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The basic prey model in «deep time», part 2: competition during MIS 3 in France?

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1. Introduction

This paper is the final of a series of four papers, which taken together present a study that was essentially built around two goals: to search for (and wherever necessary, modify) a conceptual and analytical framework that would allow us to describe, as well as explain hominin behavioural variability, and to implement that framework in the context of the Middle to Upper Palaeolithic transition (MUPT) debate in Western Europe.

The need for such a new framework originated out of our contesting of the modernity concept (Jehs, 2011), which instigated a search that started from the most basic paradigm within palaeoanthropology, i.e. the theory of evolution. As it turned out, there were multiple evolutionary approaches to behaviour and culture, each focussing on different aspects and processes, and each requiring its own kind of input data (Jehs, 2012). This entailed that not all would be "easily" adapted to being implemented in a Palaeolithic context; in fact, to us (human) behavioural ecology appeared to be the best candidate at this moment, for several reasons (Jehs, 2012; Jehs & De Smet, 2011). These, amongst which the availability of the required data was obviously a rather stringent reason, led us to one particular aspect of the MUPT, i.e. possibility of interaction between Neanderthal and modern human populations. Using optimal foraging theory, and the basic prey model in particular, we set out to analyse the differential exploitation of animal resources for the three major technocomplexes (Mousterian, Chatelperronian and Aurignacian) during the Middle to Upper Palaeolithic in France. The intention here was to use and update an existing faunal database (containing the NISP for each individual taxon for all French assemblages dated between MIS 3 to 5e with a total NISP > 20 for which a clear carnivore influence could be excluded, see Grayson & Delpech, 2006), and search for patterning pointing to resource intensification (competition) between the technocomplexes just mentioned.

As such, and for the first part of this analysis (Jehs & De Smet, 2011), we incorporated all 219 assemblages contained within the database, which were dated to the wider timeframe of MIS 3-5e. To avoid being overly repetitive here, we redirect the reader to the latter (open source) paper in which the base data, the general methodology (the prey model and its modifications), and the statistical procedure have been described in full detail. The analysis below is essentially identical to that in Jehs & De Smet (2011), but now only the MIS 3 assemblages have been taken into account.

2. Animal exploitation during MIS 3 in France

Starting from the full database, which covered MIS 3 to 5e (Jehs & De Smet, 2011), we removed all entries that could not be (securely) ascribed to MIS 3. Besides the fact that doing so allowed us to focus on the actual question of resource intensification during the transition, this may have two other advantages: for one, climatic extremes not incorporated in MIS 3 are now left out of the analysis. Moreover, while MIS 3 was a highly variable climatic phase in its own right, MIS 3 assemblages have a high chance of representing remains averaged over multiple but short-lived climatic regimes that remained unrecognised during excavation. Compared to analysing all entries, this may contribute to levelling the identifiable impact of climate on vegetation and therefore the available hunting fauna. Secondly, and perhaps more importantly, focusing on MIS 3 leads to a significant decrease of Mousterian sites (i.e. the majority of the database), such that the three archaeological traditions become somewhat more balanced in terms of numerical representation (55 Mousterian, 8 Chatelperronian, and 38 Aurignacian sites, i.e. a total of 101). As mentioned in the introduction, we refer to (Jehs & De Smet, 2011) for a full description of the general methodology, the statistical procedure and the variables involved.

2.1. Diet patterns and archaeological tradition (see appendix 1)

While the number of assemblages is about the same as those that were considered "reliable" (Jehs & De Smet, 2011), the drop in significant results we found with the latter does not occur here. In fact, we found that more than 20 diet indicators were *added* to the all entry-list of significant differences between archaeological traditions. Overall, p-values of the newly added results tend to be a bit higher, while on the other hand, the indicators that were already there score higher values of the test statistic.

As far as maximum diet breadth is concerned (the number of prey types), the pattern that was visible in the full database (i.e. a higher mean rank for the Chatelperronian vs. the Mousterian) is now evident in all four rather than just two of the parameters. Moreover, in the MIS 3 database, differences between Mousterian and Aurignacian have become significant as well, the latter displaying a larger diet breadth. Interpreted in terms of the coexistence hypothesis, resource intensification (vs. the Mousterian) can be inferred during the Chatelperronian, and the Aurignacian, judging from the behaviour of the NPREYTYPE parameter.

