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Monospecific faunal spectra in Mousterian contexts: Implications for social behavior

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ABSTRACT

This paper focuses on the question of the existence of collective hunting in Neanderthal populations. While many Mousterian sites from Western Europe exhibit faunal assemblages clearly dominated by a particular taxon, faunal spectrum alone is not enough to discuss the hunting strategies developed for their acquisition and the relative importance of the prey in Neanderthal diet. Therefore, Neanderthal hunting strategies are examined using different proxies such as prey selection and carcass exploitation in two Late Pleistocene sites: Mauran and Les Pradelles. These sites share all the characteristics (high quantity of faunal material, specialized faunal spectrum, large number of prey, catastrophic mortality profile, seasonal slaughter, possible selective transport of the richest elements) usually recognized in communal hunting assemblages. The conclusions underline that the subsistence economy of the hunter-gatherers in question involves the planned procurement of animal resources with the intention of storing surplus in anticipation of future food needs. It demonstrates that Neanderthal populations in South-western Europe already possessed the necessary technical and cognitive capacities.

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1. Introduction

A growing amount of zooarchaeological work has demonstrated that Neanderthals subsisted primarily by hunting herbivores coming from a large variety of environments, possibly complemented by scavenging (Farizy et al., 1994; Grayson and Delpech, 1994; Stiner, 1994; Gaudzinski, 1995, 1996; Gaudzinski and Roebroeks, 2000; Speth and Tchernov, 1998, 2001, 2007; Texier et al., 1998; Boëda et al., 1999; Burke, 2004; Rendu and Armand, 2009; Rendu, 2010). However, the question of the hunting techniques used by Neanderthals for the capture of large ungulates is still widely debated. According to Mellars, the increase of specialized hunting during the Upper Paleolithic would attest to a more systematic and intensive exploitation of their prey. In this view, the logistical organization of Anatomically Modern Human societies would be, as a consequence, more pronounced than the one of Neanderthal populations (Mellars, 1973, 1989, 1996, 2004). Although based on a large sample of Mousterian, Chatelperronian and Aurignacian faunal assemblage sites, Grayson and Delpech have questioned the increasing dietary specialization across the Middle to Upper Paleolithic transition

(Grayson and Delpech, 2002, 2006), as the social behavior implications are difficult to perceive at this scale of analysis. As emphasized by Mellars, “to have any meaning in cultural or behavioural terms, specialization must presumably imply deliberate selection of particular species from the total resources potentially available for exploitation” (Mellars, 1996, pp. 196). However, by using only the archaeological data, the discrimination between “faunal specialization as a deliberate economic strategies” and “purely ‘ecological’ specialization” (Mellars, 2004) is nearly impossible (Costamagno et al., 2006). The present authors have therefore decided to work towards a more accurate analysis level in the aim to identify the procurement strategies and the linked strategies developed by Neanderthals. Indeed, as underlined by Gaudzinski, analysis of monospecific archaeofaunas point to a variety of exploitation tactics used by Neanderthals (Gaudzinski, 1996, 2006). This paper focuses more specifically on the question of the existence of collective hunting linked to the killing of numerous prey during the same hunting event in order to constitute some food storage for deferred consumption. Indeed, although numerous Mousterian sites exhibit a monospecific faunal spectrum such as, for example in south-western France, La Borde (Jaubert et al., 1990), Mauran (Farizy et al., 1994), Coudoulous I (Coumont, 2005), Jonzac (Airvaux, 2004) and Les Pradelles (Costamagno et al., 2006), and the German sites of Wallertheim (Gaudzinski, 1995) and Saltzgitter Lebenstedt

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(Gaudzinski and Roebroeks, 2000), the existence of this type of strategy, which requires a considerable degree of collaboration between hunters and the anticipation of prey movement is still widely disputed for the Neanderthals (Costamagno et al., 2006; David and Enloe, 1993; Mellars, 2004; Rendu, 2007).

Ethnographically, communal hunting of large ungulate herds may have different purposes (economical, symbolic ...). When the objective is to obtain a large quantity of skins and meat, possibly stored (Binford, 1978; Driver, 1990) or consumed in an aggregation site (Todd, 1987) these particular hunting events share some specific features. In temperate and cold climates, they are characterized by a great number of slaughtered individuals from the same species, a catastrophic mortality profile, a selective exploitation of the carcasses and systematic transport of the skeletal elements of high nutritive value from the kill site to the base camp (David and Enloe, 1993; Costamagno, 1999). Furthermore, this kind of hunting strategy can only be conducted on gregarious prey.

2. Material and methods

Two sites have been considered in this paper: Mauran, dominated by bison, and Les Pradelles, where the bone assemblage is largely constituted of reindeer remains (Fig. 1).

2.1. Les Pradelles

Excavated by Vandermeersch, and then by Maureille and Mann, the site of les Pradelles (Marillac-le-Franc, Charente) is a collapsed

gallery within a karstic system (Maureille et al., 2007) (Fig. 1). Its deposits produced a Quina industry contemporaneous with the last glaciation (Bourguignon, 1996; Meignen et al., 2007). In the lowest levels, facies 2 has been retained for this analysis. The faunal spectrum is largely dominated by reindeer and is exclusively of human origin (Costamagno et al., 2005, 2006). The zooarchaeological research presented for this paper was exclusively conducted on reindeer remains. Only the material coming from the Maureille and Mann excavation was included in this study, due to the problem of sampling strategies used during the Vandermeersch excavation. However, to increase the sample size, minimum number of individuals (MNI) and age profiles were based on the products of both excavations.

The calculation of the MNI was based on all of the skeletal elements (bones and teeth). Age at death was established on the dental remains using tooth eruption sequences (Miller, 1974) and the quadratic method (Klein et al., 1983) modified for its application (Pike-Tay et al., 2000) to reindeer (Soulier, 2008). Cementum analysis was conducted to identify the hunting season (Rendu et al., submitted for publication). The techniques used in the dental seasonal increments analysis of the ungulate teeth employed polarized light microscopy and followed the protocol generally used (Pike-Tay et al., 1999, 2008; Wall, 2005; Rendu, 2010). With regard to the skeletal part profiles, all taxonomically identifiable specimens (including shaft fragments) were taken into account. In order to highlight the skeletal element representation, normed % NISP (%NNISP) was calculated for each skeletal portion (Grayson and Frey, 2004). NNISP represents “the skeletal parts NISP values

