Optimal Foraging Theory - OFT

Background, Problems and Possibilities

Mesolithic cave on the island of Stora Karlsö, Gotland, Sweden.
Photo by Ingegärd E. Malmros

University of Gotland
2012/Spring term
School of Culture, Energy and Environment
Bachelor Thesis
Author: Ingegärd E. Malmros
Supervisor: Jan Apel
Optimal Foraging Theory (OFT) has its origin in processualistic ideas in 1960s with traces back to the dawn of the archaeological science in the 19th century. The OFT model is based on the construction of an individual's food item selection understood as an evolutionary construct that maximizes the net energy gained per unit feeding time. The most common variants are diet patch choice, diet breadth/prey choice models and Marginal Value Theorem (MVT). The theory introduced experimental studies combined with mathematically data analyses and computer simulations. The results visualized in the experimental diagrammed curve are possible to compare with the archaeological records. What is “optimal” is an empirical question not possible to know but still useful as a benchmark for measuring culture. The theory is common in USA but still not in Europe. OFT seems to be useful in hunter-gatherer research looking at human decisions, energy flow, depression of resources and extinction. This literature review concludes that the prey-choice/diet-breadth model seems to be useful for hunter-gatherer research on Gotland focusing on possible causes of the hiatus in archaeological records between 5000-4500 BC.

Keywords: Darwinism, diet-breadth, evolutionary ecology, Marginal Value Theorem, MVT, Optimal Foraging Theory, OFT, patch choice, prey choice

Optimal Foraging Theory (OFT) har sitt ursprung i de processualistiska ideéerna under 1960-talet med spår tillbaka till arkeologins början som vetenskap under 1800-talet. OFT modellen baseras på konstruktionen av en individs födoämnnesval som förstår som en evolutionär konstruktion som maximär nettoenergiuttaget per tidsenhet som gått åt för försörjningen. De vanligaste varianterna är patch-choice, diet breadth/prey choice modellerna och Marginal Value Theorem (MVT). Experimentella studier genomfördes och data bearbetades matematiskt och visar datorsimulerade kurvdiagram möjliga att jämföra med arkeologiska källmaterial. Vad som är "optimalt" är en empirisk fråga omöjlig att veta men användbar ändå som en slag referens för att mäta kultur. Teorin är vanlig i USA men ännu inte i Europa. OFT förefaller användbar inom forskning av jägare-samlare om man fokuserar på beslutsfattande, energiflöde, depression av resurser och utrotning av arter. Slutsatsen i denna litteraturöversikt är att prey choice/diet breadth modellen tycks vara användbar för gotländsk jägare-samlare-forskning som fokuserar på möjliga orsaker till de arkeologiska fyndens hiatus mellan 5000-4500 BC.

Keywords: Darwinism, diet-breadth, evolutionary ecology, Marginal Value Theorem, MVT, Optimal Foraging Theory, OFT, patch choice, prey choice
Acknowledgements

I would like to thank my supervisor Jan Apel for letting me be a part of his research group in excavation and theoretical analysis, for his inspiring discussions and for supplying me with literature. His dedication to the Early Mesolithic period on Gotland, made me understand some of the exciting challenges waiting for a Mesolithic researcher and I became myself a part of that dedication.
# Table of contents

1 Introduction .................................................................................................................. 5
  1.1 Aim and Research Questions ................................................................................. 7
  1.2 Methodology and source material ......................................................................... 7
    1.2.1 Methodology ................................................................................................. 7
    1.2.2 Source Material ............................................................................................. 8
    1.2.3 Criticism of the Source Material ..................................................................... 8
  1.3 Limitations ............................................................................................................... 8
    1.3.1 Inclusion criteria ............................................................................................ 8
    1.3.2 Exclusion criteria ........................................................................................... 9

2 Previous research ......................................................................................................... 9
  2.1 The history of theoretical perspectives in archaeology .................................. 9
    2.1.1 The history of Archaeology as a science ......................................................... 10
    2.1.2 New Archaeology - Processual Archaeology ............................................... 10
    2.1.3 Postprocessual archaeology .......................................................................... 13
    2.1.4 Darwinism – theory of evolution .................................................................. 14
    2.1.5 The ecological approach .............................................................................. 15

3 Optimal Foraging Theory - OFT ............................................................................... 17
  3.1 OFT as a benchmark for measuring culture ..................................................... 17
    3.1.1 The basic variables of OFT ........................................................................... 18
    3.1.2 The Marginal Value Theorem (MVT) .............................................................. 20
    3.1.3 OFT – optimal strategy equation ................................................................. 21
  3.2 Early reviews, support and criticism of OFT 1977 – 1987 ............................ 22
    3.2.1 OFT: A selective review of theory and tests, 1977 .................................... 23
    3.2.2 OFT: Field tests of Diet and Habitat Switching, 1981 ............................... 23
    3.2.3 Anthropological applications of OFT: A critical review, 1983 .................. 24
    3.2.4 Eight reasons why OFT is a complete waste of time, 1987 ...................... 25
  3.3 Different OFT applications .................................................................................... 26

4 Results and discussion ................................................................................................. 35

5 Conclusion ................................................................................................................... 44
  5.1 Concluding remarks .............................................................................................. 46

6 References...................................................................................................................... 47
1 Introduction

This Bachelor thesis is inspired by the wish to find a suitable method for analysing Mesolithic hunter-gatherer societies in the Baltic Region, focusing on Gotland. The reason is a hiatus period between 5000-4500 BC with no Gotlandic archaeological records so far and the causes are still unknown (Apel & Vala in prep.). As humans are living within ecological systems hopefully an optimal foraging perspective can shed light upon indications of affluence or starvation during different periods on Gotland. With an ecologically oriented explanation of human past it is possible to discuss return rates and fluctuating resources using the Optimal Foraging Theory (OFT) (MacArthur & Pianca 1966; Emlen 1966). The Mesolithic pioneers on Gotland were seal-hunters during the Mastogloia Lake period with changing sea-levels and fluctuations in the economy, and the archaeological records show that their prey choices change over time (Lindqvist & Possnert 1997). Per Persson (1999), inspired by Sahlin (cited Lee & DeVore 1968), has the opinion that affluence dominated during the Mesolithic in Southern Sweden based on his analyses of ecofacts and he made his subjective assessment that the resources were plenty enough. Terrestrial big animals but not seal dominated the diet even if some seal bones were recorded (Persson 1999).

OFT is closely connected to evolutionary ecology with ties both to the Darwinian and processual archaeology. In “The American Naturalist” in 1966 Robert H. Mac Arthur & Eric R. Pianka and Stephen Emlen both presented their reports “On optimal use of a patchy environment” respective “The role of time and energy in food preference”, the framework later called “The Optimal Foraging Theory”. The theory states that organisms forage in such a way that they will maximize their net energy intake per unit time (MacArthur & Pianca 1966; Emlen 1966). Different models of OFT have been developed by evolutionary ecologists as for example James L. Boone (2002). The theory has been useful for ecological anthropologist when applying this model to hunter-gatherer systems aiming empirically quantification of predator-prey relationships (Trigger 2006). Archaeology is a diverse discipline in which a variety of professions, methods and theories are useful when looking into the past, trying to draw out as much
truth as possible out of the ancient records. It is also a discipline filled with traps when interpreting these finds. As every single researcher is allowed to use his/her own opinion in the interpreting and evaluating process it is essential to know from which perspective the evaluation is made, which bias is colouring the views and which archaeological theory is the base for the assessment. There have been many questionable romantic evaluations on happy easygoing foragers, but surprisingly few researchers seem to have been interested to discuss the hard environmental conditions and diseases of arctic and boreal hunter-gatherers. At the symposium “Man the hunter” in Chicago 1966, organized by Richard B. Lee and Irven Devore (1968:85-88), attempts were made to bring together a comprehensive look at recent ethnographic research on hunter-gatherers. At that time the common opinion was that hunter-gatherers were almost always near the brink of starvation, struggling for survival, and the new idea that a hunter-gatherer society was as Marshall Sahlins called it “an original affluent society” was challenging. This became the new consensus even if many disagreements also were presented in the book “Man the hunter” (Sahlins cited Lee & Devore 1968). Even in Scandinavia these new ideas were adopted and Persson (1999:173-177)) in his PhD dissertation “Neolitikums början” is convinced that resources were available but not used because of affluence. His statement is based on assumptions due to different hunting and fishing customs in the Baltic region. His opinion is that hunter-gatherer made conscious cultural decisions as to which prey to choose and the affluence is taken for granted. OFT discusses why food selection sometimes is broad, sometimes narrow and that especially deviations from the optimal foraging model can help to identify constraints when discussing the energy budgets (MacArthur & Pianca 1966; Emlen 1966). OFT has still not been used in Scandinavian hunter-gatherer analyses, and energy flow discussions are missing. Historically evolutionary ecology and archaeology have its root in anthropology in USA but in Scandinavia archaeology belongs to the humanistic discipline and this has interfered (Trigger 2006).

Archaeology as a scientific discipline has a short history from the 19th century and the theoretical approaches are almost hundred years younger. Bruce G.Trigger (2006:137) summarizes that Scandinavian prehistoric archaeology
owes its origin in the evolutionary, culture historical, functional and processual approaches that have characterized prehistoric archaeology thereafter. The purpose of this bachelor thesis is first to put Optimal Foraging Theory (OFT) in its historical context and thereafter to evaluate the usefulness of different OFT models for archaeological purposes. The foraging perspective has not been used in hunter-gatherer research in the Baltic Region. This bachelor thesis will analyse the background of the Optimal Foraging Theory, evaluate different OFT applications and look into problems and possibilities related to them. Finally a conclusion will be made with an evaluation of the usefulness of an optimal foraging perspective on analyses of hunter-gatherer societies on Gotland. There is a need for future studies of hunter-gatherer societies where the predator-prey relationships between humans and preys are analysed.

