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Here Be Dragons - Taxonomic Bias in Upper Palaeolithic Cave Paintings

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Here Be Dragons: taxonomic bias and ecological context in Upper Palaeolithic cave art in France and northern Spain.

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Thesis Declaration

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

---------- Annie

Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw'r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o'r blaen ar gyfer unrhyw radd, ac nid yw'n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy.

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ABSTRACT

The artwork from the Upper Palaeolithic of Europe is undoubtedly of major historical value. With hundreds of Palaeolithic archaeological sites in Europe, it is an enduring testament to the history of human occupation of the continent, and provides an important perspective on the habits and challenges faced by prehistoric humans in a dramatically changing environment. Data from sites in France and northern Spain were examined to determine whether there were patterns of taxonomic bias within depictions of animals from Upper Palaeolithic artwork, when compared to wider fossil assemblages from the region. Our results highlighted significant biases towards medium and large-bodied herbivores and carnivores, irrespective of the number and quality of depictions, and significantly less focus on smaller-bodied taxa with widespread fossil records from western Europe. Many of the larger mammal species demonstrated unstable population dynamics throughout the late Pleistocene. Emphasis often seemed to be placed on the larger animals within the ecosystem, irrespective of the number of depictions in the cave and of the distance between different sites. Particular examples of unusual or unique representations coupled with respective population dynamics could suggest that the quickly-changing climate and ecological changes at population level for many species were factors which humans may have found interesting. Critical evaluation of controversial theories such as hunting magic demonstrate that attempting to assign a single theory to the production of cave art in the Upper Palaeolithic is risky, but necessary in order to assess not only human cultural development throughout the Palaeolithic, but also to understand why researchers may seek particular explanations.

KEYWORDS, ABBREVIATIONS AND DEFINITIONS:

KEYWORDS: Palaeolithic, cave paintings, Pleistocene, fauna, ecology, humans

- Anthromorph: a figure which is comprised of the features of two or more species. In the framework of European cave paintings, these are typically human-shaped figures with animal features, such as heads.
- AS = Asturias
- BP = [Years] Before Present. May be used as a singular (BP) or a conjunction (years BP). Before Present usually denotes before the year 1950, when radiocarbon dating came into widespread use.
- c. = circa.
- CB = Cantabria
- FR = France
- LGM = Last Glacial Maximum.

1. INTRODUCTION

The Upper Palaeolithic period of Europe (40,000-11,000 BP) was characterised by dynamic and sometimes rapidly changing environments, with the advancing and retreating of the Last Glacial Maximum (LGM) causing major ecological upheaval. In western Europe, one area that experienced pronounced changes was the landmass encompassing France and Spain. This area was a patchwork of changing environments, utilised in the early part of this period by both humans and Neanderthals (Jones et al. 2018). Jones et al (2018) describe the Cantabrian region of northern Spain specifically as being a 'mosaic' of environments which generated a variety of habitat types for both human species to exploit. Around 28,000 years ago (at the end of the Mousterian) the habitat shifted to more open vegetation, supported by δ13C values from large herbivores of the region, including horses and red deer. Variability observed from isotopic δ15N values within the archaeological levels could indicate either environmental change as a whole, or foraging within different micro-habitats (Jones et al. 2018). The Upper Palaeolithic was a time of rapid and variable cultural innovation and development for both human species present in Europe, marked by a distinct cultural transition after the Middle Palaeolithic (Talamo et al. 2012). Evidence from archaeological sites separates distinctive sub-periods within the Upper Palaeolithic characterised by stone and bone tools, skeletal remains, and indicators of behaviour and culture (Herrera & Garcia-Bertrand, 2018).

The Upper Palaeolithic was often divided into a series of five set periods based on these characteristics, named after the type sites and/or artifacts, as follows:

- Châtelperronian (c. 45,000 – 40,000 years BP).
- Aurignacian (c. 39,000 – 26,000 years BP). The humans of this period are sometimes considered to be the first 'truly modern' humans in Europe.
- Gravttian (c. 29,000 – 18,000 years BP). This period is known for inventions such as game hunting spears, nets, needles and layered clothing, as well as many of the 'Venus' figurines typical of the Upper Palaeolithic.
- Solutrean (c. 18,000 – 17,000 years BP). Known for ornamental innovations such as beads, and cave art.
- Magdalenian (c. 17,000 – 11,000 BP). The final period of the Upper Palaeolithic before the Holocene/Mesolithic transition around 10,000 YBP. Known for elaborate bone, ivory and antler tools, including projectiles, burins, harpoons, and spear-throwers, and for cave art.

(Herrera & Garcia-Bertrand, 2018)

It is from the Franco-Cantabrian region, during the Aurignacian to the Magdalenian period, that some of the most sophisticated and detailed examples of Palaeolithic artwork have been found, with familiar examples of painted caves such as Chauvet and Lascaux, and sculptures such as the Hohlenstein-Stadel Lion Man enjoying global as well as regional fame. Leroi-Gourhan (1968) attempted to characterise the styles of Palaeolithic art as differing between these periods:

- Style I (Primitive): Aurignacian to mid-Gravettian.
- Style II (Primitive) Mid-Gravettian to early Solutrean.
- Style III (Archaic): Early Solutrean to Early Magdalenian.
- Style IV (Classic) Middle to Late Magdalenian.

The 'dawn of art' is thought to roughly correspond to artistic developments beginning in Africa approximately 50,000 years BP, when the oldest evidence of art and personal ornamentation was first discovered, and at which point humans were anatomically modern. Similarly, 60,000-year-old 'crayons' from Australia, and a growing collection of evidence to suggest that our close relatives, Neanderthals (*Homo neanderthalensis*) were creating sophisticated artwork (Appenzeller, 1998) suggests that the origins of artwork production certainly occurred before modern humans entered Europe, and likely stretch further back in our history than we may currently have evidence for. These artists, when they migrated, carried their artwork and ideas with them, with these practises further developing wherever humans settled (Appenzeller, 1998). Complex artwork was certainly being produced on a massive, worldwide scale by 40,000 years ago. During the Upper Palaeolithic, the Last Glacial Maximum (LGM) advanced, peaked at 22,000 years BP, then retreated, bringing with it a widespread population crash and general change in lifestyle to human groups in the area (Djindjian, 2016).

It is so far unknown which factors may be responsible for the production of artwork on a wide scale in Upper Palaeolithic Europe. Some scholars have hypothesised that the seemingly sudden appearance of the ability to produce complex and symbolic artwork represents an underexplored 'step' in the brain's cognition which may have incurred an advantage to humans at the time (Appenzeller, 1998). However, no physical evidence has been discovered to support this theory, which seems largely based on simply the number of sites and artifacts found well-preserved in Europe. However, the aforementioned population and lifestyle changes may have provided a changing social environment under which the production of artwork could have proved beneficial for social cohesion – which will be explored in greater detail later on.

Upper Palaeolithic artwork is by no means constrained to Europe; cave paintings, wall engravings, and petroglyphs (sometimes collectively referred to as "rock art") are found worldwide. Examples of painting and engraving on rock faces and inside caves are known from every continent, with recurrent themes such as animals, handprints, geometric signs and anthromorphs (figures with characteristics of more than one species, typically human and animal) noticeable from all. Discoveries from Indonesia, including figurative images of

animals and hand motifs dating to 39,000 years BP and possibly older, demonstrate that sophisticated technique was globally widespread by the beginning of the Upper Palaeolithic (Aubert et al. 2014).

FIGURE 1: CAVE PAINTINGS IN ALTAMIRA

FIGURE 2: CAVE PAINTINGS IN LASCAUX. PHOTO BY AUJOULAT, N. (2003) © MCC-CNP, VIA: CLOTTES, J. & COYE, N. (N.D.).

Figure 2: Cave paintings in Lascaux. Photo by Aujoulat, N. (2003) © MCC-CNP, via: Clottes, J. & Coye, N. (N.D.).

