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

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7 Hyena foraging

7.1 Introduction

After analysing Middle Palaeolithic sites guided by Optimal Foraging Theory (OFT), this chapter aims to provide an additional evaluation of the applicability of this reasoning to the Pleistocene by applying OFT reasoning to the foraging behaviour of the Pleistocene European cave hyena (*Crocuta spelaea*). The results of this analysis will be compared to the results of the analysis of Middle Palaeolithic sites. This species was chosen because of its important similarities to Neanderthals, most significantly the facts that both species are of roughly similar size and they are both social carnivores. It is proposed that in order for the application of OFT to Pleistocene foraging behaviour to be fruitful, the theory should be able to highlight the differences between the foraging niches of both species.

It is expected that Neanderthals and cave hyenas occupied different niches during the Middle and Late Pleistocene, since they co-existed in large areas, where both species left a rich record of their activities (e.g. Brugal, Fosse, and Guadelli 1997, Fosse *et al.* 1998). If both species occupied a similar niche, this would have resulted in the local extinction of one of the two. As this was patently not the case, we are presented with an opportunity to test whether applying OFT to cave hyenas results in a different modelled diet. Hence, this case-study provides a check of the validity of this kind of analysis. Hyenas are often seen as scavengers, which would be an important niche difference allowing them to co-exist with predators. However, this view is not correct in the case of spotted hyena (*Crocuta crocuta*), since this species is an accomplished hunter (e.g. Kruuk 1972). Genetically it is closely related to cave hyena (Rohland *et al.* 2005), suggesting that this species too was an important predator in its environment. Therefore cave hyena and Neanderthal niches were potentially very similar. It must be noted though, that the range of species consumed by a predator represents only one facet of its niche. The different niches of cave hyenas and hominins may have been defined by other adaptations than the range of species they exploited, like spatial segregation, or the use of different strategies (e.g. Stiner 1992, 446).

Studying hyena foraging has advantages over the study of foraging by other carnivores. Hyenas have long been recognised as an important taphonomic agent in the formation of bone deposits at archaeological sites, both in Plio-Pleistocene African and European studies. This has led to a great amount of actualistic and palaeontological research into the foraging strategies of hyenids and their palaeontological residues, in order to see what their role in the archaeological record has been (e.g. Binford, Mills, and Stone 1988, Brugal, Fosse, and Guadelli 1997, Diedrich and Žák 2006, Horwitz 1998, Lam 1992, Stiner 1992, Villa *et al.* 2004).

Unfortunately, not all excavated hyena sites have been published in detail and the environmental conditions of many sites are not clarified at all in the publications that were at my disposal. I will present two case studies, for which sufficient data are available, namely the French sites of Lunel-Viel and Camiac. In the case of Lunel-Viel, the bone assemblage has been published in great detail, but unfortunately, not much information is available for environmental reconstruction. At Camiac we have information about the environment in which the cave hyenas foraged. However, details about the skeletal part representation and age-structure of the species represented are scant. The information that these sites yield will be combined and supplemented with information from other sites in order to arrive at a synthesized image of foraging strategies of Pleistocene cave hyenas that can be compared to our understanding of Neanderthal foraging.

Additionally, all extant hyena species employ scavenging as part of their foraging strategies. Spotted hyenas often employ scavenging as a secondary strategy, but in some populations this strategy contributes an important part of the total calories that are consumed. Modelling hyena foraging niches with OFT may therefore also produce insight in the viability of scavenging in hominin foraging strategies.

In order to be able to construct a diet breadth model for hyenas, I will first shortly present our knowledge of extant hyenid species, emphasising the spotted hyena, because it is anatomically and genetically very similar to the cave hyena. This will be followed by a discussion on the character

of the bone accumulations that are produced by hyenas, which is crucial in order to be able to interpret Pleistocene hyena bone assemblages. After this I will present the sites used as case-studies. The knowledge on Pleistocene hyena behaviour gained from these case-studies will then be supplemented with knowledge gained from other Pleistocene sites and a scenario will be developed that interprets hyena foraging decisions and clarifies the separation between their niche and that of Neanderthals.

7.2 Hyena ecology

Hyenids are a group of feliform carnivores. They are a small Family in the class Mammalia, of which only four species are in existence today. These four species are the remnants of a much larger group. In the late Miocene, 24 species are known to have existed (Watts and Holekamp 2007, r657). The extant species show quite a wide range of adaptations. One of them, the aardwolf (*Proteles cristatus*), feeds mostly on termites and is only distantly related to the other three species. Due to the distant relationship and incongruous foraging pattern it will not be referred to in this chapter. The other three species feed mostly on meat of macrofauna, which is acquired by hunting and scavenging. These species are brown hyena (*Hyaena brunnea*) and striped hyena (*Hyaena hyaena*), which are closely related, and spotted hyena (Mills and Bearder 2006). Hyenas are distributed over a large area. Striped hyena is found in India, the Near East and areas in North and East Africa. Brown hyena is found mainly in southern Africa, while spotted hyena lives in most of Sub-Saharan Africa. (Mills and Bearder 2006, Watts and Holekamp 2007).

In Pleistocene Europe, several hyenids existed. In the late Pliocene and early Pleistocene, two forms occurred, the “gigantic” short-faced hyena (*Pachycrocuta brevirostris*) and the medium sized *Hyaena perrieri*. The latter species may be closely related to the brown hyena, the former species was probably distantly related to the modern spotted hyena. During the Middle and Late Pleistocene there is a species resembling the striped hyena, *Hyaena prisca*, and the cave hyena (Brugal, Fosse, and Guadelli 1997, Diedrich and Žák 2006).

The cave hyena will be the focus of this analysis, since its sites have been well researched and because it was the most common of the Late Pleistocene species. Anatomically it appears to be closely related to modern day spotted hyena. However, Cuvier found it sufficiently different from spotted hyena to define it as a separate species (Fosse 1997, 17). Modern genetic analysis, however, has shown that spotted hyena and cave hyena samples fall in the same group and can be regarded as belonging to a single species (Rohland *et al.* 2005, 2441). Spotted hyenas therefore present a suitable behavioural analogue. The close kinship of the Pleistocene and contemporary populations suggests that they may have been behaviourally similar. On the other hand, denning and bone accumulation occurs in all three contemporary hyena species, suggesting that it is an ancestral feature of this group. Therefore, reference to bone accumulations produced by other species will occasionally be made.

Hyenas are social carnivores living in clans. Among brown and striped hyenas, clans are small and they usually consist of related individuals. A brown hyena clan can comprise only a mother and her offspring. On the other hand, spotted hyena clans may number up to 80 individuals, but on average, clans number 25 individuals (Kruuk 1972, Mills and Bearder 2006, Watts and Holekamp 2007). These clans are multi-male, multi-female groups. Moreover, in-group relatedness in spotted hyena is low. This kind of social system is more reminiscent of that of primates than of carnivores (Watts and Holekamp 2007, r658). It contrasts sharply with the social system of the other two species.

As pointed out above, the cave hyena was closely related to the modern spotted hyena. This species has a remarkable social system in which females are the dominant sex (Watts and Holekamp 2007, 660). Females exhibit elevated levels of testosterone and the female reproductive organs in the species have been masculinised. Spotted hyena females have a penis-like clitoris, through which the females give birth (Drea and Frank 2003, 124). Furthermore, females are about 12 % larger than males. Males weigh between 45 and 62 kilos, whereas females weigh 55 to 82.5 kilos (Mills and Bearder 2006). The masculinization has important consequences for childbirth in this species. The first time a female gives birth, the clitoris has to tear, since it is too small to allow the fetal head to pass through it. The first period of labour is therefore prolonged and painful in spotted hyenas. This results in an elevated number of stillborn cubs from a female's first pregnancy and delivery. Moreover, it also leads to elevated mortality in female hyenas. As much as 36% of the female population may die during their first labour (Frank, Weldele, and Glickman 1995).

Pleistocene cave hyenas were larger than their modern day counterparts. This may be an expression of Bergman's rule (discussed in section 2.4 for Neanderthals) (Brugal, Fosse, and Guadelli 1997, 160). The body weight of Pleistocene hyenas was higher than that of Neanderthals, which is estimated by (Sorensen and Leonard 2001) as 55 kg. for females and 65 kg. for males. Moreover, female Pleistocene cave hyenas in Europe have also been described as being slightly larger than the males (Diedrich and Žák 2006, 252). This can be taken as an additional indication that Pleistocene cave hyenas had a similar social system as modern spotted hyenas.

Spotted hyenas have a very strict dominance hierarchy that regulates interactions within the group. Remarkably, the rank of a spotted hyena individual is not dependent on its size or strength, but is derived from its mother's rank. The rank of an individual in the group determines the timing of its access to food. This is very important, since competition for food seems to be more intense in spotted hyenas than in any other carnivore (Drea and Frank 2003, Watts and Holekamp 2007). In order to deal with the feeding competition, hyena individuals usually spend a lot of time in small subgroups that forage in a dispersed manner throughout the territory. They can therefore best be described as living in a fission fusion society (Watts and Holekamp 2007, r659).