1.1 Aim and Research Questions
The aim of this Bachelor thesis is to follow the development of theoretical ideas within the archaeological history and look into OFT in an evolutionary ecological perspective. An evaluation of the usefulness of the theory for research on hunter-gatherer systems and predator-prey relationships between human and prey is also included. The Mesolithic hunter-gatherer research on Gotland is in focus.
- What archaeological historical and theoretical roots can be traced in OFT?
- What are the main critical and supportive aspects of OFT?
- Can OFT in an evolutionary ecological perspective be useful for studies on eventual extinction of animals in hunter-gatherer environments?
- What main OFT versions relevant to different foraging situations are of interest to Baltic Mesolithic research, focusing on Gotland?

1.2 Methodology and source material
1.2.1 Methodology
A qualitative comparative research method is used aiming to gather information and understanding on archaeological history and theory in the chosen literature. As qualitative methods only produce information on the special cases that are studied it is not wise to draw any general conclusions but the comparative per-
spective hopefully will discover some similarities or differences in the analysed reports.

1.2.2 Source Material
The research materiel consists of archaeological literature with focus on OFT and some of its variations.

1.2.3 Criticism of the Source Material
The material used is based on secondary sources that are well documented; peer reviewed, and written by well-known archaeologists from institutions using methodological accuracy with good reputations. It is however difficult to evaluate the amount and direction of bias among the researchers. The authors and researchers themselves have used primary archaeological artefact sources as well as secondary ones (other researchers’ reports) with the potential risk that every new author may distort and bias the secondary source. The demand for updated material is fulfilled as the literature is spanning from the first original reports on OFT (MacArthur & Pianca 1966; Emlen 1966) until 2012. Both criticism and support of OFT is presented, hopefully giving the reader a reasonable possibility to make his/her own judgment of the usefulness of the theory.

Criticism of the primary source material (artefacts, geofacts and ecofacts) used in the secondary sources might be that the results of the records are depending on special environmental conditions as for example low temperature, high ph-level and a low exploitation level.

1.3 Limitations
1.3.1 Inclusion criteria
- Literature representing archaeological history and theory from 1966 when OFT was first presented until today (Internet documentation included)
- Only authors who are well-known, peer reviewed and with good academic reputation will have their books or reports analysed.
- Only the usefulness of an optimal foraging perspective on Mesolithic hunter-gatherer societies on Gotland is analysed, not the rest of Sweden.
2.1 The history of theoretical perspectives in archaeology

Matthew Johnson (2010) explores the increasing diversity of approaches to archaeological theory and states that there is no simple definition of “theory”. He proposes a definition of theory as “the order we put facts into” (2010:2) which has an impact on the decision on why and how to do archaeology and how it
will be interpreted by the researcher. Theories and methods are often confused by archaeologist he says, and disagreement over whether concepts should be considered “theoretical” or “methodological” are common. Johnson argues that all researchers are theorists and that all facts translated into meaningful accounts of the past by the set of rules that is used are explicit or implicit theoretical in nature. The archaeological history is therefore also to a great extent the history of its theoretical framework.

2.1.1 The history of Archaeology as a science
Trigger (2006:121- 137) makes a short review of two distinct movements that changed the collecting of antiquities to that of comparing and analysing the material prehistoric culture in a systematic manner. This is the dawn of the prehistoric archaeology according to him. The fist movement originated in Scandinavia in the early 19th century when the Danish archaeologist Thomsen invented a technique which made it possible to distinguish and date archaeological finds. This facilitated the introduction of comprehensive studies of the prehistory based on a solid chronological foundation. The second movement began in the 1850s in France and England with the pioneering studies of the Palaeolithic period where questions of human origin were addressed in a time depth perspective in human history that was never known or imagined before. The Palaeolithic research became extremely important in the discussions between the evolutionists and creationists that followed the publication of Charles Darwin’s *On the Origin of Species* in 1859 (Trigger 2006). The evolution influenced both scientists and political theorists. Johnson (2010) divides the evolutionary theory into socio-cultural and Darwinian approaches.

2.1.2 New Archaeology - Processual Archaeology
Systems theory and systems thinking in archaeology are introduced by Sally and Lewis Binford (1968) in “New Perspectives in Archaeology” dealing with low, middle and upper range theory, and Kent V. Flannery (1968) in “Archaeological Systems Theory and Early Mesoamerica”. Binford (1963) is a promoter of ethno-archaeological research and archaeological theory with an emphasis on the application of scientific methodologies. His research has a focus on generalities and the way human beings interact with their ecological niche. He is using hunter-gatherer and environmental data in his analytical method for ar-
chaeological theory-building (Binford 2001). Flannery (1968, 1969) looks at culture as a natural system that can be explained in an objective manner in mathematical terms when the material is broken down in its elemental system components. New Archaeology as developed in the 1960s and 1970s, defined archaeological cultures as systems and system is defined by Graham Clarke 1978 as “an intercommunicating network of attributes or entities forming a complex whole” (Bonsall 1996:2-4; Johnson 2010:72). This was an empirical definition of culture and made research on cultural system and its adaption to an outside environment very important. Cultural systems according to Johnson are adapted to an external environment and elements of culture are more or less observable. There is a strong influence by Darwinian ideas of adaption. The researcher can measure, quantify, weigh and make caloric valuations from a faunal assemblage. From these data the researcher can construct and measure a link between subsistence economies and trade off. This hypothesized link might then be tested by reference to the archaeological record. Such cultural systems can be modelled and compared from culture to culture and lead to comparative observations and generalizations about cultural processes. As elements of cultural systems are interdependent, change in one part of the system will affect the whole system and lead to a positive or negative feedback, homeostasis or transformation. Ecology, as a natural system, strives towards a state of balance when affected by external changes (for example climate or a new predator). After a period of fluctuations through modifications in the relations between the subsystems a new overall balance will emerge. Archaeologists can make their research on links between subsystems in terms of correlation rather than simple causes. New Archaeology sought to replace “culture history” with “culture process”. The idea of process relates closely to ideas of cultural evolution and cultural ecology and the search for underlying processes rather than the “noise” on top. An artefact is looked upon as a representative of trade or craft specialization and to chart the process which led to this trade or specialization is the important matter. As archaeologists are interested in long term perspectives and cultural anthropologists in the present the two disciplines together can contribute with knowledge about human beings (Johnson 2010:72-75).
Johnson (2010:80-88) has the opinion that thinking in cultural processes has many advantages when investigating the cultures in the past compared with traditional approaches. The reason is that it provides convincing explanations alongside with the development of generalizing and comparative arguments. Still there is a lot of criticism of functionalism that can be equally applied to the theories of cultural processes. Critics argue that there is a flaw when explaining something by reference to its function as it gives no explanation of the historically past from where it came. Therefore Johnson states that functional explanations seem more linked with adaptive explanations than with conscious decisions when societies develop a better adapted life style. For functionalists culture is like an organism where the different parts of the society are performing different functions and are adapted to their environment. He compares with structuralists where culture is like a language which expression is made up by a system of hidden, cognitive meanings (Johnson 2010:94-95). In the Darwinian sense these functional societies will be “selected for” in a long time perspective and found in the archaeological records. The processual researchers’ arguments therefore often are related to adaptive explanations. As processual arguments depend on functional linkages these links are weak points. The processual thinking fails to explore why a special strategy was adopted and preferred when many choices existed between particular adaptive strategies. No answer is given if it depends on the particularity of the cultural group or on cultural preferences. Cultural models seems to require an external “kick” (for example climate changes) to start changes according to Johnson. Processual thinking is a way of trying to understand society from the outside and cultures therefore often are divided in elements of general categories as subsistence, trade etc. The hard criticism on the “outside” view lacking the “inside” one opened up for the “interpretive” and “postprocessual” views of archaeology after the early 1980s (Johnson 2010:80-88).

A modified processual thinking developed where some archaeologists rejected all models of culture processes. They instead adopted postprocessual approaches according to theories by Anthony Giddens (cited Johnson 2010:84) that represents different ways of thinking about societies. Others have separated some of the processual thinking from much of the ideas of functionalism and
in that sense been able to incorporate conflict and contradiction within their parameters. In doing so, change from within the cultural system can be both understood and explored in processual terms and no external “kick” is needed for explaining transformation. Processual models will then be less dependent on theories of adaption to an external environment. Simulation and mathematical modelling on computers has been used from the late 1970s where chance, historical contingency and human decision-making have been built into models. Johnson argues that much of postprocessual archaeology is dependent on concepts of culture process even if many postprocessualists don’t want to admit it (Johnson 2010:84-88). The debate over scientific methods in archaeology are undergoing the same discussions as in any other social science says Johnson. Behavioural psychologists focus on people’s behaviour as they claim that thoughts are beyond the domain of science while Auguste Comte and Émile Durkheim in sociology used a positivistic framework for their sociological methods. In contrary the sociologist Giddens in opposition argued for the impossibility of a neutral value-free science of society and some feminists argue that science is merely a male construct (cited Johnson 2010:48 - 49).

2.1.3 Postprocessual archaeology

The postprocessual archaeology developed largely because of a growing interest in cultural phenomena in anthropology and claimed to represent the opposite pole to processual archaeology of the same theoretical spectrum. The postprocessual archaeology, labelled by Ian Hodder in 1985, began to develop in the late 1970s and early 1980s (Trigger 2006:444-483). Hodder (2009:122-138) invites Colin Renfrew to write a chapter in “Archaeological theory today” about postprocessualism, as he since long had indicated his dissatisfaction that cognitive issues had been poorly addressed by the early functional-processual phase of processual archaeology. Renfrew explains the importance of human symbolism and interpretations for the development of culture and presents a cognitive processualism. Postprocessual archaeology is an interpretive archaeology filled with diversity (Hodder 2009:122-138).
2.1.4 Darwinism – theory of evolution

Darwinian fitness discusses the rate of increase of a gene in the population and the capability of a certain genotype to reproduce. In the theory of natural selection, the process causing differences in individual genotypes affects fitness so that frequencies of genotypes with higher fitness become more and more common over generations. Selection and not development is in focus. Behavioural ecology is the study of ecological and evolutionary bases for animal behaviour and how a special behaviour promotes adaption for a species to its environment. Natural selection (Darwinian fitness) will probably favour organisms with special traits that provide selective advantages in a new environment. Adaptive significance will be visible in traits beneficial for increased survival and reproduction. Different behaviours lead to different “trade-off” affects that involves losing one quality in favour for another (Scarre 2009:31-32).

