

Large mammals, climate and resource richness in Upper Pleistocene Europe

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Abstract. A regional model for Upper Pleistocene Europe is examined from the perspective of faunal variation. A large mammal database from three regions distributed between the north and south of the continent is analysed in terms of taxa frequency and diversity. Comparisons are drawn between faunal assemblages with an archaeological association and those without. A focus on faunas with *Capra* reveals increased carnivore frequency. It is suggested that these associations provide a means to assess relative resource richness between regions and allow a chronological comparison of past hominid behaviour. The implications for characterising human exploitation of large mammals is discussed.

Key words: *Capra*, taphonomy, archaeology, hominids, specialist hunters, resource richness, community structure, Upper Pleistocene, large mammals.

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I. INTRODUCTION

In this paper I will take a hominid perspective on the issue of the influence of climate on the large mammal faunas of Upper Pleistocene Europe. The study arose from a consideration in the archaeological literature of what constitutes a specialist hunter (NITECKI & NITECKI 1987; CHASE 1989; FARIZY & DAVID 1992; STINER 1992). In many ways the problem is similar to that faced by palaeomammologists reconstructing climatic conditions either synecologically or autecologically. What is involved is an assessment of the diversity and frequency of taxa in our samples. The approach taken here is to analyze faunal data via a regional model constructed to take account of geographical variation in predator and prey behaviour.

In order to reconstruct either past climate or hunting practices from faunal data it is essential to consider taphonomy since it is the process which supplies information (GIFFORD 1981). For example, recent work has emphasised anatomical representation, cut marks and obvious carnivore damage to investigate early hominid behaviour as BRAIN (1981) showed by answering the question "the hunters or the hunted?".

However, there is another larger regional scale which remains to be tackled by studies of past behaviour. This involves the investigation of faunal regions within Europe. Their significance as units of behavioural analysis resides in their contribution to a palaeoecological framework intended to investigate evolutionary processes, both physical and behavioural, among fossil taxa, including hominids. Species do not evolve in isolation. Understanding the pattern and timing of such evolutionary processes requires a community approach, with an emphasis on reconstructing behaviour (GUTHRIE 1990).

Palaeomammalogists have generally ignored such behavioural frameworks, preferring instead indicator species to reconstruct community types. Using this procedure faunal provinces have been reconstructed, partitioned climatically and chronologically according to the significance attached to key species (e.g. HESCHELER & KUHN 1949; ZEUNER 1959; KAHLKE 1975; MUSIL 1985). In many cases such regional divisions express nothing more than the history of research and are therefore of limited value for palaeoecological research. The same approach has been followed by archaeologists plotting artifact types to reconstruct cultural provinces (e.g. MCBURNEY 1950; GABORI 1976; KOZŁOWSKI & KOZŁOWSKI 1979).

This standard procedure will fail to reconstruct either climate or hominid economy from large mammal data. The reason is simple. Animals, being mobile, vary their behaviour according to local factors. Large mammals can do this on a large spatial scale. Our regions need to be independent of such local variation if we are to hope to measure it and use it in palaeoecological analysis. The only way to achieve such independence is by stipulating regions which are larger than the behaviour we want to examine and to fix them to geographical constants which consistently affect the reasons why animals vary their behaviour. Since mobility is related to the abundance and distribution of resources for both herbivores and carnivores these geographical constants must relate to the food supply (GAMBLE 1986: 69-74).

At this scale of regional analysis and over the climatic cycles of the Pleistocene the geographical constants affecting the distribution of taxa within Europe are longitude, latitude and relief (LLR). We need to understand the possible effect of these three constants (LLR) on the variation in our faunal samples **before** we make assessments of specialist and generalist hominid lifestyles in the remote past. In the same way some caution is implied before we use the composition of assemblages via dominance and diversity indices to infer climatic régimes. The model (Fig. 1) recognizes three latitudinal provinces and nine regions based on longitude and relief (see GAMBLE 1986 Chapter 3 for discussion)

Elsewhere (GAMBLE 1983, 1984, 1986; MIRACLE 1991; MARSHALL 1993) I have argued that the variation in carnivore diversity and numerical dominance within these nine regional faunal assemblages is the result of differences in denning behaviour. Where competition was high due to resource scarcity then greater use was made of caves and rock shelters and hence carnivores contributed more to the formation of the assemblages in such locations. Not suprisingly, such competition is dependent upon LLR factors since these, at whatever point in an interglacial/glacial cycle, controlled the resource base through variation in photosynthesis which in turn influences the degree of seasonality in the various regions of Europe (Fig. 1). In this paper I want to examine a related issue by examining the regional structure of Pleistocene large mammals as an index of relative resource richness between these same geographical regions.

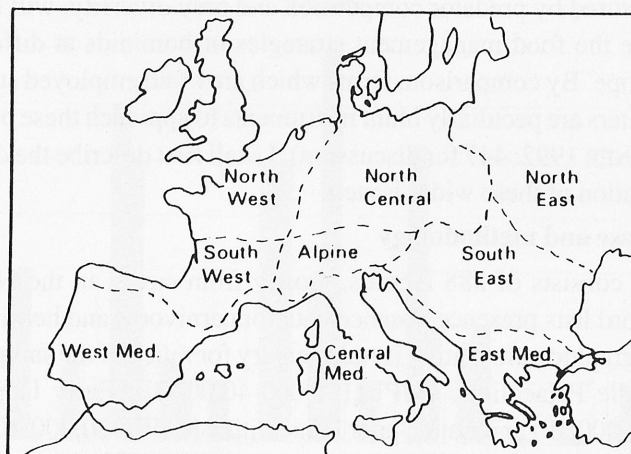


Fig. 1. Map showing the regional subdivisions of the study area. The abbreviations NC, SE and ME are used in the text for the North Central, South East and East Mediterranean regions.

II. FAUNAL COMMUNITIES AND *CAPRA*

The present study will investigate faunal variation in three regions, the North Central (NC), South East (SE) and East Mediterranean (ME) (Fig. 1). It will focus on Upper Pleistocene *Capra* to examine relative resource richness in time and space.

The species *Capra ibex*, *Capra pyrenaica* and *Capra aegagrus* were widely distributed during the Upper Pleistocene (MUSIL 1985: Fig. 26). Problems of identification are well known and especially so when *Rupicapra* and *Ovis* are present. Mountain *Capra* occur in many archaeological levels and have on occasion been cited as examples of specialist hunting by Neanderthals as at Teshik Tash in Uzbekistan (MOVIUS 1953) and Hortus in France (PILLARD 1972). During the Upper Palaeolithic *Capra* is common from Iberia (DAVIDSON 1989) to Greece (GAMBLE in press). STRAUS (1987) has discussed the specialised nature of exploitation strategies at this time while MIRACLE and STURDY (1991) have analyzed the landscape features which favour these species. In particular they note the close association between poor soils (the angry karst) and increased proportions of *Capra* and *Rupicapra* in their low altitude, eastern Adriatic sites.