All hyena species forage nocturnally. They are usually seen as obligate scavengers. This view is correct in the case of brown and striped hyenas that acquire most of their prey by scavenging. The only hunting observed in these hyena species is hunting for small species like dogs and rodents (*e.g.* Horwitz 1998, Mills and Bearder 2006). In the case of spotted hyenas scavenging is a less important foraging strategy. They are known to scavenge, but often seem to prefer fresh kills above scavenged meat (Cooper, Holekamp, and Smale 1999, 159). However, spotted hyena behaviour nowadays varies and different feeding strategies will be employed depending upon the ecological circumstances. Despite the variation in foraging behaviour in different ecological settings, medium- to large-sized ungulates form the mainstay of hyena diets in most areas (Brugal, Fosse, and Guadelli 1997, Lam 1992, Mills and Bearder 2006).

Spotted hyenas often forage alone. As pointed out, a large portion of the hyena diet is obtained by hunting, although scavenging is quite important in many populations. In this respect, it should be noted that adult spotted hyenas can also kill prey as large as wildebeest (*Connochaetes taurinus*) on their own³¹ (Mills 1985, Watts and Holekamp 2007). Solitary foraging is attractive for many individuals because of the intense competition for food in this species. This competition is more intense than in other social carnivores. Therefore it is often profitable for individuals, especially low-ranking ones, to forage alone. Additionally, while hunting success does improve when hunting in groups, this improvement is not dramatic, which may explain why 75% of successful hyena hunts were executed solitarily (Watts and Holekamp 2007, r659). After a successful hunt, group members often converge on the kill, competing for the food with the individual that obtained it (Watts and Holekamp 2007, r658). Still, group hunting does occur in this species. Furthermore, hunting in groups allows hyenas to target larger species than Wildebeest. Hyenas hunting in groups regularly kill animals like zebras (*Equus sp.*). Moreover, groups have been observed hunting buffalo (*Syncerus caffer*) and even giraffes (*Giraffa camelopardalis*). In very exceptional cases hunting of juvenile elephants (*Loxodonta africana*) has been observed (Fosse 1996, Watts and Holekamp 2007). The latter species are only attacked if the victim is very young, injured or pregnant (Cooper, Holekamp, and Smale 1999, 152).

In general therefore, spotted hyenas only hunt prey of up to about 250 kg. The preferred prey in many areas seems to consist of large antelopes like gemsbok (*Oryx gazella*) and wildebeest (Cooper, Holekamp, and Smale 1999, Kruuk 1972, Mills and Bearder 2006). Smaller species of antelope, like gazelles (*Gazella sp.*) are also exploited, but due to their smaller body size their caloric contribution to the diet is usually insignificant. During a study of a group of spotted hyenas in the Masai Mara for example, 297 instances of exploitation of a wildebeest carcass were witnessed and 240 instances of the exploitation of a Thomson's gazelle (*Gazella thomsoni*) carcass. Taking body size into account, wildebeest carcasses provided about 47.7% of the dietary biomass, while Thomson's gazelles provided an estimated 4.3% (Cooper, Holekamp, and Smale 1999, 153).

When hunting, spotted hyenas often preferentially target either young or old individuals. For example, in the Serengeti, 36% of wildebeest that are killed are under one year of age, and 30% are senile. With zebras in the same area, 48% of hunted individuals are under four years old and 17% are senile. In the Kalahari Desert, 31.7% of prey killed by hyenas are gemsbok younger than one year of age, while 11.5% of the killed animals are wildebeest of similar age (Fosse 1996, Fosse 1999).

31 This species weighs up to 230 kg. according to Mills and Bearder (2006).

In addition to hunting, spotted hyenas scavenge. However, the contribution of scavenging can be unimportant in the diet of spotted hyenas. It is thought that the amount of food procured by scavenging is dependent on the ecological situation. In areas rich in biomass, scavenging is relatively unimportant. This is the case for both the populations on the Masai Mara plains in Kenya and in the Ngorongoro crater in Tanzania. Here hunted food constitutes 95% and 82% of the consumed food respectively. In the Serengeti and other areas in southern Africa, this percentage is generally 70% or lower. In Kruger park for example, the amount of hunted and scavenged meat both account for about 50% of the consumed diet (Cooper, Holekamp, and Smale 1999, Mills and Bearder 2006).

On the richer plains of East Africa, small and medium-sized ungulates are more abundant than in southern Africa. In the latter area, megaherbivores form a much larger proportion of the herbivore guild. Therefore, larger amounts of carrion are available in southern Africa than in eastern Africa (Cooper, Holekamp, and Smale 1999, 158). At least in eastern Africa the low predictability of available carrion, as well as the low patch quality of carrion, results in spotted hyenas in a preference for hunted food (Cooper, Holekamp, and Smale 1999, 159).

In conclusion we have seen that spotted hyenas adapt their foraging behaviours to the ecological setting. For example, close to aquatic resources, they have been shown to be capable of fishing for example, and at least one population routinely hunts small Nile crocodiles (*Crocodilus niloticus*) (Lam 1992, 398). At least some of the variability in the prey categories can be explained in terms of ecological variation. In more closed areas, where group size is smaller, generally smaller species are hunted than in open areas. Moreover, the focus on young animals seems to be more important in more closed areas (Brugal, Fosse, and Guadelli 1997, 174). Most importantly, the amount of scavenged food in the diet seems to vary according to the ecological circumstances in which a hyena population finds itself (Cooper, Holekamp, and Smale 1999). However, not all the variation in the diet of spotted hyenas has a straightforward ecological explanation (Lam 1992, 404).

7.3 Hyena sites

Most important for our purpose is the fact that hyenas leave a material record of their activities. Much of their life is organised around denning sites which can be divided into two types. Natal dens are isolated sites, used by a usually low-ranking mother to give birth and nurse her cubs. More high ranking mothers usually give birth in the “communal den”, which is used by all individuals of a group (Boydston, Kapheim, and Holekamp 2006). In addition to dens, there are also places where food is cached (Diedrich and Žák 2006, Pokines and Peterhans 2007). This means that we potentially have sites that provide a glimpse of the totality of hyena foraging strategies, something that is harder to come by for other carnivores.

In spotted hyenas, the den is an important focus of the life of a clan. Cubs are raised here and the den plays an important role in social learning, because the young learn their place in the dominance hierarchy and corresponding role in group life at these sites (Drea and Frank 2003, Watts and Holekamp 2007, r658). Remains of prey are transported to these sites, sometimes over large distances (e.g. Brugal, Fosse, and Guadelli 1997, Diedrich and Žák 2006, Lam 1992, Mills and Bearder 2006).³² In contrast to striped and brown hyena, spotted hyenas do not provision their offspring with transported food. Until the young leave the den, they subsist solely on milk (e.g. Pokines and Peterhans 2007, 1915). The bones transported to communal dens are thus usually transported by adults to feed themselves. The function of this behaviour seems to be to decrease the chance of theft by other predators or by group members (Pokines and Peterhans 2007). The bone assemblages therefore reflect the diet of adult hyenas.

The location of the communal den may be relocated frequently throughout the territory of the clan. In one 10-year study, this happened once a month on average. Most denning sites were only used once, although some popular locations were re-occupied periodically (Boydston, Kapheim, and Holekamp 2006). Den moves can be prompted by several factors, like increases in ectoparasite populations, or a disturbance at the den, for example by lions. In other cases, the reasons for moves remained unclear (Boydston, Kapheim, and Holekamp 2006). Increases in foraging efficiency can be cited as reasons for den moves in areas with migratory prey. However, den moves are often made over short distances, averaging about 1.5 kilometre (Boydston, Kapheim, and Holekamp 2006). Still,

32 Unfortunately, exact minimal transport distances are only rarely specified in the literature. A minimum of 4.6 km can be given for dens analysed by Lam (1992). Here crocodiles hunted at Lake Turkana were excavated in a den 4.6 kilometres from the shore.

in areas with a lot of standing prey, the den may be moved regularly may happen in response to changing prey densities

Like foraging behaviour, denning and bone accumulating behaviour in modern hyenas is varied. In southern Africa, spotted hyenas do not seem to accumulate significant quantities of bones in their dens, in contrast to eastern Africa, where this has been observed (Sutcliffe 1970, 1111, Pokines and Peterhans 2007). The evidence from the European Pleistocene record will be discussed at a later stage, but it is clear that cave hyenas did accumulate large quantities of bone materials in their dens. In contrast to the Pleistocene situation, the number of hyena remains present in excavated modern dens is small (cf. Fosse 1997, 16), even though high juvenile mortality has been recorded for modern spotted hyena (e.g. Drea and Frank 2003, Mills and Bearder 2006).