Darwin published his “On the Origin of Species” in 1859 and “Descent of Man” in 1871 with observations grounded on the diversity and interrelationships of the species he had found among plants and animals on his voyage, mapping the coast of South America. He recognised the key role of natural selection in the way development occurred in individual species over time. The most successful individuals within a species would more likely reproduce and pass their characteristics to the offspring. Thus, features offering advantages would be reinforced and spread among the population and sub-groups could be specialized and successful within its particular environmental niche (Scarre 2009).

Darwin’s theory was revolutionary when challenging the diversity of life, not because of divine creation but of evolution, if the ideas would be true also for humans. His views brought him into fierce conflict with others but his theory successively won general acceptance. It was the most persuasive explanation of the development of diversity of life where forms and behaviours are constantly adapting and changing in response to pressures and environmental factors. Genetic studies have supported the model of evolution through natural selection and Mendel in 1860s made basic studies with plant breeding experiments showing the way in which inheritable characteristics are passed from parents to offspring (Scarre 2009:32). Boyd & Silk (2009.53-71) explains the modern syn-
thesis on Darwinism and population biology seen in population genetics where evolutionary change in a phenotype reflects change in the underlying genetic composition of the population. Evolutionary population biology analyses both how and why populations are differently developed in nature and the limitations that have a great affect the evolutionary process. During the past 50 years DNA analyses have developed and it is now possible to explain how Darwinian natural selection operates at the level of the genetic code and this evolution is still going on. Darwin’s theory introduced a new way of understanding humans, fauna and flora in the context of their shared environment. Evolutionary ecology studies the adaption of species to their environments in both biological and behavioural terms. If cultural ecology also includes an adaptive mechanism the study is called human evolutionary ecology, but many archaeologist regard this as too limited to provide a comprehensive explanation of human cultural behaviour (Boyd & Silk 2009; Scarre 2009).

2.1.5 The ecological approach
Colin Renfrew & Paul G. Bahn (2008:36-37) discuss the ecological approach with studies of the relations living organisms have with respect to their natural environment and to each other. Julian Steward (1902-1972) as an anthropologist was interested in explaining cultural changes in an anthropological perspective on how living cultures work (Steward cited Renfrew & Bahn 2008). Steward argued that cultures not only interact with one another but also with the environment and used the expression “cultural ecology” when studying ways in which adaption to the environment could cause cultural changes. Independently, Graham Clark (1907-1995) meant that by studying how human populations adapted to their environments it would be possible to understand many aspects of ancient cultures (Bonsall 1996; Clark cited Renfrew & Bahn 2008). Clive Bonsall (1996:1-4) refers to Clark’s important work in Mesolithic research, and especially on the pre-boreal site of Star Carr presented in the Star Carr monograph 1954 as “a landmark in archaeological literature for its linking of environment, subsistence and technology”. By that time, the artefact-dominated culture-historical approach still dominated around them. Thanks to new excavation techniques, examinations now could be done not only of prehistoric environments but also of prehistoric foods and economies. Careful environmental anal-
yses and recovery of organic remains gave new insights from an ecological point of view. Here the base was laid for the expanding field of environmental and dietary reconstructions (Renfrew & Bahn 2008:36-37). Evolutionary ecology is defined as the study of adaptive design in behaviour, life history and morphology and within the framework of evolutionary biology. Adaptive behaviour is seen when track variability is caused by environmental factors in ways that enhance individual’s reproduction (Bird & O’Conell 2006).

Stephen Shennan (2002) discusses archaeology and evolutionary ecology and he refers to Eric Alden Smith who has suggested that there are three styles in the evolutionary analyses of human behaviour: 1. Evolutionary psychology, 2. Behavioural ecology and 3. Dual inheritance theory. The behavioural ecology represents the classical Darwinian view with the assumption that in evolutionary terms humans are very close to animals, just another unique species. Diversity in behaviour in the present and recent past is depending on different pay-offs for different ways of action in different environments. *Culture according to behavioural ecologists has a minor role because cultural behaviour that does not lead to the best reproductive outcome will be weeded out. The most widespread methodology based on these assumptions is Optimal Foraging Theory (OFT).* It is assumed that behaviours are to some extent also genetically determined but as complex animals as humans have a great capacity for learning this also give them considerable behavioural flexibility. As the gene-behaviour link is very hard to study behavioural ecologists ignore the details of the inheritance process and look at behaviour as adaptation produced by “decision rules”, which are under selection. A large number of studies have been carried out in the field where animal behaviour is analysed for their ability of predictions, based on the assumptions that they can make sense of field observations. *OFT does not assume that animals are aware of their decisions or evolutionary aims. It simply analyses what would be optimal and from that point, comparisons with other records can be made.* The selection is assumed for a particular type of behaviour with phenotypic flexibility, learning ability and sensitivity to the environment. Shennan is of the opinion that human phenotypes are more complex than other animals because culture is more influencing them. Since culture is not acquired genetically, there are different points of views whether human genes have any
bearing on human behaviour or not. The hypothesis of optimisation is not self-verifying as it is predictable what will be optimal in a given situation, for example, what foraging strategy will give best return for a given amount of effort. However, the problem persists that there is no basis for defining what is “good enough”. Shennan summarizes behavioural ecology as a powerful and complex set of ideas for understanding animal behaviour in terms of evolutionary consequences. He also states that predictions derived from the optimality theory and how they correspond to what people actually do should be a matter for research instead of dogmatic debates (Shennan 2002:1-5).

3 Optimal Foraging Theory - OFT

3.1 OFT as a benchmark for measuring culture

When “new archaeology” emerged during the 1960s, a new interest awoke that emphasized technology, settlement patterns and subsistence on the empirical side along with ecologically oriented explanations of the human past on the conceptual side (Grayson & Cannon 1999). OFT derived from evolutionary ecology as a branch of behavioural ecology, that studies the foraging behaviour of animals in response to their environment. The foraging behaviour of animals and the payoff animals obtain from different foraging strategies are in focus, where the highest payoff measured as the highest ratio of energetic gain cost while foraging should be favoured. The theory helps biologists to understand the factors that determine the operational range of food types or diet width of the consumers. Animals with a generalist strategy tend to have broader diet than those with a specialist strategy with a narrow diet. Specialists seem to ignore many of the prey items crossing their way. As foraging is critical to the survival of animals, more successful foragers according to the evolutionary perspective are assumed to increase their reproductive fitness passing their genes on into the next generation (Grayson & Cannon 1999).

OFT was first formulated in 1966 in the journal American Naturalist and the theory got its name somewhat later. The papers by Mac Arthur & Pianka (1966:603-609) and Emlen (1966:611-617) were published independently and they both argued that a successful foraging is of greatest importance to an indi-
individual’s survival and that it should be possible to predict foraging behaviour by constructing an “optimal forager”. They demonstrated the need for a model where an individual’s food item selection could be understood as an evolutionary construct that maximizes the net energy gained per unit feeding time. It gives a better understanding of adaption, energy flow and competition and how and why food selection sometimes is broad and sometimes very narrow. The constructed model of an “optimal forager” would have perfect knowledge of how to maximize usable food intake, but real animals and humans are not that predictable. OFT as a benchmark provides a method of comparing a virtual “optimal forager” with the performance of a real forager interpreted in archaeological records. As there are no perfect real optimal foragers these discrepancies will shed light upon problems worth to discuss and analyse further (Emlen 1966; MacArthur & Pianka 1966).

3.1.1 The basic variables of OFT

MacArthur & Pianca (1966) were influenced by the development of theories in economics and population biology and focused on the geometry of the organisms and their biological environment. In their paper “On optimal use of a patchy environment“ and “Optimum theories” hypotheses were discussed for testing with the assumption that different phenotypes have different abilities at harvesting resources and that these resources are distributed in a three-dimensional patchwork in the environment. Their tests were aimed to determine in which patches a species would feed and which items would form the diet if the species acted in the most economical way. The natural selection was thought to work toward such an optimal allocation of time and energy. The basic procedure for determining optimal utilization of time or energy budgets is that an activity should be enlarged as long as the resulting gain in time spent per unit food exceeds the loss (MacArthur & Pianca 1966:603).
Time spent per eaten item is divided into time for search and time for pursuit, capture and eating. Time has an energy cost. The method of ranking proceeds from items of highest harvest per unit to those of lowest. *The decrease in pursuit time measures the adaption of the species for the items and must be empirically determined.* The model makes the assumption that the patches are equi-distance apart and that the patches are equally stocked with prey. The exact shape of the curves (fig. 1) is usually not known and varies from situation to situation which makes no general prediction of an exact diet possible. It seems an organism that has a low search/pursuit ratio should be more restricted in diet (MacArthur & Pianca 1966:604). The basic variables (fig. 1, fig. 2) are hunting time (H), travelling time (T), pursuit time (P), search time (S), kinds of prey in the diet (N) and food density (D). The pursuit time may increase when hard-to-catch items are added to the diet.

The graphical method discussed by MacArthur & Pianca (1966) allows specification of the optimal diet of a predator in terms of net amount of energy gained from a capture of prey compared to energy used in searching for the prey. Predictions are possible to do about changes in the degree of specialization of the diet as the numbers of different prey items change. Environments that are more productive should lead to diet that is more restricted and larger patches are
used in a more specialized way than smaller ones. In patchy environments, predators spend most of their time searching. Animals should be more selective in their choice of food items when the food is common and more indiscriminate when starved or when food is scarce. Food preferences seem to change readily and appropriate to changes in the environment. This model is often referred to as the patch-choice model (MacArthur & Pianca 1966; Emlen 1966).