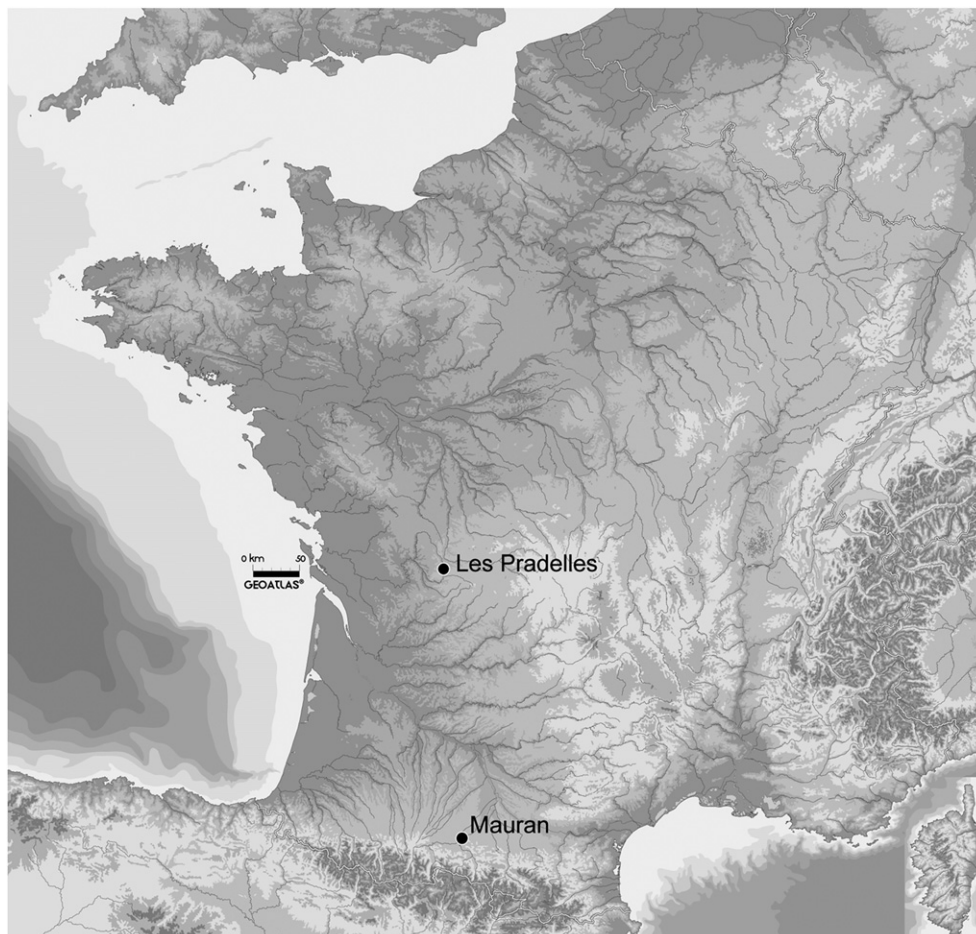


Fig. 1. Site locations. Map from Geotlas.

divided by the number of times the relevant part occurs in the skeleton of the animal involved" (Grayson and Frey, 2004, p. 31).

The skeletal elements were grouped together into large anatomical segments: cranial elements (skull, mandible), post-cranial axial skeleton (vertebrae, ribs), scapulae and pelvis, long bones of the upper limb (humerus, radio-ulna, femur, and tibia), long bones of the lower limb (metacarpal, metatarsal) and compact foot bones (carpal, tarsal, phalanges). The skeletal part profile for reindeer was analyzed using the utility index (SFUI) calculated by Metcalfe and Jones (1988) for reindeer carcasses. Following the recommendations of Jones and Metcalfe (1988), the marrow cavity volume of reindeer bones were used rather than the marrow index calculated by Binford (1978). The correlation coefficients calculated are Spearman's rho. With regard to taphonomic and zooarchaeological observations, all bone surfaces were observed under a low-angled light using a hand lens (magnification $12\times$). The criteria used to identify these traces are those listed by Blumenschine et al. (1996). The trace frequencies were calculated on the basis of the number of identified specimens, bones with unobservable surfaces having been excluded from the calculations (according to Delpech and Villa, 1993). Finally, the criteria developed by Villa and Mahieu (1991) to distinguish green- and dry-fractures were applied.

2.2. Mauran

The open air site of Mauran lay against a dismantled limestone cliff. While the excavation was concentrated on a small surface of 25 m^2 , the numerous excavation tests suggest that the site extension is higher than 1000 m^2 (Farizy et al., 1994). Its deposits yielded a Denticulate Mousterian associated with numerous bison remains (Jaubert, 1993; Farizy et al., 1994; Thiébaud, 2005) (Fig. 2). The excavation undertaken by Farizy identified two archaeological levels attributed to Marine Isotope Stage (MIS) 3. Only Layer 2 was studied. Except for the seasonal data obtained through a skeletochronological analysis (Rendu, 2007), all the results were obtained from the study published by David and Farizy (1994). The establishment of the minimal number of individuals was based on the dental remains. Sex-ratio was evaluated by these researchers using criteria in Speth (1983). Age at death was established using the tooth eruption sequences and tooth wear evaluated by recording the crown height of the M_3 (Klein and Cruz-Urbe, 1984). The skeletal part profile was calculated by using % survival (Brain, 1981) and the % MAU (Binford, 1978). It then was compared by David and Farizy (1994) to the bone density of the different skeletal portions (Kreutzer, 1992) and also to their nutritive value (Brink, 1997). A reevaluation of this relationship has recently been proposed

Table 1

NISP counts for large mammals at les Pradelles.

	NISP	% NISP
<i>Canis lupus</i>	6	0.1
<i>Vulpinae</i>	8	0.2
<i>Crocota crocuta</i>	1	0.0
<i>Panthera spelaea</i>	1	0.0
<i>Mustelidae</i>	1	0.0
<i>Bovinae</i>	49	1.1
<i>Equus caballus germanicus</i>	40	0.9
<i>Cervus elaphus</i>	3	0.1
<i>Rangifer tarandus</i>	4434	97.5
<i>Leporidae</i>	6	0.1
<i>Marmota marmota</i>	1	0.0
Total	4550	100

(Rendu et al., submitted for publication) by using the SFUI which allows the use of complete bones, thereby minimizing the impact of differential preservation (Metcalfe and Jones, 1988). Butchery marks (percussion marks, cut marks) and burned bones were systematically recorded, but the poor preservation of the cortical surfaces and the high degree of post-depositional fragmentation minimize the potential of these approaches.

3. Results

3.1. Les Pradelles

Les Pradelles is characterized by a high density of faunal remains, mostly ungulates, compared to the lithic material. The osseous collection is particularly well preserved. Facies 2 is largely dominated by reindeer (97.5%). Large bovid and horse are the second and third most important prey (Table 1). As expected, calculating the evenness of the bone assemblage ($\text{Evenness} = -\sum p_i \ln p_i / \ln S$ with S taken to be the number of taxa in the assemblage and p the proportion of specimens in the species) shows that the taxonomic diversity is low for the documented layer ($E = 0.065$). Seventeen slaughtered individuals were identified by the MINI on the Maureille and Mann teeth collection, but by considering the dental remains from the Vandermeersch collection this number can be increased to 59. The mortality profiles suggest a catastrophic mortality, but with an underrepresentation of the individuals under two years of age (Figs. 2 and 3) (Soulier, 2008). The cementum results conducted on twelve individuals attest to a seasonal hunting centered on the end of the warm season (Fig. 4) (Rendu et al., submitted for publication).

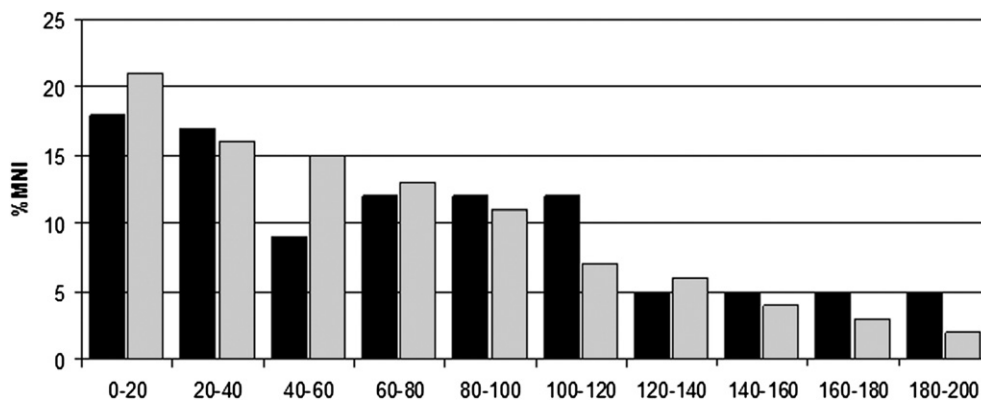


Fig. 2. Mortality profile from Les Pradelles (Soulier, 2008) compared to a present reindeer population (Miller, 1974).

