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**Studying Prehistoric hunting proficiency: Applying Optimal Foraging Theory to the
Middle Palaeolithic and Middle Stone Age**

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Abstract

Middle and Late Pleistocene bone assemblages have been analysed to infer hominin hunting competence. Interpretations in terms of competence are usually based on the species represented in bone assemblages, such as the presence or absence of large and dangerous species. However, the sophistication of hunting strategies is not the only factor that influences the exploitation of prey species. Before interpreting an assemblage in terms of hunting proficiency, more parsimonious explanations of prey choice must be eliminated. One important reason to focus on certain species is that they are more economic to exploit than others. To test whether the presence or absence of species can be explained by economic motives rather than by hunting proficiency, Optimal Foraging Theory is applied to Pleistocene bone assemblages. The motives that drive prey choice are studied by modelling the behavioural characteristics of species and scrutinizing which characteristics the exploited species had in common. Application to Middle Palaeolithic sites in the Eemian of Germany shows that large and dangerous species were exploited frequently, but that solitary species are better represented at some sites than species living in herds. In another case-study from the Middle Stone Age in South Africa, the most important characteristic of selected prey species

is their size. Large and dangerous species were preferred over smaller dangerous species. The better representation of large docile species can be ascribed to “common sense” and not, as has been suggested, to a lack of hunting proficiency.

Keywords: Middle Palaeolithic; Middle Stone Age; Optimal Foraging Theory; Neanderthals; Diet Breadth; Anatomically Modern Humans

1 Introduction

The competence of hominins in exploiting animal resources has been debated for several decades. Examples are discussions on differing hunting proficiency between the African Middle Stone Age (~250 – 50 ka) (MSA) and Later Stone Age (LSA) (e.g. Binford, 1984; Faith, 2008; Klein and Cruz-Urbe, 1996; 2000; Marean and Assefa, 1999) and of differences between Neanderthal and Upper Palaeolithic foraging strategies (e.g. Binford, 1985; Grayson and Delpech, 2006; Mellars, 2004; Stiner, 1994).

Changes in the composition of bone assemblages are commonly interpreted in terms of developing foraging strategies. However, this research is plagued by many distorting factors. Climatic changes, taphonomic influences, and differences in transport behaviour all influence the representation of different species in an assemblage. Using Optimal Foraging Theory (OFT), comparisons between foraging choices in different circumstances or by different hominin populations can be made. Although all distorting factors can never be completely filtered out, OFT avoids ideologically laden interpretations (cf. Roebroeks and Corbey, 2001). Hence, OFT presents an analytical tool that may be used to more objectively compare different faunal assemblages and isolate behavioural differences in the exploitation strategies represented therein. OFT has been successfully applied both ethnographically and to the archaeological record of (mostly) later periods (e.g. Bennett, 1991; Bird and Bird,

1997; Bliege Bird et al., 2001; Byers and Ugan, 2005; Cannon and Meltzer, 2004; Grayson and Delpech, 1998; Hames and Vickers, 1982; Hawkes, 1982; Jones, 2004; McGuire and Hildebrandt, 2005; Stiner and Munro, 2002; Winterhalder, 1987; 2001). This suggests that it presents a constructive approach to the study of Pleistocene foraging strategies.

The following section briefly introduces OFT and explores how it can be used in Palaeolithic archaeology. The use of OFT for understanding foraging strategies is illustrated with two case-studies: first an examination of the role of dangerous prey in the South African MSA, second an analysis of the influence of changing climates on Neanderthal foraging strategies in northwest Europe.

2 Optimal Foraging Theory

OFT is a body of theory derived from the domain of ecology. The central assumption guiding the construction of OFT models is that the evolutionary fitness of an individual is linked to its foraging success. Successful foraging strategies will therefore be evolutionarily selected for (e.g. Houston et al., 2007; Krebs et al., 1981; Perry and Pianka, 1997; Winterhalder, 1987; 2001). Observed foraging strategies are assumed optimal solutions to the problems the forager faces, shaped by natural selection (e.g. MacArthur and Pianka, 1966; Winterhalder, 1987).

OFT models predict the choices an organism would be expected to make if it were striving towards a particular goal. In many applications of OFT, the goal, or currency, is assumed to be maximisation of the amount of calories acquired while foraging (e.g. Bettinger, 1991; Winterhalder, 1987; 2001; Winterhalder and Smith, 1992; Winterhalder and Smith, 2000). However, other currencies such as minimising the amount of time spent while foraging, minimising risk incurred, maximising prestige or maximising the amount of rare nutrients gained, can also be incorporated in OFT models (e.g. Bliege Bird and Smith, 2005;

Bliege Bird et al., 2001; Ludvico et al., 1991; McGuire and Hildebrandt, 2005; Winterhalder, 1987).

To apply OFT models to archaeological situations, a number of variables need to be reconstructed. In order to minimise the number of reconstructed factors, a simple model, the diet breadth model, appears to be best suited for archaeological application (Sheehan, 2004, 170). Discussion will therefore concentrate on this model.

2.1 Diet Breadth Model

The diet breadth model predicts which resources a predator will exploit in a given environment. The model assumes that foraging strategies will be geared towards maximising the acquisition of a currency (MacArthur and Pianka, 1966). In most applications, the currency is assumed to be caloric gain. As models constructed based on this currency have shown a reasonable fit with prey choice observed in ethnographic studies (e.g. Broughton and O'Connell, 1999; Winterhalder, 1987, 319-322), this currency is used here.

The return rate, or profitability of different prey types is approximated by ranking them according to their caloric value. In terrestrial mammals, body size is generally directly related to the caloric yield of an animal (e.g. Ugan, 2005, 75). In the case-studies presented here, the different prey types are ranked by body weight.

If the currency is not caloric value, the predicted ranking will not fit the observed prey choice. In that case, alternative currencies can be investigated. An alternative currency can be detected by examining shared attributes of the exploited prey species and by scrutinising the archaeological context for the use of non-food animal products. In cold climates, for example, animals may be exploited for their fur in addition to their nutritional value (e.g. Jones, 2004).

The profitability of prey species not only depends on their body size, but also on the ease with which they can be exploited. This variable is generally called the “handling cost” in

OFT models. Reconstruction of this variable is difficult, since it is a composite of prey species' anti-predator behaviours and the predator's abilities in pursuit, capture and processing (MacArthur and Pianka, 1966). A high handling cost of species will result in a low ranking. Moreover, if an increased number of species is exploited, it is assumed that, because foragers are less specialised, overall handling cost will also increase (e.g. MacArthur and Pianka, 1966; Winterhalder, 1987).

An incorrect assessment of the handling cost of the available prey species will lead to deviations from the model's predictions; different species will be exploited. In this scenario, the fit between the species that are expected to be exploited and the species that actually were exploited may be better than when using an incorrect currency. In this case, studying the shared handling cost attributes of species that contrary to predictions were, and were not exploited, may provide information on the factors influencing prey choice.

In hominin hunting strategies, technological and behavioural developments can significantly alter the handling cost of specific prey species (e.g. Bright et al., 2002; Stiner and Kuhn, 2006; Ugan et al., 2003). Another important influence on prey handling costs is the social structure of predators. Predators operating in larger groups are able to tackle larger species of prey (e.g. Creel and Creel, 1995; Radloff and Du Toit, 2004). It can also increase the success rate of hunting (Funston et al., 2001; Holekamp et al., 1997), as when hunting herd animals, larger groups often result in more kills from a herd (Creel and Creel, 1995). In humans, group hunting is often employed to break through the defences of a herd (MacDonald, 2007), and group hunting often results in increased productivity (Kaplan et al., 2009). Some studies suggest that hunting in groups reduces the average nutritional gain made by individuals. However, group size may drastically reduce the impact of kleptoparasitism by other animals (Cooper, 1991; Waite and Field, 2007). Taking this factor into account increases the profitability for individuals to join groups (Waite and Field, 2007). In both the

MSA and the Middle Palaeolithic, the presence of hyenids and felids may have made the prevention of kleptoparasitism an important factor determining hominin foraging success.

As the hunting capabilities of hominins are the subject of investigation, handling costs were modelled using the anti-predator attributes of the prey species. If prey species with high modelled handling costs are represented at the sites under consideration, it can be assumed that the accumulators of the bone assemblages exhibited behaviour that was sophisticated enough to deal with the prey's anti-predator attributes. To approximate a prey species' handling costs, focus is on three specific attributes: prey size, danger posed by the species, and social behaviour.

The size of a species influences the difficulty of exploiting it: larger species are generally more difficult to kill. Moreover, the size of an animal will also influence the danger associated with hunting it, as larger species can do more damage. This is borne out in the fact that there is a relationship between predator size and prey size (e.g. Owen-Smith and Mills, 2008; Radloff and Du Toit, 2004; Woodward et al., 2005). Prey species that are larger than the maximum expected prey size for a mammalian predator are assumed to entail significantly higher handling cost than smaller species.

Some species are more likely to exhibit a flight response, while others readily stand to fight attackers. Moreover, some species, especially carnivores, have evolved "weapons", making them more dangerous than other species. The first case-study presented below examines fight vs. flight response, while the second focuses on the distinction between carnivores and herbivores. Both carnivores and species exhibiting a fight response likely had increased handling costs, especially to hunter-gatherers equipped with simple hunting weapons.

For the application of OFT to archaeology, it is important to realise that the order of ranking and the modelling of handling costs represent ordinal measures at best. Differences in

body sizes may be small but may entail large differences in the rank order. Therefore increases in ranking must not be mistaken for linear increases in return rates.

The total profitability of a prey species is a function of its body size and handling cost. Hunter-gatherers will preferably focus on the most profitable species available. However, large, highly ranked species are generally present in lower population densities than smaller low-ranked prey. In order to ensure a steady supply of food, the number of exploited species will be increased if highly ranked species are encountered only rarely. This lowers the time spent searching, since more suitable prey animals will be encountered. The diet breadth model thus predicts that an “Optimal Set” of species will be exploited. Which species are in the Optimal Set is determined by the overall cost of searching for and exploiting the most highly ranked species, as illustrated in Fig. 1 (Bettinger, 1991; Winterhalder, 1987; 2001).

The search cost depends on the abundance of different prey species in the environment of the occupied sites. As a relationship exists between a species' body size as well as between whether a species is a herbivore or a carnivore and population densities, the population density of different species can be approximated (Eisenberg, 1990; Silva et al., 2001; Silva et al., 1997; White et al., 2007). However, reconstructing a species' population density in this way only gives an estimate for a species living under ideal conditions. In reality, large deviations from the expected pattern can occur (Silva, et al., 1997). These approximations thus need to be combined with data on the suitability of the environment of the site for the different available prey species at the time of occupation.

