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Chapter 7

Selection versus Opportunism, a view from Neanderthal subsistence strategies

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Abstract

Neanderthal subsistence strategies were considered for a long time through the lens of the duality of selection versus opportunism, mostly as a comparison to the hunting behaviours developed in later periods. Based on some examples from the literature, this chapter proposes a review to discuss the presence of selection and opportunism in the different stages of the predation *chaîne opératoire* developed by Neanderthal populations in Eurasia. We underline the existence of a continuum between these two options and the impossibility of using this duality to evaluate the Mousterian subsistence strategy. We conclude that long-term organization is at the centre of the Neanderthal subsistence and is strongly connected with the adaptation of Neanderthals to the opportunity offered by their territory.

Keywords: Zooarchaeology, Middle Palaeolithic, hunting strategy, human evolution, adaptation

1. Introduction

The question of selection versus opportunism is one of our fundamental interrogations when we deal with the exploitation of a specific ecosystem by human populations. It directly questions the kind of interaction the human groups have with their environment.

Selection is understood here as the reasoned and repeated exploitation of parts of the available resources within a given environment, according to criteria related to the economic or cultural interests of the hunter. Conversely, opportunism, taken here as the expression of the absence of selection, can be perceived as "*more versatile, and allow the animal to exploit a much greater array of environmental conditions and resources*" (Parker, 1978). Thus, Newton-Fisher (2015) described many chimpanzee hunts "*as opportunistic in that they appear to decide to hunt after encountering prey during the course of normal foraging activities or travel around the home range*".

Most of the time, these two options are considered hierarchically unequal in terms of cognitive or technological capacities. Selection is now and then seen as the capacity of a human group to identify its need and to develop specific strategies for optimizing their fulfilment, implying the capacity of anticipation, scheduling and the technological resources to achieve these goals. On

the other hand, opportunism, for some scholars, would sometimes attest to a lesser development of the populations, a submission to the environment with choice limited by their social and technological progress. However, things are far more complex than this duality and numerous parameters (including the environment itself) should be taken into account before any conclusion in terms of human social and cognitive capacities. In addition, there is a continuum between selection and opportunism and these two can be sometimes strongly related and alternately practiced by the same human group.

Therefore, there is no systematic hierarchy between the two adaptive solutions except the one that the analysts decide to give based on their own cultural perspectives (Adler et al., 2006).

Selection can only be highlighted if it is repeated through time (within a site) or space (within a region and a set of sites). On the other hand, the absence of selection and an apparent opportunism can also mask the succession of several selection strategies, which follow one another and which, because of the palimpsest of the archaeological assemblages, become invisible to analysts.

Neanderthals are considered as highly skilled flint knappers, able to produce sophisticated tools following complex *chaînes opératoires* (Romagnoli et al., in this book). To this aim, Neanderthal populations conducted complex raw material procurement strategies (e.g., Kuhn, 1995, 2013) sometimes selecting specific materials for some specific productions. By the end of the Lower Palaeolithic, selection of raw materials can also be shown by the few preserved wooden productions, as for instance the exceptional Schöningen spears (Schoch et al., 2015; Thieme, 1997). These past decades, a growing number of studies have underlined the cultural complexity of Neanderthals and particularly their potential capacity to symbolic behaviour (Burdukiewicz, 2014; García-Diez, this book; Jaubert et al., this book). Evidence of this include potential engravings (Rodríguez-Vidal et al., 2014; Leder et al., 2021), the use of birds (Peresani et al., 2011; Finlayson et al., 2012; Morin and Laroulandie, 2012) and shellfish (Zilhão et al., 2010) for ornaments, the capacity to bury their dead (Rendu et al., 2014; Balzeau et al., 2020) and the exceptional Bruniquel construction (Jaubert et al., 2016), if we cite only some examples.

However, concerning their hunting strategies, for decades the ability to select a specific prey or group of prey has been questioned by scholars (Binford, 1988; Mellars, 1989, 1999, 1996; Straus, 1992, 1997). It is directly linked to the first attempts in the late 70's and early 80's to reconstruct Neanderthal subsistence. Based on the frequency of low value skeletal parts (head and feet) and the high frequency of carnivore marks compared to human impacts (cut marks mostly) on faunal remains, the Neanderthals were thought to be opportunistic hunters and scavengers, depending on carnivore dens scavenging to collect large ungulate remains (Binford, 1988, 1981). Even if these ideas were rejected by later analyses (Jaubert, 1990; Farizy et al., 1994; Stiner, 1994; Grayson and Delpech, 1994; Gaudzinski, 1995; Gaudzinski and Roebroeks, 2000), their conclusions have shaped our views on Neanderthal subsistence, deeply influencing the research for the next decades.