A number of bone assemblages of Pleistocene age that were at least mostly accumulated by hyenas have been excavated in western and Central Europe. A much larger number of sites is known where cave-use seems to have alternated between hominins and hyenas. Furthermore, even cave sites that show a clear hyena signature sometimes contain small numbers of hominin tools (e.g. Villa and Soressi 2000). Bone assemblages associated with hyena activities can be divided into different categories. One type of assemblage points to the use of a site as a denning site, while other assemblage types demonstrate the existence of prey deposit and consumption sites (e.g. Diedrich and Žák 2006). In addition some sites contain bone accumulations that appear to reflect activities of multiple, competing carnivores (e.g. Fosse *et al.* 1998, 54). We must therefore exercise caution when analysing sites in terms of hyena foraging strategies. It appears that denning sites will show the best signature of hyena foraging activities, since these reflect the results of foraging by a group over a period of time.

Some clear characteristics have been proposed to determine whether hyenas were the principal accumulators of a bone assemblage or not. Important indicators of hyena sites are the presence of large numbers of coprolites, sometimes concentrated in “latrines” (Stiner and Kuhn 1992, 437). A high ratio of carnivores to herbivores when compared to hominin accumulation is also common. Moreover, within the carnivore group hyenas themselves are often important. This is because hyenas interact frequently with other carnivores, while in general carnivores tend to avoid each other (Cruz-Uribe 1991). Moreover, the fierce intra-specific competition results in high infant mortality in dens, explaining the abundance of hyena fossils. Furthermore, the presence of abundant gnaw marks on the bones is an important characteristic (Brugal, Fosse, and Guadelli 1997, Stiner 1992). The species of hyena that accumulated the bones is usually determined by the remains of hyenas present in the accumulations, especially in the case of den sites where juveniles die inside the den. In most cases in Pleistocene Europe, the accumulating species was cave hyena.

Large numbers of coprolites and an abundance of hyenid remains are associated with denning sites. These sites can be re-used for long periods of time, especially when these are located in caves (Pokines and Peterhans 2007). This enables us to analyse large time averaged assemblages. Denning sites can be considered comparable to a “Central Place” in hominins in that they are the focal point of the activities of all individuals in a clan. Cubs are born at these sites and they remain there. Spotted hyena infants wage an important struggle for dominance with their siblings very rapidly after they are born. During these struggles 25% of all cubs that are born are killed by their siblings. In addition to cubs being killed soon after birth, in areas where food is scarce, the dominant cub may prevent a subordinate cub from feeding, resulting in death by starvation (Frank, Glickman, and Licht 1991). This results in high numbers of juvenile bones at hyena dens (Drea and Frank 2003). The use of denning sites is spatially organised. Young are raised in small niches of the cave, while food remains are concentrated in larger rooms. The clearest indication of spatial organisation is tends to be concentration of large numbers of coprolites in latrines (e.g. Horwitz 1998, Stiner 1992, Sutcliffe 1970).

However, not all bone assemblages that appear to have been accumulated by hyenas resemble denning sites. In some sites, for example, the hyena age profile is not dominated by juveniles, but by adults (Fosse *et al.* 1998, 53-54). These assemblages appear to reflect competition for prey with other carnivores or conspecifics, for example from a different clan. Another type of site is the prey deposit site, where carcasses have been deposited. This behaviour has also been observed in modern hyenas (Diedrich and Žák 2006, 250). In European contexts, the cool environments of caves provided hyenas with ideal areas for prey storage. Moreover, in some cases, vertical cave systems were available. These were difficult to access and therefore provided well protected storage sites. This analysis will be restricted to denning sites whose hyena population contains predominantly juvenile individuals. It

is hoped that this selection will result in the analysis of assemblages showing minimal influence from other carnivores as opposed to analysing assemblages in which adult hyenas are abundant.

It is hoped that bone assemblages from such sites, provide a more reliable image of cave hyena foraging strategies than sites with “mixed” assemblages. Nevertheless, the nature of hyena den assemblages already implies some biases with regard to the bone collection deposited at the site. The most important factor is the fact that cave hyenas, like modern spotted hyenas, were adapted to destroy large bones. This adaptation enables them to scavenge carcasses without much meat, because they can still exploit greasy bones and marrow, in contrast to for example felids (*e.g.* Blumenschine 1987). This behaviour results in the preferential destruction of certain categories of bone. Especially small species will be underrepresented in the Number of Identified Specimens (NISP) of a site: usually only the cranial skeleton of small ungulates is present at Pleistocene dens (*e.g.* Brugal, Fosse, and Guadelli 1997, Diedrich and Žák 2006, Fosse 1996, Lam 1992). In larger species, whose bones are more difficult to destroy, the overrepresentation of cranial remains decreases. Since more identifiable skeletal parts have survived, larger species will therefore be overrepresented in hyena den assemblages.

Another important point concerns hyena transport behaviour. Hyenas transport remains of prey animals to their dens. This transport can take place over quite great distances. Sometimes two animals even cooperate. Lam (1992, 392) for example, describes a spoor consisting of two sets of spotted hyena tracks, with the drag mark of a crocodile tail between them. The transport behaviour may introduce a bias in the species that are represented at den sites. Large species may be transported less often, as is also the case in hominin sites (see chapter 3). On the other hand, if a small animal is captured and multiple hyenas feed on it, there may be few remains left to transport to the den. Therefore, counterintuitively, small animals may be underrepresented at den sites, since they provide too small a package to share with multiple individuals.

In modern hyena sites, on the other hand, it has been observed that the ratio of represented species strongly resembles the actual ratios in which the species are present in the environment (Stiner 1992, 446). This suggests that the biases influencing the survival of bones in hyena dens sites may not be too drastic.

7.4 Expectations for the study of Pleistocene hyenas

The foregoing discussion of modern spotted hyenas enables us to model the likely behaviour of the closely related cave hyena. We will assume that cave hyenas were as large as Neanderthals, which means that 300 kilograms would be the expected upper limit of the size of their prey. In the case of group foraging, larger species may have been taken, however spotted hyenas appear to prefer foraging alone in many cases.

Therefore, we expect Pleistocene European hyenas, like modern day spotted hyenas, to focus on medium-sized ungulates, for example red deer or reindeer. These could be hunted solitarily and in groups. They are therefore expected to be well-represented in hyena bone assemblages. Larger prey species, like horses or bovids are expected to be rarer, since they had to be taken in groups. Because of the versatility of foraging strategies in spotted hyenas, consisting of solitary hunting, group hunting and scavenging, we expect that hyenas will have had a broad diet. Since scavenging is practised frequently and hunting is focussed on the weak individuals, we expect the age profiles of prey animals at cave hyena sites to be biased in favour of juvenile and senile individuals.

7.5 Case-studies

I will analyse cave hyena foraging strategies on the basis of two French sites that have been published in reasonable detail. Firstly, I will discuss Lunel-Viel, an early site. On the basis of faunal remains, this site can be dated to the Middle Pleistocene. Secondly I will discuss the site of Camiac, which is dated to MIS 3.

7.5.1 Lunel-Viel

Near the village of Lunel-Viel, located between Nîmes and Montpellier, in the Hérault département, a system of four caves has been discovered. The cave designated Lunel-Viel 1 was found to contain Pleistocene faunal remains in the 19th century. In the 20th century, a team led by Bonifay carried out excavations in this cave, which yielded a large bone assemblage (over 8000 pieces identified to

anatomical and/or species level), and a small stone artefact assemblage (Fosse 1996, 47). Based on the recovered faunal remains, the site has been dated to the middle part of the Middle Pleistocene, to about 350 ka. During the excavation, 11 *couches* were recognised. These have been grouped into two assemblages, a lower (inf.) assemblage, containing *couches* 6-11 and an upper (sup.) assemblage containing *couches* 1-5 (Fosse 1996). These two assemblages differ slightly in character. The site provides us with a large and time-averaged assemblage to which OFT can be applied.

Several lines of evidence suggest that the bones recovered were accumulated by cave hyenas. Firstly, hyena remains (mostly cave hyena, but also small numbers of *Hyaena prisca*) were found in the excavations. Additionally, numerous hyena coprolites were recovered. Moreover, gnaw marks are visible on the “quasi-totality” of recovered herbivore bone materials (Fosse 1996, 55). Indexes of the manner of fracturation of the bone have been compared to reference collections of both hunter/gatherer and hyena bone collections, compiled by Bunn (Bunn 1983). These comparisons show that the manner of bone breakage is comparable to that seen in modern hyena dens (Fosse 1996, 51-52).

However, there are some differences between the upper and lower assemblages. First, the number of bones in the Upper Assemblage is smaller than in the Lower one. Conversely the Upper Assemblage contains more stone artefacts than the Lower Assemblage. In the upper level, the identified bones outnumber artefacts by a ratio of 2.7, while in the lower level this ratio is 10.6 (Fosse 1996, 73). Refitting studies have shown that the association of the stone artefacts with the bone assemblage accumulated by hyenas is the result of post-depositional processes. The artefacts were probably displaced from the cave entrance downslope into the interior of the cave where

the hyena bone assemblage was accumulated (Villa and Soressi 2000, 209). Another difference between the Upper and the Lower Assemblage is the hyena population itself. In the Upper Assemblage, the hyena sample is dominated by adults, while in the lower assemblage it is dominated by juveniles (Fosse 1996, 70). The Lower Assemblage thus shows a stronger hyena signature. The fact that very young animals dominate the hyena population suggests that it was a denning site. Hence, during the formation of the Lower Assemblage, hyenas used this cave for long periods of time rearing their vulnerable cubs. We can therefore be certain that hominin use of the cave was ephemeral during this time. The analysis is thus limited to this assemblage.

