A view to a kill : investigating Middle Palaeolithic subsistence using a optimal foraging perspective

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4 Optimal foraging models and Neanderthal archaeology

4.1 Introduction

In the previous chapters, the biological and archaeological evidence regarding Neanderthal subsistence behaviour were reviewed. In this chapter I will outline a theoretic framework that will be used to analyse Neanderthal and hyena bone assemblages. As argued in chapter 1, Optimal Foraging Theory (OFT) provides a promising perspective for the study of Neanderthal subsistence strategies. OFT is a theoretical approach dealing with foraging strategies, stemming from behavioural ecology and economic science (*e.g.* Rapport and Turner 1977). It is designed to evaluate the way in which an individual's behaviour affects its evolutionary fitness. It shows how natural selection influences foraging strategies and as such provides a framework within which foraging strategies can be interpreted (*e.g.* Barrett, Dunbar, and Lycett 2002, Krebs and Davies 1997, Winterhalder and Smith 1992). OFT assumes that foraging is important for an animal's survival and reproductive success. Therefore, models are designed that aim to study which ecological circumstances would favour the development of observed foraging behaviours (Winterhalder and Smith 1992, 23).

Different types of model have been designed, depending on the environmental situation and the factor deemed most important for an animal's reproductive success. Archaeological data are of a much lower resolution than the ecological data for which OFT models were originally designed. Consequently, it is most productive to focus on simpler models requiring less fine-grained data. Most of these focus on how a forager can maximise his caloric intake in a given environment. This is a simplifying assumption since Neanderthals may have pursued other goals as well. However, this simplification enables us to use OFT models to produce testable hypotheses about what foraging behaviour we would expect Neanderthals to exhibit given our knowledge of their behaviour and environment.

The first goal of this chapter is to introduce the model that is best suited for archaeological application: the diet breadth model. The chapter will begin with an introduction of the general principles of OFT, the diet breadth model and criticism that has been levelled at OFT. This will be followed by a review of previous archaeological applications of OFT. The information the Pleistocene record yields with regard to the application of OFT will be discussed as well as the problems posed by the record. After this discussion the primary aim of the chapter is to develop a strategy that will allow us to apply the diet breadth model to the Pleistocene archaeological record. I will propose ways in which the variables of the model can be approximated using the archaeological and palaeontological record. This approach will be tested in the following chapters.

4.2 General assumptions and criticism

The central assumption of evolutionary ecology is the fact that relationships between animals and their environment are under evolutionary selection. Therefore an animal's foraging behaviour can be understood as shaped by natural selection in order to maximise fitness. With a proper knowledge of the environment and the specific needs of a species, models can be constructed that predict how animals will behave (*e.g.* Krebs and Davies 1997, MacArthur and Pianka 1966, Winterhalder and Smith 1992). Furthermore, it is assumed that, because of natural selection, over time foragers will have evolved to become as proficient at foraging as possible (Winterhalder 1987, 314). Foraging strategies are thus assumed to maximise the evolutionary success of the forager. It is important to keep in mind that the optimal situation is a working assumption (*e.g.* MacArthur and Pianka 1966, Winterhalder 1987), used to construct models that can test whether behaviour is optimised toward the acquisition of a certain commodity, like food. If the observed behaviour does not conform to the model's predictions, the hypothesis is rejected. In this case an alternative hypothesis explaining the observed behaviour must be formulated.

Before I go into the models themselves, it is important to realise what kind of questions OFT models can answer. Animal behaviour can be explained at several different levels; Tinbergen (1963) delineated four categories of explanation for animal behaviour, which are known as his "four whys". These four categories can be divided in two groups: proximal causes of behaviour and ultimate causes of behaviour. Proximate causes explain the function of actions for at the level of the individual. Ultimate causes explain the evolutionary causes of behaviour at species or population level. Archaeological research, especially in the Palaeolithic can often only explain patterns at Tinbergen's ultimate level. Proximate explanations require far greater resolution.

At the ultimate level, behaviour can be studied with regard to its functional cause: explaining the function of behaviour in terms of fitness for a species. The other explanation in this category is the phylogenetic explanation. This explanation focuses on how the evolutionary history of a species has influenced the behavioural solutions employed by a species (*e.g.* Barrett, Dunbar, and Lycett 2002, Krebs and Davies 1997, Tinbergen 1963). OFT models are designed to study behaviour and explain it at an evolutionary level. They are especially promising for the functional study of behaviour. The application of OFT to archaeological sites is expected to illuminate which factors were responsible for the behaviour exhibited by Neanderthals in different settings. On the other hand, by applying OFT to different periods of time we may also be able to track the development of strategies through time and thus gain insight in the phylogenetic development of behaviours.

The use of OFT models to explain human foraging behaviour has been criticised by some, because the underlying assumptions are deemed to be problematic. First, it is not clear how foraging behaviour correlates exactly with reproductive success. Therefore, in OFT models a proxy is used that is thought to correlate with reproductive fitness. This proxy is called the currency. Usually, the currency is energetic gain. It is thus assumed that maximising energetic returns from foraging activities correlates positively with the fitness of the forager. This currency tends to be a good predictor of foraging decisions (*e.g.* Waite and Ydenberg 1996, Winterhalder 1987). This assumption is certainly not universally valid, however. Optimisation of behaviour may have been selected for other elements. These can be factors like rare but essential nutrients, gaining social prestige or the reduction of risks (*e.g.* Bliege Bird and Smith 2005, Hockett and Haws 2005, Ludvico, Bennett, and Beckerman 1991). Therefore, the fact that OFT models usually focus on caloric gain can be problematic. Malnutrition is of course an important problem, with great consequences for an animal's fitness. Nevertheless, humans need 50 essential nutrients, and it has been proven that a more diverse diet lowers infant mortality and prolongs life-expectancy (*e.g.* Bliege Bird and Smith 2005, Hockett and Haws 2005, Ludvico, Bennett, and Beckerman 1991). This problem can be solved by constructing models using different currencies. This makes it possible to test whether behaviour was geared toward optimising other commodities.

A second issue is that it is often unclear how foraging behaviours are transmitted. In OFT models, inter-generational transmission of foraging behaviours is a working assumption. Natural selection on these inherited traits ensures that foraging behaviour is optimised over time. When applying OFT to human foragers, anthropologists often object that inheritance in humans is not only genetic but also cultural. Of course this is also the case in many animal species. This results in the objection that, it is unclear whether any reproductive advantages of a good forager will be transmitted to its offspring (Ingold 2000, 30). This makes the assumption that natural selection has resulted in fitness-maximising foraging behaviour over time problematic (*e.g.* Ingold 1992, Ingold 2000).

Of course, culture as a mechanism of inheritance, is also subject to selection. This selection simply operates differently from natural selection at a genetic level (Barrett, Dunbar, and Lycett 2002). This is exactly the advantage of cultural over genetic inheritance. It allows a population to deal with change much faster than would be the case if it could only adapt genetically. Especially in long-lived animals, genetically adapting to changing circumstances would take a long time and bring with it the demise of large parts of the population. Therefore, culture can be seen as an evolutionary mechanism that facilitates fast behavioural change (*e.g.* Potts 1998).

Furthermore, in hunter-gatherers, these cultural behaviours do have clear reproductive benefits. Anthropological studies show that good hunters have greater reproductive success and more extramarital affairs (*e.g.* Kaplan and Hill 1985, Smith 2004, Smith, Bliege Bird, and Bird 2003). There are also much more subtle consequences of foraging behaviour that, due to evolution being a long-term process, will filter out the people with less potential for efficient behaviour, whether this is genetic or cultural. For example, many consequences of malnutrition of foetuses may only become apparent later in life. So a child that was nutritionally stressed in the womb can appear to be very healthy, but later in life there may still be significant health consequences that inhibit fitness and reproduction (*e.g.* Lummaa 2002).Therefore in cases with cultural transmission it is still in a forager's best interest to forage efficiently. For the offspring of unsuccessful foragers, the fitness consequences may be less severe when foraging is inherited culturally instead of genetically. In a cultural society, offspring can acquire skills from individuals other than their parents. Therefore, they may be able to become more successful foragers than their parents.

An additional argument for why OFT models work is because they are grounded in economic principles (*e.g.* Rapport and Turner 1977). Foragers may not be consciously maximising their evolutionary fitness, but they are expected to serve their own interests as well as possible and thus to forage as efficiently as possible. On the other hand, it is clear from cultural anthropology that humans do not function solely as rational, purely self interested actors. Cultural norms may not prescribe optimisation of foraging strategies but in most cases, food is a valuable social currency. Therefore it is expected that human foragers make rational choices when foraging and they will not consciously practise very unrewarding strategies. It is known from ethnography that much behaviour of hunter/gatherers is rational in nature (*e.g.* Mithen 1988, Winterhalder 2001). Hunter/gatherers are not constantly computing equations in order to arrive at decisions. In many situations, rules of thumb are used and these have been selected for because they work well in most cases (Winterhalder 2001, 32). Simple heuristic mechanisms for decision making have been observed in many animals and also in modern humans. These mechanisms are used not only by hunter/gatherers, but for example also by employees in insurance companies (Todd 2000). We can thus assume that humans generally make decisions in a system of "bounded rationality". They will not consider the infinite number of possible courses of actions, but will decide rationally based on simple heuristic mechanisms (Todd 2000, 941)

In the course of hominin evolution, the greater reliance on cultural traits brought with it natural selection on traits that are associated with functioning in a cultural society. This may be visible in the steady increase in brain size in the human lineage. As has been argued in chapters 1 and 2, since large brains enable better foraging skills, natural selection on foraging skills was an important factor in this process (*e.g.* Kaplan *et al.* 2000). Furthermore, selection probably worked on decision making processes, favouring individuals that were able to make appropriate choices in foraging situations. Selection on decision making mechanism would be relevant, since not everyone's fitness benefits from similar decisions. There are clear conflicts between fitness interests of men and women for example. This selection has therefore resulted in the fact that in genetically similar populations, behaviour can be differentiated (Hawkes 1993, 342).

