Explaining the Development of Dietary Dominance by a Single Ungulate Taxon at Grotte XVI, Dordogne, France

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The Magdalenian of southwestern France has long been renowned for the frequency with which associated faunal assemblages are dominated by reindeer (*Rangifer tarandus*). The site of Grotte XVI (Dordogne, southwestern France) is no exception: 94% of the Magdalenian ungulate assemblage at this site is provided by reindeer. However, this figure represents the endpoint in a steadily increasing progression of reindeer dominance, and steadily decreasing progression of ungulate assemblage evenness, at this site during the Upper Paleolithic (*c.* 36,000–12,000 ^{14}C years BP). These changes are not correlated with faunal assemblage size, degree of bone fragmentation, or skeletal element representation, but are correlated with declines in reconstructed summer temperatures for southern France. While it is quite possible that human predators responded behaviourally to this situation through the innovation of more efficient means of prey capture, the faunal patterns that characterize the Grotte XVI Upper Palaeolithic ungulate assemblages can be accounted for by climate change alone. © 2001 Academic Press

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Introduction

In 1861, soon after a Pleistocene human presence had become established in western Europe (Grayson, 1983), Edouard Lartet (1861) began the process of ordering the ancient human occupations of this area in time, observing that there had been a sequence of such occupations and that each had been marked by a distinct set of faunal associates. Drawing an explicit analogy with the archaeological classification of the human past into Stone, Bronze, and Iron ages, Lartet divided the "period of primitive humanity" (1861: 231) into four faunal ages, those of Cave Bear, Elephant & Rhinoceros, Reindeer, and Aurochs.

Gabriel de Mortillet (1869*a*, *b*, 1873, 1883) quickly raised a lengthy series of objections to this approach, replacing it with a classification scheme based on stone tool assemblages, with the name of each resultant industry based on the best known typical site. In this system, Lartet's Reindeer Age became the Magdalenian. Reindeer, Mortillet (1883: 459) noted, were so abundant in Magdalenian sites that Lartet had proposed "to call the Magdalenian the Reindeer Epoch".

It was, of course, Mortillet who had done the calling, but the association between reindeer (*Rangifer tarandus*) and the French Magdalenian is still very much with us. Both Lartet and Mortillet had focused their analyses of this period on southwestern France, and even though reindeer are certainly not always the most abundant large mammal in Magdalenian sites here (e.g., Delpech, 1983; Delpech & Le Gall, 1983; Straus, 1987; Delpech & Villa, 1993; see the review in Costamagno, 1999), Straus's characterization of this time and place as "a land of reindeer and reindeer hunters" (1996: 90) is certainly apt.
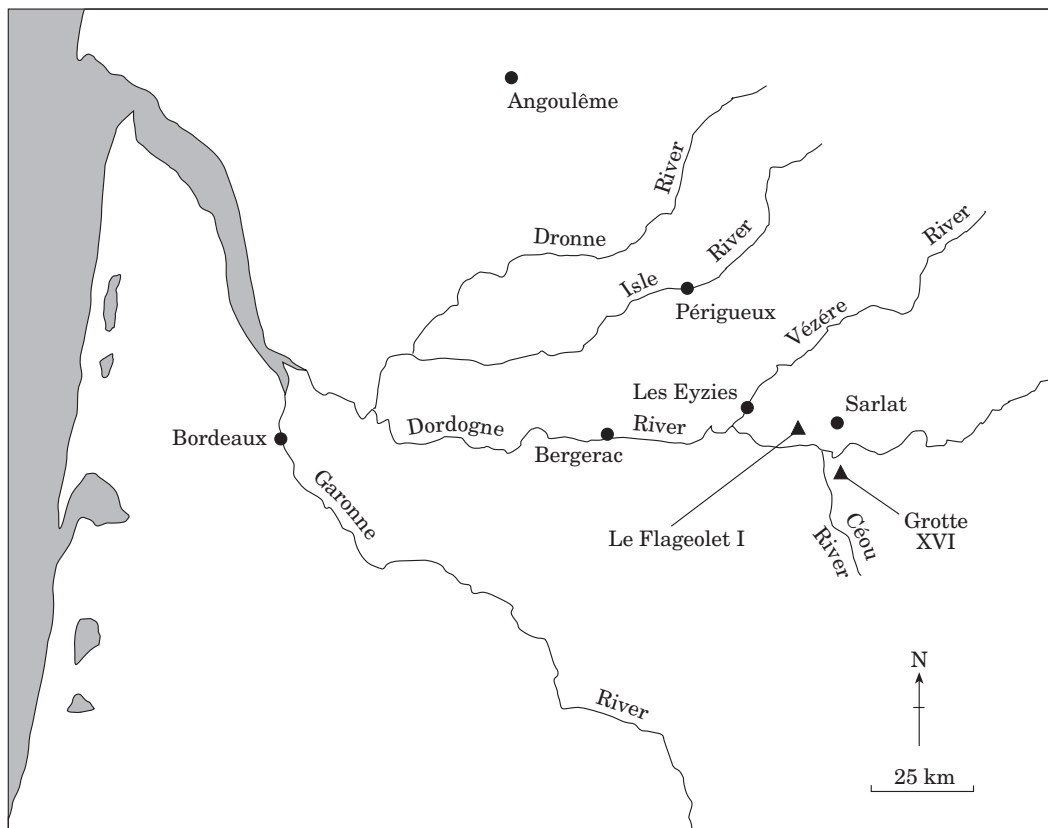
Figure 1. The location of Grotte XVI and Le Flageolet I.

The site of Grotte XVI in the Dordogne region of southwestern France is no exception to Straus's description: 94% of the identified ungulate remains from the Magdalenian unit at this site are of reindeer. Here, we provide a broad chronological view of the development of such dominance and provide an explanation for how it came to be at this particular place.