The NISP counts of the recovered bone material from Lunel-Viel are listed in table 7.1. The lower assemblage is heavily dominated by cervids, with aurochs (*Bos primigenius*) being second in importance and cave hyenas themselves in third place. For the aurochs sample, the ratio between the sexes could be determined because of their sexual dimorphism. In the lower assemblage, it appeared that 33% of the assemblage was male, while 67% was female (Fosse 1996, 78).

Cranial elements are overrepresented in the cervid sample. This corresponds to the observations about small ungulates at other Pleistocene dens mentioned in the previous paragraph. The dominance of these elements is reduced in the equids and they are quite rare compared to postcranial bones in the bovid sample (Fosse 1996, 50). With regard to the longbones, especially humerus and tibia, the distal ends are overrepresented. This is to be expected, because the proximal ends are more spongy and contain more marrow. They were therefore preferentially consumed. Moreover, cylinders, longbones missing both diaphyses, which are characteristic of hyena dens have also been recovered (Fosse 1996, 50). It appears that just like in modern spotted hy-

	NISP	
Species	Lower	Upper
Cervids (<i>Cervus elaphus</i> + <i>Euctenoceros mediterraneus</i>)	2707	523
<i>Bos primigenius trocheros</i>	893	324
<i>Crocuta spelaea intermedia</i>	562	223
<i>Equus mosbachensis palustris</i>	373	152
<i>Canis lupus lunellensis</i>	99	28
<i>Equus hydruntinus</i>	53	24
<i>Sus</i> sp.	46	14
<i>Dicerorhinus etruscus</i>	39	13
<i>Hyaena prisca</i>	16	3
<i>Cuon priscus</i>	7	1
<i>Panthera spelaea</i> ³³	5	6
<i>Felis (Lynx) spelaea</i>	5	2
<i>Ursus</i> cf. <i>deningeri</i>	5	-
<i>Capreolus</i> cf. <i>süssenbornensis</i>	4	-
<i>Panthera pardus</i> ³⁴	4	2
<i>Bison</i> cf. <i>schoetensacki</i>	2	-
<i>Meles thoralis spelaeus</i>	1	1
<i>Vulpes vulpes</i>	1	11
<i>Felis (Lynx)</i> cf. <i>pardina</i>	1	-
<i>Felis monspessulana</i>	1	-
<i>Mustela palerminea</i>	1	
<i>Lutra</i> sp.	-	2
Total	4825	1329

Table 7.1: The faunal assemblage from Lunel-Viel. Based on (Fosse 1996, 71).

33 Multiple species are listed as *Felis spelaea*. This species was listed under class A Carnivores. Moreover, Fosse (1996) refers to lions in his text.

34 Referred to as *Felis (Panthera) lunellensis* by Fosse 1996). Testu (2006) determines it to be *Panthera pardus*.

ena dens, distal appendicular bones and cranial elements are overrepresented (compare Fosse 1996, 74-76, Pokines and Peterhans 2007).

For some groups, the age structure of the represented animals could be estimated, based on the wear of their teeth. The age structure of the largest group, the cervids, is illustrated in graph 1. Age-classes I and II represent juvenile animals, while age classes X and above represent old individuals. It is clear that in the lower level, juveniles are best represented. Next to these two age-classes, young adults from age-class IV and V were present in relatively large quantities. The age structure of the horses is illustrated in graph 2. The equid sample is dominated by individuals from the 5-6 year-old and 3-4 year-old categories. However, the age categories from 7 to 10 are also quite well represented (Fosse 1996, 53, 68). Prime-age in horse is generally considered to be the age category between 6 and 9 years old (e.g. Fernandez, Guadelli, and Fosse 2006).

In the bovid sample it must be noted that dental remains are rare. However, combining dental remains with the stages of fusion of postcranial bones, some indication of the age of the animals represented at the site is listed by Fosse (1996, 53). According to him, the bovid sample from the lower assemblage contained five young animals and 28 adults. In hyenas, as discussed above, the lower assemblage is dominated by juvenile animals. In wolves, the sample consisted of ten young

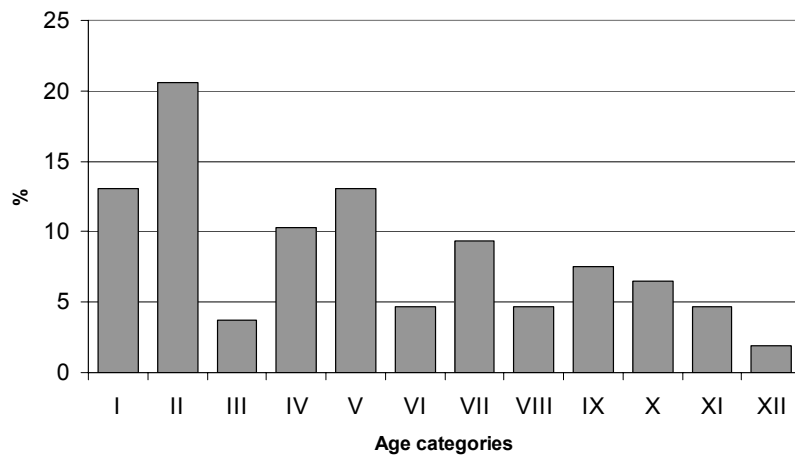


Figure 7.1: Age structure of the cervids represented in the lower assemblage. Adapted from (Fosse 1996, 68).

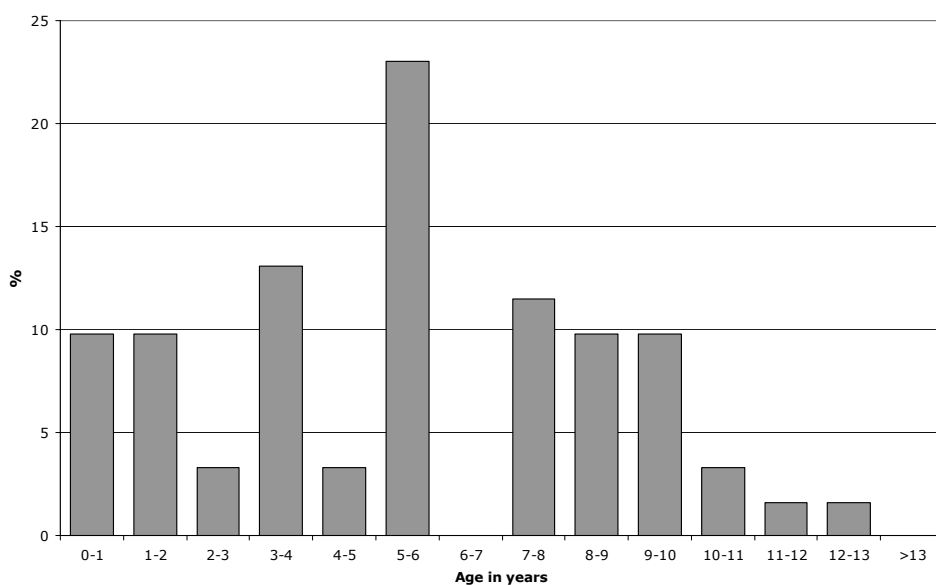


Figure 7.2: Age structure of the horses represented in the lower assemblage. Adapted from (Fosse 1996, 68).

Species	MNI Young	MNI Adult
<i>Bos primigenius</i>	5	28
<i>Equus hydruntinus</i>	3	3
<i>Sus</i> sp.	2	3
<i>Dicerorhinus etruscus</i>	3	2

Table 7.2: Age categories of the less common species represented in Lunel-Viel in terms of MNI. Based on (Fosse 1996, 54).

Rank	Species	Weight	NISP
1	<i>Dicerorhinus etruscus</i>	1250 ³⁵	39
2	<i>Bison</i> cf. <i>schoetensacki</i>	650	2
3	<i>Bos primigenius trocheros</i>	600	893
4	<i>Ursus</i> cf. <i>deningeri</i>	560	5
5	<i>Equus mosbachensis</i>	335	373
6	<i>Cervus elaphus</i>	200	2707
7	<i>Panthera spelaea</i>	195	5
8	<i>Equus hydruntinus</i>	188	53
9	<i>Panthera pardus</i>	90	4
10	<i>Sus</i> sp.	89	46
11	<i>Crocota crocota</i>	70	562
12	<i>Canis lupus lunellensis</i>	45	99
13	<i>Hyaena prisca</i>	40 ³⁶	16
14	<i>Capreolus</i> cf. <i>sussenbornensis</i>	32 ³⁷	4
15	<i>Felis (Lynx) spelaea</i>	20	5
17	<i>Cuon priscus</i>	15	7
18	<i>Felis (Lynx)</i> cf. <i>pardina</i>	10	1
19	<i>Meles thorali spelaeus</i>	10	1
20	<i>Felis monspessulana</i>	5	1
21	<i>Mustela palerminea</i>	<1	1

Table 7.3: Ranking of the animals present in the Lunel-Viel assemblage. Weights from: (Brook and Bowman 2004, Louguet-Lefebvre 2005).

adults and two adults (Fosse 1996, 54). With regard to other animals, present in smaller numbers, it appears that the small equid (*Equus hydruntinus*) is represented in the lower assemblage by three young and three adult animals. Boar (*Sus* sp.) is represented by at least two young animals, one young adult, one prime-aged individual and one very old animal. Lastly, the rhinoceros (*Dicerorhinus etruscus*), is represented by three young and two adults in the lower assemblage (Fosse 1996, 54).