The study of Upper Palaeolithic art in Europe dates back to the 1800s, to the discovery of Altamira (Cantabria, Spain) (Fig. 1) in 1868, and features a complex history of theory and discovery. While Altamira stirred academic and archaeological interest in cave art from the 19th century, the discovery of Lascaux (Fig. 2) in 1940 generated significant public attention, with the cave receiving around 120,000 visitors annually after its discovery (Lefèvre, 1974). By 1960, however, the paintings in Lascaux had been significantly damaged by algae, inadvertently brought into the cave by visitors and accelerated by the environmental disturbance caused by their respiration, CO2, and water vapour (Lefèvre, 1974). Soon after, in 1963, the caves were permanently closed to the public and access has been strictly limited since. Since then, and over the course of the 20th century, technological advancements including the development of mineral dating (such as carbon and uranium-thorium series) have allowed researchers to conduct detailed studies and make comparisons between artworks, creating a strong foundation for comparative studies. In recent decades, the discoveries of decorated cave sites including Cosquer (1985) and Chauvet (1994), demonstrate that the field is still yielding new discoveries. Chauvet cave, sometimes argued as being the most spectacular in recent years, some scientists and organisations have aimed to make ice age art sites more accessible to the general public with the use of new technologies, including 3-dimensional computer renderings of Lascaux (which users can explore in Virtual Reality), and a full replica of Cosquer cave in Marseilles, due to open in 2022.

Altamira and subsequent discoveries gave rise to new ideas about human development, particularly notions of what earlier and so-called 'primitive' humans were capable of creating. Particularly notable figures such as the Abbé Henri Breuil (1877-1961) laid the foundations for the study of and public interest in Pleistocene art, particularly cave paintings and engravings. Breuil popularised many ideas on the cultural basis for cave paintings, including hunting magic and religious practises, based on wider works into the origin and base of such practises, including that of Sir George James Frazer in "The Golden Bough". Frazer set out several 'laws' dictating the use of sympathetic magic, which included the Law of Similarity (in which a likeness or imitation equals a definitive state) and the Law of Contagion (that things which have been in contact with one another exchange permanent properties) (Frazer, 1890).

Following hunting magic theories (which are largely speculative), the school of processual archaeology, which argued for a less hypothetical and more evidence-based view of human archaeology, generated ideas about Palaeolithic art purely based on ecological function. Publications such as Mithen (1988) argued prehistoric art as an indication of game health and hunting strategy, with the number and appearance of the animals in the images representing critical statistics about the health of the ecosystem and its relevance for humans when hunting.

Many theories regarding Upper Palaeolithic cave art rest on the underlying assumption that a function had to have been gleaned from the production or viewing of the artwork. Part of the reasoning behind this theory is that the energy expended in the production of artwork is energy that could have been expended conducting more 'important' activities, and thus art had to have served an important function to have eaten into energy needed for survival (Halverson et al. 1987). Haverson et al. (1987) argue against this theory, stating that artistic production may have simply occurred during time which would otherwise have been used for other leisure activities, and that the idea that all activities conducted by prehistoric people must have been adaptive is a broad assumption. The creation of cave art in the Palaeolithic had to have come from somewhere, to have been preceded by former steps. Haverson et al. (1987) argue for the enhancing of already-present features in the environment as a likely precursor to representations with no underlying geological features – from engraving and incising, to body painting, embellishing natural features, and finally to representation without these supports. The correspondence of human vision (which perceives three-dimensional images) with two-dimensional representation is impressive, and requires a level of abstracted thought – cognition allows for two-dimensional artistic representations, and the two may have co-developed (ibid.). However, regardless of how the development of these techniques may have come about, the most significant observation put about by Halverson et al. (1987) is that the creation of images for modern people, and most likely prehistoric people, is enjoyable, rewarding, and constitutes play. It could be argued that it was not necessary for a group's immediate survival, and there needs to be no other reason to have painted or engraved animals other than the creator's ability and desire to produce those images. Such activity needs no meaning other than 'art for art's sake' (or, as Halverson et al. suggest, 'representation for representation's sake').

The lines drawn are simple enough to elicit recognition, but complex enough to betray senses of movement, space, and remarkable biological accuracy. Indeed, Melcher & Wade (2006) identified the coat colours of animal drawings as changing under different light sources, with flickering torchlight transforming yellow and red to orange and brown (seen in Fig. 1) – a more accurate representation of many coat colours. Flickering torchlight has also played a role in the theory that Upper Palaeolithic cave paintings could be interpreted as a prehistoric cinematic experience. This idea was expanded by Werner Herzog in the 2010 documentary *Cave of Forgotten Dreams*, about Chauvet Cave, in which a bison with eight legs gives the impression of running, and other figures appear to have been exaggerated to give the impression of movement (Abrams, 2021).

Wade & Melcher (2006) also highlight interesting techniques among the art of El Castillo and Altamira, including the use of 'twisted perception' (combining an animal's body in profile to a frontal view of the face). They suggest that the use of twisted perception in particular may have been an efficient way of portraying the identifiable features of an animal, including both body profile and head, antler or horn shape, as opposed to other suggested theories (including Breuil) labelling this technique as primitive. It is also suggested that the prehistoric artists were exploring depth in artwork, as evidenced by the Lascaux 'falling horse', which wraps around a rock, and the red cows at Tito Bustillo, which only appear proportional from certain angles (ibid.). The successful implementation of perspective and movement in these images is a testament to the artistic abilities of Upper Palaeolithic people, but the difficulty arises with both of the above theories due to the perception of art being unique to the observer. As stated by Wade & Melcher (2006), it is difficult to test hypotheses which rely at least somewhat on the observations of cave visitors thousands of years later, and there is no accompanying written record.

Possibly the most common recognisable figurative works of Upper Palaeolithic artwork worldwide are those of animals. Images of humans, despite the artists' undeniable talent for capturing form and accuracy, are uncommon, although composite creatures or anthromorphs are also represented.

In many places, Palaeolithic art can be used as a visual record of prehistoric and now-extinct species, providing a unique insight into the appearance and sometimes behaviour of prehistoric species. One of the best-recorded examples is that of the Irish Elk (*Megaloceros*), with depictions from sites such as Cougnac (France) recording possible coat colours and a shoulder hump supporting the large antlers (Monaghan, 2019). Another example is the cave lion (*Panthera spelaea*), determined to likely lack the conspicuous mane of its African cousins by studying cave depictions (Packer & Clottes, 2000). The accuracy of animal depictions in caves can be determined to a degree by comparing them to extant species; as such, species such as the red deer, horse, chamois and

bears are typically well-rendered and recognisable, tentatively suggesting that the same can be said of extinct species. With this in mind, species such as woolly mammoths (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*) and cave lion are recognisable, creating implications for our understanding of the surrounding ecology, such as species mix, habitat types, and prey-predator relationships. This information, rather innocently immortalised on the walls of caves and carved into ivory and bone, adds significantly more to the reconstruction of the European Pleistocene than could be gleaned from skeletal remains alone. The overall style of Palaeolithic art changed less in 40,000 years across large geographical areas (Melcher & Wade, 2006) than would perhaps be expected, to the ultimate end that observers today are able to see and study, without explanation, the same artwork that ancestors several millennia ago were able to see and understand.

The biological accuracy inherent in ice age art provides a unique insight into an early form of biological recording through a human lens, including what was relevant to humans during this pivotal period in human development. Regardless of whether the depictions had a metaphysical, ecological, or purely recreational motivation behind their creation, it can be widely seen that people were depicting animals which were seen in the environment around them. A factor which is particularly interesting is that a first impression grants the viewer a glimpse into the way people saw Pleistocene megafauna: mammoths, deer, bison, lions, bears. However, Pleistocene Europe was a complex web of different environments, and ecosystems are built from the bottom up: there seems to be a wide gap in the representation of most other classes of animal. There are few birds and fish, very few smaller mammals, and almost no representations of small vertebrates (such as rodents, reptiles, and amphibians) or invertebrates. It could be that the species which were drawn on cave walls may have had an inherent importance in some way, a selection criteria such as edibility or danger. The difference between what is depicted and what is overlooked provides the basis for this study.

As detailed in this section, the history of cave art is extensive, and the geographical extent of prehistoric art is global. Therefore, it is necessary both to outline specific hypotheses for analysis, and also to define a coherent study area (see section 1.1).

1.1 STUDY AREA AND AIMS

A map of the study area with examined sites marked is presented below (Fig. 3). The Franco-Cantabrian Upper Palaeolithic is particularly rich in cave art, with these sites unique in displaying not only numerous images and diverse taxa, but also in being situated extremely close to one another. Additionally, the fossil record for this region is extensive and well-studied, providing a firm foundation for comparing the sites to the wider fossil record. The 'sites' explored in this study are caves which contain paintings and/or engravings – wall art, which has been scribed onto a surface, for purposes of consistency. Sites which include only portable artwork or other artifacts are not included. For further project development, it would be interesting to compare sites with different artistic uses to see whether the faunal assemblage differs.

