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

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8 Discussion

This study has tested whether the diet breadth model from the domain of Optimal Foraging Theory (OFT) can be used to analyse Pleistocene foraging strategies. In this chapter I will synthesize the results of this study. As pointed out in chapter 1, understanding the Neanderthal dietary niche is very important with regard to testing a multitude of theories on hominin life-histories, group size, language abilities and the function and cause of increases in Middle and Late Pleistocene brain sizes. The use of ecological theory can greatly contribute to our insight into Neanderthal foraging niche. However, before the diet breadth model could be applied to the Pleistocene, some obstacles had to be overcome. First, I will discuss the problems that are encountered when applying the diet breadth model to Pleistocene foraging and the solutions I arrived at in this study. This will be followed by a section that deals with the specific problems that were encountered when trying to apply the model to the selected archaeological and palaeontological sites that were analysed. Finally I will summarise the results of this study with regard to our understanding of the Neanderthal foraging niche and place these results within their wider archaeological context.

8.1 Application of the diet breadth model to archaeological data

Before OFT can be used to analyse foraging strategies evidenced by the archaeological record, a number of methodological issues need to be addressed. The diet breadth model has been developed in behavioural ecology for situations where one can observe which prey is taken at what frequency. In order to apply OFT to the archaeological record we must try to distil that information from a time-averaged and biased archaeological record. This study has highlighted some of the problems of applying OFT to archaeology but also proposed solutions, which will be discussed shortly here.

In order to estimate which prey is taken at what frequency, I have chosen to analyse the Number of Identified Specimens (NISP) of the represented species as a measure of the frequency of their exploitation. As discussed in chapter 4, this measure is not unproblematic. A possible solution to the problems is to use a different index to analyse the bone assemblages. A useful measurement could be the MNI of a species present in the assemblage. This would negate the problems stemming from the different composition of skeletons and at least partly overcome biases from differential processing and transport of different species. However, there are different ways of calculating MNI, leading to different possible outcomes (*e.g.* Reitz and Wing 1999). Therefore, using MNI when comparing sites whose primary analysis has been done by different archaeozoologists may be problematic. Moreover, not all authors publish MNI's. Hence, in order to compare different bone assemblages published by different authors, NISP is the only measure that can be used for the sites studied in this thesis. Because of our awareness of the problems associated with this variable, we may be able to correct the representation of different species based on the number of skeletal elements they possess. Moreover, behaviours like transport and processing can be modelled using measures for skeletal part representation.

The problems associated with transport behaviour are part of a larger set of problems concerning the various biases in the studied assemblages. As discussed in chapters 3 and 4, hunter/gatherers characteristically exploit their territories using some form of mobility, exploiting part of their territory until resources become scarcer and then moving on to a different area. Moreover, hunter/gatherers produce several types of sites; some sites are only occupied for specific activities, while others function as a home base or central place. This has obvious and important repercussions for this study. The archaeological sites from different areas and time periods analysed cannot be taken as representative of the full array of foraging strategies of the occupants. The analysis can only illuminate the foraging behaviour reflected at Taubach and Biache-Saint-Vaast themselves. Season-specific activities due to seasonal changes in ranking of prey species cannot be studied in this way.

Nevertheless, at both Biache-Saint-Vaast and Taubach, large amounts of material were found, which suggests that these sites occupied an important position in the foraging strategies of the groups occupying them. Also, hunting was not focussed on a single species, but multiple exploited species are present at both sites. This suggests that we are not dealing with specialised hunting camps. Moreover, at least at Biache-Saint-Vaast stone tool production was important, suggesting the juxtaposition of several activities. Investment in site furniture may have taken place at Taubach if we accept reports of hearths being present at the site. Therefore we can assume with reasonable certainty that the sites represent an important proportion of the foraging activities practised by the groups occupying them.

With regard to the selection of assemblages formed by cave hyenas (*Crocuta spelaea*), similar problems are encountered. Studies show that the communal den of a spotted hyena (*Crocuta crocuta*) clan is moved regularly, on average once a month according to one 10-year study. Many sites are not re-used, but some dens are re-used periodically over long periods of time (Boydston, Kapheim, and Holekamp 2006, Pokines and Peterhans 2007) . Moreover, next to communal dens, other types of sites are also produced. For example some females (often low-ranking ones) rear their young in an isolated natal den for the first month of their life (Boydston, Kapheim, and Holekamp 2006). Furthermore, hyenas have also been alleged to produce caches (Diedrich and Žák 2006).

With regard to the hyena accumulations analysed in this study, the sheer amount of material found precludes the idea that the sites functioned as natal dens. The age-distribution of the hyena population of the analysed accumulation at Lunel-Viel suggests that the site functioned as a communal den. No information was available on the age-structure of the hyenas at Camiac, but at least the abundance of coprolites can be taken as an indication that hyenas were present at the site for a prolonged period of time, suggesting that the site did not function as a cache, but as a communal den. If den use of cave hyenas is comparable to that of spotted hyenas, the analysis of hyena sites may give more insight in the total spectrum of foraging behaviours exhibited by these species than the analysis of Neanderthal sites. This is the case because the hyena accumulations are the result of multiple occupations that took place during different seasons. If we take modern human foraging strategies as an analogue for Neanderthals, the use of specific sites may have been tied to a specific season in Neanderthals. Therefore, occupation of Neanderthal sites may habitually have taken place in the same season.

The application of the diet breadth model can be improved by selection of sites of which the Central-Place character can be more securely ascertained. This kind of site is rare in the archaeological record however. A site like Kebara in Israel, might qualify. Here the occupied space was organised in the same way over a long time, long enough to accumulate several meters of sediment, suggesting very intensive use (*e.g.* Bar-Yosef *et al.* 1992, Meignen *et al.* 1998, Shea 2003, 181). In northwest Europe, this calibre of site is unknown though.

Another improvement in the application of OFT to the Pleistocene archaeological record would be to study several sites in a micro-region that functioned in the same settlement system. This would enable studying the full scale of foraging activities practised over the course of a year. The execution of such a research design is made impossible by the fact that there are huge gaps in preservation, and therefore in some contexts almost no securely dated sites with bone assemblages can be recovered. Moreover, the uncertainties associated with the direct dating methods for this period of time are so large that it is very hard to define a set of sites that would have functioned within the same system.

Finally, when applying this method to archaeological sites, one must carefully consider the argumentation one uses. If the excavated assemblage is taken to represent the optimal diet breadth, one must then explain why some species are not included in it. This can be done by simply positing that the return rates of these species were low. Such a manoeuvre does not explain anything however, unless one can specify why the return rate was lower than that of the exploited species. Moreover this does not take into account the possibility that the assumptions of the model, i.e. the currency that was maximised, may be incorrect and therefore the model that is used can easily be perpetuated. This means that if species that are expected to be included in the optimal set were left unexploited, one must scrutinise the assumptions underlying the model carefully in order to gauge whether for example the ranking that is used may be incorrect simply because an irrelevant currency was chosen.