The single AIs provide some detail to that picture. Again, the results on the full database are a subset of those we arrive at here, based on the MIS 3 data. For the former, we concluded that there was a lack of direct evidence for intensification (i.e. in terms of abundance of the lowest-ranking prey types), accompanied by a significant increase in prey weighing over 1000 kg during the Chatelperronian (vs. both the Mousterian and the Aurignacian). While helping to explain the higher maximum diet breadth during the Chatelperronian, it was difficult to reconcile the latter pattern with the intensification signal derived from the NPREYTYPE parameter per se (unless such prey are in fact not high[est] ranking at all).

Now, for the MIS 3 selection, we can add a few more patterns. First however, we must point out that the p values associated with the Chatelperronian vs. Mousterian comparison of type F prey (i.e. primarily *Rangifer tarandus*) now become significantly smaller, again confirming the increased *Rangifer* exploitation during the Chatelperronian established by Grayson & Delpech (2006). As far as differences between Mousterian and Aurignacian are concerned, the higher exploitation of class E prey during the Mousterian (primarily *Capra*, a pattern identified by Grayson and Delpech as well) is clearly evident in AI_E differences, whereas previously it appeared only in AI_e_alt, which includes the rather uncommon *Cervus simplicidens*. The other patterns between both traditions remained intact: reindeer dominance during the Aurignacian (type II and F prey), and a higher exploitation of 200-1000 kg prey during the Mousterian (AI_G), with *Cervus* *elaphus* as the greatest contributor according to Grayson and Delpech (2006); as we have seen earlier when discussing the full database (Jehs & De Smet, 2011), the latter did not hold up when checking the correlation between the *Cervus elaphus* NISP and AI_G. Patterning between Aurignacian and Chatelperronian remains identical as well, i.e. a more important exploitation of animals weighing more than 1000 kg (and in the 2800-5500 weight range), during the Chatelperronian.

	Number of prey types	*Single prey type AIs*	*Dual prey type AIs*	*Inclusive prey type AIs*
Chatelperronian vs. Mousterian	I**(C 75.75; M 39.84)	II*(C 61.38; M 34.11)	V_vs_I**(C 62.62; M 37.80)	
	II*(C 70.81; M 41.79)	V**(= AI_H)(C 80.38; M 44.57)	V_vs_II**(C 73.25; M 42.73)	
	1***(C 81.56; M 40.73)	F**(C 72.12; M 30.91)	V_vs_III***(C 69.75; M 39.08)	
	2**(C 75.69; M 42.10)	7*(= AI_h_alt)(C 73.75; M 47.42)	V_vs_IV**(C 60.50; M 36.05)	
		8***(C 75.44; M 45.29)	H_vs_E**(C 56.00; M 30.68)	
		f_alt*(C 61.38; M 34.11)	H_vs_F**(C 65.62; M 40.65)	
			H_vs_G***(C 75.50; M 42.36)	
			G_vs_F***(C 31.12; M 69.04)	
			F_vs_E*(C 67.12; M 39.78)	
			E_vs_D**(C 17.17; M 44.31)	
			8_vs_5**(C 74.50; M 45.06)	
			8_vs_6**(= AI_i_alt_vs_g_alt)(C 67.25; M 40.79)	
			7_vs_5**(C 72.69; M 47.15)	
			7_vs_6**(= AI_h_alt_vs_g_alt)(C 66.38; M 42.20)	
			i_alt_vs_e_alt**(C 53.08; M 28.17)	
			i_alt_vs_f_alt**(C 69.38; M 42.48)	
			h_alt_vs_e_alt**(C 53.58; M 30.63)	
			h_alt_vs_f_alt*(C 66.88; M 44.30)	
			f_alt_vs_e_alt*(C 67.12; M 41.63)	
			e_alt_vs_d_alt**(C 17.17; M 44.34)	
Aurignacian vs. Mousterian	I***(A 62.97; M 39.84)	II**(A 74.00; M 34.11)	III_vs_II**(A 37.73; M 57.79)	H_G_vs_F_A* (A 42.18; M 58.13)
	II**(A 61.23; M 41.79)	E**(A 42.56; M 60.20)	H_vs_E*(A 42.38; M 30.68)	
	1**(A 60.53; M 40.73)	F***(A 76.31; M 30.91)	G_vs_F***(A 26.97; M 69.04)	
	2**(A 59.79; M 42.10)	G***(A 42.46; M 58.38)	F_vs_E***(A 60.12; M 39.78)	
		e_alt**(A 42.56; M 60.20)	E_vs_D*(A 32.12; M 44.31)	
		f_alt***(A 74.00; M 34.11)	i_alt_vs_e_alt*(A 38.98; M 28.17)	
			g_alt_vs_f_alt***(A 35.54; M 60.18)	
			f_alt_vs_e_alt**(A 60.67; M 41.63)	
			e_alt_vs_d_alt*(A 32.09; M 44.34)	
Chatelperronian vs. Aurignacian		V (= H)*(A 55.35; C 80.38)	V_vs_II*(C 73.25; A 49.31)	
		7 (= h_alt)*(A 52.69; C 73.75)	H_vs_F*(C 65.62; A 44.22)	
		8 (= i_alt)*(A 55.35; C 75.44)	8_vs_5*(C 45.06; A 74.50)	
			7_vs_5*(C 47.15; A 72.69)	
			i_alt_vs_f_alt*(C 69.38; A 50.41)	
			h_alt_vs_f_alt*(C 66.88; A 47.38)	