Grotte XVI

Grotte XVI is one of 23 caves and rockshelters that are known to dot the limestone cliffs that overlook the Céou River near its confluence with the Dordogne (Figure 1). Since 1983, this site has been the focus of intensive excavations directed by J.-Ph. Rigaud and J. F. Simek (Rigaud, 1986; Rigaud *et al.*, 1995). These excavations have revealed a stratified sequence of deposits that extend at least 3 m in depth (the bottom has yet to be reached) and that incorporates a Palaeolithic cultural sequence that begins with the Mousterian and continues through the Magdalenian (Table 1). Chronological control is provided by 14 radiocarbon age determinations and, for the Mousterian, by a series of TL dates (Rigaud, 1986; Rigaud *et al.*, 1995; Delpech, 1999*b*; Guibert *et al.*, 1999).

Because excavations in Mousterian levels are continuing, and because the identification of the vertebrate faunal material that has already been excavated from these levels is far from complete, the analysis we present here is based only on the faunal assemblages

Table 1. *A summary of the stratigraphy and chronology of Grotte XVI (see text for references)*

Stratum	Cultural assignment	^{14}C and TL ages
0	Magdalenian	12,285 ± 100 (AA-6843)
		12,530 ± 105 (AA-6842)
As	Solutrean	20,070 ± 330 (AA-2668)
		20,230 ± 270 (AA-2669)
		20,280 ± 220 (AA-2992)
		20,410 ± 380 (AA-2991)
		20,460 ± 260 (AA-2993)
Abc	Gravettian	26,430 ± 470 (AA-2670)
Abb	Aurignacian	28,140 ± 405 (AA-6840)
		29,285 ± 420 (AA-6841)
		29,710 ± 510 (GifA-94201)
Aib	Aurignacian (?)	Undated
B	Châtelperronian	35,000 ± 1200 (GifA-95581)
		38,100 ± 1670 (AA-2997)
		>39,800 (AA-2674)
C	Mousterian	64,600 ± 3100*
D–K	Mousterian	Undated

*Average of six TL dates (CRPAA).

Table 2. Numbers of identified specimens per Grotte XVI ungulate taxon by stratum

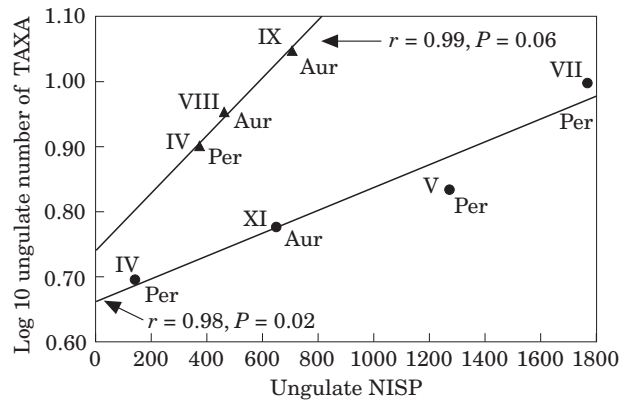| Taxon	Stratum					
	0	As	Abc	Abb	Aib	B
Bos/Bison	2	4	15	25	4	6
Capra sp.	10	12	58	82	28	26
Cervus elaphus	25	18	91	134	28	47
Rupicapra sp.	27	13	21	37	12	11
Capreolus sp.	2	5	4	8	1	2
Equus sp.	29	12	32	74	8	5
Megaceros sp.	—	—	—	1	—	—
Rangifer tarandus	2018	316	809	677	154	88
Rhinoceros	—	—	—	—	—	1
Saiga tatarica	24	—	—	—	—	
Sus sp.	2	4	3	13	4	1
Total	2139	384	1033	1051	239	187
Number of taxa	9	8	8	9	8	9

Figure 2. The relationship between numbers of identified specimens and numbers of taxa across the Upper Palaeolithic assemblages at Le Flageolet I (from Grayson & Delpech, 1998). Aur=Aurignacian; Per=Perigordian.
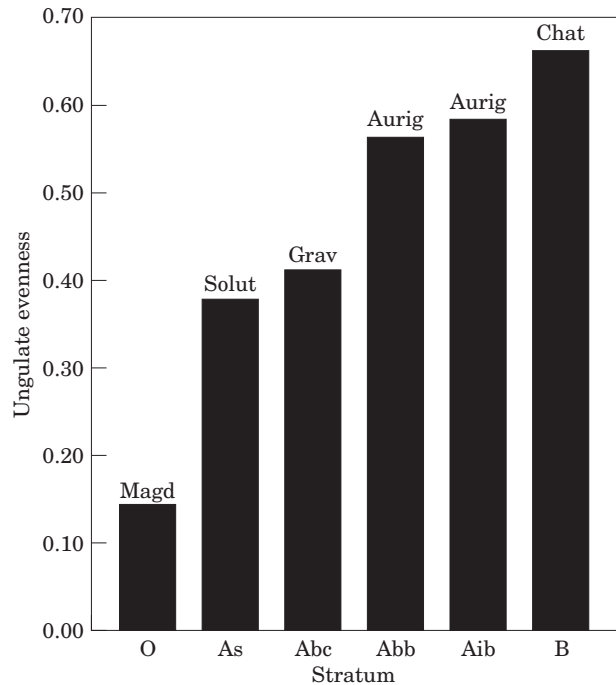

Figure 3. Upper Palaeolithic ungulate assemblage evenness at Grotte XVI. Chat=Châtelperronian; Aurig=Aurignacian; Grav=Gravettian; Solut=Solutrean; Magd=Magdalenian.

from the six Upper Palaeolithic stratigraphic units listed in Table 1. Planned excavations of these units are complete, and while small amounts of material from them remain to be analysed, the results we present here are sufficiently robust that they are not likely to be affected by additional identifications. Table 2 provides the raw taxonomic abundance data used in the discussions that follow; we note that 10 specimens of mammoth tusk have been excluded from the analysis because all are, or are likely to have been, worked.