When scrutinising faunal assemblages, the precise ranking of a species cannot be distilled from its relative importance in the assemblage. The diet breadth model assumes that all species in the Optimal Set will be exploited upon encounter. This means that, if high-ranked species are rare, more common, lower-ranked species in the Optimal Set will be

exploited more frequently. Therefore, the most common species in a faunal assemblage may be relatively low ranked (e.g. Madsen and Schmitt, 1998, 446). Given sufficient information on the environmental circumstances around the site and the species that were available, OFT provides a method to compare assemblages formed in different cultural periods in a standardised way.

3 Case-Study: hunting strategies in the South African Middle Stone Age

A difference in hunting proficiency between MSA and LSA people in South Africa has been proposed based on differences in faunal assemblages accumulated in both periods. The focus of the debate has been on the representation of eland (*Tragelaphus oryx*), African buffalo (*Syncerus caffer*), giant buffalo (*Pelorovis antiquus*), warthog (*Phacochoerus africanus*) and bushpig (*Potamochoerus larvatus*). In MSA assemblages, eland are relatively abundant, whereas buffalo and suids are rare. Moreover, the age profile of buffalo suggests that mostly juvenile and old individuals were exploited. In LSA assemblages, suids and buffalo are better represented and eland is uncommon. The LSA age profiles of buffalo show an emphasis on adults (e.g. Klein, 1978; Klein and Cruz-Urbe, 1996; 2000). Eland is a more docile species than buffalo and suids. This was used to suggest that MSA hunters were not as proficient as LSA hunters, and hence they avoided the more dangerous species (Klein, 1978; Klein and Cruz-Urbe, 1996; 2000; Steele, 2003).

Alternatively, the changes in the composition of faunal assemblages may be explained as the result of changes in encounter rate with prey species. During the LSA, high-ranked prey such as eland may have been rarer than in the MSA. This would lead to increases in the amount of low-ranked species that were exploited (Deacon, 1989; Faith, 2008; Marean and Assefa, 1999). As the abundance of species in bone assemblages depends on their encounter

rates, this scenario is convincing. However, it does not address the possibility of differences in hunting proficiency between the MSA and LSA.

Building on a previous study (Dusseldorp, 2010), OFT is used to test whether MSA people avoided dangerous prey because they were not proficient enough to hunt them effectively, or because the more profitable eland was more abundant. Focus is on the MSA only, because the available MSA assemblages are distributed over a large area and a long period of time. Comparing the MSA as a single entity to the LSA may therefore not be productive. More detailed information on the context of the assemblages under consideration, taphonomy, etc. can be found in Dusseldorp (2010).

3.1 Parameters of the model

Being large and docile, eland is a profitable prey species, which would be in the Optimal Set under all circumstances. The abundance of eland in assemblages can therefore not be used to study prehistoric hunting proficiency. To gauge hunting proficiency requires examining which species are included in the Optimal Set, in addition to eland. If hunting proficiency was limited, species with a low handling cost would be included in the optimal set. If handling cost was not an obstacle to a species exploitation, the largest species would be preferentially included in the Optimal Set.

The species under consideration are ranked in terms of body weight and anti-predator attributes (see table 1) (for more detailed discussion see Dusseldorp, 2010). Both species of buffalo have a high handling cost due to their large size. African buffalo is aggressive and lives in large groups; the extinct giant buffalo is expected to have had similar characteristics because it was closely related to African buffalo. Eland are large, but not aggressive and live in smaller groups than African buffalo. The suids are small and live in small groups. However, they are aggressive and have been known to severely wound dogs and leopards and

also to fatally attack humans (Estes, 1991). In all species, some males live solitarily, giving them a lower handling cost than their conspecifics living in groups. As this is the case in all species under consideration, this does not alter their ranking relative to each other. In this scenario, eland would always be the most desired prey item

The ideal population densities of the species were calculated using the formula from Silva et al. (2001, 477), with the animal weights taken from Smith et al. (2003) (see Table 1).

The equation used is:

$$\text{Log } D = 1.42 - 0.68(\text{Log } M)$$

The suids were modeled as herbivores, since no equation for omnivores is provided. Moreover, warthog is primarily vegetarian. Bushpig may on rare occasions eat insects and carrion (Skinner and Chimimba 2005).

These population densities can only be taken as an indication on how frequently a species might be encountered in suitable environmental conditions. However, eland generally live in very low population densities (e.g. Estes, 1991; Klein and Cruz-Urbe, 2000). The estimated population density is on the high end of the range of observed population densities in areas where the species is considered moderately common (<http://www.iucnredlist.org/apps/redlist/details/22055/0>). Actual eland population densities are commonly lower than would be expected on the basis of their body size. Hence, eland population density around the sites at the time of occupation was probably lower in most cases than the listed estimate. Other species would thus need to be incorporated in the Optimal Set to ensure maximum hunting returns. If handling cost was an obstacle for MSA hunter-gatherers, suids would be preferred over buffalo. If handling cost was not an obstacle, buffalo should be expected over suids because of their much larger size.

The species under consideration have different environmental requirements. Eland are grazers that prefer open environments. They can go without water as long as succulent

foliage is available (Skinner and Chimimba, 2005). African buffalo are grazers too, but need access to shade and water to survive and are therefore found in less arid and more closed environments than eland (Skinner and Chimimba, 2005). Warthog are found in a wide range of environments, from open woodlands to grasslands, but are not present in densely forested areas and very arid areas (Skinner and Chimimba, 2005). Bushpig are only found in densely forested areas with a perennial supply of water (Skinner and Chimimba, 2005). Giant buffalo are extinct, so no detailed information on their environmental requirements is available. However, their fossil distribution suggests that they were more adapted to open environments than African buffalo (Klein, 1994). Differences in the suitability of the habitat for the species under consideration influence the population densities of the species and hence the encounter rates. For instance, in areas suitable for bushpig, eland population densities will be much lower than estimated based on body weight, because the habitat is not very suitable for the species. This complicates the analysis.

3.2 Application of the model

An overview of the relative importance of Eland, buffalo and suids in MSA bone assemblages from South Africa was compiled, and Fig. 2 shows their location (Dusseldorp, 2010). In Table 2, the assemblages, their dating and the relative importance of the species under consideration are listed. The relative importance of the groups under consideration is illustrated in Figs. 3 and 4. Not all five species are present at all sites. However, the presence of one species of buffalo and one species of suid are sufficient to gauge whether buffalo were preferred over suids or vice versa.

At the easternmost sites, Border Cave and Sibudu, suids are most common, followed by buffalo, while eland is rare. The lowveld environment here was characterised by dense forested conditions along watercourses and woodland savannah away from the watercourses.

Eland are historically rare in the lowveld habitats of this area (Clark and Plug, 2008; Klein, 1977). Therefore the poor representation of this species in the faunal assemblages is to be expected. Suids are expected to be present in higher population densities than buffalo due to their smaller body size (table 1). The fact that buffalo were present in all assemblages suggests that they were included in the Optimal Set. The importance of buffalo in some assemblages, combined with the lower expected population density of these species than suids, suggests that they were not avoided but that the differences in their representation relative to suids were due to different encounter rates.

At Klasies River, Suids are rare or absent, while eland and buffalo are present in all assemblages. This suggests that eland and buffalo were in the Optimal Set at all times, while suids were probably added in situations where encounter rates with larger species were low.

Suids are absent from the westernmost sites under consideration: Blombos, Die Kelders, Diepkloof Rockshelter and Ysterfontein. Plug and Badenhorst (2001) compiled an inventory of the presence of animal species in South African over the past 30 ka. They show that both species have been found to the west of Klasies River, the westernmost site in this study at which they are present. Moreover, suids are present at Sea Harvest, a hyena den close to Diepkloof Rockshelter and Ysterfontein, thought to date between 130 and 40 ka (Klein, 1983). Therefore, suids may have been present around these four sites at the time of occupation. However, due to the poor dating of Sea Harvest and the paucity of other occurrences, this is not certain.

The conclusions that can be drawn from this analysis are hampered by some problems. The comparability of the different faunal assemblages is influenced by the fact that for some only Minimum Number of Individuals (MNI) and for others only Number of Identified Specimens (NISP) data are available. Better data on the abundance of the species under consideration at the time of occupation, especially of the sites in the western part of

South Africa would strengthen the conclusions. Moreover, the correlation of high-resolution climatic records with archaeological deposits is problematic (cf. Chase, 2010), impacting the understanding of species abundance at the time of occupation of sites. However, the available data suggest that buffalo were preferred over suids during the South African MSA.

With regard to age classes, information is not available for all sites and all species. Buffalo appear to be represented mainly by juvenile and aged individuals at Border Cave, Klasies River and Die Kelders. At Klasies River and Die Kelders, eland are represented mainly by adult individuals while at Border Cave the sample is too small to draw conclusions (Klein, 1976; 1977; Klein and Cruz-Urbe, 2000). This suggests that MSA hunters preferred to focus on buffalo individuals with a relatively low handling cost. At Sibudu, age information is only available for bovid size classes. In the largest size classes (encompassing both eland and buffalo), juveniles and aged individuals are represented in much smaller numbers than adult individuals. As buffalo are more common than eland in the HP and post-HP MSA 1 (Clark, 2009, 188), it appears that here adult buffalo were exploited regularly. In suids, aged individuals are absent in the post HP MSA assemblages and uncommon in the HP assemblage. Juveniles are uncommon in the HP and post HP MSA 2 assemblage, accounting for less than 10% of the sample. However, in the post HP MSA 1 assemblage the proportion of juvenile suids is 25% (Clark, 2009). On the whole, the Sibudu assemblages thus appear to be dominated by adult individuals to a larger degree than other analysed MSA assemblages.

At a number of sites, such as Klasies River, eland is much better represented than would be expected based on their population densities. This suggests that MSA hunters were familiar enough with their behaviour to successfully plan their encounters with this species. In addition to eland, at least one species of buffalo is present in most assemblages. This indicates that buffalo were regularly exploited. Suids are only represented in the more eastern assemblages. This area may have been more forested than the west. Encounter rates with

eland would have been low, and suids were added to the optimal set. Due to the relatively variable habitat preferences of (especially) warthog, their absence in the western bone assemblages cannot be dismissed out of hand to reflect their absence in the environment. Their recorded presence at archaeological and palaeontological occurrences in the modern Western Cape province suggests that their absence is at least partly a reflection of MSA prey choice.

It is important to realise that using the relationship between predator body size and prey body size, a non-human carnivore of similar size to modern human hunter-gatherers would not be expected to hunt species over 225 kg. The equation used is $\log(\text{prey body mass}) = 1.46(\log \text{ predator body mass}) - 0.17$. Modern human body mass was estimated at 53.3 kg following Sorensen and Leonard (2001). Although described as docile, eland is double this size and must have been a formidable prey species to hunt for MSA hunter-gatherers. The fact that the larger buffalo and giant buffalo were also regularly exploited suggests that MSA people were very capable hunter-gatherers.