Appendix 1 – Significant mean rank differences of diet parameters for each pair of archaeological traditions, MIS 3 entries (Kruskal-Wallis tests); Mousterian (M), Chatelperronian (C) and Aurignacian (A). All values represent significant differences at the * p≤.05 level, ** p≤.01 level, *** p≤.001 level.

When comparing the Mousterian and Chatelperronian dual AIs, it is apparent that only AI_8_vs_4, with a significant difference between both traditions in the full database (Jehs & De Smet, 2011), did not make it to the results of our MIS 3 database analysis. We consider it part of those indicators (i.e. all those in the list, but one) that illustrate the more extensive exploitation of very large animals during the Chatelperronian, so it can be considered redundant. However, the MIS 3 analysis did reveal five new ones: AI_H_vs_F, AI_F_vs_E, AI_E_vs_D, AI_h_alt_vs_f_alt, and AI_f_alt_vs_e_alt. Of these, the first and the last but one again indicate the prevalence of very large (> 1000 kg) animals during the Chatelperronian vs. the Mousterian. The second and last illustrate the more extensive exploitation of reindeer during the Chatelperronian, and interestingly, the third adds the observation that Chatelperronians exploited more type D animals than type E prey, compared to the Mousterian, or, in other words, as type D prey are very low-ranking (10-45 kg), resource intensification during the Chatelperronian was higher than during the Mousterian. This is also reflected by AI_e_alt_vs_d_alt, both in the full and the MIS 3 database, and corresponds to the larger diet breadth as found for the Chatelperronian. Note that the type E (46-100 kg) is more restrictive than type e_alt (46-175), and that the p values in the MIS 3 analysis are smaller.

A comparison of the dual AIs at the level of Mousterian vs. Aurignacian turned out to be informative as well. Again, the MIS 3 analysis provided more significant results. In fact, the two that no longer featured in the MIS 3 vs. the complete database, i.e. AI_8_vs_4 and AI_8_vs_6, had rather high p values in the latter, and were moreover suspected of having been influenced by sample size. In any case, the patterns attested in the full database are found here as well. Apart from the obviously higher *Rangifer* exploitation and that of prey larger than 1000 kg, an interesting signal in terms of resource intensification - which was not present in the full database, consists of the lower mean ranks of AI_E_vs_D and AI_e_alt_vs_d_alt for the Aurignacian, pointing to intensification during the latter. Note that the same pattern occurred when comparing the Chatelperronian and the Mousterian. Presumably, possible bursts of intensification during the Mousterian of MIS 4 and/or 5 were responsible for hiding this pattern in the full database.

The dual AIs for Aurignacian vs. Chatelperronian, while being more numerous for the MIS 3 database, essentially showed the same pattern as the one resulting from the full database: AIs with the highest ranking animal larger than 1000 kg (and those within the 2800-5500 range) are lower during the Aurignacian. This suggests (once again) that exploitation of these animals may have been higher during the Chatelperronian, which, as we argued before, is difficult to interpret in terms of resource intensification; still a more outspoken exploitation of higher ranking animals does not *necessarily* entail lower levels of intensification, and moreover, it may be that such prey may have had a (much) lower rank than assumed based on their weight only, or that non-energetic goals had come into play.