8.2 Reconstructing the model's variables

In behavioural ecology, much information needed to successfully apply the diet breadth model can be collected in the field. Such data had to be estimated for Pleistocene applications, which presented an important challenge for the successful application of the model to Neanderthal foraging behaviours. Estimating these data proved more complicated than I had initially expected. The amount of variation of estimates, even for basic attributes like animal body weight is considerable. With regard to Pleistocene applications, these problems are exacerbated by the fact that some of the available prey species are extinct nowadays.

More importantly, taphonomy precludes a full analysis of foraging strategies, since some categories of remains are only very poorly preserved. The most obvious categories of these consists of plant foods. As discussed in chapter 3, virtually nothing is known about the vegetal component of the Neanderthal diet and what little information we have is mostly from the Mediterranean. This study focuses on the faunal component of the foraging niche. However, both analysed archaeological assemblages are from periods with a "temperate" climate. Therefore, we cannot dismiss a potential vegetal component of the diet of the occupants of the sites. In terms of caloric contribution, I assume that the faunal component was much more important however. This is corroborated by the isotopic evidence of one individual from Sclayn, dating to MIS 5c or 5e, which shows a "carnivore signature" even in a warm climatic phase (Bocherens and Biliou 1998). Other sources of food may also be underrepresented in the archaeological record. As discussed in chapter 3, ichtyological remains in particular are often underrepresented in the archaeological record. But again, isotopic evidence seems to demonstrate that aquatic resources did not play an important role in Neanderthal diets.

Ethnographic data support the idea that plant foods would not have provided the mainstay of a hunter/gatherer diet at temperate latitudes (*e.g.* Kelly 1995, 67-69). Binford has extrapolated the data on extant hunter/gatherer diets to the environment of Pleistocene Europe and concludes that animal foods must have provided the mainstay of the diet, except in some areas in the Mediterranean (Binford 2001, 193, fig. 6.07). Moreover, he suggests that during glacials, the boundary of the areas where animals provided 50% or more of the diet may have moved southward to North Africa (Binford 2007, 193). Still, we must take into account that plants may have provided a highly ranked source of food at temperate latitudes at least seasonally. The role played by aquatic foods in contemporary hunter/gatherers is large at temperate latitudes. The exploitation of aquatic resources, or rather its rarity, in Middle Palaeolithic contexts is therefore an important research topic. For this study, it seemed most productive to focus on the mammal component of Neanderthal subsistence, since the available information unambiguously shows that this was the most important source of calories.

In order to construct a ranking of the available mammal species, I used body weight estimates from the literature. As pointed out in the previous chapters, many widely differing estimates for the same species can be found in the literature (Brook and Bowman 2004, Louguet-Lefebvre 2005, Pushkina and Raia 2008). The weights used can therefore not be considered anything more than "educated guesses". In addition, other attributes could influence the ranking of species. Some of these have been discussed in chapter 4. With regard to the application of OFT to Pleistocene archaeology, especially fur may have been a factor that influenced the ranking of certain prey species. In general, the fur of larger animal species is thicker than that of smaller species, which might give large fur-bearing species a bonus in the ranking. This applies especially to brown bear, whose fur has better insulating qualities than that of for example polar bear. Another interesting case is that of polar fox, which has very thick fur with good insulative qualities (Scholander *et al.* 1950, 230). This may be a valuable attribute that could be incorporated in future rankings, especially for sites situated in cold environments.

Other factors are even more difficult to reconstruct, most notably for extinct animals. Especially environmental preference and population density, both important variables, posed problems. In order to reconstruct the environmental preference of extinct animals, we can use anatomical features like dentition and manner of locomotion. This can be combined with chemical evidence on the isotopic signature of fossil remains. This reflects an animal's dietary habits and therefore to a certain degree its environment. The outcomes of these analyses can be ambiguous though. Isotopic studies of cave bears (*Ursus spelaeus*) for example have been used to argue for both a vegetarian diet (Bocherens, Fizet, and Mariotti 1994) and an omnivorous diet (Richards *et al.* 2008a). We must therefore take into account that a species' habitat may have been variable and cannot always be easily characterised.

In the case of extant species, the habitat preferences of modern populations can be observed and used to model the preferences of their Pleistocene counterparts. Therefore our knowledge of the biotope of these species is more reliable. On the other hand, some problems do exist in this domain. First, a species' adaptation needs not have remained unchanged since the Middle or Late

Pleistocene, since it has been under evolutionary selection and may have adapted to different habitats. Second, in modern-day Europe, many large mammal species have been relegated to living in marginal areas, since most of the prime land in the continent has been developed for human activities. Furthermore, due to the extinction of some animals that played an important role in the ecological structure of the landscape, like proboscideans and large carnivores, the modern guilds of animals are very different from those of the Pleistocene.

We know from the excavated assemblages that animal communities of the Pleistocene were non-analogous to those of the present (*e.g.* Stewart 2004, Stewart 2005). This is often attributed to the environment in the Pleistocene being more "mosaic" than nowadays (*e.g.* Gamble 1999, 112). In this study the problem is most clearly illustrated by the representation of horses at an interglacial site like Taubach. Pollen records indicate the environment was densely forested. Equids are adapted to grazing in open areas and are therefore not expected to be present at interglacial sites in forested environments. The environment must therefore have been more varied than nowadays. As pointed out above, elephants and mammoths were probably keystone species, with a big impact on the environment, thereby promoting open spaces and diversity of vegetation (*e.g.* Haynes 2006, Shoshani 1998). Moreover the presence of more species of predators may also have affected the opportunities of different herbivores, possible enabling more species to co-exist (Leibold 1996, Quammen 2005).

These problems seriously affect the accuracy of predictions based on habitat preferences, such as estimates of the population densities of the different species that were available. This compounds the problem of estimating population density, in turn making the encounter rate with species difficult to predict. In this study I have chosen to use simple body weight based formulas to get an idea of the population density of species in ideal circumstances. Combined with the indications about the environment we can therefore gauge the likely encounter rate with the species at stake. In the future, this formula may be improved by more precise environmental reconstructions. This will not erase this problem completely, since the analytical techniques like pollen analysis still yield information that, for example in the case of Taubach, is to some degree at odds with the excavated mammal communities. Another interesting option is to take the abundance of species in the palaeontological record as a measure of their population density. However, this may be problematic, because some species will be underrepresented in the fossil record because their ecological niche is unfavourable for fossilization. These species would not normally be encountered in areas where their bones might be preserved, something that has been proposed for Merck's rhinoceros (Billia 2008, 35).