Over such time spans and geographical range we must expect that *Capra* was part of very different community structures and hence opportunites for exploitation by humans. Moreover, even a cursory glance at the archaeological evidence shows that Upper Pleistocene *Capra* was found at much lower altitudes and with a range of species not encountered today. These obvious changes and variable associations single out *Capra* as a suitable subject for examining regional and climatic factors in palaeontological and archaeological distributions.

As an archaeologist I am interested in assessing and comparing the wider, regional communities from which prey such as ibex were selected. The structure of those communities also shaped hominid behaviour. In particular, the relative richness of community

resources, as measured by predator competition and prey diversity, will be an important means to compare the food management strategies of hominids at different times and places within Europe. By comparison, terms which are often employed such as specialist and generalist hunters are peculiarly blunt instruments to approach these palaeoecological subtleties (see STINER 1992: 447 for discussion). I shall first describe the data set and then turn to a consideration of these wider issues.

Faunal database and methodology

The data base consists of 588 records, mostly from caves, in the NC, SE and ME regions. Each record lists presence/absence data for carnivores and herbivores identified to a discrete stratigraphic unit. Dating is rudimentary for much of the sample and has been divided into Middle Palaeolithic [MP] (100,000-40,000BP) Early Upper Palaeolithic [EUP] (40,000-20,000BP) and Late Upper Palaeolithic [LUP] (20,000-10,000BP) on the basis of the associated archaeology. A further category of 246 palaeontological [PNT] collections without any archaeology, has been added as a comparative sample. These data are presented as percentage frequency histograms by region and period in Figs 2-9.

The regional analysis of community structure on the basis of presence/absence data alone is far from ideal. However, the loss of detail in such data is compensated for by the wider coverage of geographical and chronological variation. Consequently, comparative measures have to be kept simple. In this study the regions and periods have been compared by two methods. Firstly, the proportional representation of species (irrespective of which taxa are present) has been studied separately for herbivores and carnivores. Since the total number of species does not vary significantly between regions and periods it is possible to compare community profiles by means of a series of simple graphs. These are presented according to the frequency of species arranged in rank order. Attention is drawn to two

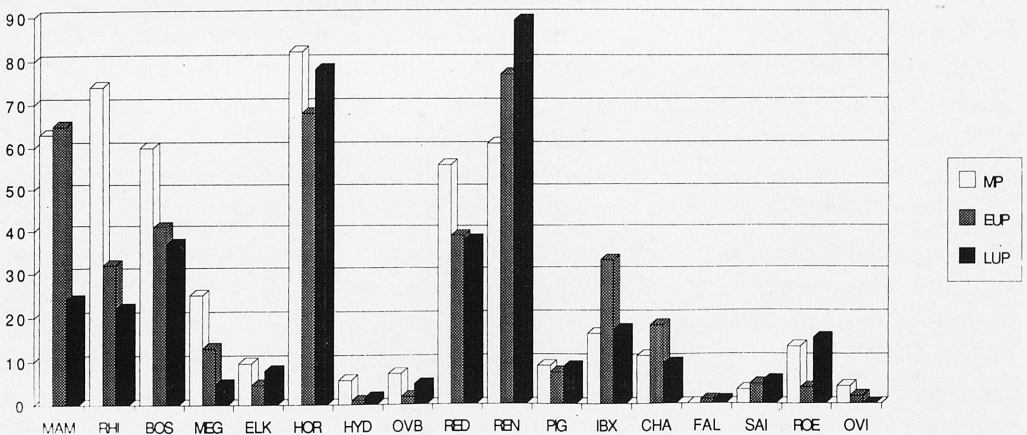


Fig. 2. Histograms showing the percentage of faunas in which the identified herbivore species were present during selected time intervals in the NC region. Legend: MAM, mammoth; RHI, rhinoceros; BOS, *Bos*; MEG, *Megaceros*; ELK, elk; HOR, horse; HYD, wild ass; OVB, *Ovibos*; RED, red deer; REN, reindeer; PIG, pig; IBX, ibex; CHA, chamois; FAL, fallow deer; SAI, *Saiga*; ROE, roe deer; OVI, *Ovis*. MP, Middle Palaeolithic; EUP, Early Upper Palaeolithic; LUP, Late Upper Palaeolithic.

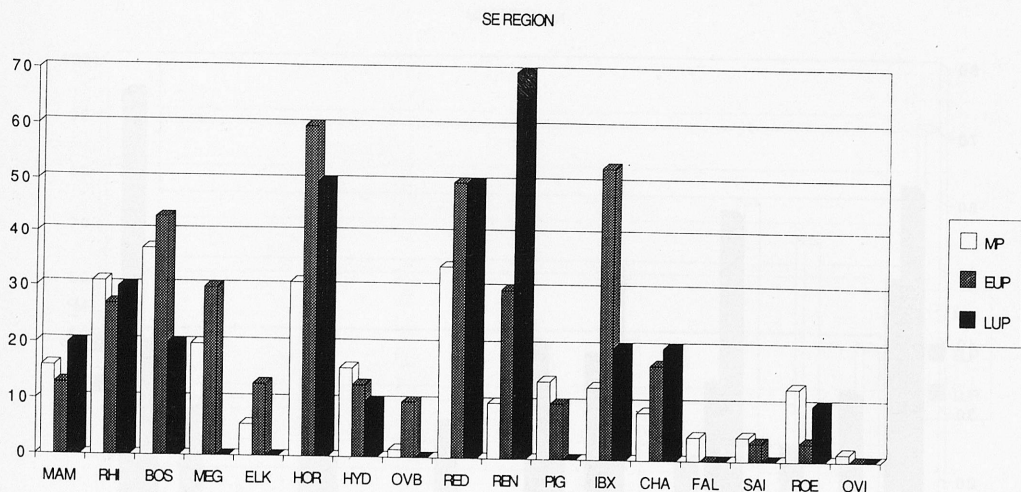


Fig. 3. Histograms showing the percentage of faunas in which the identified herbivore species were present during selected time intervals in the SE region. For legend, see Fig. 2.