As far as the inclusive AIs are concerned, there is no difference between the full and the MIS 3 database, except for the fact that the only relevant AI here, AI_H_G_vs_F_A, is far less significant in this analysis when compared to the full database.

2.2. Diet patterns and sample size (Appendix 2-3)

For our first diet indicator, i.e. NPREYTYPES, the results entail that sample size may have had a considerable impact on the maximum diet breadth differences between Mousterian and Aurignacian, and Mousterian and Chatelperronian. All differences of single AIs between Chatelperronian and Mousterian equally fall prey to the contributing effects of sample size, while three single AIs (AI_II, AI_F, and AI_f_alt) do the same in the Mousterian vs. Aurignacian comparison. The remaining three (type E, type G and type e_alt prey) are indicative of the more outspoken Mousterian *Capra* exploitation vs. the Aurignacian, as well as the higher reliance of *Bos*, *Bison* and *Cervus elaphus*, i.e. two patterns that more or less correspond to those found by Grayson & Delpech (2006). For the Chatelperronian-Aurignacian comparison of single AIs as well, sample size turns out to have impacted the inter-technocomplex differences.

The impact of sample size is again heavily felt with the double AIs, where, in the Chatelperronian vs. Mousterian situation, again three stand out that are not affected: AI_E_vs_D, AI_f_alt_vs_e_alt, and AI_e_alt_vs_d_alt. The first and the last can point to intensification in the Chatelperronian, while the second most likely signals the increased *Rangifer* exploitation during the Chatelperronian. For the Aurignacian as well, sample size has been a contributing factor. When compared to the Mousterian, the increased *Rangifer* exploitation is unaffected (AI_III_vs_II, AI_f_alt_vs_e_alt), as well as the intensification signal whereby Aurignacians focussed more on 25-45 kg and 10-45 kg prey than Mousterians did. Comparing the Aurignacian to the Chatelperronian shows that only the mean rank differences of AI_8_vs_5 and AI_7_vs_5 between both technocomplexes could have been influenced by sample size. The remaining others point to the higher exploitation of the largest animals during the Chatelperronian.

2.3. Diet patterning and climate

Of the 98 assemblages, 46 contained information on humidity, 27 of which having been classified as dry, and 19 as humid; 75 assemblages contained information on temperature, 63 of which having been classified as cold and 12 as temperate.

2.3.1. Humidity

No significant differences in diet patterning can be found between dry and humid climate sites. As such, the fact that an assumption of the chi-square test is violated as 3 out of 6 cells of the contingency table have expected counts less than 5, is irrelevant. For the sake of completeness, we can add that the result of the chi-square test is not significant. Humidity, *as recorded here*, does not seem to have an impact on diet differences between archaeological traditions.

2.3.2. Temperature (Appendix 4-5)

The chi-square test on temperature and tradition (appendix 5) is not significant, but unfortunately, an assumption of the test is violated as 2 out of 6 cells of the contingency table have expected counts of less than 5. If temperature has any impact on diet differences between traditions (see appendix 4), it would have to be sought at the level of maximum diet breadth (NPREYTYPES_II and _2, and between Mousterian and Aurignacian/Chatelperronian), the higher exploitation of type G prey (201-1000 kg) during the Mousterian vs. the

Diet pattern	r_s	*N entries*
Number of prey types		
N_PREY_TYPES_I	. 507***	102
N_PREY_TYPES_II	.460***	102
N_PREY_TYPES_1	.499***	102
N_PREY_TYPES_2	.513***	102
Single prey type AIs		
AI_II	.368**	102
AI_V	.484***	102
AI_F	.431***	102
AI_7	.454***	102
AI_8	.434***	102
AI_f_alt	.368***	
Dual prey type AIs		
AI_V_vs_I	.510***	87
AI_V_vs_II	.451***	95
AI_V_vs_III	.485***	91
AI_V_vs_IV	.478***	83
AI_H_vs_E	.501***	74
AI_H_vs_F	.432***	88
AI_H_vs_G	.487***	98
AI_G_vs_F	-.392***	97
AI_F_vs_E	.203***	99
AI_8_vs_5	.435***	101
AI_8_vs_6	.439***	93
AI_7_vs_5	.455***	101
AI_7_vs_6	.460***	92
AI_i_alt_vs_e_alt	.492***	68
AI_i_alt_vs_f_alt	.423***	95
AI_h_alt_vs_e_alt	.513***	69
AI_h_alt_vs_f_alt	.443***	94
AI_g_alt_vs_f_alt	-.264**	97
Inclusive prey type AIs		
AI_V_II_vs_I	.216*	219
AI_i_alt_f_alt_vs_e_alt_a_alt	.216*	219