4 Case study: Neanderthal responses to climate change

It is nowadays generally accepted that Neanderthals and their immediate forebears were capable hunters. This is illustrated by sites such as Schöningen, where a number of wooden spears were found with the remains of about 20 butchered horses (Thieme, 1997; Voormolen, 2008). Later sites such as Salzgitter-Lebenstedt, Wallertheim, Mauran and La Borde have shown that Neanderthals accumulated numerous bone assemblages where exploitation was focussed on prime-age individuals of a single species (Farizy et al., 1994; Gaudzinski, 1995; Gaudzinski and Roebroeks, 2000; Jaubert et al., 1990).

Although a number of bone assemblages show that Neanderthals were proficient hunters, debate about the degree of sophistication of their foraging strategies still continues. It

is currently debated whether Neanderthals were able to adapt to the same range of climatic circumstances as modern humans (e.g. Finlayson, 2004, 133; Gamble, 1999, 230-231). It has been proposed that Neanderthals were unable to cope with the very unstable climate of MIS 3 (e.g. d'Errico and Sánchez Goñi, 2003; Stewart, 2005). Furthermore, it has been suggested that they could not survive in the densely forested environments that characterised much of Europe during the Eemian interglacial (e.g. Gamble, 1992; 1999). Also, there is debate over whether Neanderthal exploitation of their territories was more opportunistic than that of modern humans, who may have taken a more planned approach (e.g. Daujeard and Moncel, 2010). Here, Neanderthal bone assemblages from full interglacial, cold-temperate and initial glacial circumstances in Northwest Europe are compared to gauge the degree to which Neanderthals could change their foraging strategies to fit these widely differing circumstances. The focus is on northwest Europe because the influence of climatic changes during the Middle and Late Pleistocene. Neanderthals were repeatedly confronted with severe glacial conditions, proposed to have led to their occasional local extinction (Hublin and Roebroeks, 2009), while at the other end of the scale they were confronted with circumstances warmer than today, which may also have led to local extinction.

OFT provides a methodology to meaningfully compare bone assemblages deposited under different climatic circumstances. Simply comparing the species represented in different environments may not be informative, as there would be important differences between the available prey species. Using OFT to model the changes in encounter rate with different species and differences in handling cost combined with predictions based on optimisation will allow evaluation of how competently Neanderthals adapted to different environments.

Unfortunately, not many sites fulfil all conditions for a successful application of OFT. Sites such as Wallertheim and Salzgitter-Lebenstedt contain bone assemblages dominated by a single species (Gaudzinski, 1995; Gaudzinski and Roebroeks, 2000). These sites can only

inform on one specific activity that was practised and not on the full suite of prey species that was exploited by Neanderthals. For other bone assemblages, the relation between the faunal remains and hominin activities is ambiguous; often tools are found with the remains of “background fauna” that may have died a natural death (e.g. Gaudzinski and Turner, 1996). At sites like Scladina and Vogelherd, Neanderthals were not the only species accumulating bones, but carnivores also contributed to the assemblages (Niven, 2007; Patou-Mathis and Bocherens, 1998).

Here, the focus is on two sites from northwest Europe (Fig. 5), Biache-Saint-Vaast in northern France, dated to the transition of MIS 7-6 (Tuffreau and Sommé, 1988), and Taubach in central Germany, dated to the Eemian interglacial (MIS 5e) (Bratlund, 1999). The occupation sequence at Biache-Saint-Vaast covers the transition from temperate, but open environmental circumstances to cold steppic climates. Taubach allows documentation of Neanderthal subsistence behaviours in forested environments during the Eemian. Both sites were probably accumulated over a considerable period of time (Auguste, 1995; Bratlund, 1999). This is advantageous for the application of OFT, since short-term fluctuations in encounter rate are averaged out, permitting study of the long-term incarnation of Neanderthal adaptation to the environment (for an in depth discussion of the study background, see Dusseldorp, 2009).

4.1 Biache-Saint-Vaast

The site of Biache-Saint-Vaast (Pas-de-Calais, France) was excavated between 1976 and 1982 (Tuffreau, 1988). The site yielded a number of stratigraphic levels, containing rich stone artefact assemblages and bone assemblages. The analysed bone assemblages are from levels IIA, Iibase, D1 and D (Auguste, 1988a, 1988b, 1992, 1993, 1995; Louguet-Lefebvre, 2005). Level IIA is a very rich assemblage (NISP=18321), while the other assemblages are

significantly smaller (level IIbase NISP=514; D1 NISP=85; D NISP=105) (Louguet-Lefebvre, 2005). Levels IIA and II base appear to have been deposited during the end of MIS 7, during conditions that were relatively temperate, yet colder than today. Levels D1 and D were deposited during the early part of the Saalian (MIS 6) (see papers in Tuffreau and Sommé, 1988)

Some methodological problems are associated with the bone assemblages. For the main assemblage, the exact numbers of species that were present in small numbers are not published. However, the assemblage accounts for 89% of the total determined NISP from the site, while the species present in small numbers account for only 4% of the total NISP of the II A assemblage (Fig. 6) (Auguste, 1993, 1995, 2003; Louguet-Lefebvre, 2005). Therefore, the initial focus is on the data from the site as a whole which, due to the numerical dominance of the assemblage from level IIA reflect the foraging strategies practised during the accumulation of this level. The developments from this that can be observed in the assemblages from level II base, D1 and D can then be considered.

The bone assemblages of the lower levels were indubitably accumulated by humans. Cut-marks are common on the bones, while signs of carnivore influence are rare. The age-profiles rule out catastrophic mortality (Auguste, 1995, 157-158). In levels D1 and D the bones are not as well preserved as in the preceding levels, obscuring cut-marks. However, the spatial configuration of stone tools and faunal remains is highly suggestive of accumulation of the bones by hominins (Auguste, 1988b; Marcy and Tuffreau, 1988a, b).

The bone assemblage from the site as a whole (fig. 6) is dominated by aurochs (*Bos primigenius*), brown bear (*Ursus arctos*) and narrow-nosed rhinoceros (*Dicerorhinus hemitoechus*) (Auguste, 1993, 1995). In all three species, adult individuals dominate the assemblage and juveniles and old individuals are very rare (Auguste, 1995).

Other species showing signs of hominin exploitation are represented in smaller numbers. In addition to brown bear, the larger Deninger's bear (*Ursus deningeri*) was exploited. Due to the similarity between the taxa, not all bear bones could be determined to species level. Brown bear is the better represented species, though (Auguste, 2003). Similarly, some individuals of Merck's rhinoceros (*Stephanorhinus kirchbergensis*) were present. This species of rhinoceros is slightly larger than the narrow-nosed rhinoceros. It is adapted to browsing. Not all rhinoceros bones were determinable to species level, but narrow-nosed rhinoceros was the better represented species (Louguet-Lefebvre, 2005). In both cases, only the most common species in the ranking is considered, assuming that the handling cost of Merck's rhinoceros is similar to narrow-nosed rhinoceros and that of Deninger's bear is similar to brown bear. Other species, such as cervids and equids do show some signs of exploitation. However, their importance in the bone assemblage is minor and the signs of exploitation less intensive than those on aurochs, bear and rhinoceros bones (Auguste, 1995, 162). In levels D and D1, bears are no longer present in the assemblages and smaller herbivores increase in importance (Auguste, 1988b).

Table 3 summarises the ranking, handling cost attributes and modelled population densities of the most important species under ideal circumstances. The size threshold of 300 kg was arrived at using the relationship between predator and prey body size published by Radloff and Du Toit (2004, 415). The equation used is:

$$\log(\text{prey body mass}) = 1.46(\log \text{predator body mass}) - 0.17$$

The Neanderthal body mass was estimated at 65 kg, following Sorensen and Leonard (2001). Predators with a similar body size as Neanderthals would thus be expected to prey on species no larger than 300 kg.

From the species listed in table 3, it becomes clear that in the assemblage as a whole, Neanderthals focussed on very large prey species. However, the largest species available,

straight-tusked elephant (*Palaeoloxodon antiquus*) is not intensively exploited and neither are animals smaller than brown bear.

Both bears and rhinoceros are solitary species. Aurochs live in groups; however, of the aurochs sample (MNI=83) of which the gender could be determined, 59% were male (Auguste and Patou-Mathis, 1994). In bison and feral cattle, adult males generally live solitary lives, except in the breeding season (Van Vuure, 2003). Although hunting of large species appears not to have been problematic, the occupants of the site focused on solitary animals. Even in ideal circumstances, the exploited species would be present in low population densities (table 3). The narrow diet breadth practised at the site thus suggests that the occupants were able to manage the encounter rates with the exploited species well, otherwise additional species would need to be exploited.

The assemblage of level IIbase (Fig. 7) presents a picture similar to that of the site as a whole. This level was deposited under similar circumstances as level IIA. The environment of the site appears to have been dominated by open forest (Louguet-Lefebvre, 2005; Sommé et al., 1986).

Levels D1 and D (Fig. 7) were deposited under colder circumstances. The mechanism of sedimentation of these levels changes. While the preceding levels were deposited in a regime of fluvial sedimentation, levels D1 and D are situated in windblown loess sediments. The environmental indicators in these layers suggest that they were formed during a feeble climatic optimum during MIS 6. During these occupations, the environment around the site was covered by herbaceous prairie (Munaut, 1988; Rousseau and Puissegur, 1988). Bears are not represented in the faunal assemblages. Instead of narrow-nosed and Merck's rhinoceros, rhinocerotids are represented by woolly rhinoceros (*Coelodonta antiquitatis*) (Louguet-Lefebvre, 2005). Although rhinocerotids remain an important group in the faunal

assemblages, the importance of large bovids decreases slightly in these levels and the percentage of equids and cervids is increased (Auguste, 1988a, b).

The colder circumstances have changed the prey choice of the occupants of the site dramatically, with the second most important species overall being dropped from the diet. The smaller herbivores, equids and cervids appear to become more important. This suggests that the Neanderthals occupying the site did not emphasise solitary prey anymore, but also targeted herbivores living in herds. The location of the site on a terrace on confluence of two river valleys was probably a strategic location allowing good visual control over migrating herds of herbivores.

4.2 Taubach

The site of Taubach (Thüringen, Germany) is located in a small travertine deposit. Pleistocene bones started to be found during mining activities in the 19th century. Large collections of bones were collected and dispersed over many European institutions. One of the largest collections from this site is housed at the *Forschungsstation für Quartärpaläontologie* of the *Forschungsinstitut Senckenberg* in Weimar. This collection was recently studied by Bratlund (1999), and this analysis is based on her data.

The fact that the assemblage was collected in the late 19th and early 20th centuries presents some analytical problems. It is unknown how systematic the collection was and whether some species may be over- or underrepresented. However, small species are quite well represented in the assemblage under consideration. Even some sesamoids of beaver (*Castor fiber*) are present (Bratlund, 1999).