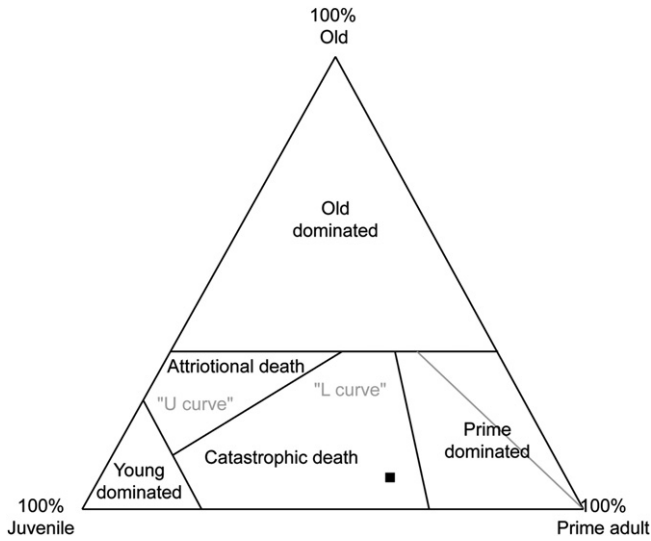


Fig. 3. Mortality profiles for Les Pradelles reindeer using a ternary diagram modified after Costamagno (1999).

At Les Pradelles, based on long bone abundance on the mid-shaft specimens, long bones are among the most abundant elements, particularly the long bones of the posterior limb (Fig. 5). Ribs, vertebrae and foot bones are extremely rare. Cranial elements are as frequent as the anterior limb bones. Due to the different degree of fragmentation between the epiphyses and the shaft fragments, the % NNISP cannot be compared to the density of the skeletal portions. However, the fact that the epiphyses of low density and the small compact bone are equally rare has to be underlined. The study of levels 9 and 10 of the Vandermeersch excavation has already highlighted a positive and statistically significant relationship between the relative abundance of skeletal parts and their density (layer 9: $r_s = 0.799, p < 0.01$ and layer 10: $r_s = 0.729, p < 0.01$) (Costamagno et al., 2006). There is a positive relationship between

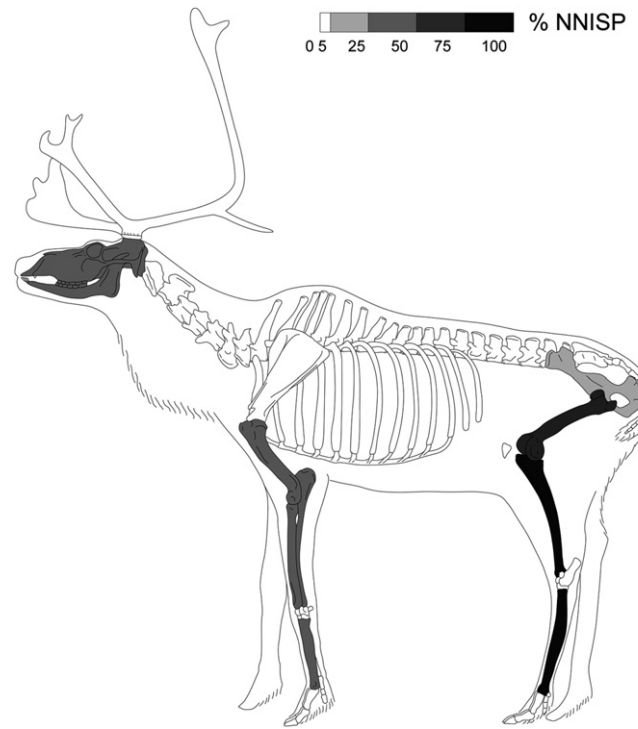


Fig. 5. Skeletal part representation for Les Pradelles Reindeer. (Drawing from Beauval and Coutureau, 2003).

the SFUI and the %NNISP but it is not statistically significant ($r_s = 0.110, p > 0.05$). Axial parts, given their high nutritional utility, are less well represented than expected, whereas and tibias and metatarsals are more abundant than expected.

The abundance of the axial parts with their high nutritional utility is clearly weaker than expected, whereas the abundance of tibia and metatarsal is much more frequent than expected. Fig. 6 compares the abundance of the skeletal elements with the volume of their medullar cavity. The nutrients within the bones better explain the relative abundance of the long bones than the SFUI ($r_s = 0.916, p < 0.01$) (Speth and Clark, 2006), suggesting selective transport of the elements.

The frequency of carnivore activity is extremely low, and less than 3% of the faunal material exhibit tooth marks or evidence of digestion. On the other hand, butchery marks are exceptionally

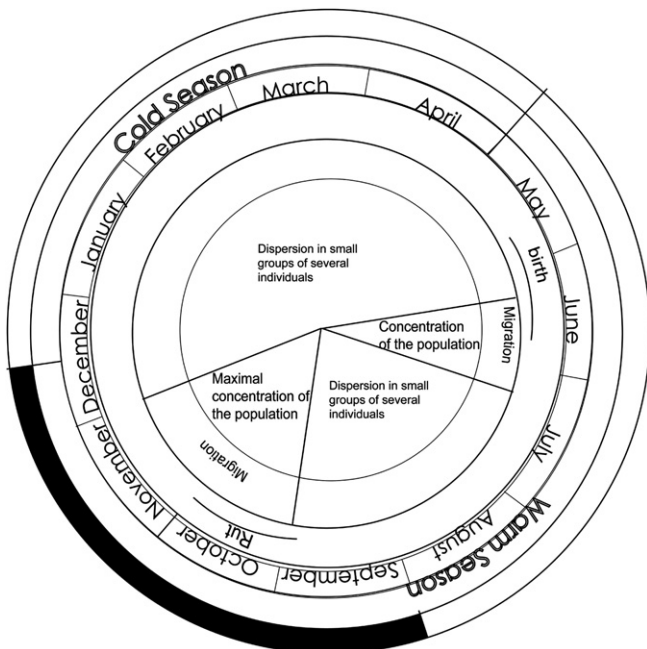


Fig. 4. Reindeer seasonal cycle (modified from West, 1997) compared to the hunting period identified by the skeletochronological analysis, underlined in black.

