shown that very efficient foragers and perfect foragers should not change their patch residence times even if the distribution of patches across the landscape changes dramatically.

In this Chapter I examined the behaviors of different foragers and the relationships between these foragers on a small spatial (patch) and temporal (couple of h) scale. A question remains open how these relationships among foragers is reflected on a longer temporal and bigger spatial scales. What are the consequences of the forager’s choices over a longer period of time (e.g. several days). These important questions certainly require more research in a simulation setting where environmental noise can be eliminated to fully understand the consequences of the MVT in relation to other foraging strategies.

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Tables

Parameter	Description	Unit	Default value	Reference
Maximum intake (M)	Maximum instantaneous intake rate of the forager	grams/hour (g/h)	960.60	Hudson and Nietfield 1985, Hudson and Watkins 1986, Wickstrom et al. 1984
Efficiency (E)	Foraging efficiency - forage biomass at which the instantaneous forage intake equals to half of the maximum intake rate.	kilograms/ hectare (kg/ha)	486.60	Hudson and Nietfield 1985, Hudson and Watkins 1986, Wickstrom et al. 1984
Digestion time (DT)	the time required by the forager to digest a specific proportion of the current stomach content that would allow the forager to resume foraging	Hours (h)	3.00	Hudson and White 1985
Digestion rate (DR)	the number of grams of consumed forage that the forager is able to digest within one hour	Proportion (/h)	0.12	Hudson and White 1985
Full stomach (FS)	the amount of forage consumed at which a forager's stomach is full	grams (g)	9180	Gedir and Hudson 2000

Table 2.1. User-defined parameters that define the intrinsic characteristics of the forager and their default values.

Parameter	**Description**	**Unit**	**Default value**	**Reference**
Patch Biomass (PB)	The initial biomass within a patch	grams (g)	2710 (the average initial biomass within a patch)	Hudson and Watkins 1986, Wickstrom et al. 1984
Initial Patch Biomass Density (IPBD)	The initial density of forage in a patch	Kilograms per hectare (kg/ha)	3011 (the average initial density of forage in a patch)	Hudson and Watkins 1986, Wickstrom et al. 1984
Patch Size (PS)	The size of a patch	square meters (m^2)	9	Hartley et al. 1997
Travel time (TravelT)	Distances between patches expressed as travel time	hours (h)	0.1 (average travel time between patches is 6 minutes)	Didkowsky 2006, Jinag and Hudson 1993, Gedir and Hudson 200, Sibly et al. 1990
Patches Equal (PE)	All forage patches are equal (they have the same initial forage biomass)	Binary (1 or 0)	0	NA
Patches are unique (PU)	Every patch has a unique, individually assigned initial forage biomass	Binary (1 or 0)	1	NA
Travel time equal (TravelTE)	Travel time between patches is the same and can have any value including zero	Binary (1 or 0)	0	NA
Travel time unequal (TravelTU)	Travel time between patches is not equal. Travel time between any consecutive patches can be arbitrary assigned and can have any value including zero.	Binary (1 or 0)	1	NA

Table 2.2. User-defined parameters that define the landscape and their default values.

Scenario	Landsacpe		Forager
	IPBD	TravelT	E
1C	3011.3 kg/ha (2564 – 3448)	0.1 h (0.0 – 0.2) – CT1	9.60
2C	3011.3 kg/ha (2564 – 3448)	0.1 h (0.0 – 0.2) – CT1	97.32
3C	3011.3 kg/ha (2564 – 3448)	0.1 h (0.0 – 0.2) – CT1	486.60
4C	3011.3 kg/ha (2564 – 3448)	0.1 h (0.0 – 0.2) – CT1	875.88
5C	3011.3 kg/ha (2564 – 3448)	0.5 h (0.4 – 0.6) – CT2	9.60
6C	3011.3 kg/ha (2564 – 3448)	0.5 h (0.4 – 0.6) – CT2	97.32
7C	3011.3 kg/ha (2564 – 3448)	0.5 h (0.4 – 0.6) – CT2	486.60
8C	3011.3 kg/ha (2564 – 3448)	0.5 h (0.4 – 0.6) – CT2	875.88
9C	3011.3 kg/ha (2564 – 3448)	1 h (0.9 – 1.1) – CT3	9.60
10C	3011.3 kg/ha (2564 – 3448)	1 h (0.9 – 1.1) – CT3	97.32
11C	3011.3 kg/ha (2564 – 3448)	1 h (0.9 – 1.1) – CT3	486.60
12C	3011.3 kg/ha (2564 – 3448)	1 h (0.9 – 1.1) – CT3	875.88
13C	3011.3 kg/ha (2564 – 3448)	2 h (3.9 – 4.1) – CT4	9.60
14C	3011.3 kg/ha (2564 – 3448)	2 h (3.9 – 4.1) – CT4	97.32
15C	3011.3 kg/ha (2564 – 3448)	2 h (3.9 – 4.1) – CT4	486.60
16C	3011.3 kg/ha (2564 – 3448)	2 h (3.9 – 4.1) – CT4	875.88
17C	3011.3 kg/ha (2564 – 3448)	4 h (3.9 – 4.1) – CT5	9.60
18C	3011.3 kg/ha (2564 – 3448)	4 h (3.9 – 4.1) – CT5	97.32
19C	3011.3 kg/ha (2564 – 3448)	4 h (3.9 – 4.1) – CT5	486.60
20C	3011.3 kg/ha (2564 – 3448)	4 h (3.9 – 4.1) – CT5	875.88

Table 2.3. Settings used in SeekSMART in landscape C.

Scenario	Landsacpe		Forager
	IPBD	TravelT	E
1B	2035 kg/ha (1702 – 2299)	0.1 h (0.0 – 0.2) – BT1	9.60
2B	2035 kg/ha (1702 – 2299)	0.1 h (0.0 – 0.2) – BT1	97.32
3B	2035 kg/ha (1702 – 2299)	0.1 h (0.0 – 0.2) – BT1	486.60
4B	2035 kg/ha (1702 – 2299)	0.1 h (0.0 – 0.2) – BT1	875.88
5B	2035 kg/ha (1702 – 2299)	0.5 h (0.4 – 0.6) – BT2	9.60
6B	2035 kg/ha (1702 – 2299)	0.5 h (0.4 – 0.6) – BT2	97.32
7B	2035 kg/ha (1702 – 2299)	0.5 h (0.4 – 0.6) – BT2	486.60
8B	2035 kg/ha (1702 – 2299)	0.5 h (0.4 – 0.6) – BT2	875.88
9B	2035 kg/ha (1702 – 2299)	1 h (0.9 – 1.1) – BT3	9.60
10B	2035 kg/ha (1702 – 2299)	1 h (0.9 – 1.1) – BT3	97.32
11B	2035 kg/ha (1702 – 2299)	1 h (0.9 – 1.1) – BT3	486.60
12B	2035 kg/ha (1702 – 2299)	1 h (0.9 – 1.1) – BT3	875.88
13B	2035 kg/ha (1702 – 2299)	2 h (1.9 – 2.1) – BT4	9.60
14B	2035 kg/ha (1702 – 2299)	2 h (1.9 – 2.1) – BT4	97.32
15B	2035 kg/ha (1702 – 2299)	2 h (1.9 – 2.1) – BT4	486.60
16B	2035 kg/ha (1702 – 2299)	2 h (1.9 – 2.1) – BT4	875.88
17B	2035 kg/ha (1702 – 2299)	4 h (3.9 – 4.1) – BT5	9.60
18B	2035 kg/ha (1702 – 2299)	4 h (3.9 – 4.1) – BT5	97.32
19B	2035 kg/ha (1702 – 2299)	4 h (3.9 – 4.1) – BT5	486.60
20B	2035 kg/ha (1702 – 2299)	4 h (3.9 – 4.1) – BT5	875.88

Table 2.4. Settings used in SeekSMART in landscape B.

Scenario	Landsacpe		Forager
	IPBD	TravelT	E
1A	1008.8 kg/ha (852-1150)	0.1 h (0.0 – 0.2) – AT1	9.60
2A	1008.8 kg/ha (852-1150)	0.1 h (0.0 – 0.2) – AT1	97.32
3A	1008.8 kg/ha (852-1150)	0.1 h (0.0 – 0.2) – AT1	486.60
4A	1008.8 kg/ha (852-1150)	0.1 h (0.0 – 0.2) – AT1	875.88
5A	1008.8 kg/ha (852-1150)	0.5 h (0.4 – 0.6) – AT2	9.60
6A	1008.8 kg/ha (852-1150)	0.5 h (0.4 – 0.6) – AT2	97.32
7A	1008.8 kg/ha (852-1150)	0.5 h (0.4 – 0.6) – AT2	486.60
8A	1008.8 kg/ha (852-1150)	0.5 h (0.4 – 0.6) – AT2	875.88
9A	1008.8 kg/ha (852-1150)	1 h (0.9 – 1.1) – AT3	9.60
10A	1008.8 kg/ha (852-1150)	1 h (0.9 – 1.1) – AT3	97.32
11A	1008.8 kg/ha (852-1150)	1 h (0.9 – 1.1) – AT3	486.60
12A	1008.8 kg/ha (852-1150)	1 h (0.9 – 1.1) – AT3	875.88
13A	1008.8 kg/ha (852-1150)	2 h (1.9 – 2.1) – AT4	9.60
14A	1008.8 kg/ha (852-1150)	2 h (1.9 – 2.1) – AT4	97.32
15A	1008.8 kg/ha (852-1150)	2 h (1.9 – 2.1) – AT4	486.60
16A	1008.8 kg/ha (852-1150)	2 h (1.9 – 2.1) – AT4	875.88
17A	1008.8 kg/ha (852-1150)	4 h (3.9 – 4.1) – AT5	9.60
18A	1008.8 kg/ha (852-1150)	4 h (3.9 – 4.1) – AT5	97.32
19A	1008.8 kg/ha (852-1150)	4 h (3.9 – 4.1) – AT5	486.60
20A	1008.8 kg/ha (852-1150)	4 h (3.9 – 4.1) – AT5	875.88

Table 2.5. Settings used in SeekSMART in landscape A.

Forager	E	M	DT	DR	FS
EE	9.60	960.60	3	0.12	9.18
E	97.32	960.60	3	0.12	9.18
ME	486.60	960.60	3	0.12	9.18
LE	875.88	960.60	3	0.12	9.18

Table 2.6. Parameters that define the four foragers.

Patch N	Travel time to Patch N (h)	Initial Biomass Density in Patch N (kg/ha)	Initial Actual Biomass in Patch N (g)
1	0.0	2,571	2313.9
2	0.0	3,102	2791.8
3	0.2	3,284	2955.6
4	0.1	3,405	3064.5
5	0.1	2,822	2539.8
6	0.0	3,340	3006.0
7	0.0	2,670	2403.0
8	0.1	3,085	2776.5
9	0.1	3,350	3015.0
10	0.2	2,621	2358.9
11	0.1	3,006	2705.4
12	0.1	2,774	2496.6
13	0.2	3,356	3020.4
14	0.0	3,195	2875.5
15	0.0	2,896	2606.4
16	0.1	2,641	2376.9
17	0.1	2,953	2657.7
18	0.0	2,635	2371.5
19	0.1	2,772	2494.8
20	0.0	3,024	2721.6

Table 2.7. Characteristics of the first 20 individual patches of forage in Landscape CT1.

Scenario	Landscape	Forager (E)	Residence time according to MVT (h)	Forage Consumed (g)
1C	CT1	9.60	2.60	2570
2C	CT1	97.32	1.70	1649
3C	CT1	486.60	1.50	1267
4C	CT1	875.88	1.30	992
5C	CT2	9.60	2.80	2710
6C	CT2	97.32	2.60	2411
7C	CT2	486.60	2.45	1922
8C	CT2	875.88	2.40	1665
9C	CT3	9.60	2.80	2710
10C	CT3	97.32	2.90	2616
11C	CT3	486.60	2.85	2158
12C	CT3	875.88	2.90	1926
13C	CT4	9.60	2.80	2710
14C	CT4	97.32	3.00	2666
15C	CT4	486.60	3.30	2379
16C	CT4	875.88	3.55	2209
17C	CT5	9.60	2.85	2710
18C	CT5	97.32	3.10	2698
19C	CT5	486.60	3.65	2509
20C	CT5	875.88	4.20	2420

Table 2.8. Patch residence times (Tr) and associated forage consumed obtained by applying the MVT to five types of foragers in landscapes of type C.

Scenario	Landscape	Forager (E)	Residence time according to MVT	Forage Consumed (g)
1B	BT1	9.60	1.65	1662
2B	BT1	97.32	1.4	1332
3B	BT1	486.60	1.1	876
4B	BT1	875.88	0.8	574
5B	BT2	9.60	1.9	1832
6B	BT2	97.32	1.9	1708
7B	BT2	486.60	1.7	1246
8B	BT2	875.88	1.7	1062
9B	BT3	9.60	1.875	1815
10B	BT3	97.32	2	1764
11B	BT3	486.60	2.1	1451
12B	BT3	875.88	2.2	1284
13B	BT4	9.60	1.875	1815
14B	BT4	97.32	2.1	1806
15B	BT4	486.60	2.6	1644
16B	BT4	875.88	2.75	1478
17B	BT5	9.60	1.9	1832
18B	BT5	97.32	2.2	1828
19B	BT5	486.60	2.8	1698
20B	BT5	875.88	3.2	1598

Table 2.9. Patch residence times (Tr) and associated forage consumed obtained by applying the MVT to five types of foragers in landscapes of type B.

Scenario	Landscape	Forager (E)	Residence time according to MVT	Forage Consumed (g)
1A	AT1	9.60	0.85	877
2A	AT1	97.32	0.70	663
3A	AT1	486.60	0.55	389
4A	AT1	875.88	0.60	329
5A	AT2	9.60	0.90	846
6A	AT2	97.32	1.05	870
7A	AT2	486.60	1.15	660
8A	AT2	875.88	1.20	547
9A	AT3	9.60	0.95	908
10A	AT3	97.32	1.10	889
11A	AT3	486.60	1.50	768
12A	AT3	875.88	1.60	657
13A	AT4	9.60	1.00	908
14A	AT4	97.32	1.20	906
15A	AT4	486.60	1.65	801
16A	AT4	875.88	2.15	765
17A	AT5	9.60	1.00	908
18A	AT5	97.32	1.20	906
19A	AT5	486.60	1.85	836
20A	AT5	875.88	2.45	805

Table 2.10. Patch residence times (Tr) and associated forage consumed obtained by applying the MVT to five types of foragers in landscapes of type A.

Figures

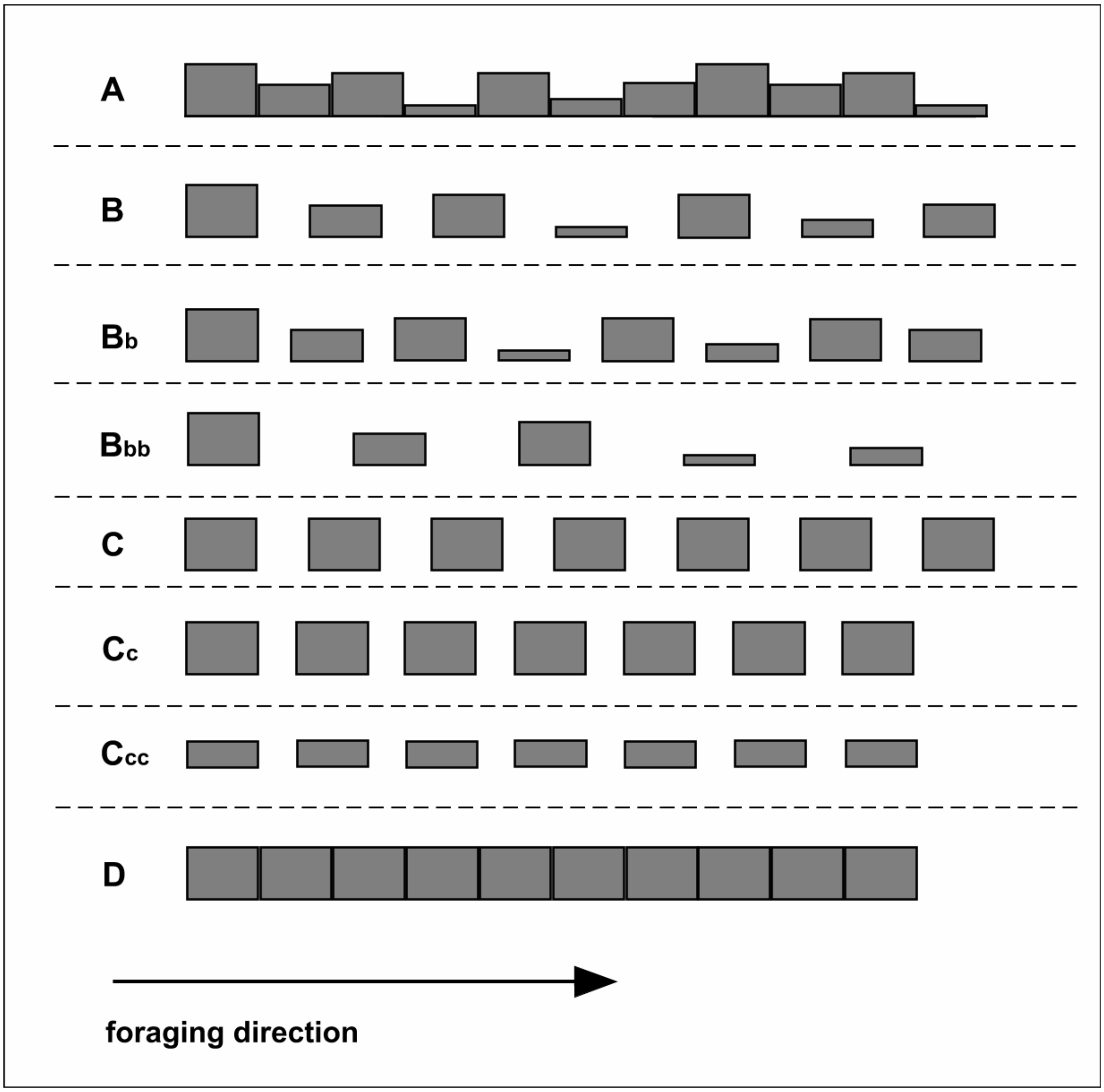

Figure 2.1. The model describes a forager feeding in a series of forage patches. Patch biomass (quality) and distribution of patches (travel time) determine the overall productivity of the landscape. For example, in scenario **A** patches are unequal and travel time between patches is 0. In scenario **B** patches are unequal and travel time between patches is greater than zero and differs among patches. In scenario **C** all patches are the same in terms of their forage biomass; travel time between patches is greater than zero but the same for any two patches. In scenario **D** patches are the same and travel time between patches is zero, which is typically described as a homogeneous landscape.

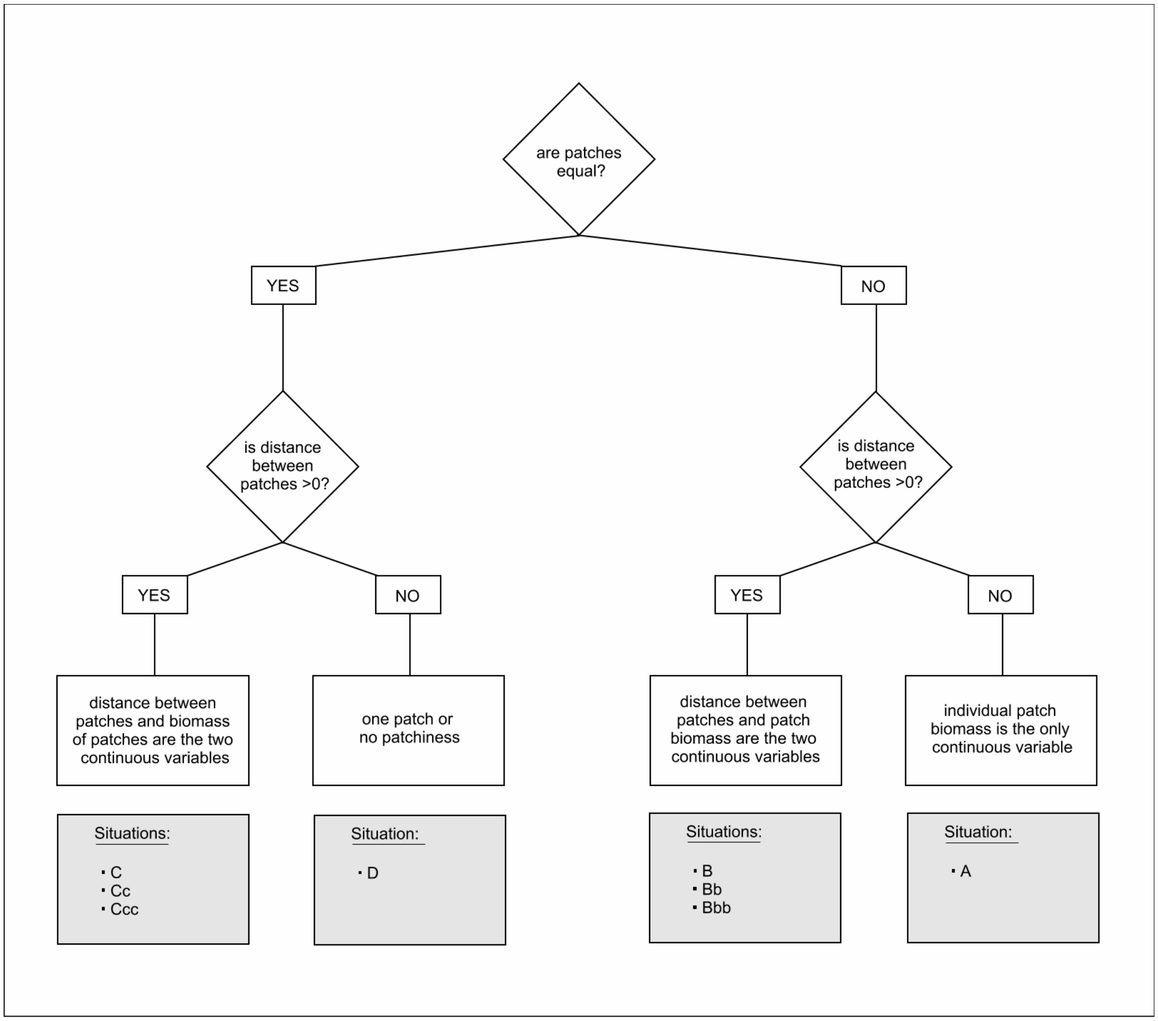

Figure 2.2. An overview of landscape patchiness helpful in assessing different scenarios with regard to patch distribution in a landscape.

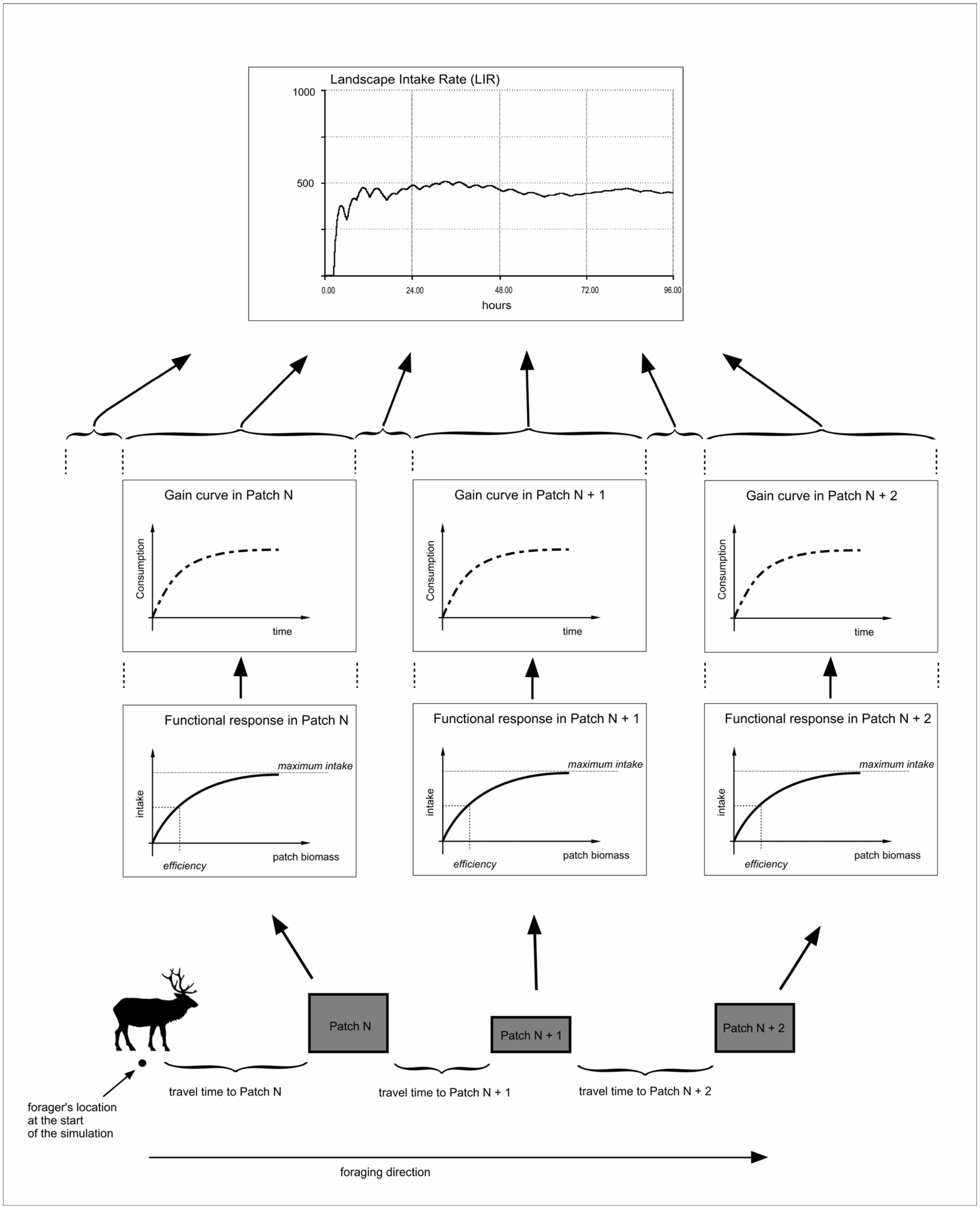

Figure 2.3. A simplified overview of the approach used to calculate the Landscape Intake Rate (LIR) in SeekSMART.

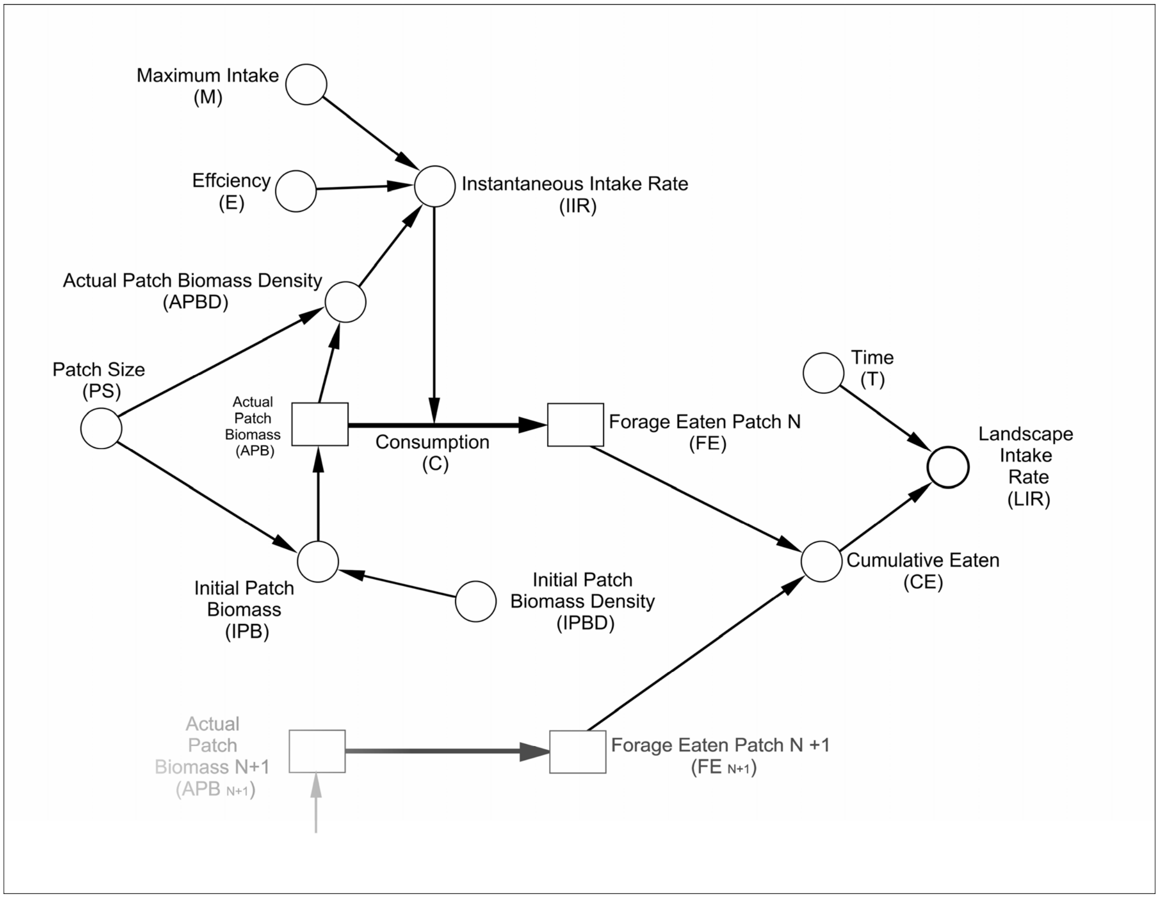

Figure 2.4. A simplified overview of the mechanisms for calculating the Landscape Intake Rate (LIR).