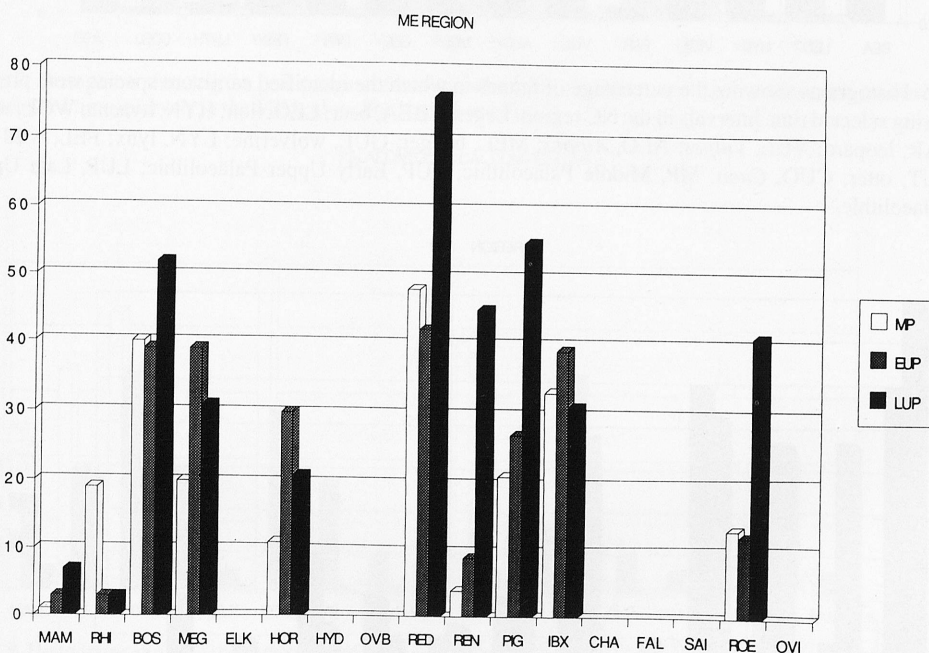


Fig. 4. Histograms showing the percentage of faunas in which the identified herbivore species were present during selected time intervals in the ME region. For legend, see Fig. 2.

profile shapes which are commonly repeated; those of incremental rank-frequency and those in the form of a primate distribution.

Two arbitrary thresholds have been set to focus on the issue of variation in taxa diversity and frequency. These are fixed at 15% and 60%. The number of taxa that exceed the 15%

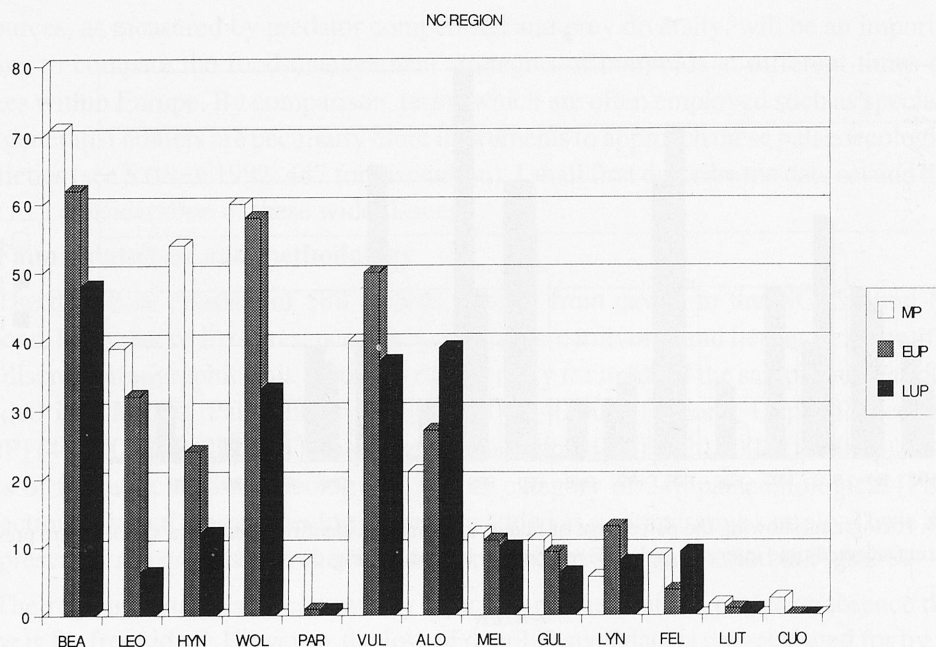


Fig. 5. Histograms showing the percentage of faunas in which the identified carnivore species were present during selected time intervals in the NC region. Legend: BEA, bear; LEO, lion; HYN, hyaena; WOL, wolf; PAR, leopard; VUL, *Vulpes*; ALO, *Alopex*; MEL, badger; GUL, wolverine; LYN, lynx; FEL, wild cat; LUT, otter; CUO, *Cuon*. MP, Middle Palaeolithic; EUP, Early Upper Palaeolithic; LUP, Late Upper Palaeolithic.

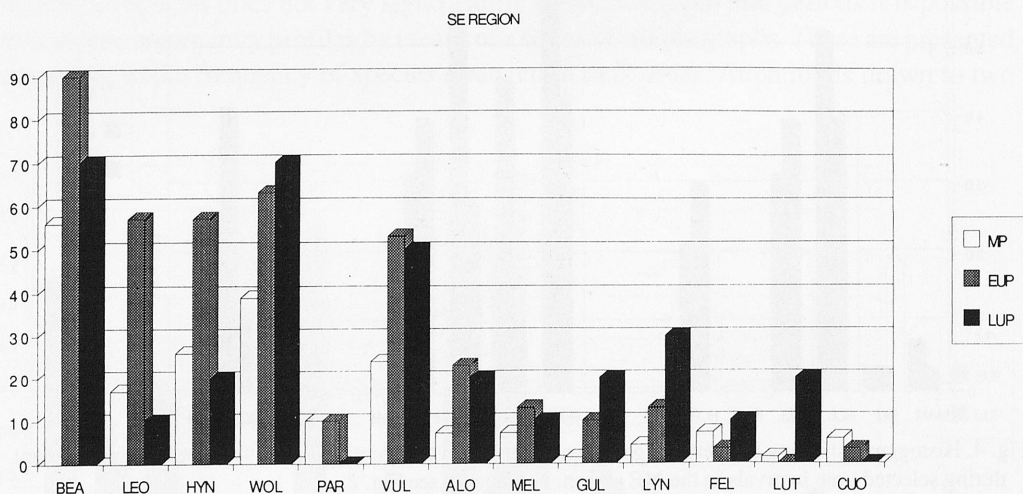


Fig. 6. Histograms showing the percentage of faunas in which the identified carnivore species were present during selected time intervals in the SE region. For legend, see Fig. 5.

threshold are seen as contributing directly to the diversity of that regional or period community. The 60% ceiling focuses attention on the number of frequent species within the community. Obviously these data provide no measure of the actual abundance of taxa