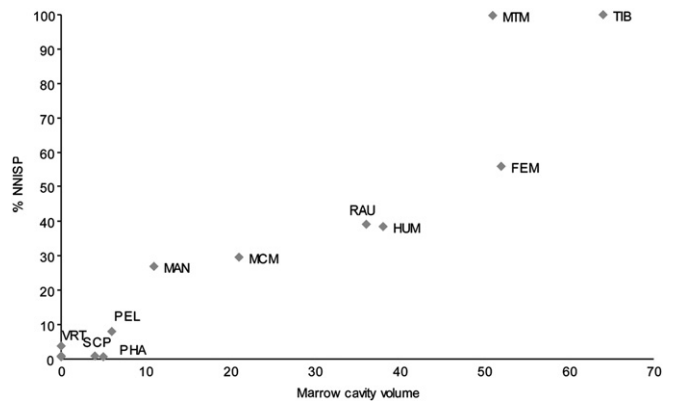


Fig. 6. Marrow cavity volume versus %NNISP at les Pradelles (MAN: mandible; VRT: vertebrae; SCP: scapula; HUM: humerus; RAU: radio-ulna; MCM: metacarpus; PEL: pelvis; FEM: femur; TIB: tibia; MTM: metatarsus; PHA: phalanges).

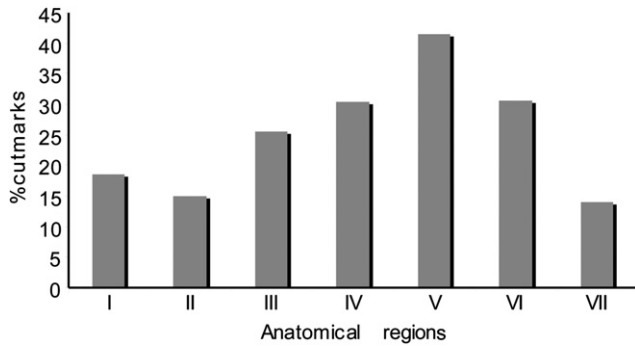


Fig. 7. Percentage of anatomical regions bearing one or more cutmarks at les Pradelles (I: skull and mandible; II: vertebrae; III: ribs; IV: scapula and pelvis; V: humerus, radio-ulna, femur and tibia, VI: metacarpus and metatarsus, VII: carpal, tarsal, phalanges).

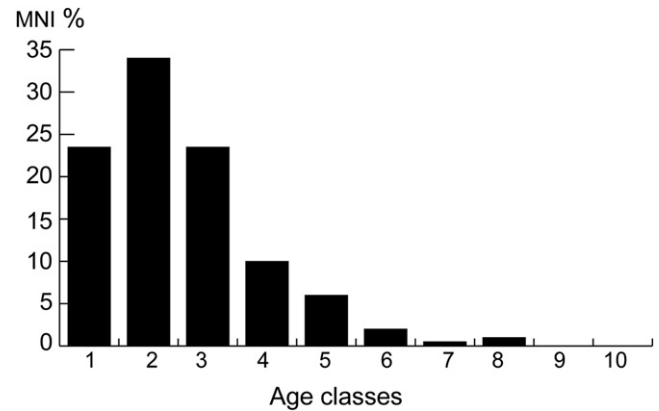


Fig. 9. Mortality profiles for Mauran bison (after David and Farizy, 1994).

numerous. Once the dental remains are excluded, cut marks can be observed on 30.3% of the faunal material and long bone remains have the highest frequency of human modifications (Fig. 7). The material is extremely fragmented and, except for a metacarpus, all long bones and most of the phalanges were found broken (76% of the first phalanges and 61% of the second phalanges). 71% of the edge of the long bone shaft and 91.5% of the phalanges exhibit evidence of fragmentation on green bones. Percussion marks are more common on the long bones than on the rest of the faunal remains (Fig. 8). The absence of burnt bone is a major characteristic of the assemblage.

3.2. Mauran

At Mauran, the faunal remains are more common than the lithic material (Farizy et al., 1994). The faunal spectrum is nearly exclusively constituted of bison remains, and the Shannon index ($E = 0.04$) is even lower than at Les Pradelles, confirming the low diversity of this faunal assemblage. Based on the jugal teeth, the minimum number of individuals attests to 137 slaughtered bison. However, by taking into account the full extent of the site, the total number of carcasses is estimated at around 4000 (David and Farizy, 1994). Female and juvenile individuals largely predominate, and male individuals are relatively infrequent in the assemblage (see David and Farizy, 1994). The mortality profile follows a catastrophic pattern, and the scarcity of individuals under two years of age is probably linked to post-depositional factors (Fig. 9).

Seasonality data were available for a large number of individuals. Twenty individuals were analyzed using the cementum

approach and, together with the fifteen juveniles for which tooth wear data were already available (Brugal and David, 1993; David and Farizy, 1994), hunting appears to have been concentrated at the end of the warm season was established (Rendu, 2007) (Fig. 10). The bison carcasses are characterized by an underrepresentation of vertebrae and of some fleshy long bones such as the femur (Fig. 11). Because of some differential preservation problems, David and Farizy (1994) argued that discussion of differential transport of these skeletal portions was impossible. However, a strong and highly statistically significant negative relationship ($r_s = -0.67$, $p < 0.01$) exists between the %MAU and the SFUI, suggesting that a possible exportation of the richest elements should be considered (Rendu et al., submitted for publication). Exploitation of the carcasses focused on the long bones rich in marrow, while significant parts of the skeletons were not affected by human activities such as phalanges that were found in anatomical connection. Moreover, 50% of the metapodials are complete and intact. Nevertheless, skeletal elements of juveniles were systematically discarded

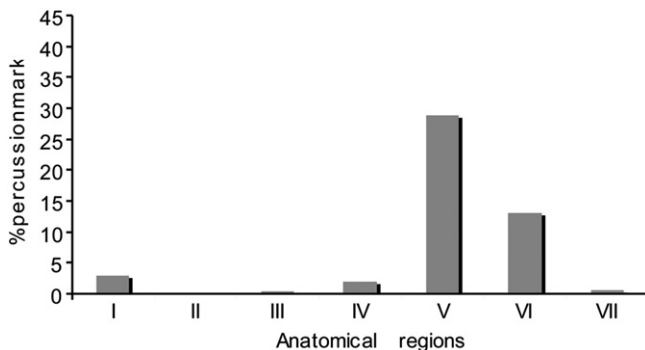


Fig. 8. Percentage of anatomical regions bearing one or more percussion marks at les Pradelles (I: skull and mandible; II: vertebrae; III: ribs; IV: scapula and pelvis; V: humerus, radio-ulna, femur and tibia, VI: metacarpal and metatarsal, VII: carpal, tarsal, phalanges).

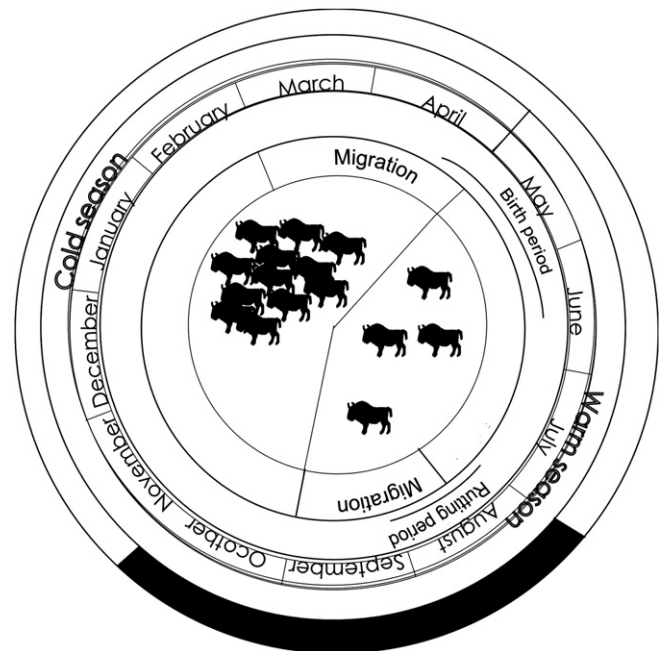


Fig. 10. Bison seasonal cycle (modified from Rendu, 2007 and Rendu and Armand, 2009) compare to the hunting period identified by the skeletochronological analysis, underlined in black.