Appendix 2 – Significant correlations (Spearman's rho) between diet parameters and sample size, MIS 3 entries. All values represent significant differences at the * p≤.05 level, ** p≤.01 level, *** p≤.001 level.

Technocomplexes	*Mean rank difference*
Aurignacian vs. Mousterian	18.112**

Appendix 3 – Significant mean rank differences (Kruskal-Wallis) of sample size between technocomplexes, MIS 3 entries. Significant at the ** p≤.01 level.

Diet pattern	*Mean rank differences*
Number of prey types	
N_PREY_TYPES_II	C 35.62; T 50.50*
N_PREY_TYPES_2	C 35.83; T 49.42*
Single prey type AIs	
AI_G	C 35.84; T 49.33*
Dual prey type AIs	
/	/
Inclusive AIs	
AI_H_G_vs_F_A	C 35.78; T 49.67*

Appendix 4 – Significant mean rank differences (Mann-Witney) of diet parameters between cold (C) and temperate (T) climate, MIS 3 entries. Values represent significant differences at the * $p \leq .05$ level

Variables	χ^2	*p*
Technocomplex & Temperature	.838	.658

Appendix 5 – Test of independency of technocomplex and temperature (Chi-Square Test), MIS3 entries.

Diet pattern	*OS vs. S*
Number of prey types	
/	/
Single prey type AIs	
AI_G	OS 69.63; S 47.35**
AI_7	OS 42.21; S 53.63*
Dual prey type AIs	
AI_V_vs_III	OS 36.05; S 48.62*
AI_H_vs_E	OS 27.64; S 39.80*
AI_H_vs_F	OS 34.28; S 47.13*
AI_E_vs_D	OS 47.75; S 35.11*
AI_7_vs_5	OS 41.81; S 52.99*
AI_7_vs_6	OS 37.16; S 48.93*
AI_h_alt_vs_e_alt	OS 26.46; S 36.98*
AI_h_alt_vs_f_alt	OS 38.11; S 49.72*
AI_f_alt_vs_c_alt	OS 45.39; S 48.00*
AI_e_alt_vs_d_alt	OS 47.82; S 35.09*
Inclusive AIs	
AI_H_G_vs_F_A	OS 69.89; S 47.29**

Appendix 6 – Significant mean rank differences (Mann-Witney) of diet parameters between open air with shelter (OS), and sheltered (S) site contexts, MIS 3 entries. Values represent significant differences at the * $p \leq .05$ level, ** $p \leq .01$ level, *** $p \leq .001$ level.

Aurignacian, and the more extensive *Rangifer* exploitation during the Aurignacian vs. the Mousterian (as captured by the inclusive AI_H_G_vs_F_A). However, all of these patterns are redundantly present in diet parameters without link to temperature.

2.4. Diet patterning and site context (Appendix 6-8)

Note that as all open air sites are older than MIS 3, only two groups remained within the parameter "site context", i.e. "open air with shelter" and "sheltered", meaning that Mann-Whitney U tests can be performed instead of Kruskal-Wallis tests.

The chi-square test on site context and archaeological tradition is significant (see appendix 7). The contingency table in appendix 8 shows that Mousterian and Chatelperronian sites contain more open air sites with shelter, but less sheltered sites, than expected. The opposite pattern is found in the Aurignacian. Looking at appendix 6, we do not see any consistent pattern: sometimes the mean ranks of the diet parameters are largest for open air sites with shelter, sometimes for sheltered sites. In order to check for the influence of site context on diet differences between technocomplexes, we have to look back at appendix 1, where we retrieve the technocomplexes for which any given diet parameter included in appendix 6 was significantly different. For example, for AI_G and AI_H_G_vs_F_A differences were found between the Mousterian and the Aurignacian. For both parameters, mean ranks were higher in the Mousterian than in the Aurignacian. In appendix 8 we see that for both diet parameters higher mean ranks can be found in the open air sites with shelter than in the sheltered sites. As appendix 8 shows that the Mousterian contains more open air sites with shelter than expected, we can conclude that for diet parameters AI_G and AI_H_G_vs_F_A site context is a relevant factor which may be partly responsible for the relation found between technocomplex and diet breadth.