### Table 1: Factors favoring increased specialization

<table>
<thead>
<tr>
<th>Of diet</th>
<th>Of patches</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leave (\Delta P) constant, but lower (\Delta S) curve</td>
<td>Leave (\Delta H) constant, but lower (\Delta T) curve</td>
</tr>
<tr>
<td>1. Greater food density</td>
<td>1. Greater food density (pursuing species only*)</td>
</tr>
<tr>
<td>2. Increased mobility of animal, or decreased environmental resistance to movement, etc.</td>
<td>2. Increased mobility of animal, or decreased environmental resistance to movement, more contiguous patch structure, etc.</td>
</tr>
<tr>
<td>Leave (\Delta S) constant, but raise (\Delta P) curve</td>
<td>Leave (\Delta T) constant, but raise (\Delta H) curve</td>
</tr>
<tr>
<td>1. Increased differences between prey types, or increased specialization of pursuing behavior</td>
<td>1. Increased differences between patch types (or sizes), or more restricted hunting technique</td>
</tr>
<tr>
<td>2. Increased mobility of prey, or greater difficulty in pursuit</td>
<td>2. Increased mobility of prey, or greater difficulty of capturing it</td>
</tr>
<tr>
<td>3. Reduction of food density in some patches by competition</td>
<td></td>
</tr>
</tbody>
</table>

*The hunting time is only independent of food density if it is all pursuit time and some search. The extent to which this is approximated determines our confidence in this effect.

Fig. 2. Variables in the Patch-choice model on optimal use of a patchy environment (MacArthur & Pianca 1966:609).

#### 3.1.2 The Marginal Value Theorem (MVT)

The Marginal Value Theorem, with the base in OFT, was first proposed by Eric L. Charnov in his thesis 1973 (Charnov 1976:129-132; Smith 1983:631). Unlike MacArthur & Pianka’s patch-choice model, the marginal value theorem states that the set of utilized patches are given. The pattern of time allocation to reach each patch that would give the highest overall rate of energy capture is analysed. As food is found in clumps or patches, the predator finds food items within a patch but spends time in travelling between patches. The predator must make a decision to which patch type to go and when to leave for the next one. Charnov’s paper has the focus on the important model assumption that while
the predator is in a patch its food intake rate for that patch decreases with time spent there and the predator depresses the availability of food to itself. The predator should leave the patch when the marginal capture rate in the patch drops to the average capture rate for the habitat. The theorem (fig. 3) makes the explicit assumption that the foraging process gradually depletes the resource level at any patch, which causes the decline in the net return rate from that patch (Charnov 1976). Eric A. Smith (1983) refers to ecological anthropological applications where some researches hold that there was a Pleistocene overkill. Others argue that human foragers practiced conservation of their prey and that the decline of vertebrates had other causes.

Fig. 3. Optimal use of a patchy habitat. The energy intake functions \( g_i(T_i) \) are shown for a habitat with two patch types. If the ray from the origin with slope \( E \sigma^* \) is plotted, the appropriate time to spend in each patch is found by constructing the highest line tangent to a \( g_i(T_i) \) curve and parallel to the ray. The lines and the resulting times are shown for the two patch types.

3.1.3 OFT – optimal strategy equation

David B. Irons et al. (1986) discusses foraging strategies when performing an informative experiment with Glaucous-winged gulls on the Aleutian Islands in the rocky intertidal habitats. They made prey preference experiments where both search and handling times of the different prey items were zero. Their experiments then showed that gulls chose chitons over urchins and mussels. Under natural conditions, though they selected urchins over chitons and the mussels were least preferred despite their high abundance. The researchers found that the intertidal zones could explain these preferences as the gulls were forag-
ing across these zones where the mean search and handling times differed (Irons et al. 1986). Their method consisted of four variables:

<p>| | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>E</td>
<td>energy content of a prey item (kJ)</td>
</tr>
<tr>
<td>h</td>
<td>handling time for a prey item</td>
</tr>
<tr>
<td>I</td>
<td>the &quot;next most-profitable item&quot;</td>
</tr>
<tr>
<td>s</td>
<td>search time for a given prey item</td>
</tr>
</tbody>
</table>

The profitability of a prey item is the ratio of the energy content to the time required for handling the item, often called the strategy equation. If a predator continues to search for the more profitable items already in its diet and ignores the "next most-profitable" ones the energy intake is decreased. Irons et al. (1986) therefore concludes that the situation in which pursuing the "next most profitable" item is the optimal strategy as it is most profitable.

OFT therefore predicts that species preying on a wide range of food items with varying profitability will be generalists. For species with long handling times relative to search times, the two sides of the equation are similar. **OFT predicts that such species will adopt a specialist strategy, preying only on items with high-energy content.** Generalist strategy sacrifice some profitability but loose less energy and time searching for prey items where specialist pursue comparatively rarer items with higher profitability but spend more time and energy searching for the prey. Many interesting perspectives are available as **experimental methods are possible to use, comparing hypothetical data with those found at an archaeological site.** The optimal foraging strategy for a species will maximize the net energy intake, and affects competition and coexistence among species in a community (Irons et al. 1986).

### 3.2 Early reviews, support and criticism of OFT 1977 – 1987

The debate concerning OFT and its usefulness is still going on and stimulates the development and use in a variety of disciplines. Many problems were discussed when OFT was introduced and many new perspectives have been add-
ed but not all researchers are still convinced. Some of the supporting or critical reports will be reviewed in this paper.

3.2.1 OFT: A selective review of theory and tests, 1977

In 1977 Pyke, Pullman & Charnov make a selective review of theories and tests in the field of optimal foraging. The reason is that many researchers are trying to develop mathematical models for predicting foragingbehaviours of animals after the introduction by MacArthur & Pianka (1966) and Emlen (1966) and the models are very similar. They all assume that the fitness of a foraging animal is a function of the efficiency of foraging measured in terms of some “currency”, usually energy, and that natural selection through evolution has resulted in animals that forage in the most optimal manner to maximize their fitness. These similar models have become known as “optimal foraging models” and the theory they represent “the optimal foraging theory” (OFT). OFT has usually been applied in situations that can be divided in four categories:
1. Optimal diet (choice by an animal of which food types to eat) - Diet breadth model, Prey choice model
2. Optimal patch choice (which patch type to feed in) - Patch choice model
3. Optimal allocation of time to different patches - Marginal value theorem
4. Optimal patterns and speed of movements

Pyke, Pullman & Charnov (1977:137) discuss both the theoretical development and the data that permits tests of predictions in a precise quantitative way. Their general conclusion is that simple models are supported reasonably well by available data and they are optimistic about the value of OFT. Their concluding argument is that these simple models discussed will require much modification for being able to deal with situations not easily put into one of the four above mentioned categories (or entail more complicated currencies than just energy).

3.2.2 OFT: Field tests of Diet and Habitat Switching, 1981

In 1981 Werner & Mittelbach make a review of the application of OFT to questions of predator behaviour and the usefulness of the model. Their focus is on experimental tests of simple models predicting prey choice with particular reference to the size-selection of prey by fish. Laboratory estimates of model parameters are used to predict prey choice in the field and the models are com-
pared with field tests. Predictions of habitat and switching is possible to obtain when parameters are habitat specific that permits predictions of net return from foraging in different habitats. It is possible to demonstrate that OFT models can be used to relate behavioural and morphological differences between species and to look at the nature of species interactions and community structure. The authors suggest this application of OFT as one of the more useful ones.

### 3.2.3 Anthropological applications of OFT: A critical review, 1983

Smith (1983) summarizes and evaluates applications of optimal foraging behaviour models to human foraging economies. The models predict patterns of prey choice, habitat use, time allocation, settlement pattern and foraging group size that will maximize some of the objective currencies (the net rate of energy capture while foraging). The constraints of resource characteristics and forager capabilities connected to a particular situation are also included. Smith has the opinion that the patch-choice model presented by MacArthur and Pianka (1966) is so similar in form to their diet-breadth model that its widespread application is prevented. As the patch-choice model does not specify how long a forager should stay in each patch, or the effect on the stock that the foraging could cause with gradual but continual decline in return rate, the classic economic situation of “diminishing returns” to inputs of time or labour has to be handled in some other way. The marginal value theorem (MVT) takes care of this problem and becomes a subgroup of foraging models (Smith 1983).

Anthropological criticism of OFT is also discussed in Smith’s paper (1983). Issues raised are the models’ degree of realism, the validity of neo-Darwinian assumptions and simple energetic-efficiency currencies, the need to incorporate the effects of risk and uncertainty and the relation of individual decision-making to processes occurring at larger spatial and temporal scales. “It is important to keep in mind”, says Smith (1983:637), “that foraging theory is not a finished product or dogma, but very much an evolving entity”. Optimal foraging models allow the researchers to frame their hypotheses in a falsifiable form, and Smith sees it as useful even when the model fails to explain all the stated questions. The missing answers will focus the search for additional determinants and thus stimulate further research and Smith has the opinion that OFT has a potential
worth developing for the future. He stresses that foraging theory allows research of diversity from a few general decision rules. This offers hope of parsimonious explanation of the heterogeneity of human foraging strategies that for orthodox cultural ecologists have been very hard to explain. Smith suggests that the theory will be even more useful if extensive efforts are made to integrate it with other analytical approaches. His vision is a new theory construction based on human foraging behaviour, resulting from a combination of optimizing decision rules and complex socio-ecological constraints. Such a theory would add general principles of adaption and culture process, paying attention to the special environments, systems of production, exchange and social formations that characterize particular societies. Smith states that more powerful and comprehensive explanations of hunter-gatherer behavioural diversity might be achieved with such a theory, never tried before (Smith 1983:640).