The Numerical Structure of the Grotte XVI Upper Palaeolithic Ungulate Faunas

The Upper Palaeolithic site of Le Flageolet I is located some 7 km northwest of Grotte XVI (Rigaud, 1982). We have previously shown that seven Aurignacian and Perigordian ungulate assemblages from this site are marked by two distinctly different relationships between numbers of identified specimens (NISP) and numbers of taxa (an eighth assemblage was eliminated from consideration because it contained only 27 identified specimens; see Figure 2 and Grayson & Delpech, 1998). We also documented that these differences cannot be accounted for by such factors as differential bone fragmentation or differential bone transport. Finally, we noted that the assemblages that comprise these two relationships are also marked by differences in faunal assemblage evenness and, very closely related, in the degree to which they are dominated by reindeer and red deer (*Cervus elaphus*). We suggested that this suite of differences reflects climatically-driven change on the faunal landscape, changes to which human populations were simply responding.

Unlike the situation at Le Flageolet I, the numbers of ungulate taxa in the Grotte XVI Upper Palaeolithic ungulate assemblages do not vary greatly (Table 2), and do not show a significant relationship with sample size ($r=0.28$, $P \gg 0.10$; see Grayson, 1991 for the protocol used to determine numbers of taxa). They do, however, differ substantially from one another in the distribution of specimens across taxa, or evenness. As we have done before, we have measured evenness as $-\Sigma p_i \ln p_i / \ln S$, with S taken as the number of non-overlapping ungulate taxa in the assemblage and p the proportion of specimens in the i-th taxon (Grayson & Delpech, 1998). As Figure 3 shows, Grotte XVI ungulate assemblage evenness declines steadily from the moderate value it displays in Châtelperronian
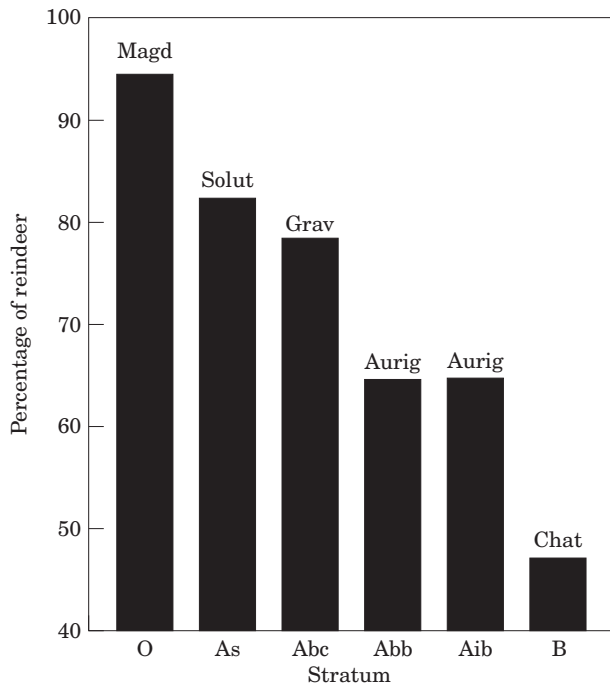
Figure 4. The changing contributions of reindeer specimens to the Grotte XVI Upper Palaeolithic ungulate assemblages. Abbreviations as in Figure 3.

Figure 5. The relationship between NISP and evenness across the Grotte XVI Upper Palaeolithic ungulate assemblages. Abbreviations as in Figure 3.

Stratum B to the very low level that marks Magdalenian Stratum 0.

Given what we have already said about the Magdalenian in general, and about the Magdalenian at Grotte XVI in particular, the very low evenness value that marks the Magdalenian here is no surprise. Now, however, it appears that the reindeer-dominated Magdalenian at Grotte XVI represents the endpoint of a steadily declining progression of evenness values. Indeed, these changing values are driven largely, though not entirely, by the degree to which particular Grotte XVI assemblages are dominated by reindeer: as reindeer dominance of these assemblages rises, evenness declines (with reindeer dominance expressed as natural logs, $r=0.96$, $P<0.001$; see Figure 4). The question, of course, is why these interrelated changes are occurring.

Sample size and evenness

Because evenness measures are prone to sample size effects (Magurran, 1988), the pattern of declining evenness values at Grotte XVI might be driven by changing sample sizes. In fact, there is a significant correlation between sample size and evenness across these six assemblages ($r= -0.814$, $P=0.05$; see Figure 5). This correlation, however, is driven by the very large and very uneven sample provided by Stratum 0 (leverage$=0.611$); the correlation between these two variables drops to insignificance with this stratum removed
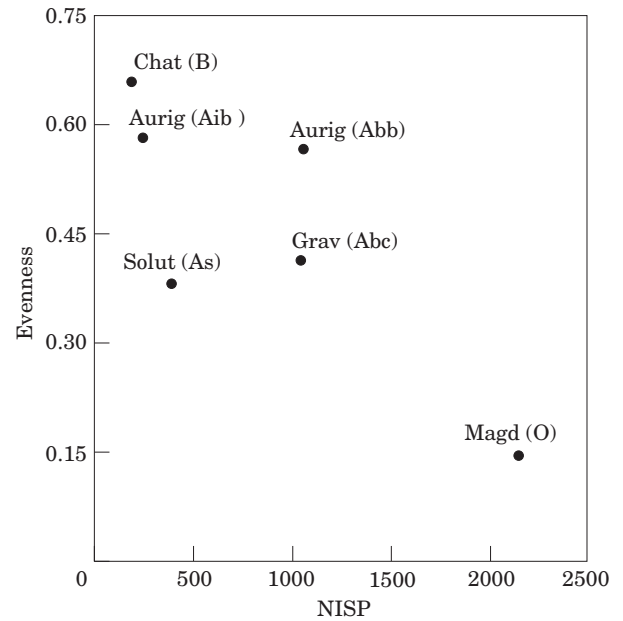
from the analysis ($r= -0.504$, $P\gg0.10$). Changing sample sizes are not causing the patterns at issue here.