These steps are repeated for each diet parameter included in appendix 6. Interpretation is not necessarily more complicated when differences are found between more than two technocomplexes in appendix 1, for example diet parameters AI_E_vs_D and AI_e_alt_vs_d_alt. For these parameters higher mean ranks are found in the Mousterian vs. the Chatelperronian and the Aurignacian. In appendix 6, we see that for these diet parameters open air sites with shelter have higher mean ranks than sheltered sites. Appendix 8 shows that indeed the Mousterian contains more open air sites with shelter than expected, and the Aurignacian contains more sheltered sites than expected. However, the Chatelperronian sites follow the same pattern as the Mousterian sites, not the Aurignacian

Variables	χ^2	*p*	*Cramer's V*	*p (Cramer's V)*
Technocomplex & site context	7.615	0.022	0.273	0.022

Appendix 7 – Test of independency of technocomplex and site context (Chi-Square Test), MIS 3 entries.

	Mousterian	*Chatelperronian*	*Aurignacian*	*Total*
Open air with shelter	15 (10.2)	2 (1.5)	2 (7.3)	19
Sheltered	40 (44.8)	6 (6.5)	37 (31.7)	83
Total	*55*	*8*	*39*	*102*

Appendix 8 – 2x3 contingency table of technocomplex vs. site context: effective count (expected count), MIS 3 entries.

ones. This means that, while we can probably still conclude that site context is a relevant factor in explaining the relation between the diet patterns and technocomplex, the evidence has become less straightforward.

Unfortunately, interpreting the role of site context is less clear-cut for other diet parameters. For example, parameters AI_V_vs_III, AI_h_alt_vs_e_alt and AI_7_vs_6 have higher mean ranks in the Chatelperronian compared to the Mousterian. For all three parameters sheltered sites have higher mean ranks compared to open air sites with shelter. This is odd, as only in the Aurignacian more sheltered sites were found than expected. The mean ranks of the Aurignacian lie each time between the Mousterian and the Chatelperronian mean ranks, but never differ significantly from both values. This might explain why, eventually, higher mean ranks are found in sheltered sites (more found than expected in Aurignacian sites) than in open air sites with shelter (more found than expected in both the Mousterian, which had high mean ranks, and the Chatelperronian, which had low mean ranks). Nonetheless, as we mentioned above, this interpretation is much less straightforward, so the conclusion that site context is a relevant factor here remains speculative at best.

Overall, for diet parameters AI_H_vs_E, AI_E_vs_D, AI_e_alt_vs_d_alt, AI_7_vs_5, AI_G and AI_H_G_vs_F_A, site context may be considered responsible for part of the relation found between technocomplex and diet breadth; for diet parameters AI_7, AI_H_vs_F, AI_h_alt_vs_f_alt, AI_ V_vs_III, AI_h_alt_vs_e_alt and AI_7_vs_6 this cannot be inferred.

3. Discussion

The conclusion of the statistical analyses are summarised in appendix 9. Basically, we were able to duplicate the findings of Grayson & Delpech (2006), i.e. a more intensive exploitation of *Capra* and *Cervus* during the Mousterian as opposed to the Aurignacian, and a bigger focus on *Rangifer* during the Chatelperronian and the Aurignacian when compared to the Mousterian. As our aims were different than theirs, we could also discern a difference in diet breadth between Chatelperronian (and Aurignacian) when

	MIS 3 assemblages	*All assemblages*
Capra & *Cervus*	M>A	M>A
Rangifer	A&C >M	A&C >M
Diet breadth	C(&A)>M	C>M
Small prey types	C&A>M	C>M
Very large prey types	C>M&A	C>M&A

Appendix 9 – Summary of the results of the statistical analysis of the MIS 3 data; Mousterian (M), Chatelperronian (C) and Aurignacian (A).

compared to the Mousterian: for the former, diet was broader, which can be interpreted as an indicator of intensification. This corresponds with our finding that small prey types (weighing less than 45 kg) have been exploited more during the Chatelperronian and Aurignacian when compared to the Mousterian. Enigmatically, and this may detract somewhat from the attested intensification signal found in the diet breadth variable, we also found that the heaviest prey types were hunted significantly more during the Chatelperronian vs. the Aurignacian and Mousterian. Moreover, the two exploitation signals attested earlier by Grayson & Delpech (2006) are also difficult to explain in terms of intensification (the climate parameters, as captured by us, only show the merest hint of a - feasible - link between these patterns and climate). Ironically, had we focused on a strict implementation of the prey model (by investigating only diet breadth and the exploitation of very small animals), we would have missed these signals entirely.

