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The basic prey model in «deep time»: the exploitation of animal resources during MIS 3-5e in France

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Abstract

Despite the considerable progress made in terms of our knowledge of the Middle to Upper Palaeolithic transition in (Western) Europe, the phenomenon remains puzzling to this day. One of the most relevant questions arguably deals with the coexistence of Neanderthals and modern humans, and the resulting economic competition and/or acculturation, in any given region of that area. This study represents the first part of an analysis of the Competition Hypothesis for France, and focuses on the broader timeframe of MIS 3-5e, both to gain some exploratory insights into the matter of resource intensification between Mousterian, Chatelperronian, and Aurignacian, and to establish the value of the basic prey model (and the modifications we applied) in this particular timeframe.

Keywords: optimal foraging, Middle Palaeolithic, Middle to Upper Palaeolithic transition, basic prey model, resource intensification.

1. Introduction

There is no doubt that Europe was a very interesting region during Isotope Stage 3 (MIS 3): the palaeoclimate has been shown to be highly variable, while overall the productivity of the primary biomass was quite high (Guthrie, 1990), allowing for a diverse set of megafauna to roam the landscape. On the human level, we can essentially witness two hominin developments, i.e. one morphological (biological), the other cultural. At the beginning of this period, only the robust (Neanderthal) morphology was found, while at the end of MIS 3 Europe was inhabited by a gracile population, which morphologically differed little from extant humans. At the cultural level, there were evident changes in material culture; transitions in other spheres of life, such as inter- and intra-group social relations or cognition, remain perhaps more elusive. In any case, MIS 3 contained a phase of cultural dynamics in which the (variants of the) Mousterian gave way to the classic Aurignacian (the so-called Middle to Upper Palaeolithic Transition, or MUPT) through regional transitional or Early/Initial Late Palaeolithic industries such as the Chatelperronian, the Uluzzian, the Szeletian, the Bachokirian and the proto-Aurignacian (see e.g. Zilhão & d'Errico, 2003). Changes include typological and technological aspects of lithic production, a more consistent inclusion of organic material in the toolkit, an increase in the internal spatial organisation of sites, and the occurrence (though not universal) of «symbolic» phenomena like cave paintings, figurines, and beads (see e.g. Mellars & Stringer, 1989; Mellars, 1991).

Unfortunately, the two developments are not easily reconciled on the empirical level, which was already well-understood in the introduction to the seminal 1989 volume by Mellars & Stringer: any synthesis of the archaeological and palaeontological records is hampered by the limited number of (diagnostic) human fossils associated with lithic remains, the problematic attribution of key archaeological levels to a given technocomplex, and problems associated with carbon dating (see e.g. d'Errico & Sánchez Goñi, 2003: 771-772). Still, multiple hypotheses have been proposed ranging from indigenous development (d'Errico *et al.*, 1998; Zilhão & d'Errico, 2000; d'Errico, 2003; Zilhão, 2006) to colonisation by a (cognitively and/

or technologically more advanced) gracile population (Mellars, 1996, 2004, 2005; Mithen, 1996; Klein, 2008). This colonisation scenario exists in several variants, which differ in the extent of biological admixture, the extent and direction of acculturation, and the geographic area. A moderate approach to the problem may assume the following (Roebroeks, 2008):

- Based on directly dated fossil evidence, there is a 1000-3000 ^{14}C year hiatus between both hominin groups.
- Archaeological data indicate that Middle Palaeolithic and Chatelperronian assemblages underlie the Aurignacian everywhere. Alleged interstratifications of the latter two have either proven false or highly disputed. In Swabia, the hiatus between the latest Middle Palaeolithic assemblages and the earliest Aurignacian is very pronounced.
- The Aurignacian appears more or less simultaneously in large parts of Europe around 35 ka ^{14}C BP; the earliest south western dates are only marginally younger than those of the easternmost parts of Europe.
- The hominin associated with the earliest Aurignacian is unknown; the later Aurignacian was produced by modern humans.
- The Chatelperronian was very likely produced by Neanderthals.
- The makers of so-called Final Middle Palaeolithic or Initial/Early Upper Palaeolithic transitional industries remain unknown until diagnostic fossil material has been found.

When we move from data to speculation, we must first acknowledge that our limited fossil sample size may overemphasise the perceived hiatus, as it is highly improbable that the last Neanderthal and the first modern human were sampled. An overlap can therefore still not be excluded, and as argued before in such a case, the demise of the Neanderthals may have been swift (Zubrow, 1989), both in the case of admixture (e.g. Zilhão, 2007; Green *et al.*, 2010) and of competitive exclusion without admixture (Mellars, 2004). Zubrow (1989) argued that even a small difference in life history characteristics of both groups may have been enough to «blip» one group out of existence, in terms of (Palaeolithic) archaeological timescales. This makes it difficult to get a grip on the situation, as our question may currently be too fine-grained for the data to answer, or, as Roebroeks suggests, there may simply be no detectable evidence left from such a rapid event.

This paper reports the results of the first phase of a study that attempts to test the Competition Hypothesis (which assumes a colonisation scenario followed by a probably brief period of coexistence of both morphologies and the subsequent cultural and morphological disappearance of the Neanderthals) for France in particular. This testing is based on a combination of readily available faunal data and an optimality model, whereby this first phase consists of an analysis of sites belonging to the last interglacial-glacial cycle (MIS 5e-3). As such, we do not primarily focus on the transition debate in this paper, but rather on the differential exploitation of animal resources[1] among technocomplexes[2] in a wider temporal context.

2. The basic prey model

The so-called basic prey model (also known as diet breadth model or prey choice model), is borrowed from Behavioural Ecology (BE), and Optimal Foraging Theory (OFT) in particular. Shaped by MacArthur & Pianka (1966), Emlen (1966), Schoener (1971), Charnov

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[1] However, still from an intensification point of view.

[2] I.e. the Mousterian, the Chatelperronian, and the Aurignacian.

& Orians (1973) and Pyke *et al.* (1977), the model was published in a definitive form by Stephens & Krebs (1986: 14-17), which also provide the mathematical derivation. A less formal derivation can be found in Giraldeau (2008: 235-238), and a graphic representation in Winterhalder (1981a). For the derivation and characterisation of variants with an increased realism, e.g. models able to deal with risk, or missing information, we refer to Stephens & Krebs (1986) as well. In essence, the prey model is an average-rate-maximising model that predicts the best set of prey types that will be exploited given certain internal and external constraints (Stephens & Krebs, 1986), in which «best» should be understood as «that which maximises the long-term average rate of energy intake». To that end, prey species need to be grouped or split into prey types, and ranked according to decreasing profitability (defined as the ratio of energy per attack to the handling time per attack, i.e. post-encounter return rate), such that the optimal diet breadth may consist of type 1, or type 1 + 2, or type 1 + 2 + 3, ...

While quite effective in ethological studies (Stephens & Krebs, 1986: 187-199), the model has known an uneasy acceptance in anthropology at large. Typically, its simplicity, its reductionist stance, its methodological individualism, and its indifference towards the origin (cultural vs. genetic) of the behaviour it describes (i.e. the phenotypic gambit) have kept the prey model from becoming wide-spread (see e.g. Joseph, 2000 vs. Winterhalder, 2002 vs. Joseph, 2003 for a recent exchange of ideas). Although even the premise of optimality itself, which roots the model firmly in evolutionary biology has been challenged, critical remarks may represent reasons why the model may be wrong in any given case, but they do not necessarily entail that it must be wrong (see also Stephens & Krebs, 1986: 215 for a similar point on optimisation models in general). On the contrary, it would appear that empirically, the model seems to be quite robust against violations of its assumptions, judging from anthropological studies in which it has been applied with success (Smith, 1991; Winterhalder, 1981b; O'Connell & Hawkes, 1981).

Even in archaeological contexts, which generally provide but a coarse-grained record of (foraging) life, this seems to be the case. While deployed primarily in Holocene studies, various scholars have used the model in «archaeological time», such as Yesner (1981), Simms (1987), Broughton (1994a,b), Grayson & Delpech (1998), Nagaoka (2002), and Dusseldorp (2009, 2010). Necessarily, these authors have used the model as a hypothesis generator, as a general background against which to organise observations about individual behaviour. This means that they did not «test» it, i.e. use the prey algorithm to predict diet breadth, verify the results with the empirically attested diet breadth, and revise the model the model to attain a closer correspondence with the empirical data, thus gaining in the end, a deeper understanding of the foraging strategies of prehistoric people (e.g. energy maximisation, time minimisation, risk reduction, ...). Rather, they «applied» the model, i.e. having *a priori* assumed that the model can describe the foraging behaviour in question, which allows the use of its qualitative predictions to guide their research and explain diet patterning. While there are several qualitative predictions to be brought into play, as will become clear further down, we have based our study on the following: any factor that causes an increase in search costs will produce an enlargement of the diet breadth. Conversely, decreasing search costs will restrict diet breadth.