In the end, these simplified models predict behaviour in a surprisingly wide variety of contexts, as pointed out in the introduction, for instance in foraging by insects, or surfing the internet (DiClemente and D. A. Hantula 2003, Waldbauer and Friedman 1991). This alone indicates that using optimal foraging as a "working model" is a valid approach. The mechanisms by which these behaviours are transmitted across generations may be unclear, but OFT can still be used to predict behaviour (Smith 1983, 627). Application of OFT-models can thus be justified by what has been called "playing the phenotypic gambit" (Barrett, Dunbar, and Lycett 2002, 9). The model is used to predict behaviour. If its predictions work out, it is assumed that the explanation that foraging behaviour is organised in order to optimise a certain currency is valid. The mechanisms of transmission of behaviour are ignored. Of course research into the mechanisms of transmission of behaviour and the interplay between genetic and cultural inheritance is important, but these problems lie within Tinbergen's proximate level of interpretation. OFT models are not designed, nor equipped to answer questions at this level.

In conclusion: The application of OFT-models is a starting point of analysis. It enables us to check how well the simplistic assumptions of OFT explain the foraging choices that are reflected at archaeological sites. If the predictions fit the attested behaviour well, the archaeological context may provide explanations on any deviations. If the fit of the model's predictions and the archaeological assemblage is poor, we are left with two explanations. First, caloric value may not have been the currency that was maximised at the site. Another currency can be proposed and a new model can be constructed if this is the case. In this way, OFT provides an avenue of research that can illuminate what factors were important in the development of Neanderthal foraging behaviours. It has to be combined with the archaeological context in order to check how valid the predictions of a certain model are. A second possibility is that the model itself is not valid. If the variables or the categorization of different categories of food used in the model differ from the variables upon which the occupants of a site based their foraging decisions, a different model must be adopted to study the foraging behaviour reflected at the site.

4.3 An example of an OFT model: The diet breadth model

After these general considerations, it is time to look at the models themselves. The most basic optimal foraging model is the diet breadth model. This model was designed to predict which species a predator exploits and which species are ignored in a given environment. It assumes that the predator lives in a homogenous environment, and that prey items are dispersed and encountered randomly. For example, a predator can choose between two species of prey, one of which is considerably larger than the other. In this case one would expect that the predator to concentrate on the larger prey, since it would provide him with more food. However, prey is encountered at random; the smaller prey will also be encountered. The diet breadth model predicts what a predator will do in this situation. If large prey is ubiquitous, the smaller species will be ignored, since exploiting it will waste time that could be spent more profitably on searching for prey of the larger species. The small species will only be exploited in situations where the large species is not encountered often enough. If the return rate of foraging for only the large species drops below the return one gets when exploiting both species, the smaller will be incorporated into the set of exploited prey (*e.g.* MacArthur and Pianka 1966, Winterhalder 1987, Winterhalder 2001).

The diet breadth model therefore predicts an optimal set of prey items that should be exploited when encountered, while other species should be ignored. Whether a species is incorporated in the optimal set depends on the profitability of its exploitation. This depends on three factors: the "value" of the species, the abundance of the species in the landscape and the cost of hunting it. Because it is assumed that a predator randomly encounters prey, the advantage of this model is that it does not require fine-grained environmental reconstructions. Most other OFT models do and are therefore not easily applicable to the archaeological record (Sheehan 2004, 170). Therefore, although this model is simplistic, it can be applied in the absence of fine-grained reconstructions of the distribution of plant and animal resources through the Pleistocene landscape. This model predicts that the prey in the optimal set will always be exploited when encountered, while prey not in the optimal set will always be ignored. The order of profitability of the available prey types is called the ranking.

In the diet breadth model, the available resources are ranked on the basis of their profitability. When using caloric value as a currency, this is the yield of the prey minus the energy that the forager had to invest in order to acquire it (Bettinger 1991, 84-85). For different currencies, different ranking can be compiled.

The energy invested in acquiring an animal is usually divided into search cost and handling cost. A forager incurs search cost while searching for food in the environment up until the moment he encounters a resource (MacArthur and Pianka 1966, 603, Winterhalder 1987, 316). The probability that an animal of a specific species is encountered is called its encounter rate; it depends on the population density of the prey species. Search time is dependent on the encounter rates of all the prey species in the optimal set. The more species are included in the optimal set, the more time spent searching for suitable prey will decrease. It is important to realise that the inclusion of a species in the optimal set does not depend on the abundance of the species itself. It depends on the abundance, or rather lack thereof, of higher ranked species. Only if searching for higher-ranked species becomes too costly will additional species be added to the diet, no matter how abundant the lower-ranked species are.

When an animal is encountered it has to be pursued, dispatched, processed and sometimes transported back to a camp or nest. The cost incurred in these activities is called handling cost. This is not a simple function like search time. The handling cost of an animal depends on both the predator's abilities with regard to pursuing and killing prey, and the prey's anti-predator strategies (MacArthur and Pianka 1966, 604). Butchering and transportation costs can also be influenced by the predator's abilities. As a general rule it can be assumed that handling cost goes up when more prey species are added to the diet. This is because species that are hard to catch will generally be lower ranked. Moreover, because hunters grow less specialised when more species are added to the diet, which will have negative repercussions for hunting and processing efficiency (MacArthur and Pianka 1966, Winterhalder 1987).

Which prey species are included in the "optimal set" and exploited upon encounter depends on the abundance of the most rewarding prey. Ideally, a forager will only exploit the most profitable

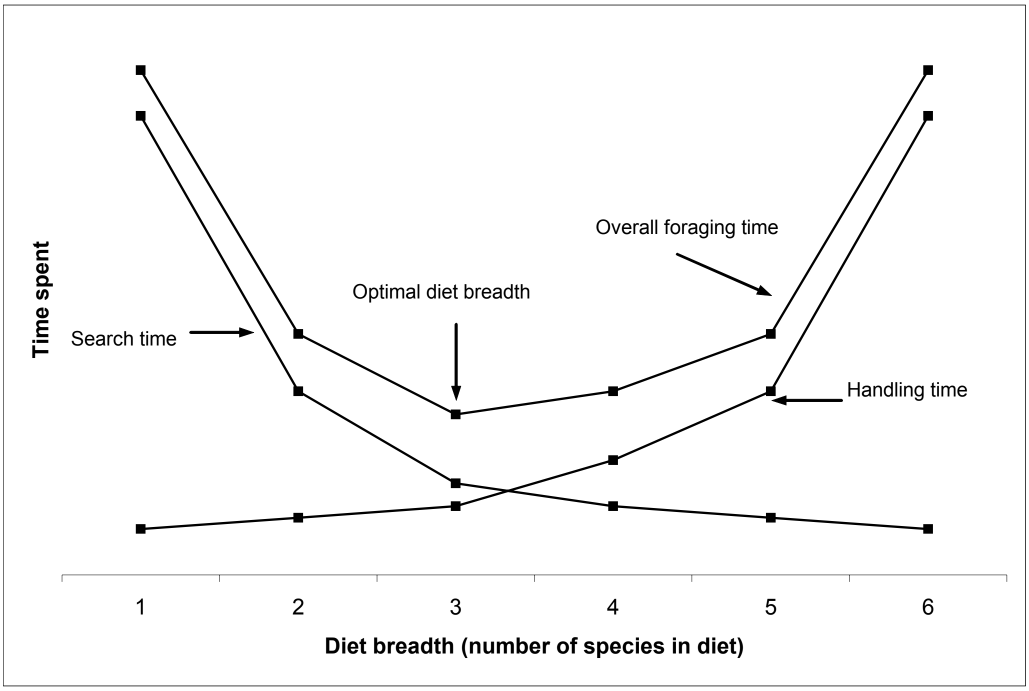

Figure 4.1: Hypothetical illustration of diet breath model. Adding species to the diet lowers search time, but raises handling time. In this situation exploiting the three most rewarding species minimizes time spent per amount of energy acquired. Graph after Bettinger (1991) and MacArthur and Pianka (1966).

species. Only if he cannot be reasonably sure that it will be encountered frequently enough will he add less lucrative species to the menu (Bettinger 1991, Winterhalder 2001). This will result in lower search time, but in a higher handling cost and consequently a lower return rate for the added species. The optimal set will be the number of species that result in the lowest overall search and handling time, as illustrated by Figure 4.1.