Even more difficult is the reconstruction of the handling costs of the various species. This variable depends on the capabilities of the predator and the anti-predator behaviours of a prey species. I have chosen to use simple attributes of the available species to get an indication of the level of difficulty hunting the species in question may have entailed. The effects of using different kinds of stone tool technology and different strategies for intercepting, killing and processing certain species is hard to estimate. I assume that no specialized tools were needed in order to butcher the different species, since all species concerned were mammals. However, one might hypothesize that skinning pachyderms may have been more costly than skinning other mammals and that this activity may thus have required specialised tools. This has not been incorporated in the handling costs of species in this study however. I do assume that the cost of butchery becomes relatively higher in smaller species since they possess similar skeletons to larger species, resulting in a similar procedure of butchery. The amount of meat that they yield is much smaller though. Especially in small mammals, handling costs may thus become prohibitively high (*e.g.* Ugan 2005).

In reconstructing handling costs, great improvements could be realised if archaeological information on hunting strategies and the killing power of the weapons used could be incorporated in the handling costs of prey species. This is hard to realise though. Information on the weaponry used is rare. Wooden spears are known from Schöningen, and Clacton, but it is uncertain how widespread their use was. Moreover there is controversy over whether these spears were thrown (Rieder 2003) or thrusted (Churchill 2002). Moreover, stone-tipped spears may also have been used in the Middle Palaeolithic (*e.g.* Shea 2006, Villa and Lenoir 2006). However, it is unsure what tool forms can be classified as spear points in Middle Palaeolithic assemblages and what percentage of points was actually used as a spear point. Strategies using traps are even harder to model, although a site like La Cotte de Saint-Brelade shows that Neanderthals were certainly capable of organising an ambush. Reconstructing handling costs in this kind of detail would be interesting in order to refine Pleistocene applications of OFT, but as some of the attributes to be modelled are very difficult to approximate, this may do little to improve the fit of the model. It was therefore thought that for the scope of this study it would be more productive to focus on simple proxies to gain insight in the handling costs.

Finally, we must realise that the variables on which the models are based have been defined not by Neanderthals, but by researchers. Identification of prey categories, for example is done based on the biological species concept. Neanderthal foragers may not have recognised all species we identify as separate categories of prey. One could hypothesise that the difference between Merck's rhinoceros (*Stephanorhinus kirchbergensis*) and narrow-nosed rhinoceros (*Dicerorhinus hemitoechus*) was not very important to Neanderthals. They are very similar animals, both falling into the heaviest category of species, leading solitary lives etcetera. Therefore, Neanderthals may have adpoted a single "rhinoceros" category in their foraging decisions. I assume that the categorizations used by Neanderthals will at least be approximated by the biological species concept used in this study. Moreover in the absence of any sources of information on "emic" categorizations used by Neanderthals, no real solution can be found for this problem.

8.3 Modelling Neanderthals

Besides the problems surrounding the reconstruction of the variables described above, reconstructing the characteristics of the predator for which the model is supposed to operate is not unproblematic either. As discussed in chapter 2, Neanderthal energetics and life histories were probably different from ours and these biological factors may have affected foraging behaviour. However, in many areas, there is little or no consensus as to how much Neanderthals differed from the modern pattern.

First, Neanderthals may have had an elevated BMR. It is thought that this trait was an adaptation to the cold, also present in modern-day hunter/gatherers in cold climates. Moreover, the increase in Neanderthal BMR may have been greater than in modern human groups according to some (e.g Churchill 2007), because they were less able to fashion insulating clothes. This in itself has no repercussions for the working of the diet breadth model, since it does not alter encounter rates or return rates. Therefore, an optimal set will still be exploited consiting of the species for which the combined encounter rate and handling cost yields the highest composite return rate. On the other hand, it does have repercussions for Neanderthal behaviour. Because of their higher energetic requirements, Neanderthals needed to realise a very high return rate (Churchill 2007, Sorensen and Leonard). This may have proven problematic in some circumstances, for example if the optimal return rate decreased, for instance because of a drop in herbivore biomass in the landscape. In such cases Neanderthals may be forced to adapt, for example by increasing their mobility rates or by changing their group size or migrating to other areas, sooner than a modern human group would.

Cold adaptations have also been used to explain the fact that Neanderthals seem to exemplify Allen's and Bergman's rule see (chapter 2). They are quite heavy for their length and have relatively short limbs. Both these factors decrease their surface area relative to their volume, thereby reducing the amount of heat loss. As discussed in chapter 2 and 4, their relatively short lower limbs have other consequences, besides minimising heat loss. They are thought to significantly increase their cost of locomotion (Steudel-Numbers and Tilkens 2004, Weaver and Steudel-Numbers 2005). This has consequences for their diet breadth, since it influences handling cost. It is predicted to favour a smaller diet breadth in Neanderthals than in modern humans in comparable circumstances. It is expected that return rates for Neanderthals would drop faster in response to higher tracking and pursuit costs, thus leading to a lower optimal diet breadth.

Recent work suggests that they may also have exhibited different activity patterns. Results of analyses of skeletal correlates of activity patterns are not always conclusive though. In a recent study, Pearson, Cordero, and Busby (2007, 150-151) argue that Neanderthal activity patterns may have been comparable to those of modern human foragers living in rugged terrain, like Epigravettians from Italy. It has been proposed though that Neanderthals were characterised by more intensive subsistence practices than their modern human contemporaries (Pearson, Cordero, and Busby 2007, 151). In light of their proposed high energetic needs, this is a logical hypothesis.

Another interesting factor is the fact that Neanderthals seem to have matured faster than modern humans. Studies into the formation of teeth have yielded conflicting results so far (Ramirez-Rozzi and Bermúdez de Castro 2004, Smith *et al.* 2007) contra (Guatelli-Steinberg *et al.* 2005). If Neanderthals did mature faster than modern humans, this would have placed a great energetic demand on the adults providing for the child. Again, this does not impact upon behaviour according to the diet breadth model, but on the other hand may have made poorer areas unfeasible for Neanderthal occupation, while a species with lower energetic needs, like *Homo sapiens sapiens*, may have been able to colonise the area.

8.4 This study

In order to apply the diet breadth model, two important Middle Palaeolithic sites are analysed in this study: Taubach and Biache-Saint-Vaast. They are compared with two Pleistocene hyena dens, Lunel-Viel and Camiac. The archaeological sites were chosen because both sites yielded large bone assemblages that have been published. These assemblages are unambiguously associated with hominin activities, since cut-marks are abundant and the occurrence of carnivore marks is minimal. Moreover, carnivore remains at the sites are rare and no other indications of their presence, like coprolites, were reported. The selected sites therefore provide a good opportunity to study hominin foraging strategies.