3. The prey model in archaeological time

As the prey model had been devised to work in «ecological time» (Grayson & Delpech, 1998: 1119), it had to be adapted to the archaeological situation. Arguably the most important aspect of this archaeological interpretation concerns the empirical determination of diet breadth itself. As such, the latter is perceived as «the total number of resources in the diet» (Kaplan & Hill, 1992: 171), or practically, «the number of taxa incorporated into the assemblage» (Grayson & Delpech, 1998: 1120). Evidently, this is not identical to «the number of resources [i.e. different prey types] taken upon encounter» (Madsen, 1993: 322). In practice prey types, by definition characterised by non-overlapping profitabilities, are generally equalled to taxa (e.g. Grayson & Delpech, 1998; Broughton, 1994a, b). As a result, overlapping profitabilities are unlikely to be avoided. Secondly, prey size (weight) is generally used as a proxy for profitability, and hence, prey type. While appearing as an over-simplification, from a logical point of view there is something to be said for a definition of prey types based on mass rather than appearance *strictu senso*: associated with each particular appearance (which does not need to be a biological species given the potentially large intra-species differences between male and female adults, and sub-adults) are a set of variables such as average encounter rate, modified energy value, and handling time, which are all known to the forager since he is assumed to have complete information. A sighting of a prey item may (consciously or unconsciously) evoke all that knowledge, and condense it into the decision variable: to exploit or not. Now, defining prey types by their profitability may very well be adequate in the human case. As optimal foraging is supposed to be a behavioural adaptation, it is highly likely that foragers have evolved a mechanism to gauge a prey's profitability (again either consciously or not) fairly accurately, e.g. by means of a rule of thumb; prey size would appear to be a simple and obvious candidate. Like prey type, prey size (as a proxy for profitability) can be determined vision, which would make it an economical (and speedy) rule of thumb. This may be true for a lot of predators (indeed weight has been routinely regarded as a proxy for prey rank by animal ecologists, see Broughton & Grayson, 1993: 333, with references) but even more so for humans, especially since the latter may be expected to gauge weight fairly accurately, arguably more so than other, less «brainy» species.

In their 1998 paper, Grayson & Delpech provided a fairly complete review of other factors that need to be taken into account when transferring the model to archaeology. Rather than discussing them in-depth here, we briefly point out their existence and refer to the paper in question for further details:

- time-averaging: taxonomic richness, or the number of taxa, refers to the maximum (not instantaneous) diet breadth that occurred during the period of bone deposition. So, while taxonomic richness measures the amplitude of the diet breadth, it does not per se tell anything about the population's average diet breadth (see also Madsen, 1993: 324-325).

- Differential time-sampling: maximum diet breadth depends on the temporal window that is sampled. So, [...] the longer an assemblage takes to accumulate, the greater the chances that it will incorporate a low-probability dietary event. If that event incorporates taxa not otherwise represented in the assemblage, NTAXA will increase (Grayson & Delpech, 1998: 1123). An analysis of the kind of taxa that are present, and the way specimens are distributed across these taxa may be of help.

- Sample size, NISP: as high-ranked taxa are always taken upon encounter, their abundances in the assemblage reflect their encounter rates in the environment. Low-ranked taxa, in contrast, are taken only when the encounter rates of the taxa with high profitabilities decline. Therefore, analyses of the distribution of specimens across taxa, such as NISP (or more complex ones, such as evenness), can help to establish how often lower-ranked taxa were included into the diet (see also Broughton & Grayson, 1993: 334; Broughton, 1994b: 376). As a diet dominated by high-ranking taxa goes hand in hand with an overall higher energetic return per unit of foraging time, preying on such taxa (presumably the larger animals) is considered to represent a higher level of predation efficiency, other things (such as seasonality and taphonomic histories) being equal (Broughton, 1994b: 376). Conversely, diets dominated by small or low-ranking prey are taken as an indication of a low foraging efficiency and resource intensification, due to depression of the higher-ranking resources (which itself may have multiple causes, such as predation pressure or climate).

- Mechanical effects: with NISP being incorporated into the analysis, there is a new issue that needs to be considered, i.e. the occurrence of mechanical effects that cause specimens to fragment, e.g. beyond recognition (lowering the attested NISP) or differentially among assemblages that are being compared. A similar reasoning involves differential bone transport and differential skeletal part representation.

The combination of the prey model's logic, the use of prey size as a proxy for profitability, and the use of NISPs lends itself naturally to the definition of relative abundance indices (AIs), which in the case at hand are calculated as the ratio of large bodied prey animals to the sum of the large and small, or to the sum of the large, medium, and small prey. High values (i.e., close to 1) of this diversity measure are assumed to be indicative of relatively high foraging returns, and conversely, low values suggest low returns. Changes through time, from high to low values are taken to indicate decreasing foraging returns (Ugan & Bright, 2001: 1309), which may be attributed to such things as over-hunting or climatological factors, depending on the available independent empirical evidence. AIs can take several forms, depending on the viewpoint and research question of the researcher (and obviously of the available fauna), see e.g. Broughton's (1994b) mammal-fish index ($\sum$ Mammals/$\sum$ [Mammals + Freshwater Fishes]), or Broughton (1994a), Nagaoka (2002), or Lupo & Schmitt (2005) for other AIs. Although these indices have been used recently, and with success (e.g. Nagaoka, 2002), caution must be applied here as well (see e.g. Madsen & Schmitt, 1998; Cannon, 1999; Ugan & Bright, 2001; Lupo & Schmitt, 2005). To conclude, although the diet model has proven to be robust in various areas of application, one must remain aware of a number of pitfalls that may or may not be relevant (and avoidable) in the case at hand.

4. Animal exploitation in France during MIS 3-5e

4.1. Methodology

4.1.1. Establishing competition

The first aim of our main study was to translate the Competition Hypothesis into the logic of the diet model. One possible means of doing so is contained within a key prediction of the prey model: a low-ranked prey animal will only be taken upon encounter (i.e. added to the diet) when the encounter rate with higher-ranked prey types drops to such a level that refraining from taking the former would lower the long-term average rate of energy intake (R). In other words, to maintain a given caloric intake, hunters will have to turn to lower-ranked animals when they find that higher-ranked animals are encountered less frequently. As the exploitation of lower-ranked prey is by definition more costly, this strategy is known as resource intensification, and should be detectable in archaeofaunas, all things being equal, by an increase of the relative numbers of low-ranking animals (i.e. a decrease of an AI as defined above), and thus also by an enlargement of (maximum) diet breadth (i.e. the number of taxa). Presumably, as according to the Competition Hypothesis both human phenotypes coexisted at the time of the MUPT, this must have led to a decrease in high-ranking prey types[3], which translates into a lowered encounter rate, and hence resource intensification.

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[3] Evidently, we assume here that both human phenotypes exploited the same prey types and ranked them identically.

4.1.2. Constructing the database

In order to establish resource intensification, we needed a database containing assemblages spread over a large enough geographical area, for which the number of identified specimens (NISP) was available. As it turned out, such a database had already been assembled by Grayson & Delpech (2006), covering France during MIS 5e-3, and containing all sites with a total NISP larger than or equalling 20 (leaving out all sites with a clearly mixed carnivore/human origin). As such, we decided to use this dataset, to which we added no new sites, but we did either leave out or add some assemblages based on (taphonomic) studies since 2006, while updating the NISP data where possible. This left us with 219 assemblages: 39 Aurignacian, 8 Chatelperronian, and 172 Mousterian. To be able to deal with the above-mentioned caveats that arise from transferring the model to archaeological time, we set out to complement the NISP data and record a multitude of other information (e.g. absolute and relative chronology, palaeovegetation, method of collection of faunal remains, fragmentation, the presence and nature of marks, seasonality, the extent of carcass exploitation, the characterisation of the site in terms of mobility, ...). In the end, as it turned out, such information was often scarce and thus not frequent enough to take along in the subsequent statistical analysis, as the majority of the sites had been excavated long ago, mostly with sub-standard techniques. We did record the nature of the site (open air, rock shelter, cave), temperature, and humidity. The latter two were necessary to find out (admittedly, in a rather rudimentary way) to what extent climate change could have had a confounding influence on the attested diet patterning between technocomplexes.

4.1.3. Data preparation

Some changes have been made to the way certain data are generally used. The nature of the site turned out to be much more specific than the classic open air - rock shelter - cave trinity, as e.g., some assemblages had been recovered entirely on the terrace of a cave. As such, we decided to describe the attested variability in terms of the amount of shelter present (open air, open air with shelter, sheltered). Although often very detailed, temperature and humidity estimations were recorded in a simple, dual way (cold vs. temperate, dry vs. humid), for several reasons: in some cases, not all analyses (e.g. based on pollen, chiroptera, coleoptera, sediments, ...) were in complete agreement, while in others the independence of the climate characterisation from our NISP data was compromised because small or large mammal associations were used to reconstruct the palaeoclimate. In addition, it is important to note the fact that such detailed estimations are often scholar or site dependent.