Differential fragmentation

The taphonomic variables that might be driving this relationship are more complex. Since our evenness measure is based on NISP, any process that differentially fragments taxa across assemblages could produce changing evenness values of the sort we have found. For instance, increasingly intense fragmentation of a given taxon across strata would, for reasons that are entirely mechanical, drive evenness downwards by increasing the numbers of specimens belonging to that taxon. Because this is the case, the potential effects of differential fragmentation on the Grotte XVI faunal assemblage evenness values must be explored.

The most elegant exploration of this issue would be provided by extensive refitting of the ungulate specimens involved, as Marean and his colleagues have compellingly argued in a different context (e.g., Marean & Frey, 1997; Marean & Kim, 1998). Such refitting would provide a direct, taxon-specific measure of fragmentation. We have not attempted this task because we do not have access to the resources that this labour-intensive approach requires, although a great deal of effort has been spent in identifying shaft fragments to the finest taxonomic level possible.

Instead, we have used taxon-specific ratios of diaphysis to epiphysis limb bone and rib fragments as our fragmentation measure, under the assumption that intensified bone fragmentation will increase the number of identifiable shaft fragments more quickly

Table 3. Diaphysis/epiphysis ratios for the Grotte XVI Upper Palaeolithic ungulate taxa

	Stratum					
	0	As	Abc	Abb	Aib	B
Reindeer						
Diaphysis NISP	656	97	254	256	69	40
Epiphysis NISP	149	34	69	43	5	10
Ratio	4·40	2·85	3·68	5·95	13·80	4·00
Shaft adjusted residual	− 0·08	− 2·31*	− 1·51	+ 1·99*	+ 2·65**	− 0·29
Other ungulates						
Diaphysis NISP	22	3	34	88	14	14
Epiphysis NISP	12	8	15	32	5	10
Ratio	1·83	0·38	2·27	2·75	2·80	1·40
Shaft adjusted residual	− 0·45	− 2·97**	+ 0·22	+ 1·69	+ 0·54	− 1·08

*$P<0.05$; **$P<0.01$.

than it will increase the number of identifiable epiphyseal fragments (Grayson & Delpech, 1998). Since the Grotte XVI evenness values are highly correlated with, and are in large part driven by, the changing relative abundances of reindeer, we focus our fragmentation analysis on this species. The data relevant to this analysis are presented in Table 3.

The diaphysis/epiphysis ratios for reindeer vary dramatically across strata, from a low of 2·85 in Solutrean Stratum As to a high of 13·80 in Aurignacian Stratum Aib. Chi-square analysis of the raw numbers on which these ratios are based shows that these differences as a whole are significant ($\chi^2=16.83$, $P<0.01$), while analysis of single-cell adjusted residuals (Everitt, 1977) shows that shafts are significantly under-represented in Stratum As ($P<0.05$) and over-represented in Strata Abb ($P<0.05$) and Aib ($P<0.01$). As Figure 6 shows, however, this measure of differential fragmentation is unrelated to ungulate assemblage evenness ($r=0.37$, $P\gg0.10$; here and below, the correlation coefficient is calculated using the natural log of the fragmentation index).

There are insufficient numbers of identified diaphyses and epiphyses to provide a comparable analysis for the other ungulate taxa represented in the Grotte XVI ungulate assemblages. Instead, we provide composite fragmentation data for these remaining taxa (Table 3). These data make it clear that these other ungulates have fragmentation ratios lower, and in some cases much lower, than those for reindeer. Insofar as this fragmentation was caused by human activities, these differences suggest that reindeer have undergone far more intensive processing than have these other taxa. In fact, pairwise χ^2 comparisons of the raw data on which these ratios are based show that reindeer shafts are significantly over-represented (at $P<0.05$) in all strata except Gravettian Stratum Abc. Since our analyses of the causes of this fragmentation are incomplete, and we thus cannot fully document those causes, we do not pursue this issue here.

Chi-square analysis of the differential distribution of diaphyses and epiphyses of these ungulates across the Grotte XVI strata shows this distribution to be significantly different from that expected by chance ($\chi^2=11.50$, $P<0.05$), with shafts significantly under-represented in Stratum As (adjusted residual=2·97, $P<0.01$). Once again, however, there is no significant relationship between this measure of fragmentation and evenness ($r=0.26$, $P\gg0.10$).

Measured in this way, then, there appears to be no reason to suspect differential taxon-specific fragmentation across assemblages as the cause of the decline in Grotte XVI evenness values through time.