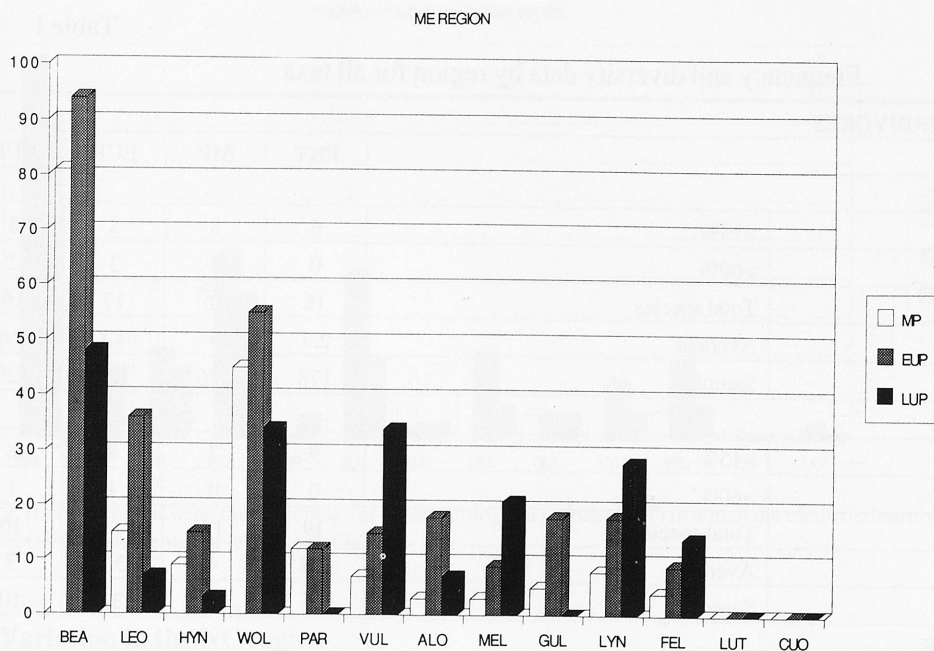


Fig. 7. Histograms showing the percentage of faunas in which the identified carnivore species were present during selected time intervals in the ME region. For legend, see Fig. 5.

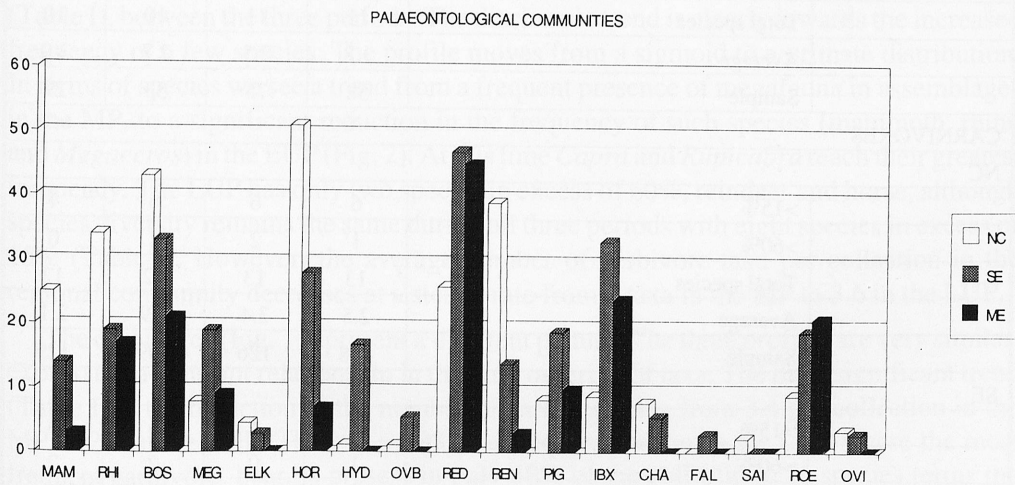


Fig. 8. Histograms showing the percentage of palaeontological faunas (PNT) in which the identified herbivore species were present. For legend, see Fig. 2.

in Upper Pleistocene animal communities. Such estimates are notoriously difficult even from well reported faunal assemblages.

Since the comparison of such graphs remains qualitative a second comparative measure is provided of simple summary values from the data base. These include (Table I) the number of species above the 15 and 60% thresholds and the average number of herbivore and carnivore taxa found in collections.

Table I

Frequency and diversity data by region for all taxa

HERBIVORES					
		PNT	MP	EUP	LUP
NC					
	>15%	6	8	8	8
	>60%	0	5	3	2
	Total species	16	16	17	16
	Average	2.7	5	4.1	3.6
	Sample	178	126	109	129
SE					
	>15%	9	7	8	8
	>60%	0	0	1	1
	Total species	19	17	15	10
	Average	2.8	4	3.7	3
	Sample	37	46	31	10
ME					
	>15%	5	6	6	8
	>60%	0	0	0	1
	Total species	11	11	10	10
	Average	1.8	2.5	2.7	3.9
	Sample	58	75	33	29
CARNIVORES					
NC					
	>15%	6	6	6	4
	>60%	1	2	1	0
	Total species	13	13	12	12
	Average	2.5	3.4	2.9	2.1
	Sample	178	126	109	129
SE					
	>15%	6	5	6	8
	>60%	1	0	2	2
	Total species	11	13	12	11
	Average	2.8	3.1	3.8	3.3
	Sample	37	46	31	10
ME					
	>15%	5	4	9	6
	>60%	1	1	1	0
	Total species	12	12	12	10
	Average	2.5	2.1	3.3	2.1
	Sample	58	75	33	29

PALAEOONTOLOGICAL COMMUNITIES

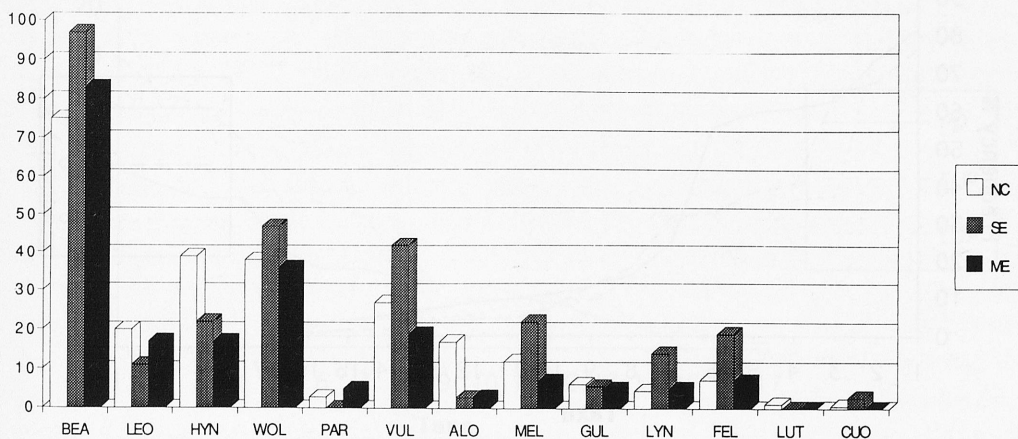


Fig. 9. Histograms showing the percentage of palaeontological faunas (PNT) in which the identified carnivores species were present. For legend see Fig. 5.