As far as our diet parameters were concerned (i.e. NTAXA and the AIs, the dependent variables in our analysis), we tried to accommodate as much as possible for the problem of overlapping profitabilities which pops up when considering taxa as prey types. We first searched the literature for existing mammal weight classifications, and came across a ranking applied in palaeoenvironmental reconstruction, more in particular the ecological diagram method (see Patou-Mathis *et al.*, 2008). As such, we arrived at the following weight classes: Class C (1-10 kg), Class D (11-45 kg), Class E (46-100 kg), Class F (101-200 kg), Class G (201-1000 kg), and Class H (> 1000 kg). We found a second classification commonly used in studies of archaeofaunas, when dealing with indeterminate bone remains, i.e. when the latter are still attributable to weight Class (e.g. Costamagno, 1999): Class I (0-100 kg), Class II (101-300 kg), Class III (301-500 kg), Class IV (501-1000 kg), and Class V (> 1000 kg). In addition, based on a literature study of weight estimates of extant and extinct species, we reconstructed the weight ranges of the taxa appearing in our database and set up a third ranking: Class 1 (0–3 kg), Class 2 (4–10 kg), Class 3 (11-25 kg), Class 4 (26-45 kg), Class 5 (46-350 kg), Class 6 (351-1050 kg), Class 7 (1051-

2800 kg), Class 8 (2801-5500). As Class 5 was rather large and could essentially be split up without too much «interpretation» of the data, we ended up with a forth ranking (i.e., a_alt to i_alt), in which Class 5 was split into Class e_alt (46-175 kg) and Class f_alt (176-350 kg).

The purpose of the four ranking systems was three-fold: (1) as mentioned above, we wanted to remain true to the model by working with prey types that had non-overlapping profitabilities as much as possible, (2) we wanted to get a rough idea of the influence a(ny) ranking system has on the results of the subsequent statistical analysis, and (3) in contrast to studies that focus on a very limited amount of assemblages (e.g. an analysis of a single site), it was impossible to better tune the prey types to the context of the assemblages at hand (e.g. with reference to the likely smaller amount of taxa in the assemblages, or to the available foraging niches). As the results of the study by Grayson & Delpech (2006) were at hand, point (2) would be easy to do.

As a result, we ended up with four measures of maximum diet breadth for each assemblage (called NPREYTYPES instead of NTAXA). The four weight rankings were also taken along when the AIs were calculated. Based on the BE literature, we decided to use two kinds of AI, i.e. the dual AI (pitting a small type against a large one, see above), and an inclusive AI (see Broughton, 1994b), in which all prey types were involved in the following way: the relative number of specimens belonging to a composite prey type was set against all others. We used the four classification systems to arrive at four maximum weight limits for our «small» prey type, i.e. 45 kg (AI_8_5_vs_AI_4_1), 100 kg (AI_V_II_vs_I), 175 kg (AI_i_alt_f_alt_vs_e_alt_a_alt), and 200 kg (AI_H_G_vs_F_A). A third «AI», the single prey type AI, was nothing more than the relative number of specimens of a given prey type within the assemblage, which was used to get a rough idea of the amount of small prey types into the diet (and hence intensification), and to facilitate the interpretation of the other two[4].

4.1.4. Statistical Analysis

For the actual analysis, we used PASW 18. We initially opted for an analysis of variance (ANOVA); however, due to severe violations of several assumptions (i.e. normality[5] and homogeneity of variances[6]) which could not be compensated for by using transformations, we proceeded by using non-parametric tests. This made the analysis both more complicated and its results less straightforward to interpret.

From the beginning, it was immediately clear that some (small) prey types only appeared in two, three, or five assemblages. Although important in itself, it does entail that abundance indices calculated with these classes will often produce missing (divisions by zero) or constant values across the entire database, making the analysis of differences between archaeological traditions for these dependent variables meaningless. As such, abundance indices based on the following prey types were ignored in the analysis:

- A (= 0), B (= 0), C (only 5 values ≠ 0),
- 1 (only 2 values ≠ 0), 2 (only 3 values ≠ 0), 3 (only 2 values ≠ 0),
- a_alt (only 2 values ≠ 0), b_alt (only 3 values ≠ 0), c_alt (only 2 values ≠ 0).

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[4] The single prey type AIs also made a comparison with the results obtained by Grayson & Delpech easier.

[5] Normality was checked using the Kolmogorov-Smirnov & Shapiro-Wilk tests

[6] We used Levene's test for equality of variances to test the second assumption for ANOVA.

While the problem of multiple zero-values also occurs with the largest prey types, it is especially troublesome with the smallest types. Still, it tells us that in general, prey smaller than 25 kg (lagomorphs, fox, beaver, wolverine, wild cat) were too low-ranking to be exploited (conservation and fragmentation issues of small prey bones left aside). The instances in which they were captured could either represent cases of an extreme intensification, or examples where the diet breadth model broke up. The first possibility may have been the case at Grotte du Renne VII (fox), Les Canalettes 3 sup (lagomorphs), and Pech-de-l'Azé Ib 7 and IV 8+Y+Z (beaver); the second possibility can involve the capture of these prey for their skin (e.g. fox at Grotte du Renne VII) or to obtain teeth or talons (e.g. Pech-de-l'Azé IV 8 + Y + Z).

For the reasons stated above, we went for the non-parametric counterpart of one-way ANOVA, i.e. the Kruskal-Wallis test[7], to test for differences in resource intensification between archaeological traditions (i.e. the main effect). Values of *p* smaller than .05 were interpreted as a rejection of the null-hypothesis (i.e. that the distribution of the dependent variable across categories is the same), and thus as differences between categories, i.e. between archaeological traditions.

To increase our certainty that diet patterns are attributable to actual resource intensification as a result of economic competition, other potential causes or contributing factors needed to be checked for. A first possible confounding factor is sample size. As a first step, we tested whether sample size correlated with the diet variables for which we had found significant differences across archaeological traditions (Spearman's correlation coefficient) For all the dependent (diet) variables which effectively correlated positively with sample size, we subsequently tested for differences in sample size between the three technocomplexes, using Kruskal-Wallis tests.

The context of the site became a second control variable. As site context consists of three categories (open air, open air with shelter, and sheltered), we made use of Kruskal-Wallis tests to check for significant differences in diet variables between the context of the site. Again, this was only done for those diet breadth variables the mean ranks of which displaying significant differences across archaeological traditions. Consequently, a frequency analysis was performed (Pearson chi-square test) to check for a possible relationship between site context (categorical variable) and archaeological tradition (categorical variable).

As a last step, we wanted to find out if any of the diet patterns we had found across archaeological traditions, could be partly due to climatic factors in the form of the climate proxies in our database (i.e. humidity and temperature). Potential links between diet and humidity/temperature were checked using the Mann-Whitney test (the non-parametric counterpart of the independent samples t-test), allowing us to check for differences between independent variables containing only two groups, i.e. wet/dry, and cold/temperate. The interpretation of the Mann-Witney test is similar to that of the Kruskal-Wallis test.

4.2. Discussion

4.2.1. All entries

4.2.1.1. Diet patterns and technocomplex: maximum diet breadth (Appendix 2)

Starting with arguably the most coarse-grained measure of resource intensification, i.e.

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[7] We used the Mann-Whitney test when testing for differences between 2, rather than K conditions e.g. in the case of climate.

changes in maximum diet breadth across traditions we see that significant differences indeed existed, between the Mousterian and the Chatelperronian: during the latter, maximum diet breadth (and hence resource intensification) was larger. If we would take the values for the Aurignacian into account (which drop below the level of the Chatelperronian, and above that of the Mousterian, but both in a non-significant way), we could make the additional suggestion that, once the Chatelperronian disappeared, resource intensification decreased in the Aurignacian. Therefore, these preliminary results seem to support the coexistence hypothesis. However, there are major caveats to be aware of:

- the pattern has been attested in two out of four prey type classification systems only. This means that finding significant differences in maximum diet breadth, i.e. the number of prey types in the diet, depends on the system used to group biological taxa into prey types.
- the pattern is significant, but only at the .05 level.

4.2.1.2. Diet patterns and technocomplex: single prey type AIs (Appendix 2)

As far as the difference between the Mousterian and Chatelperronian is concerned, single prey type AIs provide no patterning involving very low-ranking prey. It is clear however that the relative abundance of prey larger than 1000 kg, and even that of prey in the 2800-5500 range, is higher during the latter, which may (but not necessarily does) point to a decrease in intensification, i.e. seemingly the exact opposite of the finding we obtained using maximum diet breadth. Although only at the .05 level, prey in the 100-200 range were more abundant during the Chatelperronian compared to the Mousterian. As this prey type did not occur in 23 Mousterian assemblages, we are not inclined to interpret this in terms of intensification, especially when considering that in all but La Baume de Gigny XIXb and Espagnac III (both MIS3), even lower-ranking prey types occurred on site. However, it does reflect the finding by Grayson and Delpech (2006) that reindeer was significantly more abundant in the Chatelperronian than it was during the Mousterian, which is corroborated further by the very strong correlation between the reindeer NISP and AI_F ($r_s = .856$, $p = .000$, $N = 219$).