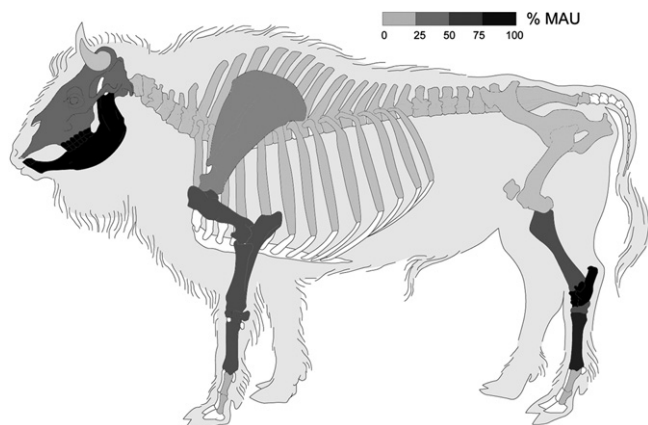


Fig. 11. Skeletal part representation for Mauran bison after David and Farizy (1994). (Drawing from Coutureau, 2003).

unexploited (David and Farizy, 1994), a pattern that is not unexpected as indicated by Speth and Clark (2006). Alterations of the cortical surfaces of the bones, a consequence of weathering, limit the observation of the cut marks, precluding discussion of the butchery activities on the site (David and Farizy, 1994) (Fig. 11).

4. Discussion

Facies 2 of Les Pradelles and Mauran are characterized by a monospecific faunal spectrum specialized on reindeer for the former and on bison for the latter. The predominance of a specific taxon and the great number of individuals raise the question of the existence of communal hunting developed by the Neanderthal population. As stated previously, the ethnographic data suggest that this kind of hunting was undertaken with the aim of providing for specific needs such as food for storage for the winter as well as hides, and also as a means for underwriting large periodic aggregations of people for social, reproductive, and other reasons. The two assemblages attest to seasonal hunting at the end of the warm season. At Les Pradelles, the reindeer would have been killed during the fall migration. At Mauran, taking into account both the skeltochronological results and the tooth wear analysis, the ethological information about modern bison and the topography of the site, a pattern of hunting at the end of the warm season, during the rut, has been proposed (Rendu, 2007).

While it is obviously impossible to identify the number of prey killed during each hunting event, several elements suggest a slaughter of a significant number of individuals. At Mauran and Les Pradelles, the mortality data seem to fit in with a catastrophic profile. An underrepresentation of juvenile individuals is, however, perceptible. While at Mauran this seems to be a consequence of a differential preservation between deciduous and permanent teeth, at Les Pradelles, the excellent preservation of the material leads to rejection of this hypothesis. However, the systematic rejection of the juvenile carcasses at Mauran must be considered. This suggests that, in both cases, exploitation was centered on the individuals which were of greater interest in terms of the quantity of meat, marrow, and perhaps grease. At Mauran, some anatomical connections, and the high frequencies of unexploited phalanges and metapodials associated with the richness in cranial elements, are strong evidence suggesting the presence of complete carcasses. The Mauran site would have been used as a kill site for bison for several generations (Farizy et al., 1994). Some topographic characteristics such as the presence of the vale, the little cliff, the swamp area, are consistent with a hunting strategy which entailed the

trapping of several individuals (Farizy et al., 1994; Rendu, 2007). Neanderthals would then have stayed there for all of the carcass processing. At Les Pradelles, the reindeer carcasses were brought to the site with a preference for the long bones rich in marrow. In the case of communal hunts leading to mass kills, carcasses are subject to standardized treatment resulting in the systematic rejection of certain parts at the butchering site (Wheat, 1972; Binford, 1978; Speth, 1983) whereas small scale hunting results generally in the exploitation of the entire carcass (Bartram, 1993; Bunn, 1993). Although specific conditions (size of the animal, how much time the hunters have, how far they are away from camp, their food needs) may modify this pattern (Bartram, 1993). At Les Pradelles, therefore, the preferential introduction of nutritionally rich elements onto the site is consistent with a slaughter of several reindeer during the same hunting event. The selective transport of adult individuals fits in well with this hypothesis. Hunting by trapping or by the interception of a part of a herd can be suggested.

Were these collective hunting events, which had for consequence the slaughter of a great number of individuals, aimed at producing a storage surplus of food, as well as hides, for later winter use? The paucity of evidence of deferred consumption of the food supplies and the even rarer evidence of skinning at these sites, make it difficult to tackle this question directly. At Les Pradelles, the conjunction of the lithic and the faunal data suggest several hypotheses. The very low density of lithic material and the systematic introduction of ready-to-use and heavily curated stone tools, are evidence of short term occupations (Meignen et al., 2007; Costamagno et al., 2006). This occupation pattern is not compatible with the consumption on the site of the whole amount of the carcasses obtained by successive hunts, nor does it suggest consumption by large temporary aggregations of people brought together for a short period by social, demographic, or other factors. In this context, the great number of prey, the high frequency of cut marks, evidence of standardization and systematization of the meat processing, the selective introduction into the site of the richest elements in marrow and grease, the nature of the occupation and the lack of living structures such as a fire place might be seen as proof of the use of the site as a secondary butchery site and sustain the hypothesis of food storage for a deferred consumption and/or preparation of the animal resources for easier transport toward a base camp (Costamagno et al., 2006). Simultaneously, the skeletal part profile from Mauran, characterized by an underrepresentation of some fleshy elements, is not very different from that seen in northern American Holocene kill sites (e.g. Speth, 1983). Furthermore, the discarding of the juvenile bones on site sustains the hypothesis of a selective exploitation of the richest elements. However, the bone surface modifications limit discussion of the intensity of the carcass butchery.

To summarize, Les Pradelles and Mauran share all the characteristics (large quantity of faunal material, specialized faunal spectrum, large number of prey, catastrophic mortality profile, seasonal slaughter, possible selective transport of the richest elements) of specialized hunting (sensu David and Enloe, 1993). This communal hunting involved the planned procurement of animal resources, very likely with the intention of storing the surplus in anticipation of future needs. Such hunting strategies require the participation of a large number of individuals. They also imply an important degree of communication among participants, active cooperation, and a defined role for everyone: thus, a social organization (e.g. Kurz, 1937; Frison, 1978; Morgan, 1980). This communal hunting implies the systematic scheduling of activities to form a year-round pattern or "annual round". The subsistence economy of the hunter-gatherers in question involves the planned procurement of animal resources with the intention of storing surplus in anticipation of future food needs, suggesting that

Neanderthal populations in Southwestern Europe already possessed the necessary technical and cognitive capacities, contrary to what has been proposed previously (Mellars, 2004). The specialisation of the faunal spectrum is not only a consequence of the specie availability in the environment, but also a result of the kind of hunting strategies developed by the Mousterians. Therefore, these sites follow perfectly the definition of the specialized hunting proposed by Mellars (1973, 1996, 2004).