The time has come however to assess the extent to which we have accomplished the goals we set out, i.e. to evaluate the potential of the prey model in Palaeolithic research (and the MUPT in particular) and to contribute to the competition hypothesis. Our assumption at the beginning has been that if the prey model would be able to deal with the necessarily incomplete archaeological record of the period in question (which could be said to be compromised further by using a necessarily time- and place-averaging database study, based on assemblages that in quite a number of cases could be considered having been excavated, analysed and published using substandard methods), and if the competition hypothesis would have been correct, we would have to find an intensification signal embedded within the NISP data. A lack of such a signal would have meant that (the implementation of) the prey model and/or the competition hypothesis was/were wrong.

In light of earlier studies pointing to the contrary, we were rather surprised that an intensification signal was actually found. It had been argued before that at sites with a good stratification covering the transition (according to Grayson & Delpech, 2008, only Roc de Combe, Grotte XVI and Saint-Césaire fit that description), no changes in exploitation strategies could be detected in the archaeofaunas at the sites (Morin, 2004; Grayson & Delpech, 2003, 2005, 2008) that could not be ascribed to climatic factors. So can or should our results be interpreted as an indication for competition?

We would prefer to consider the study as an exercise, for reasons of an empirical as well as theoretical nature. As mentioned above, our data were rather coarse-grained as our database contained a considerable number of faunal assemblages excavated long ago with techniques that we now consider substandard. This has several consequences for the data, ranging from uncertainties as to whether *Rangifer* specimens always excluded (shed) antlers or antler tools (i.e. to what extent did "utility" blur the prey model), whether the bone remains of very large animals (> 1000 kg) were kitchen waste rather than being collected for some reason (again could be argued in terms of utility, or in this case even a higher degree of "showing off" while hunting),... Additionally, the poor resolution of our data was reflected in the way we necessarily had to record climatic variation, i.e. mostly as a relative estimation based on the results of various studies using very different methods. As such, climate appeared to have no significant relationship with our diet variables, which is rather unlikely (e.g. the *Rangifer* pattern). Additionally, the intensification pattern was not unequivocal: with the exception of the increased exploitation of very

Appendix 10 – Differences in animal exploitation. The «X» marks a significant difference with at least one other technocomplex.

Technocomplex	*< 45 kg*	*Capra*	*Rangifer*	*Cervus*	*> 1000 kg*
Mousterian		X		X	
Aurignacian	X		X		
Chatelperronian	X		X		X

small animals, it was not quite independent of sample size (or site context in some cases) and, if one would actually choose to accept the attested differential exploitation patterns at face value, there seemed to be more at work than mere intensification. While based on the current evidence we would not support such a claim, appendix 10 shows that the patterning could also be interpreted as niche separation, whereby Aurignacians and Chatelperronians focused to a larger extent on both larger and smaller prey, as well as *Rangifer* as an intermediate-sized prey type situated between *Capra* and *Cervus*, which were typically hunted in the Mousterian. There is however also a theoretical reason that prevents us from regarding our results as supporting evidence for the competition (and by extension, the coexistence) hypothesis: while finding no intensification patterning would have pointed to one or both of our assumptions being wrong (i.e. the adequacy of the prey model and the competition hypothesis), actually finding a clear intensification signal does not logically allow to conclude that both our assumptions were correct and that the signal may be interpreted as resulting from competition.