Differential body part representation
By differentially altering the distribution of specimens across taxa, changing patterns of body part
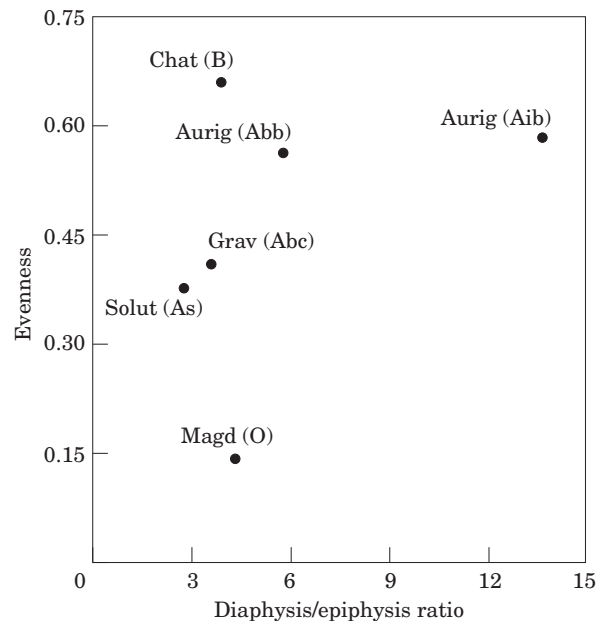

Figure 6. The relationship between evenness and reindeer diaphysis/epiphysis ratios across the Grotte XVI Upper Palaeolithic ungulate assemblages. Abbreviations as in Figure 3.

Table 4. *Numbers of identified specimens by skeletal element, strata 0 and B, and stratum 0 adjusted residuals (AR)*

	Reindeer			Other ungulates		
Element	Stratum O	Stratum B	AR	Stratum O	Stratum B	AR
Radius/ulna	95	5	+0·15	8	5	+0·68
Humerus	56	0	+1·81	5	1	+1·54
Skull/mandible/teeth	274	13	+0·68	60	51	+0·51
Carpals	21	3	− 1·57	4	3	+0·26
Ribs	224	8	+1·40	0	4	− 2·11*
Scapula	15	1	− 0·16	0	1	− 1·05
Vertebrae	33	3	− 0·81	0	1	− 1·05
Innominate/sacrum	10	0	+0·75	1	1	− 0·07
Femur	59	5	− 0·90	2	2	− 0·10
Tibia	89	9	− 1·76	5	2	+0·19
Tarsals	10	2	− 1·75	1	1	− 0·07
Metapodials	295	23	− 1·71	15	9	+1·05
Phalanges	132	2	+2·08*	9	17	− 1·94

*$P<0.05$.

accumulation by the predators—in this case, people—whose activities deposited a set of faunal assemblages could also cause the evenness pattern at issue here (Grayson & Delpech (1998) discuss this effect as applied to taxonomic richness values). Fortunately, it is relatively easy to test for the presence of this phenomenon by examining the distribution of specimens across body parts within taxa and across assemblages. If body part representation does change significantly across assemblages, then the evenness values for these assemblages must be recalculated with the elements involved eliminated from the analysis.

Here, we focus our attention on the two faunal assemblages that show the greatest differences in evenness: Magdalenian Stratum 0 and Châtelperronian Stratum B. Since much of the evenness decline that marks the Grotte XVI assemblages is driven by increases in the relative abundance of reindeer through time, we begin our examination with this taxon.

Table 4 provides NISP values by major skeletal element for reindeer from strata 0 and B (in parallel with the Le Flageolet I analysis, we have excluded such elements as the patella, sesamoids, fibula, and antler). This table also provides the single-cell adjusted residuals associated with these values. Of the 13 comparisons involved, only that for phalanges is significant. With this element removed from the comparison, there are no significant differences in reindeer element distributions between the two assemblages.

Since other ungulates are far less common in the Grotte XVI assemblages, we again analyse those ungulates as a composite group (Table 4). The only significant difference in this comparison is provided by ribs; with ribs excluded from the comparison, phalanges emerge as significantly over-represented in Stratum 0 (adjusted residual = +2·05, $P<0.05$). With both ribs and phalanges excluded, no significant differences in element representation remain between the two assemblages.

Accordingly, we have recalculated assemblage evenness values for strata 0 and B using that subset of skeletal elements listed in Table 4, but excluding ribs and phalanges. The results differ little from those obtained by analysing the entire set of specimens (Figure 3). Stratum 0, with an evenness value of 0·19, remains far less even than Stratum B, with an evenness value of 0·67.

We conclude that neither differential bone fragmentation nor differential bone transport—or any other process that can differentially alter skeletal part representation—has caused the decline in evenness that marks the Grotte XVI Upper Palaeolithic ungulate assemblages.

Explaining the Evenness Decline

If neither changing sample sizes nor taphonomic variables can account for these declining values, the cause most likely lies in some factor extrinsic to the faunal assemblages themselves. There are two obvious such factors that might be involved. First, the increasing emphasis on reindeer that is largely driving the evenness decrease might have resulted from some "cultural" variable, as is often suggested in analyses of the Magdalenian. For instance, the increasing emphasis on reindeer might have resulted from improved methods of harvesting these animals, methods that increased the energetic returns obtained from this species beyond those that could be obtained from other ungulates. Changes of this sort, whether in such hardware realms as weaponry or in such software realms as the development of highly effective communal hunting techniques (e.g., Gordon, 1988), could readily lead to the heavy emphasis on reindeer that marks Stratum 0 (see the discussion in Grayson & Cannon, 1999).

We do not dismiss this possibility, but we do not pursue it here. Instead, we observe that the pattern of

ungulate representation across the Upper Palaeolithic assemblages at Grotte XVI suggests that all of these taxa provided sufficiently high economic returns that they always remained in the diet and were always pursued upon encounter. Accordingly, we make the facilitating assumption that the evenness values at Grotte XVI reflect the abundance of these ungulates on the faunal landscape (Broughton & Grayson, 1993; Grayson & Cannon, 1999). If this assumption is correct, it follows that the increasing abundance of reindeer in the Grotte XVI assemblages must reflect increased human encounter rates with this species compared to the rates with which other species were encountered. We will argue that these altered rates were caused by climate change that was either particularly favourable to reindeer or particularly inimical to other ungulates, or both. Finally, we will return to our facilitating assumption concerning encounter rates as well as to the possibility that human behavioural change accounts for the patterns we have detected.