This region features a number of known refuge areas utilised by human hunter-gatherer groups during the colder conditions of the LGM. During these conditions, which were cold and relatively dry, human groups in Europe were driven south, into a system of low mobility and smaller territory sizes, and forcing them to modify their hunting and tool producing strategies accordingly (Djindjian, 2016). These strategies were modified from migratory herd hunting (of bison, mammoths, and reindeer) to gregarious mammal hunting (horses, deer, aurochs, and wild boar), the latter being significantly less stable (ibid). Before the LGM, the territories of these same people were large (10-100,000km ^{2}) and there was high mobility and the ability to travel between areas, with mobile hunting camps and trade between other groups (ibid.). However, the population crash after the LGM forced these groups to change to a Local Opportunistic Strategy lifestyle, characterised by low mobility, opportunistic hunting, and limited contact between other human groups (ibid). This was also accompanied by vegetation changes, with an increase in tundra and a decrease in steppe habitat, further reducing migratory prey numbers (ibid.). Djindjian (2016) suggests that cave art is a product of the former high mobility, abundant mode of living, seen in Europe prior to adverse conditions forcing human groups south. This links with the experimental approach to population size conducted by Derex et al. (2013), whose evidence suggests that population demographics and cultural complexity are closely linked. A large population size may be a prerequisite for cultural innovation, with larger populations found to have longer-lasting and improved cultural

knowledge (ibid.). This may partially explain the high number of sites demonstrating Magdalenian artwork within the study area, as the population recovered after the LGM population crash and increased contact between groups. The vegetation and conditions seen at the time is represented in a simplified format in Figure 1, which demonstrates vegetation types, elevated land and mountain ranges, glaciers, and study sites used in this thesis.

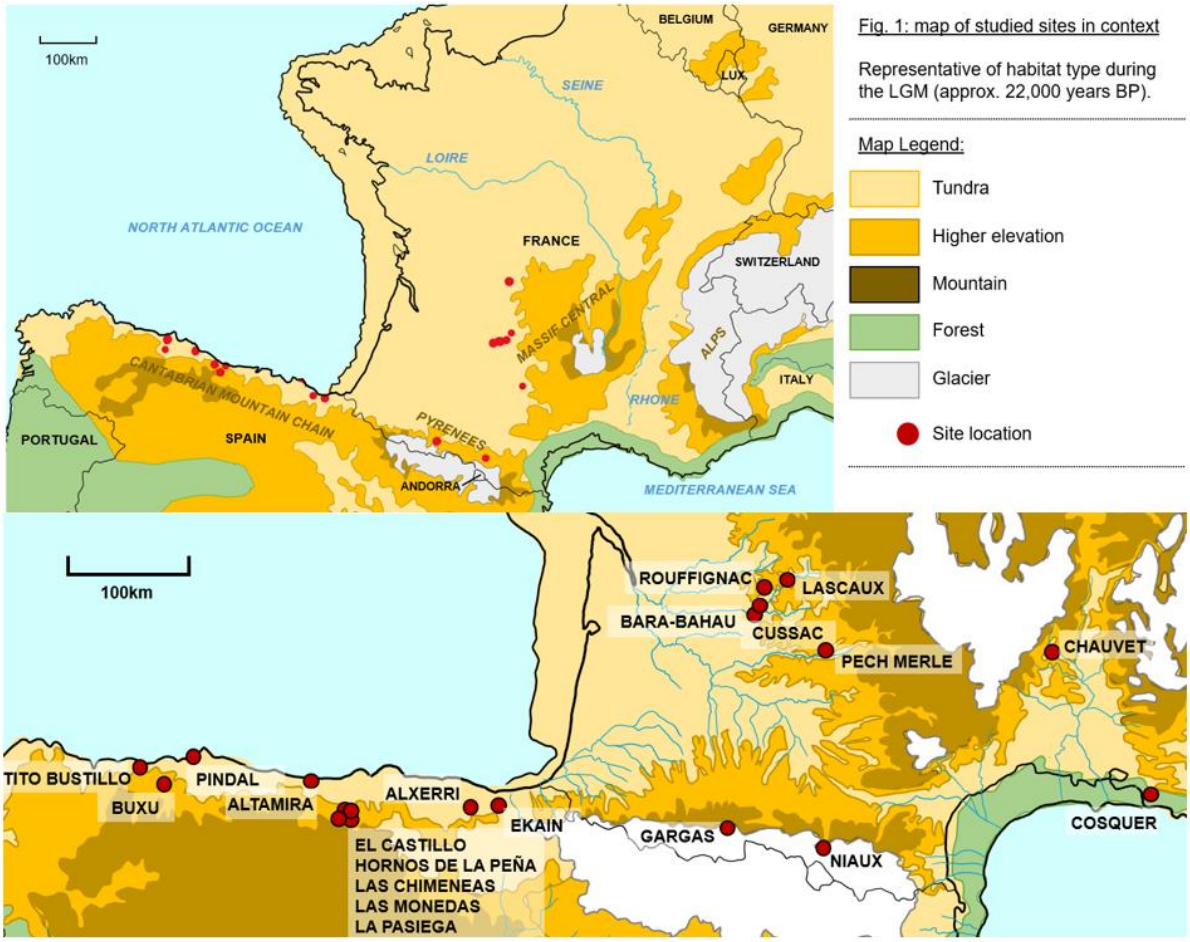

FIGURE 3: MAP OF STUDIED SITES IN CONTEXT, DEMONSTRATING HABITAT TYPES DURING THE LGM AS WELL AS MODERN AND PREHISTORIC COASTLINES. THE TOPOGRAPHY HAS REMAINED LARGELY THE SAME, WITH ADDITIONAL GLACIERS IN ELEVATED AREAS.

During the Pleistocene and associated glacials (including the LGM), the sea level fell up to 150 metres (492 feet) (Wilson & Veraguth, 2010).

Study sites for this work were selected on the basis of inventory data stating the number and species of animals depicted in each individual cave being available. The importance of this factor was imperative in both selection of study sites and also analysis of results; accurate inventory data was needed in order to build a comprehensive scope of the taxa represented at each site. Such data was not always easy to acquire, and for some sites species lists and inventories were not up-to-date. Using the available data, 30 well-represented caves containing paintings/engravings were analysed. In order to counteract a lack of comprehensive data for the whole Palaeolithic Franco-Cantabrian region, the 30 sites displayed on this map were used in direct data analysis, but further discussion of depictions from other sites were also included during the analysis and discussion. These sites are representative of a large portion of the Upper Palaeolithic, from over 30,000 BP to approximately 13,000 BP. This provides not only an insight into Pleistocene artwork as a whole, but also allows for direct comparison to floral and faunal populations at a given time, known from the fossil record.

The primary aim of the study was to evaluate whether there was evidence of taxonomic bias towards certain animal groups in European Palaeolithic art, and examine whether these trends reflect wider cultural

developments and attitudes towards animals. Europe has a well-preserved Pleistocene fossil record, as well as several hundred archaeological sites featuring Palaeolithic artwork, providing a comprehensive basis for a comparative study of presence and absence in Upper Palaeolithic art. Two hypotheses for further investigation were formed based on the possible outcomes of the results:

- H1: Distinct taxonomic bias is demonstrated in European Palaeolithic art towards certain animal groups.

This hypothesis rests on the assumption that the animals depicted in artwork from these sites had been selected specifically from the fauna that Palaeolithic humans encountered. Should this hypothesis hold true, it suggests that there were certain criteria that people were using in order to select which animals to depict.

- H0: No distinct taxonomic bias is demonstrated in European Palaeolithic artwork, and animal depictions were depicted without bias towards certain taxa.

If true, this hypothesis suggests that any apparent taxonomic bias is likely due to differing faunal communities in different areas (e.g. there were no wolves because wolves were not present, rather than being deliberately eliminated from depiction). This would suggest that a broader interest in depicting the natural world and surrounding or familiar sights may be responsible, with the focus for analysis then shifting to the cultural reasons surrounding the nature of artwork.

These hypotheses overlap to a degree; both require some analysis of the way that artwork reflects wider culture, and analysing the way that animal depictions are placed and represented. In the analysis of the results, consideration will be given to wider themes, such as the role of anthromorph depictions, as well as examining whether H1 or H0 can be definitively proven.