Variation in the NC region

Fig. 10 plots the profiles through time for one region, the NC. Among the herbivores there is a marked shift, supported by changes in the average number of taxa per collection (Table I), between the three periods. The diachronic trend is clearly towards the increased frequency of a few species. The profile moves from a sigmoid to a primate distribution. In terms of species we see a trend from a frequent presence of megafauna in assemblages in the MP, to a significant reduction in the frequency of such species (mammoth, rhino and *Megaceros*) in the EUP (Fig. 2). At this time *Capra* and *Rupicapra* reach their greatest frequency. The LUP has only two species in excess of 60%, reindeer and horse, although species diversity remains the same during all three periods with eight species in excess of 15% (Table I). However, the average number of herbivore taxa per collection in the regional community decreases at a steady rate from 5 taxa in the MP to 3.6 in the LUP.

The carnivores (Fig. 11) present a different picture. The three profiles are very similar, expressing a constant relationship in the rank ordering of taxa. The most significant trend (Table I) is the reduction in the number of carnivore taxa from 3.4 per collection in the MP to 2.1 in the LUP. There is a lack of a frequent species in the LUP where the most frequent carnivore, bear, is present in only 48% of the collections. In species terms the change between the MP and LUP centres upon the decline in the frequency of wolf, hyena and lion while fox remains important, but never above 60% throughout the time span covered. The NC region is characterized by very small frequencies of small carnivores - badger, wolverine, lynx, wild cat, otter and dhole (Fig. 5).

Discussion

The NC analysis identifies two results for inter-regional comparison,

- change through time in regional community structure can be demonstrated. These changes are irrespective of changes in the frequency of key indicator species (eg. reindeer).
- differences exist between the community structure of herbivores and carnivores.

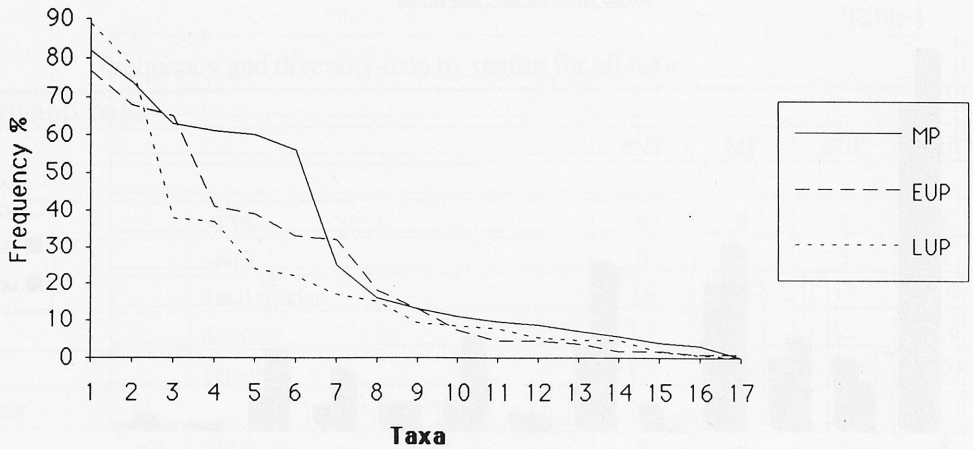


Fig. 10. Frequency distribution diagrams for herbivore taxa from the NC region by time period.

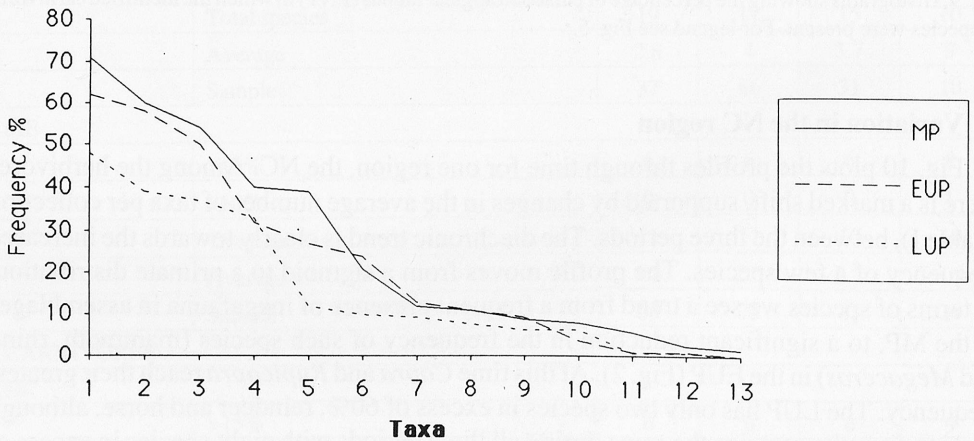


Fig. 11. Frequency distribution diagrams for carnivore taxa from the NC region by time period.

Variation in the SE region

The community profiles for the herbivore taxa in the three periods in this region (Fig. 12) do not show the same marked directional change as in the NC region. The MP and EUP display an incremental rank ordering of taxa frequency. The LUP profile shows some tendency toward a primate distribution but this is not as clear as the NC profile for the same period. Taxa diversity remains constant (Table I). Only two species are present in 60% of the collections in the EUP (horse) and LUP (reindeer). *Capra* is present in 53% of all EUP collections (Fig. 3). The average number of herbivore taxa does decline steadily from the MP to the LUP (Table I). In species terms the SE region is marked by lower frequency levels for megafauna (mammoth, rhino, *Megaceros*) but only in the case of the last species is there any significant decline in their presence during the LUP.

The carnivore profiles differ from the herbivore in a number of respects. Diversity increases through time with the number of taxa present in 15% of collections rising from 5 to 8 even though the total number of species identified declines by two species (Table I).

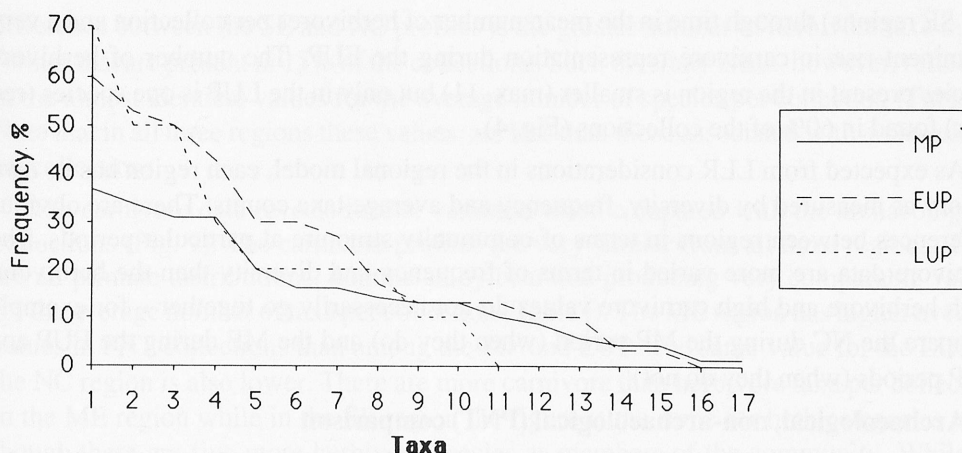


Fig. 12. Frequency distribution diagrams for herbivore taxa from the SE region by time period.