Thus until the mid-90's, Neanderthals were understood as strongly dependent on the opportunities in their way to gather food, with very limited choices to cope with their environmental constraints. However, the development of taphonomic analyses (Marean and Kim, 1998), new studies (Jaubert, 1990; Stiner, 1994; Gaudzinski, 1995; Patou-Mathis, 2000; Speth and Tchernov, 2002; Gaudzinski, 2006) and new discoveries (Farizy et al., 1994; Gaudzinski and Roebroeks, 2000) have brought new insight into the subsistence strategies

developed by our past relatives. During the 300 thousand years of their expanse in a territory going from the Atlantic costs to the Siberian Altai, they have adapted to various environments, exploiting most kinds of prey, from small ungulates to megafauna (for syntheses see Gaudzinski, 2006; Stiner, 2013), carnivores (e.g., Gómez-Olivencia et al., 2018), leporids (Morin et al., 2019), tortoises (Speth and Tchernov, 2002), but also halieutic resources like fishes (Guillaud et al., 2021; Hardy et al., 2013; Hardy and Moncel, 2011), shellfish (Stiner, 1994) and marine mammals (Stringer et al., 2008; Blasco et al., this book; Rivals et al., this book). They developed complex hunting strategies, practicing communal hunting when the circumstances made it possible (Farizy et al., 1994; Gaudzinski-Windheuser et al., 2018), killing a large number of individuals at the same time (Farizy et al., 1994; Costamagno et al., 2006), and accumulating a large quantity of food that they might have stored (Soulier and Morin, 2016). There is very limited information on the weapons they used. While close ranged ones have been evidenced (e.g., Gaudzinski-Windheuser et al., 2018), no long-distance weapons have been confirmed.

Several researchers have advanced the possibility that hunting was sometimes supplemented by scavenging (Brugal and Jaubert, 1991; Stiner, 1994; Conard and Prindiville, 2000). Thus, in the specific context of the Quercy, a limestone plateau in Southwestern France, the possibility of opportunistic scavenging of hyena dens or karstic pits, where ungulates were sometimes trapped, was proposed (Brugal and Jaubert, 1991). In this case, Neanderthals would have used the specific topographic conditions of their environments to collect carcasses, limiting the risks.

Due to the flexibility of Neanderthal subsistence strategies and the bias introduced in large scale analyses by regional and chronological variabilities, the selection capacity of Neanderthal has been questioned and sometimes even rejected, interpreted as the evidence of a lack of technological and cognitive capacities (Mellars, 2005, 2004).

Thus, this question of selection or opportunism is of prime interest for our understanding of, on the one hand, the subsistence strategies developed by this human species and, on the other hand, its flexibility and adaptability to specific environmental constraints and opportunities

These notions are expressed differently across the spectrum of predatory activities, and different criteria or methods have been developed over time by researchers to identify the presence or absence of selection in the exploitation of a particular resource type.

Regional approaches were developed by studying the faunal spectra in the same region from contemporaneous or sub-contemporaneous sites in order to identify the presence or absence of specialized economy on a specific prey. Thus, Mellars defined a specialized faunal spectrum when it was more than 80% dominated by one taxon (Mellars, 1996, 2004), arguing that such a spectrum was the consequence of a prey selection in the environment. After studying Southwestern France archaeological record, he concluded that such selection was absent from the Middle Palaeolithic subsistence while Early Upper Palaeolithic societies were specialized on reindeer exploitation (Mellars, 2004). However, this work has been criticized for 1) not taking into account the prey available in the environment (Grayson and Delpech, 2002); the Early Aurignacian in this region developed during the Heinrich 4 event and reindeer was the most common prey (see for instance Banks et al. (2013)) and 2) because Mellars combined the entire Middle Palaeolithic (Grayson and Delpech, 2003, 2002), within which a strong variability has been found (Jaubert, 2009; Discamps et al., 2011).

In parallel to the regional approaches, scholars have applied Optimal Foraging Theory (OFT) to discuss the efficiency of predation and indirectly the presence or absence of selection of specific resources. Following the OFT (MacArthur and Pianka, 1966), predators tend to focus on the prey that guarantees the best return (i.e., high rank prey) between the energy devoted to its capture and processing, and the energy obtained by its consumption (e.g., Starkovich, 2012, 2014; Lupo and Schmitt, 2016). For human hunters, even if we do not consider the symbolic or social value of prey, numerous parameters have to be taken into account to identify its economic rank (its own biological and behavioural characteristics, its distribution and frequency in the environment, the period of the year and the technological and social developments of the human group).

In general, it is accepted that in most environments, Neanderthal focused on the most nutritionally high-return species (Stiner, 1994, 2013; Churchill, 2014; Power, 2019). This selection of high rank prey can be investigated at two levels. Firstly, by discussing the frequency of high ranked species within the faunal spectrum of a site compared to their frequency within the environment; secondly, by identifying the selection of specific individuals (based on their biological conditions such as age and sex) inside the hunted population.