Analysis of results will primarily focus on whether certain patterns can be identified within the studied area of artwork, alongside whether these patterns are also reflected in species present in the fossil record. Direct comparison of population dynamics (where known) and information regarding changing climate and ecology will be the primary focus of this analysis, although an overview of theories regarding the creation and social context behind the production of cave paintings will also be included. Many of the following figures have been illustrated by me, with the intention of highlighting themes and features in a bold and simplistic manner.

2. MATERIALS AND METHODS

The primary aim of the study was comparing the species diversity found in animal depictions with the fossil record and wider fauna of late Pleistocene Europe. This comparison was designed to highlight areas of taxonomic bias or elimination present in Palaeolithic art, using systematic and multivariate analyses of data from 30 sites located in France and Spain. Depictions of animals in the caves were isolated and organised. The sites were chosen for their accessibility in online literature; fieldwork was unfortunately not possible owing to the timing of the project with the COVID-19 pandemic.

The first step taken was organising the data and which parameters to use. The cave site data was organised in a species-number table, plotting the cave site against a simplified species metric. The species metric was simplified in the interests of generating functional data and eliminating as much uncertainty as possible regarding species identification; e.g. the more generalised term “Caprinae” was used to encompass depictions described as ibex, chamois, and goats, all of which are classified in this family. Since literature regarding some species designations has not been standardised, it is sometimes difficult to ascertain which species is being discussed. Misidentification on the part of the authors of consulted literature, or the author of this paper, had the potential to skew more species-specific data, resulting in the potential for misleading conclusions. Because there were differing taxonomic groups within the table, the taxa were also organised by ecological guild in order to assess body plans and community patterns. Using Simberloff & Dayan’s (1991) definition of a guild as “a guild is defined as a group of species that exploit the same class of environmental resources in a similar way” species depicted in prehistoric caves were organised by their basic ecological role: small, medium and large-bodied herbivores, small, medium and large-bodied carnivores, avifauna, microfauna, herpetofauna and fish. This could

then be compared to papers and data regarding hunted game types. Average weight range of species groups and size categories of species are shown in Table 2. Weight-based criteria provides a baseline for dividing species into 'small' (<20kg herbivores, <15kg carnivores), 'medium' (20-500kg herbivores, 15-100kg carnivores), and 'large' categories (>1000kg herbivores, >100kg carnivores), based on average weight range of adult individuals. Extinct species weight is approximation, and some overlaps occur; e.g. overlap between adult weights of lynx and leopard.

For the cave painting data for the caves of Asturias and Cantabria, data primarily came from Echegaray & Sáinz (1994), while for France, the data sources were significantly more variable. French data was sourced from: Art préhistorique – Représentations (Hominidés, accessed Feb 2021), Barrière (1976), Cosquer Cave (Bradshaw Foundation, accessed Feb 2021), Chauvière & Kaeser (2020), Clottes (2010), Clottes (1996), Curtis (2006), Delluc & Delluc (1997), Feruglio et al. (2020), Grotte de Pech Merle (Hominidés, accessed Feb 2021), Mélard (2008) and Plassard & Plassard (2000).

Two sets of values were obtained for statistical testing. The first set investigated whether there was a correlation between the geographic closeness of the caves and the percentage similarity of the depictions between them, and the second investigating correlation between the number of depictions in each cave and the diversity of species represented.

The distance between caves was measured in Kilometres using the 'measure distance' function in Google maps, in a straight line 'as the crow flies'. The objective was to assess geographical proximity (as opposed to assessing routes between caves) under the aim of investigating whether groups of people using the same geographical areas could have been sharing ideas or common themes. Percentage similarity was assessed by comparing shared taxa between each pair of caves. From the caves studied, three distinct geographically-close 'groups' of 4 were highlighted, e.g. groups of caves within. This was conducted using a sample size of 12 caves, in which the furthest distance between two caves in a 'group' was 71km (between La Lluera and Tito Bustillo). Caves were lettered A-L, then the distance between two selected caves was measured and the percentage similarity between the two caves was calculated. The close groups were also compared to each other in this analysis. This was done using shared taxa as a proportion of the set of depictions between two sites. sets of comparative data were assumed to be normally-distributed, so a Pearson's correlation was chosen to calculate the significance – additionally, identifying the strength of the correlation between the two factors was the aim, so a simple and clear result could be obtained.

TABLE 1: GROUPINGS OF SPECIES REPRESENTED IN PALAEOLITHIC ART

Trophic category	Species included
Large Carnivores	Bears, Large felines (lions, panthers), Large canines (wolves, dogs)
Small Carnivores	Foxes, Mustelids, Small felines (lynx, wildcat)
Large Herbivores	Bovids, Mammoths, Rhinoceros
Medium Herbivores	Caprines, Cervids, Reindeer, Horse, Antelope, Boar
Small Herbivores	Lagomorphs
Micromammals	Bats, Rodents
Avifauna	Birds (all species)
Herpetofauna	Reptiles, Amphibians
Fish	Fish (all species)
Marine Mammals	Whales, Dolphins, Pinnipeds

TABLE 2: WEIGHT CATEGORIES OF DEPICTED AND FOSSIL FAUNA

Average weight range							
0-10kg	10-20kg	20-50kg	50-100kg	100-300kg	300-500kg	500-1000kg	1000+kg
Avifauna		Caprine (Ibex, Chamois)			Horse	Bison	
Mustelidae (Stoat, Weasel, Badger)		Antelope, Boar				Aurochs/Bovids	Mammoth
Microfauna	Canidae (Fox)	Canidae (Wolf, Dog)				Megaloceros	Rhinoceros
Small Felidae (Wildcat, Lynx)			Hyena		Marine Mammals (Cetaceans, Pinnipeds)		
Lagomorph		Deer (Red, Fallow, Reindeer)					
		Larger Felidae (Lion, Leopard),					
			Bear (Brown bear, Cave bear)				

Small Herbivores	Medium Herbivores	Large Herbivores
0-20kg	20-500kg	500-1000+kg

Small Carnivores	Medium Carnivores	Large Carnivores
0-15kg	15-100kg	100+kg

2.2 EVALUATION OF METHODS

The cave depictions and fossil record data were translated into trophic categories. Some fossils are identifiable only to genus or family level (e.g. bovid, genus *Bos*), while others are recognisable to species level (e.g. micro-mammalian fauna described by Cuenca-Bescós et al., 2009). Standardising both cave depictions and fossil deposits into wider, ecological guild categories allows a simple yet effective comparative method, highlighting both present and absent taxa from the artwork within the study area. This also accounts for potential inaccuracies in assigning species-specific identification to depictions, while still maintaining the flexibility to describe the characteristics of specific species.

Because the aim of the study was to identify taxonomic biases, only animal depictions were selected for use: this excluded anthropomorphs and composite depictions, humans, handprints, and geometric signs. In the interests of consistency, largely indeterminate or unidentifiable depictions were also eliminated.

A list of species found in late Pleistocene fossil deposits in northern Spain and southern France (within the boundaries of the study area) was compiled using data from archaeological sites containing fossils (Lloveras et al. (2020), Philippe & Fosse (2003), Fontana et al. (2006), Foucher et al. (2016), Cuenca-Bescós et al. (2009), López-García et al. (2011), Rufà et al. (2017)) and more general faunal trends in the Pleistocene without anthropogenic factors (Pinto-Llona et al. (2012), Sommer & Benecke (2004, 2005, 2006), Sommer & Nadachowski (2006)). Holocene species were eliminated from the list, as these species appeared or spread through Europe after the cave paintings were made. The list was organised into a table in conjunction with species depicted in the Upper Palaeolithic sites. Each cave in the study is representative of the Upper Palaeolithic period, from between 35,000 BP and 11,000 BP, which corresponds to the latter part of the late Pleistocene until the early Holocene boundary. The caves are organised into date order from oldest to newest in the bar charts.