Unfortunately, there is no pollen data that can be used to reconstruct the environment; hence reconstruction must be attempted on the basis of the species that are present in the assemblage. The large mammal fauna of the Lower Assemblage is indicative of a temperate climate. In the uppermost layer belonging to the lower assemblage, bird and tortoise remains indicate climatic warming (Fosse 1996, 48). This layer only contained about 10% of the bone assemblage from the lower assemblage. We can therefore assume that this assemblage was largely formed during a period of temperate conditions. The dominance of cervids is interpreted by Fosse (1996) as reflecting the importance of forested areas in the environment, while equids provide evidence of the existence of open areas in the surroundings of the site. Of course, the foraging preferences of hyenas may influence the data on which the environmental reconstruction is based. Fortunately, birds were also found at the site. It is unlikely that they constituted an important part of the hyena diet. These animals therefore provide us with information on the environment that is independent of hyena preferences. Three groups of bird species are important. Species preferring wooded areas are best represented, followed by species preferring rocky and open terrains (Fosse 1996, 48).

As for the hominin sites discussed in the previous chapters, I constructed a ranking of the species present based on their body weight, listed in table 7.3. A comparison of the ranking with the table listing the identified bones at species level shows that the most highly ranked species, rhinoceros, was not exploited heavily. The same is true for Bison and Deninger's bear, both of which are even rarer in the assemblage. The next most highly ranked ungulates are present in

large numbers. The smallest, cervids were exploited most intensively, but horse and aurochs are also present in large numbers. Wolves are also present in reasonably large numbers, even though they are not very highly ranked. However, many studies indicate that aggression between different carnivore species is a common phenomenon. In addition to trying to steal carcasses from carnivores of other species, carnivores often kill other carnivores (see overview in Van Valkenburgh 2001, 104-105). Usually, the killed carnivores are not consumed, though. However, since the wolves were probably transported to the site, this may have been the case here.

The hyenas responsible for the accumulation of this bone assemblage thus preferentially targeted medium to large sized ungulates. The smaller species may be underrepresented due to differential bone destruction. Moreover, smaller species may have been completely devoured at the kill site and therefore transported to the den site less often.

35 According to Louguet-Lefebvre (2005), this is a small species, with a shoulder height of 1.5 m., while for *Dicerorhinus kirchbergensis* a shoulder height of 2.5m is given. She did not provide an estimate for *Dicerorhinus hemitoechus* but does state that it is of medium height. I therefore estimated this species at 60% of *D. kirchbergensis* as listed by Brook and Bowman (2004).

36 I used the estimates provided by Brook and Bowman (2004) for *Hyaena hyaena* and *Hyaena brunnea*, since they are probably closely related to *Hyaena prisca*, for which no estimate was provided.

37 I used the estimate provided by Brook and Bowman (2004) for *Capreolus capreolus*.

Species	Density (ind/km ²)
<i>Cervus elaphus</i>	0.7166
<i>Bos primigenius trocheros</i>	0.3395
<i>Crocota crocuta</i>	0.0431
<i>Equus mosbachensis</i>	0.5046
<i>Canis lupus</i>	0.0525
<i>Equus hydruntinus</i>	0.7474
<i>Sus scrofa</i>	1.2428
<i>Dicerorhinus etruscus</i>	0.2119

Table 7.4: Reconstructed population densities of the most important species at Lunel Viel. For methodology see previous chapters.

The abundance of cervids in the assemblage can be attributed to their encounter rate. This can be approximated by reconstructing their population density. As pointed out in the previous chapters, population density is dependent on body weight. In table 7.4, the population densities for the most common species in the Lower Assemblage are listed. Based on reconstructed population density alone, we would expect equids to be better represented than bovids. The fact that this is not the case may be caused by the environment. If wooded areas predominated in the surroundings of Lunel-Viel, there would be less suitable habitat for equids than for aurochs, which are more at home in wooded areas. Modern equids spend between 80 and 99% of their time in the grassland zones of their range. Wooded areas are only sought out for shelter during storms etc. (Burke *et al.* 2008, 897). If forest was the dominant vegetation type, the area was probably more suitable for cervids and aurochs than for equids and

bison. However, the near-absence of bison is striking. They are more adapted to open areas than aurochs, but since equids were also present in large numbers, suitable habitat was probably available to them. They may have been at a disadvantage because they had to compete both with aurochs and horse in parts of their niche. These species may have been better adapted to the specific environmental facets of the area, leaving the bison that has an intermediate adaptation little forage. An alternative explanation is that its rarity is due to identification bias. *Bos* and *Bison* bones resemble each other, so bones belonging to bisons may have been erroneously classified as Aurochs.

With regard to cervids there is a clear focus on the exploitation of juvenile individuals; senile individuals are rare. I assume that most of the remains that have been recovered were obtained by hunting instead of scavenging. This is hard to prove however, since high juvenile mortality also occurs naturally. The fact that old individuals are less common than adults suggests that hunting cervids may have been preferred to their scavenging. In horses the focus is not on juvenile animals, but on young adults. However, mature individuals are also well represented. The age structure of the horses suggests that they were not obtained by scavenging, since adults are very well represented. They were thus probably hunted by hyenas. The same seems true for the bovid sample, although the data provided on the age structure are less detailed. However, juveniles form about 15% of the assemblage, while the rest of the animals represented were adults. Unfortunately, data on whether senile individuals were present in the assemblage is not presented. Still on the basis of the age-class data that show a majority of adult individuals, we can assume that hunting was the main strategy for the exploitation of aurochs.

In addition to the three dominant ungulates, a few species represent between two to just under one percent of the assemblage each. In the case of wolves, young adults are largely dominant, and the only other age-group represented is that of the mature adults. Their presence should probably be explained as being the result of aggression by cave hyenas to competing carnivores. We must assume that wolves were probably hunted on encounter. The presence of equal numbers of young and adult animals for *Equus hydruntinus* appears to be the result of hunting, although again, we cannot be certain. The pattern presented for wild boar is difficult to interpret. In addition to the two juveniles, one senile individual is present, while one young adult and one mature adult are also represented. Scavenging can account for the presence of these weak categories, but the number of represented individuals is too small to draw conclusions from.

The exploitation of rhinoceros at Lunel Viel may be explained as the result of scavenging, since this very large animal is quite difficult to hunt. Modern-day hyenas rarely hunt animals larger than 250 kg.³⁸ Moreover, pachyderms provide the best scavenging opportunities in actualistic studies in East Africa (cf. Blumenshine 1987). The fact that more young are present in the assemblage can be cited in support of this assumption, but the pattern is not conclusive. Another factor that can be cited in favour of a scavenging strategy in this case is the encounter rate. Based on reconstructed population densities cervids should be encountered 3.3 times more often than rhinoceros. In the assemblage, rhinoceros is far rarer than one would expect if it were hunted on encounter. This sug-

38 Less than 1% in a study covering 801 cases (Cooper, Holekamp and Smale 1999).

gests that exploitation of rhinoceros was quite a rare event. Presumably, the number of scavengeable carcasses in the landscape was not very high and competition was often intense (cf. Blumenschine 1987). Therefore, not too many remains may have been available to transport back to the site.

At this site hunting of medium and large sized ungulates provided the mainstay of the diet of cave hyenas. This is apparent even though smaller species may be underrepresented because they will not have been transported to the site as frequently. Still, red deer is also in the size category that is expected to suffer a large degree of bone destruction (e.g. Brugal, Fosse, and Guadelli 1997, Fosse *et al.* 1998, Villa *et al.* 2004). Therefore, the rarity of boar, *Equus hydruntinus*, roe deer and other small species must at least partly reflect hyena foraging strategies. The importance of scavenging is hard to ascertain, but is expected to be relatively insignificant in terms of its caloric contribution to the diet. This is thought to be the case in view of the age profiles of the species that are represented at the site. Still, the forested environment indicated by the faunal assemblage must have provided hyenas more scavenging opportunities than their modern savannah habitat, because visibility of carcasses is lower in wooded environments. It has been shown that in East Africa carcasses remain available to scavengers longest in wooded zones of the landscape (cf. Blumenschine 1987). The effect of the forested environment on scavenging opportunities may be augmented by the temperate climate in which decay processes are slowed compared to modern day Africa (Fosse *et al.* 2004).