Finally, during the butchery process, the differential exploitation of skeletal parts compared to their richness in meat and marrow (see for instance Morin, 2007) can help to identify the selective exploitation of some specific anatomical elements. It should be noted, however, that the perishable elements are much more difficult to interpret by zooarchaeologists.

In this chapter, considering the fact that a large part of the Neanderthal subsistence relied on ungulates (Naito et al., 2016; Wißing et al., 2019; Jaouen et al., 2019), we propose to follow these different scales of analyses: selection conducted at a regional scale, selection at a site or local scale, selection of specific individual inside a population and selection conducted by the hunter during the exploitation of the carcasses. We complete this review by opening this question of selection on the small prey and carnivore exploitation that sometimes have complemented their diet (Stiner, 2013).

Based on selected examples from the geographical range occupied by Neanderthals (at least as we perceive it for now) we discuss their choice or the absence of choice, in other word their degree of liberty in their hunting strategies.

2. Selection at a regional scale

The question of the animal populations hunted by Neanderthal is old. Since the work of Binford in the early 1980's (Binford, 1988), the limited perception of the hunting capacity of this hominin implied that in the best case, Neanderthals were exploiting the most common prey in their environments without any selection. Based on the rich record of Southwestern France, this hypothesis was later supported by Mellars in his discussion about the differences between Middle and Upper Palaeolithic hunting strategies (Mellars, 1996, 2004) stating that the later one conducted specialized hunting (thus, selection) while the former would have hunted all kinds of prey and no specific game would have been at the core of their economy. The large number of diversified faunal spectra in the Middle Palaeolithic record of Southwestern France was thus regarded as a demonstration of the opportunistic behaviour of Neanderthals and an absence of a selective strategy.

Recent analyses of old collections, new field projects associated with advances in dating methods (Guérin et al., 2012, 2017; Frouin et al., 2018) led to a global revision of the Middle Palaeolithic archaeosequences of Southwestern France (Jaubert, 2009), help to identify the succession of different cultural events during which different subsistence strategies were developed. In particular, the end of the Mousterian is marked by the succession of three major techno-complexes, the Quina deposed mostly between the MIS 4 and the early beginning of MIS 3 (see Discamps and Royer, 2017), followed by the Mousterian of Acheulean Tradition and the Discoidal Denticulate Mousterian. Several recent zooarchaeological syntheses (Delagnes and Rendu, 2011; Discamps et al., 2011) demonstrated that the Quina Mousterian was systematically associated with faunal spectra largely dominated by reindeer in the northern part of the Aquitaine Basin. From 29 stratigraphic units with fauna associated to Quina Mousterian, 24 are largely dominated by reindeer remains, half of them (18/29) present a specialized faunal spectrum (sensu Mellars, 2004) on this taxon. In total 73% of the remains found in Quina contexts are attributed to reindeer (see Discamps et al., 2011; Discamps and Royer, 2017). The reindeer abundance in the faunal spectra is considered to be linked to the major climatic deterioration of MIS 4 (Discamps et al., 2011; Discamps and Royer, 2017) and would not be a direct consequence of human selection. Can we speak here about an opportunistic specialization of the diet on reindeer? It is not so easy. Indeed, as shown by E. Discamps (2014), during this period, there was a major drop off of the ungulate biomass. In addition, the sedentary prey that were present just before this event were abruptly replaced by migratory reindeer (Britton et al., 2011). Some researchers have argued that to cope with these specific conditions (Costamagno et al., 2006; Delagnes and Rendu, 2011), Neanderthals developed a logistic mobility pattern. Costamagno and colleagues (Costamagno et al., 2006) were the first to identify the use of the site of Les Pradelles at Marillac-le-Franc (France) as a secondary butchery site where hundreds of reindeer carcasses were brought and processed before being exported for their consumption. In the same way, Niven and colleagues (Niven et al., 2012) proposed that the site of Chez-Pinaud at Jonzac was used as a butchery site in direct relation to a nearby kill site. There, carcasses would have been summarily processed before the exportation of the richest parts while the poorest elements were discarded in situ, sometimes still in anatomical articulations (Jaubert et al., 2008). These two sites exhibit several common features: evidence of short-term seasonal occupations, catastrophic mortality pattern (excluding evidence of selection of the individuals), activities specifically dedicated to hunting, the possible exportation of some elements and, crucially a large number of carcasses exploited there, several hundred (Costamagno et al., 2006), maybe several thousands in the case of Jonzac (Jaubert et al., 2008; Niven et al., 2012; Rendu et al., in press). For these sites, it has been proposed that Neanderthals came every year at the same season, to perform the same activities, at the same way attesting to the existence of an annual calendar of the activities (Figure 7.1, A). Thus, while no evidence of prey selection is apparent, a strictly opportunistic hypothesis is challenged by the scheduling of and preparation for hunting. Furthermore, the large carcass accumulations could result from several hundreds of occupations and maybe the transmission of this specific mobility pattern for several generations, rejecting the simple opportunistic hypothesis.