This presents another issue of bias in the archaeological sites; human-processed remains of small animals such as birds (Rufà et al. 2017) likely provides a restricted view of the fauna of the area. Selection of certain species for resources creates a bias of abundance in certain species in certain archaeological areas. Owing to the nature of caves as an excellent source of preservation, species which are present due to anthropological activity around these sites are more likely to be preserved, narrowing the potential for a fully objective view of the Pleistocene fauna of a given area if only these sites are available or used.
However, information about species at the population level is also available without major anthropogenic involvement, such as Sommer & Benecke's population mapping of felids, canids and mustelids from Pleistocene Europe – these are considered to provide a less subjective view of population trends for certain groups of mammals. Considering the overlaps between the species mentioned in the archaeological assemblages vs the wider populations, it is very likely that some species have been omitted from species lists on the grounds of either lack of fossils, or lack of human exploitation. It is difficult to assess the differences between what was exploited by humans and what was present in the environment at the time, although these biases still provide an interesting platform from which patterns of exploitation vs. depiction in artwork can be observed.

When studying cave paintings, our knowledge of the subject may always be considered incomplete (Bégouën & Clottes, 1987), and thus the current dataset could always be considered 'partial'. The limitations of preserved caves mean that the numbers and percentages suggested in this study should be considered conservative estimates, and that new information is always being discovered, enriching that which is already known. This includes the discovery of new depictions inside already-studied areas, such as those mentioned in Man-Estier et al. (2015) from Les Combarelles I. As mentioned in the Introduction, the Upper Palaeolithic is split into sub-divisions, each of which Leroi-Gourhan characterised as having its own distinctive style. While this methodology is not foolproof by any means, it would be interesting to be able to compare the predominance of species with respect to these styles and subdivisions. Due to the relatively simple methods used, it would be straightforward to update and expand these models with new information in future studies.

3. RESULTS

3.1: TAXA DEPICTED IN PALAEOLITHIC CAVES

There appears to be distinctive regional variation in depicted species. Figures 2-4 show the taxonomic breakdowns of each cave, organised by geographic region. In total, the 31 cave sites examined included a total of 2994 depictions of at least 21 different taxa. Animal depictions were dominated in both Spanish cave art sites by bovids; 18% in Asturias (AS) (Fig. 5), and 27.2% in Cantabria (CB) (Fig. 6). In France (FR) (Fig. 6), there were additionally higher percentages of mammoths (14.8%) and rhinoceros (3.8%). France had more large herbivores as a whole (39.5%) than both Spanish sites (AS-21.4% and CB-28%), but fewer medium herbivores (FR-53.6% to AS-77% and CB-70%).

The medium herbivores at the Spanish sites were comprised almost exclusively of deer, horses and caprines, with one of these three taxa dominant in 17 of the 20 sites. Out of these medium herbivores, most numerous taxon in both Spanish sites were deer (AS-37.8% and CB-30.8%) followed by horses (AS-21.5% and CB-25.9%), whereas in France the most frequent depictions were of horses (37.2%) followed by mammoths (14.9%) and bison (13.8%). The percentage of deer in the French cave sites was 8.3%. France had comparatively more variation in the most-depicted species, with horses predominant in 5 sites, bovids in 3, mammoths in 2 and rhinoceros in 1 of a total of 11 sites.

With regards to other taxa, France also demonstrated a higher proportion of carnivore depictions (FR-4.8%, compared to AS-0% and CB-0.8%), and slightly higher numbers of bird depictions (FR-0.6% to AS-0% and CB-0.2%). The taxonomic variation was greater overall in French cave depictions, as well as demonstrating differing proportions of dominant taxa in each cave.