3.2.4 Eight reasons why OFT is a complete waste of time, 1987

In 1987 Pierce & Ollason present serious criticism of optimizing theory applications of the behaviour and morphology of animals. They argue that optimisation theory is inappropriate for investigating the products of evolution as it is not possible to test whether an animal is optimal in its behaviour or not and that animals should not be expected to be optimal. It is no diet breadth even possible to test whether behaviour has been selected to fulfil specific functions they state, they argue, and cannot see that any optimisation model of foraging behaviour has ever been supported. Their criticism:

1. Natural selection can be assumed to maximize only reproductive output, and not as OFT assumes, maximize rewards obtained by animals engaging in independent activities since it is impossible to define the rewards or activities except circularly.
2. Animals are not designed and evolution is not purposeful.
3. Optimal strategies may not occur in nature.
4. The existence of optimal strategies is untestable and has to be assumed.
5. Functional hypotheses are untestable as models do not attempt to replicate nature exactly.
6. Optimal foraging models have not been tested.
7. Optimal foraging models have not been upheld. The authors argue that no single published test of an optimal foraging model has provided unequivocal support for the model.

8. Appeals to the heuristic value of the theory are inappropriate and the theory encourages unjustified interpretations of the behaviour of animals. The authors conclude that optimisation theory has no place in current evolutionary thought.

Stearns and Schmidt-Hempel (cited Pierce & Olasson 1987:118) have their comments added at the end of the criticism and state that most of Pierces & Ollason’s arguments are based on misinterpretations of the underlying logic of optimisation theory and the scientific method.

3.3 **Different OFT applications**

Researchers are using OFT with different modifications, adding new perspectives and determinants, revising and criticizing the theory and seem not to be able to abandon it as no better alternatives have been developed so far. From the beginning OFT was used for predicting animals (non human) behaviour but in 1990s hunter-gatherer populations were added. OFT is of value when discussing *when* it does make sense for a predator to broaden its diet and add the next most-profitable subject. When population increases, high-ranking food items probably will be over-hunted and perhaps even be driven to extinction (Winterhalder 1993, Smith 1983). Environmental factors as for example the climate, volcanic eruptions and sea level changes as well as over-hunting and other forms of depression of the prey are of importance. Many processualistic inspired researches are interested in formulating testable hypotheses that can be analysed by quantitative methods and have these results compared with anthropological data and OFT is an alternative.

3.3.1.1 **Darwinian evolutionary ecology still up to date**

"Darwinian evolutionary ecology allows us to frame some concrete expectations about what a forager should choose to gather", says David Horst Thomas (2009), scientist at the American Museum of Natural History, when the museum celebrated the 200th anniversary of Darwin’s birth and 150th anniversary of his publication of “On the Origin of Species”. Thomas uses optimal foraging theory
when he interprets the remains of thousands of meals found in archaeological sites with the assumption that individuals decide what to eat in a way that maximizes the total energy return and minimizes the energy spent on searching, collecting and preparing food items in their environment. The scientist group demonstrates excavations where they determine the amount of energy that humans could retrieve in relation to the amount of energy they spent collecting and processing the food. Series of testable hypotheses are possible to perform about what an efficient forager will choose or not choose from the available food around using the “diet breadth model”, Thomas (2008) explains. The team conducts series of foraging experiments by mapping the most efficient strategies for harvesting available foodstuffs and for each food type they record the length of time and amount of energy expended for collecting and processing. The data is comparable between different foods expressed as kilocalories per hour. “The Darwinian paradigm is like an atlas, showing the various roads available,” Thomas says, and “archaeologists use human behavioural ecology to map the options and understand the fitness benefits, making sense of the ancient stuff we find” he concludes (Thomas 2008, 2009).

3.3.1.2 OFT focusing on overexploitation and depression
In archaeological studies of temporal changes in human predation strategy OFT often is used focusing on the role of overexploitation of important prey resources and resulting resource depression. In 1993 Bruce Winterhalder publishes his report on “Work, resources and population in foraging societies” with anthropological views on the labour effect required of hunter-gatherers within an evolutionary ecology approach. Until then a suitable comprehensive theoretical framework and methodology had lacked for such an analysis. His computer simulation of evolution and population ecology models could show that equilibrium foraging efficiency is a declining function of work effort. Population density responds to work effort by first increasing and then decreasing. He states that foraging theory models have a framework with the capacity to explain observation of routine sharing, modest effort and limited material accumulation in hunter-gatherer societies, and point at diversity in the expression of these characteristics. The theory is consistent with the neo-Darwinian and neoclassical ones. Winterhalder sees no need in evolutionary ecology theory for the Zen
economy (inspired by Zen Buddhism) proposed by Sahlins (cited Winterhalder 1993). The essential questions in Winterhalder's work are: How do hunter-gatherer population growth and food choice respond to resource exploitation and depletion? What are the implications of response for work (Winterhalder 1993:323)? His results are based on a dynamic, computer simulation model that takes the number of resources initially available, subtracts any harvest and then calculates logistic recovery to determine the resources available to the forager in the subsequent round of foraging for each resource type and foraging interval. With longer foraging, resources will eventually be depleted to lower and lower levels. The optimal forager moves when the marginal return in the present location drops to the average return for the habitat as a whole, but how close foragers actually might approach this optimum is an empirical issue that Winterhalder argues is of secondary importance. An evolutionary ecological approach will look into case-specific dynamics of production, distribution and consumption that all act to diminish the extended time-reward to foraging. Some foragers will experience hard pressure and face circumstances that compel long hours of hard work but the overall tendency of the foraging economy appears to be one of limited effort according to Winterhalder. His opinion is that an evolutionary ecology approach provides a logically sufficient explanation and also focuses on the observed diversity among foragers in the subsistence behaviours related to effort and sharing linked to their material environment (Winterhalder 1993).

When Grayson & Cannon in 1999 publish their report on “Human palaeoecology and foraging theory in the Great Basin” they suggest applications of models from foraging theory to hunter-gatherer prehistory. The Great Basin already had a long history of palaeoenvironmental analyses with an ecologically oriented conceptual framework. The Stewardian cultural ecology that they used failed to explain why relationships between human behaviour and particular environmental contexts take the forms they do and a new framework was asked for. According to Grayson & Cannon (1999) foraging theory provides the best models for examining interactions between people and their environments within an evolutionary framework. Foraging theory-based applications of the resource depression concept follow from the prey-choice model. Still the models need
development and they ask for foraging theory models that can deal successfully with interrelationships between landscape change and landscape use. These models will be heavily dependent on landscape-level change through time and attempts so far have given weak results. The authors are more optimistic about the archaeological application of what they call resource depression models but notice a problem in missing knowledge of how resources were collected and processed and exactly when. There also might be a problem with experimental return rate data if they are produced by inexperienced individuals or processed in a wrong manner. The conclusion is that important insights have been provided into subsistence change and into the relationships between human impacts on the environment and human responses to those impacts (Grayson & Cannon 1999).

Some researchers like Louis R. Binford (1963, 1968), Kent Flannery (1969) and James L. Boone (2002) begin to address even the evolution of agriculture as an extreme form of resource intensification. Binford argues that human beings exist within a world composed of ecological systems (systems theory), and have the option of adopting cultural innovations as a means of coping. Flannery presents his Broad Spectrum Revolution (BSR) hypothesis in 1968, inspired by Binford’s ideas, and suggests that the diet breadth was introduced after the Ice Age first in the Middle East and then in Europe and played an active role in the emergence of the Neolithic period.

The evolutionary ecological approach attracts many researchers due to the concept of energy budget, in which time and energy allocation is conceptually divided into 1. Somatic effort (growth, development and maintenance including subsistence activities) and 2. Reproductive effort (divided in mating and parental effort) (Boone 2002). James L. Boone explores the relationship between population dynamics and subsistence intensification in his paper “Subsistence strategies and early human population history: an evolutionary ecological perspective”. The energy budget approach in conjunction with some of the general implications of foraging theory is used. He discusses two basic propositions regarding long-term human population history with the near-zero growth rates that have been persisting through much of prehistory and the broad changes in
population growth rates across subsistence modes. According to him the near-zero growth rates probably are due to long-term averages across periods with rapid local population growth interrupted by infrequent crashes caused by both density-dependent and density independent factors. The broad changes in population growth rates are explained in terms of changes in mortality due to the dampening or buffering of crashes rather than significant increases in fertility. Boone’s questions are: Why were growth rates so low when essentially all humans alive were foragers? Why did growth rates increase during Holocene? During Holocene there was a period with global warming and a wide-scale adoption of domesticates and increased sedentism (Boone 2002:7). Boone presents an alternative view of human population history where individual energetic efficiency in resource acquisition and production, rather than total productivity rates or the environmental carrying capacity, play a critical part in determining reproduction rates. Studies show that effective control of fertility has been quite rare in human history and the fertility baseline differs very little between human foragers, horticulturalists and intensive agriculturalists. Human population seems to be characterized by a saw-tooth pattern instead of series of stepped dynamic equilibriums. Human foragers are no longer seen as the natural resource conservationists they once were and overexploitation and population density must be discussed together (Boone 2002).