In the same region, bison kill sites associated with a Discoidal Denticulate Mousterian during the second part of MIS 3 are also of major interest. Among them, the site of Mauran is unique (Farizy et al., 1994). Associated with a discoidal denticulate Mousterian, the faunal spectrum is almost exclusively composed of bison remains (more than 99%). A total of 137 individuals were identified by MNI but, based on the site dimension, the authors have proposed that

more than 2000 bisons were killed in situ. The mortality profile follows a catastrophic pattern (David and Farizy, 1994). Cementum increment analyses suggested that all the different kills occurred at the end of the summer (Rendu et al., 2012). Exploitation of carcasses focused on the long bones rich in marrow and meat, while significant parts of the skeletons were not affected by human activities (phalanges and more than 50% of the metapodial are found complete), and skeletal elements of juveniles were systematically discarded.

Other contemporaneous sites share the same characteristics with a focus on bison exploitation at the end of the summer early spring, such as La Quina Layer 6C (Chase, 1999; Rendu et al., 2011) or Les Fieux (Gerbe, 2010). Conversely, the MIS3 faunal record from the region attests to a wider diversity of the paleofauna (Discamps et al., 2011; Discamps and Royer, 2017) specifically in living camps like layer EGPF at Saint-Césaire (Morin, 2012). Thus, during the MIS 3 in this region, Neanderthals presented most of the year an unselective subsistence strategy, completed at some specific moments of the annual cycle by specialized hunting of bison, when they gathered in large groups around the rut phase (Figure 7.1 B). Here these different sites clearly evidence selective hunting (Rendu et al., in press).

A similar pattern was identified in the archaeological record of Crimea during the MIS4 and 3, with the specific exploitation of the European wild ass (*Equus hydruntinus*). The site of Starosele (Layer 4, 2 and 1) is characterized by an ungulate faunal spectrum dominated by *E. hydruntinus* (%NISP= 90%) and completed by bison, cervid and saiga (Burke, 2000). Based on the skeletal part representation, the anthropogenic marks and the lithic reduction sequence, the site was interpreted as a task specific location (Burke, 2000). The assemblage seems to have resulted from specialized hunting and the site used as a seasonal butchery site, dedicated to the capture and the processing of wild ass.

Kabazi II presents some strong similarities to Starosele (Chabai et al., 2006): with a specialization on *E. hydruntinus* (%NISP= 98%) supplemented by horse, saiga, bison, cervid (red deer and megaloceros) and rhinoceros (Patou-Mathis and Chabaï, 2003). Dhole and cave lion complete the faunal assemblage. At least 38 *E. hydruntinus* were hunted within several family groups during the warm season (Ramírez-Pedraza et al., 2020). The low production of lithic industry associated with the specific exploitation of the carcasses led the authors to propose that the site was used as a task specific location dedicated to the acquisition and the first stage of butchery of E. hydruntinus carcasses (Patou-Mathis and Chabaï, 2003).

These two sites would have resulted from specialized hunting, with Neanderthals specifically focusing their interest on *E. hydruntinus,* while at other contemporaneous sites they exploited a broader variety of taxa (Burke, 2006). This spatio-temporal segmentation of the activities attests the development of logistic mobility and would reflect their seasonal selection of the wild ass.

Finally, we can highlight the fact that the development of task specific location for the specific capture of animals was not devoted only to Ungulates. Therefore, at Grotta del Clusantin (MIS3, Italy) Romandini and colleagues identified a faunal spectrum largely dominated by marmot remains (90%). Based on the anthropogenic modifications, they proposed that the site was specifically used by Neanderthal for the exploitation of the large rodent for meat and fur (Romandini et al., 2012).

FIGURE 7.1 HERE

3. Selection at a local scale

At Kebara Cave (Israel), Speth and Clark (2006) propose an interesting evolution of hunting selection strategies based on the application of OFT. The study focuses on the entire Middle Palaeolithic sequence of this cave located on Mount Carmel and attributed to the first half of the MIS 3. The authors find a regular decrease in the contribution of large ungulates (deer and aurochs) to the Neanderthal diet through time until their near disappearance. While these taxa (considered high ranked) disappeared from the faunal spectra, lower ranked species, fallow deer and gazelle, became the main prey of the hunters. Based on the absence of climatic changes that could justify an evolution of the archaeofauna and on the fact that this trend is not observed at contemporaneous sites, the authors propose that this evolution of the faunal spectrum was the consequence of overhunting the highest ranked taxa until their disappearance in the direct vicinity of the site.