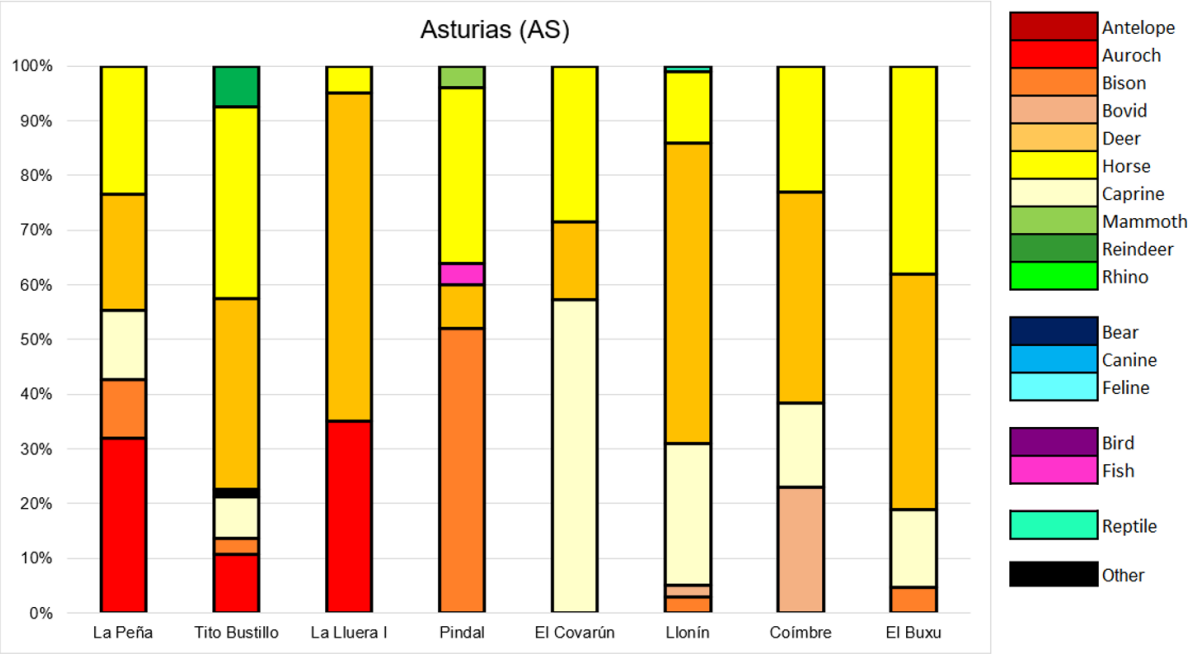

FIGURE 4: TAXONOMIC BREAKDOWN OF SPECIES DEPICTED IN DECORATED CAVES FROM ASTURIAS, NORTHERN SPAIN

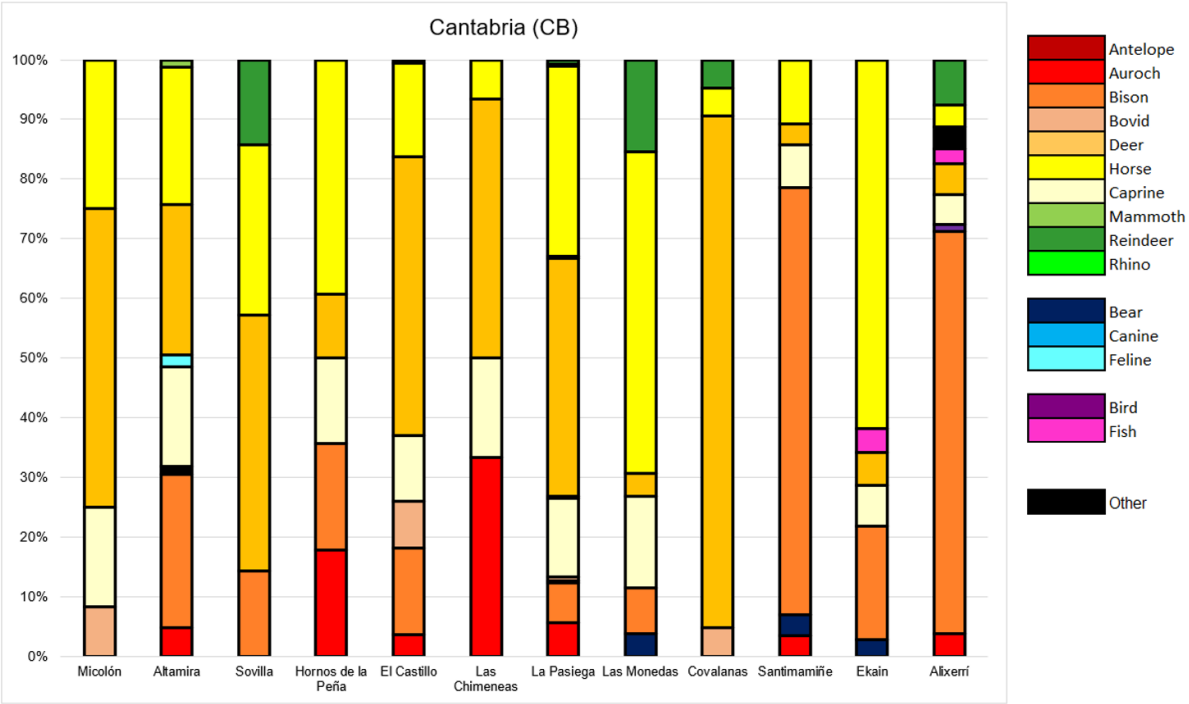

FIGURE 5: TAXONOMIC BREAKDOWN OF SPECIES DEPICTED IN DECORATED CAVES FROM CANTABRIA, NORTHERN SPAIN

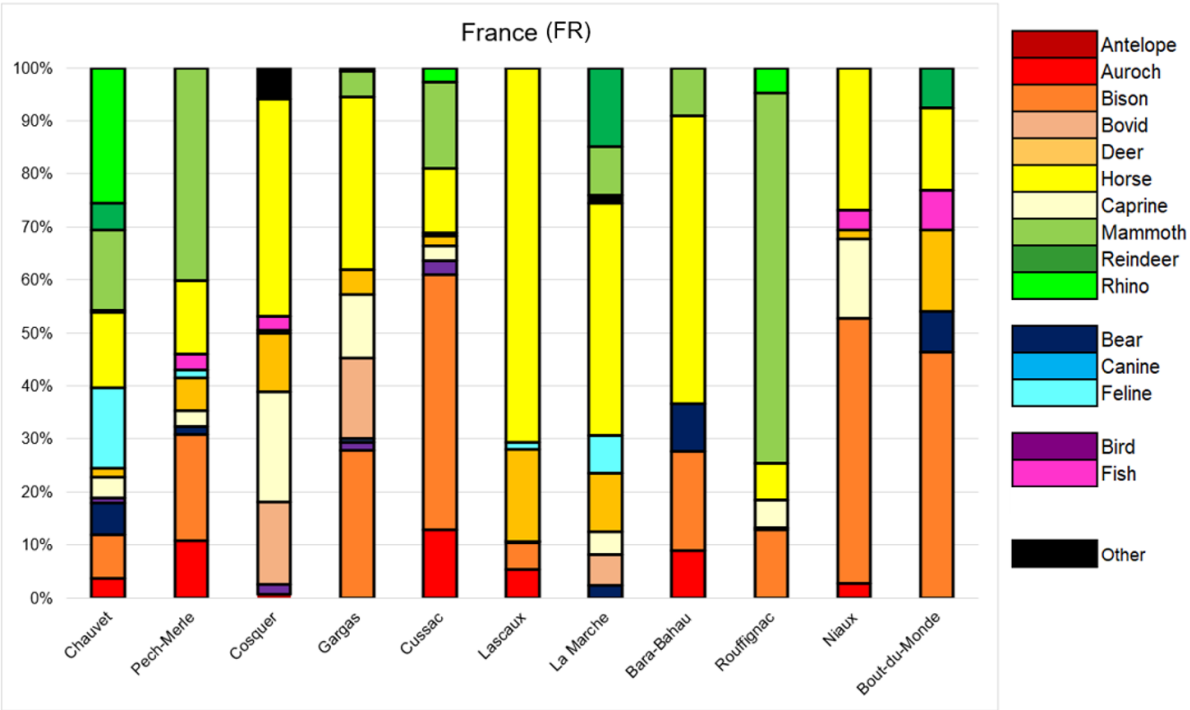

FIGURE 6: TAXONOMIC BREAKDOWN OF SPECIES DEPICTED IN DECORATED CAVES FROM SOUTHERN FRANCE.

Overall, medium herbivores were most commonly-depicted (59% of all studied depictions, Table 3), followed by large herbivores (33%); carnivores total 3% of all depictions, followed by fish (0.5%), birds (0.4%) marine mammals (0.3%), herpetofauna (0.03%) and small herbivores (0.03%).

A visual representation of the proportion of species present at different sites means that different sites can be examined and compared. The presence of Rouffignac greatly increases the proportion of mammoths in the results, although it would not rearrange the order of percentage representation outlined above. There is a relatively similar mix of species in both areas of northern Spain,

TABLE 3: PERCENTAGE OF SPECIES GROUPS IN ALL DECORATED CAVES

	Large Herbivore	Medium Herbivore	Small Herbivore	Large Carnivore	Avifauna	Herpeto-fauna	Fish	Marine Mammal
Asturias	21.4	77				0.3	0.3	0.3
Cantabria	28	70		0.8	0.2		0.6	
France	39.5	53.6	0.1	4.8	0.6		0.6	0.4
Total	33	59.3	0.03	3	0.4	0.03	0.5	0.3

The relationship between the number of species depicted in a site and the number of individual depictions returned a weak positive correlation (0.67, Table 4). This suggests that the greater the number of individual depictions present at a site, the more species are likely to be represented there.

There was no correlation between the geographical proximities of caves to one another and their similarity, which suggests that ideas regarding taxonomic bias were not being shared within small groups or individual sub-cultures, but were consistent across all locations. Correlation coefficient testing to ascertain whether proximity of cave impacted the similarity of the species mix depicted returned a result of -0.27 (Table 4), with a p-value of .536236 at $p<.05$. This indicated no significance between the geographic proximity of caves to one another and their similarity in species depictions. Within the 3 groups, pairwise similarity values varied between 71% (caves GH) and 4% (caves JL). Cave G (El Castillo) and H (La Pasiega) were the most similar, at 0.2km apart, while cave J (Bara-Bahau) and L (Lascaux) were least similar, 24.1km apart, sharing only two common taxa (bovids and horses). Six pairs of caves scored over 50% in similarity: La Lluera and Buxu (50%, 67km apart), Tito Bustillo and Hornos de la Peña (52%, 87km apart), La Pasiega and Lascaux (53%, 454km apart), Pindal and Hornos de la Peña (57%, 43km apart), Buxu and Hornos de la Peña (61%, 87km apart), and El Castillo and La Pasiega (71%, 0.2km apart). The key for similarity seemed to pivot on a number of shared common taxa, including aurochs, bison, caprids, deer and horses, which were the only taxa represented by Hornos de la Peña, explaining its larger similarity scores with multiple other caves. However, the lack of correlation overall did indicate that there did not appear to be any distinctive 'subcultures' across multiple caves where only specific taxa were drawn. The only exception was La Pasiega and El Castillo, which were extremely close to one another and shared a large pairwise similarity score.

This correlation was important in identifying the extent of geographically-close information exchange, which may have led to shared cultural significance of certain species. Overall, this result indicates that closely-associated caves were not demonstrating much skew towards one particular species (a potential indicator of special significance which could then be investigated further), but that all caves were drawing similar fauna across the whole study area, dependent on which species were present in the wider environment.

The second correlation coefficient for the study area (between number of depictions and diversity of species) returned a result of 0.67 (with a p-value of .009907 at $p<.05$) which was significant, indicating that there was a weak positive correlation between the number of depictions in a cave and the number of species depicted. It was hypothesised that in caves with lots of artwork, a greater number of species would be found. This is assumed (an area with only three images can convey a maximum of three species, whereas a site with ten images can convey a maximum of ten) but prompts the question that in sites with several hundred images, such as Chauvet, why there was not a significantly greater variety of taxa depicted. The argument behind this hypothesis was founded in the assumption that creating artwork (painted, engraved, or sculpted) takes time both to master and to create. A simplified hypothesis could be put forward that the time and energy expenditure taken to produce such artwork generates a need to depict things which were of the greatest relative importance; thus the more depictions present at a site, the more time and energy was taken there to

produce them. While an artist (or group of artists) with less time with which to make artwork may only depict what is of the greatest importance, those with more time on their hands may depict both “highly important” and “less important” images. The second reason for higher diversity could be the length of time the cave was used for; if groups of people were using cave sites over a long period of time, such as several tens of millennia, then not only could there be a cultural shift in “importance” (reflecting the cultures of human groups at the time), but the faunal composition itself could have changed.

TABLE 4: CORRELATION COEFFICIENT RESULTS.

Correlation coefficient		
1	location against % similarity	-0.27
2	# depictions against # species	0.6

Table 5 looks specifically at animals which can be identified to species level, including fossil data from the study areas throughout the Upper Palaeolithic. Compared to other figures, the species seen in the wider fossil record demonstrate higher diversity, representing a more comprehensive view of vertebrate faunas within the ecosystem. The Palaeolithic representations seem to indicate a heavy bias towards larger-bodied animals, specifically prominent species including the largest vertebrates present in the environment, and their predators, with the apparent exclusion of wolves. Smaller predatory species including foxes and wildcats, although present, do not appear to have been depicted, and micro-mammals (such as rodents and bats) do not appear to have been represented either, despite having a large presence in Late Pleistocene fossil mammalian fauna.