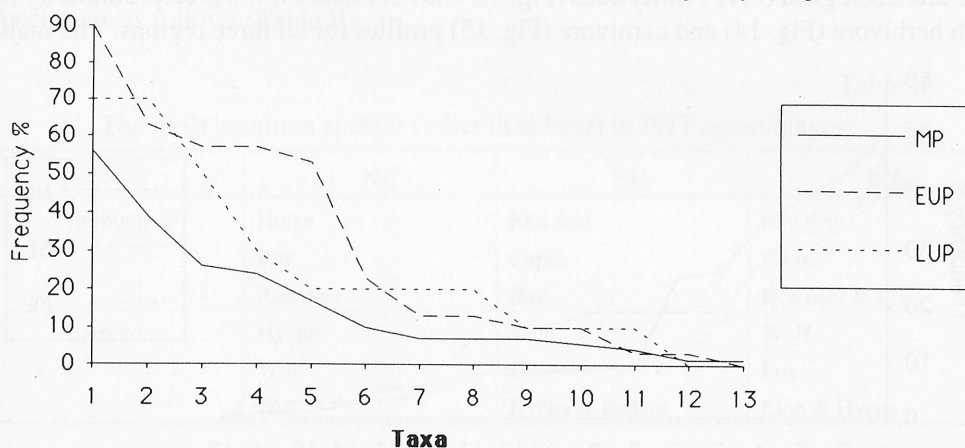


Fig. 13. Frequency distribution diagrams for carnivore taxa from the SE region by time period.

Only in the EUP and LUP are two carnivores (bear and wolf respectively) present in more than 60% of all the collections. Finally, the average number of carnivores rises from the MP to EUP and falls back slightly in the LUP. In species terms we see the sharp decline of lion and hyena between the EUP and LUP. Wolf continues to increase, in contrast to the NC region, during the three periods. It is the shift between the small and large carnivores in the EUP and LUP that is most dramatic (Fig. 13) with otter, lynx and wolverine all present in 15% of LUP collections (Fig. 6).

Inter-regional comparison

The SE data bear out the two results raised by the NC study and adds a further synchronic dimension to questions of faunal change. This is shown by the different figures for diversity and frequency. Moreover, the shape of the community profiles is sufficiently different to argue that the differences in LLR which these regions encompass are being felt in the organization of community structure. The ME region (Table I) further emphasises the synchronic variation. Here we see an increase (rather than decrease in the NC

and SE regions) through time in the mean number of herbivores per collection and a very prominent rise in carnivore representation during the EUP. The number of herbivore species present in the region is smaller (max. 11) but only in the LUP is one species (red deer) found in 60% of the collections (Fig. 4).

As expected from LLR considerations in the regional model, each region has its own history as measured by diversity, frequency and average taxa counts. There are obvious differences between regions in terms of community structure at particular periods. The carnivore data are more varied in terms of frequency and diversity than the herbivore. High herbivore and high carnivore values do not necessarily go together – for example compare the NC during the MP period (when they do) and the ME during the EUP and LUP periods (when they do not).

Archaeological, non-archaeological (PNT) comparison

However, set beside this finding of inter-regional variation are the patterns from the non-archaeological (PNT) collections (Fig. 8). The PNT data show a greater similarity for both herbivore (Fig. 14) and carnivore (Fig. 15) profiles for all three regions. The major

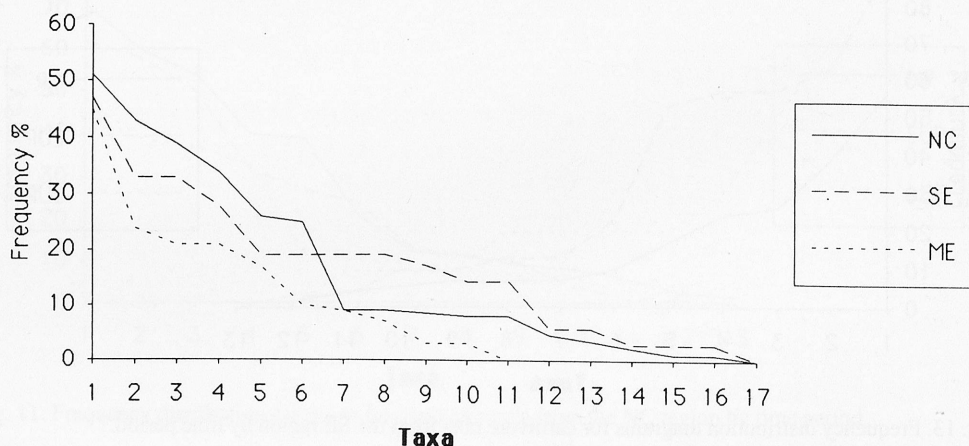


Fig. 14. Frequency distribution dirgrams for herbivore taxa from palaeontological communities (PNT) by time period.

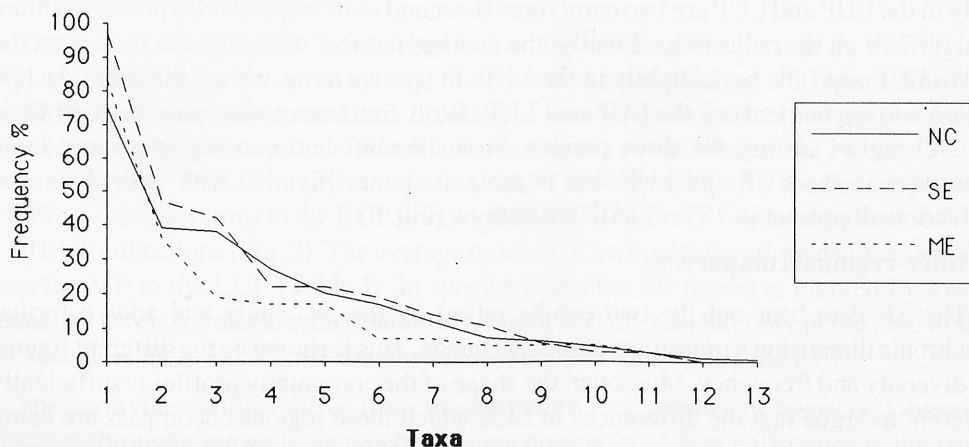


Fig. 15. Frequency distribution dirgrams for carnivore taxa from palaeontological communities (PNT) by time period.

difference between the SE and NC profiles is the greater number of herbivore taxa in the former that are present in 15% of the collections. Such diversity is not, however, reflected in the almost identical values for the average number of species per collection (Table I). Note that in all three regions these values are less than those associated with archaeological collections.