Diet differences between Mousterian and Aurignacian were not very informative either in terms of intensification, although results were highly significant. Type II (100-300 kg) and type F (100-200) prey were more abundant during the Aurignacian, the latter of which can be attributed to reindeer having been more extensively exploited during the Aurignacian (see previous paragraph), while for type II prey this effect is less prominent because *Cervus elaphus* belongs to the same type and was hunted more during the Mousterian (still, the correlation between type II prey and reindeer is considerable: $r_s = .418$, $p = .000$, $N = 219$). This again corroborates the findings by Grayson & Delpech (2006). The fact that prey types in the 200-1000 range (type G) are on the contrary more abundant during the Mousterian, could have been due to the more extensive *Cervus elaphus* exploitation during the Mousterian (see Grayson & Delpech 2006), as prey type G is the only type in our four weight classifications in which *Cervus elaphus* is not accompanied by *Rangifer tarandus* in the same class, but as it turned out *Bos* and *Bison* must have contributed quite a lot as well as the correlation between *Cervus elaphus* and AI_G was rather weak and non-significant ($r_s = .132$, $p = .052$, $N = 219$). As such, the *Rangifer* and the *Cervus* pattern, as established by Grayson & Delpech (2006) for the Aurignacian and Mousterian respectively, if at all, could only have appeared in the single prey type AIs of types F and G. Despite the fact that our prey types are not as fine-grained, and even when the assemblages we used are not entirely the same, it was reassuring to find that the reindeer pattern was confirmed (and could have been easily extracted even without the results obtained by Grayson & Delpech).

The mean relative abundance of type e_alt was higher during the Mousterian, while that of f_alt was higher during the Aurignacian. The latter is again highly influenced by extensive *Rangifer* exploitation during the Aurignacian (the reindeer NISP strongly correlates with AI_f_alt, i.e. $r_s = .576$, $p = .000$, $N = 219$). Type e_alt on the other hand, may be considered a low-ranking prey type that is not always part of the diet. Overall, it is absent from 93 assemblages, while importantly, in 51 of those, no smaller prey had been exploited. However, while type d_alt might in this respect be a better gauge of resource intensification, no significant differences were found at that weight level (i.e., 26-45 kg). Therefore, and because the upper weight limit of the type is 350 kg (which hardly qualifies as small prey) we are not willing to interpret the type e_alt pattern from a resource intensification perspective. Still, the e_alt index does reflect the abundance of *Capra* in Mousterian assemblages vs. Aurignacian ones, as found by Grayson & Delpech (2006).

No patterning involving low-ranking animals existed when comparing the Chatelperronian and the Aurignacian. However, the Chatelperronian displayed higher abundances of type V, 7, and 8 prey when juxtaposed to the Aurignacian. We can therefore note that Chatelperronians exploited significantly more animals heavier than about 1000 kg when compared to both the Mousterian and the Aurignacian.

So in conclusion, no intensification pattern could be found using single prey type abundances. However, there is a significant exploitation of high-ranking (> 1000 kg, and even > 2800 kg) animals during the Chatelperronian, which may (but not necessarily does) suggest a lower amount of resource intensification during that period, i.e. seemingly contradicting the hypothesis. A utility other than energy may have been sought after (e.g. prestige [Hawkes, 1991], or raw materials, which would argue against the use of the classic prey choice model), but there is yet another way to interpret the data, which will be discussed later on.

4.2.1.3. Diet patterns and technocomplex: dual prey type AIs (Appendix 2)

As stated before, dual prey type AIs contain more data than single prey type AIs, as they weigh the relative abundance of a low-ranking against that of a high-ranking prey type (rather than against that of the entire assemblage). Again, the idea is to choose a low-ranking prey type that is not always part of the diet. The section above already showed that choosing the latter is far from straightforward in a database study, as that choice is not tailored to a specific site with its specific ecological and topographic environment (see above).

Starting with differences between Mousterian and Chatelperronian, the relative abundance of type V (> 1000 kg) prey during the Chatelperronian as discussed in the previous section influences every dual prey type AI that can be constructed using type V as the high-ranking prey type, inducing significant differences between both archaeological traditions in every case. Because they (more or less) cover the same weight range, the same goes for types H, 7, 8, i_alt and h_alt, although the latter four typically evoke significant results when bundled with some, rather than all of the smaller classes. This can be expected, as the grain of the classification systems we constructed ourselves (and to which the latter four dual AIs belong), is somewhat finer than that of the other two. However, that finer grain in our classification is mostly found with the more low-ranking prey types, and that is exactly where no significant differences between Mousterian and Chatelperronian could be detected[8].

So, if only a limited amount of dual AIs had been calculated and analysed, we might have concluded that the Chatelperronian was characterised by a lower resource intensification than the Mousterian (i.e. by higher dual AIs), contradicting the coexistence hypothesis. However, knowing how the abundance of very large animals during the Chatelperronian skewed the results (i.e. the patterning observed with the single AIs), and seeing that

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[8] The exception here is AI_8_vs_4 (= AI_i_alt_vs_d_alt), but the significance, at just .05, is rather unconvincing.

pattern reflected as well in dual AIs that involved lower-ranking types that still out-ranked the very lowest, the effect we witnessed should not be ascribed to resource intensification at face value.

There is one dual AI that stands out from this general pattern however, as it deals with prey as light as 26-45 kg, i.e. AI_e_alt_vs_d_alt. Coincidentally, it is composed of both prey types that we thought of as being candidates for the lowest-ranking prey in the database, as even smaller prey types are very rare and thus devoid of enough variability across archaeological traditions to yield significant results (see above). This AI, which perhaps we would not have come across if we had not decided on testing all possible dual prey type AIs, actually *can* be interpreted in terms of resource intensification, and perhaps with more inferential power than the dual prey type AIs containing the very large taxa. More in particular, the mean rank is lower for the Chatelperronian, implying that during the Mousterian, relatively more e_alt prey specimens were exploited when compared to type d_alt. Basically, this means that Chatelperronians exploited the lowest-ranking of both more frequently when compared to the Mousterians, or in other words, that resource intensification was higher during the Chatelperronian. Essentially, both patterns (the abundance of the most high-ranking animals, and that of very small animals during the Chatelperronian vs. the Mousterian) corresponds to our finding that maximum diet breadth (and resource intensification) was significantly higher during the Chatelperronian (at least according to two ranking systems): they apparently exploited relatively more prey at both ends of the spectrum compared to what Mousterian hunters focused on.

When moving to the Mousterian vs. the Aurignacian, our list of significant differences becomes smaller. A first notable and very significant divergence is to be found with types F and G: the G_vs_F AI is, like for the Chatelperronian, lower for the Aurignacian vs. the Mousterian. This could be interpreted as intensification, but more in particular it is due to the focus on reindeer during the Aurignacian (the reindeer NISP correlates strongly with AI G_vs_F, i.e. $r_s = -.834$, $p = 0$, $N = 214$). The latter probably also partly explains why the mean rank of the f_alt_vs_e_alt index (176-350 vs. 46-175 kg) is larger during the Aurignacian; the more extensive exploitation of *Capra* during the Mousterian (see Grayson & Delpech 2006) and the higher exploitation of e_alt prey in general during the Mousterian (as determined above) explaining the other part. Like in our comparison between Mousterian and Chatelperronian, during the Aurignacian as well, an excess of the highest-ranking prey type could be noted when set against Mousterian animal exploitation, for multiple dual AIs (2800-5500 kg vs. 25-45 kg, 46-175 kg, and 351-1050 kg). This again suggests that the pattern cannot be interpreted in terms of resource exploitation without further consideration.

Finally, when comparing the exploitation strategies of the Chatelperronian and the Aurignacian, we see the significantly higher exploitation of very high-ranking prey (> 1000 kg and 2800-5500 kg) during the Chatelperronian reflected in all four statistically significant differences. No small prey types are part of the AIs that turned up significant results, so no firm conclusions about resource intensification could be made.

4.2.1.4. Diet patterns and technocomplex: inclusive prey type AIs (Appendix 2)

Two measures out of four have produced significant differences between archaeological traditions, i.e. AI_H_G_vs_F_A (H(2) = 16.719, p = .000) and AI_i_alt_f_alt_vs_e_alt_a_alt (H(2) = 6.947, p = .031). However, in the latter case, differences were no longer significant in the pairwise comparisons. Taken at face value, the remaining difference, between Aurignacian and Mousterian, points to a higher amount of intensification during the Aurignacian. This appears to confirm the hypothesis, and in fact, although pairwise comparisons showed no significant patterning involving the Chatelperronian, mean ranking follows a declining trend across traditions, i.e. Mousterian (118.99), Chatelperronian (92.50), Aurignacian (73.92), suggesting inclining resource intensification.