The simplest versions of the diet breadth model assume that if a prey species in the optimal set is encountered it is always exploited. Adaptations of the model have also been constructed. It has been proposed that the dichotomy between species that are exploited and species that are ignored may be modelled more realistically. To this end, the contingency model has been formulated (Bettinger 1991, 85-86). This model states that a prey species that is in the optimal set, but is not the highest ranked species, may or may not be exploited when encountered. It would be most logical for a forager to weigh the expected cost of continued searching for the highest ranked species against the profit he will make from the prey at hand. If the prey at hand is more rewarding than the expected cost of continued searching, subtracted from the yield of the preferred prey, the prey at hand will be exploited by the forager (Bettinger 1991, 86).

It is expected that the optimal set changes when one of the parameters of the model changes. Both search time and handling time of species may change and these changes will influence the composition of the "optimal set" of prey items. Search time will change when prey becomes more or less abundant for example. This can be a reflection of climatic change, but also of human impact. A species can become rarer if it is overexploited, in which case it is expected that lower-ranked species will be added to the diet (Jones 2004, 308). It is thus important to realise that addition of items to the diet depends not on their own abundance, but on the abundance of higher-ranked resources (Bettinger 1991, 87). If the prime prey is rare, other prey may be exploited more heavily, not because the forager prefers this species, but because of its high(er) encounter rate relative to the very low encounter rate with the highest ranked prey. This means, for example, that when new predators enter competition for a resource, diet breadth may be increased as the density of the resource gets lower, but it will not be dropped from the optimal set (MacArthur and Pianka 1966, 604).

Handling time is determined by the abilities of the prey and the predator. This variable can change for example through evolutionary developments of either prey or predator. More interesting for archaeology are the influence of technology and the development of hunting strategies on the handling costs of species. Increased knowledge of prey behaviour can for example affect its handling time and therefore its return rate in such a way that it becomes elevated to a higher rank. The same is the case with technological developments. One important example of technology affecting handling costs is seen in mass-collecting of small animals. Technology in the form of nets or traps may make the exploitation of small animals with low individual return rates very profitable, because they can be collected in great quantities (Stiner *et al.* 1999, 193, Ugan 2005).

As mentioned above, the diet breadth model is very simplistic and other models have been constructed on the basis of assumptions that are in many cases more realistic. Most animals for example do not live in a homogenous environment. In order to deal with heterogeneous environments, a refined diet breadth model has been developed, namely the patch choice model. This can be applied if fine-grained knowledge of the structure of the environment is available. In this case foragers are confronted with a range of patches that differ in energetic value and the amount of energy and time needed to exploit them. The different patches are ranked, much in the same way as prey types in the diet breadth model (Bettinger 1991, 88-89). The most important decision that hunter-gatherers face in patchy environments is when to leave a patch. They typically do not remain in a patch until it is depleted, usually choosing to leave at the moment return rates drop below the level where expected return rates in another patch minus the cost of moving result in higher returns overall. However, since moving to a patch whose status is unknown is risky, hunter-gatherers will sometimes remain at a given patch longer than expected (Bettinger 1991, Winterhalder 1987). In such decisions, transport cost is very important: if transport costs are high, hunter-gatherers will tend to become generalists, exploiting most resources as they are encountered in a patch. When transport costs are low they tend to specialise in few high ranked prey items and prefer departure to another patch earlier (Ingold 2000, 30).

If resources are distributed in patches, a very important variable is the predictability of their location in time. When the status of patches is predictable, people will leave their old patch sooner than if it is unpredictable. The assumptions that these models are based on usually state that patches are scattered through the landscape randomly and that they are encountered randomly. But hunter-gatherers typically have a good knowledge of the landscape and of the habits of their prey. They invest in this knowledge, and this pays off, because foraging becomes more predictable. Therefore patches and prey are not encountered at random. Furthermore, the fact that most foragers now face influences from the policy of the nation-state they inhabit implies that they are often forced to make less than optimal choices (Winterhalder 1987, 320).

Many other kinds of OFT models have been constructed, for example, models that predict group size, or resource transfers within a group and so on (*e.g.* Winterhalder 2001). These are very hard to test against the archaeological record. Therefore I will focus on the diet breadth model. This model is well-suited for research into the determining factors of prey selection in the Pleistocene. In the following sections, I will outline how the diet breadth model can be used on the sites that were selected for this analysis.

4.4 Applications of diet breadth in the study of the Middle Palaeolithic

The notion of diet breadth is not new in the study of Middle Palaeolithic subsistence. For example, the concept of diet breadth has regularly been invoked when comparing Middle and Upper Palaeolithic subsistence (*e.g.* Grayson and Delpech 1998, Richards *et al.* 2001, Stiner, Munro, and Surovell 2000, Stiner *et al.* 1999). It is often implied that Neanderthals had a smaller diet breadth than anatomically modern humans (AMH), who were therefore able to displace Neanderthals. This perspective on the problem is very interesting, but some aspects of the published studies are problematic. In this section, I will review these previous applications and point out some problems. In sections 4.5 and 4.6 I will discuss how these shortcomings can be corrected.

An important hypothesis with regard to changing diet breadth in the Late Pleistocene was put forward by Stiner *et al.* (Stiner 2001, Stiner, Munro, and Surovell 2000, Stiner *et al.* 1999). The central idea of her thesis is that anatomically modern humans were able to replace Neanderthals because modern humans were able to exploit small fast moving, fast reproducing prey more efficiently. This “broad-spectrum revolution” enabled modern humans to maintain higher population densities and recover faster from demographic crashes. This is an interesting hypothesis and, as pointed out in chapter 3, the evidence for exploiting this type of prey is indeed rare at Middle Palaeolithic sites. Stiner bases her hypothesis on research at a number of Mediterranean sites, in Israel, Turkey and

Italy. Her assertion that leporids and birds are generally better represented in Upper Palaeolithic levels at these sites seems to be true. However, leporids and birds are not absent at the Mediterranean sites of Middle Palaeolithic age, both in the sites she studied or at those examined by others (Tortosa *et al.* 2002). Moreover, the importance of small fauna seems to increase late in the Upper Palaeolithic in the western Mediterranean. For France it has been proposed that exploitation of small animals does not become important until the Magdalenian (Costamagno and Laroulandie 2004). Therefore, the increase in diet breadth and especially the increase in the importance of small mammals do not always coincide with the arrival of AMH.

Related to this hypothesis is a high-tech approach that has been used to highlight the differences between Middle and Upper Palaeolithic foraging behaviour: isotopic analysis. An important study by (Richards *et al.* 2001) compares middle to late Upper Palaeolithic foragers to Middle Palaeolithic ones. This study shows that in some cases, Upper Palaeolithic humans added resources to their diet that were absent from the diets of the analysed Middle Palaeolithic fossils, like fish. However, the Middle Palaeolithic fossils that were analysed were all recovered in Western Europe (Belgium and France) and the Mediterranean (Croatia). The upper Palaeolithic specimens to which they were compared were recovered in Russia, the Czech Republic and Britain. Moreover, they are all dated to the middle Upper Palaeolithic. Therefore, foragers operating in very different situations are compared. Since diet breadth will be adapted to a forager's specific environment, the outcome of this comparison does not necessarily tell us much about the foraging capabilities of Neanderthals and modern humans, it only informs us what solutions were chosen by different hominins in different circumstances.

Researchers have also looked at diet breadth for reindeer-dominated fauna in France (*e.g.* Grayson and Delpech 1998, Grayson and Delpech 2003). In this research, conflicting conclusions have been reported. Some authors say that the Upper Palaeolithic assemblages are characterised by increasing specialisation on one species (i.e. narrower diet breadth) (Mellars 1996, Mellars 2004), whereas other researchers do not detect a change in diet breadth until the Magdalenian (Grayson and Delpech 2003, Grayson and Delpech 2006).

None of these analyses, present a fine-grained environmental reconstruction, nor is a ranking of species available in the environment constructed. The absence of environmental reconstructions makes it difficult to evaluate whether increasing representation of species at archaeological sites reflects an increase in diet breadth, or a decrease in encounter rates with more highly ranked species. Conversely, an increasing representation of reindeer (*Rangifer tarandus*) at Upper Palaeolithic sites may indicate specialised hunting of this species, but could also signal increased encounter rates with this species, and decreased encounter rates with more highly ranked species, due to climatic factors (*e.g.* Grayson and Delpech 2008, 353-354). These studies therefore do not apply the diet breadth model as rigorously as is needed in order to draw with inferences on the foraging choices made by the hominins that produced the assemblages.

4.5 On reconstructing the model's parameters

As argued above, archaeological applications of the diet breadth model are different from "real-time" studies, that mostly predict which species a predator will exploit. Since data on prey densities and prey and predator capabilities are often available, search and handling cost can be reliably reconstructed. The archaeological record on the other hand confronts us with the results of foraging behaviour. Therefore we can assume that the diet breadth reflected at archaeological sites is the optimal diet breadth. The goal of this study is therefore to use OFT to reason back from the end result of foraging behaviour to gain insight into the variables determining the diet breadth. Search cost and handling cost are variables that are influenced by the sophistication of foraging tactics. The aim of using OFT is thus to gauge how Neanderthal behaviour influenced these variables and the profitability of exploiting available species. We will combine the known diet breadth with other known or reconstructable variables. This will enable us to model search cost and handling cost. The advantage of such a simplified model is that it will permit us to construct clear scenarios. These hypothetical scenarios will be tested against the archaeological record, which will allow us to refine them and use them in order to reconstruct Middle Palaeolithic foraging behaviour. In this section I will go into the factors that can influence the different variables of the diet breadth record and how this in turn can influence the foraging strategies that were practised. This will be followed by a section on the application of the theory within Neanderthal archaeology.