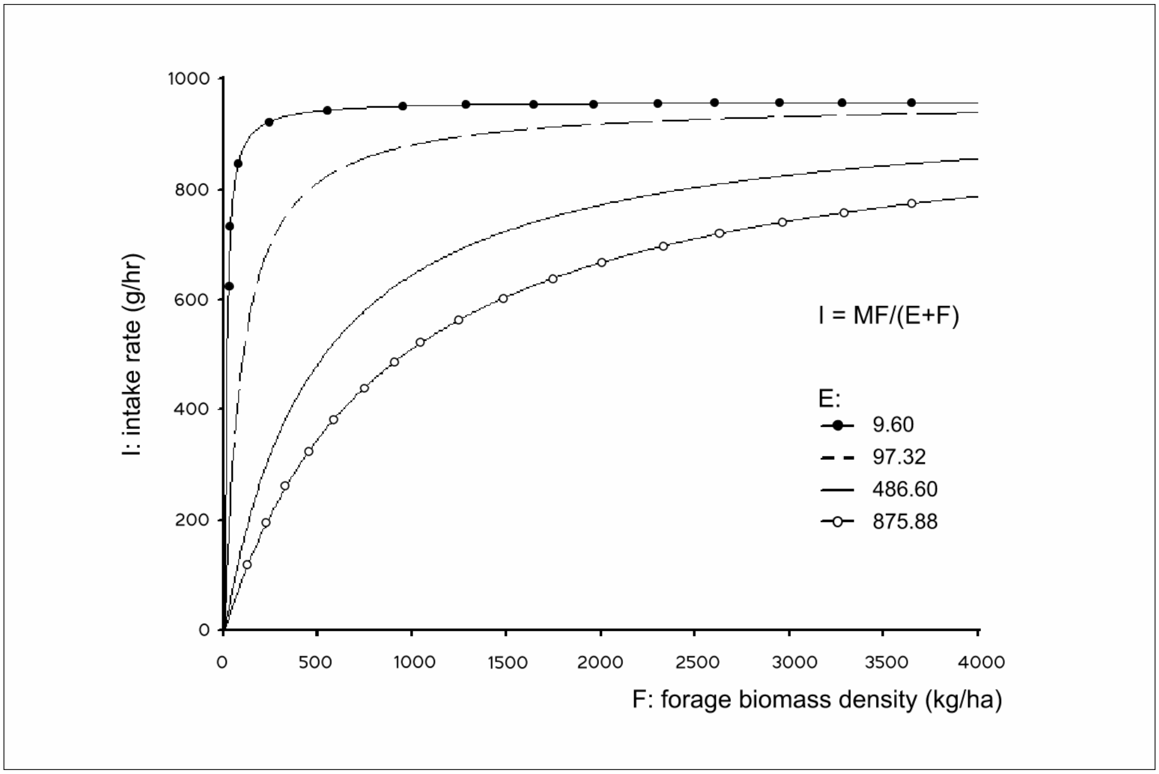

Figure 2.5. Functional response curves of the four forager types (EE: E = 9.60, VE: E = 97.32, ME: E = 486.60, LE: E = 875.88) tested in the model. If the value of the maximum intake rate (M) is constant, then the forager's efficiency defines the slope of its functional response curve.

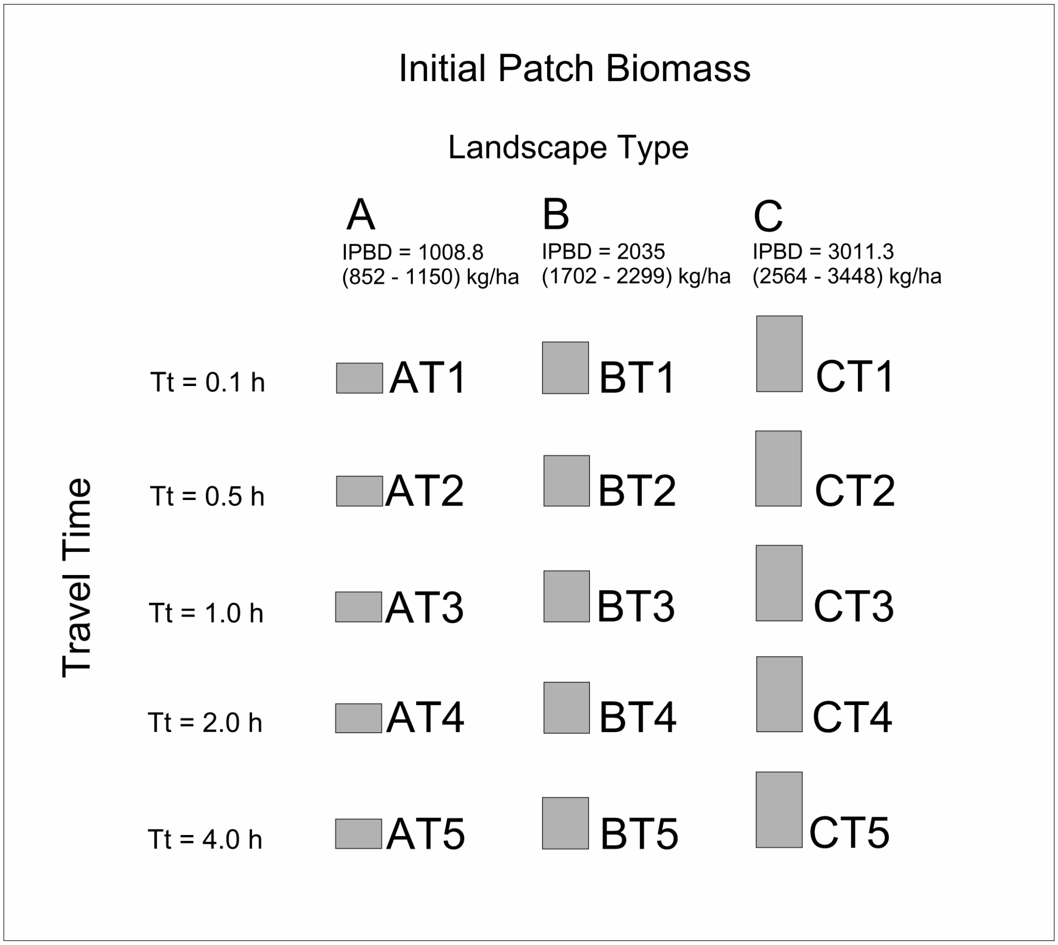

Figure 2.6. Illustration of three different types of landscapes defined by patch quality (initial patch biomass density) and further divided into specific landscapes depending on the average travel time between patches.

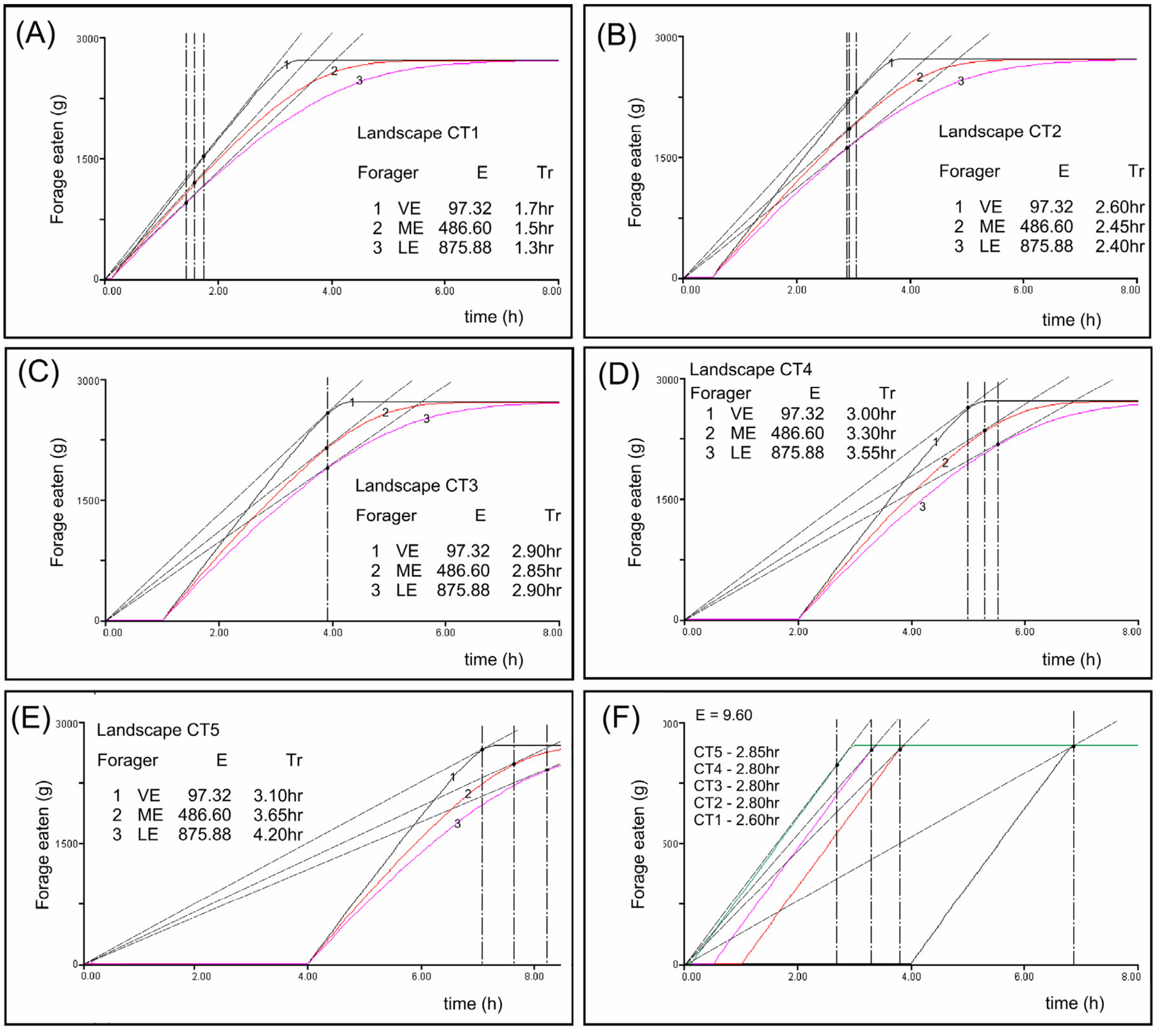

Figure 2.7. Gain curves generated for EE (E = 9.60), VE (E = 97.32), ME (E = 486.6) and LE (E = 875.88) foragers in landscapes of type C. For each habitat (average patch biomass) there is only on average travel time (TravelT) where patch residence time (Tr) for all types of foragers is the same (C). A – E: residence times (Tr) obtained for 3 types of foragers (VE, ME and LE); F: residence times for the EF Forager vary little across very different average travel times (TravelT). Vertical dashed lines indicate Tr for foragers using foraging strategies based on the MVT.

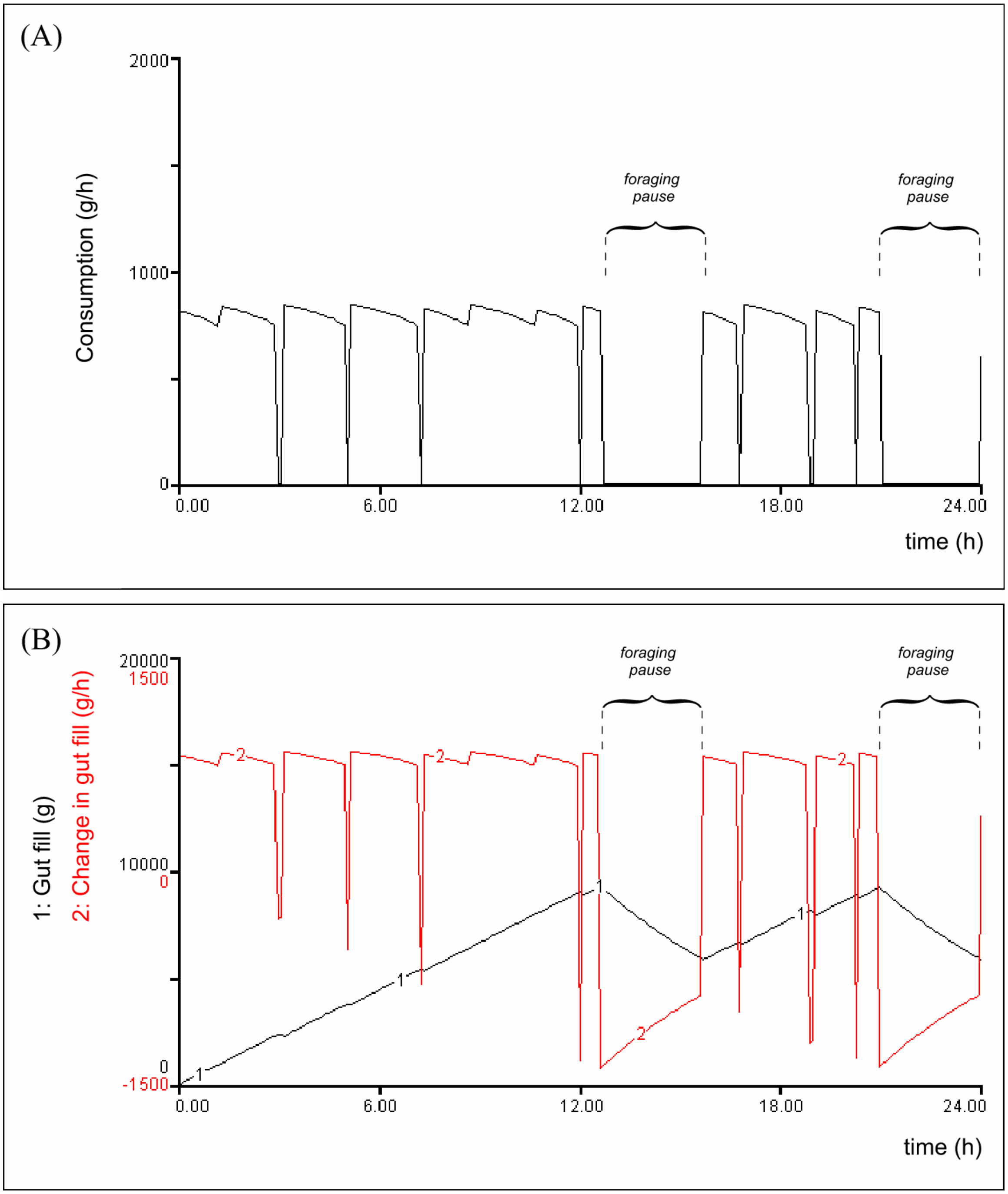

Figure 2.8. In the validation run the MVT forager visited 11 patches, however, travel times to reach patches 1, 2, 5, 6, 7 were 0.0 h. Therefore foraging in patches 1 and 2, as well as in 5, 6 and 7 could be interpreted as foraging within one patch. Foraging pauses were caused by gut fill reaching 9.18kg, which due to rumination and digestion when not foraging, was reached later than cumulative consumption of the same value.

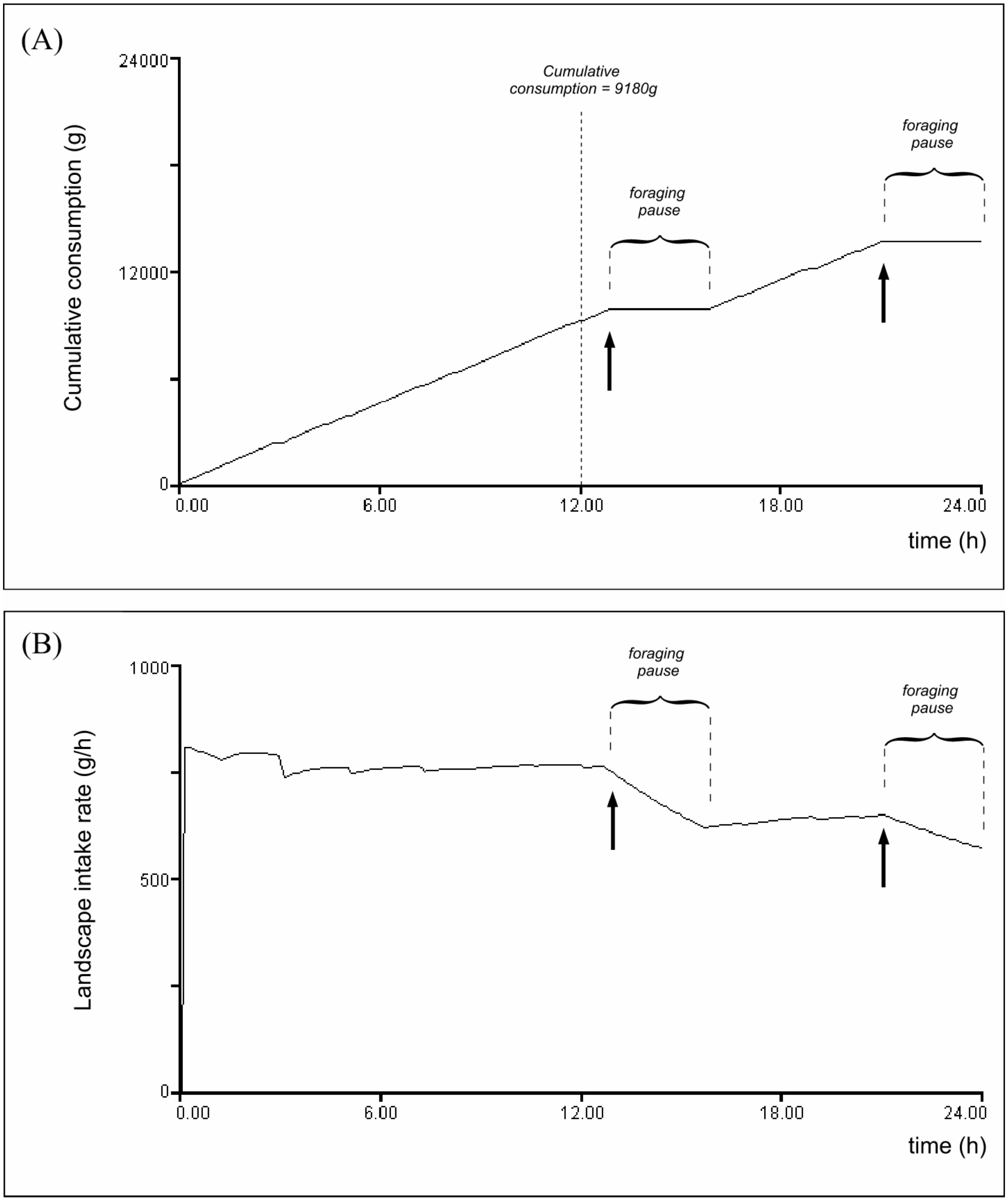

Figure 2.9. The lower limit of the required consumption (6.99kg) was reached by the virtual elk at 9.1h of the simulation. The animal needed exactly 12 h to consume 9.18 kg of forage. Arrows indicate points where the gut fill reached 9.18 kg and foraging pauses started.

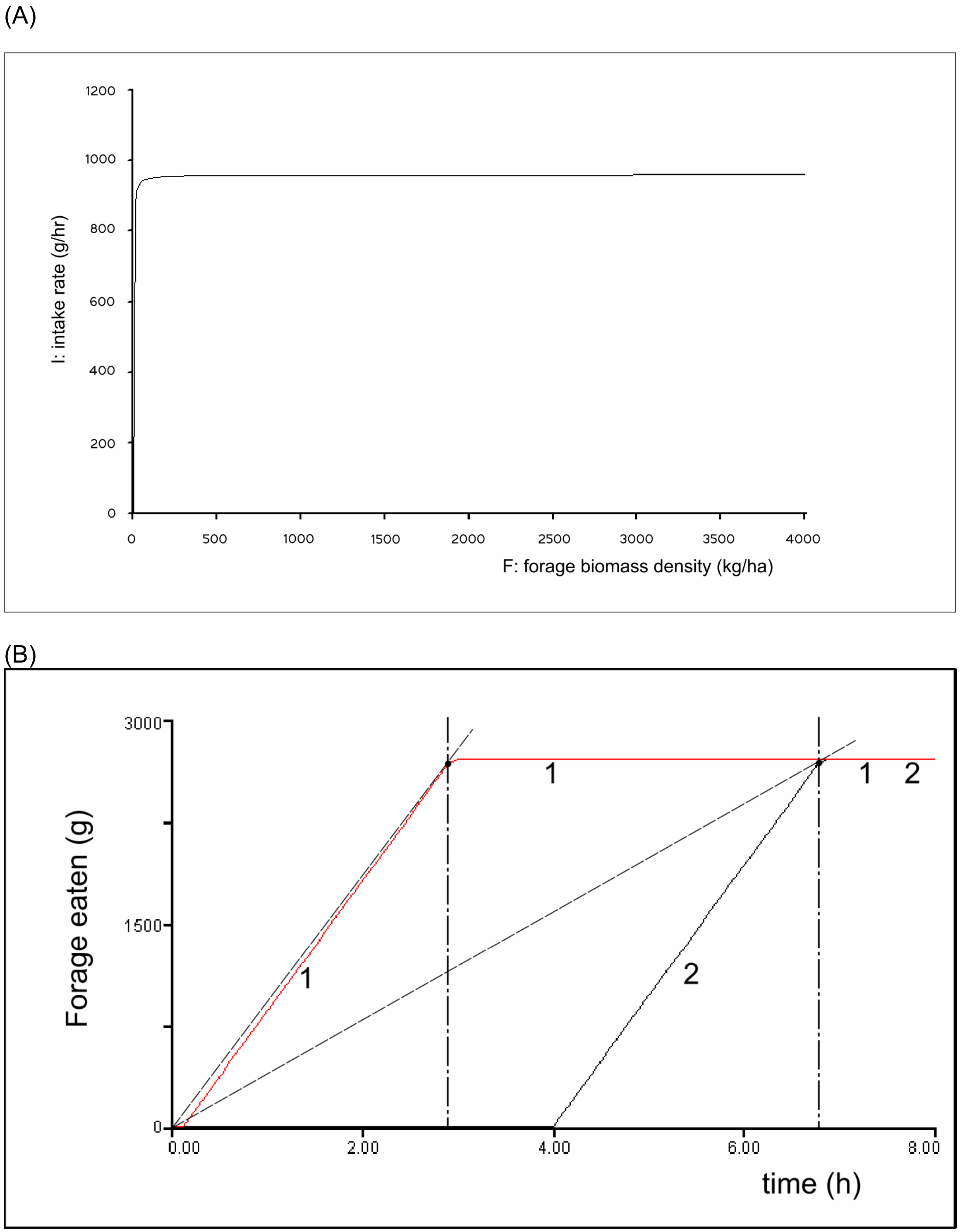

Figure 2.10. (A): Illustration of the functional response curve (FRC) of the perfect forager in landscape C; and (B): its gain curves and associated patch residence times (Tr = 2.80hr) in landscapes CT1 (1) and CT5 (2) indicated with dashed lines.

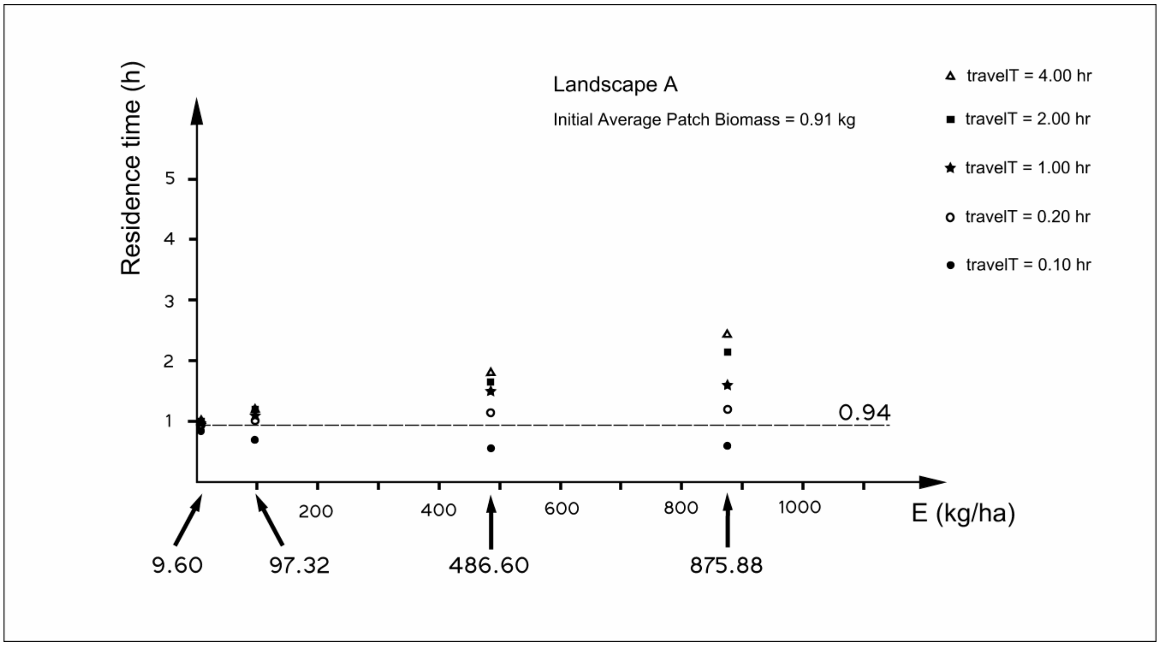

Figure 2.11. Patch residence times (Tr) obtained by applying the MVT to four types of foragers: extremely efficient (E=9.60), very efficient (E=97.32), medium efficiency (E=486.60) and low efficiency (E=875.88) with four average travel times between patches (0.10, 0.50, 1.00, 2.00 and 4.00 h) in Landscape A. Dashed line indicates the mean patch residence time for the extremely efficient (EE) forager.

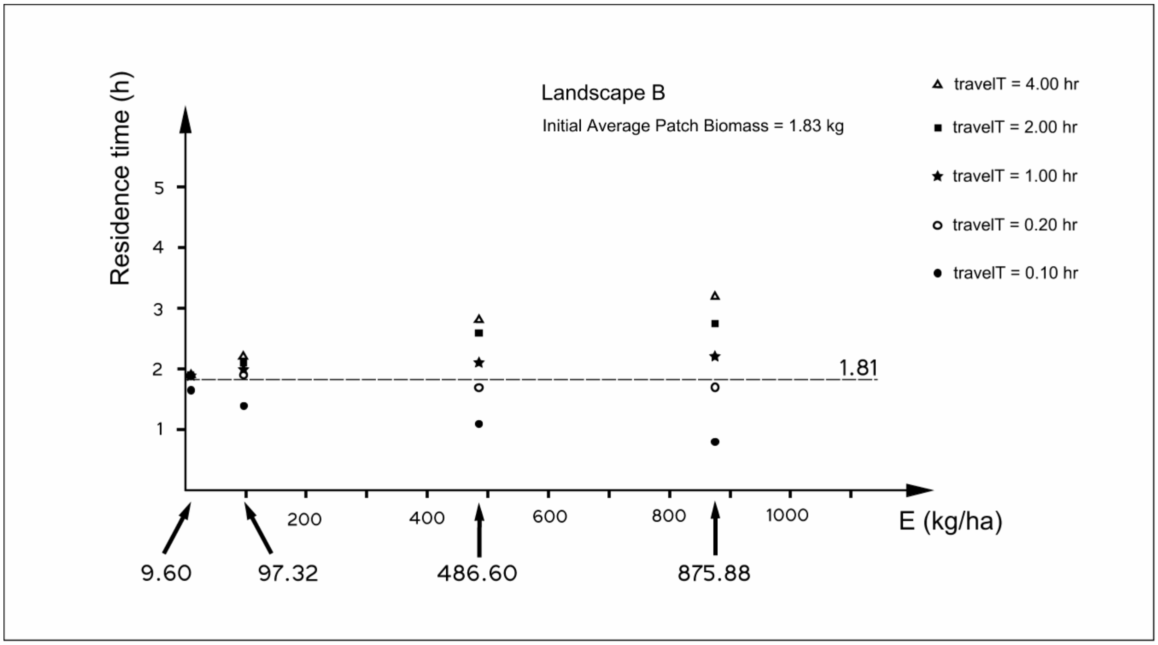

Figure 2.12. Patch residence times (Tr) obtained by applying the MVT to four types of foragers: extremely efficient (E=9.60), very efficient (E=97.32), medium efficiency (E=486.60) and low efficiency (E=875.88) with four average travel times between patches (0.10, 0.50, 1.00, 2.00 and 4.00 h) in Landscape B. Dashed line indicates the mean patch residence time for the extremely efficient (EE) forager.

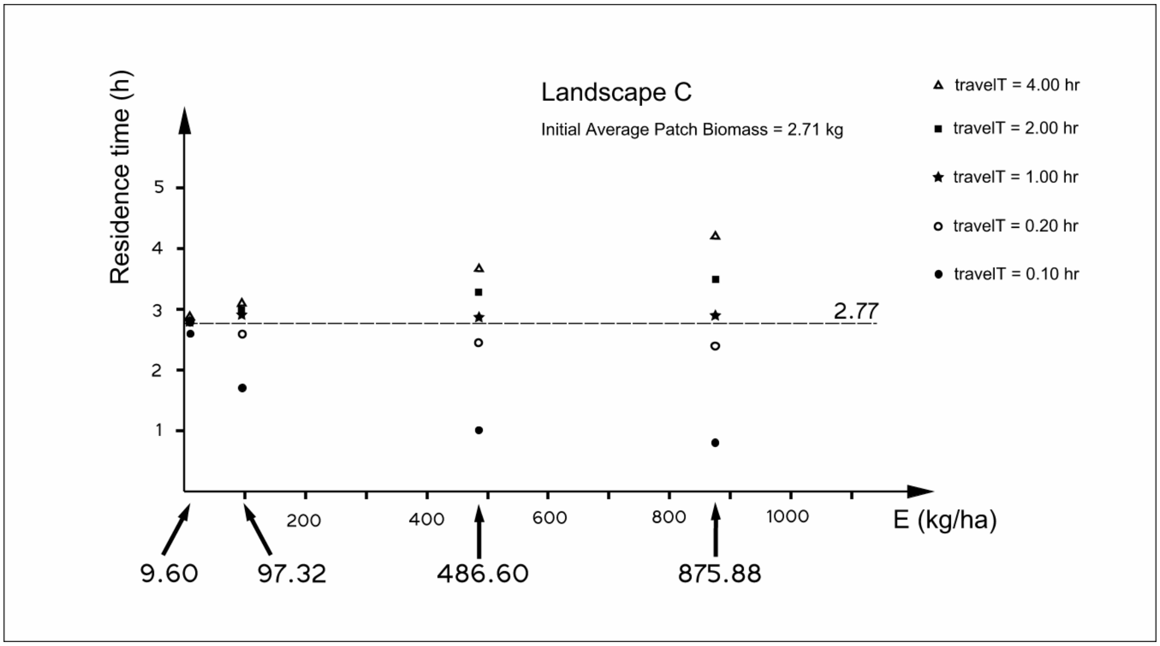

Figure 2.13. Patch residence times (Tr) obtained by applying the MVT to four types of foragers: extremely efficient (E=9.60), very efficient (E=97.32), medium efficiency (E=486.60) and low efficiency (E=875.88) with four average travel times between patches (0.10, 0.50, 1.00, 2.00 and 4.00 h) in Landscape C. Dashed line indicates the mean patch residence time for the extremely efficient (EE) forager.