In the same way, the end of the sequence is marked by a progressive enrichment of juvenile prey while no change in the hunting season is attested, leading the authors to propose that an over-hunting of the adults occurred, forcing Neanderthal to focus more and more on the young individuals that are usually considered as the lowest rank prey to fulfil their needs (Speth and Clark, 2006).

Here, it is interesting to see that this selection conducted by Neanderthals towards the most profitable resources according to OFT had a direct impact on the human environment. In addition, this example shows that the selection process was adapted to the evolution of the faunal composition in the site vicinity in order to meet the needs of hominins.

An interest in high ranked prey has been identified in a large variety of environments. At Klissoura Cave 1 (Greece) from the late MIS 5 to the transition to the Upper Palaeolithic (Starkovich, 2014), Neanderthal focused on high ranked ungulates (notably the Mediterranean fallow deer) supplemented by tortoises, the highest ranked small game available within the site vicinity (Starkovich, 2012). There, a shift occurred during the Early Upper Palaeolithic with the inclusion of low ranked prey in the diet of the human population (Starkovich, 2012, 2014). By taking into account the absence of major environmental change and the diversity of the activities evidenced by the archaeological material, the author suggests that this change in the diet resulted in the increase of demographic pressure on the ecosystem. It also suggests that, contrary to Kebara, Neanderthal occupations in southern Greece were not intense enough to directly affect the ecosystem.

4. The hunter's choice

In addition to demonstrating the selection of animal populations by Neanderthals, Kebara also attests to the selection of individuals within these same populations (Speth and Clark, 2006). Indeed, depending on their age and sex, and considering the season of hunting, not all the individuals have the same physical (e.g. quality of the skin, quantity and quality of grease) and behavioural characteristics and might not have the same potential interest for hunters. Thus, identifying the sex-ratio and the age structure of the hunted population offers us the possibility to discuss the prey selection criteria (or their absence) developed by the predator.

As stated by M. Stiner (1990, 1994), human hunting activities tend to generate catastrophic mortality patterns, which reflect the living population (dominated by young individuals) and prime dominated patterns (with a strong selection of adults). The first one is expected to be produced by an ambush predator, opportunistic encounter, and or slaughtering (Lubinski, 2013). The second one would illustrate a strong selection of the highest ranked individual within a population (Stiner, 1990).

Since the Lower Palaeolithic, the existence of prime dominated archaeological assemblages has been established (e.g. Qesem Cave, Israel; Stiner et al., 2011). In some cases, this pattern is particularly pronounced: Neumark 1 (MIS 5, Germany), remarkable for its preservation and the quantity of carcasses it provides, demonstrates a marked selection of prime adult males (78% of the total) among the 160 fallow deer hunted by Neanderthals (Gaudzinski-Windheuser et al., 2018). While prime dominated assemblages are not uncommon during the Middle Palaeolithic (but see for instance: Gaudzinski and Roebroeks, 2000; Hoffecker and Cleghorn, 2000; Patou-Mathis, 2000), it is at the end of this period that they become more frequent (Stiner, 2013). During most of the Middle Palaeolithic, the two patterns, selective and non-selective hunting in terms of age and sex seem to coexist (David and Farizy, 1994; Stiner, 1994; Conard and Prindiville, 2000; Costamagno et al., 2006; Rendu, 2010; Conard et al., 2012; Daujeard et al., 2012).

The example of the Abric Romaní (MIS 3, Spain) is surely one of the best demonstrations of the coexistence of multiple strategies during the Middle Palaeolithic. Marín and colleagues (Marín et al., 2017) conducted an analysis of the exploitation of the two main prey of this late Middle Palaeolithic site, horse and red deer. Based on the analysis of 259 and 227 horse and red deer teeth representing respectively 47 and 50 individuals, they reconstruct the evolution of the mortality patterns for the two ungulates in seven stratigraphic units (E to M). While horses are characterized by the over-representation of prime adults, red deer show a catastrophic age profile suggesting the absence of selection. Thus, the authors identify two drastically opposed hunting strategies: selective hunting of horses and opportunistic hunting of red deer. This example is particularly striking because the same choice seems to have been made repeatedly throughout the stratigraphy, demonstrating the coexistence of selective and opportunistic strategies within the same hominin populations. This example also illustrates that the absence of selection does not necessarily reflect the inability to select and might result from specific cultural choices made by Neanderthals.