The most important variable that we need to understand is the currency that was optimised by Neanderthals, since this determines both how Neanderthals ranked their prey and what motivated their foraging decisions. Most OFT scenarios assume that caloric value is the most important factor guiding foraging decisions. On the other hand, there are many other options, like rare but essential nutrients, or socially motivated currencies. Therefore very complicated foraging patters can in some cases be expected. Plants represent a relatively poor source of energy, but they provide the building blocks for vitamins A, C and E. These are also present in animal livers, but not in great quantities in other tissues. Liver consumption is problematic, because it can lead to toxic levels of vitamin A (Hockett and Haws 2003, Hockett and Haws 2005). Another example is provided by birds. They are excellent suppliers of fats and may yield twice as many calories per 100g of flesh than for example mammals or fish. Marine animals produce carbohydrates and lipids generally not available from terrestrial resources (Hockett and Haws 2003, 212). Moreover, some resources may not even be targeted for dietary purposes, but for other commodities like fur or feathers (Jones 2004, 311). As many sites seem to present evidence of hunting large and dangerous animals, social prestige may also have played a role.

In some areas food can be so abundant that rather than foraging success, other activities like searching for mates, are important in determining fitness (Schoener 1971, 372-373). In such cases foraging is still done effectively, rather than maximising the amount of calories that is acquired, the amount of time spent foraging is minimised (Rapport and Turner 1977, 369). This may result in a wider diet breadth than would be expected when adopting the caloric value of a species as currency.

Furthermore, it may be the case that distinct groups in society rank foods differently. OFT hypothesizes that foraging strategies are optimised in order to optimise reproductive success. In human and also primate society, males often have different reproductive goals than females, which results in the two sexes practising different foraging strategies. (*e.g.* Bird 1999, Stanford 1999). The currency that is used to rank resources may thus not be uniform within a foraging group.

It is often thought that women's foraging is geared mainly towards provisioning the family, while the more risky to acquire big game is hunted by men and shared more widely than just among members of the nuclear family. The reasons for this difference are debated. Some researchers have argued that males share more widely in order to build a network upon which they can fall back when their hunting returns are disappointing. Big game would be the ideal food for such strategies, since it is too large for one family to eat all at once (*e.g.* Isaac 1978, Winterhalder 2001, 27). Others think that males may use their foraging spoils more to further their own political interests and may invest in order to increase their mating possibilities. It is thought that for males, mating with multiple women will almost always have a higher reproductive payoff than investing in increasing the chances of survival of their offspring. Therefore they will often choose to invest in potential partners (Bird 1999, 67). This seems to be supported by the fact that proficient hunters have greater access to extramarital affairs (Kaplan and Hill 1985, 132).

Females have other reproductive priorities. Firstly, they have certainty of parenthood of their offspring. Therefore their main foraging goal will be providing for their offspring. Furthermore, since nutrition can influence ovulation, pregnancy and lactation, foraging success or failure has more severe reproductive consequences for women than for men. Therefore it will in all probability be a higher priority for women to minimize short-term fluctuations in foraging success instead of maximizing the average returns (Jochim 1988). This means that women are expected to concentrate on abundant, low risk resources, such as plant foods.

Since the political and social role of food is very hard to test archaeologically, I will take caloric value as the starting point of my enquiry. The use of caloric value as a currency that is maximised may be simplistic but its application is reasonably straightforward. Caloric value however, is not as easily quantifiable as it appears. Body mass is generally a good indicator of caloric value. However, this is not an absolute law. As discussed, birds provide almost twice as many calories per 100g of meat than do mammals (Hockett and Haws 2003, 212, Ugan 2005, 75). In terrestrial mammals, the relationship between body size and caloric value holds up. Not only because larger animals provide more meat, but also because the meat of larger animals contains more fat (Rabinovich and Hovers 2004, 301). Since terrestrial mammals form by far the most important category of food remains found at Middle Palaeolithic sites, I will focus on body mass as a proxy for a prey's caloric value and thus its ranking.

Moreover, using this currency, deviations from the predicted patterns can be picked up, highlighting that foraging decisions were based on different factors. These will then be investigated bearing in mind the possibility of different currencies. In some cases the ranking according to caloric value and rankings based on other or multiple variables will not differ very much, however. This problem of equifinality cannot be solved by the application of the diet breadth model in isolation. By examining the archaeological context and data on for example butchery patterns we may be able to discern additional factors based upon which foragers ranked the available species.

When the caloric ranking is constructed, handling cost and search cost must be modelled in order to predict how they influence prey choice. Handling cost is an interesting variable, since Neanderthal foragers could have consciously modified it. It is a complicated factor to reconstruct, since this variable is a composite function of the predator abilities in pursuit and processing costs, and the prey species' skills at evading capture (*e.g.* MacArthur and Pianka 1966, 603). Therefore, developments in a predator's behavioural repertoire can in some cases significantly alter the return rate of a prey species and thus its ranking. Furthermore, the ranking of species may vary across individual foragers. For example, hunting skill and therefore pursuit costs of certain prey species may improve with experience, resulting in different rankings of prey species between age-groups (*e.g.* Walker, Hill, and McMillan 2002).

The most obvious way in which handling cost of prey species can be altered is by using technology for their exploitation. As shown in the previous chapter however, relating Middle Palaeolithic tools to subsistence strategies is far from straightforward. Furthermore, while technology may influence return rate it may also require a considerable amount of investment. Therefore it need not always be the most profitable solution for foragers. Increased investment in more sophisticated technology will not always yield large increases in return rates. Hence it can be more rewarding to keep technology simple (Ugan, Bright, and Rogers 2003).

An interesting example of lowering handling costs using technology and the problems connected to recognising this in Neanderthal archaeology is the case of mass collecting of small animals. When one is able to catch many of small animals simultaneously, for example by driving them into a trap, handling cost can be significantly decreased. Therefore mass collection can, in some cases, lead to return rates that match, or are even higher than those of encounter hunting of large mammals (Ugan 2005). Mass collection presents an exception to the rule that the inclusion of prey does not depend on its own abundance, but on the abundance of the higher-ranked prey types, since the return rate of mass collecting is dependent on the abundance of the prey. If population densities go up, so do return rates. Basically, it can "overtake" originally higher-ranked species (Madsen and Schmitt 1998, 447).

On the other hand, an important factor determining the handling costs are processing costs. These can account for a large percentage of the total handling cost of a species. For example, for large mammals processing can amount to between 1.3 and 40% of the total handling costs, in on-encounter hunting. In general, small animals require more processing per calorie than large animals (Ugan 2005, 82). This leads to an important point. It is often assumed that if animals are mass-collected, handling costs can be lowered sufficiently to make this more rewarding than encounter hunting of large mammals. For certain species this is the case, but generally mass collecting is not enough and efficiency gains must also be made in processing (Ugan 2005, 84). It appears that mass collecting of especially birds and mammals does not significantly improve return rates. Mass collecting does pay off in invertebrates and fish. This is because processing costs of large fish and insects are low, while they are not in mammals and birds (Ugan 2005, 78-80). Furthermore, a lot of time often has to be invested in the drives, nets etc., used in mass collecting, thus increasing the handling cost of mass-collected animals. On the other hand, trapping can be combined with other foraging activities and it is known that other resources are often exploited during animal drives. These are usually not quantified however, but this may result in an increased return rate for these activities.

As argued in section 3.3.6, the exploitation of small animals is an important topic in the study of Middle Palaeolithic subsistence. Mass collecting shows that in some cases exploiting these species is very profitable. Problematic is the fact that much of the material culture that could be used in catching animals, like snares or traps will have been made of organic materials. These will be next to invisible archaeologically. Furthermore, technology like gill-nets may take weeks or even months to produce, and for this investment to be worthwhile the tools must be used for a long time (*e.g.* Kelly 2001, 45). In mobile societies, investing in such technology may not have been worthwhile. In order to deduce what choices Neanderthals made we have to be aware of the problems surrounding lowering of handling cost. Since we know what species were exploited at sites and we can rank them on the basis of body size, we may be able to come up with educated guesses about the exploitation strategies used by Neanderthals.

Mass collection is just one example of how ranking of animal species can be altered by strategic and technological change. Ideally we would like to see a link between technology and exploited prey species. If changes in technology are accompanied by changes in the species that are represented at sites this provides an indication of changes in handling cost. It can also happen that animals that are in the exploited set change in ranking because of changes in the behavioural strategies used in their exploitation. This is a development that is more difficult to detect archaeologically. It might show up in changing representation of prey species through time. In the case of Middle Palaeolithic archaeology, the versatility of the stone tools may point to an absence of specialised technology in order to hunt specific prey. If different species of animal require different kinds of hunting or processing tools, the cost of the technological investment in the tools may influence prey choice. In some cases it can be more profitable to invest in a tool for a more common species, but one that will certainly be encountered, than in a tool for a species that may or may not be encountered (Ugan, Bright, and Rogers 2003, 1323). On the other hand, in order to exploit large mammals, generic tools will generally suffice for different species.