7.5.2 Camiac

Camiac is another example of a cave site with a bone assemblage accumulated by hyenas (Guadelli *et al.* 1988, Guadelli 1989). It is located in the southwest of France, and is situated at the edge of calcareous terrace, overlooking the valley of tributary of the Canodonne river. This valley is connected to the Dordogne valley (Guadelli *et al.* 1988, Guadelli 1989). This site was strategically situated near the confluence of different river valleys and provided an excellent location to monitor prey. The site has been dated using ^{14}C of a bone fragment, yielding an age of $35.100 \pm 2000/-1500$ bp. (Guadelli *et al.* 1988, Guadelli 1989).

The site consists of a small cave and an area of plateau in front of it, from which a large collection of bone materials was recovered. The excavation also yielded a small stone assemblage, which shows that the site was used by both hominins and hyenas. There are convincing arguments to interpret the bone assemblage as reflecting hyena foraging strategies though. First, the concentration of bones was excavated in the southern part of the excavated area, while the majority of artefacts was

recovered in the northern part of the excavation. Second, there are no hominin traces of exploitation on the bones, while hyena traces are abundant. Gnaw marks are very common, on most long-bones, the epiphyses have been destroyed and many bones show signs of having been ingested by hyenas (Guadelli *et al.* 1988, 61). Moreover, hyena coprolites were also common in the excavated area. Unfortunately, no age profile is available for the hyena remains, but the fact that they are relatively numerous may also be cited in support of the interpretation of this assemblage as having been accumulated by hyenas.

The faunal assemblage of Camiac is presented in table 7.5. It is quite a diverse assemblage, especially in view of the number of bones that was identified (compare the number of species with Taubach or Biache-Saint-Vaast for example). The assemblage is dominated by horse (*Equus caballus*), bovids (mostly bison (*Bison priscus*)) and woolly rhinoceros. If we assume that the bones determined as “bovid” represent both bison and aurochs in the same proportions as the bones that could be determined to species level, 260 of the bovid bones would have belonged to bison. I will therefore assume that 299 bison bones are represented in the assemblage and 38 aurochs bones. Following this line of reasoning, bison would be the second best represented species at the site, while aurochs would be fifth best represented, falling between cave hyena and mammoth.

Some data about the age-structure of the taxa present in the assemblage is reported by Fosse (1996). He bases his report on a

Species	NISP	MNI
<i>Equus caballus gallicus</i>	337	12
Bovines indet.	293	
<i>Coelodonta antiquitatis</i>	200	26
<i>Crocota crocuta spelaea</i>	76	9
<i>Bison priscus</i>	39	10
<i>Mammuthus primigenius</i>	22	5
<i>Megaloceros giganteus</i>	19	4
<i>Cervus elaphus</i>	12	1
<i>Equus hydruntinus</i>	8	2
<i>Panthera spelaea</i>	5	2
<i>Bos primigenius</i>	5	1
<i>Vulpes vulpes</i>	5	1
<i>Ursus spelaeus</i>	4	2
<i>Canis lupus</i>	2	2
<i>Panthera spelaea</i> var. <i>cloueti</i> ?	2	1
<i>Alopex lagopus</i>	2	1
<i>Sus scrofa</i>	2	1
<i>Rangifer tarandus</i>	2	1
Total	1035	81

Table 7.5: The faunal assemblage recovered at Camiac. From (Guadelli *et al.* 1988, 62).

	NISP	
Group	Young	Adult
Cervids	-	12
Equids	19	326
Bovids	3	327
Rhinocerotids	11	182
Proboscideans	4	15

Table 7.6: The age structure of the main taxa present in the faunal assemblage, as reported in (Fosse 1996, 78).

personal communication by the lead author of the paper on Camiac that was available to me. Unfortunately, the age structure is not given in MNI counts based on dentition, but in NISP (nombre de restes). This data is reproduced in table 7.6. These counts do not seem very reliable to me, since all the identified bones are incorporated in the age structure. Not every skeletal part is very suitable for age-determinations however. Different types of bone fuse at different moments in time, etc. Moreover, juvenile bones will also be preferentially destroyed. Bones of adults have a much better chance of survival, therefore juveniles may be underrepresented using this method.

Only small percentages of the bones identified to species show indications of belonging to juvenile individuals. For the best represented group, equids this is about 5.5%, in rhinocerotids this is about 5.7%. In bovids, the percentage is lowest, at 0.9%, while in mammoths, it is 21%. Regarding the latter species, it has to be realised of course that the sample is very small. The same is true for cervids, in whose sample none of the bones belonged to a juvenile individual.

The environment of the site at the time of occupation can be reconstructed from the faunal assemblage and from pollen recovered from the coprolites found at the site. The species list reveals a number of cold adapted species, like reindeer (*Rangifer tarandus*), polar fox (*Alopex lagopus*), mammoth (*Mammuthus primigenius*) and woolly rhinoceros (*Coelodonta antiquitatis*). In addition, the large number of horse remains and the dominance of bison over aurochs bones suggest that the environment was quite open. The presence of red deer and especially wild boar (*Sus scrofa*) shows that forested areas were also present in the surroundings of the site.

The environmental reconstruction based on the species that are present in the assemblage is corroborated by analysis of pollen present in the hyena coprolites that were recovered at the site. 48% of the pollen in the coprolites is arboreal. Pine (*Pinus*) makes up 46.8% of the pollen, while one percent belonged to birch (*Betula*) (Guadelli *et al.* 1988, 63). The sediments of the site were also analysed for pollen, yet these yielded a Mediterranean flora. These pollen must be intrusive in the sediments, since both the bone assemblage and the coprolites point to radically different environmental circumstances.

A ranking of the species present in the assemblage has been compiled in table 7.7. It is clear instantly, that apart from mammoth, the heaviest groups of species present, woolly rhinoceros and bovids are intensively exploited. The most heavily exploited species, horse (*Equus caballus*), is ranked lower, but is still a large species. Other species are represented less strongly in the assemblage.

It is striking that the represented prey species are mainly large herbivores and in the case of woolly rhinoceros even a megaherbivore. As has been pointed out, it is likely that smaller species are underrepresented in hyena den assemblages. Therefore, it can be hypothesised that cervids like red deer and reindeer were probably more important in cave hyena foraging strategies practised at this site than their representation in terms of NISP suggests. On the basis of this assemblage it seems clear that the focus of hyenas was probably geared towards the larger species that were present in the environment. Moreover, cranial remains of smaller ungulates preferentially survive the hyenas' destruction, if these species were important in hyena foraging strategies, at least cranial remains would have been well represented at this site, yielding a higher MNI. The importance of cervids and other smaller species like boar was therefore limited.

Since only very imperfect information on the age structure has been published for this site we cannot draw too many conclusions about the age classes exploited by cave hyenas here. Adult bones are dominant in all taxa except for the proboscideans. Based on this data, for most cases, we would expect the represented animal species to have been exploited by hunting adults. Juvenile bones are more prone to destruction by hyenas however, so that juvenile individuals are probably underrepresented in the bone assemblage. Therefore the importance of scavenging may be underestimated slightly.

This site shows that hyenas preferentially exploited very large species. Equids seem to have been the most heavily exploited species, closely followed by bison. Most striking is the fact that woolly rhinoceros accounts for almost 20% of the assemblage. Considering that it would probably have been present in low population densities (See table 7.8) compared to the smaller species, we can conclude

Rank	Species	Weight	NISP
1	<i>Mammuthus primigenius</i>	5000	22
2	<i>Coelodonta antiquitatis</i>	2900	200
3	<i>Bison priscus</i>	650 ³⁹	39 ⁴⁰
4	<i>Bos primigenius</i>	600 ⁴¹	5 ⁴²
5	<i>Ursus spelaeus</i>	500	4
6	<i>Megaloceros giganteus</i>	450	19
7	<i>Equus caballus</i>	335	337
8	<i>Cervus elaphus</i>	200 ⁴³	12
9	<i>Panthera spelaea</i>	195 ⁴⁴	5
10	<i>Equus hydruntinus</i>	188	8
11	<i>Sus scrofa</i>	89	2
12	<i>Rangifer tarandus</i>	86 ⁴⁵	2
13	<i>Crocota crocuta</i>	70	76
14	<i>Canis lupus</i>	45	2
15	<i>Alopex lagopus</i>	5	2
16	<i>Vulpes vulpes</i>	5	5

Table 7.7: Ranking of the animals represented in the assemblage of Camiac. Weights based on (Brook and Bowman 2004, Louquet-Lefebvre 2005).

Species	Density (ind/km ²)
<i>Equus caballus</i>	0.5046
<i>Bison priscus</i>	0.3216
<i>Coelodonta antiquitatis</i>	0.1163
<i>Crocota crocuta</i>	0.0431
<i>Bos primigenius</i>	0.3395
<i>Mammuthus primigenius</i>	0.0803

Table 7.8: Reconstructed population densities for the most important species at Camiac.

that woolly rhinoceros was preferentially targeted by hyenas. The low number of juvenile bones in the sample may even point to them being hunted with a focus on adults. On the other hand, it is unclear how many of the adult bones in the sample actually belonged to old individuals. In view of this species' body size I prefer to regard scavenging or hunting of weak individuals as the explanation for their presence at the site.