Travertine is only formed during warm climatic intervals. The travertine at Taubach was formed during MIS 5. The combination of species found at the site, among which the European pond turtle (*Emys orbicularis*), which can only survive in climates warmer than

today at the location, suggests that the large mammal assemblage was deposited during MIS 5e (e.g. Bratlund, 1999; Mlynarski and Ullrich, 1977; Van Kolfschoten, 2002). Bratlund (1999) further suggests that the mammal assemblage was probably deposited during one of the earlier pollen phases of the Eemian. The most parsimonious interpretation is that the large mammal assemblage was deposited during pollen stage 3 of MIS 5e. This would mean that the climate was warmer than nowadays (Kühl and Litt, 2003, 210). Pollen cores from Germany suggest that deciduous trees grow in importance during pollen phase 3, with oak (*Quercus*) being dominant. Although the climax vegetation has not fully developed during this pollen phase, non-arboreal pollen are only present in very small percentages in pollen cores (e.g. Zagwijn, 1996).

Gamble (1986, 1992, 1999) has hypothesised that Neanderthals could not cope with the forested Eemian environments, because available herbivore biomass was low and dispersed. This position is supported by a paucity of sites in Western Europe securely dated to this period. However, there are compelling taphonomic arguments that can account for this scarcity (e.g. Roebroeks et al., 1992; Roebroeks and Speleers, 2002). The site of Taubach shows that Neanderthals could indeed survive in Eemian forested environments.

The composition of the faunal assemblage is illustrated in Fig. 8. The faunal spectrum resembles that of Biache-Saint-Vaast. However, at Taubach brown bear is dominant, followed by Merck's rhinoceros, bison (*Bison priscus*) and beaver. These species show significant numbers of cut-marks. Red deer is represented by over 200 specimens, but only 2 were cut-marked, while one horse bone was possibly cut-marked (Bratlund, 1999). Most of the remaining species can be assumed to have been part of the background fauna. In addition to Merck's rhinoceros, some narrow-nosed rhinoceros bones were present. In addition to bison, some aurochs bones were present. Both rhinoceros and large bovids have been lumped in the analysis (Bratlund, 1999).

Neanderthal faunal exploitation at Taubach concentrated on bear, Merck's rhinoceros, bison and to a lesser degree beaver. Of the bison sample, the horncores were examined to ascertain the sex of the animals: all were males (Bratlund, 1999). In bears and bison, the age profiles are dominated by adult individuals (Bratlund, 1999, 113, 124). However, in Merck's rhinoceros, the age profiles were dominated by young individuals, of about 1.5 years of age (Bratlund, 1999, 100).

The ranking, handling cost attributes and population densities for the species are reconstructed in table 4. Again, the focus is on very large species, although the largest species, straight-tusked elephant does not show signs of exploitation. The species is well-represented, but its size may have ensured more frequent collection of this species by miners than smaller species. In contrast to Biache-Saint-Vaast, the focus is on hunting young rhinoceros here. Moreover, the focus is exclusively on male bison, which are likely to have been solitary.

4.3 Discussion

In both the warm forested environment of Taubach and the open woodland environment of levels IIA and IIbase of Biache-Saint-Vaast, the diet breadth of Neanderthals was narrow. Neanderthals focussed the largest available animals outside proboscideans: rhinocerotids and large bovids. In addition they heavily exploited the smaller ursids. Smaller herbivores, such as equids and cervids, were only occasionally exploited. Bears and rhinoceros live alone or in small groups, suggesting a focus on solitary species, and this interpretation is reinforced by the focus on male bison at Taubach. A similar focus is seen at Biache-Saint-Vaast, but the presence of significant numbers of female aurochs suggests that herds were also targeted sometimes. The emphasis on solitary species disappears during the occupation of levels D1 and D at Biache-Saint-Vaast. Here, smaller herbivores living in herds are exploited.

A possible explanation of this pattern is that the reduced productivity of forests versus more open environments precipitated changes in Neanderthal demography. The warm environments of the Eemian and to a lesser degree late MIS 7, may have resulted in a decrease in Neanderthal group sizes due to the lower availability of animal biomass (e.g. Delpech, 1999). Moreover, in modern climates, dependence on plant foods drops significantly below 50% to the north of 40°N (Mussi, 2007). Hence, although Neanderthals did consume plant foods (Henry et al., 2011), their importance may have been small. This is supported by stable isotope analyses (Bocherens et al., 2005; Richards and Trinkaus, 2009). Moreover, ethnographically recorded return rates of plant foods are often relatively low (e.g. Bright, et al., 2002; Cordain et al., 2002). Processing of many vegetable resources entails grinding and grindstones are virtually unknown from the Middle Palaeolithic archaeological record (e.g. Kuhn and Stiner, 2006), suggesting that plant food return rates may have been lower still. Therefore, Neanderthal population densities may have decreased due to the lower productivity of the forested environments of MIS 5e.

In this situation, hunting large solitary prey may have been preferred over targeting herds of animals. To deal with herds of animals one needs to isolate individual animals, requiring larger hunting parties than when dealing with solitary animals (e.g. MacDonald, 2007, 115). This pattern is seen most clearly at Taubach, where all large bovid horncores belonged to males. Moreover, in the largest prey species, Merck's rhinoceros, hunting was focussed on subadult individuals of about 1.5 years (Bratlund, 1999). Using modern-day rhinoceros as an analogue, these individuals would likely have just left their mother and have been living alone. Focussing on these individuals, instead of adults weighing over two tonnes, may have been a way to reduce the danger associated with hunting this species. The assemblages IIA and IIBase from Biache-Saint-Vaast were deposited in the closing stages of an interglacial. The environment surrounding the site was dominated by open woodland. In

this environment, herbivore biomass was probably present in higher densities than in closed forests.

In the assemblages deposited during MIS 6, bears are no longer exploited, while cervids and equids become more important. Now animals living in groups dominate the bone assemblages. The mammoth-steppe environment was probably characterised by a high availability of herbivore biomass (e.g. Delpech, 1999). This allowed Neanderthals to live in larger groups, which may have allowed them to more efficiently target animals living in herds. Being able to target herds may have afforded them the possibility to drop brown bear from the diet. Brown bear is a very dangerous species to hunt, therefore when other foraging options to targeting solitary species were available; this was the first species to be dropped from the optimal set.

At both Taubach and Biache-Saint-Vaast, two large species are conspicuously left unexploited. The absence of the largest available species, straight-tusked elephant may be due to its very large size (being more than twice as large as the rhinoceros that are exploited). Giant deer (*Megaloceros giganteus*) is also not exploited. This species is larger than brown bear and may have been less dangerous, because it is not a carnivore. A few possible reasons for this pattern can be proposed. First, the difference between the body sizes of both species is not large. Second, brown bear contains more calories per kg of meat than most other mammals (e.g. Byers and Ugan, 2005). Third, at both Taubach and Biache-Saint-Vaast, bears were exploited for their fur. If the procurement of fur also played a role in foraging decisions, brown bear may have been more highly ranked than giant deer. A further argument is dependent on the season of hunting; if occupation of the sites took place in autumn, brown bear would be building up fat reserves to prepare for hibernation. In that case, the ranking of the species would be increased.

Only a small number of Eemian sites is known. In Germany, two sites with a single elephant carcass and a small number of stone tools are known. In both cases the elephants were aged males; at one of the sites, Gröbern, the animal was diseased and may have been scavenged. At Lehringen, a wooden spear was found with the carcass. Another site is known with a single aurochs skeleton and some small tools (Gaudzinski, 2004). These sites corroborate a focus on solitary species. They do not confirm the pattern with regard to the avoidance of elephant. However, in both cases, the fact that the individuals were old and in one case diseased, may have sufficiently lowered their handling cost.

At Scladina Cave, the remains of a number of Chamois (*Rupicapra Rupicapra*) that were hunted by Neanderthals were found (Patou-Mathis, 1998). Chamois females and juveniles live in herds. At Scladina, juveniles and old individuals are represented, but no prime-aged animals (Patou-Mathis, 1998, 300). Therefore, here Neanderthals did sometimes hunt animals living in herds. However they focussed on weaker individuals. In addition, although the level was originally assigned an Eemian age, it has been suggested that it actually dates to MIS 5a (Van Kolfschoten, 2000, 277). If the level dates to MIS 5a, the environment will have not have been covered in a dense interglacial forest, making herbivore biomass more abundant. Excavations at the Eemian sites of Neumark-Nord in Germany (Hublin and Roebroeks, 2009, 504) and Caours in northern France (Antoine et al., 2006) will add to the knowledge of Neanderthal interglacial foraging strategies in the near future.

During cold periods, Neanderthals appear to have specialised in intercepting herds of herbivores at a large number of sites. Large bovids were systematically exploited at a number of sites (e.g. Gaudzinski, 1996). In still colder episodes they also focussed intensively on horses and especially reindeer at a large number of sites (e.g. Costamagno et al., 2006; Gaudzinski and Roebroeks, 2000; Grayson and Delpech, 2006). The importance of cervids and equids during the later phases of occupation at Biache-Saint-Vaast fits in this pattern.

The colder environments supported larger populations of herbivores and this allowed Neanderthals to live in larger social groups. These groups could apparently efficiently deal with herds of herbivores.

5 Discussion and Conclusion

The application of OFT to prehistoric foraging strategies helps to evaluate bone assemblages accumulated in different periods without applying double standards to interpretations (cf. Roebroeks and Corbey, 2001). Moreover, it allows a comparison in meaningful terms of bone assemblages deposited under very different environmental circumstances.

Unfortunately, some problems are associated with the application of OFT. First, the search cost is very difficult to model, since data on the prehistoric abundance of prey species is difficult to acquire. Using changes in a species' abundance from the archaeological sites themselves as indications for their changing abundance is fraught with problems since differences in a species' abundance at a site can also be due to changes in hominin behaviour. Looking at the abundance of species in natural death assemblage may provide a solution. However, since the error margin associated with radiometric dates for the Middle Palaeolithic and Middle Stone Age is often in the order of several millennia, contemporaneity of natural bone assemblages and archaeological assemblages is difficult to establish. Due to the very unstable climate during most of the Pleistocene, small temporal differences could have entailed dramatic changes in the abundance of the available prey species. The population densities of the available species are modelled based on the global relationship between body size and population density. This approach has its own problems. Although the relationship between body size and prey size is significant in mammals, large deviations from the pattern

have been observed. Moreover, in marginal environments, many species will not attain the same population densities as in their ideal habitat.

Pleistocene environments are often characterised as non-analogous to modern-day environments (e.g. Markova et al., 2010; Stewart and Lister, 2001). Therefore, the suitability of the environment to the available prey species is difficult to model. In addition, multiple species are extinct, further complicating reconstructions of population densities.

Reconstructing both rankings and population densities is also complicated because estimations for body mass of Pleistocene species in some cases diverge by large amounts. Using different published estimates may result in different rankings and different modelled population densities (see discussion in Dusseldorp, 2009).