With regard to the comparison between the archaeological materials and the hyena sites, there is certainly much room for improvement. Ideally, one would use hyena dens without any indications for hominin activity, while the sites used in this study both yielded small stone artefact assemblages. Unfortunately, almost all published Pleistocene hyena dens harbour stone tools. Because of the character of the bone assemblage, the presence of hyena traces on the bones and the absence of traces of hominin activities on the bones I have assumed that the accumulation of the bone assemblages can be attributed mainly to hyena activities. Moreover, the hyena dens used in such a comparison should ideally be located in the same region and dated to the same period as the archaeological sites that are being analysed. Unfortunately, no well-published hyena dens in the vicinity of Taubach and Biache-Saint-Vaast were available for analysis. Therefore, the choice of sites used in the present study, although far from ideal is the best available at present.

With regard to the archaeological sites, other sites from the same latitude containing well preserved and well published bone assemblages are uncommon. Although for future applications, analysis of some other sites may be very useful, many of the sites that are available provide little information. One well-published site with regard to Neanderthal hunting strategies is the site of Wallertheim. This site, which has been analysed by Gaudzinski (1995, 1996) might be expected to be included in this study. It has been left out of this analysis for two important reasons. First, two excavations at the site have yielded very different results. The assemblage that was analysed by Gaudzinski was excavated in the early 20th century and points to specialised hunting of bison. However, excavations in the vicinity of the early excavations in the nineties by Conard *et al.* (*e.g.* Conard *et al.* 1995, Conard and Prindiville 2000, Conard, Prindiville, and Adler 1998) failed to replicate the results reported by Gaudzinski. Multiple find levels were identified, some containing bone assemblages and stone tools, but it could not always be ascertained that the artefacts were associated with the bone assemblages. None of the findlevels yielded a bone collection comparable to the one studied by Gaudzinski (Conard and Prindiville 2000, 295). Second, the assemblage analysed by Gaudzinski provides indications for exploitation of only one species, namely bison (*Bison priscus*). The site may therefore have functioned as a special-purpose site and analysis would probably not yield insight in the full suite of Neanderthal foraging strategies and the set of species that they exploited. This is underscored by the large variety of species that is represented in the layers that were researched in the nineties. The possibility of a site not yielding a representative picture of Neanderthal foraging strategies is also the reason for the exclusion of other sites, like Salzgitter-Lebenstedt, which show focussed exploitation of one animal species only.

For other sites that contain large bone assemblages in which multiple species of animal are present, the association of the species with hominin activities was not unambiguous. At Buhlen for example, mammoth, woolly rhinoceros and horse remains are present in large numbers. The number of cut-marks on the other hand is quite small and gnaw marks have also been observed (*e.g.* Prins 2005). Other sites like the caves of Scladina (Pathou-Mathis 1998), that yielded both hominin remains and lithic artefacts, seem to have functioned as a carnivore den as well, making it difficult to separate hominin from carnivore activities. The number of sites suitable for the application of OFT therefore proved to be quite limited.

In the end, the sites of Taubach and Biache-Saint-Vaast appeared to be the only sites in north-western Europe that satisfied most of the requirements for the application of the diet breadth model. This does not mean that they were wholly unproblematic. The amount of information about the bone assemblage was not ideal, most obviously in the case of Biache-Saint-Vaast, but to a lesser degree in the case of Taubach as well. Furthermore, the amount of environmental information could be improved for both sites.

In the case of Biache-Saint-Vaast, the publication of a second monograph, which was announced in 1988, might resolve some of the issues that currently hamper the application of OFT to the site. With regard to Taubach, some of the information needed is now lost forever, since bones have been destroyed or lost and the stratigraphic provenance of the old collections may be hard to reconstruct. If the location of the supposed *Knochensand* can be ascertained, the application of radiometric dating methods may at least resolve the issues surrounding the date of the assemblage. With a solution to this problem, the certainty with which the environment can be reconstructed increases. Some of the information needed for Taubach may yet be gained. Further studies may clarify exactly how many narrow-nosed rhinoceros (*Dicerorhinus hemitoechus*) bones are present in the rhinoceros sample and how many aurochs (*Bos primigenius*) bones are included in the bison sample.

8.5 Application of OFT to Biache-Saint-Vaast and Taubach

The analysis of Biache-Saint-Vaast and Taubach has shown that applying the principles from the diet breadth model on archaeological assemblages is a valuable approach in order to interpret excavated bone assemblages. On the other hand, it is abundantly clear that the ranking that was used, based on the weight of the animals represented, does not in itself fully explain the set of species that was exploited. In some cases a high handling cost could be used to explain the patterns, but for some species the fact that they were apparently left unexploited cannot be explained satisfactorily using the diet breadth model.

As argued in chapter 4, using a ranking based on caloric values, or in this case animal body weights as a proxy of caloric value, the diet breadth model predicts that the heaviest species present in the environment would be exploited. Because of the fact that they are usually present in quite low population densities, it would predict that several species would be exploited on encounter in order to ensure a high enough encounter rate to guarantee a steady food supply. As shown in the previous chapters, these predictions have been proven to be correct. Diet breadth at both analysed Neanderthal sites proved to be narrow. Moreover, the species that were exploited consisted of very heavy species, with one notable exception, namely the beaver exploited at Taubach.

However, some exceptions to the predictions are also obvious. At both analysed Middle Palaeolithic sites, the most highly ranked species, straight-tusked elephant (*Palaeoloxodon antiquus*) was not or only rarely exploited. On the other hand, since this was by far the heaviest species present in the environment, the encounter rate for this species was low. Therefore, the poor representation of this species at sites does not necessarily mean that it was not exploited on encounter, but might signal that is was simply not encountered very often. However, if we use the reconstructed population densities and compare the projected densities of elephants with the projected densities of the rhinoceros species, the proboscidean population density is about half as high as that of rhinoceros. Since rhinoceros were heavily exploited at both analysed Palaeolithic sites, it is proposed that if exploiting elephants was an important activity of the occupants of both Biache-Saint-Vaast and Taubach, it would have left a more visible signature.

In the case of elephants, invoking handling cost does seem reasonable. As predators usually hunt species of up to about twice their own size (*e.g.* Owen-Smith and Mills 2008), hunting a species about 80 times as heavy as themselves may have simply been too dangerous for Neanderthals. This problem is exacerbated by the fact that the smaller females and young, the categories that one might overcome more easily than adult males, live in herds, making their exploitation potentially even more difficult than that of lone males.

Another large species that was not exploited at either site is giant deer (*Megaloceros giganteus*). The average weight of this species and thus its rank is hard to ascertain, with estimates ranging from 388 to 700 kilo's (Brook and Bowman 2004, Pushkina and Raia 2008). A weight of 450 kg. as posited by Louguet-Lefebvre (2005) seems reasonable though. If this estimate is correct, the only species that weighs less but is regularly exploited is brown bear (*Ursus arctos*). It seems therefore that this species is close to the lower limit of species that would be exploited by the occupants of Biache-Saint-Vaast and Taubach. On the other hand, at Biache-Saint-Vaast smaller species are said to have been exploited at least occasionally. At Taubach, red deer (*Cervus elaphus*) bones and possibly a horse bone (*Equus taubachensis*) have been cut-marked; if these smaller species were exploited ephemerally, it is hard to understand why this kind of exploitation would not have focused on the larger giant deer. An alternative explanation may be that distinguishing between remains of giant deer and large specimens of red deer can be difficult. Therefore, the amount of red deer may be overrepresented relative to giant deer.