However, there is again a cautionary note to be made: the (composite) low-ranking prey type that yielded the results, i.e. 0-200 kg, is problematic. All three other indices, which set apart composite prey types that were much lower-ranking, showed no significant differences between traditions. This suggests that the non-composite prey type or taxon responsible for the pattern is to be found in the upper part of the 0-200 kg weight range. Indeed, when we compare the taxa in prey type F to types e_alt and f_alt, the likely suspect is *Rangifer tarandus*, and indeed, reindeer NISP correlates with AI_H_G_vs_F_A ($r_s = -.437$, $p = .000$, $N = 219$). The question that needs to be asked is whether this species, which is responsible for quite a number of significant results, can really be interpreted as low(est)-ranking within the theoretical context of diet breadth model and the empirical reality condensed into the database. As it can hardly be interpreted as a species that enters or leaves the diet as a function of higher-ranking prey availability because of the very real focus on this taxon during the Aurignacian (see also Grayson & Delpech), the answer to this question tends to be «no».

4.2.1.5. Diet patterns and sample size

It was only to be expected that sample size would correlate frequently with diet breadth: the bigger the sample, the more likely that more taxa will be included. Importantly, a Kruskal-Wallis test showed that sample size was significantly higher in the Aurignacian than in the Mousterian; however, this is true only at the $p = .05$ level. Nevertheless, we still need to check for which diet indicators these results are relevant. For this, we need to compare Appendices 2 and 3.

As it turns out, maximum diet breadth is not affected at all, as no significant difference existed between these both archaeological traditions. As mentioned before, differences in prey type abundance (the single prey type AIs) reflect primarily the patterns established before by Grayson & Delpech (2006), i.e. the greater focus on *Rangifer* by Aurignacians, and that on *Capra* and *Cervus* by Mousterians. Of these, only AI_II and AI_F correlate with sample size, but rather weakly so. However, all dual AIs which differ significantly between Aurignacian and Mousterian correlate with sample size, and with the exception of AI_G_vs_F and AI_f_alt_vs_e_alt, this correlation is moderate. This means that in the remaining cases, i.e. AI_8_vs_4, AI_8_vs_6, and AI_i_alt_vs_e_alt, we can say that the diverging ranks for the Aurignacian and the Mousterian have been influenced by sample size. This means that the significantly larger number of very big animals (> 1000 kg) in the Aurignacian vs. the Mousterian is likely to be partly due to sample size.

4.2.1.6. Diet patterns and humidity

We found several significant differences in diet patterns between dry and humid climates (see Appendix 4). However, humidity and archaeological tradition are independent from each other ($X^2 = .501$, $p = .901$). Therefore humidity cannot (help) explain the differences in diet patterns found between archaeological traditions (see Appendix 2).

The patterns between diet indicators and humidity attested here, are mostly of palaeoecological importance, albeit in a diluted form: while abundances obviously arose through human intervention, they also reflect in part the natural occurrence of taxa and prey types. For example, a humid climate is characterised by higher abundances of type G prey compared to a dry climate, and this is unsurprising when we check the taxa contained within this type (*Bos* and *Bison*, *Cervus*, *Megaloceros*, *Alces*). Type F prey on the contrary (*Rangifer*, *Equus hydruntinus*) are associated with a dryer climate. For *Sus*, the third taxon in type F, this may not be true, but its contribution to the prey type is swamped by those of the other two taxa.

4.2.1.7. Diet patterns and temperature

We found several significant differences in diet patterns between cold and temperate climates (see Appendix 5). However, like with humidity, temperature and archaeological tradition are independent from each other (X^2 = 1.049, p = .901). Therefore temperature cannot explain the differences in diet patterns found between archaeological traditions (found in Appendix 2). As such the data in Appendix 5 could prove more useful for palaeoecological analyses, and in fact, confirms some general ideas about taxa and temperature (e.g. the preference for cold environments by *Rangifer*, the preference for more temperate environments by *Bos* and *Bison*).

4.2.1.8. Diet patterns and site context

When testing for the independency of technocomplex and site context, one of the assumptions of the chi-square test was violated: expected counts for three out of nine cells of the contingency table were lower than 5 (as opposed to the allowed 20 %). Therefore, the result of this chi-square test (X^2 = 20.021, p = .002) is not valid. When the Chatelperronian is left out of the comparison, only one expected value (out of 6) is lower than 5 (i.e. that of Aurignacian open air sites). As this is less than 20 %, and as the value in question (1.48) is higher than 1, the results of this chi-square test (X^2 = 19.362, p = .000) are considered valid. The value of Cramer's V (.303, p = .000) indicates a medium effect size.

Although the chi-square test including Chatelperronian entries cannot be considered valid, we will incorporate the Chatelperronian data in interpreting the results, assuming that technocomplex and site context are not independent for these entries as well. It must be remembered that the number of Mousterian assemblages far outweighs that of Chatelperronian or Aurignacian entries, and as such, the percentages given in the contingency table of site context and archaeological tradition are skewed and must be interpreted with care. Therefore, we compare the effective counts with the expected counts for each cell of the matrix. A quick inspection of Appendix 7 shows:

- that open air sites are very rare in the entire database, and they are all Mousterian;
- that open air sites with shelter are more abundant;
- that sheltered sites, i.e. caves and rock shelters, are the most abundant;
- an overrepresentation of open air sites with shelter and open air sites in the Mousterian, and an underrepresentation of sheltered sites;
- an overrepresentation of sheltered sites, and an underrepresentation of open air sites (with and without shelter).

As far as the relationship between site context and diet differences between technocomplexes is concerned, it is evident from Appendix 6 that no significant differences in the number of prey types exist between site types. It is also evident that all but one of the remaining diet variables (i.e. AI_e_alt_vs_d_alt) have a higher mean rank in open air sites than in open air sites with shelter (so generally, for all diet variables, the following is true: open air > sheltered). Similarly, except for three diet variables (AI_II, AI_G, and the inclusive AI), a higher mean rank can be observed in sheltered sites when compared to open air sites with shelter. So again in general, sheltered > open air with shelter, which combined indicates that the mean ranks of the diet parameters between site contexts adhere to the following rule: open air > sheltered > open air with shelter.

Note that Appendix 2 shows the following relationship between mean rank diet differences between technocomplex: Chatelperronian > Mousterian (except for AI_G_vs_F, and AI_e_alt_vs_d_alt[9]), Chatelperronian > Aurignacian, and Aurignacian > Mousterian

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[9] In the case of AI_e_alt_vs_d_alt, site context does not explain the attested differences between Chatelperronian and Mousterian (C < M). More in particular, we find a higher mean rank in open air sites with shelter than in open air sites. Although there are more open air sites with sites than expected in the Mousterian, there are no more open air sites than expected in the Chatelperronian.

(except for AI_G, AI_e_alt, and AI_G_vs_F), which combine into the following pattern: Chatelperronian > Aurignacian > Mousterian.

Thus, if it is so that site context partly explains the differences in diet patterns found between technocomplexes, then we should generally find relatively more open air sites in the Chatelperronian, relatively more sheltered sites in the Aurignacian, and relatively more open air with shelter sites in the Mousterian than expected. However, in Appendix 7 we see different patterns: Mousterian sites have more open air and open air with shelter sites than expected, and both Chatelperronian and Aurignacian sites have more sheltered sites than expected. As these patterns are not consistent with the relation found between site context and diet parameters, we can exclude site context as an explaining factor in the relations found between technocomplex and the diet parameters.

4.2.1.9. Summary

The following differences in animal exploitation strategies between archaeological traditions could be discerned:

- Chatelperronians exploited significantly more of the highest-ranking prey (> 1000 kg, and even in the 2800-5500 kg range), compared to both Mousterians and Aurignacians. This may or may not be significant in terms of resource exploitation. In the former case, and at face value, it would contradict the coexistence hypothesis.
- More extensive reindeer exploitation, and smaller relative amounts of *Cervus elaphus* and *Capra* during the Aurignacian vs. the Mousterian, patterns established by Grayson and Delpech, were discernable here as well. We chose not to regard *Capra* (or by extention, type e_alt), as a very low-ranking prey type given the abundances of type d_alt, and as such, the former's relative abundance has not been interpreted in terms of intensification. Chatelperronians too exploited more reindeer than Mousterians (but less than Aurignacians).
- On average, Chatelperronians exploited the smallest prey (26-45 kg, or type d_alt), more frequently than Mousterians, supporting the coexistence hypothesis.