The diet breadth model searched the answer the question what kind of factors affect how humans choose which food items to pursue process and consume, as the same food items are used by some foragers and ignored by others. Assumptions in the model are that foragers encounter potential food items in the environment at random. Foraging costs are measured in terms of time and total foraging time is divided in search time and handling time (pursuing, capturing, processing and consuming). Prey profitability is defined as the net energy return obtained per unit of time. The result is that foragers should take low-ranked prey only as long as the return rate per encounter (profitability) is greater than the average return rate gained from searching for and handling higher-ranked prey. That also implies that high-ranked prey should be taken whenever encountered and depletion of foraged resources is nearly inevitable states Boone (2002). The adoption and cultivation of domesticates can be seen in some parts as the
culmination of the historical trend at the end of Pleistocene towards lower individual energetic efficiency in human subsistence strategies. A corresponding increase in spatial efficiency, defined as increased average total productivity of land becomes necessary. Boone has the opinion that the commonly accepted definition of carrying capacity is unrealistic as depletion of resources is always occurring and has an ongoing dynamic relationship with forager population size. Two major modelling efforts have been done to put OFT and long-term population processes into a dynamic, integrative framework with respect to human forager populations by Belowsky and Winterhalder (cited Boone 2002). Boone refers to two models that both integrate three dynamic processes that are essential to the population-resource relationship: 1. The effects of resource acquisition and consumption on the human population, 2. The effects of changing prey densities on resource selection and 3. The effects of resource exploitation on population densities of prey. The models show how resource selection and growth rates of the forager population change as a function of resource density and how density of prey responds and changes as a function of their exploitation. Under domestication, the production rate reduces individual efficiency but increases total yields per unit area of land that in turn increases the sustainable human population. Boone has the opinion that this specific aspect of domestication may be one of the most critical distinguishing characteristics for a change in the subsistence pattern. The adaption of domesticates might also be expected to dampen the amplitude of growth and crash phases and in that way push long-term average growth rates to a higher level. Probably the population crashes are not atypical and when domesticates were introduced crashes decreased and the growth rates increased markedly (Bone 2002). The fertility rates of traditional populations across all subsistence modes vary around nearly the same mean which also other studies confirm (Pennington 2001).

In 2002 Kristen J. Gremillion publishes a report concerning foraging theory and hypothesis testing in archaeology dealing with methodological problems and solutions. He proposes a strategy to probe the model’s failures by manipulating constraints and variables. By doing so the model’s performance under varying environmental conditions constitutes a partial test of alternative explanations of behaviour. He illustrates his statement by a case study involving plant use by
early food producers in Kentucky during the 3rd millennium B.P. Possible explanations for these changes were evaluated using linear programming. The finding could point out vulnerabilities in economic efficiency-based explanations for the origins of agriculture in eastern North America.

3.3.1.3  **OFT focusing on environmental changes as climate stress**
An alternative use of the prey-choice model framed under OFT is to investigate the influence of environmental changes caused by increases in climate stress on the prey availability. Steve Wolverton (2005) presents a report where he uses the same analytical technique usually used to study the effects of over-predation and resource depression caused by humans. Now it is used to analyze response to fluctuations in prey availability related to climate changes during the Holocene in Missouri. Environmental change produces many of the same effects on human predation strategy as resource depression. Climate change was a very important factor that had an impact on for example prey diets, body sizes and biographic distributions.

3.3.1.4  **OFT and MVT used in butchery studies**
Researchers in New Zealand were among the earliest ones to use foraging theory applications to archaeological situations. A number of detailed analyses examining the effects of resource depression on human foraging have been published. Butchery as well as transport studies have been incorporated. The methodological advances have increased the understanding of the processes of subsistence change in southern New Zealand (Nagaoka 2002). Butchery studies are not common. Burger, Hamilton & Walker (2005) present their paper “The prey as patch model: optimal handling of resources with diminishing returns” where they use the Marginal Value Theorem (MVT) for examining the ecological constraints on foraging decisions in processed material. Their opinion is that MVT gives a better prediction of the optimal amount of time to spend in a patch based on the relationship between an energetic gain function for a patch of a given type and the overall foraging return rate. The prediction is conditioned by the frequency with which patches are encountered. Archaeological applications of foraging theory have instead focused on understanding the range of items that enter the diet and/or how they are transported. They state that MVT is an optimisation model, just like the diet-breadth model, but the decision variable is
resource processing time or effort (optimal patch residence time) rather than specific array of resources that are acquired (e.g. optimal diet-breadth). The authors suggest MVT as a useful tool for analyses of resource processing, as it identifies how mean foraging return rate conditions the optimal effort to extract energy from prey after they are acquired. The approach is widely applicable to any prey or patch where the rate of gain decelerates with time or effort (Burger, Hamilton & Walker 2005).

Ethno-archaeological case studies also support the predicted relationship between carcass-processing intensity and overall return rate (Burger, Hamilton & Walker 2005). MVT has theoretical implications for the archaeological analysis of human hunters and their behavioural response to changes in mean foraging return rate. Processing intensity is directly recognizable from archaeological records as signatures in the carcass processing as impact fractures, green bone breaks and the relative degree of long bone fragmentation when taphonomic agents are excluded. Processing effort is used as a proxy for patch residence time and the travel time between patches (time between kills) reflects the mean foraging return rate. MVT differs from the prey-choice model in that the decision variable is time spent in a patch (measured as processing intensity) rather than the decision whether or not to attack a prey item. It also differs from the patch-choice model that applies the logic of the diet-breadth model to aggregated resources. In analysis of carcass butchery, MVT has been very useful. Fat in bone marrow is a very essential macronutrient and marrow extraction from the highest-ranked bones to the lowest is usually detectable in the degree of fragmentation (Burger, Hamilton & Walker 2005: 1147-1150). In contemporary human foraging groups there is a consistent relationship between the mean foraging return rate and the degree of carcass-processing intensity, as predicted by the prey as patch model. Three different habitats from the Arctic Circle, African Congo and Australia have been examined with very different habitat types and faunas and the prey as a patch model is applicable for all of them, showing that within-bone nutrients are more limiting to foragers than calories gained from meat. Quantitative ethno-archaeological studies of carcass use and butchery practices can be used to present marginal gain curves. Archaeologically visible butchery practices including the intensive extraction of within-bone
macronutrients, suggest extremely low encounter rates with high-ranked resources and it might stand for possible periods of nutrient stress for local hunter-gatherer groups (good times and bad times). Limitations to the prey as a patch model is seen where all possible energy is extracted from all acquired carcasses through intensive processing and boiling (Burger, Hamilton & Walker 2005:1154-1155).

3.3.1.5 OFT used in engineering design and information foraging
As time passes OFT is spreading out to new disciplines. In 1994 Pamela Sandstrom explores OFT in her work “An optimal foraging approach to information seeking and use” for its potential to clarify and operationalize studies of scholarly communication. Her approach assumes that scholars make strategic decisions when they exploit their information environments and that these decisions can be modelled mathematically.

In 2007 Theodore P. Pavlic presents his master thesis in computer science where he generalizes ideas from OFT to allow for its easy application to engineering design. In 2011 Pavlic & Passino present a paper “Generalizing foraging theory for analysis and design” using foraging theory as an inspiration for several decision-making algorithms for task-processing agents facing random environments. As engineering designs are favoured that maximize returned value (e.g. profit) or minimize the probability on not reaching performance targets, they find OFT useful as nature selects foraging behaviours that maximize lifetime calorie gain or minimize starvation probability. They present a general modelling framework for solitary agent behaviour, many new examples that apply to it, and generic methods for design and analyses of optimal task-processing behaviours that fit into OFT. They conclude that their results extend the key mathematical features of OFT to a wide range of other optimisation objectives in biological, anthropological and technological contexts (Pavlic & Passino 2011).

Bartumeus & Catalan (2009) uses random walk methods and diffusion theory as methods to analyse and describe animal movements. In their report they critically re-evaluate classic ecological questions on animal foraging and stress the
need to bring together the general encounter problem within foraging theory as a mean for making progress in the biological understanding of random searching. Animal searches can be viewed as decision-making processes that result in a series of displacements and orientations. A more mechanistic approach to the search/encounter problem within the framework of OFT will light up and explore the direct connections between animal behaviour and stochastic properties of motion, and open up the discussion whether stochastic mechanisms exist and play a role in animal foraging or not, they state.

4 Results and discussion

This Bachelor thesis on Optimal Foraging Theory is based on a literature study using a methodology that seems suitable for the purpose and there is no crucial criticism of the source material. The thesis is leaving many challenging thoughts and ideas for future studies of hunter-gatherer societies in the Baltic region. Which theoretical model is useful to Gotland? The population hiatus indicated in the lacking archaeological records between 5000-4500 BC (Apel & Vala in prep.) is in focus. When looking into the human predator - marine prey relationship many diverse causes interfere and many different interpretations can be made. It is of interest to analyse if the affluence proposed by Persson(1999) in Southern Sweden is applicable also to Gotland. OFT includes processualistic perspectives and wish to go one step further and gain objective facts on the energy strategy in an economy, using the assessment of energy resources and energy costs. It is of interest to know how far from an “Optimal Forager” a Mesolithic pioneer on Gotland is, because the difference will be an indication of affluence or starvation.

The original context of a theory is valuable when evaluating which parts can be useful in a new context. OFT has its origin in processualistic ideas in the New Archaeology in the 1960s with roots into the dawn of archaeology as a scientific discipline in the 19th century (Binford 1963, 1968; Flannery 1968, 1969; Grayson & Cannon 1999; Binford 2001; Hodder 2001; Trigger 2006; Renfrew & Bahns 2008; Scarre 2009). MacArthur & Pianca (1966) and Emlen (1966) were influenced by processualistic ideas and human behavioural ecology when they
developed what would later be called Optimal Foraging Theory, starting with the patch-choice model. As different resources, ranked according to their food value and processing costs, are distributed unevenly in the environment, the diet breadth (syn. prey choice) model was developed. The highest ranked resources are taken first (providing the highest net return) but if the dietary stress increases a forager will be willing to increase the diet breadth and include also low ranked food. The Marginal Value Theorem (MVT) created by Charnov (1976) uses the patch-choice model with time allocation in focus. Foraging theory provides the best models for examining interactions between people and their environment within an evolutionary framework states Grayson & Cannon (1999) as OFT provides important insights into subsistence changes and analyses the relationship between human impacts on the environment and the human response. They propose prey-choice models of OFT in foraging theory-based applications of resource depression. Winterhalder (1993) analyses required labour effects of hunter-gatherers within an evolutionary ecological approach. Winterhalder’s main question is how hunter-gatherer’s population growth and food choice respond to resource exploitation and depletion. His results show that longer foraging resources will eventually be depleted to lower and lower levels. The optimal forager moves when the marginal return in the actual patch drops to the average return for the habitat as a whole. Nevertheless, it is impossible to know how close foragers actually are but Winterhalder has the opinion that these facts are of secondary importance. For analysing Early Mesolithic hunter-gatherers on Gotland and their environmental conditions during a period that probably experienced difficulties in the seal-hunting economy the diet breadth model seems most useful.