Reconstructing handling costs of potential prey species is also a difficult proposition. Simple proxies are used to model the anti-predator behaviour that might influence a species' handling cost. However, hominin technology and behaviour also influences the handling cost. Looking at changes in prey species attributes and seeing if these changes coincide with changes in technology is an avenue of research that may shed light on this. Another factor that can in some cases be reconstructed is group size: increasing the size of hunting parties can significantly lower handling costs. However, improvements in tracking skills, improvements in coordination of hunting activities due to evolving linguistic skills and a host of other behaviours are not easily traceable in the archaeological record. Their influence on development of foraging strategies is more difficult to detect.

As hunter-gatherers are residentially mobile, studying single sites will not give insight in the full foraging spectrum. The selection of time-averaged assemblages negates this problem at least partly. However, different species may have been exploited in different areas of the territory of hominin groups and not be represented at the analysed sites. Therefore comparing several contemporaneous sites in a microregion would be a promising approach.

Unfortunately, for the MSA and Middle Palaeolithic, the resolution of the archaeological record does not allow identification of sites that definitely functioned within the same system.

Finally, the use of NISP or MNI may influence the results of the analysis. Transport differential processing and transport of different animal classes leads to differential representation of the species. It has been argued that using NISP and MNI generally yields similar results (Clark and Plug, 2008; Grayson and Frey, 2004). However, large differences between analyses based on MNI and NISP can occur (e.g. Dusseldorp, in press). This can have important repercussions in terms of species representation. Hence, in terms of NISP small species may be overrepresented in assemblages (e.g. Lyman, 1994, 111). However, using MNI can lead to an overrepresentation of rare species. Moreover, calculating the MNI presents methodological problems, and it has been suggested that it cannot be used to estimate the relative abundance of species (Lyman, 2008; Plug and Plug, 1990). Ideally, when information on both indices is available, comparing the two may provide information on differential processing and transport of different species. In the MSA case-study, at Sibudu, this is illustrated by the importance of suids during the HP phase, which are much more important in terms of NISP than in terms of MNI, suggesting that they were transported more complete to the site than eland and buffalo (see also Dusseldorp, 2010; in press). The representation of buffalo and eland relative to each other will probably not be distorted to a large degree, since the species are of comparable size and processing and transport economics will have been similar for them.

The case studies that were presented here have shown how the application of OFT can produce important insights in hominin faunal exploitation strategies. Examining fauna from the MSA of South Africa shows that the danger associated with hunting buffalo did not preclude their exploitation. The emphasis that was placed on hunting large buffalo could be evaluated better if more detailed data on the abundance of suids in the western part of the

study area were available. However, based on the reviewed assemblages, the conclusion is inescapable that MSA hunters were capable of dealing with dangerous prey. The differences in age-structure between MSA and LSA assemblages show that hunting strategies were not identical in both periods. However, the presence of juvenile buffalo in the assemblages demonstrates that MSA hunter-gatherers could and did target herds of buffalo.

The case-study on Middle-Palaeolithic bone assemblages suggests that using OFT to document changes in foraging behaviour through time can lead to insights in hominin palaeodemography. More sites should be studied in order to test the ideas set forth here. Fortunately, at least two interglacial sites are currently being excavated in northwest Europe, which will provide a valuable addition to knowledge about Neanderthal survival in the Eemian.

In colder periods a large number of sites showing specialised exploitation of a single species are known from the Middle Palaeolithic. The study of more sites presenting a succession of bone assemblages deposited under differing climatic conditions, as well as sites located in different biozones, i.e. in more southern regions, can add to knowledge on the full flexibility of Neanderthal faunal exploitation strategies.

One of the themes dominating research into the MSA and Middle Palaeolithic is the search for differences from what is termed “modern behaviour”. By analysing assemblages from a purely economic angle, OFT allows initial examination of the more obvious null-hypothesis, namely that prey species were selected mainly for economic reasons. However, comparison of the handling cost attributes that prey species have in common do allow insight in the strengths and weaknesses of specific foraging methods. The focus on solitary species at Taubach and Biache-Saint-Vaast suggests that the Neanderthals that produced these bone assemblages preferentially targeted solitary animals. The emphasis on juvenile Merck’s rhinoceros at Taubach, and juvenile and aged buffalo and during the MSA, respectively,

suggests that the hunter-gatherers tried to reduce the danger associated with exploiting these species. Examining more assemblages to see under which circumstances these strategies are adopted will address how economic motives and prehistoric hunting competence interacted to produce the bone assemblages that are excavated.

The data presented here cannot be used to say much about the capability of Neanderthals to exploit aquatic species and small-fast moving prey. This is a development which has been associated mainly with modern humans (e.g. Stiner et al., 1999, 2000). The exploitation of these animals is often less profitable and when available, larger, higher-ranked prey is expected to be preferred. At the Middle Palaeolithic sites discussed here, outside beaver, which was probably exploited at least in part for its fur (Bratlund, 1999), small animals and aquatic resources are not represented. In the future, studying assemblages from circumstances where high-ranked prey is rare or absent could illuminate, if, under similar circumstances, Neanderthals did not exploit these resources to a similar degree as modern humans did.

Finally, Neanderthals and anatomically modern humans had differing energetic requirements and were anatomically different. Neanderthal energetic requirements were significantly higher than those of modern humans. This resulted in their needing to realise very high return rates from foraging (Snodgrass and Leonard, 2009). Decreases in environmental productivity will therefore have had more severe demographic impacts on Neanderthals than on modern humans. Moreover, Neanderthals had shorter lower limbs than modern humans, increasing their cost of locomotion (Weaver and Steudel-Numbers, 2005). This would increase the handling cost of resources, since moving from the camp to exploit them and transporting resources back to camp would be energetically costly compared to the modern human situation. This would lead to a smaller foraging radius around a camp (e.g. MacDonald et al., 2009). This may have influenced the viability of exploiting specific resources. For instance, high-technological investment in remote capture devices for small, fast-moving or aquatic prey (cf. Ugan, et al., 2003), may be less rewarding for Neanderthals

than modern humans because of their higher residential mobility. Technology that is difficult to transport could be used for shorter periods by Neanderthals, making the circumstances under which the investment could be recouped rarer. Comparing foraging decisions between modern humans and Neanderthals needs to take these factors into account. However, due to the focus on a limited number of animal species of the presented MSA case study and the very different environmental circumstances a meaningful comparison is beyond the scope of the current study.

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References

- Antoine, P., Limondin-Lozouet, N., Auguste, P., Loch, J.-L., Galheb, B., Reyss, J.-L., Escude, E., Carbonel, P., Mercier, N., Bahain, J.-J., Falgueres, C. and Voinchet, P., 2006. Le tuf de Caours (Somme, France): Mise en évidence d'une séquence Eemienne et d'un site Paléolithique associé. *Quaternaire* 17, 281-320.
- Auguste, P., 1988a. Apports paléontologiques et archéozoologiques de l'étude de la faune des grands mammifères de Biache-Saint-Vaast (Pas-de-Calais). *Revue Archéologique de Picardie*, 63-68.

- Auguste, P., 1988b. Etude des restes osseux des grands mammifères des niveaux D, D1, II base. In: A. Tuffreau and J. Sommé (Eds.), *Le gisement Paléolithique Moyen de Biache-Saint-Vaast (Pas-de-Calais) Volume I. Paquez et fils, Chalons-sur-Marne*, pp. 133-169.
- Auguste, P., 1992. Étude archéozoologique des grands mammifères du site pleistocène moyen de Biache-Saint-Vaast (Pas-De-Calais, France): Apports biostratigraphiques et palethnographiques. *L'Anthropologie* 96, 49-70.
- Auguste, P., 1993. Acquisition et exploitation du gibier au Paléolithique moyen dans le nord de la France. Perspectives paléo-écologiques et palethnographiques. In: J. Desse and F. Audoin-Rouzeau (Eds.), *Exploitation des animaux sauvages à travers le temps. APDCA, Juan-les-Pins*, pp. 49-62.
- Auguste, P., 1995. Chasse et charognage au Paléolithique moyen: L'apport du gisement de Biache-Saint-Vaast (Pas-de-Calais). *Bulletin de la Société Préhistorique Française* 92, 155-167.
- Auguste, P., 2003. La chasse à l'ours au Paléolithique moyen: Mythes, réalités et état de la question. In: M. Pathou-Mathis and H. Bocherens (Eds.), *Le rôle de l'environnement dans les comportements des chasseurs-cueilleurs préhistoriques. Archeopress, Oxford*, pp. 135-142.
- Auguste, P. and Patou-Mathis, M., 1994. L'aurochs au Paléolithique. Aurochs, le retour, Aurochs, vaches & autres bovins de la préhistoire à nos jours *Centre Jurassien du patrimoine, Lons le Saunier*, pp. 13-26.
- Bennett, I.M., 1991. Barí Loricarid collection and the value of information: An application of the optimal foraging theory. *Human ecology* 19, 517-527.
- Bettinger, R.L., 1991. *Hunter-Gatherers, Archaeological and evolutionary theory*. Plenum Press, New York/London.
- Binford, L.R., 1984. *Faunal remains from Klasies River Mouth*. Academic Press, New York.
- Binford, L.R., 1985. Human ancestors: Changing views of their behavior. *Journal of Anthropological Archaeology* 4, 292-327.

- Bird, D.W. and Bird, R.L.B., 1997. Contemporary shellfish gathering strategies among the Meriam of the Torres Strait Islands: Testing predictions of a central place foraging model. *Journal of Archaeological Science* 24, 39-63.
- Bliege Bird, R. and Smith, E.A., 2005. Signaling theory, strategic interaction and symbolic capital. *Current Anthropology* 46, 221-248.
- Bliege Bird, R., Smith, E.A. and Bird, D.W., 2001. The hunting handicap: Costly signaling in human foraging strategies. *Behavioural Ecology and Sociobiology* 50, 9-19.
- Bocherens, H., Drucker, D.G., Biliou, D., Pathou-Mathis, M. and Vandermeersch, B., 2005. Isotopic evidence for the diet and subsistence pattern of the Saint-Césaire Neanderthal: Review and use of a multi-source mixing model. *Journal of Human Evolution* 49, 71-87.
- Bratlund, B., 1999. Taubach revisited. *Jahrbuch des Römisch-Germanischen Zentralmuseums* 46, 61-174.
- Bright, J., Ugan, A. and Hunsaker, L., 2002. The effect of handling time on subsistence technology. *World Archaeology* 34, 164-181.
- Brook, B.W. and Bowman, D.M.J.S., 2004. The uncertain blitzkrieg of Pleistocene megafauna. *Journal of Biogeography* 31, 517-523.
- Broughton, J.M. and O'Connell, J.F., 1999. On Evolutionary Ecology, Selectionist Archaeology, and Behavioral Archaeology. *American Antiquity* 64, 153-165.
- Byers, D.A. and Ugan, A., 2005. Should we expect large game specialization in the late Pleistocene? An optimal foraging perspective on early Paleoindian prey choice. *Journal of Archaeological Science* 32, 1624-1640.
- Cannon, M.D. and Meltzer, D.J., 2004. Early paleoindian foraging: Explaining the faunal evidence for large mammal specialization and regional variability in prey choice. *Quaternary Science Reviews* 23, 1955-1987.
- Chase, B.M., 2010. South African palaeoenvironments during marine oxygen isotope stage 4: A context for the Howiesons Poort and Still Bay industries. *Journal of Archaeological Science* 37, 1359-1366.