In the end, we will have to evaluate this variable largely on the basis of the species that are represented at the archaeological sites. In this study, handling cost will be modelled by using simple attributes of prey behaviour. If anti-predator behaviour of the available species does not influence their representation at archaeological sites, this indicated that strategies were in place to counter these behaviours. If species with well-developed anti-predator behaviours are absent from sites, we can infer that Neanderthals preferred species that were easier to catch.

A final influence on handling cost that does not receive much attention in most applications of the model is the transport cost of harvested resources. Hunter/gatherers need more than one resource, therefore they often operate out of a central place that is located in order to minimize the total transport cost of all crucial resources (Winterhalder 2001, 21). As discussed in chapter 3, the large amount of materials deposited at some sites over long periods of time seems to point to their use of these sites as a central place or home-base. This assumption is debated (*e.g.* Kolen 1999), but in this study I will assume that their foraging did have a focus at a central place from which the surrounding environment was exploited.

From the central place, the area closest to the site is usually exploited first. The more the area surrounding the site gets depleted, transport costs increase. As return rates become lower as resources in the site's vicinity become depleted, at a certain point a residential move will be in order. However, transport costs of certain resources can be lowered, for example by processing in the field, so only the most valuable elements of a resource are transported (Winterhalder 2001, 22). Transport costs can have important repercussions for hunting decisions in the field. It may become less interesting to capture large prey when one is further away from the base-camp for instance. Moreover it may lead to investment in processing equipment, in order to process the resource as fully as possible in the field, thereby minimizing transport costs. Developments in processing strategies can also influence handling cost and thus the ranking of species.

The third variable in the model is search cost. This is determined by the encounter rate with the prey. In the diet breadth model, the environment is assumed to be homogeneous, and encounter with prey is assumed to be at random (*e.g.* MacArthur and Pianka 1966). Therefore manipulation of the search time through knowledge of prey behaviour is assumed to be absent. In this case, variations in search time for the highest ranked species will have direct repercussions for the diet breadth. This is an unrealistic assumption with regard to Neanderthals; since we can assume that they knew how animals behaved and could therefore influence their encounter-rate with prey species. Hopefully, deviations from the expectations will enable us to determine how sophisticated Neanderthals were at manipulating encounter rates with high-ranked prey species, for example when certain high-ranked species are represented in higher proportions than one would expect based on reconstructed population densities.

One obvious example of influencing handling cost can be found in the exploitation of plants. The location of plants is stable, in contrast to that of animals. Especially long living plants like trees, will be at known locations for many years. This knowledge can be used to minimize search time to values close to zero. On the other hand, the harvesting of plants does have to be timed, since the moment at which they bear fruit depends on circumstances during the growing season. In order to harvest efficiently, it is best to arrive at the plants, before seeds or fruits have fallen to the ground, where they may become lost and before animals like birds arrive to harvest the plants (*e.g.* Kelly 2001, 49, 54). Similar strategies can be applied to the locations of animals. Especially migratory animals may be at easily predictable locations, enabling predators to manipulate search costs.

In conclusion, the research strategy that appears most productive is to compare the resources present in the environment, ranked according caloric value, with the exploited resources present at archaeological sites. This is the approach that is adopted in this study. I will focus predominantly on the faunal aspect of foraging strategies. This focus is dictated by taphonomic considerations but is defensible as meat appears to have been the most important component of the Neanderthal diet.

Therefore, we need to reconstruct the animal communities that were present in the vicinity of archaeological sites, so we know what species there were to choose from. As a starting point for this reconstruction we will use the analysed assemblages themselves. Because the sites that were selected were palimpsests, species that were not exploited by Neanderthals may be present in small numbers in the assemblages as a result of non-human processes. We will try to compare a species representation with a reconstructed population density. This will enable us to signal whether a species is represented in the same proportion as it would be encountered in the environment. If an animal is rare in the environment, but present in large numbers at the analysed sites we can conclude that is was exploited. If a species is underrepresented, we can conclude that it was not usually exploited at the site. Any bones of these species in the assemblage may be explained by other factors, as part of the “background fauna”, or they may represent an exceptional foraging episode.

Reconstructing the species’ population density will allow us to reconstruct encounter rates and therefore search cost of the species present. This is a tricky proposition however, since many of the species are extinct nowadays and it appears that Pleistocene environments do not have analogues in the present. In general, the population density of mammal species is correlated with body weight (*e.g.* Eisenberg 1990, Silva, Brimacombe, and Downing 2001, Silva, Brown, and Downing 1997). This correlation allows us to arrive at rough estimates of population densities of the available prey species.

Body weights of the species under consideration need to be obtained in order to construct a ranking of the available species. Various authors provide body weights of both fossil and extant species (*e.g.* Brook and Bowman 2004, Louguet-Lefebvre 2005, Macdonald 2006, Owen-Smith 1988 [1992], Pushkina and Raia 2008, Waguespack and Surovell 2003), values that will be combined to provide rankings for the selected archaeological and palaeontological sites. They will also be used in order to reconstruct the population densities of the species, following the equations provided by Silva, Brimacombe, and Downing (2001).

Handling cost of prey species is hard to reconstruct, but an inventory can be made of basic behavioural parameters. Based on this information, some insight into logical targets for exploitation should be gained. The ranking that is constructed can then be compared to the species present at an archaeological site. The final step is to evaluate how well the species that were exploited were predicted by the model.

First, we will look at size of the prey species. Among mammalian carnivores, body size is related to the maximum size of their prey (Radloff and Toit 2004). Therefore the size of prey is an important characteristic for the handling cost of prey species among mammalian predators in general. We can calculate the maximum prey size for a mammalian predator of 65 kg.[5], to be 300 kg.[6] Species weighing over 300 kg. will therefore be considered difficult to hunt for Neanderthals. This means that if prey larger than 300 kg. was hunted by them we can assume that they developed behaviour that allowed them to breach this important threshold. One of the ways in which this can be achieved is by coordinated group hunting (Radloff and Toit 2004).

Secondly, we will look at whether the species of prey was a carnivore. It is assumed that carnivorous species are more difficult to hunt successfully than herbivorous species, since carnivores are equipped with “weapons” like claws and teeth to kill prey (*e.g.* Webb 1989). Hunting these species will therefore be a dangerous endeavour.

Thirdly, we will look at whether the species of prey are solitary or living in groups. This is an important handling cost variable, since it appears that many species living in groups do so mainly in order to reduce the risk of predation (*e.g.* Barnard 2004, 407-416). Minimising this risk is achieved

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[5] The weight of an average male Neanderthal (Sorensen and Leonard 2001).

[6] The equation used is log(prey body mass) = 1.46(log predator body mass) – 0.17 (Radloff and Du Toit 2004, 415).

by "safety in numbers", because a predator has many potential victims, the risk for any individual is lowered. Moreover, living in groups also has the effect of increasing handling costs for predators. More individuals are on hand to spot approaching predators and when grouped, can even attack and chase away predators. Therefore if Neanderthal prey species lived in groups we can deduce that Neanderthals had developed behaviour to deal with this increase in handling cost.

In order to apply the model we also need to decide which variable we use to measure the abundance of species in archaeological assemblages and thus the importance of its exploitation in the foraging strategies of the hominins that deposited the assemblage. The number of bones identified to species level is usually expressed in Number of Identified Specimens (NISP). This measure has some disadvantages when comparing different species and assemblages though. First, different species of animals have different skeletons. Some species'skeletons have more bones than others, which means that these species may be overrepresented (Lyman 1994, 98, Reitz and Wing 1999, 60-62). Second, some animals may be processed in the field more fully than others, which will result in an underrepresentation of the processed species at central places (Lyman 1994, 111). Moreover if a bone is fragmented, several pieces of the same bone may be identifiable. This may also lead to overrepresentation of species. However, if bones are processed very intensively, the degree of fragmentation may result in the fact that no fragments belonging to the bone may be identifiable by an analyst (Lyman 1994, 281).

In order to get a more realistic view of the represented animals in an assemblage, many archaeozoologists calculate the Minimum Number of Individuals (MNI). This index specifies how many individuals must at least have been present to account for the NISP of a species (Lyman 1994). This counters the differential representation of species due to the fact that there are different numbers of bones in their skeleton. Moreover, the best represented element of a species is selected in order to calculate the number of represented individuals, so this measure also counters the differential representation of species due to different processing procedures. MNI as an index is problematic too. Most importantly, this index is not always calculated or provided in reports. Moreover, some archaeozoologists use a different definition of MNI and thus a different way of calculating it (Lyman 1994, 100, 104). Some critics even argue that using MNI as a measure of species abundance is logically flawed and should not be practised (*e.g.* Plug and Plug 1990). Even if these problems can be resolved, MNI results in an overrepresentation of rare species. Of some species often one or two fragments are present in an assemblage (Auguste 1995a, 157). Therefore it is not the ideal index to compare different bone assemblages.

Another variable that is sometimes used in order to compare the relative importance of animal species in an assemblage is bone weights. This may circumvent some problems associated with other indices. For example, the degree fragmentation of bone in a collection has less effect on the weight of bones of a species than on the NISP. Moreover, differences in size of animals and thus of economic importance will not be visible in either NISP or MNI, but they will be reflected in the weight of the bones. Unfortunately, many processes profoundly influence the weight of specimens, for example heating, but also processes in the soil during deposition (Reitz and Wing 1999, 170). Moreover, not many studies of Palaeolithic bone assemblages provide the weight of the recovered bones.