We preface our argument by observing that harsh abiotic conditions often create landscapes that are dominated by a small number of species, presumably because relatively few species can thrive in such contexts (e.g., May, 1975; Ehrlich et al., 1980; Brown, 1981, 1988; Brown & Lomolino, 1998). Most studies of organic diversity on abiotically-stressed landscapes have depended on short-term direct observations of modern communities (e.g., Lewellen & Vessey, 1998), but both observation and theory document that the development of severe abiotic stress through time should lead to the increasing relative abundance of those few species that can tolerate such stress and to the decline in relative abundance of the far greater number of species that cannot (Menge & Sutherland, 1987). As this occurs, of course, community evenness will decline.

An empirical example of this phenomenon under circumstances very different from those represented at Grotte XVI is provided by the small mammal faunal assemblages of Homestead Cave, located in the northeastern Great Basin of intermountain western North America and, more specifically, in the northern Bonneville Basin of north-central Utah (Grayson, 1998, 2000). The area in which this site is located is quite arid, receiving only some 23 cm of precipitation a year under conditions of high summer temperatures and thus of high evaporation rates. Indeed, there are no permanent sources of water in the area, and the site itself is adjacent to the barren salt flats left behind as a result of the final desiccation of Pleistocene Lake Bonneville sometime after 12,000 ^{14}C years ago.

Excavated under the direction of D. B. Madsen, Homestead Cave provided an enormous and well-stratified vertebrate sample, representing the results of about 11,000 years of owl pellet accumulation. Some 184,000 small mammal bones and teeth from this site have been identified to at least the genus level, with
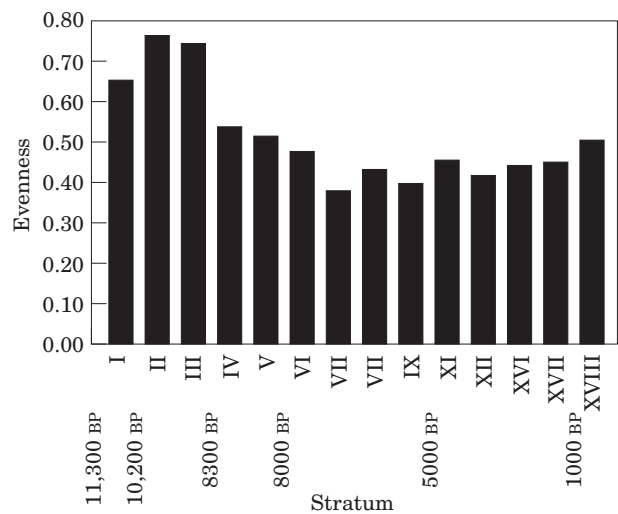

Figure 7. Small mammal assemblage evenness at Homestead Cave, Utah (from Grayson, 2000).

chronological control over the depositional sequence provided by 21 ^{14}C determinations.

The latest Pleistocene and Holocene climatic history of this general region is well understood (e.g., Madsen & Currey, 1979; Grayson, 1993; Rhode & Madsen, 1995). Sacrificing details for brevity, we note that within the northern Great Basin as a whole, a generally cool and moist latest Pleistocene and Early Holocene (c. 11,000 to 7500 years ago) was followed by a generally hot and dry Middle Holocene (c. 7500 to 4500 years ago), after which climatic conditions more closely resembling those of the present began to emerge. While the Middle Holocene was not monolithically hot and dry (e.g., Mehringer, 1985), it was far warmer and drier than what came before and after, to the extent that archaeological sites from this episode are difficult to find, suggesting in turn that human population densities in this region declined in response to increased aridity (Grayson, 1993, 2000; Kelly, 1997). Where Middle Holocene temperatures have been directly estimated from palaeoclimatic indicators in the Great Basin, they suggest summer temperatures of at least 2°C above modern (LaMarche, 1973), but much higher summer temperatures for part of this episode have also been inferred (L. V. Benson, pers. comm.).

The evenness values for the Homestead Cave small mammal assemblages track these changes closely (Figure 7). As the relatively cool and moist Early Holocene came to an end here, small mammal community evenness underwent a significant decline. Evenness values remained generally low during the Middle Holocene, then climbed as this hot and dry episode ended. While the ultimate cause of these changes lies in regional climate, the proximate cause lies in the response of local species of mammals to that climate. During the Middle Holocene, many species of mammals that had previously been common declined dramatically in abundance, some to the point of local
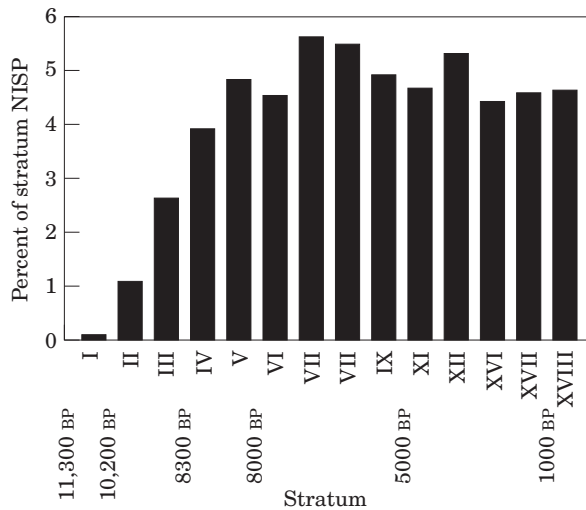
Figure 8. The changing contributions of chisel-toothed kangaroo rat specimens to the Homestead Cave small mammal assemblages.
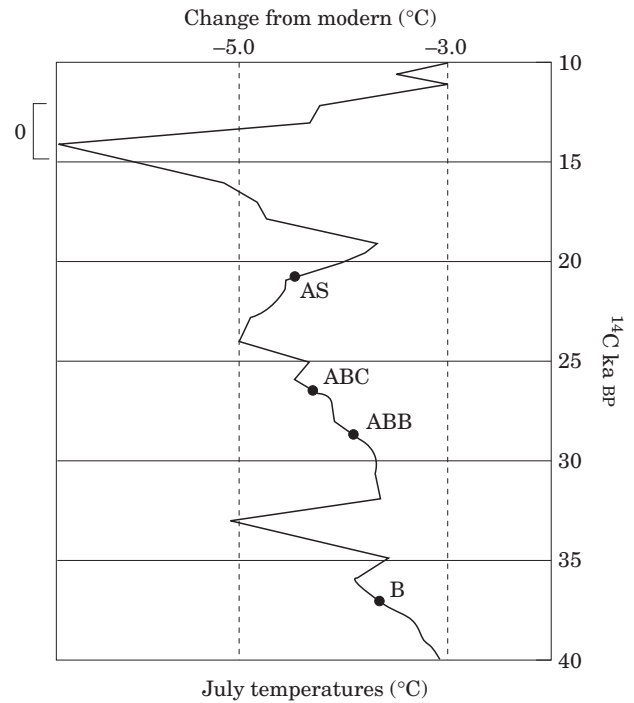