Pech de l'Azé I (MIS 3, France) (Soressi et al., 2008) provides a slightly different view by highlighting the influence of seasonality in the selection strategy. The three archaeological levels (4, 6 and 7), largely dominated by red deer remains, underline the succession of different hunting strategies according to the season. At the top of the stratigraphy, adult male deer were hunted in late summer-fall around the rut when a lot of individuals are weakened by fighting and by the fact that they stop feeding during this period (Varin, 1980). Conversely, level 6 shows the hunting of young and females from spring to early summer, around the birth season, when females are weaker and when the matriarchal groups are slower in their movements and are easier to locate (Varin, 1980). Finally, layer 4 exhibits a catastrophic mortality pattern for the two groups (male, female and young) over the year, interpreted as the succession of the two previous hunting strategies (Armand et al., 2001) (Fig. 7.2). It was hypothesized that the selection here was driven by opportunism, with Neanderthals choosing the easiest prey to trap or approach depending on the deer conditions during the year, adapting their selection to the seasons without changing their strategy (Rendu, 2010).

FIGURE 7.2 HERE

5. Selection within animal carcasses

The motivations for exploiting a specific animal are almost unlimited, going from need for food (meat, grease, and marrow), skin, bones, antlers to symbolic and social purposes. While these two last points are rarely addressed when dealing with Neanderthals (but see for instance: Peresani et al., 2011; Stiner et al., 2011; Morin and Laroulandie, 2012; Majkić et al., 2017), the processing of carcasses has been well documented and brought valuable perspectives on Neanderthal selection strategies. In particular, identifying the selective transport within the sites of specific carcass portions allows us to address the question of the choices made by the hunters and thus of their potential selective or non-selective exploitation. Following the Schlepp effect (Perkins and Daly, 1968), the hunters usually discard the less interesting parts of the carcasses at the kill sites and bring the most desired elements into their consumption site (Speth, 1983).

The question of selective transport is usually addressed by comparing the differential representation of anatomical elements with their expected nutritional value (e.g. Lyman, 1994). Although this method is constrained by numerous biases, e.g. taphonomic (Lyman, 1994), methodological (notably the reliability of the indexes used; see Morin, 2007), or even related to the taxa themselves and the weights to be transported (Morin et al., 2016), it remains one of the preferred ways for discussing the choices made by human populations in their strategy. Indeed, since at least the Lower Palaeolithic (e.g. Qesem Cave, Israel; Stiner et al., 2011), the selective exploitation of specific parts of carcasses is attested to and numerous Middle Palaeolithic occupations demonstrate such behaviour (e.g. Costamagno et al., 2006; Daujeard and Moncel, 2010; Daujeard et al., 2012). Morin and Ready (2013) conducted a review of a large part of the Mousterian records on Neanderthal selective transport through time and identified a frequent correlation of the selection of parts of the carcasses with their richness in marrow (using the Unsaturated marrow index (UMI); Morin, 2007). This trend seems to be stronger for cold periods (Morin and Ready, 2013). This strong selection for parts of the carcasses based on marrow during these cold phases is linked to the need for its high energetic value (Speth and Spielmann, 1983; Morin and Ready, 2013).

However, for Neanderthals, carcasses are not only a source of food but also of non-food materials. Bone elements were used at certain sites as fuel (Théry-Parisot et al., 2005), as soon as fire was mastered (Roebroeks and Villa, 2011). It seems difficult here to imagine that animals were selected specifically for this purpose; it is easier to assume an opportunistic exploitation of fat-rich elements of carcasses (i.e. the axial skeletal bones and articular extremities) for burning as fuel.

Simultaneously, since at least the beginning of the 20th century and the work of L. Henri Martin (1906), the production of retouchers from bones directly collected from butchered prey is demonstrated in numerous deposits, sometimes in very large quantities (Niven et al., 2012; Mallye et al., 2012; Daujeard et al., 2014; Costamagno et al., 2015; Mateo-Lomba et al., 2019). Retouchers are bone elements (sometimes teeth) used in the process of shaping and sharpening lithic tools with the main objective being to modify the active part of stone artefacts. Retouchers are a very good example of the continuum existing within Neanderthal

subsistence between opportunism and selection. Indeed, while their blanks are directly taken from the waste of butchery and the bone breakage process for obtaining the marrow (opportunism), at many sites a selection of pieces (both in terms of anatomical elements and in terms of species) is attested. Thus, at Denisova and Chagyrskaya caves in the Siberian Altai (Russia), there is a preferential use of long bone fragments and elements from large ungulates (mostly bison bone fragments) for the retoucher blanks compared to the rest of the fauna (Baumann et al., 2020; Kolobova et al., 2020; Kozlikin et al., 2020). At Payre (France), although red deer is the main prey, Neanderthals preferentially selected larger ungulate bone fragments to produce retouchers (Daujeard et al., 2014). Still, selection is not a rule and several occurrences of randomly sampling blanks within the faunal assemblage have been demonstrated (see Daujeard et al., 2014). Nevertheless, in some cases the production and selection of blanks might have occurred as early as during the butchery of the carcasses, and in the Les Pradelles (France) MIS 4 deposits, the breakage for marrow extraction of bone could have been conducted in order for the splinters to be used as blanks for retouchers (Costamagno et al., 2015). At the same time, recent analyses of retouchers from Chagyrskaya Cave (Russia) concluded that blanks were strongly selected based on their dimensions, and even some of them were modified with lateral removal of cortical tissue (Fig. 7.3) to fit to a specific standardized width (Kolobova, 2020; Bauman, 2020). This “opportunistic selection” of bone fragments resulting from carcass processing is another evidence of Neanderthal technical flexibility.