Other indices are also available, but, like the weight of the bones, they are not listed for the sites that were selected for this study. Moreover, these are all derived measures and are not always calculated in the same way. Therefore in this study it was decided to use NISP as the measure of species abundance at a site. In order to correct for the problems of overrepresentation the archaeological context can be taken into account. For example looking at skeletal completeness will inform us whether certain species are overrepresented in the NISP. Moreover, the different composition of artiodactyl, perissodactyl and carnivore skeletons is known (Lyman 1994, 98, see table), so we can correct for overrepresentation of species as a result of their different skeletal composition.

With regard to the application of the diet breadth model it is important to realise that abundance in terms of NISP or MNI does not inform us as to a species' rank. Well-represented species need not be the highest ranked, they are simply most often encountered. The highest ranked species may be rare and therefore only sporadically encountered.

Based on the predictions of the model and the archaeological reality, the following research questions emerge. First, whether the ranking based on caloric value is reliable, or whether we need to explore other currencies in order to predict Neanderthal foraging decisions. This may well be the case, since the mammoth-steppe has been envisaged as an area rich in large mammal biomass, so calories may not have been scarce. A second interesting query is whether we can see the results of manipulating handling costs. The prime example of manipulating handling costs may be the inclusion of small prey in the diet, but also of large dangerous prey. If handling cost of these species can be manipulated so that they can be hunted relatively safely, this may lead to their inclusion in the diet. Looking into this problem is also interesting in a longer temporal perspective, in order to see if for example changes in technology and behaviour coincide with shifts in diet breadth (cf. Stiner, Munro, and Surovell 2000, Stiner *et al.* 1999). Third, manipulation of encounter rates is also an interesting factor. Identifying signs of manipulation of encounter-rates may be more complicated. If species turn up in higher proportions than expected this would be a likely explanation. But this interpretation also depends on the accuracy of the environmental reconstructions used. Furthermore, if the highest ranked prey also happens to be relatively common this kind of pattern may not be easily visible in the archaeological record.

4.6 Possible confounding factors in the archaeological record

The application of the diet breadth model to the archaeological record is not straightforward. Certain taphonomic factors influence the composition of bone assemblages and constrain the research questions we can answer by studying them. First, there is the problem of temporal resolution. Sites are often palimpsests, containing the remains of multiple, and possibly many separate occupations and foraging episodes. Ranking of resources need not have been uniform over all these episodes. This means that we will lose sight of short-term variations, like seasonal fluctuations in prey ranking, because these ecological phenomena operate during a shorter time than is perceptible in the archaeological assemblages (*e.g.* Lyman 2003). These differences will be almost impossible to deduce from zooarchaeological assemblages.

On the other hand, the temporal scale of the archaeological record also presents us with advantages. Since short-term fluctuations will have been averaged out in palimpsests, it will be possible to reconstruct the strategy that Neanderthals developed to deal with their environment in the long term. Furthermore, an important criticism of foraging models in biology is the fact that they try to study the role of foraging in an animal's evolutionary fitness, but usually OFT models study short-time optimisation, while fitness is a lifetime measure (cf. Smith 1983, 638). Because of the temporal resolution of the archaeological record, applying OFT in prehistory always deals with the long-term results of foraging strategies, and can therefore show how long term developments of foraging strategies may influence a population's fitness. This issue can be turned into a methodological strength by focussing on palimpsests and research questions that adress long-term developments.

Another issue when studying bone assemblages is the fact that the behaviour responsible for their accumulation may produce assemblages that do not reflect the full suite of foraging activities equally. An obvious problem concerns the vegetable contribution to the diet, as has been discussed in section 3.3.6. The fact that Neanderthals lived during cold climatic phases may alleviate the problem, since plant foods are less important in colder climes. Moreover, as shown in chapter 2, the Neanderthal remains that have been isotopically analysed in order to reconstruct their diet suggest that plant foods were insignificant components of their diet (*e.g.* Bocherens and Drucker 2003, Bocherens *et al.* 2005, Richards *et al.* 2000, Richards *et al.* 2008b). Therefore we can assume that, especially for the colder areas of the Neanderthal range and in cold periods, plant foods will not have been very important economically. Even when we focus on the faunal component of the diet only, the archaeological record is likely to be biased. As discussed in section 3.2, hunter/gatherers lead a mobile way of life, producing different types of site. Therefore we need to take into account differences in site function and differences in seasonal occupation. Bone assemblages must not be studied in isolation, but should be compared with other sites from comparable regions and time periods. Furthermore, looking into additional features, such as bone assemblages and site architecture found at sites may provide clues as to the function of sites.

Intricately connected with the problems posed by the organization of mobility are transport decisions. In transport of food, the long-standing assumption is that limbs, especially the hindlimbs of carcasses, are the most highly prized parts of an animal and that these will therefore be transported to central places (*e.g.* Bunn and Kroll 1986, Potts 1983). Especially with increasing distance and/or carcass size, selection for the most valuable parts should become obvious (Monahan 1998, 406). The problem is that in practice, this assumption does not seem to hold true in a large number of cases (*e.g.* Domínguez-Rodrigo 2002). There is no standard transport sequence and therefore no standard pattern of bone accumulation, but there are important differences between different hunter/gatherer groups. As seen in the previous chapter, these kinds of decisions can have profound implications for the representation of species and activities at specific sites.

Still, there are some general patterns in the way in which carcasses are treated; with animals of different sizes often being treated differently (*e.g.* Bunn and Kroll 1986, Rabinovich and Hovers 2004). It is thought that smaller animals, especially if they are caught near a central place, will be transported to the camp in their entirety. The reasoning behind this is that because a round trip with the carcass would be less time and energy consuming than processing in the field and transporting processed parts to the camp. Larger animals will often be processed in the field, but the extent to which they are processed and which parts will be transported depends on many factors, for example predation risk or cultural preferences (*e.g.* Domínguez-Rodrigo 2002, Monahan 1998). Problems may arise if transport distances increase. When a forager encounters a resource, in deciding whether to exploit it, he has to consider that he can only carry a set quantity. So if he then were to encounter another, more valuable resource, he might not be able to exploit it, or would have to drop whatever he already had, making its exploitation a wasted effort. Of course, containers can alleviate this problem to a degree (Winterhalder 2001, 22). Still, this factor may cause a forager not to exploit species in the optimal set in some cases. Because of the problems regarding transport costs, care has to be taken when interpreting archaeological bone assemblages, because in the most severe case, if meat from large mammals was filleted, no bones may have been transported back to the site at all (Rabinovich and Hovers 2004, 301).

Finally, there is the difference in foraging strategies between individuals or subgroups of society. Most problematic in this regard are the different reproductive interests of males and females. Applying the diet breadth model to the archaeological record will not enable us to resolve matters at that resolution; it can only shed light on the foraging strategies at the level of the groups responsible for forming an archaeological site. In the Neanderthal situation, if we accept the evidence for a division of labour between sexes and the role of males as hunters of big game as discussed in the previous chapters, this might lead to a problematic situation, especially in cold phases in the northern parts of their range. The mammoth steppe was rich in low quality plant foods and animals subsisting on plants in this environments needed guts geared to fast processing of large amounts of food (Guthrie 2006, 208). This means that including a large amount of plant foods in the Neanderthal diet is effectively ruled out. This severely limits women's foraging possibilities. Although hunting or trapping of small animals especially is an activity that they might have practised, small animals are uncommon at many Neanderthal sites. This may mean that males could almost monopolize food distribution in some environments and this may have been a very important social currency. This situation does exist in some contemporary hunter/gatherers living at high latitudes too, but in these cases women forage for alternative resources like fish and small game in order to procure resources (Kelly 1995, 264, 267). In warmer periods and more southern environments, plants may have played a larger role in the diet. This may have had consequences for the use of food as a political tool, but also at a more basic level for the organization of mobility and male hunting strategies.

In all likelihood, food, and especially meat had an important role in the social life of Neanderthals. We can assume that it was used in order to cement bonds between people and maybe also as a tool used for reproductive purposes. One thing about Neanderthal society is important in this respect, however. It is often suggested that Neanderthals were less capable of maintaining extensive social networks and alliances than anatomically modern humans, based on evidence for long-distance trade, or lack of it (*e.g.* Gamble 1999, 267, 416). This leads to the hypothesis that the role of meat within local society may have been less extensive than what we see in contemporary hunter-gatherers. Gift-giving or exchanging may not have been very important and the social role of meat may thus have been less important than what we might expect based on modern human hunter-gatherer societies. Therefore, more food may have been used for provisioning females and children.

It is clear that we must take into account the role of taphonomic and behavioural processes when interpreting archaeological bone assemblages. Selection of suitable sites for analysis may allow us to overcome some of these problems. However, other factors like transport decisions will have been a universal factor in Neanderthal foraging behaviour.

4.7 Modelling Neanderthal diet breadth

Combining the diet breadth model with our knowledge of Neanderthal behaviour as discussed in chapters 2 and 3, we can formulate a number of hypotheses on the way that Neanderthal adaptations influenced their diet breadth. Of course Neanderthals operated over a large area under different climatic regimes and therefore diet breadth will have been variable and adapted to the regional environmental circumstances. In this section I will advance hypotheses on Neanderthal diet breadth that will be examined in the following chapters.