If we assume that the poor representation of giant deer was not the result of misidentification of their remains, the explanation of their poor representation at the studied sites is not straightforward. For females and young, we may envisage high handling costs, since they presumably lived in herds, but males lived solitarily for most of the year, except during rut. It is proposed that the species was too small to form part of the optimal set at the analysed sites. The inclusion of smaller bears in the diet may be related to other factors, which will be dealt with later. Signs of occasional hunting as exhibited for red deer at Taubach are less likely to be found in this species since it was present at lower population densities. Biache-Saint-Vaast on the other hand does seem to be located in an ideal environment for this species. It would be interesting to see whether it is represented among the species showing occasional cut-marks.

Falling under the optimal set of species at both sites are Merck's rhinoceros (*Stephanorhinus kirchbergensis*) and narrow-nosed rhinoceros. Both weigh in excess of two tons and are only outranked by the proboscideans (and in cold periods by woolly rhinoceros (*Coelodonta antiquitatis*). At Biache-Saint-Vaast, narrow-nosed rhinoceros dominates, while at Taubach Merck's rhinoceros is the most abundant. As argued in the previous chapters, this difference in representation is dependent on the environmental circumstances at both sites and not on Neanderthal preferences.

Another difference in the selection of rhinoceros does seem to reflect different hominin hunting behaviour, namely the age-classes of the animals represented at the different sites. At Biache-Saint-Vaast young adult animals were preferentially targeted, while at Taubach, juveniles are the best represented age-category. The dominant age-category at Taubach, determined using stages of tooth eruption is that of individuals of about 1 year of age (Bratlund 1999, 100). At Biache-Saint-Vaast animals between 6 and 9 (see chapter 5) years of age predominate. It is thought that rhinoceros reach their largest size at about 9 years of age. The animals exploited at Biache-Saint-Vaast are thus much larger than at Taubach. They were probably harder to exploit because of their size, but also because they were older and more experienced. Since the MNI of rhinoceros at both sites is high this pattern is unlikely to be coincidental. It is proposed that the difference may lie in the fact that the hominins responsible for the accumulation of the bone assemblage at Biache-Saint-Vaast lived in open environments, with higher animal biomass densities. They therefore probably lived in larger groups and were able to more efficiently pursue and kill mature animals.

Bovids are the next highest ranked category of prey. They were also exploited at both analysed sites. At Biache-Saint-Vaast aurochs is the exploited species; it is hard to ascertain from the literature whether bison was also present. At Taubach, bison is the best represented species, but some aurochs bones have also been identified. The relative importance of bovids is very different at the sites. At Biache-Saint-Vaast, aurochs accounts for almost half of the NISP of the site. At Taubach, the importance of bovids is much less, they represent about 12% of the total NISP for the site. At both sites, adults are clearly in the majority with regard to the other age-classes. At Biache-Saint-Vaast, with an MNI of 196, 145 individuals were adults (Auguste and Patou-Mathis 1994, 22). At Taubach, the MNI is much smaller, but adults still account for more than half of the MNI (Bratlund 1999, 128). At both sites, males predominate. At Taubach, analysis of the horn cores shows that they are all derived from males, although the rest of the bone sample suggests that a small proportion of the animals represented at the site must have been female. At Biache-Saint-Vaast, the sex of 83 individuals could be determined, among which were 49 males and 34 females. This suggests that the emphasis on males was stronger at Taubach than at Biache-Saint-Vaast.

It is proposed that the hunting of adult male bovids again indicates a strategy geared toward exploiting the largest solitary species present in the environment. The emphasis on solitary species may have been less stringent at Biache-Saint-Vaast, since it is thought that the occupants at this site lived in larger social groups, thus making it more feasible to deal with animals living in herds. This might be reflected in the larger ratio of female animals at the site. It would be interesting to see whether the emphasis on males over females changes in the different layers sampled at this site. It is proposed that in more open environments, Neanderthals were able to live in larger groups, due to the fact that more secondary biomass would be available to them. Therefore in these circumstances, the hunting of animals living in herds can be predicted to have occurred more frequently.

The final important category of prey at both sites is bears. Brown bear (*Ursus arctos*) is present at both sites. Moreover, at Taubach, cave bear is present, while at Biache-Saint-Vaast its predecessor, Deninger's bear (*Ursus deningerii*) has been found. At both sites, emphasis was on the smaller brown bear. This species accounts for about 15% of the NISP at Biache-Saint-Vaast and about 35% at Taubach. Deninger's bear accounts for about 3% of the total NISP at Biache-Saint-Vaast and at least some of the bones show traces of exploitation similar to those present on brown bear bones at the site (Auguste 2003, 138). Moreover, as shown in chapter 5, its age distribution is not a natural one as it is dominated by adults. Cave bear is very rare at Taubach and does not show traces of exploitation. The near-absence of these animals at both sites is hard to explain in terms of environmental circumstances. When we look at their reconstructed population densities, it appears that cave bear was present in larger numbers than brown bear. Even when reconstructing their population density as carnivores, their population density is estimated to have been slightly lower at 0.315 individuals per km^2 instead of 0.356, which is still much higher than the population density of brown bear.[46] It has been proposed that cave bears were better suited to closed environments than to open environments. This could explain why they are rare at Biache-Saint-Vaast. The environment here was open and a competitor like brown bear might have been able to realise high population densities in this environment, marginalising the potential for cave bears to live there. We would expect the opposite pattern at Taubach, since this site was situated in a closed environment. Yet here brown bear is again dominant and there are no traces of exploitation on the cave bear remains. Therefore, the species would be more highly ranked than brown bear and would have a higher encounter rate, especially in the case of Taubach. This suggests that the lack of signs of exploitation must be explained in terms of hominin activities instead of a very low encounter rate with this species.

In this case, the interpretation is proposed to lie in the realm of handling costs. Both species of bear fall in the order of Carnivora and even though cave bears may have been largely herbivorous (but see Richards *et al.* 2008a), they were certainly equipped with dangerous attributes, like claws and canines. In addition, cave bears were about 30% larger than brown bears. For the latter species it is suggested that hunting is best carried out using a "large calibre gun" and even then multiple shots are usually required to dispatch it (Charles 1997). An even larger species may have been even harder to hunt. This may have led Neanderthals to prefer the exploitation of brown bear, which may have been less dangerous to them. Again, this problem may have been more serious in the case of Taubach when group size is thought to have been smaller. Some caution is necessary with regard to this interpretation. It is also possible that my reconstruction of their population densities is incorrect. Even though the vegetation was suitable for this species, the surroundings of the analysed sites did not provide other important aspects of their niche. It has been proposed that cave bears decline when humans compete with them for caves as living space (*e.g.* Grayson and Delpech 2003). Since the sites that are analysed are in areas devoid of caves, cave bears may simply not have found denning sites in these areas and therefore may never have been present in large numbers. Nevertheless, since both species of bear hibernate, one would expect both species to be rare if this were a problem.