This means that Chatelperronians apparently exploited both more very high-ranking animals and more very low-ranking animals (hence leading to the broader diet we attested) when compared to the Mousterians. While the latter supports the coexistence hypothesis (as does the wider diet), the former is a bit odd from a diet breadth perspective. As this pattern of high-ranking prey exploitation is also apparent when comparing the Chatelperronian to the Aurignacian, it could be interpreted in three ways, the latter two of which lying outside the logic of the diet breadth model:

- Very large animals (> 1000 kg) may in reality have been relatively low-ranking, rather than very high-ranking:
  - their large size may have required extremely high handling costs (therefore lowering the profitability) in terms of pursuit, killing and butchering (+ drying ?);
  - this may have been augmented by the fact that considerable group sizes may have been required to handle the animal before the meat got spoiled (therefore lowering the per capita profitability[10]). In absence of such group sizes, these large animals may only have been consumed partly; therefore, only (an unknown) part of the weight may have been used by the forager to rank the taxon.

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[10] In contrast to social foraging models (Giraldeau & Caraco, 2000), the basic prey model assumes that the hunting is done by a single hunter.

- Aurignacians, upon contact, may have targeted reindeer more so than Mousterians (which dispatched primarily *Cervus elaphus* and *Capra*) as to partially occupy another niche[11]. If certain Mousterian populations were contemporaneous with Chatelperronian groups, the focus of the latter on reindeer as well, but primarily on species that were hunted less by both Mousterians and Aurignacians (i.e. very small and very large animals), could point to a process of niche separation (i.e. essentially a form of specialisation) by Chatelperronians and Aurignacians, in order to alleviate economical competition. This may or may not be related to the obvious changes in material (lithic) culture, but in any case, it would support the coexistence hypothesis, all things being equal[12].
- A maximisation of more than energy alone, or of another currency altogether. In this scenario, the exploitation of very large game may have ...
    - had some sort of utility value[13] (ivory, bone, ...),
    - been part of a showing-off tactic (Hawkes, 1991).

As far as possible confounding effects are concerned, we should note that the significantly larger number of very big animals (> 1000 kg) in the Aurignacian, when compared to the Mousterian, is likely to be partly due to sample size. Climate and site context however, as recorded here, do not appear to be relevant to the main patterns we attested.

4.2.2. Reliable entries

As discussed before, the assemblages contained within the database suffer from several deficits that make them less suitable to a diet breadth analysis when compared to anthropological, and even Holocene archaeological data. What are now considered sub-standard excavation and retrieval methods, the often limited areas covered during excavation, and a more limited understanding of taphonomic processes have blurred the information that was originally present at the sites. Originally, we intended to use parameters such as the date of excavation, the name of the excavator, retrieval methods (sieving vs. recovery by hand), the total NISP, the carnivore NISP, marks (either anthropogenic or inflicted by animals) on the bones, etc. as discriminating factors to make a selection of so-called «reliable» sites, i.e. sites with bone assemblages that were exclusively anthropogenic in nature, well-preserved, excavated and retrieved with care, and thoroughly studied.

However, when the majority of data had been assembled, it became clear that there were always some data missing (or perhaps more accurately, there was always but a very limited amount of data present), such that making a selection of the most suitable sites, if done at all, could only be based on a few, readily available criteria. These became the following:

- a NISP of > 100: in contrast to Grayson & Delpech (2006), we increased the limit for inclusion from 20 to 100 (herbivore) bone specimens. The analysis on all entries clearly showed that a considerable number of our diet variables co-varied with sample size, so this was an obvious constraint.
- a carnivore abundance below 10 %: the criterion was directed against species that could skew the relative and absolute numbers of prey taxa, both by bringing prey to the site themselves or by processing human kitchen waste. Note that Grayson & Delpech

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[11] This may explain the significant differences between Mousterian and Aurignacian exploitation strategies attested both by Grayson & Delpech (2006) and our own analysis.

[12] I.e. in case climate and other variables did not influence prey choice.

[13] Note that this utility value may have been the reason why Aurignacians focused on reindeer in the first place.

(2006) already removed certain sites from consideration when carnivore influence was obvious; evidence for this are the rather low amounts of carnivore damaged bones (whenever these data were available). It is obvious that the topic is quite complex and cannot possibly be captured by something as carnivore abundance; the matter of carnivore presence and dens is elaborated on by Costamagno (1999, with references) for example. Nevertheless, based on the values referred to in this source (16-93 % of the fauna being hyena in the case of dens), we may assume that our criterion is certainly adequate to expose carnivore dens (if any should have escaped the scrutiny of Grayson & Delpech), and presumably (but with quite some reservations), a too large carnivore influence in general.

As it turned out, this left us with 105 assemblages (79 Mousterian, 3 Chatelperronian, and 23 Aurignacian entries), spread over 30 sites.

4.2.2.1. Diet patterns and technocomplex

Some interesting patterns emerge when comparing this analysis of our diet indicators (see Appendix 9) with the corresponding one involving the entire database:

- the number of significant differences between archaeological traditions has dropped from 40 to 6.
- the 6 diet indicators displaying differences between traditions were all part of the 40 found earlier. For example, the pattern between Mousterian and Aurignacian whereby dual AIs with animals larger than 1000 kg as the high-ranking prey type were higher during the latter, is gone. Of course, as we saw earlier, the strategy could have been a partial artefact of sample size differences between archaeological traditions rather than caused completely by intensification, and raising the herbivore NISP threshold for inclusion to the analysis conducted in this section may have eliminated that factor to the extent that the pattern was no longer significant.
- significant differences are to be found between the Mousterian and the Aurignacian only (and they are the same as before, only represented by fewer indicators) rather than between all sets of traditions, or put differently, none of the differences involving the Chatelperronian survived.
- while p values remained more or less the same, all 6 differences found in this instance had lower values of the test statistic (i.e. H), meaning that the patterns, in the form of mean rank differences, have become less prominent.

This means that what we found when studying the restricted database, is a subset of our previous results. We can come up with two explanations:

- carnivore action has been filtered out more effectively, reducing the number of significant differences overall, and all patterning (falsely) attributed to the Chatelperronians in particular, i.e. a focus on very small and very large animals, in particular;
- shrinking our database (decreasing the number of entries by 58 %, and the number of Chatelperronian sites by 63 %, to a mere 3) had primarily effects of a statistical nature: the reduced variability led to a decrease of the amount of significant ($p < .05$) results, and the total disappearance of the Chatelperronian and Mousterian-Aurignacian patterns.

We believe the second explanation to be the most logical, as the first assumes a link between carnivores and the exploitation of very large animals (i.e. part of the Chatelperronian pattern) which we believe to be tenuous at best. Even if it is not, this hypothesis would not be compatible with the drop of the test statistic values, as that would mean that carnivores produced both the Chatelperronian pattern, while enhancing the differences between Mousterian and Aurignacian.

Moreover, reducing the database inevitably entailed a reduction of its variability, and thus the amount of significant differences a statistical analysis can bring to the surface. Using the single AIs (backed up by the compatible exploitation patterns discovered by Grayson & Delpech, 2006), some significant differences between traditions could be explained fairly easily in the context of the previous section; because of the multiple weight classification systems we used, those same differences were apparent in quite lot of (from a point of view, redundant) diet indicators, providing the analysis with some robustness. As the current analysis entailed a drop in the amount of significant differences, this led to a removal of redundancy. In cases where such redundancy is not present (i.e. in studies where a single weight classification system would be used, or in case of the Chatelperronian), this can be problematic.

4.2.2.2. Diet patterns and sample size

A Kruskal-Wallis test showed no significant differences in sample size between technocomplexes. We did not find any significant correlation (Spearman's rho) between diet parameters and sample size. As we cannot find a relationship between diet and sample size, nor between technocomplex and sample size, the latter cannot have been a confounding factor in the relation between diet and archaeological tradition.

So, while inspection of the full database learnt that sample sizes during the Aurignacian were significantly greater than those during the Mousterian, this is no longer the case here. In other words, the diet patterns found for the 'reliable' sites are no longer partly dependent on sample size, due to the elimination of sites with a herbivore NISP smaller than 100.

4.2.2.3. Diet patterns and humidity

Results are the same as those for the full database (see Appendix 10), although the values of the test statistic are lower here, and AI_8_vs_4 is no longer significantly different between categories of humidity. So again, we are left with a subset of our previous findings.

The chi-square test on humidity and archaeological tradition was not significant ($X^2 = .078$, $p = .962$). Unfortunately, an assumption of this test was violated as 4 out of 6 cells of the contingency table had expected counts less than 5. However, following our reasoning when considering all database entries, we can assume that humidity does not explain the differences in diet patterns found between technocomplexes.

4.2.2.4. Diet patterns and temperature

Again, our results are a subset of those of the entire database, and again, values of the test statistic are lower (see Appendix 11). An exception to this is AI_f_alt, which did not display significant differences among categories of temperature in the analysis on the full database.

The chi-square test was not significant ($X^2 = 5.474$, $p = .065$) but as in the previous section an assumption of the test was violated: 3 out of 6 cells of the contingency table had expected counts of less than 5. However, we may assume, in line with the interpretation of the full database's analysis, that temperature does not help explain the differences in diet patterns found between archaeological traditions.