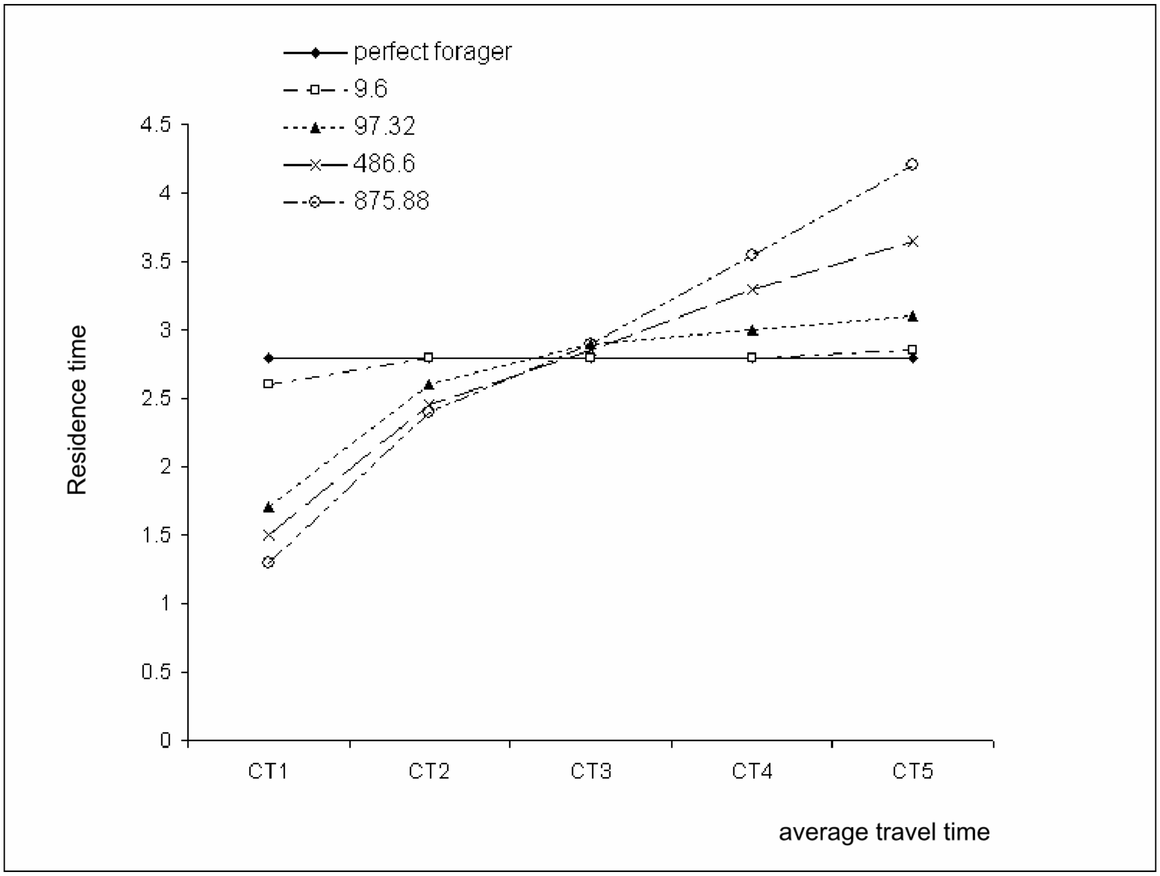

Figure 2.14. Illustration of α - the foragers' hub. The residence times of different foragers in any given habitat with patches of the same average quality, but with increasing average distances between patches rotate around α that becomes a foragers' hub in a given habitat.

Chapter 3: Why large herbivores are not slaves to the Marginal Value Theorem – importance of foraging strategies alternative to the MVT.

3.1. Introduction

To utilize forage resources, each individual needs to respond to environmental factors that affect the availability and accessibility of forage in a given landscape. Individual animals have specific abilities to exploit available resources and may use different foraging strategies to satisfy their basic food requirements needed for survival, and these are known for most of the common herbivores (Burness et al. 2001, Nagy 2001). The Marginal Value Theorem (MVT) proposed by Charnov (1976) describes foraging behaviour in a patchy landscape and links an expected transit time among patches and an observed intake rate within each patch to formulate an optimal foraging strategy. Numerous research support the MVT (Best and Bierzychudek 1982, Bonser et al. 1998, Jiang and Hudson 1993, Laca et al. 1993, Pyke 1978, Wajnberg et al. 2000) and it is widely accepted that the MVT explains foraging behaviors observed in nature and describes the optimal foraging strategy. Therefore, the MVT is generally believed to be the foundation of the classical foraging theory. However, other authors (Carmel and Ben-Haim 2005, Moen et al. 1998, Nonacs 2001, Searle et al. 2005, Wajnberg et al. 2006) argue that foraging strategies other than the MVT could be used by animals.

In a simulation modeling study, Moen et al. (1998) showed that moose (*Alces alces*) using the MVT stopping rule created a landscape that resulted in extinction of the moose population in less than 40 years. In another study, Alonso et al. (1995) illustrated that foragers only use MVT strategies under specific circumstances and attributed the deviations from the MVT to the imperfect knowledge that animals have about their environment and social behavior. Recently, Nonacs (2001) argued that the reason for refuting the MVT by several studies (e.g., Hansen 1987, Hansen and Green 1989, Howell and Hartl 1980, Kamil et al. 1993, Moen et al. 1998, Schulter 1982) is that the MVT lacks biological realism. Whereas Alonso et al. (1995) concentrated on how habitat productivity and social behavior affects the applicability of the MVT, Nonacs (2001) argued that animals are simultaneously doing more than just searching for food. For example, most individuals need to be vigilant to avoid predation. Similarly to Nonacs (2001), Fortin et al. (2004) concluded that mammalian herbivores can carry out multiple tasks without interrupting food processing, but this possibility is not considered in existing foraging models. One could argue that other factors (i.e., mating opportunities, climatic conditions, other inter-specific interactions (e.g., insect harassment on herbivores) could potentially also affect foraging strategies and result in further deviations from the predictions of the classic MVT.

The above arguments point to environmental noise as factors that result in deviations from the predictions of the MVT and that this noise needs to be accounted for if one is to precisely describe foraging strategies. This reasoning focuses on the fact that the classic MVT lacks biological realism (an animal that aims at maximizing its fitness should actually do more than just look for food in an optimal way). In other words, in an ideal world, a healthy animal secure from predation, not exposed to competition for forage resources, free from any other forms of harassment, and foraging outside the breeding season, should always follow the MVT while foraging. The large number of above mentioned papers that provide observations contradicting the MVT (including simulation studies), suggest that arguments provided by authors who believe that the MVT appropriately describes foraging behavior in an ideal world (e.g., Nonacs 2001, Alonso et al. 1995), although important, may not account for all factors responsible for the observed deviations from the MVT.

I examined this subject in detail to assess if a forager in a perfect world should deviate from the MVT, or if there are any specific incentives for foragers to deviate from the MVT even if environmental noise is not present. To examine how a forager feeding in a perfect world (i.e. not exposed to factors that would distract it from using a foraging strategy that produces the highest ratio of benefits to costs and ensures the highest cumulative consumption) foraging in a landscape consisting of a number of patches distributed over a specific area (distances between patches greater than zero) should behave depending on its foraging strategy (MVT versus alternatives) and what the consequences (in terms of cumulative gains and the benefit-cost ratio over a period of time) of these strategies are, I employed a computer simulation model. This allowed me to address the following questions: 1) what are the consequences of using a strategy that is different than predicted by the MVT (leaving patches earlier or later)?; and 2) is it possible for foragers using a foraging strategy different than the MVT to perform better than the MVT foragers?

Based on a series of simulation experiments that use elk (*Cervus elaphus*) as a focal species, I show that depending on time limitations, foraging strategies other than the MVT approach may provide advantage to foragers not using the MVT. I also argue that the widely assumed advantage of MVT over other foraging strategies applies only under specific circumstances and depends on the time scale. In this process I describe the relationship between the total time, foraging time and search time that is responsible for strategies other than the MVT being more profitable. To illustrate the instances where alternative strategies should be preferred to the MVT by foragers, I define a concept of a foraging cycle and explain its importance and the importance of the shape of the functional response curve (FRC) for foragers, and discuss how these concepts relate to the proposed model of an alternative foraging strategy that accounts for time limitation.

3.2. Methods

My first goal was to assess the consequences (daily cumulative forage consumption) of using a foraging strategy based on the MVT by foragers of varying efficiencies (slope of the functional response curve) and feeding across landscapes that differ in the quality of the average patch and the average travel time between patches, and to see if the MVT foragers are able to meet or exceed their daily food requirements in these landscapes (Phase 1). Based on my previous research described in Chapter 2, I expected that very efficient foragers using the MVT should be able to exceed their daily requirements. Therefore, my second goal (Phase 2) was to perform a sensitivity analysis for the giving up density (GUD) in an average patch to see if, by using a foraging strategy alternative to the MVT, the very efficient foragers could still meet their requirements, and if there is a strategy that would allow foragers to meet their daily food requirements in landscapes where they were not able to satisfy their needs by following MVT. Therefore, in Phase 1 of this research I looked at the MVT strategy in a daily foraging activity of different foragers across a variety of landscapes, and in Phase 2, based on the outputs from Phase 1, I explored the consequences of alternative foraging strategies in a 12 h period.

To achieve these goals, I developed and employed a computer simulation model SeekSMART. A detailed discussion of the structure of this comprehensive simulation model is provided in Chapter 2. In this Chapter I provide a short overview of the main characteristics of the model necessary for understanding the simulations and their outputs.

To set the discussion in a specific context I chose elk (*Cervus elaphus*) as an experimental subject. The well known ecology and foraging behavior of elk allowed parameterization of all components of the model with real field data. This makes elk an ideal subject for a simulation modeling study.

SeekSMART is a mechanistic and deterministic model that describes foraging by a virtual animal in a simulated landscape. It assumes that at the start of a simulation run the animal is located at a specific point in a predefined landscape consisting of patches of arbitrarily assigned biomasses and distributed according to the assigned travel times among the patches. From the starting point the animal has to travel to patch N for a user-specified units of time. Upon entering patch N, the forager has to decide whether to stay within this patch and start foraging, or whether to skip the patch and start traveling to patch N +1. This decision, as well as the forager's next decision on how long to feed in a patch, are made by the animal based on the foraging strategy that it uses according to the parameters specified in the model. The following 4 rules defining the patch leaving decisions can be examined in SeekSMART:

1) The density of forage available in the current patch drops to an arbitrary assigned value (the forager may or may not know the landscape);
2) The density of forage available in the current patch drops to the average of forage density in all patches (assumes that the forager knows the landscape);

3) The forager follows the Marginal Value Theorem (MVT). In this case the average travel time between patches and the forager's gain curve determine when the forager leaves the current patch (N) and moves to the next patch (N+1), (assumes the forager knows the landscape);

4) The forager feeds in a patch for an arbitrary assigned patch residence time (the forager may or may not know the landscape).

While feeding within a patch, the forager's consumption rate is driven by the instantaneous intake rate described by the type II functional response curve based on the Michaelis-Menten kinetics that is generally accepted as a formula explaining type II functional response curve for foraging ungulates (Fryxell 2004, Hudson and Watkins 1986, Wickstrom et al. 1984). The forager continues to feed within the patch until either its gut is full or if the time to leave the patch, based on the forager's strategy has elapsed. After leaving patch N the forager travels to patch N +1 and the process described above starts again. A forager may use the same foraging strategy defined at the onset of the simulation run for the entire total time of the run or its foraging strategy can be changed at any given time by adjusting the parameters that define the forager and the landscape.

To examine foraging strategies and their consequence in response to specific distributions of resources in absence of factors that are generally proposed as the explanation for animals not displaying MVT behaviors in natural conditions (e.g., inter- and intra-species interactions), I eliminate environmental noise and make important assumptions about the virtual forager that apply to all simulations. First, the forager is free from the risk of predation. Second, there are no other animals in the foraging area, and there are no factors that destruct the forager from choosing the best strategy to maximize its forage intake or to satisfy its forage requirements from the entire foraging area consisting of a series of patches distributed across the landscape. Moreover, the nutritional state of the animal is neutral, which means that the forager is neither satiated nor malnourished, but its gut is close to empty at the onset of a simulation run.

To determine if there are reasons to use a strategy different than predicted by the MVT for an animal that is involved only in foraging activities, I intentionally eliminated activities other than searching for food and feeding within a patch and composed the simulation trails of searching and foraging periods only. Research on elk suggests that the maximum daily foraging time is around 12 h (Clutton-Brock et al. 1982; Gates and Hudson 1983) and the simulation runs reflect that time constraint (the default total time of all simulation runs is 12 h).

SeekSMART allows for defining the following landscape characteristics by adjusting the main attributes of the patches:

1) Initial patch biomass density (kg/ha) – IPBD;
2) Patch size (m^2)- PS;

3) Initial patch biomass (g) - IPB. This value is calculated by the model based on the values provided for PS and IPBD according to the following equation: $IPB = IPBD*(0.0001*(PS^2)))*1000$
4) Distances between patches expressed as travel time (h).

Additionally, the following settings of the landscape can be specified in the model allowing examination of the effects of distribution of patches, their initial biomass densities, and overall landscape productivity:

1) all forage patches are equal (they have the same initial forage biomass density);
2) patches are different, i.e. every patch has a unique initial forage biomass density;
3) travel time between patches is the same and can have any value including zero;
4) travel time between patches is not equal. Travel time between any consecutive patches can be arbitrary assigned and can have any value including zero.

I created three main types of landscape depending on the average patch biomass. To avoid bias, instead of arbitrarily assigning IPBD for each individual patch, I used STELLA Research (ieee systems 2008) to randomly generate these values within each of the three landscape types (Landscape A: mean = 1008.78; SD = 89.67, range = 852-1150 kg/ha; Landscape B: mean = 2035.05; SD = 192.62, range = 1702.49-2299.23 kg/ha; and Landscape C: mean = 3011.35, SD = 275.84, range = 2564.41-3448.26 kg/ha). Each landscape type was further divided into sub-types depending on the average travel time between patches (AT1, BT1, CT1: TravelT = 0.1 h; AT2, BT2, CT2: TravelT = 0.5 h; AT3, BT3, CT3: TravelT = 1.0 h; AT4, BT4, CT4: TravelT = 2.0 h; AT5, BT5, CT5: TravelT = 4.0 h. Forage biomass within each patch was assigned randomly and the sequence of patches in the foraging path was predetermined. Table 3.1 illustrates the composition of patches in the three landscape types.

3.2.1. Phase 1

To assess if the MVT foragers are able to meet or exceed their daily food requirements I used three MVT foragers of varying efficiencies of resource utilization (three different slopes of the functional response curve: efficient (EF) forager (E = 97.32 kg/ha), medium efficiency (ME) forager (E = 486.6 kg/ha), and low efficiency (LE) forager (E = 875.88 kg/ha)). The MVT foragers were feeding across landscapes that differed in the density of biomass of an average patch and in the average travel time between patches. I used the patch residence times (Tr) calculated in Chapter 2 according to the MVT (i.e., based on gain curves and travel times). Next, using the obtained patch residence times (Tr) and the gain curves, I calculated the giving-up-densities (GUD), which were subsequently used in defining the behavior of the MVT foragers of the above three foraging efficiencies. During the simulation runs I tracked the landscape intake rate (LIR) and the cumulative consumption (CC) of the foragers and recorded: 1) the time (Tmin) when the foragers met the value corresponding to the lower range of the daily food requirements of elk (6990 g); and 2) the time (Tmean) when the average value of the daily requirements was achieved by the foragers (9180 g). The values for the daily food requirements were based on data obtained in the field by Gedir and Hudson (2000a). Because the data used to describe the patch biomass density in landscape C seemed most realistic, I decided to start the simulations with the most abundant landscapes (type C) and next conduct simulations for the landscapes of the other two types (B and A) that represented poorer habitats. The specific settings used in Phase 1 are summarized in Table 3.2a– b.

3.2.2. Phase 2

In the second phase, based on the outputs of Phase 1, I performed sensitivity analysis for the giving-up-density (GUD) for foragers that (based on their efficiency (E) and landscape type) were either able to exceed their daily food requirements or that were close to achieving the minimum requirements when employing the MVT as their foraging strategy. I used the GUDs calculated for the MVT foragers as starting points for the sensitivity analyses and gradually increased and decreased the GUD at 100 kg/ha increments to test alternative foraging strategies. A sensitivity analysis was terminated when either the GUD was too low to continue (less than 100 kg/ha), or if the resulting values of CC at 12 h were lower then the CC of the MVT and continued to decline for at least 8 consecutive runs (i.e. the GUD was at least 800 kg/ha higher than the GUD of the

MVT forager and, in most cases, close to the average patch biomass density (when the GUD is at the landscape average, the forager should skip all patches that have the density of forage at the landscape average or lower regardless of travel time). My goal was to test if, in a given landscape, a specific forager could use a strategy alternative to the MVT to either lower its CC, but still consume enough to satisfy its daily needs, or to increase its CC to meet its minimum requirements if it was not possible to do so using the MVT strategy. By doing this I tested foraging strategies alternative to the MVT. Based on outputs from Phase 1, I created Landscape CT1a with average travel time = 0.3 h (the average between travel times in landscapes CT1 and CT2) and decided to perform sensitivity analyses for GUDs for three foragers: efficient (E=97.32), medium and low efficiency (E = 486.6, E = 875.88 respectively) across three landscapes: CT1, CT1a and CT2. Therefore, the sensitivity analysis resulted in a total of 217 scenarios. Tables 3.4a – 3.4c provide an overview of the settings used in Phase 2.

3.3. Results

3.3.1. Phase 1

Increasing travel time between patches affected the Tmin and Tmean for all MVT foragers in all landscapes (Table 3.3 provides an overview of the results obtained in Phase 1). The efficient (EF) forager feeding in landscape CT1 was able to satisfy its daily needs within 10.4 h (travel and foraging time combined) and exceed it at the end of the simulation run (10631 g). In landscape CT1a, the EF forager reached its requirement at 11.3 h and was able to exceed the mean daily food requirements at the end of the trial (CC at 12 h = 9762 g). Its high foraging efficiency allowed the efficient (EF) forager to meet its lower threshold of daily food requirement (6990 g) also in a landscape with the average travel time of 0.5 h (30 minutes, landscape CT2). This travel time, however, was too long for the efficient (EF) forager to reach 9180 g within 12 h (cumulative consumption (CC) at 12 h = 9064 g).

The medium efficiency (ME) forager in landscape CT1 required 9.2 and 12.0 h to meet the minimum and mean forage requirements respectively. The ME forager in landscape CT1 a exceeded the minimum forage requirement (CC = 8078 g at 12 h) but failed to reach the mean daily food requirement of 9180 g. In landscape CT2 the ME forager reached CC of 7678 g at 12 h when average travel time was 0.5 h. This was higher then the lower threshold (6990 g), but lower then the mean daily consumption reported for a lactating female elk (9180 g). This indicated that 30 minute travel between patches may constitute a landscape in which an average lactating elk female would not be able to satisfy its daily food requirements even if patches were abundant in forage. Therefore, I decided to exclude all landscapes that had lower patch quality than landscapes of type C and travel times longer than 0.5 h from further analysis.

The low efficiency (LE) forager feeding in landscape CT1 required 10.2 h to meet the minimum daily forage requirements, but failed to reach CC corresponding to the mean requirements (CC at 12 h = 8169 g). In landscape

CT1a the LE forager exceeded the lower range of the daily requirement with CCs at 12 h of 7145 g, but also failed to reach the mean daily food requirement of 9180 g. In landscape CT2 the LE forager was not able to reach even the lower range of the expected forage consumption (CC at 12 h = 6786 g). This indicated that for elk that have gentle slope of the FRC (E = 875.88 kg/ha) and are feeding in habitats with the average patch quality as defined in landscapes of type C (high quality habitat), when travel times between patches are 6 minutes or more, it may be not possible to satisfy forage requirements for successful reproduction.

3.3.2. Phase 2

The EF forager employing the MVT strategy was most successful in landscape CT1a where it reached CC of 9762 g. All other foraging strategies for a forager of this efficiency in this landscape resulted on lower CC at 12 h. In the other two landscapes (CT1 and CT2) the EF forager employing the MVT consumed less forage than alternative foragers of the same efficiency. In landscape CT1 the EF forager that decided to leave patches earlier (GUD higher by 200 kg/ha than the MVT's GUD) consumed 10657 g that was 26 g more than the MVT forager. Similarly, in landscape CT2, the efficient (EF) forager that left the patches at a GUD 200kg/ha higher than the MVT forager, consumed more than the MVT forager (9121 as opposed to 9064 g, that was 57 g more), (Table 3.5a, Figure 3.1a).

The medium efficiency (ME) forager that used the MVT was most successful in landscape CT1 when its CC was 9185 g and equal to the assumed daily forage requirement of a lactating female elk. The ME MVT forager was less successful than foragers of the same efficiency using alternative strategies in landscapes CT1a and CT2. In landscape CT1a the difference between the CC of the more successful alternative strategy and the CC of the MVT forager was most pronounced and equal to 165 g. The ME forager that decided to leave patches much earlier than the MVT forager (GUD higher by 700 kg/ha) reached CC of 8243 g, higher than that of the MVT forager (8078 g). In landscape CT2 the difference in CCs between the more successful alternative ME forager and the MVT ME forager was less pronounced (7696 vs. 7678 g) and equal to 18 g (Table 3.5b, Figure 3.1b).

Similar to the EF and ME foragers, the LE forager employing the MVT strategy was able to reach a CC higher than foragers using alternative foraging strategies in only one landscape. When the LE forager used the MVT, it was most successful in landscape CT2 only where it reached CC of 6786 g. In the remaining two landscapes, the LE forager that employed the MVT performed inferior to alternative foragers. This difference was highest in landscape CT1a where an alternative LE forager that left patches at GUD 500 kg/ha higher than the MVT GUD consumed 172 g more then the MVT forager (7317 versus 7145 g). This difference between the alternative forager and the MVT forager was smaller in landscape CT1 (8193 – 8169 = 25g) (Table 3.5c, Figure 3.1c).

In summary, the foraging strategy based on the MVT produced the highest CC only in 3 out of 9 combinations of different efficiency foragers feeding in landscapes with different average travel times. In the other 6 instances foraging strategies alternative to the MVT were more successful in maximizing CCs.

3.4. Discussion

My findings reveal several interesting patterns. The most interesting is that the majority of foragers that employed foraging strategies different than the MVT performed better within the limited time frame (12 h) than foragers that followed the MVT. It contradicts the commonly accepted view that the MVT is the optimal foraging strategy, and the assumption that if an animal is observed to deviate from the MVT, it is because it is engaged in other activities important for survival and not related to foraging (predator avoidance, mating, competition for other resources, care of young, etc.). In my research I eliminated all these factors; yet, foragers using strategies alternative to the MVT, in most cases, were more successful in maximizing their cumulative consumption than the MVT foragers within a specific timeframe. My work clearly demonstrates that even if environmental noise is not present, in most cases, time-limited foragers perform better if they use strategies other than the MVT behaviors. Examination of a number of foragers feeding across a spectrum of landscapes enables to address the critical question about the causes for the alternative foragers to outperform the MVT foragers and the mechanisms of this outcome.

Inspection of the main variables (CC, consumption rate and LIR) of the MVT forager and an alternative forager of the same efficiency that performed better (had higher CC and LIR) is necessary to identify the main factors responsible for the observed deviation from the MVT. I will first examine the case of the ME forager feeding in landscapes CT1a and CT2 (Figure 3.1b). The trajectories of its CCs in these landscapes are intriguing because of the considerable differences in the GUDs for the MVT forager and the alternative (ALT) forager that used the optimal foraging strategy. In landscape CT1a the ALT forager that left at GUD of 700 kg/ha higher than the MVT GUD achieved the highest CC. It was the biggest difference in GUDs for the ALT foragers outperforming MVT foragers in all scenarios. However, in landscape CT2 the most successful strategy for the ME forager was based on GUD that was just 100 units higher than the MVT GUD (Figure 3.1b).

I will now examine the changes to the CC at 12 h in comparison to the number of patches fed on until total time T = 12 h, as a function of using a specific GUD by the ME foragers feeding in the landscape CT2 (Figure 3.2a) . Both the MVT and the ALT forager entered the first patch at T = 0.4 h and started feeding with the same consumption rate (Figure 3.2b). The ALT forager, however, using higher GUD than the MVT forager, left the first patch at T = 2.3 h that is 0.1 h (6 minutes) earlier than the MVT forager. The MVT forager stayed in the first patch longer than the ALT forager and its CC when it left the patch at T = 2.4 h was higher than the CC of the ALT forager at T = 2.4 h (Figure 3.2c). Because both foragers where feeding in the same landscape, the travel times and patches were the same and this is why the ALT forager (Figure 3.2b) reached the second patch earlier (T = 2.8 h) than the MVT forager (T = 2.9h) and started feeding with its maximum (for a given forage density) intake rate. Both foragers continued to repeat their feeding cycles (travel + foraging within the patch) during the total simulation time (12 h). At the end of the simulation the total travel time (Tt) and total residence time (Tr) as well as the number of patches fed on were the same for both foragers despite the fact that the ALT forager was leaving the patches earlier and had higher GUD and lower Tr (this seems contrary to the logic, but is actually possible if none of the foragers is able to complete the last feeding cycle, as it was in this case where both foragers were still feeding in the patch when simulation time reached the 12 h mark – Figure 3.2b). What does cause, then, the difference in CCs at the end of the simulation? At the end of the simulation run (T = 12 h) none of the foragers were able to finish feeding in the last patch (patch number 4). The ALT forager, however, was feeding at a higher consumption rate, on average, than the MVT forager, which by staying longer in each patch, was feeding for some time with a lower consumption rate than the ALT forager. This illustrates that the quality of the time (QT) that the forager spends in the patch is of critical importance to its CC at any given time. It can be shown that during the 12 h trial:

$$QT = C/Tr \qquad \text{(eq. 1)}$$

Where:

C - consumption in the average patch, and

Tr - average residence time in the patch

was higher for ALT forager than for the MVT forager:

$$QT_{ALT} > QT_{MVT} \qquad \text{(eq. 2)}$$

Then:

$$C_{ALT} / Tr_{ALT} > C_{MVT} / Tr_{MVT} \qquad \text{(eq.3)}$$

A close examination of the ME forager feeding in a landscape CT1a (Figure 3.3a), reveals another important relationship responsible for the observed advantage of foraging strategies alternative to MVT. In this landscape, the most successful strategy for maximizing CC at 12 h was based on GUD that was 700 units higher than the MVT GUD. This translates to a difference in the average patch residence time (Tr) of 0.94 h ($Tr_{MVT} = 2.45$ vs. $Tr_{ALT} = 1.73$ h). Similar to the situation observed in the landscape CT2, the ALT forager left each patch earlier than the MVT forager (Figure 3.3b). These differences in Tr caused the apparent ‘pendulum’ pattern in CCs of the two competing foragers (Figure 3.3c). The CC of the forager that leaves the patch drops below the CC of the forager that feeds in the patch due to a pause in foraging caused by travel between patches. For these two particular ME foragers in landscape CT1a the shifts occurred at 1.4, 2.4, 3.5, 5.3, 6.1, 7.8, 8.3, 8.7, 10.1, and 11.8 h (Figure 3.3c). The ALT forager achieved higher CC during the following time intervals: 2.4 – 3.4, 5.3 – 6.0, 7.8 – 8.2, 8.7 – 10.0, and 11.8 - 12 h (cycles). At other times the MVT forager had higher CC. This clearly shows that timescale is a critical factor in determining the optimal foraging strategy. If I were to end the simulation run at, for example, 2, 4, 7 or 11 h, the MVT would have been identified as the optimal strategy.

In landscape CT1a, in contrast to landscape CT2, the difference between the average Tr for both the MVT and ALT foragers during the total length of the simulation resulted in the ALT forager feeding in a different number of patches than the MVT forager (Figure 3.3a). The ALT forager fed in a total of 6 patches as opposed to 4 patches for the MVT forager (4 patches fed on by both the MVT and ALT foragers in landscape CT2 (Figures 3.2a and 3.3a)). Therefore, it was not only the quality of the residence time (QT) that was associated with the ALT forager outperforming the MVT forager, but also the number of foraging cycles (higher for the ALT forager) that contributed to the observed phenomenon.

A foraging cycle (FC) of any forager consists of travel time (Tt) to reach the patch (also called search time) and foraging (residence) time (also called handling time) in the patch (Tr):

$$FC = Tt + Tr \qquad \text{(eq.4)}$$

An animal has no control over Tt because the distances between patches are intrinsic characteristics of the landscape. It could be argued that an animal could increase it movement speed to decrease Tt, however, that would, in most cases, increase energetic costs. Assuming that an animal travels between patches at a speed that produces an optimal cost benefit ratio, it can be assumed that foragers have no control over Tt. They can, however, control Tr depending on their needs. If a forager is limited by time it should adjust its foraging cycle FC so that its CC and LIR at the end of the specific total time T are the highest possible. Therefore, the total time T, travel time Tt and residence time Tr are the key parameters that should be of interest to a forager.

Because the total time (T) is composed of travel time (Tt) and residence time (Tr), the following relationship should be important for the foraging strategy of an animal:

$$T / (Tt + Tr) \qquad \text{(eq.5)}$$

Another reason why this relationship is important is that it allows for calculating the number of feeding cycles (FC) at any time (T):

$T / (Tt + Tr) = N$ (eq.6)

If the sum of total Tt and total Tr is not the same as total time T, it can be shown that N can be less than 1 unit higher or lower than the number of patches (M) that the animal fed on until time T (Figure 3.4).

If

$N > M$ (eq. 7)

then CC_{ALT} of the alternative forager at any given time T_h (Figure 3.4) is higher than CC_{MVT} only if the sum of his CC_{ALT} at T_0 when $N_{ALT} = M_{ALT}$ and consumption (C) during the proportion of the next foraging cycle $N_{ALT} – M_{ALT}$ ($T = T_h – T_0$) is higher than the sum of the CC_{MVT} of the MVT forager at T_1 when $N_{ALT} = M_{ALT}$ and consumption (C) achieved during the proportion of the next foraging cycle $N_{MVT} – M_{MVT}$ ($T = T_h – T_1$).

This can be expressed as follows:

$CC_{ALT}T_0 + C_{ALT}T_h\text{-}T_0 > CC_{MVT}T_1 + C_{MVT}T_h – T_1$ (eq.8)

In other words, it is possible for a forager that uses a strategy alternative to the MVT to achieve CC and LIR (Figure 3.5) higher than those achieved by an MVT forager if the sum of CC after all fully completed cycles plus the consumption (C) in the last cycle are higher for the alternative forager. Therefore:

$$CC_{ALT} + C_{ALT} > CC_{MVT} + C_{MVT} \qquad \text{(eq.9)}$$

Where:

CC – cumulative consumption during the fully completed cycles

C – Consumption in the last cycle

ALT – denotes the alternative forager

MVT – denotes the MVT forager

The critical question, however, is as follows: how should a time limited forager adjust its patch residence time (Tr) to achieve higher LIR and CC than the MVT forager at any given time? It is logical that at any given time (T) for an alternative strategy to be more beneficial than the MVT strategy a forager using the alternative strategy has to have higher CC and LIR, than the CC of MVT forager at T:

$$CC_{ALT} / T > CC_{MVT} / T \qquad \text{(eq. 11)}$$

Because total time (T) consists of the total travel time (Tt) and total residence time (Tr) and travel time is intrinsic characteristics of the landscape, the above can be compared as follows:

$$CC_{ALT} / (Tt + Tr_{ALT}) = CC_{MVT} / (Tt + Tr_{MVT}) \qquad \text{(eq. 12)}$$

The above can be solved for Tr_{ALT}:

$$CC_{ALT} * (Tt + Tr_{ALT}) = CC_{MVT} * (Tt + Tr_{MVT}) \qquad \text{(eq.13)}$$

$$CC_{ALT} * Tt + CC_{ALT} * Tr_{ALT} = CC_{MVT} * Tt + CC_{MVT} * Tr_{MVT} \qquad \text{(eq. 14)}$$

Therefore, the alternative forager, to achieve CC at any given time higher by $CC_{ALT} - CC_{MVT}$ than the MVT forager, should use patch residence time Tr according to the following:

$$Tr_{ALT} = [(CC_{MVT} - CC_{ALT}) * Tt + CC_{MVT} * Tr_{MVT})] / CC_{ALT} \qquad \text{(eq. 15)}$$

One of my key findings is that time scale has an effect on the applicability of the MVT as a foraging strategy. While I present evidence for this based on simulations focused on a large herbivore, it is further supported by Wajnberg et al. (2006) who focused on invertebrates. In a study of female parasitoids *Anaphes victus* exploiting egg patches of its host, the carrot weevil *Listronotus oregonensis*, the authors found that females, in their foraging strategy, deviated from the MVT by remaining for a longer time on host patches when they approached the end of their life. In this case Wajnberg et al. (2006) found a relationship between the patch residence time (Tr) and the age of the individual. The importance of temporal scale in optimization studies has been also emphasized by Gass and Roberts (1992) who examined the feeding behavior of hummingbirds feeding on nectar. Gass and Roberts (1992) suggested that energy intake rate related to handling time should be sensitive to temporal scale and that this generalization should apply to other systems. In this research I demonstrated how temporal scale affects optimal foraging of a large herbivore.