Figure 9. July temperatures, expressed as departures from modern, as reconstructed by Guiot (1990) for eastern France, showing the position of the Grotte XVI ungulate faunal assemblages for which ^{14}C ages are available.

extinction (Grayson, 2000). At the same time, the chisel-toothed kangaroo rat (*Dipodomys microps*), which is extremely well-adapted to hyperarid environments (Hayssen, 1991), became increasingly common in the local small mammal community (Figure 8). The increase in abundance of this species played a major role in driving the evenness of the Homestead Cave small mammal assemblages downwards during the Middle Holocene.

We suggest that Upper Palaeolithic faunal assemblages from Grotte XVI reflect a similar response in a very different set of environments and at a very different time. While there are no detailed palaeotemperature reconstructions available for southwestern France, there is such a reconstruction, developed by Guiot and his colleagues (Guiot *et al.*, 1989; Guiot, 1990; Pons *et al.*, 1992), for eastern France, based on the pollen records available from Les Echets (Beaulieu & Reille, 1992) and La Grande Pile (Beaulieu & Reille, 1984). This reconstruction is, in turn, consistent with a separate analysis of pollen assemblages from Lac du Bouchet, located some 140 km east–northeast of Grotte XVI (Pons *et al.*, 1992). Importantly, the pollen spectra from this latter site are also climatically consistent with magnetic susceptibility data from the same deposits, which in turn correlate with the Greenland ice-core oxygen isotope record (Thouveny *et al.*, 1994). There is little reason to think that Guiot's palaeotemperature reconstruction is of local significance only.

Figure 9 presents estimated July temperatures for the past 40,000 ^{14}C years, presented as departures from modern, from Guiot (1990). We also indicate the placement of Grotte XVI strata B, Abb, Abc, As, and 0 on this curve.

In situating the Grotte XVI assemblages on Guiot's curve, we have relied entirely on the ^{14}C chronology available for this site (Table 1). Because there are no ^{14}C ages available for Stratum Aib, its position is not

indicated. Because the ^{14}C ages available for Stratum 0 coincide with a significant plateau in ^{14}C activity, we have indicated its position as a range; precise calibration is not possible for the earlier determinations (Stuiver *et al.*, 1998). We have placed Stratum B at the midpoint of the two finite radiocarbon ages available for this stratum, but observe that the exact chronological placement of this unit on the curve within the age range indicated by the ^{14}C data is not critical to our arguments. We have, however, assumed that the infinite age provided by AA-2674 for this stratum pertains to underlying Mousterian Stratum C.

We could not be more aware of the hazards involved in correlating the Grotte XVI Upper Palaeolithic faunal sequence with Guiot's temperature curve in this fashion. This is especially true since Guiot's curve has been dated in very much the same way. We are, in essence, comparing one set of age estimates with another.

Nonetheless, we observe that if temperature extremes are driving the evenness decline at Grotte XVI, we expect to see that the assemblages involved intersect the temperature curve at ever-decreasing values. As Figure 9 shows, they do exactly that. We also note that there is no relationship between the Grotte XVI evenness values and Guiot's average annual temperature reconstruction for this period, or with his reconstruction of January temperatures (Guiot, 1990).

Guiot (1990) also provides a precipitation curve for this period of time. The Grotte XVI evenness

values are not correlated with either average annual or January precipitation. They are, however, correlated with July precipitation: in each instance, the Grotte XVI occupations, with their ever-decreasing evenness values, intersect the July curve at times of ever-increasing precipitation.

The decreasing evenness values at Grotte XVI are thus associated with both decreasing July temperatures and with increasing July precipitation. Even though this is the case, we hypothesize that the evenness structure of the Upper Palaeolithic ungulate assemblages at Grotte XVI (Figure 3) is to be explained by the effects of decreasing summer temperatures. We argue this for two reasons. First, the July temperatures in Guiot's reconstruction never rise above 3·0°C below modern during the time Grotte XVI was occupied, while the precipitation values are quite close to modern during the time that strata Abb, Abc, and As accumulated. Perhaps more importantly, modern reindeer do not thrive under conditions of summer warmth, in part because they are not well-endowed with sweat glands, but they do exist under a wide variety of precipitation regimes (Heptner *et al.*, 1988).