This study raises the question of the place of this particular hunting technique in the Middle Paleolithic subsistence strategies. Especially, is it possible to suggest the recurrence of communal hunting at other monospecific sites? Although the zooarchaeological analyses in the Mousterian context of Southwestern France are still limited, some recent studies bring new insight to this specific topic. At Puycelsi, the slaughter of 39 bison and their partial exportation for deferred consumption of the meat (Griggo, cited in Rendu et al., submitted for publication) shares important similarity with what has been identified at Muraan. Fewer individuals might simply be the consequence of fewer hunting events. Similarly, during the deposition of layer 6c at La Quina, a large number of bison were killed at the end of the warm season (Rendu and Armand, 2009) and the richest segments were selectively exported (Debénath and Jelinek, 1998; Chase, 1999). In layer 22 of the Jonzac site, where reindeer represent more than 80% of the %NISP, the occurrence of anatomical connections and the possibility of an underrepresentation of the richest part of the carcasses indicate that the individuals were introduced in great numbers to be partially exploited (Jaubert et al., 2008) before eventual selective transport. For all these sites, their repetitive use with the goal of producing a surplus of food to be consumed later at another site has been suggested (Chase, 1999; Jaubert et al., 2008; Griggo, cited in Rendu et al., submitted for publication). For these three sites, as for Muraan and les Pradelles, the large quantity of faunal material, the highly specialized faunal spectrum, the catastrophic mortality profile, the seasonal slaughter and the possible selective transport of the nutritionally most valuable elements seem to indicate a specialized hunt. These examples from MIS 4 and 3 suggest that communal hunting may have played an important role in late Middle Paleolithic subsistence strategies and become a more or less regular practice (Costamagno et al., 2006; Delagnes and Rendu, submitted for publication). This particular shift in hunting behavior (Delagnes, 2010; Delagnes and Rendu, submitted for publication) had as a consequence the differentiation of site functions (Rendu et al., submitted for publication) at the end of the Mousterian.

The repeated use of specific locations at a precise moment of the year so as to acquire and process carcasses of particular taxa is evidence of hunting activities that are scheduled according to a year-round pattern. These task specific locations would have acted as satellites of a principal base camp, to which part of the resources would have been introduced. The segmentation in both time and space of predation activities would fit in with a logistical mobility pattern (Binford, 1980).

This diversification of site function devoted to hunting activities has to be underlined. Indeed, the regular predominance of reindeer in the Early Upper Paleolithic faunal spectra is generally interpreted as proof of specialized hunting developed by Early Aurignacian populations (Mellars, 1973, 1996, 2004). However, there is no evidence of specific hunting sites for this period in Southwestern France (Bachelier et al., submitted for publication). By taking into account the fact that specialization should be seen as a deliberate economic strategy (Mellars, 2004) and cannot be based only on the recurrent association of a taxon and a techno-complex, and bearing in mind the definition given by David and Enloe (1993) of specialized hunting, it can be assumed that communal hunting in the Early Upper Paleolithic is not yet established.

5. Conclusion

The question of specialized hunting conducted by Neanderthal populations was investigated in two major Mousterian sites in Southwestern France. Basing the analysis not only on the overrepresentation in the faunal spectrum by a particular taxon but by integrating element from prey selection and the choice in the transport and exploitation of the carcasses, it has been shown that, in these late Mousterian sites, communal hunting involved deferred consumption in anticipation of future needs. Mousterian specialized faunal spectra are not exceptional (c.f. Gaudzinski, 2006, for a general discussion) but data attesting to a segmentation of the butchery activities within the territory are extremely rare. The generalization of zooarchaeological studies in close relationship to techno-economical analyses of the stone tool industries is of first interest to access to the spatiotemporal organization of Mousterian economies. Based on these two sites, occupied toward the end of the Mousterian in Southwestern France, it is clearly impossible to generalize this pattern to the whole southwestern France record. Nevertheless, these two studies raise important question about the conditions (cultural, demographic, social organization) that might favor the use of communal hunting strategies and involved deferred consumption.

However, it can be asked, when this kind of hunting strategy appeared for the first time and if its development followed a particular pattern. This raises the question of the spatiotemporal extension of this phenomenon in the Mousterian context. Does this kind of hunting strategy show cultural elements shared by the whole Neanderthal population or, on the contrary, does it reflect a regional variation which characterized the Mousterian population of Southwestern Europe at a particular period?

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References

- Airvaux, J., 2004. Le site paléolithique de chez-Pinaud à Jonzac, Charente-Maritime. *Préhistoire du Sud-Ouest, Cressensac (Suppl. 8)*.
- Bachelier, F., Bon, F., Deschamps, M., Eizenberg, L., Henry-Gambier, D., Mourre, V., Normand, C., Pelegrin, J., Primault, J., Scanduzzi, R., L'organisation sociale de la chasse à la charnière du Paléolithique moyen et du Paléolithique supérieur. Moustériens, Châtelperroniens et Aurignaciens dans l'espace pyrénéen. *P@lethnologie 3*. submitted for publication.
- Bartram, L.E., 1993. Perspectives on skeletal part profiles and utility curves from eastern kalahari ethnoarchaeology. Occasional Paper No. 21, Center for Archaeological Investigations. In: Hudson, J. (Ed.), *From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains*. Southern Illinois University at Carbondale, Carbondale, pp. 115–137.
- Beauval, C., Coutureau, M., 2003. <http://www.archeozoo.org/IMG/ai/Renne.ai> (accessed 22.07.10).
- Binford, L.R., 1978. *Nunamiut Ethnoarchaeology*. Academic Press, New York.
- Binford, L.R., 1980. Willow smoke and dog's tails: hunter-gatherer settlement systems and archaeological site formation. *American Antiquity* 45, 4–20.
- Blumenshine, R.J., Marean, C.W., Capaldo, S.D., 1996. Blind tests of interanalyst correspondence and accuracy in the identification of cut-marks, percussion marks and carnivore tooth marks on bone surface. *Journal of Archaeological Science* 23, 493–508.