The incorporation of brown bear in the diet is quite peculiar, since it weighs roughly the same as the unexploited giant deer, maybe even less. Its ranking may have been elevated for two reasons however. First, its ranking may have been higher shortly before it started hibernation, since it would have built up large energy reserves. Some ethnographically known groups considered this the only time that the species was "fit" for eating (Charles 1997, 256-257). Second, this species may have been valued for other attributes, like its fur. Cut-marks on their bones at both Biache-Saint-Vaast and Taubach indeed suggest that they were skinned.

At Biache-Saint-Vaast, bears are the second most common species in the assemblage as a whole. Strikingly, they disappear during the formation of the upper levels as has been discussed in chapter 5. Since bears are thought to be cold-tolerant species and species indicative of temperate environments like red deer are still present in the assemblages, it is thought that this cannot be explained in terms of climatic deterioration. When the climate cooled, hunting herd animals became ever more important. In this circumstance a dangerous species like brown bear, also the lowest ranked exploited species, would be the first to be dropped from the exploited set in favour of ungulates that could be "mass-collected".

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[46] The function for carnivores has a parabolic shape, resulting in higher population densities for the largest carnivores compared to medium-sized species (Silva, Brimacombe and Downing 2001).

This interpretation must also be treated with caution though. First, the bone assemblages of the upper levels are much smaller than of the lower levels and most notably of level II A. We can therefore not be certain that these levels reflect Neanderthal exploitation strategies over long periods of time. Exceptions to the normal pattern may also be reflected in these levels andwill not be "averaged out" in these smaller assemblages. Second, the bone surfaces of the D-levels are weathered; therefore traces of exploitation could not be studied. It is therefore uncertain to what extent hominins interfered with the bones.

At Taubach, one small species was regularly exploited, namely beaver (*Castor fiber*). This species is not highly ranked, weighing less than 20 kilo's on average. On the other hand, the exploitation of this species may be explained at least in part by the fact that it could be exploited very close to the site, dramatically lowering search cost. Moreover, the caloric value of this species was seasonally elevated because in autumn, beavers build up important fat reserves in their tail (Jankowska *et al.* 2005).

The rare traces of exploitation on the bones of quite small species at both sites seem problematic at first. In the original model an optimal set was defined of highly ranked species that would be exploited on encounter and all species outside this set would not be exploited upon encounter. Using the reconstructed population densities of equids and cervids it is clear that they must have been encountered much more frequently than some of the exploited species. The number of bones of these species bearing cut-marks is very small however. This indicates that they were not automatically exploited on encounter. It does show on the other hand that they were at least occasionally exploited.

This may be explained by the fact that both analysed sites represent palimpsests that were formed over long periods of time. The composition of the optimal set of species exploited by a predator may change over very short periods of time, however. Predators respond to fluctuations in the density of prey species that are highly ranked. If the most highly ranked species are present in large numbers, the diet breadth will become narrower. If the highly ranked species are rare, diet breadth will widen. The exploitation of smaller species at both sites may therefore be a reflection of responses to periods of shortage of the preferred prey.

The foregoing shows that there is a reasonable fit in terms of species exploited between the predictions made by the diet breadth model and foraging strategies practised at the analysed sites. The number of exploited species is small and the exploited species are among the largest species available with the exception of proboscideans. This suggests that using body weight as currency approximates the currency Neanderthals used in ranking the available prey species well.

There is one additional factor that may have played a role in the ranking of species at both sites. This is the value of the fur of a prey species. This is illustrated by the exploitation of brown bear at both sites and of beaver at Taubach. Brown bear is the smallest exploited species, it is about as large as giant deer, which is left unexploited. Its ranking and also that of beaver may have been boosted by the value of their fur, which is of high quality (*e.g.* Scholander *et al.* 1950). The exploitation of beaver cannot be easily explained using its weight or caloric value as currency. As argued, its search cost may have been lowered significantly for hominins occupying Taubach, thus increasing the return rate. In addition, it possessed high quality fur that again could have significantly increased return rates, when compared to the returns from exploiting its meat alone.

One argument against the importance of this factor in the ranking of species is the fact that ursids disappear from the layers in Biache-Saint-Vaast that were formed during the coldest climate. This is hard to account for. The exploitation of bears had clearly been geared towards the fur (*e.g.* Auguste 1995a, Auguste 2003), yet just when hominins would have most need for insulative furs they disappeared from the record. It is possible that the season of the last occupations was different from the season of occupation during which the other levels were accumulated. It may be that fur was either not needed (summer) or not available (winter), yet this proposition is very hard to test.

Another factor that plays an important role in the ranking of foodstuffs by both modern humans and chimpanzees is the political gain that it can bring. Meat is a valued resource and in the case of modern humans the meat of some animals is valued more than that of others. Hunting of specific species may thus have provided benefits to the hunter, increasing their return rate beyond the caloric value alone. This is another attribute that may have elevated the ranking of brown bear. Since cave bear is rare, and I expect it to have been a more prestigious prey because of its size, I assume that prestige did not play a large role in the ranking of prey species.

Both sites thus show a focus on rhinoceros, ursids and bovids. The differences in importance of the groups between the sites are difficult to account for using the diet breadth model. The original model predicts that animals that are in the optimal set will be exploited upon encounter. This would lead us to expect the species with the highest population density to be the best represented species. The representation of species at Biache-Saint-Vaast follows this expectation reasonably well.[47] This is not the case at Taubach though, where rhinoceros and brown bear are dominant over bison, which, based on its reconstructed population density, would have been expected to be more common.

An important factor that can explain this pattern is the emphasis on the males of bison at Taubach. This has been interpreted as being the result of a preference for solitary animals. Female bison live in herds, while males are either solitary or live in bachelor groups, except during the mating season. If only male bison were included in the optimal set, the population density of the individuals of the species that would be exploited on encounter would be drastically lowered when compared to the population density of the species as a whole.

The application of OFT to these sites has thus provided interesting insights in the foraging decisions that were made by the occupants of the sites. It does not provide perfect predictions or explanations of the foraging behaviours that were practised though. Its function is mostly as a starting point of analysis, especially since many of the interpretations that were put forward still need to be tested. This is the case for example with proposed differences in Neanderthal group size and their implications for foraging behaviour. All in all, the application of the diet breadth model does allow us to gain more insight into why which species were exploited.