The carnivore data reveals further variation when compared with the archaeological collections (Fig. 9). The carnivore profiles are very similar from all three regions. They are all primate distributions, dominated by bear and producing very comparable values for the average number of taxa per collection (Table I). The ME region has higher average values in PNT collections than among the MP and LUP. The same value for the LUP of the NC region is also lower. There are more carnivore than herbivore taxa per collection in the ME region while in the SE region the figure is the same for both categories even though there are five more herbivore species as members of the community. While no species (other than bear) achieves 60% in the collections the next three most common species are as follows (Table II)

Table II

The most common species (other than bear) in PNT assemblages

	NC	SE	ME
Herbivores	Horse <i>Bos</i> Reindeer	Red deer Capra <i>Bos</i>	Red deer <i>Capra</i> Roe deer & Bos
Carnivores	Hyena Wolf Fox	Wolf Fox Hyena & Badger	Wolf Fox Lion & Hyena

Discussion

The PNT data are obviously a chronological palimpsest. They do however focus attention on the similarities and differences between regions and periods. In particular they suggest that the route to understanding the differences in basic community structure and composition depends on appreciating the taphonomy and ecology of the carnivores. This variation can be interpreted in two ways,

- increased carnivore presence, both syn- and diachronically, points to harsher climates and a move to types of denning behaviour, such as the use of caves. Such behaviour increased their chances of survival in the archaeological and palaeontological records (GAMBLE 1984)

- increased carnivore presence, both syn- and diachronically, points to the location of richer areas for prey resources. Competition between predators will still be high, hence their contribution through denning and feeding behaviour to the faunal record.

Capra faunal communities

The route I have adopted to examine these two propositions is through the community associated with those collections containing *Capra* remains. Distinguishing between

climate or competition as explanations for variability among the carnivore community will be tackled by considering competition as a measure of environmental richness. The key to determining which regions or periods were 'rich' in resources brings the *Capra* data into play. The data set (Tables I and IV) emphasises the period between 40,000 and 20,000BP as a preferred time for *Capra*. The frequency of *Capra* is highest in the SE and ME regions.

Table III

Faunas assemblages with and without *Capra*

Archaeological faunas with <i>Capra</i>	152
Archaeological faunas without <i>Capra</i>	436
Total archaeological faunas	588
Palaeontological faunas with <i>Capra</i>	43
Palaeontological faunas without <i>Capra</i>	203
Total palaeontological faunas	246
Total all faunas	834

Table IV

Assemblages with *Capra* by period and region

<i>Capra</i> faunas by period	Total archaeological sample	<i>Capra</i> % of sample
LUP 33	168	20
EUP 65	173	38
MP 54	247	22
<i>Capra</i> faunas by region		
NC 78	364	21
SE 27	87	31
ME 47	137	34

The summary data are presented in Table V for all regions and periods. While sample size is small (in particular for the SE and ME regions) even these data are informative of the general pattern. The main finding is that collections with *Capra* are characterized by substantially increased values for frequency (number of taxa >60%), diversity (>15%) and average number of carnivores and herbivores per collection. The carnivores are especially well represented in these ibex collections. The only exception being the PNT sample from the SE region and the MP period in the ME region (average only).

Table V

Frequency and diversity data by region for *Capra* faunas

HERBIVORES					
		PNT	MP	EUP	LUP
NC <i>Capra</i> only					
	>15%	9	11	8	9
	>60%	3	7	4	4
	Total species	14	16	14	12
	Average	5.5	7.6	5.5	5.4
	Sample	16	20	36	22
SE <i>Capra</i> only					
	>15%	6	10	10	6
	>60%	1	5	3	2
	Total species	11	16	13	6
	Average	2.7	6.2	4.2	4
	Sample	13	9	16	2
ME <i>Capra</i> only					
	Average	3.2	2.9	4.1	3.2
	Sample	14	25	13	9
CARNIVORES					
NC <i>Capra</i> only					
	>15%	6	10	7	7
	>60%	2	4	3	1
	Total species	12	13	11	11
	Average	3.5	5.5	4	3.4
	Sample	16	20	36	22
SE					
	>15%	8	8	7	7
	>60%	1	4	1	4
	Total species	8	11	11	7
	Average	2.5	4.8	3.9	5.5
	Sample	13	9	16	2
ME					
	Average	3.3	2	4.5	3.3
	Sample	14	25	13	9

These findings strongly suggest that Pleistocene *Capra* are indicative of richer resource conditions. They are found where a range of habitats and feeding opportunities are concentrated by relief to produce a diverse animal community at low altitude. The three most frequent species, excluding bear and *Capra*, are as follows (Table VI)

Table VI

The most common species (other than bear and *Capra*) in *Capra* assemblages

NC	LUP	Reindeer	Wolf
		Horse	Fox
		Red deer	Wild cat
	EUP	Reindeer	Wolf
		Horse	Fox
		Mammoth	Lion
SE	MP	Horse & Rhino	Wolf
		Reindeer	Hyena
		Mammoth	Fox
	EUP	Horse	Wolf
		Reindeer	Lion & Hyena
		Rhino & Red deer	Fox
	MP	Rhino & <i>Bos</i>	Wolf
		Red deer	Fox & Hyena
		Horse	Lion

The importance of wolf in these *Capra* collections should be noted.

But even though these samples point to a community richness there are also trends to be seen. The larger NC sample (Table V) records a dramatic reduction in the carnivores from the MP to LUP. In particular there is a reduction in the number of frequent species from 4 to 3 to 1, while in terms of diversity the reduction is only from 10 to 7 taxa per collection. The result are values for the LUP which mimic those from the non-archaeological PNT.

The small sample sizes in the other regions makes it harder to identify the patterns. However, the *Capra* faunas in the ME region produce very high values for the EUP, a point emphasised by MIRACLE (1991) in his analysis of the data.

III. DISCUSSION

The aim of this regional analysis of large mammal faunas has been to identify different community structures. This has been approached in terms of species frequency and diversity within the faunal collections which make up a regional community. We have now seen that carnivores common to these three regions, and the multifarious local habitats within them, do vary considerably. We can also see a general, but by no means universal, trend through time towards smaller, less rich herbivore communities and a reduction in

the frequency of large carnivores. It is now possible to explore the implications of a community approach to faunal regions for the interpretation of past behaviour among hominids and carnivores.

Hominids and animal communities

The aspect of community structure which would most affect hominids relates to predictability. Predictability depends primarily on factors of animal mobility and secondarily on their density and aggregation (JOCHIM 1976; AMBROSE & LORENZ 1991). These last two factors are more important when dealing with the local tactics of risk reduction by human predators. Site location, settlement duration and population size will be heavily influenced by the local arrangement of animal density and aggregation. All three factors are indicative of resource richness.