Accordingly, we argue that as temperatures declined in this area, reindeer populations became increasingly abundant on the landscape compared to the abundances of other larger ungulates on that landscape. That is, we argue that the relative abundance of reindeer increased at times of decreased July temperatures. As this occurred, human encounter rates with reindeer increased relative to rates at which other ungulate taxa were encountered, and reindeer came to dominate the human diet as it is monitored at Grotte XVI. Assemblage evenness values declined in response to this climatically-driven dominance increase.

This suggested process differs little from that which led chisel-toothed kangaroo rats to increase substantially in abundance at Homestead Cave as temperatures increased during the Great Basin Middle Holocene, a process that drove small mammal assemblage evenness downwards at this site. While the predators involved at Homestead Cave were owls, not people, both situations appear to register the effects of mammalian responses to temperature extremes.

Because we are extremely aware of the weakest link in our argument—the use of a relatively small number of uncalibrated radiocarbon ages to correlate the Grotte XVI data with the July temperature curve—we note that the lack of ^{14}C age determinations for Stratum Aib provides us with a potential test of our argument. The evenness of this assemblage is much lower (0·58) than that for Stratum B (0·66), but not dramatically different from that for Stratum Abb (0·56). When ^{14}C ages become available for this stratum, they should indicate that this assemblage intersects the July temperature curve at a point compatible with our suggested explanation. An age of *c.* 30,000 ^{14}C years BP would provide support for our argument; an age of *c.* 33,000 ^{14}C years BP would strongly suggest

that we are wrong. Unfortunately, the radiocarbon chronology available for Le Flageolet I (Grayson & Delpech, 1998) is insufficiently precise to support an independent assessment of the arguments we have presented here.

Conclusions

It is hardly novel to suggest that the dominance of many Magdalenian faunal assemblages by reindeer in southwestern France Magdalenian faunas was climatically driven, nor is it novel to suggest that the changing nature of faunal assemblages in a site such as Grotte XVI, or in the Perigord as a whole, was driven by climate change (e.g., Geikie, 1881; Lubbock, 1865; Mortillet, 1883; Mortillet & Mortillet, 1900; Simek & Snyder, 1988; Boyle, 1990; Delpech, 1983, 1989, 1992, 1999*a*; Enloe, 1993, 1999; Straus, 1995). In fact, it is not even novel to suggest that reindeer abundance correlates with depressed summer temperatures: Lartet (1867, 1875) himself made the same suggestion over a century ago (see Grayson (1984) for a discussion of the context of Lartet's position). Instead, we see the contribution that we have attempted to make here as lying in the approach we have taken to measure diachronic changes in human subsistence, and in the means we have used to examine whether the subsistence changes we have detected can be attributed to climate change.

Most approaches to monitoring the degree to which Palaeolithic diets were dominated by single taxa have relied heavily on examining the percentage contribution of the target taxon to the faunal assemblages involved. While we certainly have no objection to that, and have used that approach ourselves (Figure 4), evenness measures, including the one we have used here, have the advantage that they summarize specimen distributions across all taxa within an assemblage while being independent of the particular taxa involved. As a result, they can provide a quantitative measure of dietary specificity that can be applied in, and compared across, very different faunal landscapes. They also have the advantage of being related to a rich body of theory that attempts to explain why individuals are distributed across taxa the way they are distributed (e.g., Magurran, 1988). Indeed, it was that theory that led us to the arguments we have made here.

The measure of climate change that we have used—Guiot's reconstructed temperature curve for the later Pleistocene—can certainly be criticized. Most importantly, the pollen sequences used by Guiot for the period of time of interest here are not as well-controlled chronologically as one might wish. Nonetheless, this reconstruction provides a far more precise understanding of both the nature and chronology of past climates in this region than do more traditional approaches that, while based on similar palaeoclimatic indicators (for instance, pollen sequences), simply summarize past climatic episodes with such terms as

"warmer" or "cooler" (see, for instance, Grayson (2000) for the Great Basin, or Boyle (1990: 140) for southwestern France), and that often infer such conditions from the faunal assemblages themselves (e.g., Bordes & Prat, 1965).

In short, we hypothesize that the declining evenness values that mark the Upper Palaeolithic ungulate assemblages at Grotte XVI, and that culminated in a Magdalenian assemblage that is 94% reindeer, were caused by the fact that the occupations at Grotte XVI intersected the Late Pleistocene summer temperature curve at ever-decreasing values. We posit that those declining temperatures increased the abundances of reindeer on the landscape relative to the abundances of other ungulate taxa. People responded to these changes by incorporating relatively greater numbers of reindeer into their diet as registered at Grotte XVI.

In making this argument, we are not suggesting that human behavioural innovations played no role in producing the pronounced patterns in ungulate abundance that mark the Grotte XVI faunal sequence. We are also not suggesting that the Grotte XVI ungulates were necessarily taken in strict accordance with their abundance on the landscape. We are instead suggesting that reindeer relative abundances at this site increased through time because the human occupations here happened to occur at times of ever-decreasing summer temperatures, and that climate alone can account for the patterns we have found. Given this context, it would not be surprising if humans responded behaviourally with more efficient ways of capturing prey, just as non-human predators can innovate more efficient predation behaviours under the appropriate selective conditions (Anholt & Werner, 1999). If so, the evolution of increasingly efficient means of taking reindeer would likely cause the relative abundances of reindeer in the Grotte XVI assemblages to be correspondingly greater than those that marked the surrounding faunal landscape.

We do not know whether our explanation of the development of faunal dominance at Grotte XVI is correct. It is clear, though, that this explanation can be tested not only by obtaining radiocarbon ages for Stratum Aib, but also by extending the analysis back in time, into the Grotte XVI Mousterian. In fact, this approach would seem to provide a particularly sensitive way to improve our understanding of subsistence change across the Middle-to-Upper Palaeolithic "transition".

Acknowledgements

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