TABLE 5: SPECIES REPRESENTED FROM FOSSILS IN SOUTH-WESTERN FRANCE AND NORTHERN SPAIN, ALONGSIDE REPRESENTATIONS IN CAVE ART

Trophic category	Fossils from late Pleistocene deposits		Present in study area artwork
Large Carnivores	Brown bear	*Ursus arctos*	✓
	Cave bear	*Ursus spelaeus*	✓
	Hyena	*Crocuta crocuta (spelaea)*	✓
	Leopard	*Panthera pardus*	✓
	Wolf	*Canis lupus*	✓
Small Carnivores	Arctic fox	*Vulpes lagopus*	
	Badger	*Meles meles*	
	Red fox	*Vulpes vulpes*	
	Marten	*Martes sp.*	
	Wildcat	*Felis sp.*	
Large Herbivores	Aurochs	*Bos primigenius*	✓
	Bison	*Bison sp.*	✓
	Bovid (unspecified)	Bovidae	✓
	Woolly Rhinoceros	*Coelodonta antiquitatis*	✓
	Mammoth	*Mammuthus primigenius*	✓
Medium Herbivores	Boar	*Sus scrofa*	✓
	Chamois	*Rupicapra rupicapra*	✓
	Giant deer	*Megaloceros sp.*	✓
	Horse	*Equus caballus*	✓
	Ibex	*Capra ibex*	✓
	Red deer	*Cervus elaphus*	✓
	Reindeer	*Rangifer tarandus*	✓
	Roe deer	*Capreolus capreolus*	✓
Small Herbivores	Lagomorpha	*indet.*	✓
Micromammals	Bat	*Chiroptera*	
	Desman	*Galemys pyrenaicus*	
	Garden dormouse	*Eliomys quercinus*	
	Red squirrel	*Sciurus vulgaris*	
	Mole	*Talpa europaea*	
	Rodent	*Pliomys lenki*	
	Shrews	*Sorex sp.*	
	Shrews	*Crocidura sp.*	
	Shrews	*Neomys sp.*	
	Voles	*Microtus sp.*	
	Water vole	*Arvicola sp.*	
	Wood mice	*Apodemus sp.*	

Trophic category	Fossils from late Pleistocene deposits		Present in study area artwork
Avifauna	Ducks	*Anser sp.*	
	Geese	*Branta sp.*	
	Diving duck	*Aythya sp.*	
	Golden eagle	*Aquila chrysaetos*	
	Northern goshawk	*Accipiter gentilis*	
	Falcons	*Falco sp.*	
	Buzzard	*Buteo sp.*	
	Partridge	*Alectoris sp.*	
	Partridge	*Perdix perdix*	
	Common quail	*Coturnix coturnix*	
	Partridge	*Perdicinae*	
	Ptarmigans	*Lagopus sp.*	
	Grebe	*Podiceps sp.*	
	Water rail	*Rallus aquaticus*	
	Spotted crake	*Porzana porzana*	
	Common crane	*Grus grus*	
	Great bustard	*Otis tarda*	
	Little bustard	*Tetrax tetrax*	
	Stone curlew	*Burhinus oedicnemus*	
	Wader	*Tringa sp.*	
	Landfowl	*Gallinago sp.*	
	Gull	*Larus sp.*	
	Pigeons	*Columba sp.*	
	Tawny owl	*Strix aluco*	indeterminate sp.
	Eagle owl	*Bubo bubo*	
	Little owl	*Athene noctua*	
	Scops owl	*Otus scops*	
	Barn owl	*cf. Tyto alba*	
	Chough	*Pyrrhocorax sp.*	
	Crows	*Corvus sp.*	
	Magpie	*Pica pica*	
	Jay	*Garrulus glandarius*	
	Mistle thrush	*Turdus viscivorus*	
	Passeriformes		

The fossil data (representing approximately 70 species of vertebrate) is most likely not representative of the whole vertebrate fauna of the area, owing to the exclusion of groups such as freshwater and marine species, some of which are represented in Palaeolithic artwork but not here. Additionally, the presence of some species from archaeological sites may have overstated their abundance. The diversity of species present in cave art is not high overall, but appears to be fairly representative of the large vertebrate fauna, in particular those which would likely have direct relevance for human beings, in primarily terrestrial environments. Large vertebrate fauna also has the benefit of more resilience during fossilisation due to size.

3.2 PATTERNS OF BIAS IN PALAEOLITHIC ART

In order to further assess whether cave painting depictions accurately reflected the fauna present in the area, it is necessary to examine the ecological context of the areas throughout this period. During the Late Pleistocene and Upper Palaeolithic, human populations were as susceptible as animal populations to the elements and changing climate. The environment of middle and southern Europe during the Palaeolithic was a dynamic and changing landscape dominated in places by areas of mammoth steppe – an unusually rich tundra environment supporting a large mammalian diversity (Bocherens, 2003). This steppe environment completely covered the study sites. The rich fossil record of the mammal populations within this environment allows a picture to be assembled of the specifics of the habitat: low-nutrient grazers such as horses and woolly rhinoceros, alongside bovine grazers (e.g. bison and aurochs) which require additional short grass and leaves as a dietary supplement (Bocherens, 2003). Differing isotopic compositions of herbivore bones found in this environment signify the probability that mammoth steppe was a complex 'mosaic' environment (Bocherens, 2003), able to support a range of different species. This also made it a fertile hunting ground for humans.

Soubrier et al. (2016) compared bison ecotypes found in cave paintings such as Lascaux (Fig. 7) to mtDNA and nuclear DNA of various Palaeolithic specimens in order to separate them out into steppe bison-like and wisent-like ecomorphs, concluding that the modern-day wisent (*Bison bonasus*) could be the result of interbreeding between ecotypes. They conclude that both *Bison* and *Bos* should be ascribed to the genus *Bos*. This hybrid origin is further reiterated by Flannery (2018) who states that the current European wisent is a stable hybrid between the aurochs (*Bos primigenius*) and steppe bison (*B. priscus*), arising 150,000 years ago. Soubrier et al. (2016) observe that bison and aurochs constitute roughly 21% of known cave depictions, with drawings demonstrating two distinct ecomorphs: a long-horned, robust form similar to steppe bison, and a short-horned, proportional wisent-like form. The steppe-bison-like morph dominates in art predating the LGM, while the wisent-like morph is more populous in more recent cave paintings (Soubrier et al. 2016). The alternation of these forms recorded in cave art can give possible insights into the adaptations of the two bison types to different environments.

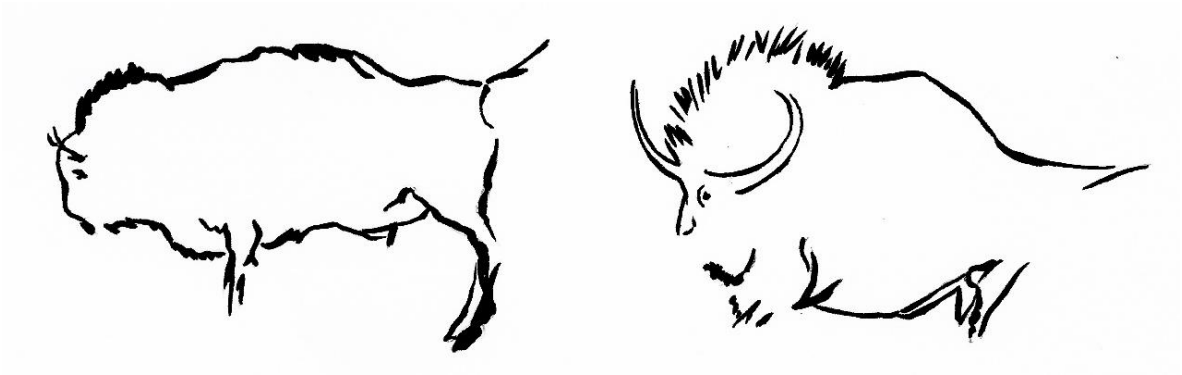

FIGURE 7: BISON ECOTYPES; WISENT-LIKE ON THE LEFT, STEPPE-LIKE ON THE RIGHT. ADAPTED FROM SOUBRIER ET AL. (2016).