Does this mean that the prey model, or a behaviour ecology logic for that matter, should be ignored in Palaeolithic studies? We belief our study shows that the model is quite capable of contributing to the investigation of faunal exploitation patterns, in a capacity that surpasses that of a mere hypothesis generator. In fact, we see an increasingly important role for the model in faunal studies of well-excavated sites with multiple assemblages. As demonstrated by Morin (2004) and Grayson & Delpech (2003), such sites are particularly well-suited because they offer much more detailed information (faunal and climatic) that can be incorporated into the analysis. Their fine grain also allows to pay proper attention to taphonomy, and bring independent evidence to bear on the research question at hand. In the case of intensification this could be the degree of carcass exploitation, butchery intensity, and the extent of marrow and grease extraction. Additionally, (dual and inclusive) AIs could be tailored to the specific circumstances dictated by the site and the research questions (the differential exploitation of certain niches, for example). So, while we conducted a general, coarse-grained study of an entire region, we would argue that the model has indeed a lot of potential, and would advise for it to be included in zooarchaeological site-based research as a standard tool alongside those currently in use when attempting to establish fine-grained fluctuations in animal exploitation between archaeostrata.

Bibliography

GRAYSON D. K. & DELPECH F., 2003. Ungulates and the Middle-to-Upper Paleolithic transition at Grotte XVI (Dordogne, France). *Journal of Archaeological Science*, 30: 1633-1648.

GRAYSON D. K. & DELPECH F., 2005. Pleistocene reindeer and global warming. *Conservation Biology*, 19: 557–562.

GRAYSON D. K. & DELPECH F., 2006. Was There Increasing Dietary Specialization Across the Middle-to-Upper Paleolithic Transition in France? In: CONARD N. J. (ed.), *When Neanderthals and Modern Humans Met*, Kerns Verlag, Tübingen: 377-417.

GRAYSON D. K. & DELPECH F., 2008. The large mammals of Roc de Combe (Lot, France): The Châtelperronian and Aurignacian assemblages. *Journal of Anthropological Archaeology*, 27: 338-362.

JEHS D., 2011. The modernity myth. *Notae Prehistoricae*, 31: 69-85.

JEHS D., 2012. Evolutionary theory and the Palaeolithic. *Notae Prehistoricae*, 32: 257-287.

JEHS D. & DE SMET D., 2011. The basic prey model in "deep time": the exploitation of animal resources during MIS 3-5e in France. *Notae Prehistoricae*, 31: 157-182.

MORIN E., 2004. *Late Pleistocene population interaction in Western Europe and modern human origins: new insights based on the faunal remains from Saint-Césaire, southwestern France*. Ph.D. thesis, University of Michigan, Michigan.

Abstract

Evolutionary approaches to behaviour and culture are slowly gaining acceptance in archaeology, and Palaeolithic archaeology in particular. As it has been deployed in numerous ethological, ethnological and even archaeological (Holocene) contexts, behavioural ecology (BE), one such approach, has earned an exceptional empirical and analytical track record. As such, multiple models exist for each subfield of the BE, awaiting modification for use in Palaeolithic "deep time". In this paper, which is the second and final part of a study on differential animal exploitation strategies between Mousterian, Chatelperronian and Aurignacian, we deploy the so-called diet breadth model or prey model in the context of the well-known competition hypothesis, while also evaluating our results in terms of model utility.

Keywords: optimal foraging, Middle to Upper Palaeolithic transition, basic prey model, resource intensification, competition, MIS 3.

Samenvatting

Evolutionaire benaderingen van gedrag en cultuur duiken steeds meer op in archeologische studies, en zo ook in de Paleolithische archeologie. Gedragsecologie, één zo'n benadering, kan terugvallen op een lange geschiedenis van succesvolle toepassingen binnen de ethologie, etnologie en archeologie van het Holoceen, waardoor ze kan terugvallen op een indrukwekkende empirische en analytische basis. Concreet bestaan er meerdere modellen voor elke subdiscipline binnen de gedragsecologie, die mits de nodige aanpassingen gebruikt kunnen worden in de "deep time" van het Palaeolithicum. In dit artikel, dat het tweede en laatste deel uitmaakt van een studie rond de differentiële exploitatiestrategieën tussen Mousteriaan, Chatelperroniaan en Aurignaciaan, zetten we het zogenaamde diet(breedte)model of prooimodel in in de context van de competitiehypothese, terwijl we de onderzoeksresultaten ook evalueren in termen van de bruikbaarheid van het aangewende model.

Trefwoorden: optimal foraging, overgang van Midden- naar Laat-Paleolithicum, standaard prooimodel, intensificatie, competitie, zuurstofisotopenfase 3.

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