Another important finding of my research is that the difference between the MVT and other strategies, as far as the cumulative consumption (CC) at the end of the 12 h period is concerned, is subtle and in many cases almost unnoticeable. In the most extreme case this difference between the MVT and the least optimal strategy was 975 g at 12 h (that is 11.9%). It was observed when the LE foragers were tested in the landscape with the shortest travel times. In all other cases the difference between the MVT forager and foragers employing less optimal strategies was smaller than 11.9% of the daily CC (Figure 3.6).

Simulation outputs indicate that for very efficient foragers it does not really matter what foraging strategy they use – their CCs and LIR differ only slightly (Figures 3.6 and 3.7). It is beneficial to be an efficient forager – an efficient forager is more flexible with the GUD (a wide range of GUDs results in very similar CCs) and consequently its patch residence times. As a result, efficient foragers can allocate more time to activities other then feeding. Therefore, it may be more important for animals to increase their feeding efficiency (morphology, diet selection in relation to specific morphology) than to use MVT and stick to their ‘default’ foraging efficiencies at all times. In other words, to increase its fitness an animal should aim to keep the slope of its functional response curve (FRC) as steep as possible. This is supported by Iason et al. (1999) who found that sheep with a daily foraging time constraint were able to increase their instantaneous intake rate compared with those given unlimited time to graze. It should be noted however, that all foragers are more or less constrained by time to meet their requirements. In this sense, it can be argued that Iason et al. (1999) compared two groups of foragers that had different time constraints and the group that was more constrained was able to increase the instantaneous intake rate. Similar results were obtained by Bergman et al. (2001) who found that young bison behave as time minimizers. The authors found that, depending on the temporal scale, a different foraging strategy was preferred by young bison that behave as time minimizers on the longest temporal scale and energy maximizers over short periods of time by foraging at the maximum instantaneous rates. Using the QT concept described earlier, it is clear that young bison aim at maximizing QT.

Therefore, the efficient foragers, which are close to the perfect forager, have the greatest flexibility in adjusting their foraging strategy in response to changing environmental factors and consequently in allocating more time to other activities that increase fitness (predator avoidance, producing more offspring by having another clutch, etc.). This implies that natural selection should favor efficient foragers that have a steep type II functional response curves (FRC) in relation to individuals of the same population utilizing the same food. Due to evolutionary changes, steep FRC (i.e., having a low foraging coefficient F) should be more common than gently sloping type II functional response curves with higher foraging coefficient F when individuals from the same population feeding in the same landscape are compared.

My results indicate that in some cases a forager had the average residence time in a patch during the 12 h trial period, a bit higher then suggested by the average Tr calculated based on the entire landscape. This was caused by the difference between the average biomass of the patches that the animal was able to feed on within the 12 h and the landscape average. In my research I used the density of forage as the trigger for the forager to leave the patch. This suggest two things: 1) the forager should either choose residence time as the trigger to leave the patch and ignore the density of forage in the patch, or 2) foragers should not use the landscape averages if they are limited by time.

In the first case, if the forager chooses to use residence time as the trigger to leave the patch, it will stay too long in a low productivity patch and not long enough in a productive patch. Therefore, this option does not seem practical. Thus, a forager should use the remaining forage density as a trigger to leave a patch. This suggests that foragers limited by time should leave patches earlier than suggested by the MVT. Because most animals are limited by time, they should stay in a patch on average shorter than implied by MVT. It also suggests that instead of remembering the entire landscape average, it may be more important to remember the daily landscape average, because these two things may not always be the same. Ollason (1980) developed a foraging model for patchy environments that accounts for the forager ability to remember its previous foraging bouts. According to Ollason (1980), the ability of an animal to choose the best strategy depends on the balance between the animal's feeding efficiency and the productivity of the foraging area and the animal's ability to memorize and the amount of remembrance. Ollason (1980) argues that the forager needs to remember its past foraging experience and to leave each patch if it is not feeding as fast as it remembers doing. The main concept in Ollason's model is similar to the MVT, however, it is based on the recent experience of the forager as opposed to the landscape average. My research supports the notion that time limited foragers should respond to their recent memory of the landscape rather than to values representing the entire landscape.

In this research I used data on lactating female elk to analyze foraging behavior of an animal that has the highest daily food requirements when compared to other kinds of individuals of the same population. If an individual that has the highest food requirements is able to satisfy its needs and successfully reproduce at the potentially maximum rate (maximize its fitness) using a strategy different than MVT, then, it can be assumed that other individuals in the population with lower food requirements are even more likely to use alternative foraging strategies, especially if these strategies allow them to engage in other activities that could improve fitness (any non-feeding time can be allocated to searching for mate, a more productive habitat, vigilance and predator avoidance).

An important factor of the foraging strategy is the quality of the food in the patch. Most foraging herbivores have been shown to forage selectively within the patch and consume the best quality forage first (Christianson and Creel 2007, Danell et al.1994, Hirata et al. 2008). Therefore, it could be argued that if GUD is measured in the field without accounting for the quality of the biomass of forage, then all large herbivores should leave the patch earlier than suggested by the MVT. In my research I have shown that even if the quality of the forage is distributed homogeneously in the patch and forge density is the only factor that declines with foraging time, elk have no reasons to strictly follow the MVT and can instead use an alternative foraging strategy that allows them to satisfy the extreme needs of a lactating female.

My overall conclusion is that elk can satisfy their daily food requirements without using the MVT in most situations. Therefore, there is no real need for elk to use the MVT at all times and elk should not be expected to use the MVT as their default foraging startegy. Instead it may be more beneficial for elk, in terms of maximizing their fitness, to use alternative foraging strategies. I believe that to further develop the optimal foraging theory and to deepen the understanding of foraging mechanisms, future research should focus on strategies alternative to the MVT.

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Tables

	Biomass density (kg/ha)		
	Landscape A	**Landscape B**	**Landscape C**
Patch 1	852	1,709	2,571
Patch 2	1,011	1,745	3,102
Patch 3	1,032	1,826	3,284
Patch 4	1,045	1,880	3,405
Patch 5	1,080	2,021	2,822
Patch 6	1,138	2,251	3,340
Patch 7	863	1,754	2,670
Patch 8	1,109	2,138	3,085
Patch 9	939	2,056	3,350
Patch 10	1,058	1,931	2,621
Patch 11	1,001	1,702	3,006
Patch 12	975	2,200	2,774
Patch 13	1,140	2,258	3,356
Patch 14	1,022	1,787	3,195
Patch 15	988	2,254	2,896
Patch 16	1,060	1,940	2,641
Patch 17	895	1,879	2,953
Patch 18	1,059	1,938	2,635
Patch 19	975	2,199	2,772
Patch 20	1,103	2,111	3,024
Patch 21	996	2,283	2,962
Patch 22	1,082	2,027	2,836
Patch 23	1,143	2,272	3,387
Patch 24	981	2,224	2,829
Patch 25	900	1,900	3,001
Patch 26	1,129	2,215	3,258
Patch 27	1,139	2,258	3,355
Patch 28	1,126	2,203	3,231
Patch 29	1,150	2,299	3,448
Patch 30	907	1,929	3,065
Patch 31	946	2,085	3,416
Patch 32	909	1,938	3,085
Patch 33	986	2,244	2,873
Patch 34	989	2,257	2,904
Patch 35	875	1,798	2,771
Patch 36	920	1,981	3,182
Patch 37	1,042	1,866	3,374
Patch 38	973	2,193	2,758
Patch 39	861	1,745	2,651
Patch 40	952	2,106	2,564
Mean	1008.775	2035.046	3011.3545
Standard Deviation	89.67	192.62	275.84
Minimum	852	1702.49	2564.41
Maximum	1150	2299.23	3448.26

Table 3.1. Characteristics of the first 40 patches in the feeding sequence in the three landscape types. Biomass density expressed in kg/ha.

Scenario	Forager (E)	Average TravelT	Landscape	MVT Tr	MVT GUD
1	97.32	0.10	CT1	1.70	1178.88
2	486.6	0.10	CT1	1.50	1603.98
3	875.88	0.10	CT1	1.30	1909.53
4	97.32	0.50	CT2	2.60	332.42
5	486.6	0.50	CT2	2.45	875.60
6	875.88	0.50	CT2	2.40	1161.28
7	97.32	1.00	CT3	2.90	104.73
8	486.6	1.00	CT3	2.85	614.06
9	875.88	1.00	CT3	2.90	871.74
10	97.32	2.00	CT4	3.00	49.41
11	486.6	2.00	CT4	3.30	368.29
12	875.88	2.00	CT4	3.55	557.26
13	97.32	4.00	CT5	3.10	13.47
14	486.6	4.00	CT5	3.65	223.15
15	875.88	4.00	CT5	4.20	322.44

Table 3.2a. Settings that defined the foragers and the landscapes of type C in Phase 1.

Scenario	Forager (E)	ave travelT	Landscape	MVT Tr	MVT GUD
16	97.32	0.10	BT1	1.4	554.61
17	486.6	0.10	BT1	1.1	1062.09
18	875.88	0.10	BT1	0.8	1397.07
19	97.32	0.50	BT2	1.9	137.83
20	486.6	0.50	BT2	1.7	650.61
21	875.88	0.50	BT2	1.7	854.98
22	97.32	1.00	BT3	2	75.27
23	486.6	1.00	BT3	2.1	373.02
24	875.88	1.00	BT3	2.2	608.83
25	97.32	2.00	BT4	2.1	28.72
26	486.6	2.00	BT4	2.6	208.81
27	875.88	2.00	BT4	2.75	375.37
28	97.32	4.00	BT5	2.2	4.40
29	486.6	4.00	BT5	2.8	148.32
30	875.88	4.00	BT5	3.2	258.96

Table 3.2b. Settings that defined the foragers and the landscapes of type B in Phase 1.

Scenario	Forager (E)	Average TravelT (landscape)	MVT Tr	MVT GUD	Tmin	Tmean	Cumulative Consumption at 12 h
	97.32	0.10 (CT1)	1.70	1178.88	8.0	10.4	10631
	486.6	0.10 (CT1)	1.50	1603.98	9.2	12.0	9185
	875.88	0.10 (CT1)	1.30	1909.53	10.2	NA	8169
	97.32	0.30 (CT1a)	2.55	375.73	8.6	11.3	9762
	486.6	0.30 (CT1a)	2.45	875.60	10.3	NA	8078
	875.88	0.30 (CT1a)	2.30	1223.49	11.8	NA	7145
	97.32	0.50 (CT2)	2.60	332.42	9.2	NA	9064
	486.6	0.50 (CT2)	2.45	875.60	11.1	NA	7678
	875.88	0.50 (CT2)	2.40	1161.28	NA	NA	6786

Table 3.3. Outputs from runs completed in Phase 1 for landscapes of type C.

Landsacpe	GUD
CT1	178.88
CT1	278.88
CT1	378.88
CT1	478.88
CT1	578.88
CT1	678.88
CT1	778.88
CT1	878.88
CT1	978.88
CT1	1078.88
CT1	**1178.88**
CT1	1278.88
CT1	1378.88
CT1	1478.88
CT1	1578.88
CT1	1678.88
CT1	1778.88
CT1	1878.88
CT1	1978.88
CT1	2078.88

Landscape	GUD
CT1a	75.73
CT1a	175.73
CT1a	275.73
CT1a	**375.73**
CT1a	475.73
CT1a	575.73
CT1a	675.73
CT1a	775.73
CT1a	875.73
CT1a	975.73
CT1a	1075.73
CT1a	1175.73
CT1a	1275.73
CT1a	1375.73
CT1a	1475.73
CT1a	1575.73
CT1a	1675.73

Landscape	GUD
CT2	32.42
CT2	132.42
CT2	232.42
CT2	**332.42**
CT2	432.42
CT2	532.42
CT2	632.42
CT2	732.42
CT2	832.42
CT2	932.42
CT2	1032.42
CT2	1132.42
CT2	1232.42

Table 3.4a. The giving-up-densities (GUD) that were used in sensitivity analysis of alternative foraging strategies for the **efficient (EF) forager (E = 97.32)**. The GUD for the MVT forager is indicated in bold font.

Landsacpe	GUD
CT1	703.98
CT1	803.98
CT1	903.98
CT1	1003.98
CT1	1103.98
CT1	1203.98
CT1	1303.98
CT1	1403.98
CT1	1503.98
CT1	**1603.98**
CT1	1703.98
CT1	1803.98
CT1	1903.98
CT1	2003.98
CT1	2103.98
CT1	2203.98
CT1	2303.98
CT1	2403.98
CT1	2503.98

Landscape	GUD
CT1a	75.6
CT1a	175.6
CT1a	275.6
CT1a	375.6
CT1a	475.6
CT1a	575.6
CT1a	675.6
CT1a	775.6
CT1a	**875.60**
CT1a	975.6
CT1a	1075.6
CT1a	1175.6
CT1a	1275.6
CT1a	1375.6
CT1a	1475.6
CT1a	1575.6
CT1a	1675.6
CT1a	1775.6
CT1a	1875.6
CT1a	1975.6
CT1a	2075.6
CT1a	2175.6
CT1a	2275.6

Landscape	GUD
CT2	75.6
CT2	175.6
CT2	275.6
CT2	375.6
CT2	475.6
CT2	575.6
CT2	675.6
CT2	775.6
CT2	**875.60**
CT2	975.6
CT2	1075.6
CT2	1175.6
CT2	1275.6
CT2	1375.6
CT2	1475.6
CT2	1575.6
CT2	1675.6
CT2	1775.6

Table 3.4b. The giving-up-densities (GUD) that were used in sensitivity analysis of alternative foraging strategies for the **medium efficiency (ME) forager (E = 486.60)**. The GUD for the MVT forager is indicated in bold font.

Landsacpe	GUD
CT1	1109.53
CT1	1209.53
CT1	1309.53
CT1	1409.53
CT1	1509.53
CT1	1609.53
CT1	1709.53
CT1	1809.53
CT1	**1909.53**
CT1	2009.53
CT1	2109.53
CT1	2209.53
CT1	2309.53
CT1	2409.53
CT1	2509.53
CT1	2609.53
CT1	2709.53

Landscape	GUD
CT1a	523.49
CT1a	623.49
CT1a	723.49
CT1a	823.49
CT1a	923.49
CT1a	1023.49
CT1a	1123.49
CT1a	**1223.49**
CT1a	1323.49
CT1a	1423.49
CT1a	1523.49
CT1a	1623.49
CT1a	1723.49
CT1a	1823.49
CT1a	1923.49
CT1a	2023.49
CT1a	2123.49
CT1a	2223.49
CT1a	2323.49
CT1a	2423.49
CT1a	2523.49
CT1a	2623.49

Landscape	GUD
CT2	361.28
CT2	461.28
CT2	561.28
CT2	661.28
CT2	761.28
CT2	861.28
CT2	961.28
CT2	1061.28
CT2	**1161.28**
CT2	1261.28
CT2	1361.28
CT2	1461.28
CT2	1561.28
CT2	1661.28
CT2	1761.28
CT2	1861.28
CT2	1961.28
CT2	2061.28

Table 3.4c. The giving-up-densities (GUD) that were used in sensitivity analysis of alternative foraging strategies for the **low efficiency (LE) forager (E = 875.88)**. The GUD for the MVT forager is indicated in bold font.

Landscape CT1	
GUD	**CC**
178.88	10346
278.88	10295
378.88	10372
478.88	10444
578.88	10493
678.88	10521
778.88	10548
878.88	10581
978.88	10607
1078.88	
1178.88	**10631**
1278.88	10650
1378.88	**H** 10657
1478.88	10585
1578.88	10596
1678.88	10518
1778.88	10529
1878.88	10352
1978.88	10268
2078.88	10182

Landscape CT1a	
GUD	**CC**
75.73	9438
175.73	9662
275.73	9726
375.73	**H 9762**
475.73	9613
575.73	9569
675.73	9623
775.73	9647
875.73	9663
975.73	9495
1075.73	9521
1175.73	9541
1275.73	9553
1375.73	9467
1475.73	9389
1575.73	9395
1675.73	9132

Landscape CT2	
GUD	**CC**
32.42	8595
132.42	8842
232.42	8989
332.42	**9064**
432.42	9100
532.42	**H** 9121
632.42	9044
732.42	8708
832.42	8738
932.42	8761
1032.42	8777
1132.42	8785
1232.42	8431

Table 3.5a. Cumulative consumption (CC) in grams at 12 h for **the efficient (EF) forager (E = 97.32)** resulting from different GUDs. The CC for the MVT forager is indicated in bold font, the highest CC for a given landscape is indicated with an **H**.

Landscape CT1	
GUD	**CC**
703.98	8670
803.98	8728
903.98	8799
1003.98	8889
1103.98	8901
1203.98	9008
1303.98	9092
1403.98	9116
1503.98	9152
1603.98	**H 9185**
1703.98	9164
1803.98	9112
1903.98	9170
2003.98	9030
2103.98	8980
2203.98	8928
2303.98	8802
2403.98	8831
2503.98	8604

Landscape CT1a	
GUD	**CC**
75.6	7124
175.6	7441
275.6	7408
375.6	7686
475.6	7900
575.6	8014
675.6	8138
775.6	8193
875.60	**8078**
975.6	8072
1075.6	8182
1175.6	8212
1275.6	8223
1375.6	8171
1475.6	8222
1575.6	**H** 8243
1675.6	8112
1775.6	8141
1875.6	7950
1975.6	7889
2075.6	7772
2175.6	7629
2275.6	7245

Landscape CT2	
GUD	**CC**
75.6	6719
175.6	7237
275.6	7258
375.6	7105
475.6	7252
575.6	7382
675.6	7538
775.6	7630
875.60	**7678**
975.6	**H** 7696
1075.6	7388
1175.6	7443
1275.6	7484
1375.6	7519
1475.6	7244
1575.6	7295
1675.6	7330
1775.6	7276

Table 3.5b. Cumulative consumption (CC) in grams at 12 h for **the medium efficiency (ME) forager (E = 486.60)** resulting from different GUDs. The CC for the MVT forager is indicated in bold font, the highest CC for a given landscape is indicated with an **H**.

Landscape CT1	
GUD	CC
1109.53	7740
1209.53	7826
1309.53	7855
1409.53	7969
1509.53	8046
1609.53	8083
1709.53	8136
1809.53	8105
1909.53	**8169**
2009.53	8163
2109.53	**H** 8193
2209.53	8026
2309.53	7846
2409.53	7889
2509.53	7850
2609.53	7663
2709.53	7194

Landscape CT1a	
GUD	CC
523.49	6689
623.49	6690
723.49	6915
823.49	7066
923.49	7159
1023.49	7225
1123.49	7184
1223.49	**7145**
1323.49	7221
1423.49	7262
1523.49	7176
1623.49	7272
1723.49	**H** 7317
1823.49	7215
1923.49	7172
2023.49	7082
2123.49	6905
2223.49	6959
2323.49	6690
2423.49	6358
2523.49	6689
2623.49	6690

Landscape CT2	
GUD	CC
361.28	6261
461.28	6402
561.28	6457
661.28	6341
761.28	6386
861.28	6551
961.28	6677
1061.28	6751
1161.28	**H 6786**
1261.28	6742
1361.28	6558
1461.28	6624
1561.28	6654
1661.28	6407
1761.28	6496
1861.28	6537
1961.28	6277
2061.28	6304

Table 3.5c. Cumulative consumption (CC) in grams at 12 h for the **low efficiency (LE) forager (E = 875.88)** resulting from different GUDs. The CC for the MVT forager is indicated in bold font, the highest CC for a given landscape is indicated with an **H**.

Figures

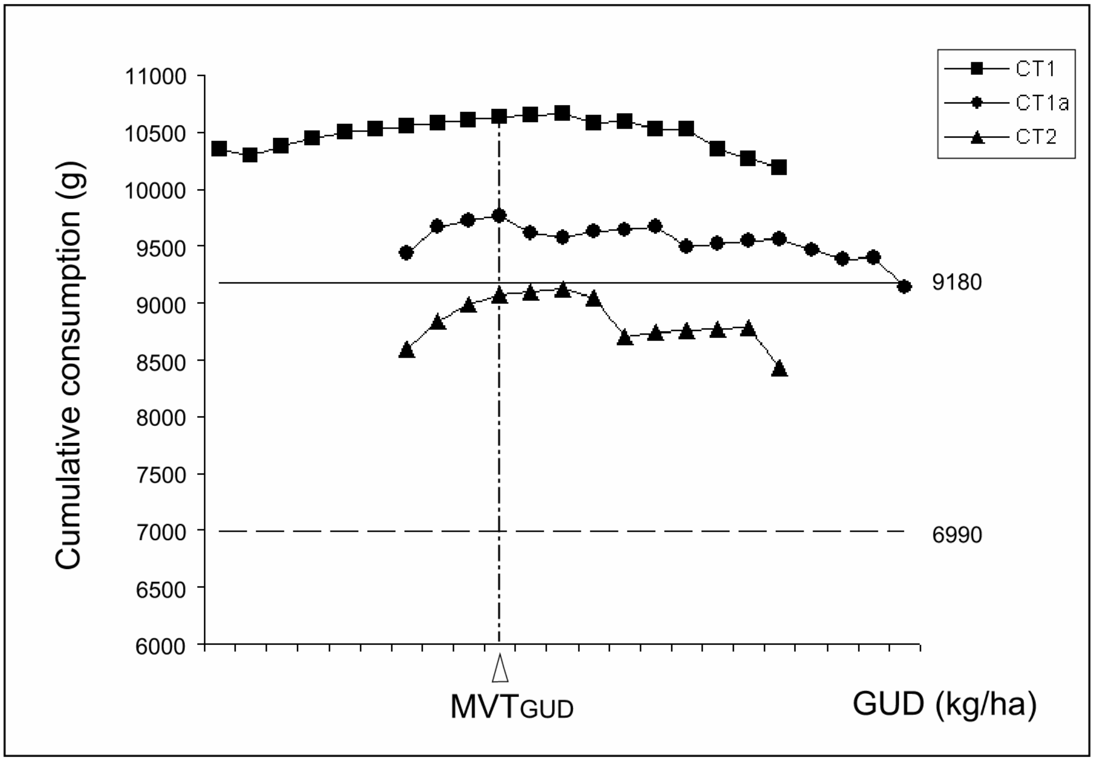

Figure 3.1a. Cumulative consumptions (CC) at 12 h as a function of GUD obtained as a result of the sensitivity analysis of the giving-up-density (GUD) for landscapes with different travel times (CT1: Tt = 0.1 h (squares); CT1a: Tt = 0.3 h (circles); CT2: Tt = 0.5 h (triangles)) for **the efficient (EF) forager (E = 97.32 kg/ha)**. The GUD obtained for the MVT forager (in a given landscape) is indicated with an arrow and dashed vertical line. The horizontal dashed (6990) and continuous (9180) lines represent the minimum and mean daily food requirements for a lactating female elk respectively.

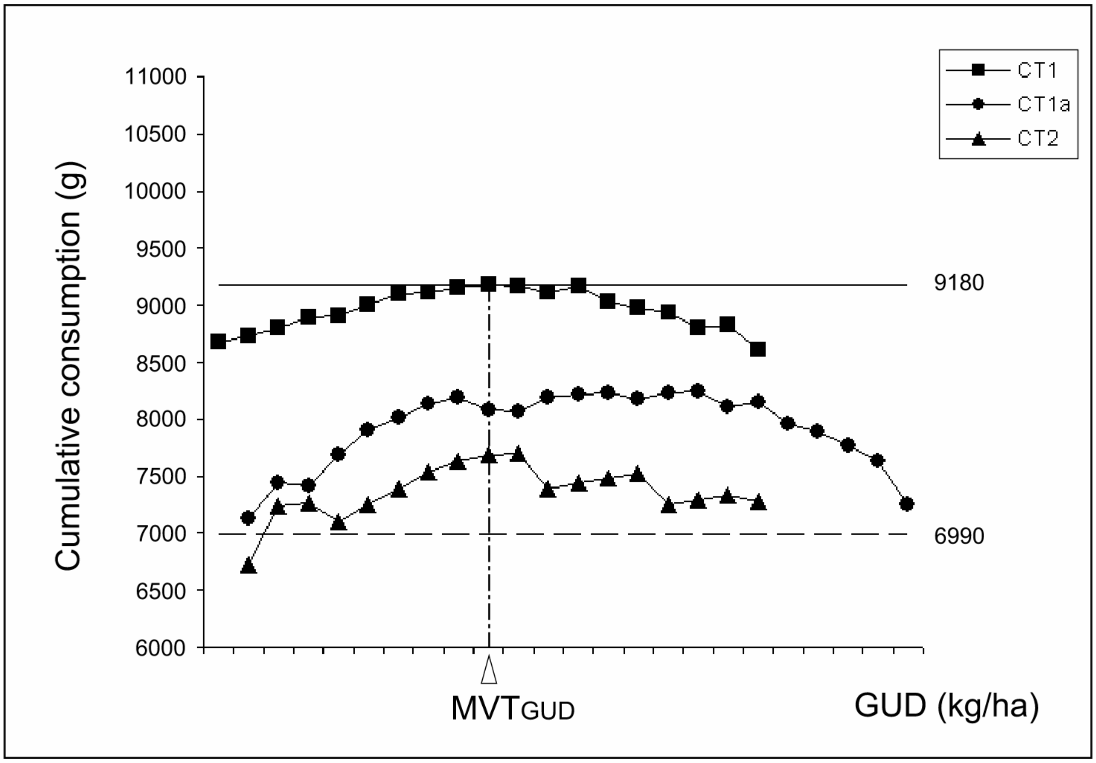

Figure 3.1b. Cumulative consumptions (CC) at 12 h as a function of GUD obtained as a result of the sensitivity analysis of the giving-up-density (GUD) for landscapes with different travel times (CT1: Tt = 0.1 h (squares); CT1a: Tt = 0.3 h (circles); CT2: Tt = 0.5 h (triangles)) for **the medium efficiency (ME) forager (E = 486.6 kg/ha)**. The GUD obtained for the MVT forager (in a given landscape) is indicated with an arrow and dashed vertical line. The horizontal dashed (6990) and continuous (9180) lines represent the minimum and mean daily food requirements for a lactating female elk respectively.

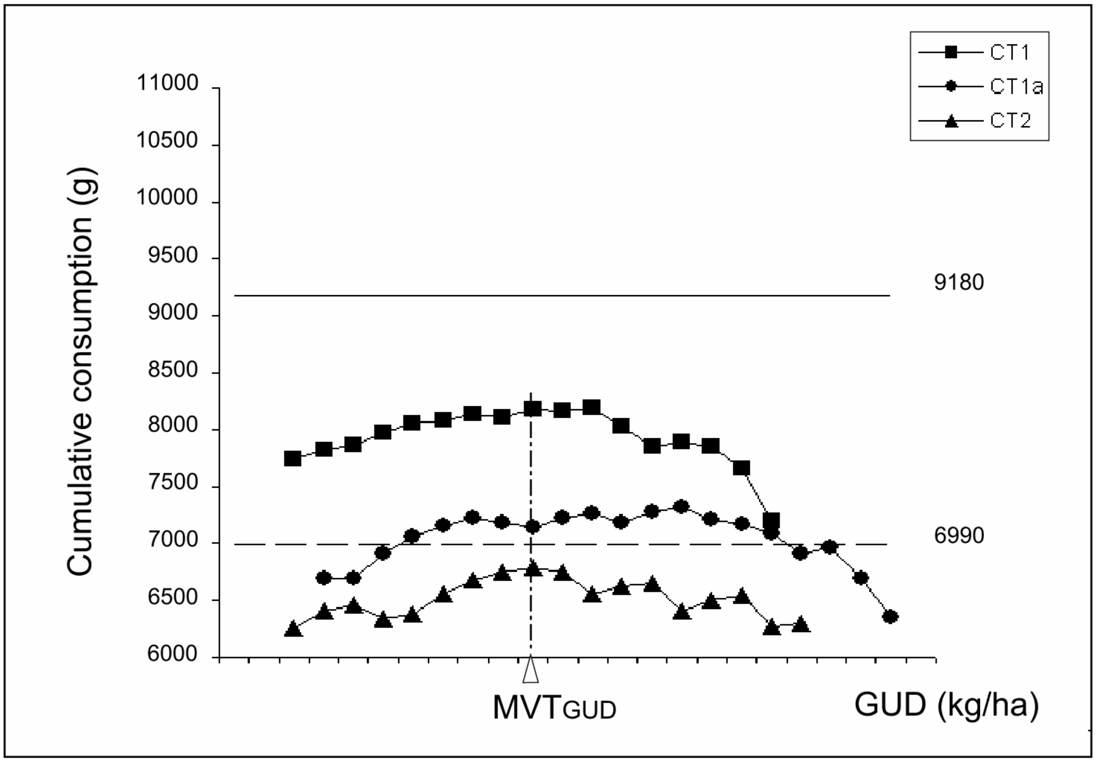

Figure 3.1c. Cumulative consumptions (CC) at 12 h as a function of GUD obtained as a result of the sensitivity analysis of the giving-up-density (GUD) for landscapes with different travel times (CT1: Tt = 0.1 h (squares); CT1a: Tt = 0.3 h (circles); CT2: Tt = 0.5 h (triangles)) for **the low efficiency (LE) forager (E = 875.88 kg/ha)**. The GUD obtained for the MVT forager (in a given landscape) is indicated with an arrow and dashed vertical line. The horizontal dashed (6990) and continuous (9180) lines represent the minimum and mean daily food requirements for a lactating female elk respectively.