Two factors of Neanderthal biology are likely to have had an important impact on their diet breadth. First there is the fact that locomotion in Neanderthals was energetically more expensive than it is in modern humans because of their comparatively short lower limbs. Second, Neanderthals required more energy compared to modern humans, because of the fact that they were larger and, especially in cold environments, because they likely had a higher BMR.

Since locomotion was expensive, Neanderthals are expected to have had smaller foraging ranges than modern humans. Return rates of prey-items would drop faster as distance from the site increases than they do for modern humans. Especially small animals would only be worth pursuing when encountered close to the camp. The further from a camp foraging took place the more energetic gain one would need in order to compensate the high locomotion cost. This leads us to expect that in a similar environment, Neanderthals would practise foraging with a smaller diet breadth than modern humans. Higher transport costs also increase the importance of processing resources in the field. Since processing will affect transport cost, it is expected that this will have been an important strategy pursued by Neanderthals in order to minimise this cost.

Neanderthals had a larger body weight and lived in colder environments than AMH. Therefore it is thought that their BMR will have been significantly higher than that of AMH (Sorensen and Leonard 2001, Steegman, Cerny, and Holliday 2002). This does not automatically have consequences for Neanderthal diet breadth. The diet breadth model states that species will be added to the diet as long as the animal's return rate is higher than the average return rate for all higher ranked prey items including the expected search time for the higher-ranked items (Smith 1983, 628). Consequently diet breadth is not solely dependent on the energetic needs of the predator, but also on its abilities to search and find prey. On the other hand, Neanderthals will get into trouble sooner if for some reason finding and dispatching prey becomes more difficult. Furthermore the point at which combined search and handling cost start to outweigh the energetic gain will also be reached earlier by Neanderthals than by anatomically modern humans. The most important consequence of Neanderthals' energy demands is the fact that energetic returns are more likely to be a constraining factor in Neanderthal foraging strategies. Therefore it is even more likely than in modern humans that energetic value was in fact the currency maximised by Neanderthals. This has another implication, namely that Neanderthals were probably unable to cope with the same range of environments as anatomically modern humans. Especially the more marginal, less productive areas and maybe also a patchy landscape in which much travelling may have been necessary in order to fulfil their diverse needs may have been shunned.

Both these factors, but especially the cost of locomotion will have influenced the system of mobility that was practised by Neanderthals. The most obvious consequence of the increased cost of locomotion is that the area that can be profitably exploited from a central place will be smaller for Neanderthals than for modern humans. If we take the energetic budget spent on locomotion to be constant across mammals, then the average round trip for Neanderthals, applying the formulas provided by Steudel-Numbers and Tilkens (2004), would be 12.9 km when using the highest estimates of Neanderthal energetic requirements and 10.5 using the moderate estimates (Steudel-Numbers and Tilkens 2004, Weaver and Steudel-Numbers 2005).[7] Among modern human hunter/gatherers, there is a lot of variation in the length of foraging trips. The maximum listed by Binford (2001) is 30 km, the average distance is about 12.2 kilometres. If we take the estimate of moderate activity levels in Neanderthals to be comparable to the situation in hunter/gatherers, we see that the average distance of a foraging trip is significantly smaller.

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[7] According to table 4 in (Steudel-Numbers and Tilkens 2004), based on limb length and body weight, Neanderthals probably used up 12.39 ml O_2 per meter. Since using 1 ml of O_2 translates as burning 0.004801 kCal, (Weaver and Steudel-Numbers 2005), Neanderthals used 0.05948 kCal per meter. Energetic estimates given by (Weaver and Steudel-Numbers 2005) are 4480 kCal/day for moderate and 5500 kCal/day for extreme activity levels in Neanderthals. According to them these would translate into energy budgets of 627 kCal and 770 kCal per day respectively.

What would be the implication for the mobility practised by Neanderthals? First, a smaller area is exploited around each site, which means that resources in the foraging radius will be depleted faster than among AMH. Therefore, residential mobility will have been higher. Another way to deal with this issue is by limiting group size. If less people need to be fed, resources will be depleted at a slower pace and residential mobility will be lower (Binford 2001, 239-241). Higher locomotion costs also have implications for transport; it seems logical to minimize the weight of things that need to be transported in order to save energy. Therefore, transport of food to and from sites will be affected. One would expect high degrees of processing in the field in order to minimize the weight to be transported. On the other hand, if a large number of animals, or very large animals were caught, one might also expect the base camp to move to the meat, instead of the other way around. This would lead us to expect higher residential mobility and also somewhat weakens the assumption of central-place foraging. However, since many European sites containing large mammals show activities spanning extended periods of time, there is an indubitable spatial focus in Neanderthal foraging.

As argued in the previous section, this study will focus on the faunal component of Neanderthal subsistence strategies. Hunting is a risky hunting strategy however. In many hunter-gatherer societies the high-risk/high-yield foraging strategies of males are buffered by women's foraging for low-risk plant foods. If such a division of labour was in place among Neanderthals, we would expect the women to forage for plant foods. The importance of plant foods is very hard to determine, but the evidence from the southern part their range discussed in the previous chapter shows that, in some settings it played a significant role in the diet. However, in more northern areas, especially in glacial environments, relying on plant foods is an unlikely foraging strategy. Another risk-reducing possibility is increasing diet breadth and also exploiting small animals (*e.g.* Kelly 1995). As shown in chapter 3, this latter strategy appears not to have been very important for Neanderthals. In the colder phases one might therefore expect women to engage in the less dangerous tasks associated with hunting larger mammals. Among modern day hunter/gatherers, women's assistance in tracking animals is an important factor determining a male's hunting success for example (Biesele and Barclay 2001). Aiding in the less dangerous tasks of driving animals into an ambush has also been proposed (Kuhn and Stiner 2006, 958-959).

We have one important indication that Neanderthals did manage to buffer the risk of fluctuations in hunting returns as well as modern humans. This is provided by the analysis of Neanderthal teeth, discussed in chapter 2, which shows that the incidence of hypoplasias in their teeth is comparable to that of modern-day Inuit. In addition, the number of perikymata showing hypoplasias is lower in Neanderthals than in Inuit, pointing to shorter periods of nutritional stress among Neanderthals (Guatelli-Steinberg, Larsen, and Huchinson 2004).

Since the exploitation of a broad set of small animals was not the solution adopted by Neanderthals, they must have used a different strategy to buffer the risk of fluctuations in the returns of hunting large animals. One logical strategy is to exploit areas less intensively, and leave before prey density drops significantly (*e.g.* Kelly and Todd 1988). This would enable high returns, but only in the short term, since large-bodied species are generally present in low population densities. Consequently, this would lead to a drastically elevated degree of residential mobility. This would enable Neanderthals to focus on the very largest animals only. However, since large species have a slow rate of reproduction, they are easily overexploited. Therefore such a strategy would only be viable if Neanderthals were present in low population densities too. Another way of buffering short-term fluctuations in hunting returns would be by developing ways to store meat. Drying meat is not very complicated apparently, hanging it out to dry for two days appears to be sufficient to preserve it for some time and this process furthermore reduces the weight of the meat by up to 60% (Kelly 2001, 56). Since Neanderthals are known to have focussed on large animals, storage of surplus meat is a likely strategy.

In warmer periods and richer areas diet was likely broadened. However, as argued by Stiner *et al.* (Stiner 2001, Stiner, Munro, and Surovell 2000, Stiner *et al.* 1999), it is striking that Neanderthals did not exploit small, fast-moving prey as intensively as some modern humans. This is not necessarily related to differences in capabilities though. The fact that small fast game was not exploited more heavily may be due to reliance by women on "top-end" resources. Neanderthal foraging may have been characterised by focussing on a very narrow set of species. Slow moving species like tortoises and shellfish, which were exploited by Neanderthals, may have had much lower handling costs and therefore much higher return rates than fast moving species. Therefore, in warmer conditions, the widening of the diet to include plants and slow moving species might lead to the expectation that residential mobility would have decreased. However, even when foraging for low-risk resources, Neanderthals would have focused on the items with the highest return rates. They are thus expected to maintain higher rates of residential mobility compared to AMH under these circumstances.

This is compounded by the fact that these slow-moving animal species generally are slower reproducing species than fast moving prey like small mammals or birds (*e.g.* Stiner *et al.* 1999). Still, because of their role as top-carnivores and their heavier build, Neanderthals were probably present in lower population densities than modern humans. Combined with the hypothesis that they were more residentially mobile, it may have been possible for them to exploit these populations without their return rates dropping too dramatically. Over-exploitation of some species of small prey probably did occur in the late Middle Palaeolithic; however, this becomes much more apparent in the Upper Palaeolithic. It may also be a critical difference between Neanderthal and AMH foraging strategies, which do often show a greater reliance on small game: they may therefore have been able to exploit territories more intensively than Neanderthals could.