7.6 Discussion

The two case-studies have shown that foraging behaviours in Pleistocene European cave hyenas deviate from the expectations that were formulated on the basis of comparative studies of spotted hyenas. The focus on cervids in Lunel-Viel is in keeping with what would be expected on the basis of spotted hyena behaviour in Africa. However, the importance of bovids at both Lunel-Viel and Camiac is remarkable. Animals of that size are only rarely hunted by spotted hyenas. The largest prey species they take down regularly is zebra (Cooper, Holekamp, and Smale 1999). The presence of large numbers of aurochs at Lunel-Viel and bison at Camiac shows that the Pleistocene European hyenas were capable of routinely killing much larger prey.

The presence of woolly rhinoceros at Camiac is even more surprising. This species is more than three times larger than the large bovids that were present. Woolly rhinoceros is present at other hyena sites in France, but usually contributes small percentages of the NISP. Nevertheless at a number of sites in the Bohemian Karst, in accumulations produced by hyenas, quite a large number of woolly rhinoceros remains have been found, sometimes accounting for more than 20% of the NISP. In these cases hunting of juvenile animals up to about one year of age seems to have been practised,

39 My estimate since I deem the estimates provided by both Brook and Bowman (2004) and Louquet-Lefebvre (2005) to be unrealistically low.

40 A large number of the bones identified as "bovines indet." can be assumed to have belonged to this species

41 My estimate, since I deem the estimates provided by both Brook and Bowman (2004) and Louquet-Lefebvre (2005) to be unrealistically low.

42 Some of the bones identified as "bovines indet." must be added to this figure

43 My estimate, since the estimates provided by both Brook and Bowman (2004) and Louquet-Lefebvre (2005) are unrealistically high.

44 *Panthera spelaea* var. *cloueti* is assumed to be equal in rank to *Panthera spelaea*.

45 I used the estimate provided by Pushkina and Raia (2008) since the estimate provided by Brook and Bowman (2004) is very low (60 kg.).

while adults were probably scavenged (Diedrich and Žák 2006, 258). Whether scavenging or hunting provided the bulk of woolly rhinoceros at the site, it is clear that this species was preferentially targeted by cave hyenas. We would expect this species to be present in low population densities, therefore encounter rate with this species would have been low; much lower at least than encounter rates with cervids, bovids and equids would have been. Even though this species is overrepresented because its bones are very hard to destroy (*e.g.* Diedrich and Žák 2006, 264), the importance of this heavy species must have been high in caloric terms.

As pointed out, the scavenging opportunities provided by pachyderms are good, since meat is available for a long time and large amounts of it are available. Their availability will have lasted longer in MIS 3, compared to the modern day African ecosystems in which actualistic studies are executed (*e.g.* Blumenshine 1987). Therefore scavenging of pachyderms may have been a productive foraging strategy. However, if this was practised by hyenas, we would also expect a greater number of proboscideans at hyena den sites. These are rare at both Camiac and the Bohemian Karst (Diedrich and Žák 2006). I deem it possible that hunting woolly rhinoceros was practised by hyenas. They would probably have focused on juvenile or weakened individuals. In this regard a detailed study of the remains from Camiac would be helpful.

There is another possible explanation though. Actualistic research suggests that not even hyenas are able to exploit pachyderm carcasses fully, since the skin is difficult to penetrate. When hyenas leave these carcasses, food would still have been available. If Neanderthals had primary access to megaherbivores, their activities may thus have opened up new scavenging opportunities to hyenas. Since scavenging is a well-established foraging strategy in hyenas and the large amounts of food provided by pachyderms will probably not have been exploited fully by Neanderthals, ravaging megaherbivores exploited by Neanderthals may be a likely scenario.

This brings us to the important methodological problem of identifying the accumulating agent of the assemblages under consideration. Both sites that were analysed contain stone artefact assemblages in addition to the bone assemblages. This is not uncommon in the case of hyena dens (Villa and Soressi 2000), however it does open up the possibility that the bone assemblages were not solely accumulated by hyenas. At Lunel-Viel the association of artefacts with the bone assemblage was probably the result of post-depositional processes (Villa and Soressi 2000, 209). This view is strengthened by the strong presence of juvenile hyenas. Hyenas were able to raise their vulnerable cubs in this cave, which suggests that there was minimal disturbance by hominins. Unfortunately, the case is not as clear-cut at Camiac. The bone assemblage has all the characteristics of a hyena assemblage. Moreover, an abundance of coprolites and the important presence of hyena itself all suggest use as a den. This is strengthened by the absence of hominin inflicted marks on the bones. Yet hominin influence cannot be totally ruled out. The case for the interpretation of Camiac as a den may be boosted by the publication of the age-structure of the hyenas. If juveniles are an important category this would show that cubs were raised there and hominin influence was minimal.

Few well published age-profiles are available for the prey species represented in hyena dens. The age profiles for the lower assemblage from Lunel-Viel suggest that in cervids the emphasis was on juveniles, although the other age classes are by no means absent. The highest peaks in the graph showing the age-profile for horses concern young adults, but mature adults are well represented. In bovids, the emphasis may have been on adults, but the data are insufficient to be certain. The available data on the age categories of the species represented at Camiac are even poorer, but except for mammoth, the number of juvenile bones seems to be small.

Most authors expect hyenas to focus on weak individuals in populations. It is generally assumed that only hominins consistently hunt prime-aged prey (*e.g.* Steele 2002, 307). In many studies of modern spotted hyenas, a preference for juvenile and senile individuals is apparent. The age profiles for Pleistocene hyena dens do not always conform to this pattern. The pattern for equids at Lunel-Viel for example shows that adults are well represented. A recently published study shows even more clearly that cave hyena strategies may also have focussed on adult animals. At Fouvent, located in the Haute-Saône, a large faunal assemblage was recovered. Only a study of the horse remains found at the site has been published. With 41.2% of the NISP, they were the dominant species represented at the site though, followed by cave hyena with 34.7% (Fosse 1997, 17). The age profile of the equids present at the site is indistinguishable from that of equids at the Middle Palaeolithic sites of Bau de l'Aubesier and Combe Grenal, showing a dominance of horses aged 6-9, or prime-aged individuals (Fernandez, Guadelli, and Fosse 2006, 180).

However, there is a lot of variation in the age profiles of prey animals found in hyena dens. At some sites, young animals do make up an important part of the ungulate animals, and in some cases even represent a majority (Brugal, Fosse, and Guadelli 1997, Fosse 1999). However, some sites show that they were definitely capable of hunting primarily adults of large species like horse.

The fact that cave hyenas hunted larger species of prey than spotted hyenas do, can at least in part be explained by the fact that they were larger than their modern-day counterparts. In general there seems to be a relationship between predator size and prey size, with prey size increasing disproportionately in relation to predator size (see formula in section 4.5) (Radloff and Toit 2004, 410). On the other hand, the estimated weight of the largest common spotted hyena prey, zebra, is about 288 kilos. (Brook and Bowman 2004, Cooper, Holekamp, and Smale 1999). Buffalo is only rarely hunted and according to Cooper Holekamp and Smale (1999, 152-153), only when weakened. This species weighs between 500 to 600 kilos. Bison is heavier than buffalo and was exploited regularly at Camiac, but also at other excavated hyena dens, like Bois Roche (Villa *et al.* 2004). This suggests that in some Pleistocene cave hyena populations, hunting in groups may have been more important than it was to modern-day spotted hyenas, allowing them to take larger prey more often.

A final remark concerns an interesting category of finds amidst hyena bone accumulations, namely antler material. Especially red deer (*Cervus elaphus*) antlers were collected by hyenas. These antlers had nutritional value, since hyenas could chew them and digest the bone collagen. Many of the antlers that are found in these deposits are shed. For example, at Guattari, 56 shed antlers were found, against 13 unshed ones (Fosse *et al.* 1998, 55). This shows that we need to be careful when interpreting collections of shed antlers as the results of hominin activities, since hominins are clearly not the only agents that can be responsible for the accumulation of these items. Whether antler material was collected by hominins or hyenas is often easily distinguished, however. Hyenas are thought to have collected antlers in order to exploit their fat content and they will therefore be gnawed (Fosse *et al.* 1998, 55).

7.7 Conclusion

This chapter has shown that using OFT to differentiate between cave hyena and Neanderthal foraging strategies is difficult. European hyena dens and Middle Palaeolithic bone assemblages show a large overlap in the categories of prey that are present. Both hyenas and Neanderthals were apparently able to systematically target large ungulates, such as horses and bovids. Still, both cave hyena and Neanderthals appear to have been successful in Pleistocene Europe. This suggests that they were both able to monopolise large amounts of biomass. Therefore some differentiation in niches must have existed, otherwise both species would not have been able to co-exist. The results of the analysis do indeed point to a number of differences in the foraging niches of both species which will be listed and discussed below.

The most important difference is in the greater variation in species and age-categories of prey present in hyena dens. This is not unexpected. In modern-day Africa there is a lot of competition among different species of carnivore for similar species of prey. The composition of the carnivore guild in a region is shaped by this competition. In many areas of Africa, the presence of small species of carnivores like cheetah or wild dog is severely limited by the fact that larger predators like lion and spotted hyena consume most of the available biomass and moreover frequently kill smaller predators. In addition, in some areas, the number of hyenas seems to be limited by lions, while in other areas it is the other way round (Owen-Smith and Mills 2008, Van Valkenburgh 2001).