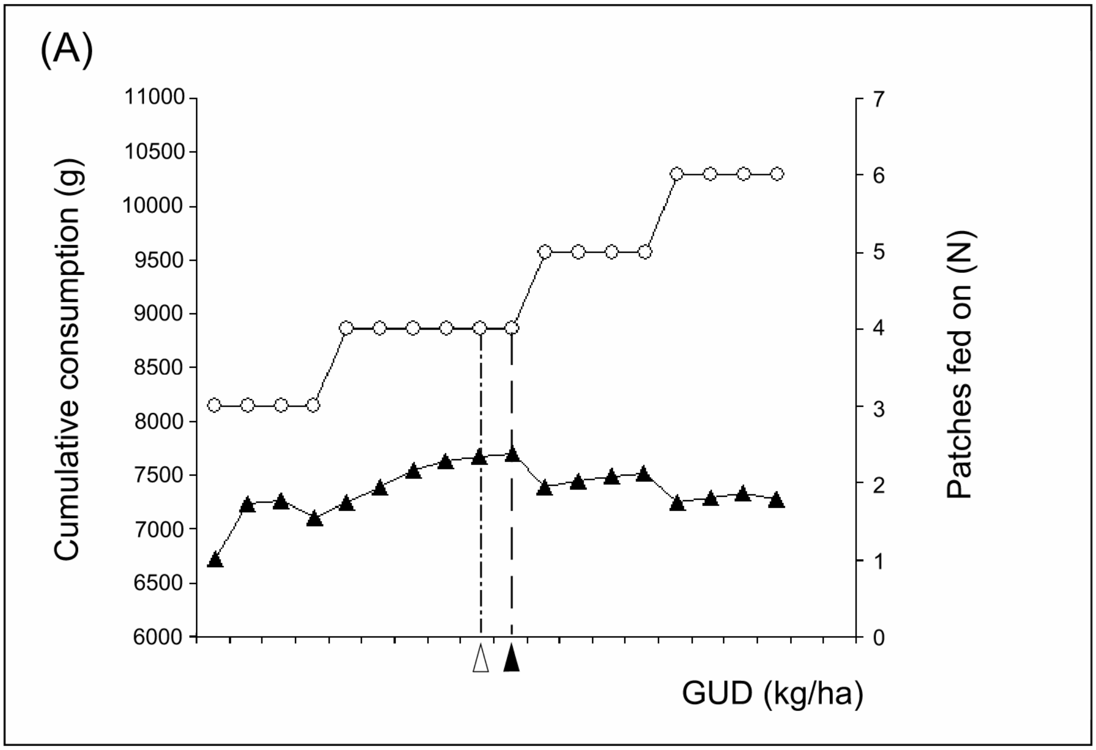

Figure 3.2a. 1) Triangles: cumulative consumptions (CC) at 12 h obtained as a result of the sensitivity analysis of the giving-up-density (GUD) for the ME forager (E = 486.60) feeding in landscape CT2 (Tt = 0.5h). The GUD obtained for the MVT forager (875.60) is indicated with an open arrow; the GUD for the strategy that produced highest CC at 12h (975.60) is indicated with a dark arrow. 2) Circles: number of patches fed on until time T=12h as a function of a specific foraging strategy (GUD).

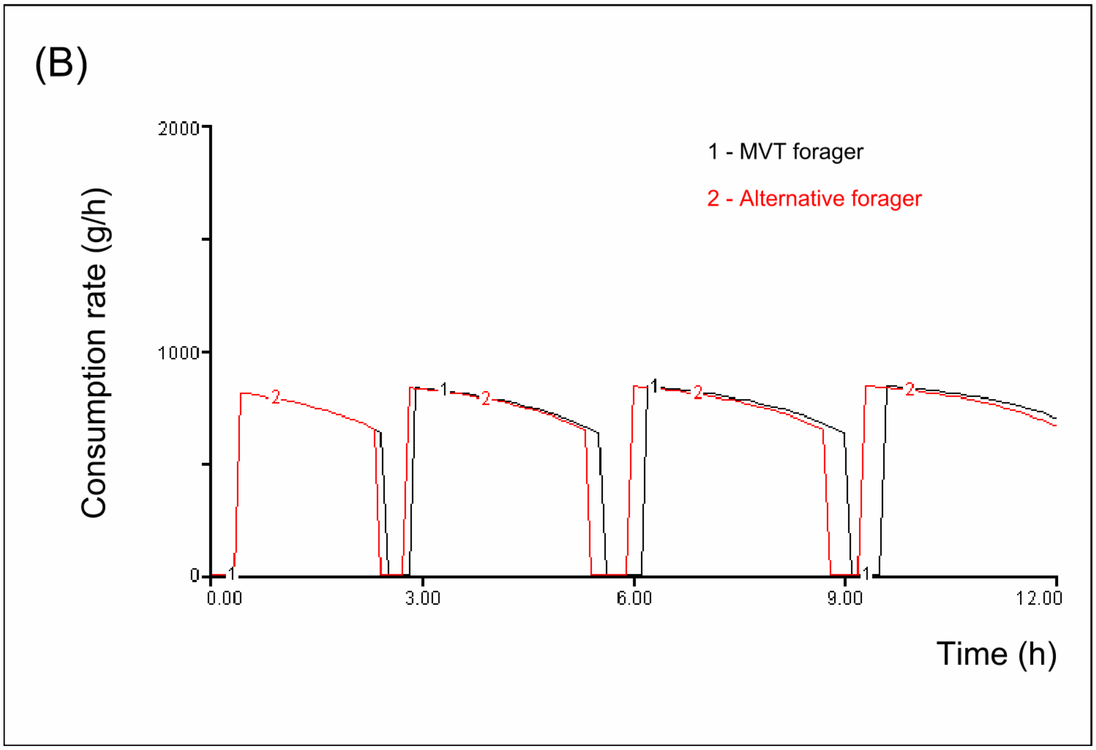

Figure 3.2b. Consumption rate for the ME foragers (E=486.6) feeding in landscape CT2. The MVT forager: 1-black line; the alternative forager: 2 – red line. Alternative forager performed better at the end of the 12 h simulation. Consumption rate drops to 0 when the animal is in transit.

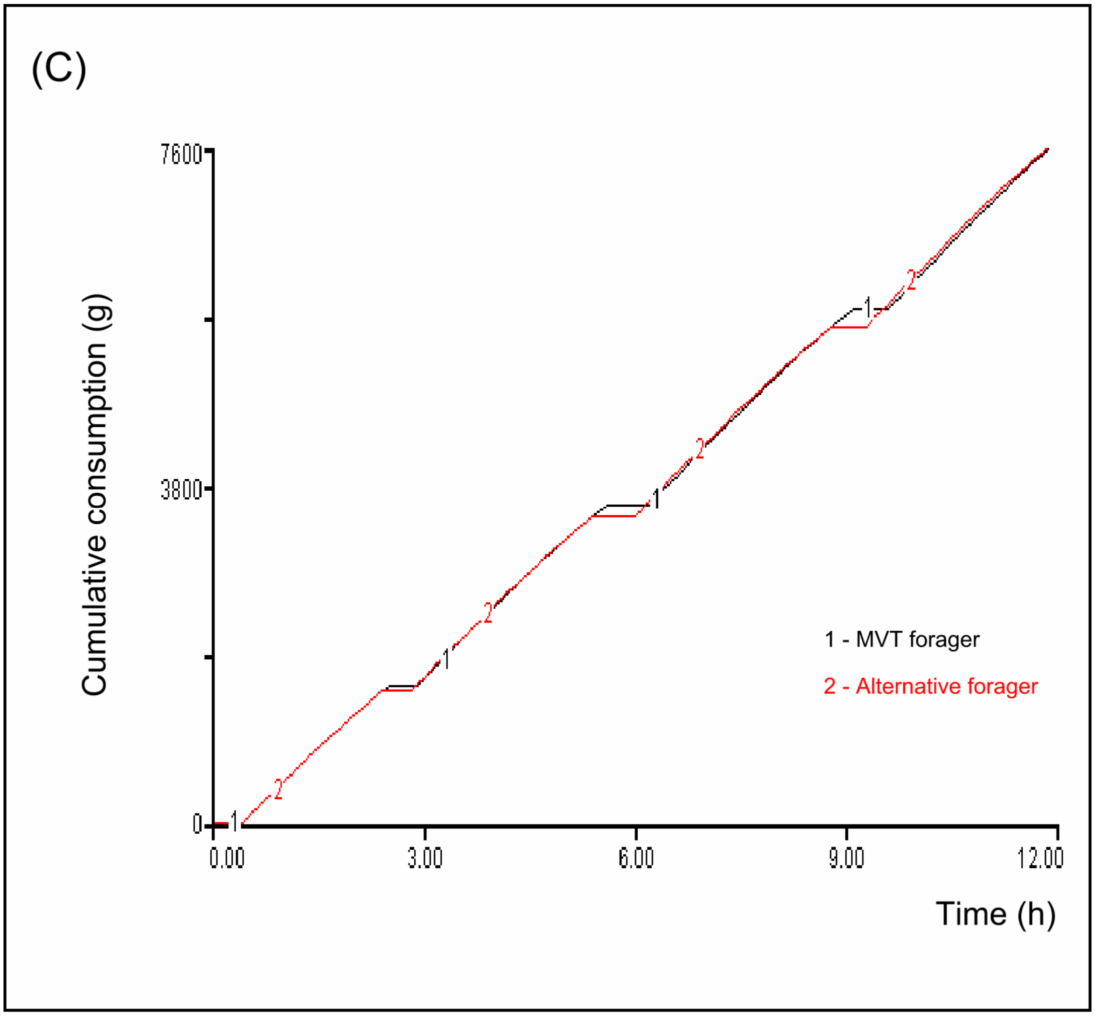

Figure 3.2c. Changes to cumulative consumptions (CC) of the MVT (1 – dark line) and the alternative forager (2 – red line) for the ME foragers (E=486.6) feeding in landscape CT2.

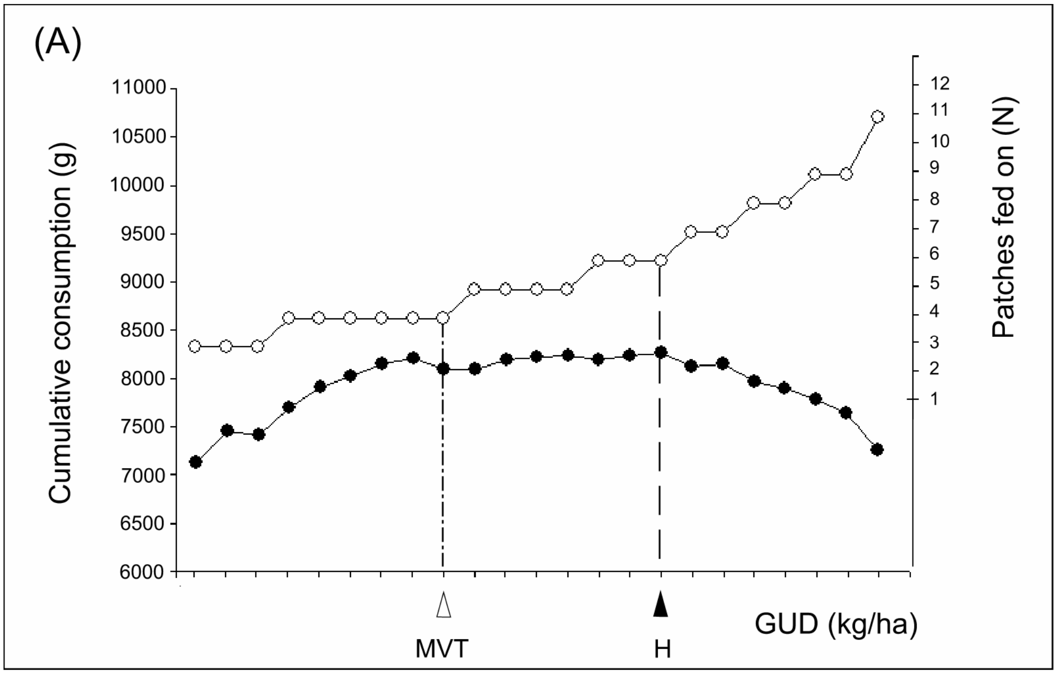

Figure 3.3a. 1) Dark circles: cumulative consumptions (CC) at 12 h obtained as a result of the sensitivity analysis of the giving-up-density (GUD) for the ME forager (E = 486.60) feeding in landscape CT1a (Tt = 0. 3h). The GUD obtained for the MVT forager (875.6 kg/ha) is indicated with an open arrow; the GUD for the strategy that produced the highest CC at 12h (1575.6 kg/ha) is indicated with a dark arrow. 2) Open circles: patches fed on until time T=12 h as a function of a foraging strategy (GUD).

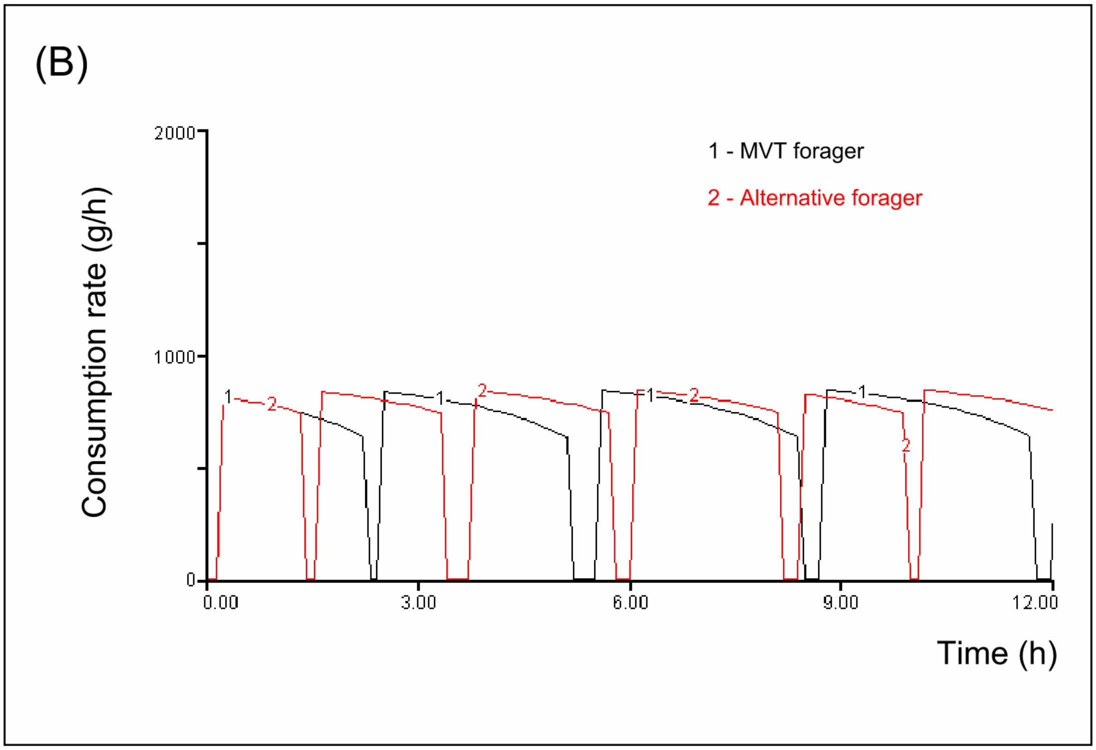

Figure 3.3b. Consumption rate for the ME foragers (E=486.6) feeding in landscape CT1a. MVT forager: 1-black line; the alternative forager: 2 – red line. Alternative forager performed better at the end of the 12 h simulation. Consumption rate drops to 0 when the animal is in transit.

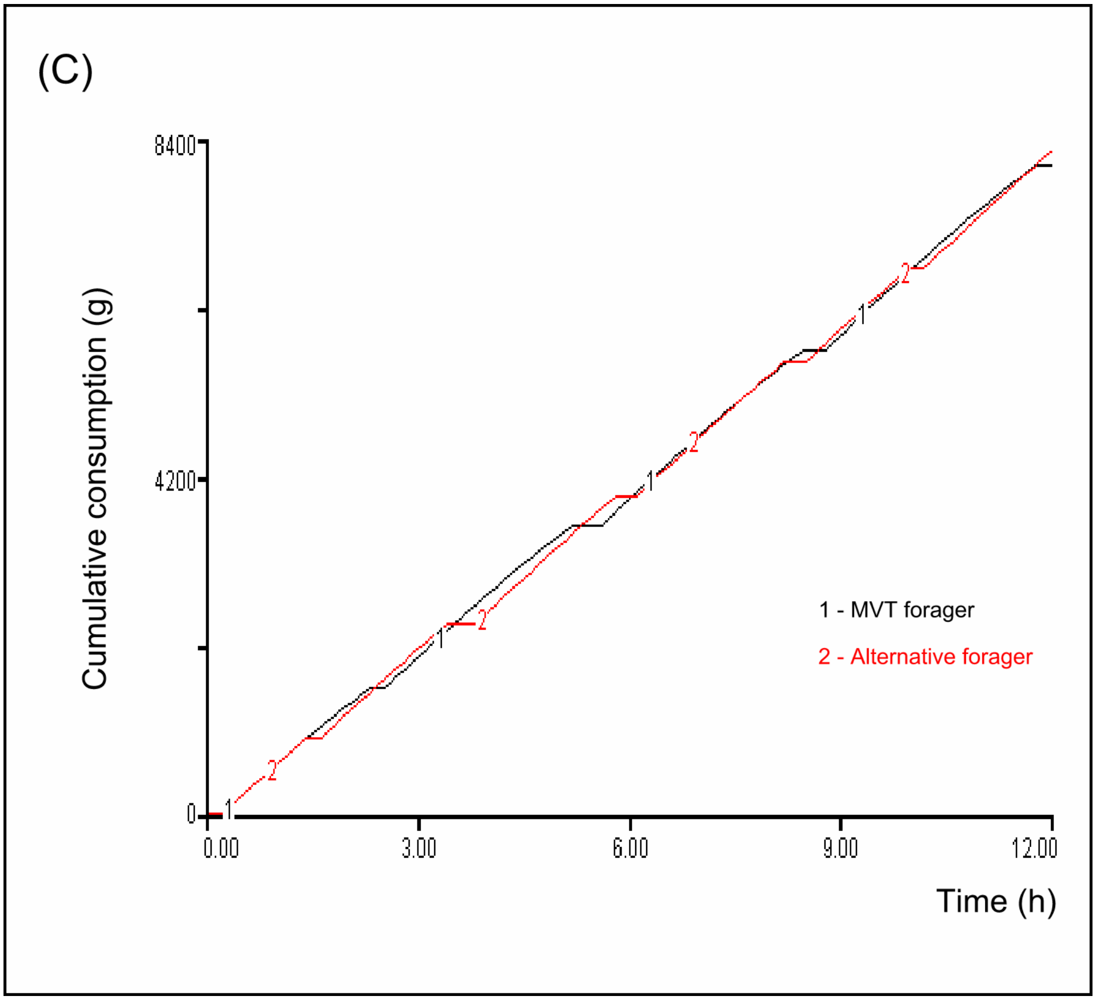

Figure 3.3c. Changes to cumulative consumptions (CC) of the MVT (1 – dark line) and the alternative forager (2 – red line) for the ME foragers (E=486.6) feeding in landscape CT1a.

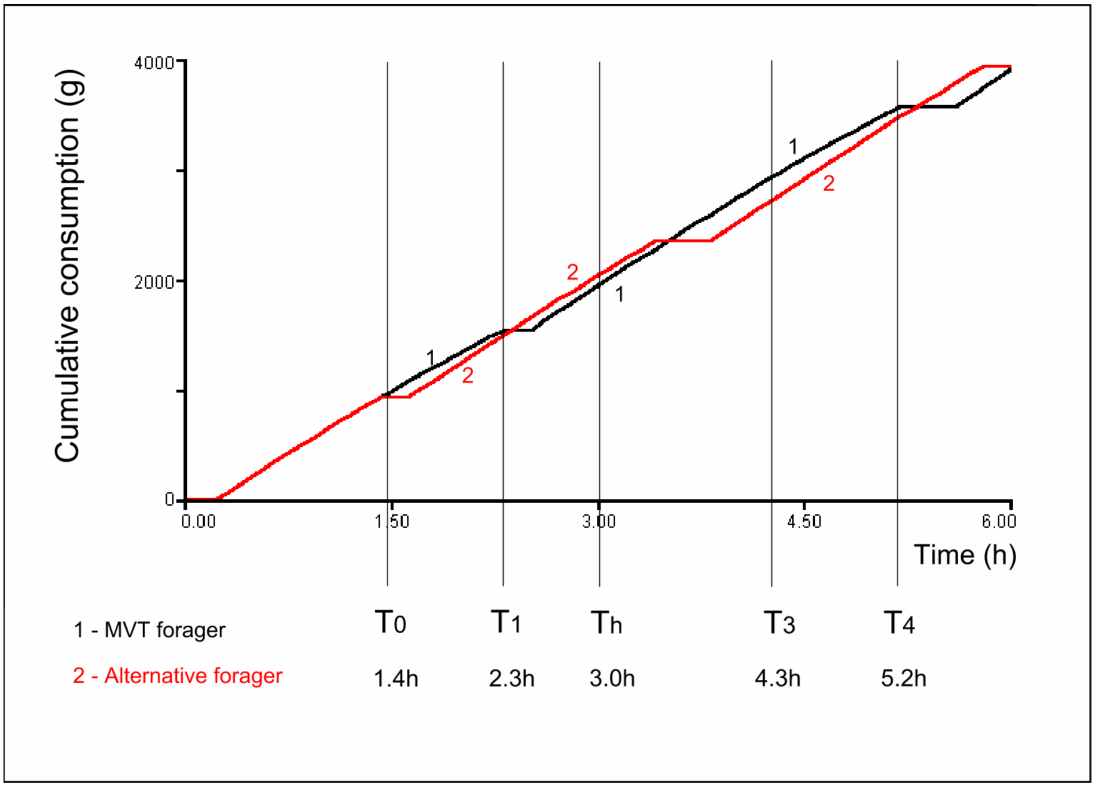

Figure 3.4. Cumulative consumptions (CC) of the MVT forager (1 black line) and the ALT forager (2 – grey line). Following relationships between the number of feeding cycles (N) and patches fed on (M) are true for the indicated points in time:

T_0: $N_{ALT} = M_{ALT}$ $N_{MVT} < M_{MVT}$
T_1: $N_{ALT} < M_{ALT}$ $N_{MVT} = M_{MVT}$
T_h: $N_{ALT} < M_{ALT}$ $N_{MVT} < M_{MVT}$
T_3: $N_{ALT} < M_{ALT}$ $N_{MVT} < M_{MVT}$
T_4: $N_{ALT} < M_{ALT}$ $N_{MVT} = M_{MVT}$

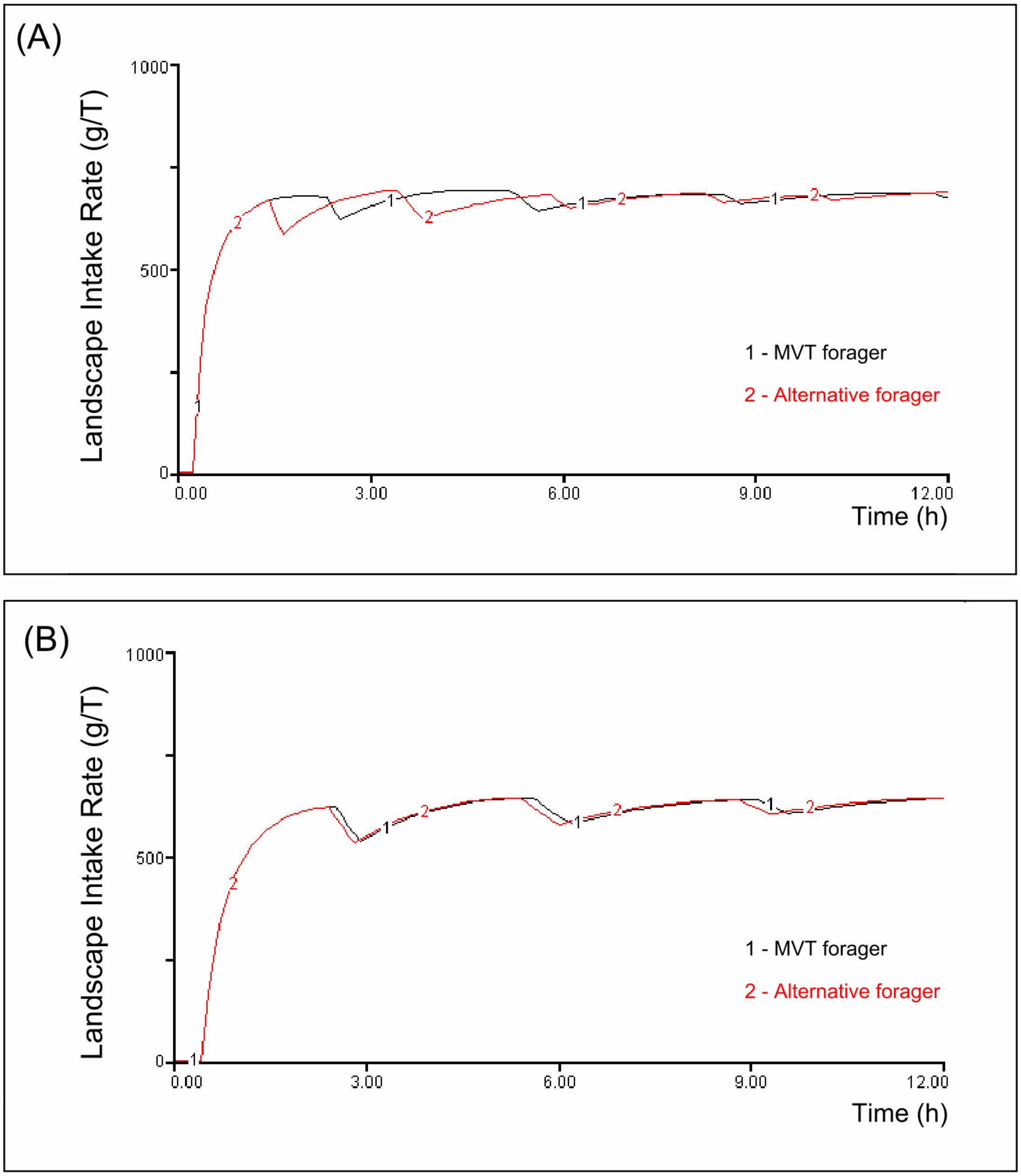

Figure 3.5. The alternative forager achieves CC higher then the MVT forager only in the time intervals when its LIR is higher than the LIR of the MVT forager. The LIR trajectories of the ME forager feeding in A: Landscape CT1a, 1 – the MVT forager (GUD = 875.6kg/ha), 2 – the alternative forager (GUD = 1575.6); B: Landscape CT2, 1 – the MVT forager (GUD = 875.6kg/ha) 2 – the alternative forager (GUD = 975.6 kg/ha).

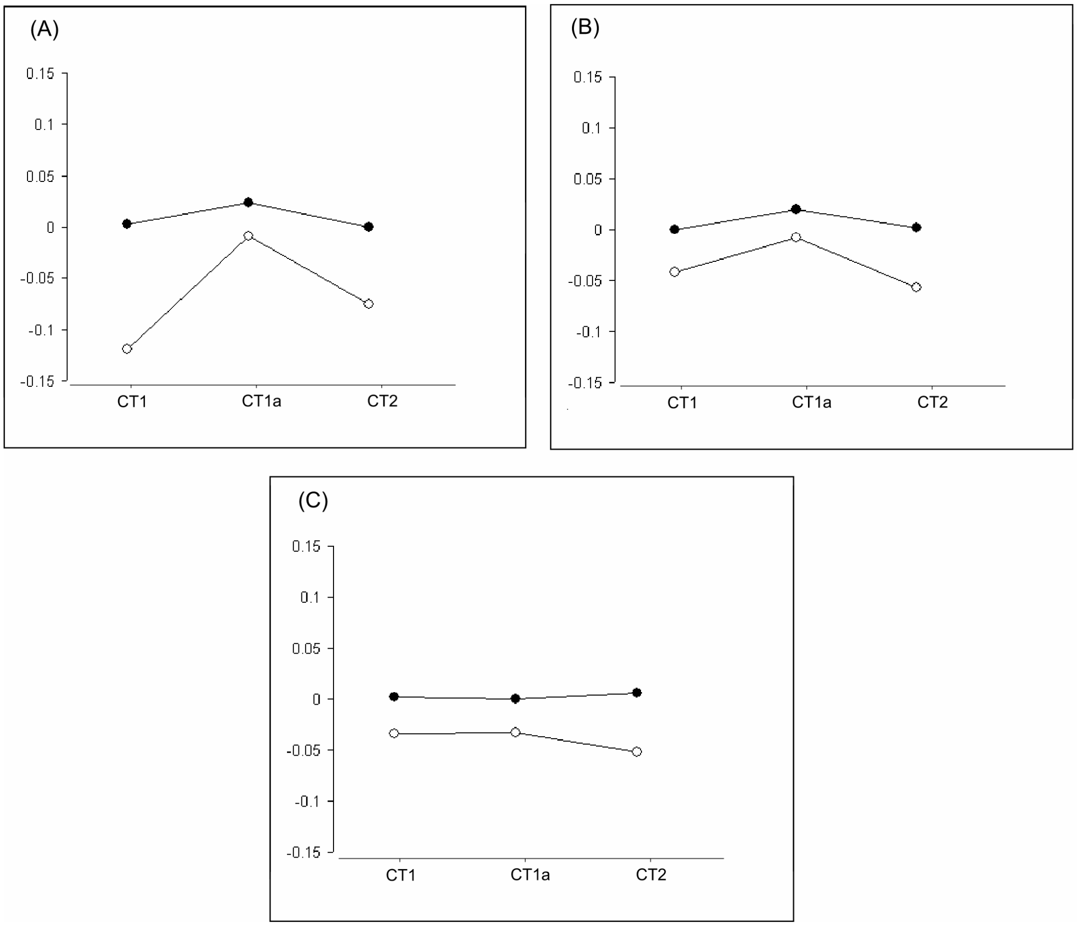

Figure 3.6. Proportional deviations in CCs from the CC obtained by the MVT forager at 12 h in response to different foraging strategies (GUD). Closed circles indicate the proportional difference between the highest CCs and the MVT CC in a given landscape; open circles indicate the difference between the lowest CCs and the MVT CC in a given landscape. A: LE foragers (E = 875.88 kg/ha), B: ME foragers (E = 486.6 kg/ha), C: E foragers (E = 97.32 kg/ha).