The optimal foraging strategy for a species will maximize the net energy intake and affect competition and coexistence among species in a community. MacArthur & Pianca (1966) and Emlen (1966) argued that it should be possible to predict foraging behaviour by constructing an “optimal forager”. A model was constructed where an individual’s food item selection could be understood as an evolutionary construct that maximizes the net energy gained per unit feeding time – the “Optimal Forager” was born. As the energy budget in OFT includes evolutionary behavioural and ecological approaches, empirical observations are
possible to operationalize. It is possible to mathematically find out the optimal choice of patches and food items. Simulation techniques can visualize these choices as different scenarios that are comparable with real archaeological records. Deviations from the optimality can help to identify unexpected constraints in the individual’s behavioural, cognitive or genetic repertoire or in the environment, but the genetic-behavioural link is still very unclear (MacArthur and Pianca 1966; Emlen 1966; Charnov 1976; Irons et al. 1986; Smith 1983; Boone 2002; Shennan 2002; Wolverton 2005; Johnson 2010). An analysis using an optimal foraging perspective will hopefully help to find some discrepancies between the period before 5000 BC and after 45000 BC that can tell something about the hiatus period that looks like a bottleneck in Gotlandic pioneer economy.

MacArthur & Pianca (1966) states that the basic procedure for determining optimal utilization of time or energy budgets is that an activity should be enlarged as long as the resulting gain in time spent per unit food exceeds the loss. The result is that foragers should take low-ranked prey only as long as the profitability is greater than the average return rate gained from searching and handling higher-ranked prey. The diet breadth model was developed for analysing what kind of factors affect human choices of which food items to pursue process and consume as the same food items are used by some and ignored by others. The model assumes that foragers encounter potential food items in the environment at random. Foraging costs are measured in terms of searching and handling time and the net energy return obtained per unit time defines the prey profitability. High-ranked prey should always be hunted and therefore depletion of foraged resources is almost inevitable according to MacArthur & Pianca (1966), Winterhalder 1993, Grayson & Cannon (1999) and Boone (2002). This model could be applied on any region with foragers living nearby and still have different economies or different food habits as in Persson’s (1999) material from Southern Sweden compared with the records from Gotland (Lindqvist & Possnert 1997; Apel & Vala in prep.).

OFT is useful as a benchmark for measuring culture, as the economies are analysed as objectively as possible when comparing the real archaeological rec-
ords with the mathematically simulated models of the choices of an “optimal forager”. The pioneers on Gotland during the Mesolithic show in their records that their prey choices change over time (Lindqvist & Possnert 1997). OFT seems suitable to use when analysing the choices of optimal high-profitable prey available on Gotland (seals) and its energy content compared with the “optimal forager’s” energy needs, and to evaluate the discrepancies and discuss the probably reasons. Humans and preys must be placed in their context that includes their environment, the climatologically conditions, sea levels, flora and fauna etc. In a hunter-gatherer society according to OFT an optimal forager will forage the most profitable items, but in the archaeological record it is not always so. Often environmental causes interfere (Irons et a. 1986; Wolverton 2005; Grayson & Cannon 1999). In a study of Gotland it would be of interest to analyse available food species found outside settlements and compare these with archaeological records related to human activity for getting information on their food choices, what they prefer and what they neglect.

An analysis of diet choices and deviation would be of interest in a comparison between Gotland and the mainland in southern Sweden. Will an OFT perspective on Mesolithic research give the same results as in Persson’s hypothesis on affluence (1999)? As food choices are different in a relatively short distance hopefully OFT could gain some new perspectives. For being able to use OFT for simulation some basic variables must be available, but even if variables are missing, OFT can be used as a benchmark for heuristic discussions useful for the Gotlandic pioneers and their economy. The graphical method constructed by MacArthur & Pianca (1966) used basic variables as hunting time, travelling time, pursuit time, search time and kinds of prey in the diet and food density. The method of ranking proceeds from items of highest to lowest harvest per unit time where especially the relative frequency of prey and related hunting period dictate which prey to hunt,. A discussion on seal hunting on and around Gotland ought to be done related to hunting periods and seal-ecology. Smaller terrestrial preys as hare also have to be discussed. MacArthur & Pianca (1966) and Pyke, Pullman & Charnov (1977) were both seeking for the reason why out of a wide range of available food items still animals preferred a few often restricted items in the diet. The prediction is that the individual tries to achieve a balance be-
tween spending a long time searching for highly profitable food while losing energy, and spending minimal time using less energy to more common but less profitable food items. Why deviation still occurs may have many reasons and starvation seem to be a main one. Boone (2002) concludes that high-ranked prey should be taken whenever encountered why eventually overexploitation will follow. This statement is of interest from a Gotlandic perspective as Lindqvist & Possnert (1997) presents a material with large fluctuations in the amount of finds among humans and preys.

Burger, Hamilton & Walter (2005) and Thomas (2008, 2009) find that both highest-ranked food and very low-ranked food, hardly worth the effort to harvest and prepare, with a very low return are used. The fragmentation of the osteological remains increases in low-return records as bone marrow is highest ranked before meat. Foragers are able to make shifts in diet breadth and change strategies to fit present circumstances. As population increases, high-ranked food items probably will be overused and sometimes even driven to extinction. Different age groups and genders may also use different foraging strategies (Burger, Hamilton & Walter 2005; Thomas 2008, 2009). Usage of OFT theory on the Gotlandic pioneers with their changing economy might help to analyse over-consumption where resource use has outpaced the sustainable capacity of the ecosystem with risk for starvation. Boone (2002) argues that the definition of carrying capacity is unrealistic as depletion of resources always occurs related to forager population size. Boone (2002) has the opinion that domestication increases the sustainable human population as the intensification rate reduces individual efficiency but increases total harvest per unit land. This has a dampening effect on population growth and crash phases. He does not consider human foragers to be natural resource conservationists.

The concept of energy budget in OFT is divided into somatic effort and reproductive effort (Boone 2002). Boone’s main question is why growth rates are so low among foragers and why growth rate increases with domestication and sedentism. Effective control of fertility is quite rare in human history and fertility is almost the same anywhere (Pennington 2001; Boone 2002). Boone’s interpretation is that human populations seem to be characterized by near-zero
growth due to long-term averages across periods with rapid local population growth interrupted by infrequent crashes. The broad changes in population growth rate are instead explained in terms of changes in mortality rather than increases in fertility. Boone’s opinion is that individual energy efficiency in resource acquisition and production has a greater impact on determining reproduction rates than total productivity rates or the carrying capacity of the environment. Human population therefore is characterized by a saw-tooth pattern instead of stepped dynamic equilibriums and this explanation gives new perspectives on fertility, domestication and sedentism (Pennington 2001; Boone 2002). Pennington (2001) finds almost the same fertility rates of traditional populations across all subsistence modes.

Humans or preys change behaviour due to adaption to the environment. When the sea level in the Baltic Sea changes it has a great impact on both fauna and flora (Lindqvist & Possnert 1997). Boyd & Silk (2009) explains the importance of environmental impact on population genetics as an evolutionary change in a phenotype that reflects change in the underlying genetic composition of the population, a link possible to trace back to the very first human beings. The modern Darwinist synthesis presents genetic analyses that show how and why populations are differently developed in nature as a part of an ongoing evolutionary process. Darwinian natural selection operates at the DNA-level of the genetic code and this evolution is still going on. Darwin’s theory introduces a new way of understanding the total environmental context with humans, flora and fauna (Body & Silk 2009; Scarre 2009). “Darwinian fitness” describes natural selection as the process where genes are selected due to their higher fitness to reproduce and evolutionary ecology studies the adaption of species to their environments as foraging is critical to the individual’s survival. Only behaviours that lead to the best reproductive outcome will last (Boyd & Silk 2009; Scarre 2009). Shennan’s (2002) opinion is that since culture is not acquired genetically humans have phenotypes that are more complex and are more influenced by culture than animals why genetically determined behaviours are very difficult to analyse. Evolutionary ecology analyses adaptive behaviour when track variability caused by environmental factors enhances individual’s reproduction (Shennan 2002; Bird & O’Connell 2006).
OFT does not tell when a genetic mutation has changed the behaviour, but notices that something has occurred when discrepancies between the archaeological material and the simulated model of “optimal forager” choices are changing. These changes will help to formulate new research questions. There is a need for discussions on the gene-behaviour link and as the DNA-technique is making progress, DNA-analyses ought to be possible to include in a new extended OFT model. On Gotland osteological remains often are very well preserved due to the lime stone soil why ancient DNA (Shennan 2002; Boyd & Silk 2009) can be possible to extract.