The favoured environments for hominid and carnivore occupation throughout the Upper Pleistocene were those with high animal biomass where several dietary alternatives existed due to higher species diversity. These communities would be preferred to those where biomass was dominated by one numerically abundant animal.

These communities represent 'secure' environments. These are found in areas of diverse, but not extreme topography, where ecological niches are compressed and hence biomass is high because species diversity is high. Good examples of such ecotonal settings surrounded by high risk plains environment are provided by the Crimea and the Prut/Dnestr valleys skirting the Russian plain (SOFFER 1989), the Swabian and Frankonian Albs in southern Germany (GAMBLE 1979) and the Cantabrian mountains which border the submerged continental shelf (CLARK & STRAUS 1983).

By contrast, the difficult, unpredictable, environments for hominids and carnivores were those in high, rugged topography where species diversity was low and animals scattered. The same goes for many forest conditions where animal biomass declines and which, in the case of hominids, is not compensated for by alternative cheap supplies of plant food. Technology can offset the problem but only at a considerable organizational cost.

Predators and resource richness

Similar factors of predictability affected the large carnivores during the Upper Pleistocene – bear, lion, wolf, hyena and leopard. While their strategies to reduce such risks ranged from hibernation to tree climbing, food sharing to bone digestion, omnivory to dedicated carnivory, and while the intensity of these strategies varied under environmental selection, the inter-specific competition among the guild of social hunters – wolf, lion and hyena – must be recognized as a significant indicator of community richness and predictability. The frequent presence of all three species points to precisely those environments where hominids were best adapted. Inter-predator competition was high due to resource richness. However, in more unpredictable environments inter-predator competition was lower although environmental (climatic) selection was hard.

I would suggest therefore that the faunal records collected by hominids and carnivores are essentially presenting us with a record of the 'good times' and 'favoured areas' during the climatic cycles of the Upper Pleistocene. On the evidence presented here 'poor times' and 'unfavourable areas' are rarely represented in the regional faunal record, a point which

palaeomammologists and archaeologists will want to keep in mind. Consequently, any comparative study of faunal evolution needs to assess the extent to which resource rich conditions varied over time and between regions since they provide our best samples for reconstructing faunal evolution and hominid subsistence.

The evidence from palaeontological data

I would offer as support for these conclusions about resource richness the non-archaeological, PNT data. The high equivalence of herbivore and carnivore counts in all three regions points to the fact that by comparison with the archaeological communities the carnivores which created these PNT collections were hurting. Competition was severe and environmental selection, in the form of climate, was hard enough to override the LLR differences between regions. The absence of hominids in such collections is telling. It is also the case that the frequency of bear, presumably as a result of hibernation, is highest among these PNT collections. Significantly, the exception comes from the ME region. Here it is the EUP which sees the greatest frequency of bear, interpreted by MIRACLE (1991) as evidence for increased hibernation as a result of environmental selection. It is also this period in the ME region which sees (as already noted) the one significant reversal in the number of herbivores and carnivores. During the EUP the carnivores exceed the average number of herbivores per collection (Table I), a pattern only approached elsewhere in the SE region for the same period. It must also be remembered that in both regions the EUP is the period when *Capra* is most frequently represented (Table II). As MIRACLE notes (1991:214) changes in the presence of carnivores in sites from the ME region,

"suggests the lowest intensity use by humans during the EUP, and an almost equally poor hominid showing during the MP. It is not until the LUP that humans appear to have had a significant presence in the area."

To support these conclusions further work is needed to date the PNT collections and investigate the taphonomy of cave sites from which these samples are mostly drawn.

Conclusion: faunal communities and specialist *Capra* hunters

By adopting a regional approach to the study of European palaeomammals it can be seen that during the Upper Pleistocene there were four main types of faunal communities. These can be determined by the presence of hominids and large and small carnivores. They are the result of differing resource conditions that arose from the translation of the prevailing climatic regime through LLR (the basis of the regional divisions; Fig. 1). The four communities are as follows (Table VII).

Table VII

Four communities in Upper Pleistocene Europe

	Hominids	Carnivores		Conditions
		Large	Small	
1.MP, EUP, LUP	X	X	X	Resource rich
2.PNT		X	X	
3.LUP	X		X	
4.PNT			X	Resource poor

Which communities favoured *Capra*? I would predict that if we had adequate data on species abundance as measured by bone counts, MNI or other means, we would discover that *Capra* was present in significant numbers in two types of faunal assemblage. The first (community 1) would be associated with many other frequent species particularly carnivores. EUP sites such as Bacho Kiro in the SE region (KOZŁOWSKI 1982) and Subalyuk (MOTTI 1941) in the NC region would fall into this category. Outside my study area I would expect Hortus (PILLARD 1972) with its *Capra ibex* and fragmentary Neanderthals to be an assemblage of this type. Gnawing and bone breakage will be high while anatomical representation will be dominated by heads and hooves (STINER 1991).

In terms of regional community structure these assemblages will be associated with incremental rank-frequency distributions for the herbivore taxa. These might be translated into high species diversity and high biomass. By definition such conditions would only be found in mosaic habitats at low to middle altitude.

The second type of assemblage (community 3) would find *Capra* as a truly numerically dominant species, associated with few carnivore bones and species. Herbivore diversity may also be much reduced. Carnivore gnawing and bone breakage will be absent or greatly reduced. Cut marks will be common. Anatomical representation will extend beyond head and hooves.

These assemblages are equivalent to where we find *Capra* today; in high altitude settings with broken, rugged relief. These are the settings described by STRAUS (1987) for Cantabria. Other sites would include the late glacial rock shelters in the ME region at Klithi (GAMBLE in press) and Badanj (MIRACLE in press). In the case of the latter we have already noted the geographical features (MIRACLE & STURDY 1991) which account for the low altitude appearance of *Capra* at the site. In terms of regional community structure these assemblages will be associated with primate-type distributions for the herbivore taxa. These might be translated into conditions of low diversity and low dominance as found in mountainous regions.

I would therefore conclude by agreeing with FREEMAN (1973) and STRAUS (1987) that it is not until the LUP that we see specialist *Capra* hunting. Prior to this either no suitable faunal communities existed (eg. the EUP) or the hominids of the time (ie. the MP) had not developed the necessary skills to secure a living in an unpredictable, climatically controlled environment. This is why the MP and the EUP can look so similar (Table I) although the hominids had radically different organizational capacities when it came to exploiting community richness (STRINGER & GAMBLE 1993). Finally, with this regional perspective on behaviour, a specialist hunter can now be defined as exploiting an animal community in a region where climatic stress rather than inter-predator competition for resources is the major selective pressure.

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