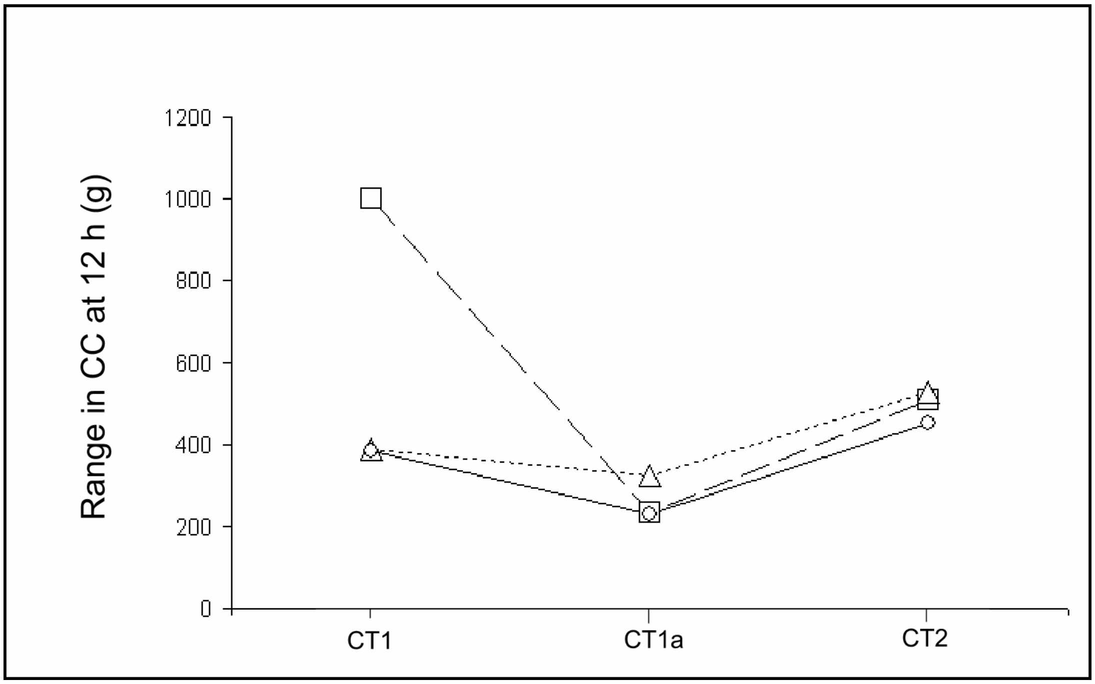

Figure 3.7. Range in CC at T = 12 h depending on the landscape (travel time) and the efficiency of the forager (E). Squares: LE forager (E = 875.88 kg.ha): Circles: ME forager (E = 486.6 kg/ha); Triangles: E forager (E = 97.32 kg/ha).

Chapter 4. Smart foraging: rules and implications.

4.1. Introduction

Natural selection favors behaviors that maximize fitness by increasing the proportion of genes responsible for the specific behavioral trait in the next generation. It is commonly assumed that natural selection should, therefore, favor the development of foraging behaviors that maximize the net energy/nutrient intake per unit of time (or cost). Consequently, it was generally accepted that animals should use the marginal value theorem (MVT) proposed by Charnov (1976) while foraging to optimize their benefit-cost ratio and the MVT became the basis of the foraging theories. The MVT describes a forager's behavior in a patchy habitat and links an expected travel time among patches and an observed intake rate within each patch to obtain the patch residence time. According to Charnov (1976), the MVT describes the use of a patchy habitat by an optimal predator that optimizes its benefit-cost ratio.

Although the MVT received support from field research across different taxa (Cassini et al. 1990, Cuthill et al. 1994, Jiang and Hudson 1993, Nolet and Klaassen 2009, Tentelier et al. 2009, Van Gils and Tijsen 2007,Zhang et al. 2009), investigators identified examples of animals not using MVT (Alonso et al. 1995, Moen et al. 1998, Searle et al. 2005, Thiel and Hoffmeister 2004, Wajnberg et al. 2006). These inconsistencies raised questions about the MVT and suggested the theory may lack biological realism. Nonacs (2001) proposed that it should be amended by incorporating biological and ecological conditions describing a particular animal and its habitat. More recently, the applicability of the MVT was found to depend on the scale at which the forager operates (Wajnberg et al. 2006), and that strategies alternative to MVT behaviors may be more efficient in maximizing long term forage intake if the forager is limited by time (Chapter 3).

Accepting the MVT as the optimal foraging strategy assumes that individuals should always aim at achieving the highest possible gains, consume as much as possible and optimize its benefit-cost ratio while foraging. The flaw is the assumption that an individual can out-compete other members of its population only by performing at the maximum of its ability and by maximizing its food intake. In terms of foraging behaviors, for an animal to survive and reproduce at the highest possible level, it is enough to meet dietary requirements for maximum reproduction. To win a competition it is sufficient to be better than competitors and for some individuals that could translate into behaviors that result in gains lower than could be achieved by performing at the maximum potential. In other words, at least some animals in a population should not be expected to do their best while foraging and it should be sufficient for them to do just "enough" so that this "enough" satisfies their needs associated with maximizing fitness. It could be argued that depending on foraging skills, habitat productivity, and other external circumstances, this could be achieved by performing below the animal's maximum potential.

If there are reasons for foragers not to maximize their consumption at all times and the MVT is not the best model to describe foraging behaviors in most situations then, how should the optimal foraging strategy be described? According to Darwin's theory of natural selection, individuals should maximize their fitness. Maximizing one's fitness, however, may not be the same as maximizing one's food consumption. On the contrary, it may be more beneficial, in terms of fitness, to simply satisfy basic foraging requirements and focus on activities other than foraging that maximize fitness (predator avoidance, mating, and care of the offspring). The concept and term 'satisficing' was introduced by a Nobel Laureate in economics Herbert Simon (Simon 1956). He pointed out that organisms have insufficient abilities and knowledge to discover an optimal path, and therefore, should pursue a "satisficing" path that would allow satisfaction at some specified level of all of its needs. Although the idea of satisficing has been widely applied in many disciplines ranging from psychology to computer sciences (Durbach 2009, Fu and Pirolli 2007, Oppenheimer et al. 2009, Tyson 2008), including economy (Galand 2009), where it originated (Simon 1955, 1956), it remains poorly explored in ecology. One of the first attempts to examine the applicability of satisficing in biology was the work of Ward (1992) who reviewed research on foraging behaviors in ecology and associated foraging models. He found that diet selection by Columbian ground squirrels (*Spermophilus columbinaus*) and ants (*Lasius pallitarsis*) was not optimal and argued that it was an indication of the foragers using satisficing. On the other hand, Nonacs and Dill (1993) argued that satisficing fails as a coherent alternative to optimality because its predictions are not testable and therefore cannot be refuted. However, contrary to the arguments by Nonacs and Dill (1993) more recent research suggests that animals may actually use satisficing strategies (Killen et al. 2007, Nolet et al. 2006). Recent work by Caramel and Ben-Haim (2005) is a rare example of applying a satisficing foraging model for describing animal behaviors.

The ongoing debate on strategies that animals should employ in utilizing resources (Caramel and Ben-Haim 2005, Searle et al. 2005, Wajnberg et al. 2006), the apparent applicability of the same concepts in ecology and economics (Maynard-Smith 1982, Lomincki 1978, 1988), and the need for more integration between economic and ecological concepts (Hammerstein and Hagen 2005) triggered this study.

Based on the existing models of foraging (i.e. the MVT and satisficing), I aimed to identify a foraging strategy or a set of foraging rules that an animal should follow to meet its daily food requirements sufficient to reproduce at the highest possible rate and still be able to engage in other activites increasing fitness thus maximizing it. I was also interested if any patterns in these satisficing foraging behaviors could be identified and if it would be possible to describe these patterns in a form of a mathematical model that would allow formulation of a testable foraging behavior model.

4.2. Methods

4.2.1. Simulation tool

To analyze a vast spectrum of foraging behaviors of elk (*Cervus elaphus*), I designed and employed a computer simulation model SeekSMART. A detailed description of this simulation tool is provided in the second Chapter of the thesis. The simulator allows for examining forage consumption by a forager having its own intrinsic characteristics (i.e., functional response curve (FRC) and digestive mechanisms) and feeding in different landscapes by using a variety of foraging strategies (such as the MVT and alternatives). SeekSMART is a mechanistic and deterministic model that has a fine temporal and spatial resolution and the ability to inspect the foraging behavior across multiple spatial and temporal scales.

For the purpose of this research SeekSMART was calibrated based on data obtained from research on elk (*Cervus elaphus*). The well known ecology and foraging behavior of elk allowed populating all components of the model with real field data, and to validate the outputs of the model against the results of findings from field research. This makes elk an ideal subject for a simulation modeling study.

SeekSMART allows for examination of foragers having specific functional response curves (FRC) by defining the *maximum intake rate* (M) and the slope of the FRC (foraging biomass at which intake rate is equal to half of the maximum intake rate, called the *efficiency* (E)). By adjusting the maximum intake rate and the efficiency of the forager, any shape of type II FRC can be assigned to the forager. Another set of parameters that define the forager is digestion time (DT), digestion rate (DR) and gut capacity (full stomach FS). The DT is the time required by a satiated forager to digest a specific proportion of the current stomach content that would allow the forager to resume foraging. Full stomach (FS) is a parameter that specifies the amount of forage consumed (grams, dry matter (DM)) at which a forager's stomach is full and the forager is satiated. The model assumes that a forager will pause its foraging if its stomach is full. The digestion rate (DR) is the proportion of consumed forage that the forager is able to digest within one hour. The model assumes that the forager is not ruminating (digesting) while foraging and rumination and digestion occur only when the forager moves from one patch to another patch or when the animal pauses its foraging bout due to full stomach.

In addition to the characteristics of the forager described above, the model allows variation in and specifing of the decision-making processes that the forager uses to decide when to leave a patch. For example, the forager may leave patches when forage available in the current patch drops to an arbitrary assigned value. Another option allows the forager to leave the patch due to the density of forage available in the patch dropping to the landscape average. The third approach that can be tested is that the forager follows the Marginal Value Theorem (MVT). In this case, the average travel time between patches and the average forage availability in a patch determine when a specific forager leaves the current patch (N) and moves to the next patch (N+1). Another patch departure rule that can be tested in SeekSMART is that the forager feeds in a patch for an arbitrary assigned residence time.

Because I was interested in analyzing a spectrum of foraging behaviors of undisturbed animals (no inter or intra-species interactions) feeding in several different landscapes, the following important assumptions were applied to all simulations. First, I assumed that the forager was free from the risk of predation. The second assumption was that there were no other animals in the foraging area, and there were no factors that obviated the forager from applying its chosen foraging strategy. Moreover, the nutritional state of the animal was neutral, which means that the forager was not nutritionally stressed, but its gut was almost empty at the onset of a simulation run.

SeekSMART describes an animal feeding in a landscape of forage patches with specific distributions defined by travel times between patches, and quality defined by forage biomass density (or biomass). The model assumes that forage in a patch is homogeneous in terms of nutrients and calories. For the initial assessment of foragers characterized by specific functional response curves (value of parameter E) feeding in a spectrum of landscapes, I created 3 main landscapes based on the quality of patches: landscape A was a poor quality habitat with the average initial density of forage at 1008.8 kg/ha (range: 852 – 1150). Landscape B was more abundant in forage (average: 2035, range: 1702 – 2299 kg/ha) and landscape C was the best quality landscape (average: 3011.3 kg/ha, range: 2564 – 3448). To avoid bias, quality of individual patches in each landscape type was assigned by a random number generator within the above mentioned ranges. These 3 main types of landscape were further divided depending on travel times between patches into 5 subtypes: T1 (average Tt = 0.1 h), T2 (average Tt = 0.5 h), T3 (average Tt = 0.1 h), T4 (average Tt = 2 h), and T5 (average Tt = 4 h). This resulted in a total of 15 landscapes (e.g., CT1, CT2, CT3, CT4, CT5, etc.). In the simulation experiments completed for the discussion described in Chapter 3, to generate a more realistic spectrum of landscapes, I created one additional landscape CT1a with the average Tt = 0.3 h.

Although SeekSMART allows for testing the effects of patch size, to focus this discussion on the effects of patch quality and travel times, the size of all patches was constant at 9 m^2. Chapter 2 provides a more detailed explanation of the rationale for this size of a patch as well as more detailed description of landscapes created in the model.

4.2.2. Scenarios

First, I analyzed the results from Chapter 3 obtained from examination of different foragers (i.e., having different shapes of the functional response curve

(FRC)) using a variety of foraging strategies (different patch giving-up densities (GUD)) across a spectrum of landscapes, to determine if there are potential candidates (foragers that at the end of the 12 h simulation time reached cumulative consumption (CC) higher than or equal to the CC required for successful reproduction in a specific landscape) for using strategies other than MVT to satisfy their daily food requirements.

In the second phase, I examined the behavior of foragers selected in the first phase and the associated foraging strategies. Because benefits are represented in SeekSMART by forage consumption and time is a surrogate for costs, a foraging strategy can be defined as a specific allocation of travel time (Tt) and patch residence time (Tr) with the associated giving-up density (GUD) to achieve specific cumulative consumption (CC) at any given total time (T). Therefore, to assess the applicability of different foraging strategies, I monitored the following variables for each scenario: CC at 12 h, total time needed for the forager to reach the required consumption of 9180 g (Total T required), time remaining to 12 h after the food requirement was met (extra T), total travel time during the 12 h period (TTt), total residence time during the 12 h period (TTr), and the number of patches fed on until T = 12 h (M). Based on data from Gedir and Hudson (2000a), I assumed that 9180 g (DM) is the daily forage requirement for a lactating female elk, and that this is equivalent with a consumption required for successful reproduction. Forage requirements for elk reach highest values for lactating females (Gedir and Hudson 2000b) and fitness of a pregnant or lactating female is limited by her ability to raise her young. Thus, if predation and disease are excluded, the only limiting factor for maximizing fitness is the ability of the female to satisfy her food requirements for maximum reproduction (as opposed to males that could further increase their fitness by mating with more females). Based on this rationale, I decided to use data on forage requirements of lactating female elk to examine a variety of foraging strategies in the context of satisficing.

I wanted to (1) identify all foraging strategies other than MVT strategies that would allow foragers to satisfy their daily consumption requirements needed for successful reproduction (to achieve this goal I conducted sensitivity analysis for GUD for the selected foragers and landscapes. I conducted this analysis at 100 kg/ha intervals until a CC at 12 h equal to 9180 g was achieved and a clear declining trend in CC at 12 h was determined); and (2) categorize these strategies depending on travel time and patch residence time allocated by the forager in each strategy and by the extra time (extra T) that the forager would gain using a specific strategy. This would allow the examination of the behaviors associated with foraging strategies and potentially help in formulating a satisficing model more complex than the trivial assumption that satisficing is just ‘laziness’ (Ward 1992, Nonacs and Dill 1993). I also expected that categorizing foraging strategies that allow the forager to satisfy its daily forage requirements sufficient for maximum reproduction without maximizing forage intake at the end of the trial (it is sufficient to eat enough to reproduce at the highest possible rate), could reveal a pattern or trend that would describe a foraging behavior that is based on the satisficing principle and allows for fitness maximization.

4.3. Results

Outputs of the sensitivity analysis indicate that only two foragers where able to meet or exceed CC of 9180 g, which is the daily consumption required by lactating female elk (Gedir and Hudson 2000a): the efficient (E) forager in landscapes CT1 and CT1a, and the medium efficiency (ME) forager in landscape CT1 (Figures 4.1a – 4.1c).

The goal of the previous sensitivity analysis for GUD conducted in Chapter 3 was to identify a foraging strategy (a specific GUD) that produces the highest CC at time = 12 h. In this research, I was interested in identifying all foraging behaviors that would allow for satisfying the needs of a lactating female elk. Therefore, a wide spectrum of GUDs was included in the sensitivity analysis (Tables 4.1 – 4.3). This extensive analysis reveals that depending on the combination of forager's efficiency (E) and the distribution of resources, the potential for using strategies that do not maximize consumption increases with increasing E and decreasing travel time (Tt). The efficient (EF) forager could use a wide range of GUDs (0 – 2578.88) and the animal would be able to exceed its daily food requirements in all cases when foraging in landscape CT1 using GUDs within this range (Figure 4.1a). The same forager (EF) feeding in landscape CT1a (more travel required) would have to be more careful in choosing its strategy (GUD): if the value of GUD was higher than 1575.73 kg/ha or lower than 75.73 kg/ha, the forager was not able to meet its daily food requirements (Figure 4.1b). The situation was more difficult for the medium efficiency (ME) forager: the virtual elk with E = 486.6 kg/ha was able to meet its daily food requirements only in the landscape with shortest travel times (CT1) when using only one GUD: the value associated with the MVT strategy (1603.98 kg/ha), which was the strategy that produced the maximum CC at 12 h (Figure 4.1c). Across the entire spectrum of GUDs the ME forager was not able to achieve CC that would allow attaining the required consumption by using strategies other than MVT.

Figure 4.2 reveals opposite trends in the total travel time (TTt) and extra time (extra T). With increasing GUD, TTt increased and extra T, after reaching a peak, decreased. As could be expected, the highest values of extra T were associated with maximizing strategies and the highest value of TTt was associated with a behavior that allowed to satisfy the required CC, but demanded continuous foraging by the animal during the entire duration of the trial.

This analysis reveals two main types of foraging behaviors that efficient foragers could use: 1) maximize the CC at the end of the trial, and 2) satisfy the requirements for successful reproduction. Whereas there is only one strategy that maximizes CC at the end of the trial, and this may or may not be the MVT (Figures 4.1 and 4.3), a variety of satisficing foraging behaviors (GUDs) exists.

The most efficient foragers feeding in landscapes with short travel times have the broadest selection of satisficing behaviors (Figure 4.1a). Less efficient foragers, depending on their efficiency in utilizing resources and the distribution of these resources, could be left with no choice but to use a strategy that maximizes CC (e.g., ME forager, Figure 4.1c). To maximize the CC, time limited foragers should adjust their patch residence times (Tr) as described in Chapter 3. This could result in an animal using a strategy different than the MVT. To satisfy the requirements of successful reproduction, efficient foragers could use a spectrum of foraging strategies that reflect a "satisficing" range of GUDs and are different than the MVT GUD.

4.4. Discussion

The simulation results obtained in this research indicate that satisficing behaviors should be expected in nature. My outputs reveal that, similarly to economic systems, where firms adjust their prices only if their profits fall below a "normal" or "fair" level defined by the satisficing level (Galand 2009); at least some animals should be able to use satisficing foraging behaviors and still maximize fitness. Depending on the productivity of the habitat (distribution and quality of patches) and the efficiency of the forager (shape of the FRC), the difference between the minimum required consumption (to survive and reproduce at the highest rate) and the maximum potential cumulative consumption that the forager can achieve may be quite large (Figures 4.1a and 4.1b). The bigger this difference is the more choices the forager has when deciding on its foraging strategy and a wider range of foraging behaviors could be employed by the forager. This finding indicates that satisficing, widely applied in economics (Galand 2009) and other disciplines (Durbach 2009, Fu and Pirolli 2007, Oppenheimer et al. 2009) should be observed in ecology. My simulation results allow for close examination of a variety of satisficing behaviors.

As pointed out by Ward (1992), two aspects of satisficing theory are applied in ecology: one pertains to satisfying minimum requirements, and the other aims at describing behaviors that should be applied by animals in situations of information or time constraints. Originally satisficing was proposed (Simon 1955, 1956) as behavior that could be applied in situations where individuals have limited knowledge of the environment and thus are not able to find the optimal solution. The ecological model developed by Caramel and Ben-Haim (2005) is designed for these situations where animals have limited knowledge of the landscape (info-gap satisficing). Because most animals have annual home ranges and many are territorial, it could be argued that in most cases foragers have some knowledge of their landscape. Only dispersing individuals exploring new habitats have little knowledge of the environment and resources that could be expected. In this research, I related these two main currents of satisficing theory: the virtual forager in the simulations was limited by time and the sensitivity analysis of GUD could be applied to foragers that had different knowledge of the habitat (depending on the goal of the forager and its knowledge, the animal could use different GUDs).

If the goal of the animal is to achieve a specific CC at the end of the trial (e.g., satisfy minimum requirements), then the total sum of forage consumed from all patches (CC) should be equal to the predefined goal. This is quite obvious and was described as trivial by Nonacs and Dill (1993), who failed, however, to describe it mathematically. The mathematical expression to describe the above statement is:

$$\sum_{i=1}^{n} \int_{To}^{Te} C = CCr$$

where:

To – time when the animal starts foraging in patch N,
Te – time when the animal terminates foraging in patch N (thus Te – To = Tr),
C – consumption from patch N
CCr – daily required cumulative consumption

Because consumption within a patch is described by type II functional response, the above can be expressed in a more detailed form:

$$\sum_{i=1}^{n} \int_{F(To)}^{F(Te)} M\,(\,F/\,(E+F)\,) \;=\; CCr$$

where:

M – maximum consumption rate (asymptotic intake rate)

E – efficiency of the forager: the forage biomass density at which the intake rate drops to 50% of the maximum intake rate (defines the slope of the FRC).

F - current forage biomass density in the patch.

F(To) – forage biomass density in the patch when the animal starts foraging in patch N

F(Te) – forage biomass density in the patch when the animal terminates foraging in patch N.

According to my results, the above can be accomplished by using a spectrum of satisficing foraging strategies delineated by the following two extremes in foraging behaviors.

In the first case, the forager uses a GUD that maximizes CC and terminates its foraging when the CC at the desired level is achieved (Figure 4.3). An animal using such behavior could be called a maximizing satisficer. It uses a GUD that maximizes the CC at the end of the day, but only to satisfy its requirements, and decides to stop foraging when the required consumption is attained. The EF forager using this strategy in landscape CT1 should leave patches at GUD = 1378.88 (note that the MVT GUD was 1178.88, therefore, the behavior based on the MVT was not the optimal foraging strategy for this time-limited forager) and terminate its foraging at time T = 10.4 h when its CC reaches the required 9180 g (Gedir and Hudson 2000a). This strategy is an extension of the MVT and supports the idea presented by Nonacs and Dill (1993) in the sense that it is a subset of optimal foraging. It also is consistent with the suggestion from Ward (1992) that it has little heuristic value to ecologists because any animal that does not feed continuously may be considered to have achieved the satsficing criterion (assuming that external circumstances, e.g., predation avoidance, are not disrupting foraging activities). It is important to note that if animals were using the above foraging strategy, all foragers with steep FRC, feeding in good quality habitats would satisfy their requirements well before the end of the day and would never be seen foraging in the evening (unless constrained by digestive processes). In other words, foraging activity of efficient foragers would be concentrated in the morning and should rarely be observed in the evening. This is contrary to field observations of foraging elk (Gedir and Hudson 2000b) and other species (Gates and Hudson 1983, Gillingham and Bunnell 1985, Gillingham et al. 1997).

My research reveals that the other end of the spectrum of satisficing behaviors, however, is not related to the MVT. It is to choose a GUD that would ensure that the required CC is achieved at the end of the 12 h period without using a GUD that generates the optimal cost-benefit ratio, but that is 'good' enough (Figures 4.1a-b, Figure 4.3). This could be achieved by the E forager in landscape CT1 by using a GUD of 2578.88 kg/ha and foraging for the entire period of 12 h. It is important to note that in this case the forager is actively foraging during the entire time and is still satisficing. This is contrary to the commonly accepted assumption that satisficing can only be assumed if the animal is not feeding continuously (Nonacs and Dill 1993, Ward 1992). Although wild animals are often seen "doing nothing" (e.g., bedding), research on elk and other ungulates suggest that they spend most of their time actively foraging (Gedir and Hudson 2000b, Gillingham and Bunnell 1985, Gillingham et al. 1997). My work suggests that animals may actually choose a satisficing foraging strategy and be active all the time (EF forager in landscape CT1 using GUD = 2628.88 kg/ha, or EF forager in landscape CT1a using GUD = 1625.73 kg/ha , Figures 4.1a-b, Figure 4.3). All other strategies based on GUDs from within the above two extremes would allow the forager to meet the required CC at different total T required (Figures 4.1a and 4.1b) and therefore, are satisficing strategies.

This begs a question about the value of a foraging strategy that requires the animal to be active at all times if an alternative strategy would allow it some extra time “to do nothing”. In addressing this problem, it is important to keep in mind that for all satisficing foragers (animals whose CCs at the end of the time interval is equal to the required cumulative consumption: CC = 9180 g) the average consumption rate, or the landscape intake rate (LIR) introduced in Chapter 2, is the same regardless of the strategy they choose. Therefore, a satisficer should allocate its travel time (Tt), patch residence time (Tr), and foraging brakes (extra T) in such a way so that it maximizes the forager’s fitness. It could be argued that exploring the landscape could maximize fitness (better knowledge helps to exploit new resources, find more mates, etc.,), thus more travel should be preferred. At the same time, travel is costly (energetic costs, predator encounters, etc.). On the other hand, extra time (extra T) is an important bonus that could be allocated to any activity that increases fitness such as mating, predator avoidance, care of the offspring, or even more travel). Extra time gives the forager more flexibility and a wider spectrum of tools to increase fitness. Therefore, a satisficing forager should search for a balance between its required total travel time (TTt) and extra time (extra T) that could be allocated to other activities. Figure 4.2 illustrates the trajectories of total travel time (TTt) and extra time (extra T) as a function of foraging behavior (GUD). For each GUD a difference (Tdiff) between the TTt and extra T can be calculated. The GUDs for which the Tdiff is closest to zero represent the balance between the costs of more required travel and extra time that benefits fitness. I argue that it represents the optimal foraging behavior in the sense that it should maximize fitness (Figure 4.4). Therefore, an optimal satisficing strategy that maximizes the forager's fitness could be formulated as follows. The forager should use a GUD at which the value of Tdiff is closest to zero:

$$\text{Tdiff (GUD)} = \text{TTt (GUD)} - \text{extra T(GUD)} \rightarrow 0$$

This relationship could be adjusted further to reflect external circumstances. Depending on the environment (e.g., predation risk), a satisficing forager may want to travel more than required by the maximizing strategy (it may be profitable to explore more patches and be less predictable for predators), or to reduce travel to levels lower than required by the maximizing strategy (e.g., reduce movement to decrease predator encounter rates). Therefore, there should be two GUDs that are the balance points that maximize the fitness of a satisficing forager: one (S1) that results in the lowest absolute value of Tdiff for all GUDs bigger than the MVT GUD, and second (S2) that results in the lowest absolute value of Tdiff for all GUDs smaller than the MVT GUD (Figure 4.4):

$$\left.\begin{array}{l} \text{S1 if GUD} > \text{MVT GUD then S1} = \\ \text{S2 if GUD} < \text{MVT GUD then S2} = \end{array}\right\} \text{Tdiff (GUD)} \longrightarrow 0$$

Behaviors based on this principle (Figure 4.5) enable forgers to reproduce at the highest possible rate, ensure significant exploration of the landscape, and allow time for other activities that could further maximize fitness. An animal that uses this foraging behavior could be described as a smart forager. A smart forager (e.g., the efficient forager (E = 97.32) using GUD = 0.001 or 2128.88 kg/ha in landscape CT1) is an animal foraging with an efficiency that would allow it to satisfy the required CC before the end of the time interval (for most diurnal animals that would be within 12 h) and uses a GUD that results in the optimal balance between travel time and extra time adjusted for its specific mobility needs.

I have shown that contrary to the approach suggested by Ward (1992) an animal’s behavior alone cannot be used to assess whether the animal is satisficing or optimizing. To determine the strategy that the forager is employing, it is crucial to examine its behavior in relation to its efficiency in exploiting resources and its cumulative consumption. This reveals the crucial importance of the functional response curve (FRC). That the shape of the FRC is an important ecological indicator was realized early in ecological research (Emlen 1966, Takahashi 1968) and significant research has been devoted to this concept since its inception (e.g., Hayes and Harestad. 2000, Hobbs et al. 2003, Hudson and Watkins 1986, Lovvorn and Gillingham 1996, Wickstrom et al. 1984), however, my work in concert with the recent findings of Nolet and Klaassen (2009) suggest that the significance of the shape of the FRC in the context of forging behaviors was not fully realized. Nolet and Klaassen (2009) argue that foraging behavior (patch exploitation) can be predicted from foragers’ functional responses and point out that the functional response derived for swans (*Cygnus columbianus bewickii*) seems to correctly predict the observed GUDs. This reinforces the concept of smart foraging and supports the perfect forager theorem (PFT) presented in Chapter 2. The PFT predicts that patch residence times are related to the shape of the FRC and that the most efficient foragers are little affected by changing travel times among patches. On the other hand, the MVT predicts that the patch residence time (Tr) should depend on the transit time between patches and the expected gain from the patch (and the gain is a result of the quality of the patch and the efficiency of the forager).

Considering this crucial importance of the slope of the FRC, I was interested in examining whether a forager should aim at achieving the highest possible efficiency (steep slope of the FRC) or focus on choosing the most appropriate foraging behavior, or both.

To examine the effects of the FRC of the forager (the slope of the type II functional response curve) and different foraging strategies I compared the trajectories of CC resulting from three types of FRC (three values of *efficiency* E) and several foraging behaviors (wide range of GUDs) in three different landscapes. As a starting point I used the slope of the FRC that represented the average from the literature (Hudson and Watkins 1986, Wickstrom et al. 1984) on elk foraging (E = 486.6) to define medium efficiency (ME) forager and next increased it by 80% to simulate a low efficiency (LE) forager (E = 875.88) and decreased by 80% to simulate an efficient (EF) forager (E = 97.32). I also calculated the MVT GUD for each of these foragers in 3 landscapes (CT1, CT1a and CT2 – I chose these three landscapes because the parameters that defined them were more realistic (travel time ranging from 0.1 to 0.5 h, initial patch biomass density in the range from 2564 to 3448 kg/ha) than other landscapes defined in the previous Chapters). Next, I established a range of GUDs by calculating GUDs that were 80% higher and lower than the MVT GUD for each forager in each of the three landscapes. Because the ranges of the forager's efficiency (E) and GUD were the same, any overlap in the trajectories of the resulting CCs would indicate that the forager could balance its low efficiency by choosing an appropriate foraging behavior (GUD). No overlap in the trajectories of the CCs would indicate that the slope of the FRC has a stronger effect on CC than a foraging behavior (GUD). Figures 4.6a-c illustrate the results of this analysis. It clearly indicates that the efficiency of the forager (slope of the FRC) has a much stronger effect on CC than an animal's foraging behavior (GUD). When GUD is changed by the same value, the CCs of foragers having different slopes of the FRC are always different (there is no GUD that would generate a CC higher for the less efficient forager). The analysis reveals that a forager of lower efficiency was able to reach CC higher than the more efficient forager only when the less efficient LE forager used GUDs (within a range of 1509.53 to 2209.53) associated with behaviors that would maximize its CC as the end of the 12 h trail and when the more efficient ME forager used a GUD (2703.98) that would not allow it to satisfy the required CC of 9180 g at the end of the 12 h period. It is highly unlikely that any forager would deliberately use a strategy not allowing for satisfying the basic requirements needed for successful reproduction. This reinforces the importance of the FRC as an ultimate driver for foraging behaviors.

When analyzing the importance of the FRC it is also interesting to note that the above mentioned overlap in the ranges of CCs (Figure 4.6a) was only possible in the landscape (CT1) with shortest travel times. In the remaining two landscapes (CT1a and CT2) there was no overlap of CCs between the foragers. It suggests that if travel times are short, foragers of different efficiency have very limited potential to balance their low efficiency by choosing a specific foraging behavior to increase their long-term gains by adjusting their foraging behaviors. However, as travel time increases, the efficiency of the forager remains equally important, but significance of the foraging behavior (GUD) for the CC decreases. This indicates that a foraging animal should focus more on increasing its efficiency then on choosing the best foraging strategy (GUD). In the context of the theory of natural selection this implies a stronger evolutionary pressure on being an efficient forager than on being able to choose the best foraging behavior. Indeed, my previous simulation outputs described in Chapter 2 suggest that for extremely efficient foragers (the PFT), the residence time in a patch is not related to travel times between the patches.