- Clark, J.L., 2009. Testing models on the emergence and nature of modern human behavior: Middle Stone Age fauna from Sibudu Cave (South Africa), Ph.D-thesis. University of Michigan.
- Clark, J.L. and Plug, I., 2008. Animal exploitation strategies during the South African Middle Stone Age: Howiesons Poort and post-Howiesons Poort fauna from Sibudu Cave. *Journal of Human Evolution* 54, 886-898.
- Cooper, S.M., 1991. Optimal hunting group size: The need for lions to defend their kills against spotted hyenas. *African Journal of Ecology* 29, 130-136.
- Cordain, L., Eaton, S.B., Miller, J.B. and Hill, K., 2002. The paradoxical nature of hunter-gatherer diets: Meat-based, yet non-atherogenic. *European Journal of Clinical Nutrition* 56, S42-S52.
- Costamagno, S., Meignen, L., Beauval, C., Vandermeersch, B. and Maureille, B., 2006. Les Pradelles (Marillac-de-Franc, France): A Mousterian reindeer hunting camp? *Journal of Anthropological Archaeology* 25, 466-484.
- Creel, S. and Creel, N.M., 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour* 50, 1325-1339.
- d'Errico, F. and Sánchez Goñi, M.F., 2003. Neanderthal extinction and the millennial scale climatic variability of OIS 3. *Quaternary Science Reviews* 22, 769-788.
- Daujeard, C. and Moncel, M.-H., 2010. On Neanderthal subsistence strategies and land use: A regional focus on the Rhone Valley area in southeastern France. *Journal of Anthropological Archaeology* 29, 368-391.
- Deacon, H.J., 1989. Late Pleistocene palaeoecology and archaeology in the southern Cape, South Africa. In: P. Mellars and C. Stringer (Eds.), *The human revolution: Behavioural and biological perspectives on the origins of modern humans*. Edinburgh University Press, Edinburgh, pp. 546-564.
- Delpech, F., 1999. Biomasse d'ongulés au Paléolithique et inférences sur la démographie. *Paleo* 11, 19-42.
- Dusseldorp, G.L., 2009. A view to a kill: Investigating Middle Palaeolithic subsistence using an optimal foraging perspective. Sidestone Press, Leiden.

- Dusseldorp, G.L., 2010. Prey choice during the South African Middle Stone Age: Avoiding dangerous prey or maximising returns. *African Archaeological Review* 27, 107-133.
- Dusseldorp, G.L., in press. Tracking the influence of Middle Stone Age technological change on modern human hunting strategies. *Quaternary International*. DOI: 10.1016/j.quaint.2011.02.011.
- Eisenberg, J.F., 1990. The behavioral/ecological significance of body size in the mammalia. In: J. Damuth and B. Macfadden (Eds.), *Body size in mammalian paleobiology, Estimation and biological implications*. Cambridge University Press, Cambridge, pp. 25-37.
- Estes, R.D., 1991. *The behavior guide to African mammals, Including hoofed mammals, carnivores, primates*. The University of California Press, Berkeley/Los Angeles/London.
- Faith, J.T., 2008. Eland, buffalo, and wild pigs: were Middle Stone Age humans ineffective hunters? *Journal of Human Evolution* 55, 24-36.
- Farizy, C., David, F., Jaubert, J. and Leclerc, J., 1994. Fonctionnement du site: Hommes et bisons. In: C. Farizy, F. David and J. Jaubert (Eds.), *Hommes et bisons du paléolithique moyen à Mauran (Haute-Garonne)*. CNRS Éditions, Paris, pp. 239-245.
- Finlayson, C., 2004. *Neanderthals and Modern Humans: An ecological and evolutionary perspective*. Cambridge University Press, Cambridge.
- Funston, P.J., Mills, M.G.L. and Biggs, H.C., 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology* 253, 419-431.
- Gamble, C., 1986. *The Palaeolithic settlement of Europe*. Cambridge University Press, Cambridge.
- Gamble, C., 1992. Reply to Roebroeks *et al.* *Current Anthropology* 33, 569-571.
- Gamble, C., 1999. *The Palaeolithic societies of Europe*. Cambridge University Press, Cambridge.
- Gaudzinski, S., 1995. Wallertheim revisited: A re-analysis of the fauna from the Middle Palaeolithic site of Wallertheim. *Journal of Archaeological Science* 22, 51-66.
- Gaudzinski, S., 1996. On bovid assemblages and their consequences for the knowledge of subsistence patterns in the Middle Palaeolithic. *Proceedings of the Prehistoric Society* 62, 19-39.

- Gaudzinski, S., 2004. A matter of high resolution? The Eemian interglacial (OIS 5e) in North Central Europe and Middle Palaeolithic subsistence. *International Journal of Osteoarchaeology* 14, 201-211.
- Gaudzinski, S. and Roebroeks, W., 2000. Adults only. Reindeer hunting at the Middle Palaeolithic site of Salzgitter-Lebenstedt. *Journal of Human Evolution* 38, 497-521.
- Gaudzinski, S. and Turner, E., 1996. The Role of Early Humans in the Accumulation of European Lower and Middle Palaeolithic Bone Assemblages. *Current Anthropology* 37, 153-156.
- Grayson, D.K. and Delpech, F., 1998. Changing Diet Breadth in the Early Upper Palaeolithic of Southwestern France. *Journal of Archaeological Science* 25, 1119-1129.
- Grayson, D.K. and Delpech, F., 2006. Was there increasing dietary specialization across the Middle-to-Upper Palaeolithic transition in France? In: N. J. Conard (Ed.) *When Neanderthals and Modern Humans met*. Kerns Verlag, Tübingen, pp. 377-417.
- Grayson, D.K. and Frey, C.J., 2004. Measuring skeletal part representation in archaeological faunas. *Journal of Taphonomy* 2, 27-42.
- Hames, R.B. and Vickers, W.T., 1982. Optimal diet breadth theory as a model to explain variability in Amazonian hunting. *American Ethnologist* 9, 358-378.
- Hawkes, K., 1982. Why hunters gather: Optimal foraging and the Aché of Eastern Paraguay. *American Ethnologist* 9, 379-398.
- Henry, A.G., Brooks, A.S. and Piperno, D.R., 2011. Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). *Proceedings of the National Academy of Sciences* 108, 486-491.
- Henshilwood, C.S., J.C.Sealy, Yates, R., Cruz-Urbe, K., Goldberg, P., Grine, F.E., Klein, R.G., Poggenpoel, C., Niekerk, K.v. and Watts, I., 2001. Blombos Cave, Southern Cape, South Africa: Preliminary Report on the 1992-1999 Excavations of the Middle Stone Age Levels. *Journal of Archaeological Science* 28, 421-448.
- Holekamp, K.E., Smale, L., Berg, R. and Cooper, S.M., 1997. Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). *Journal of Zoology* 242, 1-15.

- Houston, A.I., McNamara, J.M. and Steer, M.D., 2007. Do we expect natural selection to produce rational behaviour? *Philosophical Transactions of the Royal Society B: Biological Sciences* 362, 1531-1543.
- Hublin, J.-J. and Roebroeks, W., 2009. Ebb and flow or regional extinctions? On the character of Neandertal occupation of northern environments *Comptes Rendus Palevol* 8, 503-509.
- Jaubert, J., Lorblanchet, M., Laville, H., Slot-Moller, R., A.Turq and Brugal, J.-P., 1990. Les chasseurs d'Aurochs de La Borde. Editions de la maison des sciences de l'homme, Paris.
- Jones, E.L., 2004. Dietary evenness, prey choice and human-environment interactions. *Journal of Archaeological Science* 31, 307-317.
- Kaplan, H.S., Hooper, P.L. and Gurven, M., 2009. The evolutionary and ecological roots of human social organization. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364, 3289-3299.
- Klein, R.G., 1976. The Mammalian Fauna of the Klasies River Mouth Sites, Southern Cape Province, South Africa. *The South African Archaeological Bulletin* 31, 75-98.
- Klein, R.G., 1977. The Mammalian Fauna from the Middle and Later Stone Age (Later Pleistocene) Levels of Border Cave, Natal Province, South Africa. *The South African Archaeological Bulletin* 32, 14-27.
- Klein, R.G., 1978. Stone age predation on large African bovids. *Journal of Archaeological Science* 5, 195-217.
- Klein, R.G., 1983. Palaeoenvironmental implications of Quaternary large mammals in the fynbos region. In: H. J. Deacon, Q. B. Hendey and J. J. N. Lambrechts (Eds.), *Fynbos palaeoecology: A preliminary synthesis*. Cooperative Scientific Programmes Council for Scientific and Industrial Research, Pretoria, pp. 117-138.
- Klein, R.G., 1994. The Long-Horned African Buffalo (*Pelorovis antiquus*) is an Extinct Species. *Journal of Archaeological Science* 21, 725-733.