Studies of contemporary predators suggest that overlapping prey choice is a common phenomenon in the predator guild. Differentiation of niches may not be effectuated in the range of species that is taken, but can be effectuated in another field. For example in the timing, with some predators taking certain species at other times than others, *i.e.* differences in seasonality (*e.g.* Stiner 1992, 433). This kind of niche separation may have been present in the exploitation of bears for example. It appears that in many areas hyenas exploit caves in which bears hibernate, scavenging on the remains of bears that died during hibernation (Diedrich and Žák 2006, 260-262). Neanderthals, as shown by both Taubach and Biache-Saint-Vaast assemblages, actively hunted these large predators.

Another obvious difference between the Neanderthal and hyena niche lies in the mode of acquisition and exploitation of prey species. Hyenas practise a significant amount of scavenging in addition to hunting. The amount of scavenging practised may be quite minor in some spotted hyena populations, but it is practised in all populations and in many it does play an important role with

regard to subsistence. Scavenging is such an important strategy in hyenas, that they evolved adaptations geared toward a scavenging way of life, including an acute sense of smell that is used to locate carcasses, a gastro-intestinal tract that can cope with decaying meat, teeth that can crush bones in order to be able to profit from carcasses with little or no meat, etc. (*e.g.* Tooby and DeVore 1987). Hominins probably had different adaptations in order to intercept prey. Instead of an acute sense of smell, they may have used their increased intelligence to predict locations where prey would be and will have ambushed or hunted them at strategic locations. This is shown by the consistent use of sites like Biache-Saint-Vaast and Taubach to kill fixed species of prey.

Subtle niche differences between Neanderthals and cave hyenas may be found in the categories of prey that were taken by both species. Many recent analyses show that Neanderthals most often focussed specifically on prime-aged individuals in ungulates (see examples in chapter 3). Hyenas were able to target prime-aged ungulates, as shown by the equids represented in Fouvent, but it appears that the focus on prime-aged individuals is less clear-cut than in Neanderthals. At present, a focus on prime aged individuals has been demonstrated for some species at some sites, but this focus is less obvious in other den sites and other prey species (*e.g.* Brugal, Fosse, and Guadelli 1997, 174, Fosse, 1999 #696, 82). This suggests that hunting strategies practised by hyenas may have been more variable and more opportunistic than those practised by Neanderthals. This impression is reinforced by the fact that bone assemblages recovered from hyena dens are usually more diverse than those from hominin sites (Fosse 1997, 18).

Both species largely focussed on the same range of prey species. In similar circumstances, Neanderthals would probably focus on a narrower set of species and age categories of prey. Cave hyenas accumulations show more variety, in the form of a larger diversity of species and in represented age-categories.

Another important difference between their niches may be the fact that hyenas are adapted to nocturnal foraging. We assume that Neanderthals, like modern humans and apes were diurnal foragers. Temporal partitioning of resources by adapting activity cycles is a mechanism of niche differentiation that has been observed in nature (Kronfeld-Schor and Dayan 2003, Richards 2002).

Moreover, Neanderthals may have routinely hunted categories of prey slightly higher up in the “spectrum of danger”. In the case of woolly rhinoceros in the Bohemian Karst, cave hyenas seem to have preferentially hunted animals under the age of one. When we compare this with hunting of rhinoceros at Taubach and Biache-Saint-Vaast, Neanderthals seem to have focussed on slightly older individuals. In the case of bears, Neanderthals apparently hunted bears at some sites, while hyenas seem to have profited mostly from individuals that died during hibernation.

As discussed earlier, there is a significant relationship in most predators between predator size and prey size (Radloff and Toit 2004). Hyenas and hominins being in the roughly the same range of weight, would naturally also select the same range of prey categories. Therefore this small difference in focus of hunting may point to a difference in strategies.

One of the ways in which the relationship between predator and prey size can be circumvented is by hunting in groups. Wild dogs in Africa are able to bring down much larger prey relative to their size than most other predators in the same environment. This is because they always hunt in packs (Radloff and Toit 2004, 416). As I have argued, pack hunting was probably more important in cave hyena than it is in modern day spotted hyena. However, if social structure and feeding competition in cave hyena were anything like they are in spotted hyena, hunting large prey in large groups may not have been as profitable for individual cave hyenas. Sharing of food from kills does not seem to be important in spotted hyenas (Mills 1985, Watts and Holekamp 2007), so lower-ranked individuals may not have had much to gain from cooperative hunting.

At Lunel-Viel where the forested environment may have limited visibility and speed of movement when compared to more open areas, individual hunting of cervids may have been a very profitable strategy for solitary individuals, since other group members would have converged on kills and carcasses more slowly than in open areas. Moreover, prey will have been more dispersed through the landscape than in open areas, where animals prefer to concentrate in large herds for safety. This means that carcasses and kills would have occurred more dispersed through the environment, and so presumably would foraging cave hyenas.

Sharing of meat seems more important in both modern humans and our primate cousins, chimpanzees (*e.g.* Hawkes 1993, Stanford 2001a, Stanford 2001b). In chimpanzees for example, meat is available to low-ranking individuals. If they capture prey, they can divide it, even if high-ranking individuals arrive on the scene (De Waal 2005, 197). Given the behaviour of their closest relatives it

is predicted that division of meat was also common among Neanderthals. Therefore they had more incentive to form larger groups of hunters, able to hunt larger species than cave hyenas. Cave hyenas probably preferred to forage in smaller groups or solitarily if circumstances permitted. At Lunel-Viel for example, the closed environment may have led to the occurrence of many cervids in small groups. The hyenas were probably able to exploit them in a solitary fashion. At Camiac, in more open environments, hyena groups were probably more attuned to hunting in groups. Cervids were less important for the diet here. They probably occurred in larger groups due to the open environment, necessitating exploitation by hyenas hunting in packs. In these circumstances hunting cervids became less important in favour of larger species offering larger “packages” of meat.

Scavenging is another foraging activity that can be done solitarily. Scavenging opportunities were also probably more abundant in Pleistocene Europe than in modern African savannahs where most actualistic work on scavenging as a subsistence strategy has been done (Fosse *et al.* 2004). In colder periods with animals concentrated in herds, this may have been an interesting strategy. However, in this period, the open landscape would also have improved visibility. In East Africa, it appears that scavenging opportunities are most abundant in riparian zones in the landscape (Blumenshine 1987). Therefore more scavenging opportunities may have been available to hyenas in the forested environments at Lunel-Viel than around Camiac.

In this case OFT can be invoked to explain why this role of scavenging is not expected to be important in Neanderthals. Since Neanderthals presumably had a different social organisation, with less intra-group competition for meat, scavenging ungulates was probably not rewarding for them. If food-sharing was practised, it would be more rewarding for individual Neanderthals to cooperate and concentrate on hunting large prey. This has the advantage of safe-guarding a more reliable, steady supply of food is procured. Moreover return rates for the cooperative hunting of herbivores would be higher than the return rates that could be achieved by scavenging their carcasses. Only scavenging of very large animals like rhinoceros or proboscideans is predicted to have been profitable for Neanderthals.

Another facet of the explanation of the signalled pattern may lie in spotted hyena social structure. Hyenas live in multi-male, multi-female groups, much like primates do. Females are solitarily burdened with the raising of their cubs. Alloparental care is unknown in spotted hyenas (Mills 1985, Watts and Holekamp 2007). Females therefore need to hunt in order to feed their offspring. Hunting dangerous prey would result in losing reproductively active females, and their dependent offspring from a pack. Losing reproductively active females from a population has much greater negative consequences than losing reproductively active males. The rate of reproduction of a population does not hinge on the available amount of sperm, since one male has much more sperm than needed to fertilise a female. The amount of available uteri is much more important for the reproductive rate of a population and these can be fertilised by a small number of males.

Males are thus more expendable than females in a population. If hunting was done by male Neanderthals, they could afford to hunt dangerously. Moreover, if reproductive success was linked to success in hunting, something that is seen in both hunter/gatherers and chimpanzees, it may have been profitable for males to pursue dangerous categories of game. If successful this probably provided them with better mating opportunities than the hunting of smaller less dangerous prey would have. In hyenas, where no division of labour was in place, hunting the most dangerous prey species would result in potentially losing both females and their offspring and was therefore probably avoided. On the other hand, this applied only to large carnivores like bears and megaherbivores like rhinoceros. The horse age-profile at Fouvent shows that when confronted with ungulates living in herds they were able to focus on the prime-aged, and thus most dangerous, individuals.

Application of OFT to hyenas and comparing the results of the analysis with the results of analyses of Neanderthal foraging produces better understanding of both species' foraging behaviour. This shows that OFT is a productive approach to studying Pleistocene foraging strategies. Moreover, the information available for both the hyena and the Middle Palaeolithic sites that were used in this thesis was not ideal. This suggests that the results of similar analyses may be improved in the future.