As an additional test to see how useful the model is in interpreting past foraging strategies, it was applied to foraging by cave hyenas in Pleistocene Europe. As argued in chapter 7, Neanderthals and cave hyenas share a lot of characteristics. Moreover, although hyenas are slightly larger, the difference in size between the two is quite small. One would therefore expect both species to concentrate on prey of similar size. On the other hand, both species have left a rich record of their activities in Middle and Late Pleistocene Europe. Moreover many archaeological sites contain evidence of hyena presence, for example in the form of gnaw-marks on bones and most known hyena dens contain at least a few archaeological artefacts (*e.g.* Villa and Soressi 2000). This suggests that the species occupied different niches, since otherwise one or the other would have gone extinct. This presents an excellent opportunity to see whether interpreting bone assemblages using OFT enables us to define a niche difference between the species.

The analysis of the dens of Lunel-Viel and Camiac showed that there is considerable overlap in the species that were exploited by hyenas and hominins. At both sites, bovids are well represented. In addition, at Camiac, woolly rhinoceros is one of the best represented species. Moreover, looking at the age-distribution of the equids at Lunel-Viel, we see that a large proportion of the bones present at the site belonged to adult animals. The recent analysis of the equids of the hyena den of Fouvent shows that an even more pronounced focus on prime-aged individuals is visible there (Fernandez, Guadelli, and Fosse 2006). This suggests that cave hyenas and Neanderthals often competed for similar resources.

Some differences in their respective niches can also be pointed out, though. First, the number of species that were present in the analysed hyena dens was greater than at the archaeological sites, even though at Camiac, the total assemblage is much smaller than at Taubach, while the assemblage at Lunel-Viel is roughly similar in size to Taubach. This can be attributed in part to the fact that hyenas scavenge. Since scavenging eliminates the need to hunt the prey, the handling cost of a carcass that is encountered may be very low and this may lead to the consumption of small species that would not be hunted. Another factor that may play a role is the fact that solitary hunting expeditions by hyenas may have targeted other species than group hunting episodes. Therefore, the fact that hyenas used a greater number of strategies in order to exploit the animal biomass that was available led to a wider diet breadth. The den in most cases represents a palimpsest of the results of all these strategies and therefore contains a larger number of prey categories. A similar pattern can be observed with regard to the age-categories of the prey species that were hunted by hyenas. As pointed out, at some sites hyenas focus on prime-aged adults of certain species. This is not the case for all sites and all prey

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[47] If we take the optimal set to comprise narrow-nosed rhinoceros, aurochs and brown bear. Adding up the modeled population densities of the species yields a total population density of 0.732 individuals of animals inside the set per km^2. The proportion of aurochs in this number is about 50%, brown bear about 26% and narrow-nosed rhinoceros 24%.

species though. This may also be related to varied foraging tactics, scavenging and solitary hunting may lead to the exploitation of a larger amount of young and old individuals, while group hunts may lead to the killing of large numbers of prime-aged individuals.

The greater variation in the number of prey species and vulnerable age categories represented at hyena dens is likely to be underestimated by looking at NISP-counts. This is caused by the fact that hyenas are able to destroy bones, and the bones of smaller species and especially young individuals are more likely to have been removed from the assemblages.

When looking at the totality of hyena dens that were surveyed in chapter 7 it also appears that hyenas may have focussed on less dangerous prey categories than Neanderthals did. The sites where a focus on ursids is exhibited seem mostly to represent scavenged animals that died during hibernation. Moreover, in the rhinocerotids, the focus of exploitation seems to have been on very young animals. However, at some of their sites, carnivores are quite common, as is the case with wolves at Lunel-Viel, which is unexpected if dangerous prey was avoided. On the other hand, as mentioned before, carnivores often interact aggressively, sometimes even killing individuals of different species (Van Valkenburgh 2001). This behaviour must therefore be placed at least partly outside the foraging domain, since such aggression probably takes place for different reasons than for the direct procurement of food only. Moreover, outside of the probably scavenged bears, large carnivores are rare at the sites.

It is proposed that this difference may be caused by a difference in social structure between hyenas and Neanderthals. In hyenas, the male's role in reproduction is limited to copulation. Males play no part in provisioning of offspring. This task is carried out solely by the mother, also without assistance from relatives. The loss of a female is therefore evolutionarily damaging. The loss of a male less so, since there are usually enough males to ensure successful reproduction.

Because hunting in hominins is thought to have been a mainly male activity, especially the dangerous tasks, the death of one of the hunting party may have been more acceptable to Neanderthals than to hyenas. Of course, in the case of Neanderthals, such risky activity would only have been undertaken if the payoff was high enough. In the case of hunting bears, this latter factor shows that some prestige or privileged access to females might still be associated with hunting larger prey. As argued above, this is not in evidence however, so possibly the payoff of the selected prey in terms of calories and fur was high enough to entice Neanderthals to hunt adult bears and rhinoceroces.

The comparison with hyenas thus shows that the niche of Neanderthals and hyenas overlapped. This is also the case with contemporary predators in many areas, like the African savannah. However, important differences have also been observed. Hyenas exhibit a more variable, opportunistic kind of prey selection. This is thought to reflect the practice of quite different activities while foraging: scavenging, hunting solitarily and hunting in groups. These activities in part yielded different kinds of prey.

These differences can also be explained in terms of their social structure. Because of the strict dominance hierarchy in hyenas and the fierce competition for food, solitary foraging becomes a very productive strategy, especially for low-ranked individuals. Therefore scavenging and hunting solitarily are probably practised extensively. When the dominance hierarchy is not as strict and some form of food-sharing is in place, as is thought to be the case in Neanderthals, hunting in groups for very specific high-ranked prey may become more rewarding.

8.6 The analysis in context

The analysis of the bone assemblages of sites studied in this thesis has ignored other sources of evidence. First, we can also study the artefacts that are found and try to tie them in with our interpretations of Neanderthal foraging tactics. Second, more Middle Palaeolithic bone assemblages are known that show that the strategies deployed at Taubach and Biache-Saint-Vaast were part of a wider repertoire of subsistence strategies. This is to be expected since OFT predicts that different circumstances will have led to the adoption of different foraging strategies by Neanderthals. These sources of evidence have been discussed in chapter 3, so here it suffices to make some general points that are important to contxtualise the results of this study.

With regard to the stone tools we know that Middle Palaeolithic sites are in most cases characterised by a Mode 3 technology. The tool types at most sites are dominated by scraper types and weapons are generally considered to be rare. This view needs to be modified in some respects. First, a lot of variability exists in Middle Palaeolithic assemblages. The bandwidth of this variability is generally regarded as quite small, but this view needs revision. For example, a large number of sites is known in the Late Pleistocene where the reduction strategy is based on blade production. Second, weapons may not be as rare as often thought. For example, analysis of convergent scrapers has shown that they may have functioned as spear points of thrusted spears (Villa and Lenoir 2006). With regard to these findings it is interesting to point out that the majority of Biache-Saint-Vaast "scrapers" were apparently hafted (Beyries 1988). Moreover, we can assume that the use of wooden weapons as known from Clacton, Schöningen and Lehringen was widespread.