- Klein, R.G., Avery, G., Cruz-Urbe, K. and Steele, T.E., 2007. The mammalian fauna associated with an archaic hominin skullcap and later Acheulean artifacts at Elandsfontein, Western Cape Province, South Africa. *Journal of Human Evolution* 52, 164-186.
- Klein, R.G. and Cruz-Urbe, K., 1996. Exploitation of large bovids and seals at Middle and Later Stone Age sites in South Africa. *Journal of Human Evolution* 31, 315-334.
- Klein, R.G. and Cruz-Urbe, K., 2000. Middle and Later Stone Age large mammal and tortoise remains from Die Kelders Cave 1, Western Cape Province, South Africa. *Journal of Human Evolution* 38, 169-195.
- Krebs, J.R., Houston, A.I. and Charnov, E.L., 1981. Some recent developments in optimal foraging. In: A. C. Kamil and T. D. Sargent (Eds.), *Foraging Behavior: Ecological, Ethological and Psychological Approaches*. Garland STPM Press, New York,
- Kühl, N. and Litt, T., 2003. Quantitative time series reconstruction of Eemian temperature at three European sites using pollen. *Vegetation history and Archaeobotany* 12, 205-214.
- Kuhn, S.L. and Stiner, M.C., 2006. What's a mother to do? The division of labor among Neanderthals and Modern Humans in Eurasia. *Current Anthropology* 47, 953-980.
- Louguet-Lefebvre, S., 2005. *Les mégaherbivores (Éléphantidés et Rhinocerotidés) au Paléolithique moyen en Europe du Nord-Ouest*. Archeopress, Oxford.
- Ludvico, L.R., Bennett, I.M. and Beckerman, S., 1991. Risk sensitive foraging behaviour among the Barí. *Human ecology* 19, 509-516.
- Lyman, R.L., 1994. *Vertebrate taphonomy*. Cambridge University Press, Cambridge.
- Lyman, R.L., 2008. *Quantitative Paleozoology*. Cambridge, Cambridge University Press.
- MacArthur, R.H. and Pianka, E.R., 1966. On optimal use of a patchy environment. *American Naturalist* 100, 603-609.
- MacDonald, D.W., 2006. *The Encyclopedia of Mammals*, New edition. Oxford University Press, Oxford.
- MacDonald, K., 2007. Ecological hypotheses for human brain evolution: Evidence for skill and learning processes in the ethnographic literature on hunting. In: W. Roebroeks (Ed.) *Guts and*

- Brains: An integrative approach to the hominin record. Leiden University Press, Leiden, pp. 107-132.
- MacDonald, K., Roebroeks, W. and Verpoorte, A., 2009. An energetics perspective on the Neandertal record In: J.-J. Hublin and M. P. Richards (Eds.), *The evolution of hominin diets, Integrating approaches to the study of Palaeolithic subsistence*. Springer Verlag, Dordrecht, pp. 211-220.
- Madsen, D.B. and Schmitt, D.N., 1998. Mass collecting and the diet breadth model: A Great Basin example. *Journal of Archaeological Science* 25, 445-455.
- Marcy, J.-L. and Tuffreau, A., 1988a. Le niveau D. In: J. Sommé and A. Tuffreau (Eds.), *Le gisement Paléolithique Moyen de Biache-Saint-Vaast (Pas-de-Calais) Volume I*. Paquez et fils, Chalons-sur-Marne, pp. 291-299.
- Marcy, J.-L. and Tuffreau, A., 1988b. Le niveau D1. In: J. Sommé and A. Tuffreau (Eds.), *Le gisement Paléolithique Moyen de Biache-Saint-Vaast (Pas-de-Calais) Volume I*. Paquez et fils, Chalons-sur-Marne, pp. 263-289.
- Marean, C.W. and Assefa, Z., 1999. Zooarcheological evidence for the faunal exploitation behavior of Neandertals and early modern humans. *Evolutionary Anthropology: Issues, News, and Reviews* 8, 22-37.
- Markova, A.K., Puzachenko, A.Y. and Van Kolfschoten, T., 2010. The North Eurasian mammal assemblages during the end of MIS 3 (Brianskian-Late Karginian-Denekamp Interstadial). *Quaternary International* 212, 149-158.
- McGuire, K.R. and Hildebrandt, W.R., 2005. Re-Thinking Great Basin Foragers: Prestige Hunting and Costly Signaling during the Middle Archaic Period. *American Antiquity* 70, 695-712.
- Mellars, P.A., 2004. Reindeer specialization in the early Upper Palaeolithic: the evidence from south west France. *Journal of Archaeological Science* 31, 613-617.
- Mlynarski, M. and Ullrich, H., 1977. Amphibien und Reptilienreste aus dem Pleistozän von Taubach. In: H.-D. Kahlke (Ed.) *Das Pleistozän von Taubach bei Weimar*. Akademie Verlag, Berlin, pp. 167-170.

- Munaut, A.V., 1988. Étude palynologique. In: A. Tuffreau and J. Sommé (Eds.), *Le gisement Paléolithique Moyen de Biache-Saint-Vaast (Pas-de-Calais) Volume I. Paquez et fils, Chalons-sur-Marne*, pp. 77-88.
- Mussi, M., 2007. Women of the middle latitudes. The earliest peopling of Europe from a female perspective. In: W. Roebroeks (Ed.) *Guts and Brains: An integrative approach to the hominin record*. Leiden University Press, Leiden, pp. 165-183.
- Niven, L., 2007. From carcass to cave: Large mammal exploitation during the Aurignacian at Vogelherd, Germany. *Journal of Human Evolution* 53, 362-382.
- Owen-Smith, N. and Mills, M.G.L., 2008. Predator-prey size relationships in an African large-mammal food web. *Journal of Animal Ecology* 77, 173-183.
- Patou-Mathis, M., 1998. Les espèces chassées et consommées par l'homme en couche 5. In: M. Otte, M. Pathou-Mathis and D. Bonjean (Eds.), *Recherches aux grottes de Sclayn, Volume 2: l'Archéologie*. Université de Liège, Liège, pp. 297-310.
- Patou-Mathis, M. and Bocherens, H., 1998. Comportements alimentaires des hommes et animaux à Scladina. In: M. Otte, M. Patou-Mathis and D. Bonjean (Eds.), *Recherches aux grottes de Sclayn, vol. 2, L'Archéologie*. Université de Liège, Liège, pp. 329-336.
- Perry, G. and Pianka, E.R., 1997. Animal foraging: Past, present and future. *Trends in Ecology and Evolution* 12, 360-364.
- Plug, C. and Plug, I., 1990. MNI Counts as Estimates of Species Abundance. *The South African Archaeological Bulletin* 45, 53-57.
- Plug, I. and Badenhorst, S., 2001. The distribution of macromammals in Southern Africa over the past 30 000 years. *Transvaal Museum, Pretoria*.
- Pushkina, D. and Raia, P., 2008. Human influence on distribution and extinctions of the late Pleistocene Eurasian megafauna. *Journal of Human Evolution* 54, 769-782.
- Radloff, F.G.T. and Du Toit, J.T., 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. *Journal of Animal Ecology* 73, 410-423.

- Richards, M.P. and Trinkaus, E., 2009. Isotopic evidence for the diets of European Neanderthals and early modern humans. *Proceedings of the National Academy of Sciences* 106, 16034-16039.
- Roebroeks, W., Conard, N.J. and Van Kolfschoten, T., 1992. Dense forests, cold steppes and the Palaeolithic settlement of Northern Europe. *Current Anthropology* 33, 551-586.
- Roebroeks, W. and Corbey, R., 2001. Biases and double standards in palaeoanthropology. In: R. Corbey and W. Roebroeks (Eds.), *Studying Human Origins, Disciplinary history and epistemology*. Amsterdam University Press, Amsterdam,
- Roebroeks, W. and Speleers, B., 2002. Last interglacial (Eemian) occupation of the North European plain and adjacent areas. In: A. Tuffreau and W. Roebroeks (Eds.), *Le dernier interglacière et les occupations humaines du Paléolithique moyen*. Université des Sciences et Technologies de Lille, Lille, pp. 31-39.
- Rousseau, D.-D. and Puissegur, J.-J., 1988. Analyse de la malacofaune continentale. In: A. Tuffreau and J. Sommé (Eds.), *Le gisement Paléolithique Moyen de Biache-Saint-Vaast (Pas-de-Calais) Volume I*. Paquez et fils, Chalons-sur-Marne, pp. 89-102.
- Sheehan, M.S., 2004. Ethnographic models, archaeological data and the applicability of modern foraging theory. In: A. Barnard (Ed.) *Hunter-gatherers in history, archaeology and anthropology*. Berg, Oxford/New York, pp. 163-173.
- Silva, M., Brimacombe, M. and Downing, J.A., 2001. Effects of body mass, climate, geography and census area on population density of terrestrial mammals. *Global Ecology and Biogeography* 10, 469-485.
- Silva, M., Brown, J.H. and Downing, J.A., 1997. Differences in population density and energy use between birds and mammals: A macroecological perspective. *Journal of Animal Ecology* 66, 327-340.
- Skinner, J.D. and Chimimba, C.T., 2005. *The mammals of the southern African subregion*, third edition. Cambridge University Press, Cambridge.

- Smith, F.A., Lyons, S.K., Ernest, S.K.M., Jones, K.E., Kaufman, D.M., Dayan, T., Marquet, P.A., Brown, J.H. and Haskell, J.P., 2003. Body mass of late quaternary mammals. *Ecology* 84, 3403-3403.
- Snodgrass, J.J. and Leonard, W.R., 2009. Neandertal energetics revisited: Insights into population dynamics and life history evolution. *PalaeoAnthropology* 2009, 220-237.
- Sommé, J., Munaut, A.V., Puisségur, J.J. and Cunat, N., 1986. Stratigraphie et signification climatique du gisement Paléolithique de Biache-Saint-Vaast (Pas-de-Calais, France). In: A. Tuffreau and J. Sommé (Eds.), *Chronostratigraphie et faciès culturels du Paléolithique Inférieur et Moyen dans l'Europe du Nord-Ouest*, 26. Société Préhistorique Française, Paris, pp. 186-196.
- Steele, T.E., 2003. Using Mortality Profiles to Infer Behavior in the Fossil Record. *Journal of Mammalogy* 84, 418-430.
- Stewart, J.R., 2005. The ecology and adaptation of Neanderthals during the non-analogue environment of Oxygen Isotope Stage 3. *Quaternary International* 137, 35-46.
- Stewart, J.R. and Lister, A.M., 2001. Cryptic northern refugia and the origins of the modern biota. *Trends in Ecology & Evolution* 16, 608-613.
- Stiner, M. and Kuhn, S., 2006. Changes in the 'Connectedness' and Resilience of Paleolithic Societies in Mediterranean Ecosystems. *Human Ecology* 34, 693-712.
- Stiner, M.C., 1994. *Honor among thieves, A zooarchaeological study of Neandertal ecology*. Princeton University Press, Princeton.
- Stiner, M.C. and Munro, N.D., 2002. Approaches to Prehistoric Diet Breadth, Demography, and Prey Ranking Systems in Time and Space. *Journal of Archaeological Method and Theory* 9, 181-214.
- Stiner, M.C., Munro, N.D. and Surovell, T.A., 2000. The tortoise and the hare: Small game use, the broad-spectrum revolution and Paleolithic demography. *Current Anthropology* 41, 39-73.
- Stiner, M.C., Munro, N.D., Surovell, T.A., Tchernov, E. and Bar-Yosef, O., 1999. Paleolithic population growth pulses evidenced by small animal exploitation. *Science* 283, 190-194.