4.2.2.5. Diet patterns and temperature

No significant differences in diet patterning could be found between site contexts, so the latter is irrelevant in explaining diet differences between technocomplexes.

4.2.2.6. Summary

In conclusion to the analysis of the reliable entries, we found that reducing the number of assemblages (by means of a quality criterion) brought problems of a statistical nature to the surface. At that point, even the built-in redundancy (in terms of the four weight rankings and the different measures of intensification, i.e. NPREYTYPES and the three AIs) was not enough to render the picture that had emerged from the analysis of all entries. Importantly, such redundancy would normally not be present in a study of a more limited amount of assemblages, which represents a case where we believe the prey model may be of more use, e.g. as one way of determining intensification in a fine-grained analysis that also includes carcass exploitation, butchery intensity, marrow and grease extraction (see e.g. Morin, 2004). In any case, we can say that the analysis of only the MIS 3 assemblages (55 Mousterian, 8 Chatelperronian, and 38 Aurignacian), which nears completion, was certainly surprising in terms of redundancy.

As far as our evidence for intensification goes, there are indeed some indications, e.g. the higher exploitation of small animals during the Chatelperronian. On the other hand, their preoccupation with the biggest animals appears enigmatic in the context of the prey model; likewise, the extensive exploitation of reindeer during the Aurignacian (and to a lesser degree, the Chatelperronian) is difficult to comprehend in terms of the predictions of the prey model, as reindeer cannot be considered small animals. Here as well, the soon to be published analysis of the MIS 3 assemblages was revealing.

Based on the latter and the results we obtained here, we would like to argue that if there was indeed an intensification process going on at the MUPT (as predicted by the Competition Hypothesis), and if our results are more or less representative for MIS 3, the basic prey model can provide but a partial description of the foraging behaviour of the MIS 3-5e hominins in our database. Indeed, we believe that yet another mechanism (i.e. aside from an increase in diet breadth) would have to have been at work to explain our results. This may not be very remarkable, as Morrison (1994, cited by Betts & Friesen, 2004) pointed out that intensification can take three general forms, which are not in all cases mutually exclusive:

- specialisation (an increasing focus on a small number of resources),
- diversification (an increasing focus on a broad number of resources, as predicted by the basic diet model),
- investment (the development of new technologies and procurement strategies).

This indicates that the basic prey model, while perhaps not able to offer an all-encompassing explanation (most likely, such an explanation does not exist anyway), can be a great heuristic device in terms of generating testable hypotheses and directing future research.

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Site		*Level(s)*
1	*Abri Bourgeois-Delaunay*	8, 8', 9, 9', 10
2	*Abri Pataud*	7, 8, 11, 12, 13, 14
3	*La Baume de Gigny*	VIII, XV, XVI, XIXb, XIXc, XX
4	*La Baume Moula-Guercy*	IV + VIII
5	*Beauvais*	C1, C2
6	*La Borde*	IIIb
7	*La Brèche de Genay*	série rouge, série brune
8	*Caminade-Est*	F
9	*Les Canalettes*	2, 3 sup.
10	*Chez-Pinaud*	8 (zone 2 + *locus* W), 10 (zone 2), 12, 14, 16, 18, 20, 22, 24
11	*Combe-Grenal*	6, 7, 8, 9, 10, 11, 12, 13, 14, 15 + 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39 + 40, 41, 42 + 43, 44 + 45, 46 + 47, 48 + 49, 50, 50A, 51, 52, 53, 54
12	*Espagnac*	II, III, IVa, IVb
13	*La Ferrassie*	F frontal, G frontal, H, I, J, K1-3, K4, K5 until base of K (= K5 + K6), L3a-b sagittal
14	*Les Fieux*	J, K
15	*Le Flageolet I*	VIII, IX, XI
16	*La Grande Roche de la Plématrie*	Ej, Em
17	*Grotte de l'Adaouste*	20 + 21 + C + D + E + F + 9 + 9a + 9b2 + 9c + 10b + 11 + III + IV
18	*Grotte de l'Hyène*	IVb6
19	*Grotte des Hyènes*	2A, 2C, 2DE, 2F
20	*Grotte du Renne*	VII, Xa, Xc, XI, XII
21	*Grotte Ouest* du Portel	C, D, F, F1, F2, F3, G
22	*Grotte Tournal*	IA, IIB
23	*Grotte Vaufrey*	I, II
24	*Grotte XVI*	Abb, Aib, B, C
25	*Hortus*	9A-10A2, 10A3-B, 11C, 12A-B, 13A-14, 15, 16B, 17-21B, 23B2, 24, 26B, 27, 28A, 28CD, 29
26	*Maldidier*	5
27	*Mauran*	C1 + C2
28	*Mont-Dol*	6, 7, 8, 9
29	*Mutzig I*	C3-4, C5, C6
30	*Payre*	D
31	*Pech de l'Azé Ib*	4, 6, 7
32	*Pech de l'Azé II*	2E, 2G, 2G', 3, 4A, 4B (in the cave) + 4 (in front of the cave), 4C1, 4C2, 4E
33	*Pech de l'Azé IV*	G, H1, H2, I1, I2, J1, J2, J3, J3a, J3b, J3c, J4, 8 (new campaign)+Z+Y
34	*Le Piage*	G-I + F + b + d, K
35	*La Quina* (station amont)	2a, 2b, 4a, 4b, 6a, 6b, 6c, 6d, 8
36	*Ramandils*	I, II, III, IV, V
37	*Raysse*	2
38	*Regourdou*	2, 3, 4, 5, 7
39	*Roc de Combe*	5, 6, 7, 8
40	*Roc-en-Pail*	30 (?)
41	*La Roche-à-Pierrot*	EGC (14), EGPF (10), EJOP sup. (8), EJO sup. (6), EJF (5), EJM (4), EJJ (3)
42	*Saint-Marcel*	F, G, H, I, J', J
43	*Salpêtre de Pompignan*	V, VI, VII, VIII, XI
44	*La Salpêtrière*	14a (= CG5-SLC4)
45	*Trou de la Chèvre*	3,4

Appendix 1 - Sites and assemblages appearing in the study.

Techno-complexes	*Number of prey types*	*Single prey type AIs*	*Dual prey type AIs*	*Inclusive prey type AIs*
Chatelperronian vs. Mousterian	I*(C 156.25; M 103.75) 1*(C 168.56; M 105.27)	V**(= H) (C 170.56; M 105.63) F*(C 152.25; M 95.74) 7*(= h_alt) (C 154.00; M 108.14) 8***(C 163.00; M 104.83)	V_vs_I*(C 135.19; M 89.24) V_vs_II**(C 162.62; M 102.96) V_vs_III**(C 150.12; M 94.75) V_vs_IV*(C 142.06; M 93.04) H_vs_E*(C 110.29; M 71.18) H_vs_G**(C 166.88; M 102.95) G_vs_F*(C 66.19; M 121.39) 8_vs_4 (= AI_i_alt_vs_d_alt)*(C 94.06; M 65.70) 8_vs_5**(C 161.69; M 104.54) 8_vs_6**(= AI_i_alt_vs_g_alt) (C 154.50; M 99.62) 7_vs_5*(C 152.31; M 107.77) 7_vs_6*(= AI_h_alt_vs_g_alt) (C 145.31; M 102.50) i_alt_vs_e_alt**(C 121.25; M 69.91) i_alt_vs_f_alt**(C 154.00; M 100.29) h_alt_vs_e_alt*(C 119.00; M 72.88) e_alt_vs_d_alt*(C 36.50; M 88.08)	
Aurignacian vs. Mousterian		II**(A 138.50; M 103.90) F***(A 164.24; M 95.74) G***(A 75.28; M 118.97) e_alt**(A 84.15; M 117.77) f_alt***(A 147.81; M 101.11)	G_vs_F***(A 56.49; M 121.39) 8_vs_4 (= i_alt_vs_d_alt)*(A 83.52; M 65.70) 8_vs_6 (= i_alt_vs_g_alt)*(A 117.66; M 99.62) i_alt_vs_e_alt*(A 90.33; M 69.91) f_alt_vs_e_alt**(A 136.99; M 101.34)	H_G_vs_F_A***(A 73.92; M 118.99)
Chatelperronian vs. Aurignacian		V*(= H) (C 170.56; A 116.83) 7*(= h_alt) (C 154.00; A 109.18) 8*(= i_alt) (C 163.00; A 121.92)	V_vs_II*(C 162.62; A 109.97) H_vs_G*(C 166.88; A 117.68) 8_vs_5*(C 161.69; A 120.53) i_alt_vs_f_alt*(C 154.00; A 114.51)	

Appendix 2 - Significant mean rank differences (Kruskal-Wallis) of diet parameters between technocomplexes, all entries. Values represent significant differences at the * p≤.05 level, ** p≤.01 level, *** p≤.001 level.