After the Middle Palaeolithic, "transitional industries" have been found over large areas of Europe. At least in the case of the French Châtelperronian, Neanderthal fossils have been found associated with these industries. In these assemblages artefacts have been found with dimensions that, based on ethnographic evidence, point to a use as projectile points (Shea 2006). This may indicate that in the latest phase of their existence, Neanderthals used spearthrowers.

The Middle Palaeolithic weapons, thrusted spears but also Schöningen spears that may have been thrown (*e.g.* Rieder 2003) are suitable only for "close encounter hunting". This suggests that Neanderthals must have deployed strategic behaviour, like driving animals into ambushes. First to get close enough to the prey to use their spears. Second, because ethnographic studies suggest that hunting with these types of weapons is usually practised only when animals are first put at a disadvantage (*e.g.*Binford 2007).

With regard to the osseous evidence, it is important to realise that even though proboscideans were not exploited at the sites in this study, their exploitation is not unknown from the archaeological record, as discussed in chapter 3. A number of sites is known where artefacts and proboscidean remains occur together. At many of these the manner of exploitation remains unclear, but hunting can certainly not be excluded for sites like La-Cotte-de-Saint-Brelade and Lehringen. In the context of this analysis of Taubach, the sites of Lehringen and Gröbern are very interesting. They date to the Eemian, like Taubach. Gröbern is even situated very close to Taubach, and can therefore be expected to be environmentally similar. Both these sites contain the carcass of a single old male elephant and a small collection of artefacts. At Lehringen a spear was found in association with the remains as well. For Gröbern it has been proposed that the carcass was scavenged. The spear at Lehringen suggests that here hunting may have been practised. These sites demonstrate the exploitation of elephants in contrast to Taubach. However, the fact that weakened, solitary individuals were exploited shows that this exploitation was limited to cases in which handling cost was significantly lowered. These cases therefore do not contradict the interpretation put forward in this study.

La Cotte-de-Saint-Brelade is slightly younger than Biache-Saint-Vaast, dated to a cold phase in MIS 6. Here, on two occasions a group of mammoths and woolly rhinoceros died at the base of a cliff. It has been proposed that they were driven off the cliff (Scott 1980, Scott 1986). This suggests that during cold phases in the open landscapes hominins were capable of living in large enough groups to organise this activity. This conforms to the interpretations put forward here. It suggests that when hominin groups were large enough, even mammoth fell within the range of prey that could be captured. This could only be accomplished through lowering handling costs by driving them into a natural trap. If the landscape lacked such opportunities handling cost may not have been lowered enough to allow these animals to be exploited.

Hominin involvement with bears has long been a controversial topic. Because many caves show the juxtaposition of Mousterian artefacts with bear remains, in the early 20th century a "cave bear cult" was proposed to have been practised by Neanderthals. This hypothesis came under fierce attack in the second half of the previous century. It is now thought that many ursid bones found in caves belonged to animals that died during hibernation (Auguste 2003, Pacher 2002, 244). The caves were later occupied by hominins, resulting in the co-occurrence of bones and Middle Palaeolithic artefacts. On the other hand, some sites do show unambiguous evidence for the exploitation of cave bear by Neanderthals. The most well-known example is the Grotte du Renne at Arcy-sur-Cure. At this site, layer Xc has yielded cave bear bones showing clear hominin exploitation traces (David 2002). The German site of Balver Höhle also harbours evidence for the intensive exploitation of cave bear by Neanderthals (Kindler 2008).

The exploitation of brown bear is also rare in the Middle Palaeolithic archaeological record and it must be realised that Biache-Saint-Vaast and Taubach are exceptions with regard to the large amounts of brown bear materials that were exploited at these sites. At other sites in Italy and France cut-marked bones of this species have been found though (Auguste 2003).

The largest contrast with the studied assemblages are the many sites where the focus of exploitation was clearly on medium-sized ungulates. Most of these sites are situated in cold and open environments, and the faunal assemblages are dominated by reindeer (*Rangifer tarandus*), like Salzgitter-Lebensted in Germany or equids, as at Zwoleń in Poland. These do not contradict the predictions made in this study but represent groups operating on the mammoth steppe, focussing on large groups of ungulates that were in more or less predictable locations. These herds probably formed predictable patches, whose exploitation yielded high payoffs.

On the other hand, many assemblages dominated by cervids, most importantly red deer are known, especially in more southern areas (see for an overview of French sites Grayson and Delpech 2006). Exploitation of this species was minimal at the sites analysed in this study. Moreover it was predicted that when faced with closed environments, hominins would focus on very large and solitary prey species. These sites therefore contradict the deductions arrived at in this study, since one would expect exploitation at these sites to focus on megafauna like rhinoceros or aurochs. This suggests that when faced with a more or less closed environment, some populations may have adopted a strategy in which diet breadth was widened significantly and in which a focus on medium-sized ungulates was adopted.

Some comments need to be made in relation to the patterns observed at these sites however. First, many of the assemblages dominated by cervids listed in (Grayson and Delpech 2006) also contain quite large amounts of horse (*Equus caballus*)[48] suggesting open environments. Some of these sites even contain reindeer remains, pointing to a setting in cold, possibly "Mammoth-steppic" environments.[49] These sites may therefore be grouped with sites in open areas where the focus was on herd animals whose movements were more or less predictable. Second, many of the sites are located in more southern, Mediterranean areas. In these areas, broadening the diet may have been a more suitable response, since growing seasons are longer and the density of suitable resources may have been higher (Roebroeks 2003). Here, broadening the diet may have led to more drastic decreases in search costs than in the northern sites that were analysed, which would have made this a more profitable strategy. A third point of interest is the fact that many of the sites listed by Grayson and Delpech (2006) are located in rockshelters. These may represent sites to which animal remains were transported by hominins. This may have led to an overrepresentation of the smaller species. This may also be the reason why the sites in (Grayson and Delpech 2006) contain very few remains of rhinoceros.

This suggests that the focus on the heaviest species present in the environment as supported by the sites analysed in this study was by no means universal in Neanderthals, especially in the Late Pleistocene. It may be that the strategies proposed to have been responsible for the accumulation of the analysed bone assemblages were mostly adaptive in the more northern areas. Still, isotope analysis of Neanderthals at Arcy-sur-Cure suggests that they did maintain a focus on the heavier animals (Bocherens *et al.* 2005). Therefore the results of this study should be thoroughly tested against more southerly sites in the future.

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[48] *e.g.* Canalettes 2, 3; Pech de l'Azé 4B4

[49] *e.g.* Combe-Grenal 9, 34, 35; Regourdou 3, 4; Grotte XVI C.