Owen-Smith (2002) and Spalinger and Hobbs (1992) described the FRC of browsers as having very steep slopes. This indicates that browsers are highly efficient foragers with efficiency similar to the one I used for the efficient (E) forager. Therefore, if my suggestions are true, browsers should have more potential to satisfice than other herbivores. Research on ungulates suggests different slopes of FRC (Hobbs et al. 2003, Hudson and Watkins 1986, Risenhoover 1987, Trudell and White 1981, Spalinger and Hobbs 1992, Wickstrom et al. 1984), but rarely links it to a specific foraging behavior. Searle et al. (2005) stressed the importance of the shape of the gain functions and noted that it can have profound effects on predictions of patch models. My work confirms this observation and provides the mechanism for the relationship between the shape of the FRC and forgaing behavior. Similar to herbivores, very different slopes of FRC, have been proposed for carnivores (Hayes and Harestad 2000, Messier 1995) and some indicate a very steep FRC (Hayes and Harestad 2000). This indicates that animals indeed attempt to increase their efficiency when possible.

Field research that would simultaneously examine the FRC, cumulative consumption and behavior of the foragers in the same habitat feeding at the same time could further test my conclusions. Projects of this broad scope are rare (Searle et al. 2005, Bergman et al. 2001) because require significant resources. Searle et al. (2005) pointed out that the shape of gain functions can have a strong effect on the predictions of foraging models. Because gain functions are shaped by the FRC, this supports my findings that the efficiency of the forager ultimately determines its foraging strategy. The findings of Bergman et al. (2001) support my conclusion that foragers (especially time limited) should attempt to maintain the highest possible efficiency that would enable them to minimize foraging time. Although the research conducted by Bergman et al. (2001) was quite extensive, results presented does not allow for testing of how the FRC changes across different landscapes and the associated response of the foragers (my conclusion suggests that animals should select landscapes that would allow them for the steepest FRC). Although the concept of resource selection functions (RSF) does not directly link intake rates and habitat selection, as stated by Boyce and McDonald (1999), foraging theory is behind the prediction of resource selection, providing the mechanisms that shape patterns of resource use. Research that directly links habitat selection to intake rates of foragers is rare. Gillingham et al. 2001 found that winter habitat use by black-tailed deer (*Odocoileus hemionus*) cannot be predicted by intake rates, they found, however, a positive correlation between intake rates and habitat use by deer in summer. Iason et al. (2002) found that free-living wild rabbits (*Oryctolagus cuniculus*) did not select habitats that provided the maximum potential rate of intake, however, the population under study, similarly to the animals observed by Gillingham et al. (2001), was exposed to predators and predation avoidance was the main factor responsible for habitat selection. Findings of Reuda et al. (2008) indicate that foragers less exposed to predation select habitats that allow for high instantaneous intake rates, which is further confirmed by Bergman et al. (2001).

Current technology such as modern GPS and other systems tracking animal behavior combined with advanced techniques in assessing consumption and intake rates (e.g., Gedir and Hudson 2000a, Kuzyk and Hudson 2006) should allow for completing a project that would test my conclusions that foragers should behave accordingly to the set of rules, which I call smart foraging.

The following rules of smart foraging are derived from the findings of this research and the abovementioned discussion on the importance of the slope of the FRC and foraging strategies (GUDs):

1) Always attempt to be a perfect forager (Chapter 2 provides a detailed description of the Perfect Forager Theorem (PFT)). Strive to increase foraging efficiency (slope of the FRC) to be a perfect forager. This is especially important if animals are in a new habitat.
2) Being a perfect forager an animal does not have to worry about its knowledge of the landscape or habitat because distances between patches have little impact on its GUD and patch residence time (Tr) when choosing to use an optimizing (consumption maximizing) strategy.
3) For non-perfect foragers, stick to the highest efficiency achieveable in a given habitat.
4) In stable habitat use satisficing: adjust the GUD (and associated Tr) in a way that the difference between the total travel time (TTt) and extra time (extra T) is closest to zero. Apply the extra time when required (e.g.,

predator avoidance) or when an opportunity (e.g., mating) to increase fitness arises.

5) In unstable unenvironment (likely to be interrupted when foraging during a limited time interval), start foraging with a foraging strategy that maximizes CC at the end of the time interval. This strategy may be different than the MVT (likely stay shorter in each patch than expected from the MVT if the total foraging time is limited). Calculate the GUD and associated residence time (Tr) depending on the expected gain from an average patch, the travel time required to reach that patch and time limitations (Chapter 3 provides detailed explanation).

I believe that the smart foraging principle presented in this Chapter is an interesting concept. First, it is based on satisficing principle that is very well established in many scientific disciplines (ecologists seem to be surprisingly reluctant to explore this idea). Secondly, it incorporates the basic principles of foraging in a patchy environment (however, is not a subset of the MVT). And, finally, it is built on the functional response curve that defines the skills of the forager in exploiting resources.

4.5. Conclusions

My research findings clearly indicate that efficient foragers have a wide choice of foraging behaviors that are in fact satisficing behaviors. By this I argue, contrary to Nonacs and Dill (1993), that satisficing is a very strong alternative to optimal foraging. I also argue that satisficing is not only a strong alternative, but, considering the wide spectrum of satisficing strategies that allow efficient foragers to reproduce at the highest rate, should be commonly used by animals.

I support other research (Caramel and Ben-Haim 2005, Killen et al. 2007, Nolet et al. 2006, Ward 1992) that identifies satisficing as one of the foraging models that accurately describe foraging behaviors. Furthermore, I propose that optimal foraging behavior is better described by the concept of smart foraging, which is a set of rules based on key ecological concepts: the efficiency of the forager (the functional response curve), satisficing, the MVT, and incorporates time limitations.

My work provides support for satisficing in ecosystems and thus reinforces this important link between biology and economy, the two disciplines that have been shown to share the main theories such as cooperation (Maynard Smith 1982), distribution (Lomnicki 1978, 1988) and utilization of resources by individuals (MacArthur and Pianka 1966, Emlen 1966, Charnov 1976). I concur with Hammerstein and Hagen (2005) that more interdisciplinary collaboration between economists and biologists is needed to advance research in both disciplines.

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Tables

GUD	CC (g)	Total T required (h)	extra T	Total Tt (h)	Total Tr (h)	M
0.00	9633	11.50	0.50	0.3	11.7	4
78.88	10156	10.95	1.05	0.3	11.7	4
178.88	10346	10.65	1.35	0.3	11.7	4
278.88	10295	10.60	1.40	0.4	11.6	4
378.88	10372	10.55	1.45	0.4	11.6	5
478.88	10444	10.50	1.50	0.4	11.6	5
578.88	10493	10.45	1.55	0.4	11.6	5
678.88	10521	10.55	1.45	0.4	11.6	5
778.88	10548	10.50	1.50	0.4	11.6	6
878.88	10581	10.45	1.55	0.4	11.6	6
978.88	10607	10.45	1.55	0.4	11.6	6
1078.88	10623	10.45	1.55	0.4	11.6	6
*1178.88	10631	10.40	1.60	0.4	11.6	7
1278.88	10650	10.40	1.60	0.4	11.6	7
1378.88	**10657**	10.35	1.65	0.4	11.6	7
1478.88	10585	10.35	1.65	0.5	11.5	8
1578.88	10596	10.45	1.55	0.5	11.5	8
1678.88	10518	10.45	1.55	0.6	11.4	9
1778.88	10529	10.45	1.55	0.6	11.4	9
1878.88	10352	10.55	1.45	0.8	11.2	10
1978.88	10268	10.75	1.25	0.9	11.1	11
2078.88	10182	10.85	1.15	1.0	11.0	12
2178.88	10008	10.90	1.10	1.2	10.8	13
2278.88	10015	11.10	0.90	1.2	10.8	14
2378.88	9835	11.10	0.90	1.4	10.6	17
2478.88	9748	11.40	0.60	1.5	10.5	20
2578.88	9292	11.70	0.30	2.0	10.0	22
2678.88	9020	12.25	0.00	2.3	9.7	22
2778.88	8562	12.65	0.00	2.8	9.2	23

Table 4.1. Consequences of using specific giving-up densities (GUD) by the efficient forager (**E = 97.32**) feeding in **landscape CT1** on: cumulative consumption at 12 h (CC), total time needed to reach the required consumption of 9180 g (Total T required), time remaining to 12 h after the food requirement was met (extra T), total travel time during the 12 h period (Total Tt), total residence time during the 12 h period (Total Tr), and the number of patches fed on until T = 12 h (M). The MVT GUD is indicated with an asterix, bold font indicates the highest CC.

GUD	CC (g)	Total T required (h)	extra T (h)	Total Tt (h)	Total Tr (h)	M
0.00	8898	12.30	0.00	1.1	10.9	4
75.73	9438	11.70	0.30	1.1	10.9	4
175.73	9662	11.50	0.50	1.4	10.6	4
275.73	9726	11.40	0.60	1.5	10.5	4
*375.73	**9762**	11.35	0.65	1.6	10.4	4
475.73	9613	11.30	0.70	1.7	10.3	4
575.73	9569	11.25	0.75	1.7	10.3	4
675.73	9623	11.50	0.50	1.4	10.6	5
775.73	9647	11.50	0.50	1.4	10.6	5
875.73	9663	11.45	0.55	1.5	10.5	5
975.73	9495	11.45	0.55	1.7	10.3	5
1075.73	9521	11.65	0.35	1.6	10.4	6
1175.73	9541	11.60	0.40	1.6	10.4	6
1275.73	9553	11.60	0.40	1.6	10.4	6
1375.73	9467	11.60	0.40	1.7	10.3	6
1475.73	9389	11.75	0.25	1.8	10.2	7
1575.73	9395	11.75	0.25	1.8	10.2	7
1675.73	9132	12.05	0.00	2.1	9.9	8
1775.73	9141	12.05	0.00	2.1	9.9	8
1875.73	8874	12.35	0.00	2.4	9.6	9
1975.73	8883	12.75	0.00	2.4	9.6	9
2075.73	8519	13.05	0.00	2.8	9.2	10
2175.73	8247	13.30	0.00	3.1	8.9	11
2275.73	7974	13.70	0.00	3.4	8.6	12
2375.73	7610	14.10	0.00	3.8	8.2	13

Table 4.2. Consequences of using specific giving-up densities (GUD) by the efficient forager (**E = 97.32**) feeding in **landscape CT1a** on: cumulative consumption at 12 h (CC), total time needed to reach the required consumption of 9180 g (Total T required), time remaining to 12 h after the food requirement was met (extra T), total travel time during the 12 h period (Total Tt), total residence time during the 12 h period (Total Tr), and the number of patches fed on until T = 12 h (M). The MVT GUD is indicated with an asterix, bold font indicates the highest CC.

GUD	CC (g)	Total T required (h)	extra T (h)	Total Tt (h)	Total Tr (h)	M
3.98	5760	18.60	0	0.2	11.8	3
103.98	7591	14.55	0	0.2	11.8	3
203.98	7729	13.85	0	0.3	11.7	4
303.98	8182	13.40	0	0.3	11.7	4
403.98	8362	13.15	0	0.3	11.7	4
503.98	8538	12.95	0	0.3	11.7	4
603.98	8646	12.90	0	0.3	11.7	4
703.98	8670	12.80	0	0.3	11.7	4
803.98	8728	12.60	0	0.4	11.6	5
903.98	8799	12.50	0	0.4	11.6	5
1003.98	8889	12.45	0	0.4	11.6	5
1103.98	8901	12.35	0	0.4	11.6	5
1203.98	9008	12.20	0	0.4	11.6	6
1303.98	9092	12.15	0	0.4	11.6	6
1403.98	9116	12.10	0	0.4	11.6	6
1503.98	9152	12.05	0	0.4	11.6	7
*1603.98	**9185**	12.00	0	0.4	11.6	7
1703.98	9164	12.05	0	0.5	11.5	8
1803.98	9112	12.05	0	0.6	11.4	8
1903.98	9170	12.00	0	0.6	11.4	9
2003.98	9030	12.15	0	0.8	11.2	9
2103.98	8980	12.25	0	0.9	11.1	11
2203.98	8928	12.50	0	1.0	11.0	12
2303.98	8802	12.45	0	1.2	10.8	13
2403.98	8831	12.55	0	1.2	10.8	15
2503.98	8604	12.70	0	1.5	10.5	19
2603.98	8385	13.40	0	1.8	10.2	22
2703.98	8000	13.50	0	2.3	9.7	21
2803.98	7783	14.40	0	2.6	9.4	23

Table 4.3. Consequences of using specific giving-up densities (GUD) by the medium efficiency forager (**E = 486.6**) feeding in **landscape CT1** on: cumulative consumption at 12 h (CC), total time needed to reach the required consumption of 9180 g (Total T required), time remaining to 12 h after the food requirement was met (extra T), total travel time during the 12 h period (Total Tt), and total residence time during the 12 h period (Total Tr), and the number of patches fed on until T = 12 h (M). The MVT GUD is indicated with an asterix, bold font indicates the highest CC.

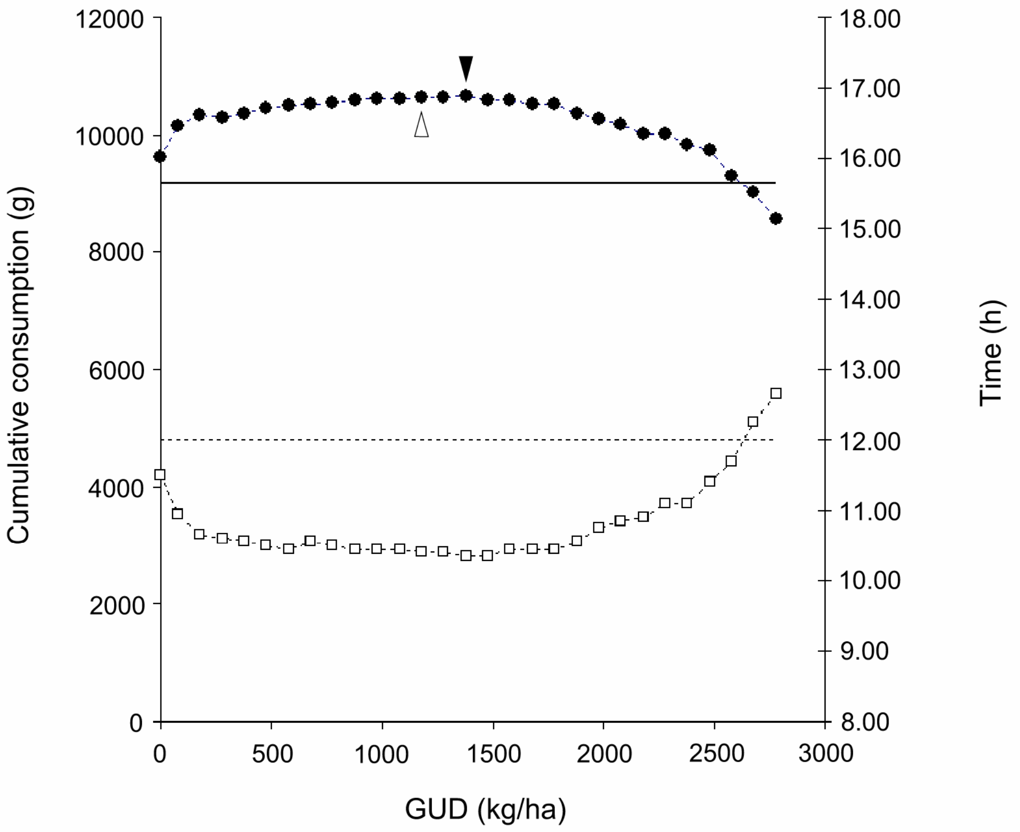

Figure 4.1a. Cumulative consumption (CC) at 12 h (circles, left axis) and time required to reach the requirement of 9180g (squares, right axis) for the efficient forager (**E = 97.32**) in landscape **CT1** as a function of giving-up density (GUD). The solid line indicates 9180 g and the dashed line indicates 12 h. The open arrow indicates the CC of the MVT forager and the corresponding GUD, the dark arrow indicates the alternative forager that achieved the highest CC using its specific GUD.

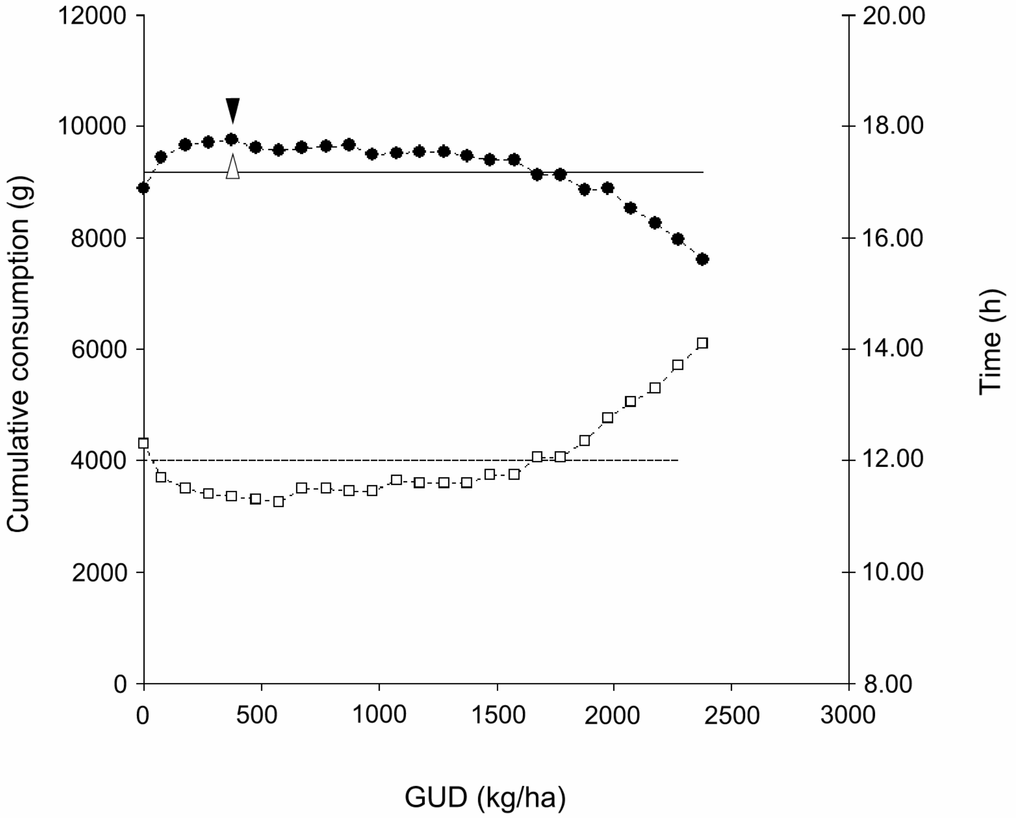

Figure 4.1b. Cumulative consumption (CC) at 12 h (circles, left axis) and time required to reach the requirement of 9180g (squares, right axis) for the efficient forager (**E = 97.32**) in landscape **CT1a** as a function of giving-up density (GUD). The solid line indicates 9180 g and the dashed line indicates 12 h. The open arrow indicates the CC of the MVT forager and the corresponding GUD, which was the strategy that resulted in the highest CC (dark arrow).

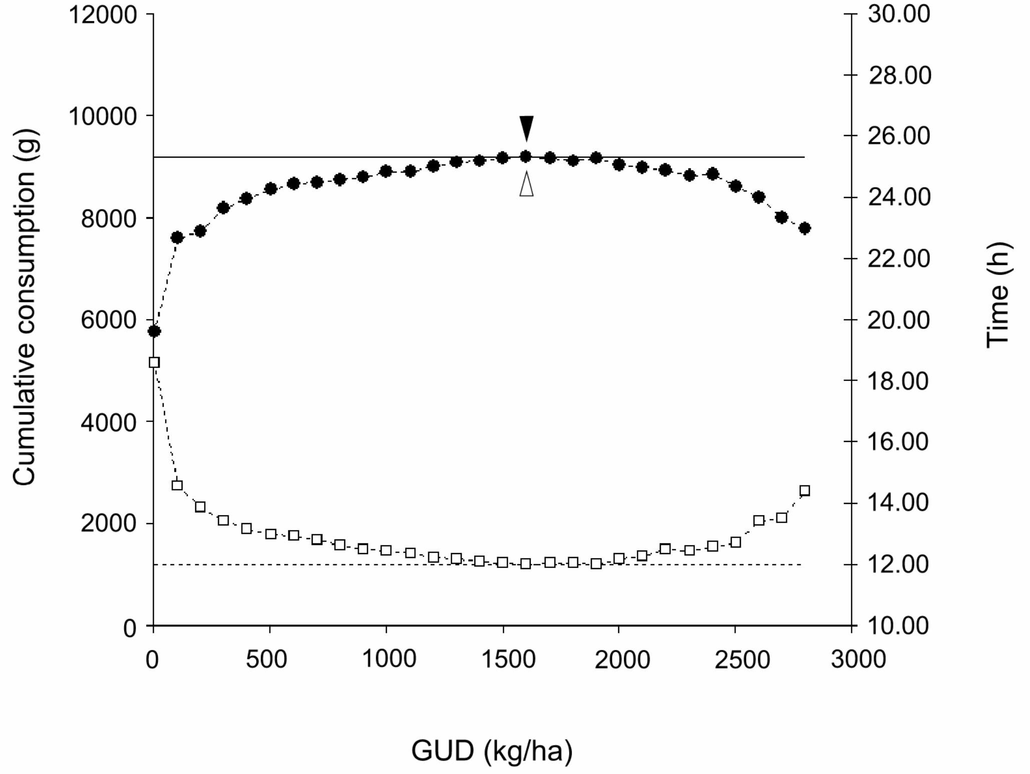

Figure 4.1c. Cumulative consumption (CC) at 12 h (circles, left axis) and time required to reach the requirement of 9180g (squares, right axis) for the medium efficiency forager (**E = 486.6**) in landscape **CT1** as a function of giving-up density (GUD). The solid line indicates 9180 g and the dashed line indicates 12 h. The open arrow indicates the CC of the MVT forager and the corresponding GUD, which was the strategy that resulted in the highest CC (dark arrow).

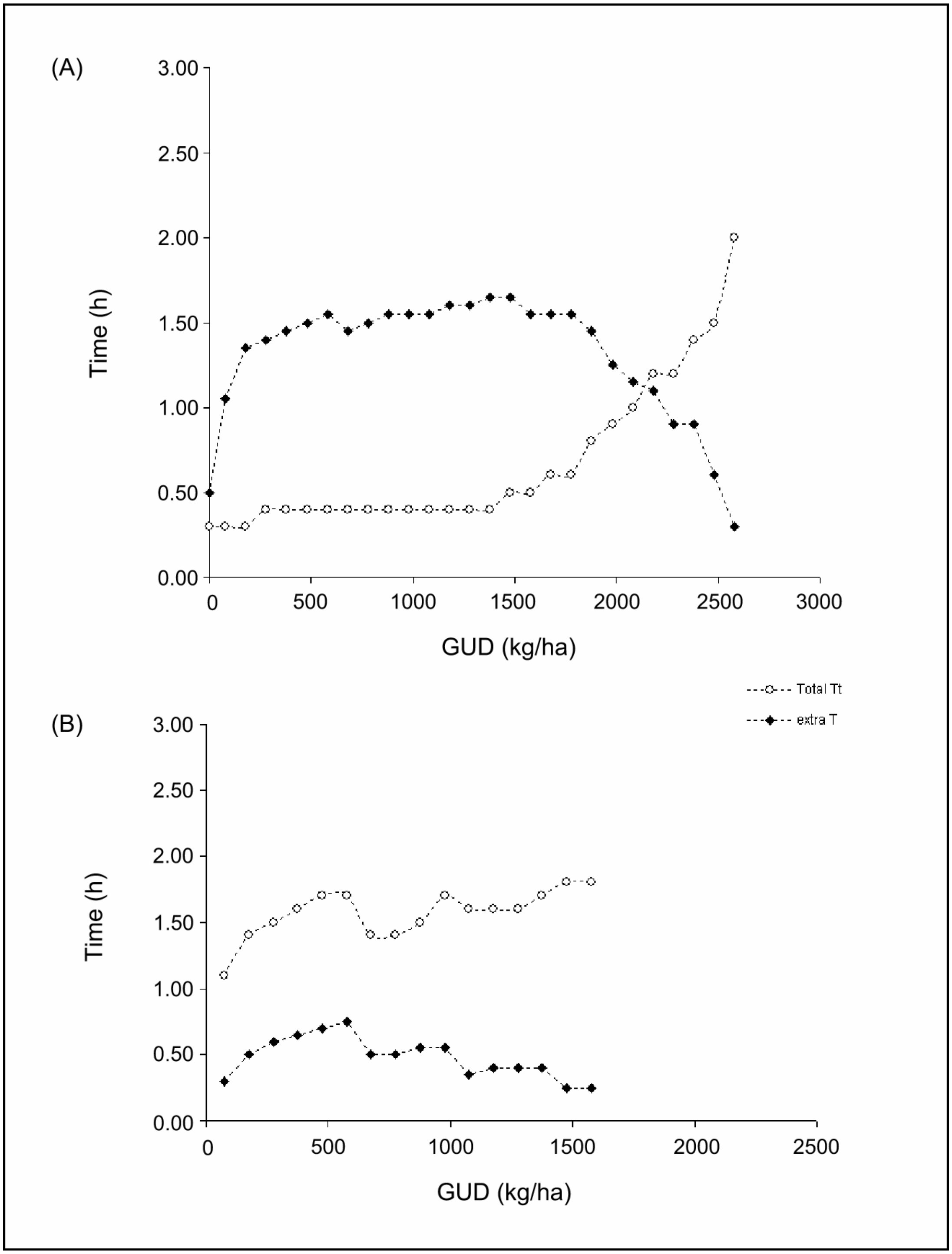

Figure 4.2. Trajectories of total travel time (TTt - open circles) and extra time (Extra T – black dimonds) for the two situations that allowed for satisficing behaviors: the efficient forager (E = 97.32) feeding in (A) landscape CT1 and (B) in landscape CT1a.

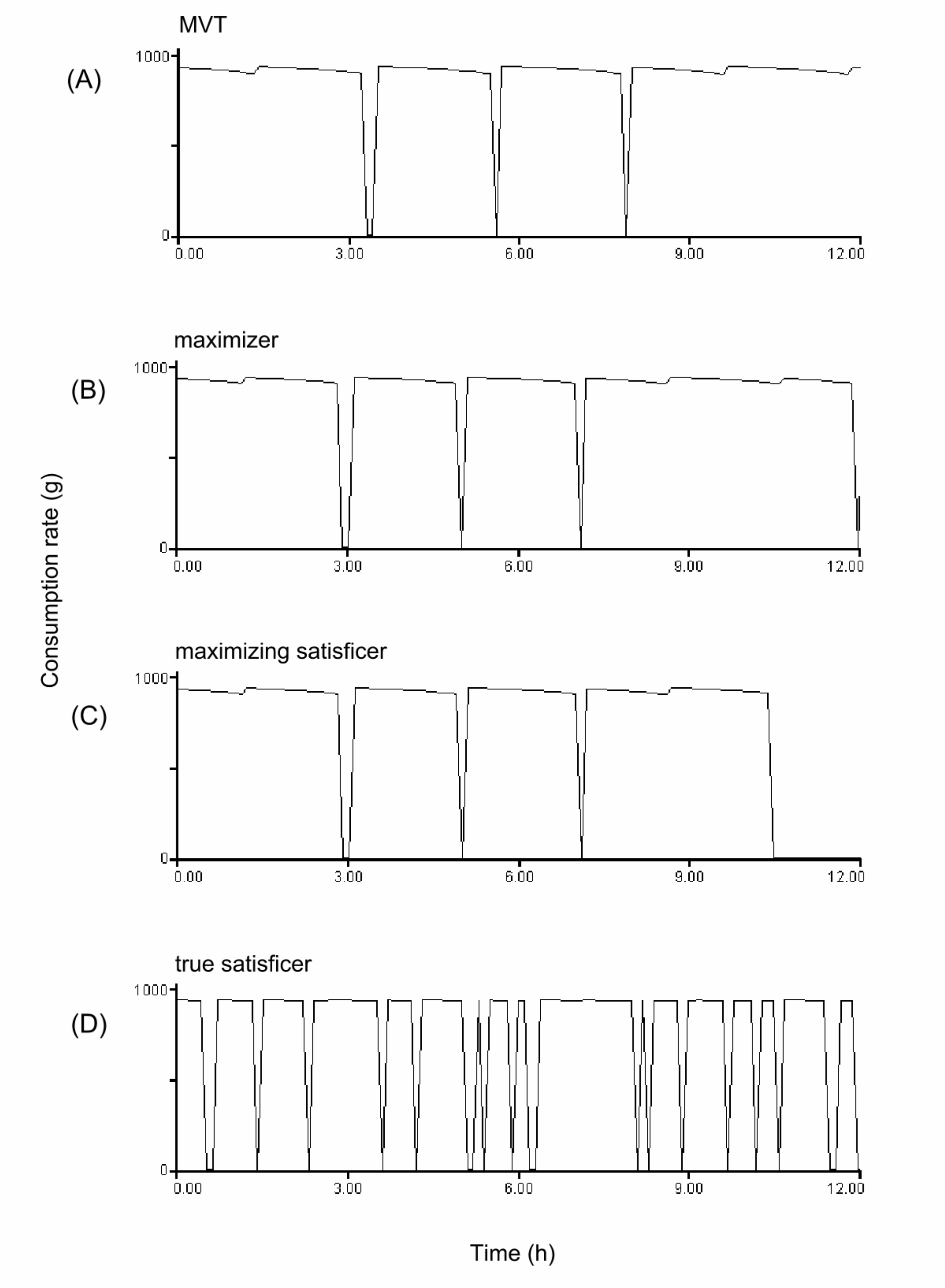

Figure 4.3. Based on efficient forager (E = 97.32 kg/ha) feeding in landscape CT1. Four main types of foraging behaviors. A: an MVT forager leaves patches at GUD = 1178.88 kg/ha; B: a forager that maximizes the CC at 12 h leaves patches at GUD = 1378.88; C: a maximizing satisficer leaves patches at GUD = 1378.88, but terminates its foraging when its CC reaches the requirement of 9180 g (at T = 10.4 h); a true satisficer leaves patches at GUD = 2600 kg/ha and forages for the entire duration of the trial.