- Thieme, H., 1997. Lower Palaeolithic hunting spears from Germany. *Nature* 385, 807-810.
- Tuffreau, A., 1988. Historique de fouilles effectuées à Biache-Saint-Vaast. In: A. Tuffreau and J. Sommé (Eds.), *Le gisement Paléolithique Moyen de Biache-Saint-Vaast (Pas-de-Calais) Volume I. Paquez et fils, Chalons-sur-Marne*, pp. 15-24.
- Tuffreau, A. and Sommé, J., 1988. *Le gisement Paléolithique Moyen de Biache-Saint-Vaast (Pas-de-Calais) Volume II Mémoires de la Société Préhistorique Française. Paquez et fils, Chalons-sur-Marne*.
- Ugan, A., 2005. Does size matter? Body size, mass collecting and their implications for understanding prehistoric foraging behaviour. *American Antiquity* 70, 75-89.
- Ugan, A., Bright, J. and Rogers, A., 2003. When is technology worth the trouble? *Journal of Archaeological Science* 30, 1315-1329.
- Van Kolfschoten, T., 2000. The Eemian mammal fauna of central Europe. *Geologie en Mijnbouw* 79, 269-281.
- Van Kolfschoten, T., 2002. The Eemian mammal fauna of the northwestern and central european continent. In: A. Tuffreau and W. Roebroeks (Eds.), *Le dernier interglaciare et les occupations humaines du Paléolithique moyen. Université des Sciences et Technologies de Lille, Lille*, pp. 21-30.
- Van Pletzen, L., 2000. The large mammal fauna from Klasies River, MA-thesis. University of Stellenbosch, Stellenbosch.
- Van Vuure, C., 2003. *De Oeros, Het spoor terug*. Wageningen UR, Wageningen.
- Voormolen, B., 2008. Ancient hunters, modern butchers : Schöningen 13II -4, a kill-butchery site dating from the northwest European Lower Palaeolithic. Ph.D-thesis. Faculty of Archaeology. Leiden University, Leiden.
- Wadley, L., Plug, I. and Clark, J.L., 2008. The contribution of Sibudu fauna to an understanding of KwaZulu-Natal environments at ~60 ka, ~50 ka and ~37 ka. In: S. Badenhorst, P. Mitchell and J. C. Driver (Eds.), *Animals and people: Archaeozoological papers in honor of Ina Plug*. Archaeopress, Oxford, pp. 34-45.

- Waite, T.A. and Field, K.L., 2007. Foraging with others: Games social foragers play. In: D. W. Stephens, J. S. Brown and R. C. Ydenberg (Eds.), *Foraging behaviour and ecology*. University of Chicago Press, Chicago/London, pp. 331-362.
- Weaver, T.D. and Steudel-Numbers, K., 2005. Does climate or mobility explain the differences in body proportions between Neandertals and their Upper Palaeolithic successors. *Evolutionary Anthropology* 14, 218-213.
- White, E.P., Ernest, S.K.M., Kerkhoff, A.J. and Enquist, B.J., 2007. Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution* 22, 323-330.
- Winterhalder, B., 1987. The analysis of hunter-gatherer diets: Stalking an optimal foraging model. In: M. Harris and E. B. Ross (Eds.), *Food and evolution, Toward a theory of human food habits*. Temple University Press, Philadelphia, pp. 311-341.
- Winterhalder, B., 2001. The behavioural ecology of hunter-gatherers. In: C. Panter-Brick, R. H. Layton and P. Rowley-Conwy (Eds.), *Hunter-gatherers, An interdisciplinary perspective*. Cambridge University Press, Cambridge, pp. 12-38.
- Winterhalder, B. and Smith, E.A., 1992. Evolutionary ecology and the social sciences. In: B. Winterhalder and E. A. Smith (Eds.), *Evolutionary ecology and human behaviour*. Aldine de Gruyter, New York, pp. 3-23.
- Winterhalder, B. and Smith, E.A., 2000. Analyzing adaptive strategies: Human Behavioral Ecology at twenty-five. *Evolutionary Anthropology* 9, 51-72.
- Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. and Warren, P.H., 2005. Body size in ecological networks. *Trends in Ecology & Evolution* 20, 402-409.
- Zagwijn, W.H., 1996. An analysis of Eemian climate in Western and Central Europe. *Quaternary Science Reviews* 15, 451-469.

Table 1: Ranking, handling cost attributes and modelled population densities for the species under consideration.

Species	Ranking			Handling cost			Population density
	Rank	Weight	Size	Social structure	"Fight/flight"	Composite	ind/km ²
Giant buffalo	1	1000	5	=4	=4	5	0.24
African buffalo	2	580	4	=4	=4	4	0.35
Eland	3	570	3	3	1	3	0.35
Bushpig	4	97.5	2	=1	3	2	1.17
Warthog	5	82.5	1	=1	2	1	1.31

Table 2: The assemblages under consideration and the importance in percentages of eland, buffalo and suids relative to each other. Suids were taken together as in some studies they were not systematically distinguished.

Assemblage	MIS	Eland		African buffalo		Giant buffalo		Suids		African buffalo/Giant buffalo		Reference
		NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	
BlombosM3	5c - 5b	94	67	6	33	0	0	0	0	0	0	(Henshilwood et al., 2001)
Blombos M2	5b - 5a	100	100	0	0	0	0	0	0	0	0	(Henshilwood, et al., 2001)
Blombos M1	early 4	96	83	4	17	0	0	0	0	0	0	(Henshilwood, et al., 2001)
Border Cave MSA 1	5e-5a	-	14	-	29	-	0	-	57	-	0	(Klein, 1977)
Border Cave MSA 2	4	-	0	-	50	-	0	-	50	-	0	(Klein, 1977)
Border Cave MSA 3	3	-	14	-	21	-	0	-	64	-	0	(Klein, 1977)
Die Kelders total	4	79	62	3	10	6	10	0	0	11	19	(Klein and Cruz-Urbe, 2000)
Diepkloof	5d - 3	54	67	0	0	54	33	0	0	0	0	(Klein et al., 2007)
Klasies River MSA I	5e - 5d	-	45	-	18	-	27	-	10	-	0	(Klein, 1976)
Klasies River MSA II	5c - 5a	-	60	-	20	-	22	-	2	-	0	(Klein, 1976)
Klasies River HP	late 4 -3	-	37	-	40	-	23	-	0	-	0	(Klein, 1976)

Klasies River MSA III	3	-	44	-	44	-	11	-	0	-	0	(Klein, 1976)
Klasies River MSA IV	3	-	33	-	44	-	22	-	0	-	0	(Klein, 1976)
Klasies River LBS	5e - 5d	36	-	21	-	36	-	7	-	0	-	(Van Pletzen, 2000)
Klasies River Sas	5c - 5a	72	-	30	-	5	-	3	-	0	-	(Van Pletzen, 2000)
Klasies River Upper	late 4 - 3	15	-	31	-	46	-	8	-	0	-	(Van Pletzen, 2000)
Sibudu HP	late 4 - 3	1	11	5	22	0	0	94	67	0	0	(Clark and Plug, 2008)
Sibudu Post HP MSA 2	3	17	14	3	14	0	0	79	71	0	0	(Clark and Plug, 2008)
Sibudu Post HP MSA 1	3	4	13	43	25	31	25	22	38	0	0	(Clark and Plug, 2008)
Sibudu Late MSA	3	14	-	39	-	6	-	51	-	0	0	(Wadley et al., 2008)
Sibudu Final MSA	3	33	-	48	-	0	-	19	-	0	0	(Wadley, et al., 2008)
Ysterfontein	5c or 5d	100	100	0	0	0	0	0	0	0	0	(Wadley, et al., 2008)

Table 3: Ranking, handling cost and population density of the most important species at Biache-Saint-Vaast. Animal weights from (Brook and Bowman, 2004), unless otherwise indicated. A + for a handling cost attribute signifies that the species handling cost is increased for that attribute. In some herbivores males are solitary.

Species	Ranking		Handling cost			Population density ind/km ²
	Rank	Weight	Size >300 kg	Social structure	Carnivore	
Straight-tusked elephant	1	5500	+	+	-	0.075
Narrow-nosed rhinoceros	2	1600	+	-	-	0.15
Aurochs	3	600 ¹	+	+	-	0.34
Giant deer	4	450 ²	+	+	-	0.41
Brown bear	5	400	+	-	+	0.19 ³
Horse	6	272 ⁴	-	+	-	0.51
Red deer	7	200 ⁴	-	+	-	0.72
Wild ass	8	188	-	+	-	0.75
Wild boar	9	89	-	+	-	1.24
Roe deer	10	23 ⁴	-	+	-	3.12

¹ Estimate based on Van Vuure (2003)'s statement that aurochs weighed as much as modern bison

² Estimate from Louguet-Lefebvre (2005)

³ Calculated brown bear as omnivore $\text{Log } D = 1.41 - 1.83(\text{Log } M) - 0.34(\text{Log } M^2) + 0.28(\text{Log } M^3)$ (Silva et al., 2001).

⁴ Estimate from Pushkina and Raia (2008)

Table 4: Ranking, handling cost and population density of the most important species at Taubach. Animal weights from (Brook and Bowman, 2004), unless otherwise indicated. A + for a handling cost attribute signifies that the species handling cost is increased for that attribute. In some herbivores males are solitary.

Species	Ranking		Handling cost			Population density
	Rank	Weight	Size	Social structure	Carnivore	ind/km ²
Straight-tusked elephant	1	5500	+	+	-	0.075
Merck's rhinoceros	2	2000	+	-	-	0.15
Bison	3	687 ⁵	+	+	-	0.31
Giant deer	4	450 ⁶	+	+	-	0.41
Brown bear	5	400	+	-	+	0.19 ⁷
Horse	6	272 ⁸	-	+	-	0.51
Red deer	7	200 ⁸	-	+	-	0.72
Wild boar	8	89	-	+	-	1.24
Roe deer	9	23	-	+	-	3.12
Beaver	10	18	-	-	-	3.69

⁵ Estimate from MacDonald (2006) .

⁶ Estimate from Louguet-Lefebvre (2005).

⁷ Calculated brown bear as omnivore $\text{Log } D = 1.41 - 1.83(\text{Log } M) - 0.34(\text{Log } M^2) + 0.28(\text{Log } M^3)$ (Silva et al., 2001).

⁸ Estimate from Pushkina and Raia (2008).

Figure captions

Fig. 1: Illustration of diet breath model. Adding species to the diet lowers search time, but increases handling time. In this situation exploiting the three most rewarding species minimises time spent per amount of energy acquired. Graph adapted from Bettinger (1991) and MacArthur and Pianka (1966).

Fig. 2: Map showing the location of the South African sites under consideration. 1: Ysterfontein, 2: Diepkloof, 3: Die Kelders, 4 Blombos Cave, 5: Klasies River, 6: Sibudu, 7 Border Cave.

Fig. 3: Graph showing the relative importance of eland, buffalo and suids in terms of NISP at the sites under consideration.

Fig. 4: Graph showing the relative importance of eland, buffalo and suids in terms of MNI at the sites under consideration.

Fig. 5: Map showing the location of the European sites under consideration. 1: Biache-Saint-Vaast, 2: Taubach.

Fig. 6: Graph showing the composition of the bone assemblage of Biache-Saint-Vaast in terms of NISP. N=20658. Adapted from Auguste (1993).

Fig. 7: Graph showing the composition of the bone assemblage of levels IIbase (n=412), D1 (n=85) and D (n=106) in terms of NISP from Biache-Saint-Vaast. Adapted from (Auguste 1988b).

Fig. 8: Graph illustrating the composition of the faunal assemblage of Taubach in terms of NISP (n=4343). Data from Bratlund (1999).