- Boëda, E., Geneste, J.-M., Griggo, C., 1999. A Levallois point embedded in the vertebra of a wild ass (*Equus africanus*): hafting projectiles and Mousterian hunting weapons. *Antiquity* 73 (280), 394–402.
- Bourguignon, L., 1996. La conception de débitage Quina. *Quaternaria Nova* 11, 149–166.
- Brain, C.K., 1981. *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. University of Chicago Press, Chicago.
- Brink, J.W., 1997. Fat content in leg bones of *bison bison*, and applications to archaeology. *Journal of Archaeological Science* 24, 259–274.
- Brugal, J.-P., David, F., 1993. Usure dentaire, courbe de mortalité et saisonnalité: les gisements du Paléolithique moyen à grands bovidés. In: Desse, J., Audouin-Rouzeau, F. (Eds.), *Exploitation des animaux sauvages à travers le temps*. APDCA, Antibes, pp. 62–77.
- Bunn, H.T., 1993. Bone assemblages at base camps: a further consideration of carcass transport and bone destruction by the Hadza. *Occasional Paper No. 21, Center for Archaeological Investigations*. In: Hudson, J. (Ed.), *From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains*. Southern Illinois University at Carbondale, Carbondale, pp. 156–168.
- Burke, A., 2004. The ecology of Neandertals. *International Journal of Osteoarchaeology* 14.
- Chase, P.G., 1999. Bison in the context of complex utilization of faunal resources: a preliminary report on the Mousterian zooarchaeology of La Quina (France). In: Brugal, J.-P., David, F., Enloe, J.G., Jaubert, J. (Eds.), *Le Bison: gibier et moyen de subsistance des hommes du Paléolithique aux Paléochasseurs des grandes plaines*. APDCA, Antibes, pp. 159–184.
- Costamagno, S., 1999. *Stratégies de chasse et fonction des sites au Magdalénien dans le sud de la France*. Thèse de Doctorat. Université de Bordeaux I, Bordeaux.
- Costamagno, S., Beauval, C., Lange-Badré, B., Vandermeersch, B., Mann, A., Maureille, B., 2005. Homme ou carnivores? Protocole d'étude d'ensembles osseux mixtes: l'exemple du gisement moustérien des Pradelles (Marillac-le-Franc, Charente). *Archaeofauna* 14, 43–68.
- Costamagno, S., Meignen, L., Beauval, C., Vandermeersch, B., Maureille, B., 2006. Les Pradelles (Marillac-le-Franc, France): A Mousterian Reindeer Hunting Camp? *Journal of Anthropological Archaeology* 25, 466–484.
- Coumont, M.-P., 2005. *Taphonomie préhistorique: mammifères fossiles en contexte naturel, les avens-pièges, apport pour l'étude des archofaunes*. Thèse de doctorat. Université Aix en Provence 1, Aix en Provence.
- Coutureau, M., 2003. <http://www.archeozoo.org/IMG/ai/Bison.ai> (accessed 22.07.10).
- David, F., Enloe, J.G., 1993. L'exploitation des animaux sauvages de la fin du Paléolithique moyen au Magdalénien. In: Desse, J., Audouin-Rouzeau, F. (Eds.), *Exploitation des animaux sauvages à travers le temps*. APDCA, Antibes, pp. 29–47.
- David, F., Farizy, C., 1994. Les vestiges osseux: étude archéozoologique. XXX^e supplément à *Gallia Préhistoire*. In: Farizy, C., David, F., Jaubert, J. (Eds.), *Hommes et bisons du Paléolithique moyen à Mauran (Haute-Garonne)*. C.N.R.S., Paris, pp. 177–234.
- Debénath, A., Jelinek, A.J., 1998. Nouvelles fouilles à la Quina (Charente). Résultats préliminaires. *Gallia Préhistoire* 40, 29–74.
- Delagnes, A., 2010. *Systèmes techniques, subsistance et mobilité au Paléolithique moyen: interactions et implications diachroniques*. Habilitation à diriger des Recherches. Université Bordeaux I, Talence.
- Delagnes, A., Rendu, W., Shifts in neandertals mobility: Mousterian technological and subsistence strategies in Western France. *Journal of Archaeological Science*. submitted for publication.
- Delpech, F., Villa, P., 1993. Activités de chasse et de boucherie dans la grotte des Eglises. In: Desse, J., Audouin-Rouzeau, F. (Eds.), *Exploitation des animaux sauvages à travers le temps*. APDCA, Antibes, pp. 79–102.
- Driver, J.C., 1990. Meat in due season: the timing of communal hunts. In: Davis, L.B., Reeves, B.O.K. (Eds.), *Hunters of the Recent Past*. Unwin Hyman, London, pp. 11–33.
- Farizy, C., David, F., Jaubert, J., 1994. Hommes et bisons du Paléolithique moyen à Mauran (Haute-Garonne). C.N.R.S. XXX^e supplément à *Gallia Préhistoire* Paris.
- Frison, G.C., 1978. *Prehistoric Hunters of the High Plains*. Academic Press, New York.
- Gaudzinski, S., 1995. Wallertheim revisited: a re-analysis of the fauna from the middle palaeolithic site of Wallertheim (Rheinhessen/Germany). *Journal of Archaeological Science* 22, 51–66.
- Gaudzinski, S., 1996. On Bovid Assemblages and their Consequences for the Knowledge of Subsistence in the Middle Palaeolithic. In: *Proceedings of the Prehistoric Society*, 62, pp. 19–39.
- Gaudzinski, S., 2006. Monospecific or Species-Dominated Faunal Assemblages during the Middle Paleolithic of Europe. In: Hovers, E., Kuhn, S. (Eds.), *Transitions before the Transition*. Springer, New-York, pp. 137–147.
- Gaudzinski, S., Roebroeks, W., 2000. Adults only, reindeer hunting at the middle paleolithic site Salzgitter Lebenstedt, northern Germany. *Journal of Human Evolution* 38, 497–521.
- Grayson, D.K., Delpech, F., 1994. The evidence for middle palaeolithic scavenging from Couche VIII, grotte Vaufrey (Dordogne, France). *Journal of Archaeological Science* 21, 359–375.
- Grayson, D.K., Delpech, F., 2002. Specialized early upper palaeolithic hunters in southwestern France? *Journal of Archaeological Science* 29, 1439–1449.
- Grayson, D.K., Frey, C.J., 2004. Measuring skeletal part representation in archaeological faunas. *Journal of Taphonomy* 2, 27–42.
- Grayson, D.K., Delpech, F., 2006. Was there increasing dietary specialization across the middle-to-upper paleolithic transition in France? In: Conard, N. (Ed.), *When Neandertals and Modern Humans Met*. Tubingen Publications in Prehistory, Tubingen, pp. 377–405.
- Jaubert, J., 1993. Le gisement paléolithique moyen de Mauran (Haute-Garonne): techno-économie des industries lithiques. *Bulletin de la Société Préhistorique Française* 90, 328–335.
- Jaubert, J., Lorblanchet, M., Laville, H., Slott-Moller, R., Turq, A., Brugal, J.-P., 1990. Les chasseurs d'Aurochs de la Borde: un site du Paléolithique moyen (Livernon, Lot). *Maison des Sciences de l'Homme*, Paris.
- Jaubert, J., Hublin, J.-J., Soressi, M., McPherron, S., Bailey, S., Bordes, J.-G., Claud, E., Mallye, J.-B., Michel, A., Niclot, M., Rendu, W., Richards, M., Richter, D., Roussel, M., Steele, T., Taylor, G., Texier, J.-P., 2008. La fin du Paléolithique moyen et le début du Paléolithique supérieur à Jonzac (Charente-Maritime): premiers résultats des campagnes 2004–2006. In: Jaubert, J., Bordes, J.-G., Ortega, I. (Eds.), *Les sociétés Paléolithiques d'un grand Sud-Ouest: nouveaux gisements, nouvelles méthodes, nouveaux résultats*. Mémoire XLVII. Société Préhistorique Française, Paris, pp. 203–244.
- Jones, K.T., Metcalfe, D., 1988. Bare bones archaeology: bone marrow indices and efficiency. *Journal of Archaeological Science* 15, 415–423.
- Klein, R.G., Cruz-Urbe, K., 1984. *The Analysis of Animal Bones from Archaeological Sites*. University of Chicago Press, Chicago, 266.
- Klein, R.G., Allwarden, K., Wolf, C., 1983. The calculation and interpretation of ungulate age profiles from dental crown heights. In: Bailey, G. (Ed.), *Hunter-gatherer Economy in Prehistory: A European Perspective*. University of Cambridge Press, Cambridge, pp. 47–57.
- Kreutzer, L.A., 1992. Bison and Deer bone mineral densities: comparisons and implications for the interpretation of archaeological faunas. *Journal of Archaeological Science* 19, 271–294.
- Kurz, R.F., 1937. *Journal of Rudolph Friederich Kurz. An Account of His Experiences Among Fur Traders and American Indians on the Mississippi and the Upper Missouri Rivers during the Years 1846 to 1852*. Bureau of American Ethnology - Smithsonian Institution, Washington D. C.
- Maureille, B., Mann, A., Beauval, C., Bordes, J.-G., Bourguignon, L., Costamagno, S., Couchoud, I., Lacrampe-Cuyaubère, F., Laroulandie, V., Marquet, J.-C., Meignen, L., Texier, J.-P., Vandermeersch, B., 2007. Le gisement moustérien des Pradelles (Marillac-le-Franc, Charente): passé, présent, futur. In: Evin, J. (Ed.), *Un siècle de construction du discours scientifique en Préhistoire*. Société préhistorique française, Paris, pp. 249–261.
- Meignen, L., Costamagno, S., Beauval, C., Bourguignon, L., Vandermeersch, B., Maureille, B., 2007. Gestion des ressources lithiques au Paléolithique moyen dans une halte de chasse spécialisée sur le renne: Les Pradelles (Marillac-le-Franc, Charente). In: Moncel, M.H., Moigne, A.-M., Arzarello, M., Peretto, C. (Eds.), *Raw Material Supply Areas and Food Supply Areas. Integrated Approach of the Behavior*. British Archaeological Research International Series 1725, Oxford, pp. 127–139.
- Mellars, P., 1973. The character of the middle-upper palaeolithic transition in southwest France. In: Renfrew, C. (Ed.), *The Explanation of Cultural Change*. Duckworth, London, pp. 255–276.
- Mellars, P., 1989. Major issues in the emergence of modern humans. *Current Anthropology* 30, 349–384.
- Mellars, P., 1996. *The Neandertal Legacy*. Princeton University Press, Princeton.
- Mellars, P.A., 2004. Reindeer specialization in the early upper palaeolithic: the evidence from south west France. *Journal of Archaeological Science* 31, 613–617.
- Metcalfe, D., Jones, K.T., 1988. A reconsideration of animal-part utility indices. *American Antiquity* 53, 486–504.
- Miller, F., 1974. *Biology of the Kamuriak Population of Barren Ground Caribou*. Part 2: Dentition as an Indicator of Age and Sex; Composition and Socialization of the Population. *Canadian Wildlife Service Reports*, Ottawa.
- Morgan, R.G., 1980. Bison movement patterns on the Canadian plain: an ecological analysis. *Plains Anthropologist* 25, 143–160.
- Pike-Tay, A., Cabrera Valdés, V., Bernaldo de Quiros, F., 1999. Seasonal variations of the middle-upper paleolithic transition at El Castillo, Cueva Morin and El Pendo. *Journal of Human Evolution* 36, 283–317.
- Pike-Tay, A., Cosgrove, R., Garvey, J., 2008. Systematic seasonal land use by late Pleistocene Tasmanian Aborigines. *Journal of Archaeological Science* 35, 2532–2544.
- Pike-Tay, A., Morcomb, C.A., O'Farrell, M., 2000. Reconsidering the quadratic crown height method of age estimation for rangifer from archaeological sites. *Archaeozoologia* 11, 145–174.
- Rendu, W., 2007. *Planification des activités de subsistance au sein du territoire des derniers moustériens*. Thèse de doctorat. Université Bordeaux I, Bordeaux. Available online at: <http://tel.archives-ouvertes.fr/tel-00444154/fr/>.
- Rendu, W., 2010. Hunting behavior and Neanderthal adaptability in the late Pleistocene site of Pech-de-l'Azé I. *Journal of Archaeological Science* 37, 1798–1810.
- Rendu, W., Armand, D., 2009. Saisonnalité de prédation du Bison du gisement moustérien de la Quina (Gardes-le-Pontaroux, Charente), niveau 6c. Apport à la compréhension des comportements de subsistance. *Bulletin de la Société Préhistorique Française* 106, 679–690.
- Rendu, W., Bourguignon, L., Costamagno, S., Meignen, L., Soulier, M.-C., Armand, A.B.C., David, F., Griggo, C., Jaubert, J., Maureille, B., Park, S.J., Des sites moustériens spécialisés? Approche interdisciplinaire et réflexions méthodologiques sur une question récurrente. [P@lethnologie 3](http://lethnologie3.com/), accepted for publication.
- Soulier, M.-C., 2008. Etude des dents de Renne du gisement des Pradelles (Charente, France): revue critique des méthodes d'estimation d'âge dentaire, saisonnalité