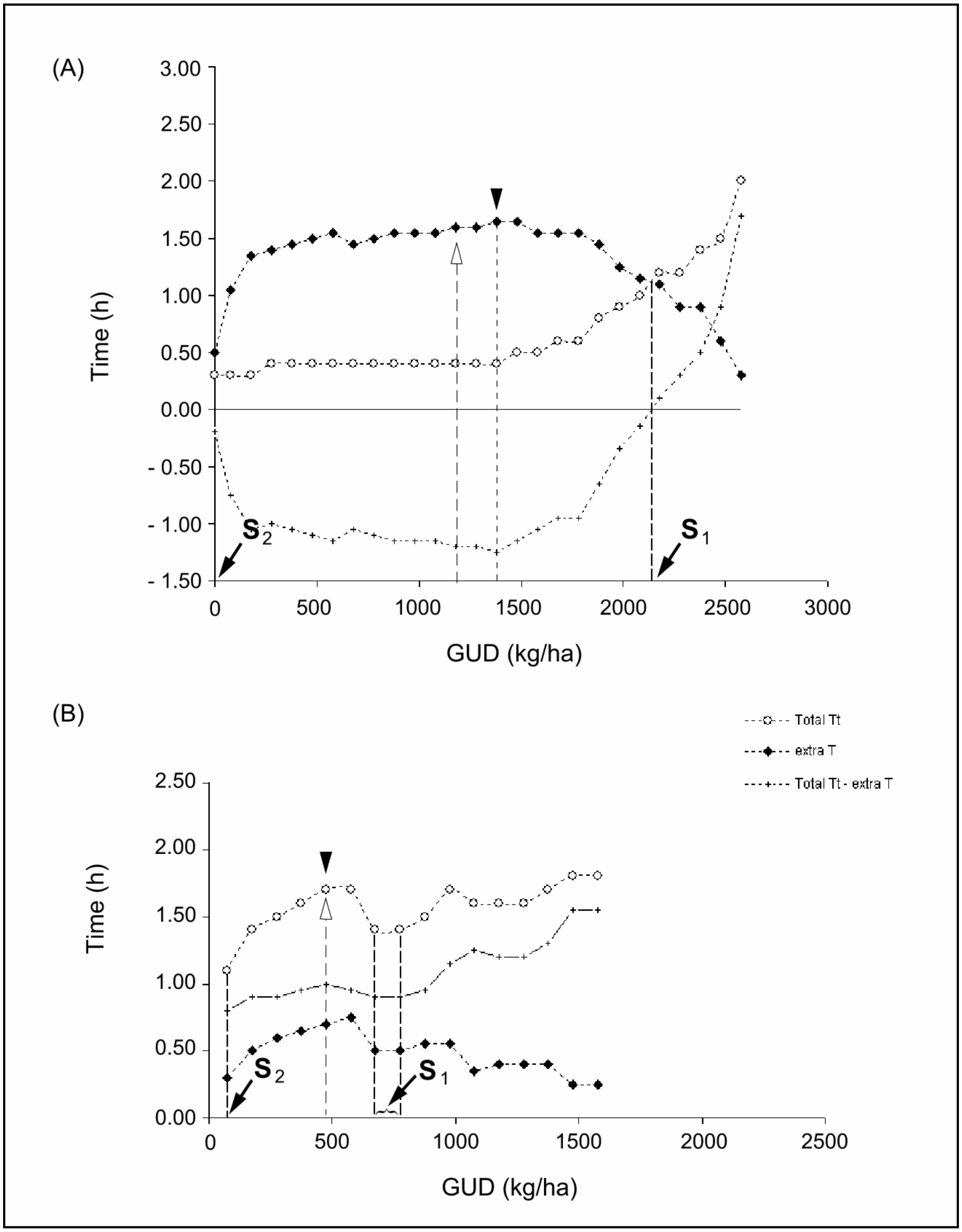

Figure 4.4. Based on the analysis of foraging behavior of the efficient forager (E = 97.32) in (A) landscape CT1 and (B) in landscape CT1a. Illustration of Smart Foraging. From all satisficing strategies (GUDs) a smart forager should use a GUD that corresponds to the point (S) where the difference between the total required travel time (open circles) and extra time (dark diamonds) is closest to zero (0). This balance point can be found for GUDs bigger (S1) and smaller (S2) than the maximizing GUDs. Dark arrows indicate the MVT GUDs and open arrows indicate the maximizing GUD that results in highest CC at time T = 12 h.

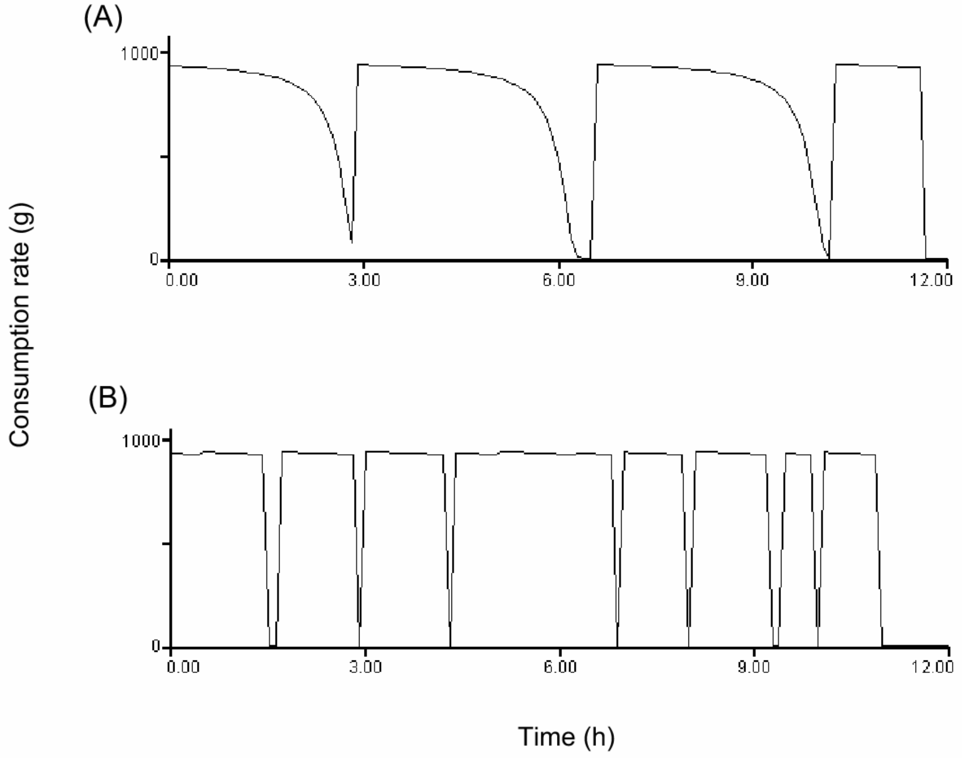

Figure 4.5. Two smart foraging behaviors of the efficient forager (E = 97.32 kg/ha) feeding in landscape CT1 (from Figure 4A). A: forager uses point **S2** as the GUD for its foraging strategy. This GUD (0.001 kg/ha) is lower than the MVT GUD, it minimizes the absolute value of Tdiff (0.2) and results in relatively short TTt (0.3 h) and extra T (0.5 h). B: The forager uses point **S1** for its foraging strategy. This GUD (2128.88 kg/ha) is bigger than the MVT GUD, it minimizes the absolute value of Tdiff (0.05) and results in relatively long TTt (1.2 h) and long extra T (0.9 h).

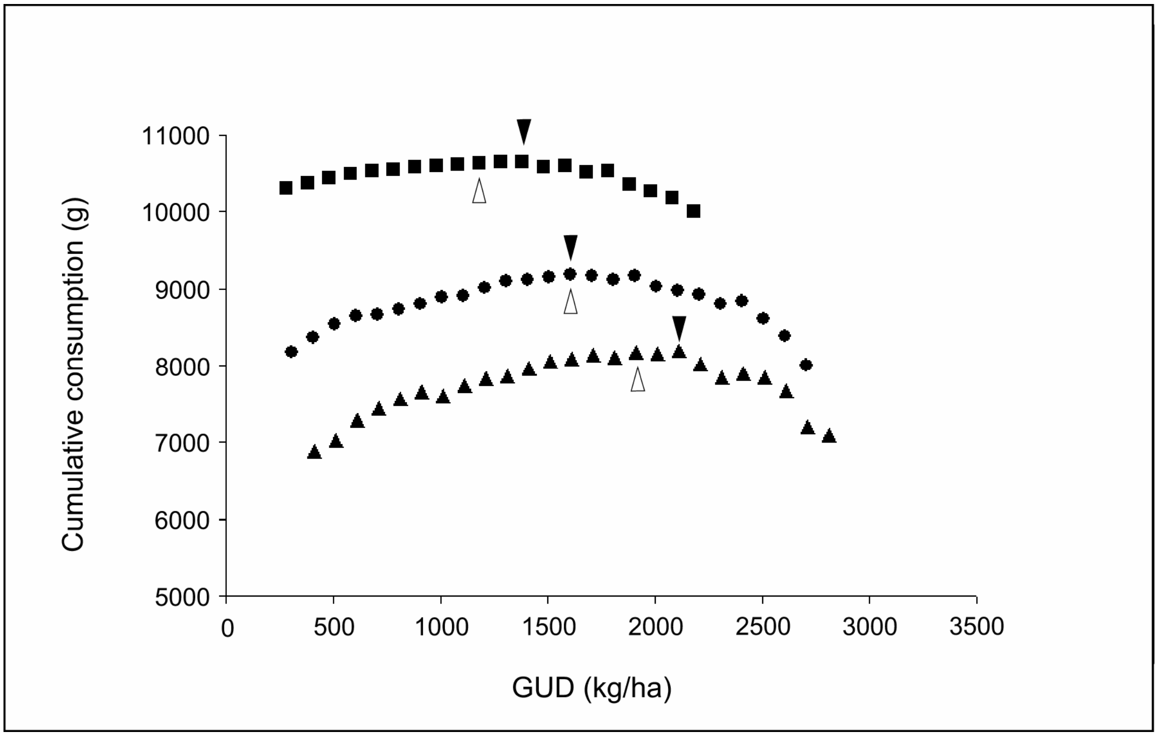

Figure 4.6a. Cumulative consumption (CC) at 12 h of three types of foragers (efficient (E=97.32, squares), medium efficiency (E = 486.6, circles), and low efficiency (E=875.88, triangles)), as a consequence of using different GUDs in landscape **CT1**. The highest and lowest GUDs for each forager represent GUDs 80% lower and higher than the GUD of the MVT forager respectively. Open arrows indicate the CC and corresponding GUD of the MVT foragers, dark arrows indicate the CC and corresponding GUD of the foragers that achieved the highest CCs.

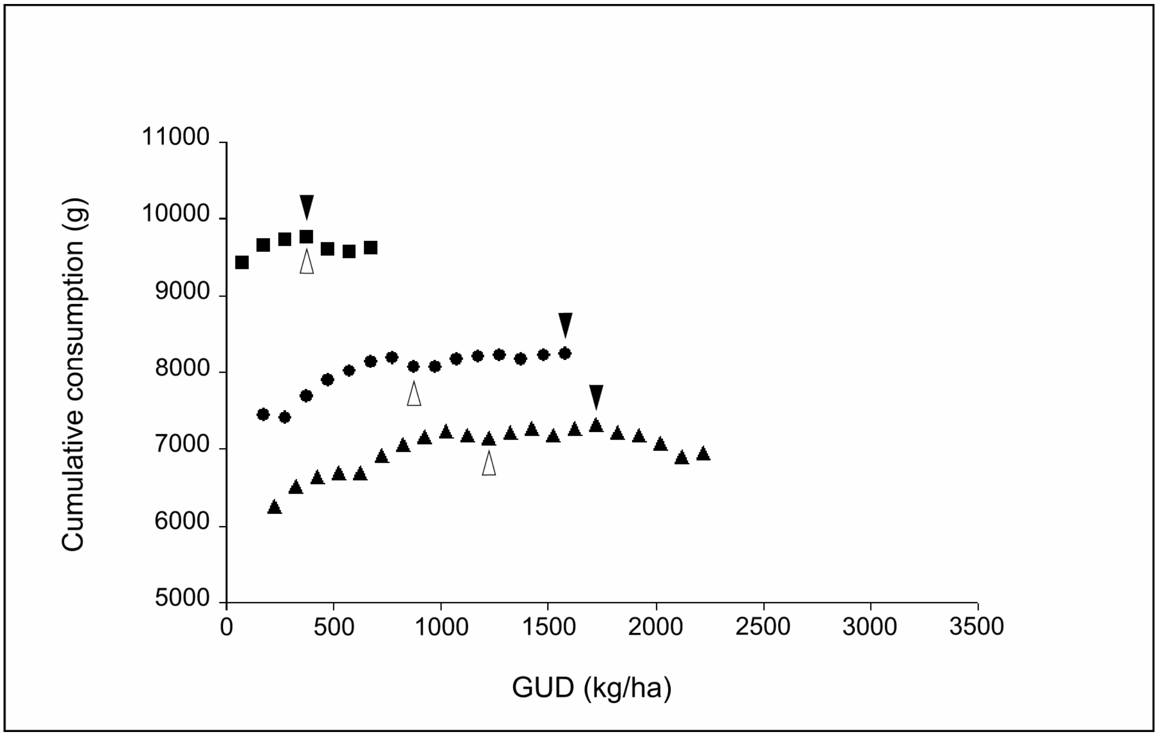

Figure 4.6b. Cumulative consumption (CC) at 12 h of three types of foragers (efficient (E=97.32, squares), medium efficiency (E = 486.6, circles), and low efficiency (E=875.88, triangles)), as a consequence of using different GUDs in landscape **CT1a**. The highest and lowest GUDs for each forager represent GUDs 80% lower and higher than the GUD of the MVT forager respectively. Open arrows indicate the CC and corresponding GUD of the MVT foragers, dark arrows indicate the CC and corresponding GUD of the foragers that achieved the highest CCs.

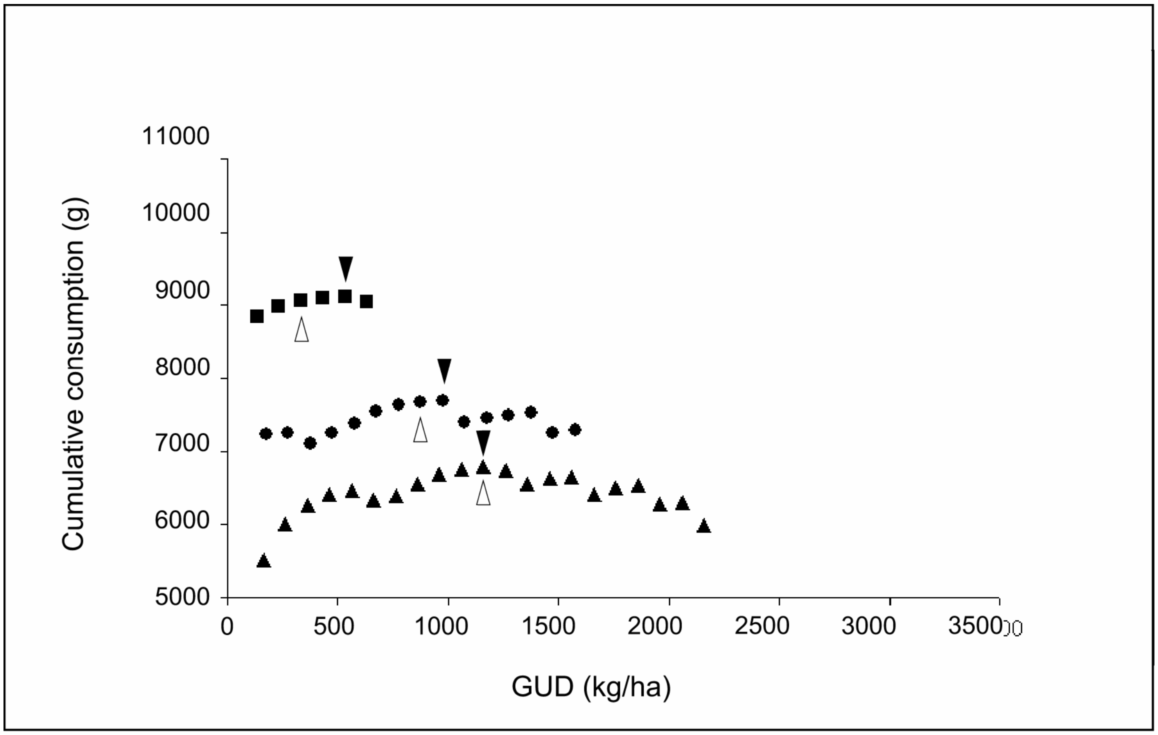

Figure 4.6c. Cumulative consumption (CC) at 12 h of three types of foragers (efficient (E=97.32, squares), medium efficiency (E = 486.6, circles), and low efficiency (E=875.88, triangles)), as a consequence of using different GUDs in landscape **CT2**. The highest and lowest GUDs for each forager represent GUDs 80% lower and higher than the GUD of the MVT forager respectively. Open arrows indicate the CC and corresponding GUD of the MVT foragers, dark arrows indicate the CC and corresponding GUD of the foragers that achieved the highest CCs.

Chapter 5. Synthesis

5.1. Main findings

The perfect forager theorem (PFT), concepts of the foragers' hub (α) and the foraging coefficient (F) and their importance for animals' foraging behavior, illustration of the consequences of time limitations for the optimal foraging strategy, and the significance of the shape of the functional response curve (FRC) in determining foraging behavior of animals are the main scientific contributions of this work.

In Chapter 2, based a series of simulation experiments, I introduced the perfect forager theorem and proposed that a perfect forager is a very efficient forager for which the foraging coefficient F (the ratio of the parameter E defining the slope of the FRC, and parameter M that determines the asymptote of the FRC) is close to zero (in other words a perfect forager is a forager whose FRC has a very steep slope). I also argued that foraging behaviors of perfect foragers are not affected by the distances between patches of forage, and proposed a relationship that exists between the perfect forager and all other forager types in a given landscape. To describe this relationship, I proposed the concept of the foragers' hub and argued that a specific foragers' hub could be identified for each habitat. Therefore, forager's hub could be a useful ecological indicator of within-population stability and diversity.

After examining foraging behavior at the scale of landscape averages: the average patch and the average travel time required to reach that patch, I shifted my focus to the landscape scale. The fact that the time scale affected the applicability of the Marginal Value Theorem (MVT) as the optimal foraging strategy (Charnov 1976) was the main finding of the research described in Chapter 3. I argued that for time-limited foragers, depending on the distribution and quality of forage patches, foraging behaviors different than MVT may be optimal and maximize the cumulative consumption at the end of the foraging trial. When time limitation was integrated in simulations, in most cases, animals were able to maximize their cumulative consumption by foraging differently than suggested by the MVT. This suggested that time-limited foragers should not be expected to use the MVT as their default foraging strategy and the MVT was a special case that only in some instances may result in maximization of resource consumption.

I also argued that, as far as cumulative consumption at the end of the time interval is concerned, the difference between the MVT and alternative foraging strategies is very small and that this difference in CC was never bigger than 11.9% in all the examined scenarios. Research described in Chapter 3 supported the perfect forager theorem by indicating small difference in CC of very efficient foragers that used a variety of foraging behaviors in different landscapes.

The concept of the perfect forager was further reinforced in Chapter 4 where I demonstrated that the ultimate factor determining the optimal foraging strategy is the slope of the FRC, which can be described by the foraging coefficient F. Although the importance of the FRC has been realized a long time ago (e.g., Emlen 1966, Takahashi 1968) and significant research has been devoted to its analysis (e.g., Hayes and Harestad 2000, Hobbs et al. 2003, Hudson and Watkins 1986, Lovvorn and Gillingham 1996, Wickstrom et al. 1984), my study has illustrated its importance in the context of foraging behavior. I was able to show that the slope of the FRC has greater consequences (in terms of cumulative consumption) for the foraging animal than the foraging strategy (patch residence time and allocation of the total patch residence time and total travel time during the total time interval) that the forger chooses.

Also in Chapter 4, based on the concepts well established in ecology (the MVT) and economics (satisficing), and research described in the previous chapters of my thesis (the importance of time limitations and the shape of the FRC for the optimal foraging behavior) I proposed a set of rules, which I called smart foraging, that should allow for fitness maximization, and thus should be considered the optimal foraging strategy in the context of natural selection. I argued that animals should focus more on increasing the slope of their FRC than on choosing a specific foraging strategy; and that natural selection should, therefore, favor foragers with steep FRC.

5.2. Support from field research

Existing field research supports the main ideas presented in the thesis. Evidence of very steep slopes of the type II FRC (Hayes and Harestad 2000, Owen-Smith 2002, Spalinger and Hobbs 1992) provides initial support for the hypothesis that animals should aim to maximize their efficiency (E). Observations of foraging behaviors (e.g., Bergman et al. 2001, Heindrich, 1979, 1993) and gain curves (Illius et al. 2002) further support this concept and indicate that perfect foragers do exist in nature and could be expected in a variety of taxa. Findings of Wajnberg et al. (2006) confirm my conclusion that the MVT is, in most cases, not the optimal foraging strategy for time-limited foragers. The work by Bergman et al. (2001) and findings of Iason et al. (1999) further reinforce the idea that time-limited foragers should attempt to maximize their foraging efficiency (E), and the findings of Nolet and Klaassen (2009) illustrate that patch exploitation by foragers can be predicted from their FRCs. The concept that I described as the foragers' hub (α) is, at least partially, supported by observations of Searle et al. (2005) who examined feeding behaviors of mule deeer (*Odocoileus hemionus*) and blue duikers (*Cephalophus monticola*) and observed a pattern that represents a small portion of the relationship described in Chapter 2.

Owen-Smith (2002) and Spalinger and Hobbs (1992) noted that browsers have steep FRC. Thus, their foraging coefficient (F) could be calculated as having small values. According to my findings these foragers should be able to use strategies other than the MVT and smart foraging described in Chapter 4 seems to be the optimal strategy that these efficient foragers should employ. This could explain at least some instances where animals were found to deviate from the MVT (Alonso et al. 1995, Searle et al. 2005, Thiel and Hoffmeister 2004, Wajnberg et al. 2006).

Model validation completed for SeekSMART generated outputs consistent with field observations of foraging elk. Gedir and Hudson (2000a) found that female elk graze longest in late lactation (12.8 h per day), when they spent 94% of their active time foraging and consume around 9.18 kg of dry matter per day (Gedir and Hudson 2000b). Gates and Hudson (1983) suggested that the upper limit on daily foraging time for elk is around 12 h. Other research supports this observation (Clutton-Brock et al. 1982, Heydon et al. 1992) and similar findings for time spent foraging were reported by Gillingham et al. (1997) and Gillingham et al. (2001) who examined forage intake and habitat use of black tailed deer (*Odocoileus hemionus sitkensis*). Jiang and Hudson (1993) observed that foraging female elk used MVT as their foraging strategy. In the model simulation run completed for the medium efficiency forager using the MVT as the foraging strategy, the virtual elk needed exactly 12 h to consume 9.18 kg of forage (DM). The model validation run also indicated time allocations (diurnal activities and foraging behavior) similar to these reported from field observations: the number of foraging bouts during the 24 h period for the virtual elk was 9.1 in the validation run, a value very close to the values obtained by Jiang and Hudson

(1993) and Gedir and Hudson (2000a, 2000b) who reported 9.2 bouts and 9.7 bouts per day respectively.

5.3. Future research needs, model limitations and assumptions

Although findings from some field studies support my conclusions, concepts presented in this thesis need to be tested in field research to confirm their applicability and test their validity.

For example, looking at more foragers with more diverse FRC (value of the parameter E) and feeding in habitats similar to that described by Searle et al. (2005), but characterized by a wider spectrum of travel times between patches should, according to the perfect forager theorem and the principle of forager's hub, produce the pattern illustrated in Figure 2.14 of Chapter 2 (the foragers' hub (α)).

My findings indicate that efficient foragers (those having steep slope of the FRC and low coefficient F) have a much wider spectrum of choices when deciding on their foraging strategies. To increase F, which defines the slope of the FRC, the forager can do two things: 1) select a habitat that, under the forager's specific morphological constraints, allows for the highest intake rates, and 2) adjust the foraging mechanism (e.g., bite rate, bite size, ability to find and handle prey). The above can be achieved in different ways. The short term and most immediate solution is to respond behaviorally. This implies that the shape of the FRC could be used in assessing the effectiveness of habitat in which the forager is feeding and whether habitat (i.e., availability of resources) is limiting for a population. A high value of the F and gentle slope of the FRC would indicate a forager inhabiting landscape of a low effectiveness that can be potentially limiting the population. In this sense, contrary to some researchers (e.g., Messier 1994), I believe there is no single right slope of the FRC for any species. Indeed, field research on herbivores and carnivores indicates a spectrum of FRC for the same species (e.g., Hayes and Harestad. 2000, Hobbs et al. 2003, Hudson and Watkins 1986, Lovvorn and Gillingham 1996, Wickstrom et al. 1984). This seems quite logical considering the differences in study locations and habitats investigated. I believe that the slope of the FRC reflects the interaction between a forager feeding in a particular habitat. One could imagine a situation where a herbivore has a steep slope of its FRC (is highly efficient) due to the structure of the vegetation present in a given landscape and the same herbivore having a gentle slope of the FRC is a different habitat due to a different structure of the vegetation even though the density of forage biomass is the same. Indeed, it has been shown that plant structure affects herbivores' intake rates (Hobbs et al. 2003). Similarly, it could be argued that predators hunting prey populations consisting of high proportion of young and inexperienced individuals would have a much steeper FRC than if they were preying upon an older population comprised mostly of individuals more experienced in predator avoidance, even though prey population density had the same values in both cases. Research findings presented by Hayes and Harestad (2000) and Messier (1994) support this idea.

The points mentioned above imply that a long-term goal of any forager should be to respond evolutionary in a way that would minimize the value of F. In other words, natural selection should favor morphological and behavioral traits that increase the efficiency of the forager. To verify this hypothesis, more field research should focus on analyzing FRC of species and populations inhabiting habitats of similar productivities, but differing in the structure of the resource, and on linking habitat selection (Boyce and McDonald 1999, Gillingham et al. 2001) to intake rate and population growth (RSF and FRC).

SeekSMART is based on some important simplifying assumptions that should be further tested in simulation experiments and field research. One of the key simplifications in the model is the assumption that quality of forage is distributed evenly in the patch. The model uses forage as one pool that includes digestible energy, protein and nutrient content and does not distinguish between these components. Depending on circumstances, animals may select different types of forage (Christianson and Creel 2007, Danell et al.1994, Hirata et al. 2008), and in an attempt to focus the discussion on the foraging strategy as opposed to diet selection, I used a homogeneous pool of forage as the currency in the model.

The model also assumed that the animal had neutral energy status at the beginning of the trial. This assumption was important, if the model was to exclude environmental noise that was suggested as the main factor responsible for the deviations from the MVT observed in field experiments (Nonacs 2001), and assess a variety of foraging strategies in 'perfect environment' where the MVT was supposed to be the optimal strategy.

Selection of patches of forage is linked to foraging behavior and a variety of approaches has been proposed to describe selection of forage patches by animals (Barton et al. 2009, Fortin et al. 2005, Fryxell et al. 2008). In this work I was not interested in examining the process that foragers use to decide on which patch to forage. Rather, I focused on strategies that animals use to optimally utilize resources in a patchy environment once the decision on patch selection has been made by the foraging animal. I believed that excluding the selection process was critical if one was to examine the consequences of variety of foraging strategies (defined by the giving-up density (GUD) and related patch residence time (Tr), as well as travel times (Tt) between patches). I also believed that including patch selection mechanism in the model would not inform the discussion on the differences between foraging strategies (the selection has been already made) and would only confound the analysis of foraging behavior as defined above. Further simulations that would account for patch selection could validate this assumption used in this thesis.

Finally, the landscapes that I designed for simulation purposes had considerable patchiness and were characterized by long travel times between patches. This design was intentional and with a purpose of examining a vast spectrum of significantly different landscapes. One of the advantages of simulation models and reasons for their application in ecology is to test situations that are difficult or impossible to examine in real experiments. I expected that testing situations that were never tested in field experiments could reveal some new patterns. Therefore, it was my intention to design landscapes that were not examined in field research. The generated spectrum of landscapes was very wide and simulations described in Chapter 3 indicated that in the habitats with travel times between patches equal to or longer than 18 minutes it would be very difficult for foraging elk to satisfy their forage requirements. However, it was this particular design of the landscapes that allowed for identification of important relationships and formulation of some of the key concepts of this thesis such as the PFT and forager's hub.

Another important assumption of the model was that the virtual animal was not involved in any inter and intra-species interactions. In nature, situations of complete isolation of an individual animal are rare. My work however, reinforces the importance of individual-based models in ecology (Lomnicki 1999) and indicates some future needs for agent-based behavioral modeling in ecology. My preliminary testing reveals that one of the instances where individual based models could further contribute to the optimal foraging theory is detailed examination of the importance of patch size, and idea also proposed by WallisDeVries et al. (1999). For clarity of the discussion about the consequences of travel times between patches, their quality and forager's characteristics, I used constant patch size for all simulations. It could be argued that variable patch size would affect the choice of foraging behavior as the optimal strategy. I believe that another aspect of foraging in a patchy environment that could affect behaviors of animals is how foragers perceive a patch of forage and whether they should respond to the amount of forage in a patch or to the density of forage in that patch. Unequal distribution of forage quality within a patch is common in nature, yet difficult to assess in field experiments and challenging for simulation modeling conducted in a broader context. It is definitely another key aspect of foraging theory that begs a detailed investigation.

5.4. Conclusions

I believe there is no one 'right' foraging strategy that is always optimal and optimality should be assessed in the context of natural selection. According to natural selection, an optimal strategy should be a behavior that maximizes fitness. Therefore, a strategy that maximizes the caloric and nutrient (forage) input and optimizes the cost-benefit ratio may not be the optimal strategy. Depending on time limitations, the structure of the landscape and foragers' efficiency in utilizing the resource, it may be the MVT or satisficing, or smart foraging that would be the optimal strategy. I argue that in most cases a set of rules that I call smart foraging should be the optimal foraging strategy.

The Marginal Value Theorem proposed by Charnov (1976) was used to explain not only foraging by animals, but also as a mechanisms for a variety of human behaviors ranging from hunting decisions and agricultural choices of early societies (Smith and Wishnie 2000) to modern internet searches (Pirolli 2005). This further emphasizes the importance of the basic concepts in the optimal foraging theory, which aims at explaining animal and human behaviors, and invokes a need for more interdisciplinary research. I believe that my work clearly indicates that transfer of ideas between disciplines (e.g., satisficing that originated in economics) can shed a new light on an old problem and result in novel ideas. This even further stresses the necessity of interdisciplinary research, and I suggest that research combining economics and biology promises progress in both disciplines. Economics is a social science that aims to explain how economies work and how economic agents (e.g., decision makers, individual players) interact. Therefore, the principles of both economics and animal ecology are based on the understanding of the mechanisms that govern behaviors of individuals. Indeed, as pointed out by Landa and Ghiselin (1999) an increase in the transfer of ideas between economics and biology should result in building new theorems, theories and paradigms. Based on my work, I believe one of the areas that should be further explored in the discipline of bioeconomics is rational choice theory that underlines microeconomics and that should be the foundation of the optimal foraging theory.

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