FIGURE 7.3 Here

6. Diversification of the diet and the exploitation of non-ungulate animals.

Different degrees of selection are now identified in the Neanderthal exploitation of high ranked ungulates, which are considered to have been at the centre of their diets. In parallel, the modality of exploitation of other vertebrate resources (sometimes considered as lower rank ones) such as mesofauna or carnivores, shows a broader regional and chronological variability, and might be the real key to understand diversity in Mousterian subsistence (Stiner, 2013). Often presented as secondary resources, acquired in opportunistic encounters (see Stiner, 2013 for discussion) their exploitation is sometimes presented as an efficient way to diversify the diet and cope with ungulate fluctuations in availability (Morin et al., 2019). These resources include carnivores, birds, fishes, and most mesofauna in general.

Most Middle Palaeolithic assemblages attest to carnivore remains in their faunal spectra. One of the problems with carnivore remains found in anthropogenic layers is to establish the origin of their accumulation: are they the result of human activities, a contamination due to taphonomic processes or the result of a short carnivore occupation of the site between two human ones? Indeed, while most carnivore species seem to have been exploited, carnivore remains with cut marks are usually not numerous, corresponding in most of the cases to one or two isolated individuals (for a review see Gómez-Olivencia et al., 2018). They seem to have been the result of opportunistic encounters or scavenging. There is, however, an exception to that pattern with the site of Biache-Saint-Vaast in France (Auguste, 1995) and Taubach (Germany) where 292 brown bear remains exhibit cut marks (Bratlund, 1999). This interest for carnivore seems to increase during the Middle to Upper Palaeolithic transition (Rendu et al., 2019).

The exploitation of birds exhibits a complex pattern. Their exploitation, starting at least during MIS 9 (Blasco et al., 2013), is well identified in numerous Mousterian sites (Gómez-Olivencia et al., 2018) yielding sometimes a large quantity of remains such as at Gorham's Cave (Gibraltar) (Finlayson, 2013; Blasco et al., 2016). While exploitation for food is usually not rejected, one of the objectives of the bird procurement seems to have been for non-utilitarian (and probably symbolic) purposes. Indeed, at Fumane (Italy) (Peresani et al., 2011; Romandini et al., 2016) and Gorham's Cave (Gibraltar) (Finlayson, 2013), the extraction of feathers is attested. Simultaneously, claws were recovered from raptors notably in several sites from Southwestern France (Morin and Laroulandie, 2012) and Italy (Romandini et al., 2014). However, the comparison of Mousterian faunal spectra with later periods and natural accumulations (Finlayson et al., 2012) underlines the over-representation of scavenging birds (vulture, corvid, golden eagle). As stated by Laroulandie and colleagues "The predatory and scavenging behaviour of these birds—which overlaps in terms of habitats with humans—may, in part, explain why they were targeted by Middle and Early Upper Palaeolithic foragers" (Laroulandie et al., 2020). Thus, an opportunistic exploitation cannot be completely ruled out in some cases.

For the meso-mammals, the most striking example of Neanderthal exploitation are of leporids (see also Blasco et al., this volume). Rabbits were exploited frequently and repeatedly in the Northern part of the Mediterranean Basin (Spain, France, and Italy) since the beginning of the Middle Palaeolithic (for a review see Cochard and Brugal, 2004; Morin et al., 2019, 2020). Morin and colleagues (Morin et al., 2019, 2020) argue that climatic fluctuations directly modified the abundance of rabbits within the environments of Mousterian hunters, increasing the probability of encounters. This would have increased the rank of this taxon and thus its interest for Neanderthal populations in the area of its distribution. Consequently, Neanderthal would have selected this resource during specific climatic episodes when the population of leporids increased, enlarging Mousterian diet long before the late Pleistocene Broad Spectrum Revolution (Morin et al., 2020). The same remarks may apply to some halieutic resources exploited by Neanderthals in different contexts. In Gibraltar (Vanguard and Gorham's cave) the repetitive exploitation of marine mammals (seals and dolphins) through the stratigraphy (especially at Vanguard Cave), led the authors to propose that the exploitation was a "focused behaviour" (Stringer et al., 2008) in the environment of the site that provided these specific opportunities.

7. Final remarks

These several examples from different chronological and geographical contexts underline that selection and opportunistic exploitation were part of Neanderthal subsistence strategies and that they were closely related. As for lithic tool production, Neanderthal behaviour was characterized by efficient technology and flexibility toward its transposition to specific resources (Stiner and Kuhn, 2006; Kuhn, 2013; Romagnoli et al, in this book).