- et profils de mortalité. Mémoire de Master 2. Université Toulouse 2 Le Mirail, Toulouse.
- Speth, J.D., 1983. *Bison Kills and Bone Counts: Decision Making by Ancient Hunters*. University of Chicago Press, Chicago.
- Speth, J.D., Clark, J.M., 2006. Hunting and overhunting in the Levantine late middle palaeolithic. *Before Farming* 3, 1. 2006.
- Speth, J.D., Tchernov, E., 1998. The role of hunting and scavenging in Neandertal procurement strategies. In: Akazawa, T., Aoki, K., Bar-Yosef, O. (Eds.), *Neandertals and Modern Humans in Western Asia*. Plenum Press, New-York, pp. 223–239.
- Speth, J.D., Tchernov, E., 2001. Neandertal hunting and meat-processing in the Near-East. Evidence from Kebara Cave (Israel). In: Stanford, C.B., Bunn, H.T. (Eds.), *Meat-eating and Human Evolution*. Oxford University Press, Oxford, pp. 52–72.
- Speth, J.D., Tchernov, E., 2007. The middle paleolithic occupations at Kebara Cave. In: Bar-Yosef, O., Meignen, L. (Eds.), *Kebara Cave Mt. Carmel, Israel. The Middle and Upper Paleolithic Archaeology, Part 1*. Peabody Museum Press, Cambridge, pp. 165–260.
- Stiner, M., 1994. *Honor Among Thieves: A Zooarchaeological Study of Neandertal Ecology*. Princeton University Press, Princeton.
- Texier, P.-J., Brugal, J.-P., Lemorini, C., Wilson, L., 1998. Fonction d'un site du Paléolithique moyen en marge d'un territoire: l'abri de la Combette (Bonnieux, Vaucluse). In: Brugal, J.-P., Meignen, L., Patou-Mathis, M. (Eds.), *Economie préhistorique: les comportements de subsistance au Paléolithique*. APCDA, Antibes, pp. 325–348.
- Thiébaud, C., 2005. *Le Moustérien à denticulés: variabilité ou diversité technico-économique*. Thèse de doctorat. Université de Provence, Aix-en-Provence.
- Todd, L.C., 1987. Analysis of kill-butcher bonebeds and interpretation of Paleoindian hunting. In: Nitecki, M.H., Nitecki, D.V. (Eds.), *The Evolution of Human Hunting*. Plenum Press, New York, NY, pp. 225–266.
- Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. *Journal of Human Evolution* 21, 27–48.
- Wall, C.M., 2005. The seasonality of site deposition of Gibraltar Neanderthals: evidence from Gorham's and Vanguard Caves. *Journal of Iberian Archaeology* 7, 9–22.
- West, D., 1997. *Hunting Strategies in Central Europe during the Last Glacial Maximum*. British Archaeological Research international series, Oxford.
- Wheat, J.B., 1972. The Olsen Chubbuck site: a paleo Indian bison kill. *American Antiquity* 37, 1–181.