OFT has probably the possibility to give new answers on old questions as the meaning of earlier observations put into an OFT model might produce diverging results. That is one of the reasons why OFT might shed some new information on foraging strategies in pioneer societies on Gotland including technology with focus on craft specialization. Johnson (2010) draws a parallel between ecology as a natural system that tends towards a state of balance when affected by external changes (for example climate or a new predator) and elements of cultural systems and the two are interdependent. A change in one part of the system will affect the whole system and lead to a positive or negative feedback. Johnson (2010) prefers research on links between subsystems in terms of correlation rather than simple causes. The idea of processual archaeology relates closely to ideas of cultural evolution and the search for underlying processes and processual archaeology is interested in processes that lead to craft specialization (Binford 1963, 1968, 2001; Flannery 1968, 1969; Johnson 2010). An artefact is looked upon as a representative of trade or craft specialization and the process that led to this trade or specialization is in focus (Johnson 2010). Technology is often crucial for new hunting- and fishing-methods as the highest pay-off measured as the highest ratio of energetic gain cost is depending on suitable equipment. Technology development has a cost which is not discussed in Persson’s hypothesis (1999) and depending on type of technology, travel time, pursuit time, search time, hunting time and kind of prey that can be foraged or hunted might be influenced. Which prey will be chosen is depending on food density but also season, geography, culture etc. A lacking use of high-
profitable prey in the diet, when there still are traces from that animal in the archaeological records, does not necessarily mean that the hunter-gatherer has made a voluntarily cultural choice not to hunt that optimal prey, or that there are huge amounts of other food items around. Could it be lacking technology that hinders hunter-gatherers to catch up high-ranked prey in one region but not in another? MacArthur & Pianca (1966), Emlen (1966), Irons et al. (1986) Burger, Hamilton & Walter (2005) and Thomas (2008, 2009) all noted that animals are more selective in their choice of food items when food is common (specialist strategy) and becomes more indiscriminate when food is scarce or when they are starving (generalist strategy). According to them food preferences change very quickly to changes in environment. More productive environments are therefore expected to lead to more restricted diet. In southern Baltic Region during the Mesolithic the mainland is almost lacking high-profitable prey as seals in their diet and on Gotland at some distance the diet is dominated by this food. The differences are interesting to discuss with focus on the prey choice, as there are terrestrial big preys in the mainland that are lacking on Gotland. The OFT model will offer help to future discussion.

Is OFT just so useful? Of course criticism exists and Pierce & Ollason (1987) give eight reasons why OFT is a complete waste of time and they argue that nobody can know what is exactly optimal and that the OFT hypothesis is self-verifying. Stearn & Schmidt-Hempel (cited Pierce & Ollason 1987) contradicts all the points with the summarizing statement that Pierce’s & Ollason’s arguments are based on misinterpretations of the underlying logic of optimisation theory and the related scientific method. MacArthur & Pianca (1966) are aware of the problem that the simulated curves have no exact known shape, and vary from situation to situation, why no general prediction is possible to make of an exact diet. Still they state that these curves are of interest as they are possible to use for predictions about changes in the diet and the numbers of different prey individuals. Shennan (2002) states that the OFT hypothesis is not self-verifying, which some opponents proclaim, as it is predictable what will be optimal in a given situation. However, there is a problem that the basis for defining what is “good enough” is lacking and has to be assumed. The increase and decrease in pursuit time measures the adoptions of the species for the items and
must be empirically determined according to Mac Arthur and Pianca (1966). Thomas (2008) uses the OFT “diet breadth model” when testing hypotheses where a team conduct foraging experiments by mapping the most efficient strategies for harvesting available food. Grayson & Cannon (1999) points out a warning that inexperienced test person might ruin test results and there is no way to know the skill level of the foragers. Smith (1983) has the opinion that the patch-choice model presented by MacArthur and Pianca (1966) was too similar to their diet-breadth model (prey choice) which prevented the applications to spread. He also criticizes the patch-choice model failing to specify how long time a forager should spend in each patch or the effect the foraging could cause on the stock causing gradual decline in return rate for that patch. Charnov (1976) realized the time allocation problem and created the Marginal Value Theorem. Smith’s (1983) conclusion is that OFT has a potential worth developing as it allows analyses of diversity from a few general decision rules important for explaining parsimony and heterogeneity of human foraging strategies. He suggests a new theory construction with added integrated analytical approaches from a combination of optimizing decision rules and complex socio-ecological constraints (Smith 1983). Pyke, Pullman & Charnov (1977) are optimistic about the value of OFT and conclude that simple models seem to be supported reasonable well by available data. Werner & Mittelbach (1981) are looking for an OFT application for predator behaviour research and find the OFT model useful for relating behavioural and morphological differences between species, as well as looking at the nature of species interaction and community structure.

MacArthur & Pianca (1966), Smith (1983) and Winterhalder (1993) are all aware that an animal’s optimality can not be properly measured, just assumed, but judge that fact as a minor problem and focus on the very important possibility OFT offers when using the “Optimal Forager” as a reference in discussions comparing cultures with different economical strategies. What is really striking is the possibility to compare the archaeological real records with the “Optimal Forager” that makes discrepancies visible and possible to discuss and analyse further. Grayson & Cannon (1999) are positive to OFT applications of resource depression but ask for models that can deal successfully with interrelationships
between landscape change and landscape use. The models so far are not useful enough. They also see problems with experimental return rate data if inexperienced individuals are performing the tests or processing them in a wrong manner.

There is a growing interest to use OFT in diverse disciplines and the theory and related models are now used also within computer science and any science where decision makings are in focus (Sandstrom 1994; Pavlic 2007; Bartumeus & Catalan 2009; Pavlic & Passino 2011).

5 Conclusion
An “optimal pioneer forager” on Gotland is one with a foraging strategy with the highest caloric payoff related to available fauna and flora taking into account all energy costs (MacArthur & Pianca 1966; Emlen 1966), but also species owing “Darwinian fitness” described as natural selection process where genes are selected due to their higher reproductive fitness (Boyd & Silk 2009; Scarre 2009). There is a gene-behaviour link still not analysed because it is hard to study and behaviour has been looked upon mostly as an adaption produced by “decision rules”, which are under selection. According to behavioural ecologists culture has a minor role as only cultures with successful adaptive foragers are assumed to pass their genes on into the next generation, as foraging is critical to survival of animals as well as humans. Unsuccessful cultures are weeded out (Smith 1983; Shennan 2001). When using OFT as a benchmark for measuring cultures it is possible to discuss differences between them, comparing them with an “Optimal Forager”. With OFT, it seems reasonable to be able to find constraints in the population development of Gotlandic pioneers that would help to understand the pressure on available resources, and to find possible indications of over-exploitation or other reasons for the lacking archaeological records between 5000-4500 BC. DNA-analyses can tell about the heritage link and disruption due to population crashes if populations with different DNA are identified after a population hiatus (Pennington 2001; Boone 2002; Scarre 2009). The analysed reports on different perspective of OFT (MacArthur & Pianca (1966) and Emlen (1966) seem to present a well-documented theory suitable for Mesol-
lithic research as a benchmark for measuring hunter-gatherer cultures and their economies. As the pioneers on Gotland were hunter-gatherers with a changing environment and economy (Lindqvist & Possnert (1997) with many archaeological remains still available for DNA analyses, a promising future lays ahead for research.

OFT is grounded in the New Archaeology in the 1960s that defines culture as systems which is an empirical definition (Binford, 1968; Flannery 1968, 1969; Johnson 2010). Cultural systems are adapted to an external environment (Darwinian ideas of adaption) with observable elements possible to measure, why fluctuating energy recourses are possible to caloric evaluate in archaeological records. OFT uses a simulated mathematical model of an “optimal forager” built on predicted various decision mechanisms. The analysis is based on the foraging strategy that gives the highest payoff measured as the highest ratio of energy gain. It is possible to construct a hypothesized link between subsistence economies and trade off and then test it by reference to the archaeological finds (MacArthur & Pianca 1966; Emlen 1966; Charnov 1976; Grayson & Cannon 1999). Opponents (Pierce & Ollason 1987) argue that OFT is self-verifying, what is optimal is impossible to test and animals should not be expected to be optimal. However MacArthur & Pianca (1966), Smith (1983), Winterhalder (1993) and Grayson & Cannon (1999) argues it is of secondary importance as OFT serves as an benchmark and how close foragers might approach this optimum is an empirical issue and Shennan states that OFT is not self-verifying as it is predictable what is optimal in a given situation (2002). All agree about the fact that “good enough” has to be assumed. These predictions are used in the simulated “optimal forager” model without assuming that animals are aware of their decisions, but the model analyses what would be optimal. The same can be said for humans. As OFT can be used for research of diversity from a few general decision rules, hopefully parsimonious explanation of the heterogeneity of human foraging strategies will be possible to explain (Smith 1983).

Cognitive science but also computer science has adopted OFT due to the use of decision rules in the model that can be transferred into their disci-
Mesolithic hunter-gatherers on Gotland analysed with an OFT model would compare the “optimal Mesolithic pioneer forager” in this special cultural system with the actual archaeological records. The results can be compared with other places and economies as cultural systems can be modelled and compared from culture to culture with OFT as a benchmark. These comparative observations might lead to generalizations about cultural processes. As elements of cultural systems are interdependent leading to positive or negative feedback, homeostasis or transformation (Johnson 2010) in hunter-gatherer societies on Gotland ought to be possible to analyse. A challenging suggestion is to use an OFT model on Persson’s material for checking if the simulated model will show an affluent society or not and compare with the material from Gotland. If one region is lacking high-profitable prey in their diet and a close region is dominated by this food questions are still unanswered. According to the OFT model high-ranked prey always is hunted first. In the Baltic Region hunter-gatherers were living nearby and still had different economies and food habits. An optimal foraging perspective will probably tell more about the causes of differences in foraging strategies in different places and different times (the hiatus).

5.1 Concluding remarks
The Bachelor thesis concludes that the research questions have been answered and OFT as a benchmark for measuring culture and foraging strategies seems useful and suitable for Mesolithic hunter-gatherer research on Gotland. An analysis using some variant of the diet breadth (prey choice) model based on the construction of an “optimal Gotlandic pioneer forager’s” food item selection, compared with archaeological records from Gotlandic Mesolithic settlements, probably would shed some new light on questions concerning eventual overexploitation correlated to the Gotlandic hiatus between 5000-4500 BC. Then one more answer will be added to the global Mesolithic question: affluence or starvation.
6 References


**Internet links:**