This duality between selection and opportunistic hunting can be observed in all the aspects of Neanderthal ungulate exploitation. During MIS 3, they developed seasonal hunting selection (Mauran, France) while being opportunistic in their hunting during the rest of the year; they adapted their selection strategies to the opportunities of paleofauna as it evolved due to the over-hunting of some high-ranking species (Kebara, Israel); they conducted at the same time selective and opportunistic hunting depending on the taxa (Abri Romaní, Spain). Finally, it is probably within the bone industry, and specifically with the retouchers, that selection and

opportunism intersect the most with the use of carcass wastes to produce standardized tools, with blanks sometimes being highly selected. As Marín and colleagues (Marín et al., 2017) demonstrated at Abri Romaní (Spain) the absence of selection is not necessarily the proof of the incapacity to select but might just be the consequence of choices made by the population. While prey selection has been seen by researchers as evidence of specific cognitive developments for Upper Palaeolithic humans (Mellars, 1996, 2004), these different examples attest to the same capacities in the Neanderthal populations (Stiner, 2013). The absence of selection, thus opportunism, does not necessarily imply a lack of organization and social complexity in the Neanderthal population. In this sense, the Quina from Southwestern France is very demonstrative. While Neanderthals were limited in the range of prey with the large preponderance of reindeer within the environment (Discamps et al., 2011; Discamps and Royer, 2017), they developed a highly complex mobility pattern (Delagnes and Rendu, 2011), including the development of different task specific locations in order to optimize the exploitation of this resource (Costamagno et al., 2006; Niven et al., 2012). Simultaneously, there is not always a strong discontinuity between selection and opportunism as underlined by the zooarchaeological analysis of Abri Romaní (Marín et al., 2017) and seasonal variation in selection occurred. The seasonal bison specialized sites in the late Middle Palaeolithic of Southwestern France are a good demonstration of this (Farizy et al., 1994; Rendu et al., 2012), such as the evolution of the selection strategies at Pech de l'Azé I (Rendu, 2010). These different examples illustrate how the exploitation of prey by Neanderthals followed complex mechanisms that might have involved at the same time both opportunism and selection depending on the context and the taxon.

Neanderthal subsistence appears thus to be more complex than was previously understood. For too many years, we have been blocked in our perception by systematic comparisons with the Upper Palaeolithic behaviour. When we take some distance to it, it is possible to have a better perception of what was Neanderthal subsistence.

Despite the 300 thousand years of their history and their large geographic extents, Neanderthals show that some common trends and the same types of hunting strategies were conducted by different populations. While the kill site of Mauran (France) is impressive for the quantity of the carcasses accumulated, the hunting techniques are not unique and the mass capture of ungulates was developed in other contexts (Gaudzinski and Roebroeks, 2000; Costamagno et al., 2006; Daujeard et al., 2019). The focus on ungulates and on the highest rank prey, and the selective transport of the richest elements are visible in a large part of the Middle Palaeolithic archaeological record. It seems also that the opportunistic exploitation of resources accompanied this deep selective behaviour. Thus, as it was previously demonstrated for lithics, Neanderthal strong technical capabilities in hunting is characterized by a high flexibility in its application. This selection capacity, expressed through the entire hunting *chaîne opératoire*, is also evidence of anticipation and scheduling in order to answer specific needs. This long-term organization within the subsistence activity is strongly connected with the adaptation of Neanderthals to the opportunity offered by their territory.

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Figure captions:

Figure 7.1. Schematic representation of the A) Quina subsistence pattern (MIS4-early MIS3) B) Discoidal Denticulate pattern (MIS3) in Southwestern France. Quina hunted principally reindeer, which was the most common species in the environment. Thus, no selection can be established, but they developed a very complex mobility pattern to deal with the specificity of their prey. Discoidal Denticulate Mousterians seem to have been opportunistic hunter most of the year, hunting what was present in the environment but might have conducted some specific communal hunting of bison at some specific moment of the year (selection). Modified from Delagnes and Rendu (2011).

Figure 7.2. Schematic representation of the hunting selection, depending of the season for the different level of Pech de l'Azé I. The circle on the right represent the period of the year when the hunting happened (Level 7: late summer-early fall; Level 6: spring early summer; level 4: year round).

Figure 7.3. Example of retoucher from Chagyrskaya (Russia) exhibiting some modification of the blank. Flowchart identify the blank modification sequence proposed by Kolobova et al. (2020). This long bone fragment results from the breakage of a long bone shaft of a large ungulate for the extraction of the marrow. The fragment was opportunistically selected and modify to fit to the standardize dimension looked for by Neanderthal. The letters refer to the scar pattern analysis.