Diet variable	*r*	*N entries*
Number of prey types		
N_PREY_TYPES_I	.417***	219
N_PREY_TYPES_1	.419***	219
Single prey type AIs		
AI_II	.196**	
AI_V	.351***	219
AI_F	.278***	219
AI_7	.321***	219
AI_8	.350***	219
Dual Prey type AIs		
AI_V_vs_I	.391***	186
AI_V_vs_II	.336***	212
AI_V_vs_III	.342***	197
AI_V_vs_IV	.337***	193
AI_H_vs_E	.360***	149
AI_H_vs_G	.359***	215
AI_G_vs_F	-.232***	214
AI_8_vs_4	.398***	140
AI_8_vs_5	.349***	218
AI_8_vs_6	.350***	209
AI_7_vs_5	.324***	218
AI_7_vs_6	.319***	208
AI_i_alt_vs_e_alt	.402***	150
AI_i_alt_vs_f_alt	.339***	209
AI_h_alt_vs_e_alt	.386***	151
AI_f_alt_vs_e_alt	.164*	218
Inclusive prey type AIs		
AI_V_II_vs_I	.198**	219
AI_i_alt_f_alt_vs_e_alt_a_alt	.210**	219

Appendix 3 - Significant correlations (Spearman's rho) between diet parameters and sample size, all entries. Only those diet parameters that showed significant differences between technocomplexes are displayed here (see also the following appendices). Values represent significant differences at the * p≤.05 level, ** p≤.01 level, *** p≤.001 level.

Diet variable	*Mean rank differences*
Number of prey types	
Single prey type AIs	
AI_F	D 78.64; H 54.90***
AI_G	D 48.11; H 81.59***
Dual prey type AIs	
AI_G_vs_F	D 49.04; H 75.83***
AI_8_vs_4	D 46.23; H 35.76**
Inclusive prey type AIs	
AI_H_G_vs_F_A	D 48.15; H 81.56 ***

Appendix 4 - Significant mean rank differences (Mann-Witney) of diet parameters between dry (D) and humid (H) climate, all entries. Values represent significant differences at the * p≤.05 level, ** p≤.01 level, *** p≤.001 level.

Diet variables	*Mean rank differences*
Number of prey types	
N_PREY_TYPES_I	C 77.90; T 97.68**
N_PREY_TYPES_1	C 76.04; T 102.38***
Single prey type AIs	
AI_V	C 79.40; T 93.87*
AI_F	C 93.10; T 59.41***
AI_G	C 68.68; T 121.02***
AI_7	C 78.82; T 95.34**
Dual prey type AIs	
AI_H_vs_E	C 55.97; T 72.97**
AI_G_vs_F	C 69.32; T 109.33***
AI_7_vs_5	C 78.36; T 94.65**
AI_7_vs_6	C 73.82; T 87.91*
AI_h_alt_vs_e_alt	C 58.24; T 70.74*
AI_e_alt_vs_d_alt	C 69.53; T 53.01*
Inclusive prey type AIs	
AI_H_G_vs_F_A	C 68.53; T 121.32***

Appendix 5 - Significant mean rank differences (Mann-Witney) of diet parameters between cold (C) and temperate (T) climate, all entries. Values represent significant differences at the * p≤.05 level, ** p≤.01 level, *** p≤.001 level.

Diet variables	*O vs. OS*	*OS vs. S*	*O vs. S*
Number of prey types			
Single prey type AIs			
AI_II		OS 129.68; S 101.13**	
AI_V	O 172.88; OS 96.01***		O 172.88; S 113.26**
AI_G		OS 126.93; S 101.89*	
AI_8	O 180.25; OS 95.52***	OS 95.52; S 113.08*	O 180.25; S 113.08***
Dual prey type AIs			
AI_V_vs_I	O 170.33; OS 76.44***	OS 76.44; S 98.56**	O 170.33; S 98.56***
AI_V_vs_II	O 165.25; OS 91.50***	OS 91.50; S 110.54*	O 165.25; S 110.54*
AI_V_vs_III	O 151.88; OS 84.51***	OS 84.51; S 103.49*	O 151.88; S 103.49*
AI_V_vs_IV	O 147.44; OS 83.55***		O 147.44; S 100.92*
AI_H_vs_E	O 128.50; OS 62.07***		O 128.50; S 77.82**
AI_H_vs_G	O 169.50; OS 92.94***	OS 92.94; S 111.96*	O 169.50; S 111.96**
AI_8_vs_4 (=AI_i_alt_vs_d_alt)	O 126.08; OS 55.78***	OS 55.78; S 74.20**	O 126.08; S 74.20***
AI_8_vs_5	O 179.88; OS 95.04**	OS 95.04; S 112.46*	O 179.88; S 112.46***
AI_8_vs_6 (=AI_i_alt_vs_g_alt)	O 170.50; OS 90.17***	OS 90.17; S 108.78**	O 170.50; S 108.78***
AI_i_alt_vs_e_alt	O 138.50; OS 60.05***	OS 60.05; S 80.12**	O 138.50; S 80.12***
AI_i_alt_vs_f_alt	O 171.25; OS 90.44***	OS 90.44; S 108.19*	O 171.25; S 108.19***
AI_h_alt_vs_e_alt	O 139.00; OS 65.25**		O 139.00; S 80.01*
AI_f_alt_vs_e_alt	O 172.50; OS 91.28***	OS 91.28; S 114.68*	O 172.50; S 144.68*
AI_e_alt_vs_d_alt	O 21.00; OS 96.16*		
Inclusive prey type AIs			
AI_H_G_vs_F_A		OS 126.66; S 101.15*	

Appendix 6 - Significant mean rank differences (Kruskal-Wallis) of diet parameters between open air (O), open air with shelter (OS), and sheltered (S) sites, all entries. Values represent significant differences at the * p≤.05 level, ** p≤.01 level, *** p≤.001 level.

	Mousterian	*Chatelperronian*	*Aurignacian*	*Total*
Open air	8 (6.3)	0 (0.3)	0 (1.4)	8
Open air with shelter	65 (54.2)	2 (2.5)	2 (12.3)	69
Sheltered	99 (111.5)	6 (5.2)	37 (25.3)	142
Total	172	8	39	219

Appendix 7 - 3x3 contingency table of technocomplex vs. site context: effective counts (expected counts), all entries. Values represent significant differences at the * p≤.05 level, ** p≤.01 level, *** p≤.001 level.

	Mousterian	*Aurignacian*	*Total*
Open air	8 (6.5)	0 (1.5)	
Open air with shelter	65 (54.6)	2 (12.4)	67
Sheltered	99 (110.9)	37 (25.1)	136
Total	*172*	*39*	*211*

Appendix 8 - 3x2 contingency table of technocomplex vs. site context: effective count (expected count), all entries, without Chatelperronian sites. Values represent significant differences at the * p≤.05 level, ** p≤.01 level, *** p≤.001 level.

	Number of prey types	*Single prey type AIs*	*Dual prey type AIs*	*Inclusive prey type AIs*
Chatelperronian vs. Mousterian				
Aurignacian vs. Mousterian		II**(A 71.41; M 48.07)	G_vs_F*** (A 26.35; M 60.80)	H_G_vs_F_A*** (AU 30.09; M 59.76)
		F***(A 80.91; M 44.47)		
		G***(A 31.61; M 59.44)		
		f_alt***(A 73.87; M 47.18)		
Chatelperronian vs. Aurignacian				

Appendix 9 - Significant mean rank differences of diet parameters for each pair of archaeological traditions, 'reliable' entries (Kruskal-Wallis). Values represent significant differences at the * p≤.05 level, ** p≤.01 level, *** p≤.001 level.

Diet variables	*Mean rank differences*
Number of prey types	
Single prey type AIs	
AI_F	D 41.69; H 25.59***
AI_G	D 26.14; H 42.59***
Dual prey type AIs	
AI_G_vs_F	D 24.27; H 42.00***
Inclusive AIs	
AI_H_G_vs_F_A	D 26.20; H 42.53***

Appendix 10 - Significant mean rank differences (Mann-Witney) of diet parameters between dry (D) and humid (H) climates, 'reliable' entries. Values represent significant differences at the * p≤.05 level, ** p≤.01 level, *** p≤.001 level.

Diet variables	*Mean rank differences*
Number of prey types	
Single prey type AIs	
AI_F	C 47.58; T 20.62***
AI_G	C 32.24; T 63.71***
AI_f_alt	C 43.78; T 31.29*
Dual prey type AIs	
AI_G_vs_F	C 31.75; T 60.52***
Inclusive AIs	
AI_H_G_vs_F_A	C 32.17; T 63.90***

Appendix 11 - Significant mean rank differences (Mann-Witney) of diet parameters between cold (C) and temperate (T) climate, 'reliable' entries. Values represent significant differences at the * p≤.05 level, ** p≤.01 level, *** p≤.001 level.