Another expectation that ties in with this proposed higher residential mobility is a reliance on simple, versatile and transportable toolkits. Because their residential mobility was high, it may not have been very rewarding to invest in “fixed” technology such as snares and traps, even if they were able to produce these. Tools for very specific activities will only have been made if the predictable returns were high enough and the activity was executed regularly enough to warrant this specialised investment. This may be the case with nets for fishing or trapping birds, whose construction costs are thought to be very high. Therefore unless densities of birds or fish were high enough to warrant construction of nets, we should expect more simple technologies to predominate.

If residential mobility was high it would be important for Neanderthals to optimise the weight to be transported. Therefore we expect Neanderthal tools to be versatile, in the sense that one tool could be used in the exploitation of multiple resources. This could be achieved by focussing on simple technologies, geared towards the category of prey that was most profitable, which would in most cases be large mammals. Artefacts like spears are used for other activities like fishing among modern hunter/gatherers, but specialised equipment for these activities may have yielded to little to warrant the investment. If residential mobility was lowered in richer environments, investment in trapping and snaring technology is expected to become more rewarding. This lowering of residential mobility would be expected in more temperate climatic phases. On the other hand, in forested environments, biomass is very hard to exploit for animals and hunter/gatherers, since most of it is locked up in the trees (*e.g.* Binford 2001, 106). In this situation as well, concentrating on the largest animals around, would have been the most profitable course of action. Since these animals would be present at low densities residential mobility would still be high. Trapping and snaring would thus presumably to have occurred mostly in the biomass rich southern parts of the Neanderthal range.

Testing these expectations will not be straightforward. A lot of the expectations hinge on high residential mobility because of a focus on large game. However, because of the temporal resolution of the archaeological record, it will be hard to deduce whether sites are palimpsests representing multiple short periods of use, or whether sites were used for a longer time and hence residential mobility was not very high. If we succeed in reconstructing likely population densities for the exploited species we can put constraints on the interpretative scenarios. Furthermore, it will be important to try to determine whether the picture of subsistence strategies presented by a site is representative of what Neanderthals were doing in that kind of environment. This can be achieved by comparing the sites to sites in similar settings. This will show whether for example small game is under or over-represented at sites under consideration.

4.8 Modelling hyena diet breadth

As pointed out in chapter 1, this study aims to evaluate the benefits of applying OFT to Middle Palaeolithic assemblages by also using it to analyse foraging strategies of Pleistocene cave hyenas (*Crocuta spelaea*). In order to do this, we need to reconstruct the model’s parameters for this species too. This species is closely related to spotted hyenas (*Crocuta crocuta*) (Rohland *et al.* 2005) and analysis of their behaviour allows us to assemble a model for cave hyenas. It appears that spotted hyenas are similar to Neanderthals in at least two important respects. They were of roughly similar size, cave hyena being slightly larger. Second, both were social carnivores. In contrast to living primates, however, spotted hyenas and presumably cave hyenas are adapted to scavenging and hunting (*e.g.* Tooby and DeVore 1987). Since Neanderthals and Cave hyenas were sympatric in large areas and they appear to have been successful in the Pleistocene, it is expected that their niches were differentiated. For OFT to prove a useful tool, it should be able to differentiate between their niches.

In order to apply the diet breadth model for cave hyenas we will use the same approach as we did in Neanderthals. We have selected sites with large bone assemblages for analysis. It is hoped that they provide us with time-averaged results of hyena foraging strategies. We will use the reconstructed weights of the prey species to construct a ranking of the available prey species. Again, we will start using caloric value of the available species as the currency that hyenas tried to maximise. Moreover we will use the same simple characteristics to try to model handling costs. Encounter rates will also be modelled using reconstructed population densities.

It is proposed that applying the same model, we should be able to see differences in selection of prey between Neanderthals and cave hyena. If this is not the case we need to either refine the model's parameters, or use a different method of analysis to study Pleistocene foraging behaviours.

4.9 Summary and conclusion

The application of OFT to the archaeological record is a promising approach. OFT provides a framework that links foraging behaviour to evolutionary fitness and as such can be used to evaluate the dramatically changing ideas surrounding the evolution of hominin foraging. The goals for this study are simple. We will use a simple version of the diet breadth model to see how well OFT predicts Neanderthal foraging decisions.

The currency that we will use is prey size as a proxy for the caloric value of the prey. This currency works well in ethnographic studies (Winterhalder 1987, 319-322), although it does not fully explain foraging decisions in all cases. After comparing archaeological bone assemblages with the constructed ranking, we can evaluate whether this currency predicts the results of foraging behaviour well. If this is not the case, other currencies will be considered. If other currencies do not explain the set of exploited species we may assume that Neanderthals ranked species differently, because they were able to influence the return rate of certain species by manipulating the search and/or handling cost of certain species. We will use simple proxies to model encounter rate and handling cost. The encounter rate will be modelled using reconstructed population densities. If species that were rare in the environment are abundant at sites we can assume that Neanderthals were able to focus on these species because of an intimate knowledge of their behaviour. Handling costs will be modelled using simple proxies to gauge whether species were dangerous or hard to approach. If they are well represented in assemblages despite these factors we can assume that the foragers were able to overcome these difficulties. The results of the application of the diet breadth theory to Neanderthal sites will then be compared to the results of similarly analysed hyena dens. It is hoped that differences in their respective niches can be recognized and, ideally that the reasons underlying these differences can be explained.

Based on the foregoing some hypotheses with regard to the foraging strategies used by Neanderthals can be formulated. In interglacial periods, if the environment was dominated by closed forests, available biomass for Neanderthals was low. Most biomass would be locked up in trees, so the combined amount of edible plant foods and herbivores was likely limited. I assume that this led to low Neanderthal population densities. Fluctuations in hunting returns could not be buffered by female foraging for plant foods in most seasons. Therefore residential mobility is expected to have been high. Herbivores providing high return rates would have been hunted in an area and residential moves would have been made before the return rates of this activity dropped considerably. In this scenario foraging activities are expected to be concentrated on the largest species. Since fluctuations in return rate needed to be minimised in contingencies smaller species would also have been exploited.

During warmer periods the environment may have more open than it is nowadays as has been proposed by Gamble (1986, 1999) for the Eemian of occupations in Germany. This may have been caused by continental conditions in Germany. However, the presence of megaherbivores may also have resulted in more open environments in Atlantic climates. The presence of horses at some sites may support this view. In these environments, more animal biomass may have been available. Furthermore, animals may have been less dispersed, but may have moved more in herds with predictable locations. This may have led to an increase in Neanderthal group size. Smaller ungulates may have been exploited more readily in such environments, thus widening diet breadth and lowering residential mobility. Whether these developments took place is dependent on how much more animal biomass was available in the environment.

In mammoth steppe environments, biomass was likely very high (*e.g.* Delpech 1999). Moreover, in open environments, animals are likely to be concentrated in larger herds (*e.g.* Guthrie 1990, 155). Therefore, the higher amount of available biomass allowed Neanderthals to be present in larger groups, but may also have necessitated larger hunting parties in order to deal with the fact that most prey was now concentrated in herds. In these richer conditions diet breadth will have been lowered, since encounter rates with high ranked prey were probably favourable. On the other hand, in conditions of affluence, other considerations may become important. The time spent foraging may have been a valuable commodity itself. In these larger groups, the fitness of individuals could have been better served if time was allocated to other activities, such as investing in bonding with mates (*e.g.* Schoener 1971). In this situation diet breadth may therefore be kept wide in order to increase encounter rates with suitable prey, resulting in shorter foraging time and leaving more time available for other activities. I propose that in this situation a focus on the most ubiquitous ungulates may be developed. On the other hand, if women's foraging was unimportant in these environments, successful foraging could also have been linked to fitness benefits. In these circumstances prestige may have played a role in foraging decisions.

In Mediterranean environments, the role of plant foods and small animals and therefore the role of women's foraging increases. These conditions may also be termed affluent and in these circumstances Neanderthals may have strived to minimize foraging time and therefore have focussed on broader diets. Prestige hunting in these circumstances is less likely, since women are more able to fend for themselves. An additional factor in widening the diet breadth is the fact that residential mobility may be lowered since fluctuations in the abundance of prey species in the optimal set can be better buffered, seeing that more species can be exploited. This in turn has implications for investing in more specialised technology. These investments become more rewarding in this situation. The widening of diet breadth may then reinforce itself, since investing in a more elaborate toolkit may allow for the profitable exploitation of more species.

Hyena foraging is expected to be more diversified than Neanderthal foraging. Scavenging animals may result in more species being exploited, since if a carcass is encountered, handling cost is drastically lowered, because no pursuit or kill has to take place. This means that even small carcasses may be profitably exploited. This may also be reflected in the age classes of exploited prey, since weak age classes will be overrepresented if this foraging tactic is used. On the other hand, spotted hyenas are capable hunters, and in rich environments, scavenging is not a very important foraging strategy (see chapter 7). It is expected that in warm periods scavenging was more important than in cold periods when the environment was more open and more herbivore biomass was available. This means that in colder periods, the average prey size may increase when compared to warmer periods. It is thought that because hyenas hunt by pursuit, weaker age categories may be overrepresented when compared to hominin hunting, since it is hypothesised that hominins were more likely to be ambush hunters.

In the next chapters we will test these hypotheses by analysing selected sites dating to the Middle and Late Pleistocene of northwestern Europe. Of course this is a small sample of sites, but it will give a good indication of whether application of the diet breadth model in this form is a fruitful approach to studying Pleistocene subsistence strategies.