This reliance on stable prey populations is a potential reason for the consistent occupation of Cantabrian Spain throughout the Upper Palaeolithic; the area was considered a genetic refuge for species including humans, red deer, and salmon, and often labelled a 'cultural hub' (Jones et al. 2020). The adaptability of these particular species to different environments, such as those dominated by temperate forests (favoured by humans as refugia) as well as tundra and steppe, is likely to have contributed to their success (Jones et al. 2020). Owing to the immense importance of herbivores as prey species for humans during this period, it is perhaps unsurprising that deer are highly prevalent in the artwork of the time and region, representing 32% of all studied depictions across Asturias and Cantabria. Across northern Spain, medium herbivores (including deer, ibex and horses) account for 72% of all depictions, compared with just over 50% in France. Straus (1987) highlights the importance of ibex as a resource during the Upper Palaeolithic of France and Spain, with specialised drives of ibex collecting potentially conducted by certain groups, as well as hunting of willow grouse and salmon. Pushkina and Raia (2008) also demonstrate a strong association between humans and medium-sized herbivores including deer, reindeer, horse and saiga. Boar were uncommon until the Holocene (Pushkina & Raia, 2008) which provides a plausible explanation of their patchy distribution in artwork. Kowalski (1967) examining bison fossils in Europe and Asia also suggests that the bison is an indicator of other large vertebrates in the same environment, such as woolly rhinoceros, cave bear, and mammoth, all characteristic of steppe environments.

Differences between depiction frequencies of mammoths and rhinoceros, both present in the mammoth steppe environment, may be in part due to the changing distribution of these species during the Late Pleistocene. During the Last Glacial Maximum (22-17ka BP) woolly mammoths were widespread but already retreating from southern climates, and during the latter half of the Late Glacial (17-12.5ka BP) the species was becoming much scarcer (Markova et al. 2013). A population contraction coupled with a shift towards more northerly climes may explain the species being largely absent from the Palaeolithic art of Asturias and Cantabria. It is widely theorised that the dramatic decline in mammoth populations was due to a combination of changing climate and human impact (Markova et al. 2013), and it can be inferred that the authors of Magdalenian works from these areas may have been infrequently or rarely encountering mammoths, instead shifting the large herbivore bias

towards bovids, which were also exploited as a food resource. There is also evidence to suggest that in some areas, such as the Southern Levant, megafaunal hunting exploited the largest animals first, and over a period of 1.5 million years the average body size of mammoths decreased, as hunting progressively favoured the largest animals (Dembitzer et al. 2022). Based on the small sample evidenced in this paper, there is an increase in the depiction of bovids in artwork over time, corresponding with a decrease in mammoths and rhinoceros (with Rouffignac a glaring exception). More bovid depictions seem to occur at the expense of deer drawings – throughout all sites studied, a predominance of bovid depictions nearly always corresponds with a deficit of deer depictions, suggesting that selection of the larger organism may have been a factor in artwork production as well. Interestingly, three caves which have more numerous bovid depictions also have depictions of fish.

Yravedra et al. (2017) state that during the Gravettian, there was a predominance of large bovids in fossil assemblage layers in Coímbre cave, the location of which suggests that the remains could have been transported from nearby valleys. By the Magdalenian, however, taphonomic evidence suggests that the hunting seemed to consist almost exclusively of deer and ibex (ibid.). This is likely a result of the Local Opportunistic Strategy lifestyle (Djindjian, 2016) which put greater emphasis on targeting local species instead of moving with migratory herds. In northern Spain, hunting strategies during the Upper Palaeolithic fell approximately into two categories: increased hunting specialisation for deer and ibex, or diversification into smaller taxa, such as birds, small mammals (including carnivores), crustaceans, molluscs, echinoderms, and similar (Yravedra et al. 2017). Hunting and exploitation of large bovids, suids, roe deer, horses, birds, small mammals, fish, and other marine resources were considered rare, except at certain sites (ibid.). The environments mediating the availability of such resources included plains environments for deer, and mountainous regions for ibex (ibid.).

It could be hypothesised that the interaction of humans in northern Spain with a range of smaller taxa should result in a diversification of taxa depicted in cave art, particularly during the Magdalenian period, but this is not the case. The consistent depiction of deer and caprids (such as ibex and chamois) across the Spanish sites does fall in line with the specialised deer and ibex hunting strategies of the time, and it could readily be suggested that people were drawing primarily what they were eating in many cases. However, it doesn't seem to be the case that people who were exploiting smaller game were also drawing it on cave walls. Perhaps the drawing of smaller species was reserved for open-air or ephemeral materials only, or perhaps the difference between drawn significance was in the effort taken to obtain food resources. Hunting an ibex across rocky mountain terrain is both a more energetically-costly practise and likely required greater social cohesion than collecting molluscs or catching fish.

Fossil data from Markova et al. (2013) demonstrates a general absence of woolly rhinoceros remains from Spain, as well as highlighting the fragmentary nature of woolly rhinoceros populations when compared to more extensive woolly mammoth ones. Reduction of woolly rhinoceros populations are likely to have begun before that of mammoths (Markova et al. 2013), resulting in lower probability of encounter after the LGM, and increasing in rarity over time. The dates obtained from Chauvet cave (France) of 32,000 BP (Cuzange et al. 2007) correspond well with the rhinoceros timeframe outlined in Markova et al. (2013): during this time, the species had yet to undergo the severe decline seen during and after the Last Glacial Maximum. The numerous depictions of rhinoceros from Chauvet cave, including two individuals locking horns (Stuart & Lister, 2012) are more likely to represent direct observation of healthy population behaviour, rather than the occasional singular encounter.

Predatory species represent only 3% of all studied depictions, but this differs widely by range: predators account for only 0.8% of depictions in Spain but 4.8% of depictions in France. Certain caves contain more predators than others, such as Chauvet cave with over 30 carnivore depictions, including lions, leopards, and what appears to be a hyena; within Chauvet cave itself, carnivores account for 12% of all identifiable depictions. Felines are the most common carnivore depicted overall at all sites, accounting for 65% of representations, while the second most frequent are bears (29%) representing either cave bears (*Ursus spelaeus*), or brown bears (*U. arctos*).

FIGURE 8: CAVE BEAR SKULL ON A PLINTH, CHAUVET CAVE. ADAPTED FROM DELANOY ET AL. (2015)

Cave bears, like contemporary bears, were most likely omnivorous, consuming both plant and animal matter. Although sometimes hypothesised to be entirely herbivorous, dental microwear analysis conducted by Pinto-Llona (2013) suggests that cave bears may have consumed bones as part of their diet. Pinto-Llona (2013) also identifies that due to the proximity in which other hominids such as Neanderthals lived to cave bears, they could represent either a potentially dangerous but largely inoffensive species, or a competitor for meat-based food resources and/or scavenged remains. The inferences from their depiction therefore have an open interpretation: bears are not infrequently depicted in ice age artwork, and indeed objects such as bear teeth were also utilised by humans. Despite the popular 20th century idea of Upper Palaeolithic cave bear 'cults', there is little evidence supporting special significance of bears over other predators (Pinto-Llona, 2013). Certainly both of the most frequently-depicted carnivores could represent threat to human life, as evidenced by Camarós et al. (2015), but the contribution of carnivores to human communities for resources such as food and fur is also very likely (Charles, 1997). Chauvet cave contains many animal remains, including a minimum number of 190 cave bears (Bocherens et al. 2006) which used the cave as a hibernaculum. A skull placed on a natural rock 'plinth' (Fig. 8) is evidence of direct interaction of humans with the remains of bears.

Large carnivores are unevenly distributed in cave art among the studied sites. Cave bears and cave lions were both present in Spain during the Upper Palaeolithic, and cut bones evidencing at least one instance of lion exploitation in La Garma, Cantabria demonstrates that humans and lions came into direct contact in northern Spain during this time (Cueto et al. 2016). Generally, felines seen in cave paintings are limited to primarily lions (and a singular leopard) despite widespread distributions of smaller feline species (such as wildcats and lynx) throughout Europe at the time (Sommer & Benecke, 2006). Lions are by far the most predominant felid represented, featuring in caves such as Chauvet (Fig. 9), Lascaux, Trois- Frères and Les Combarelles (Stuart & Lister, 2011). Stuart & Lister (2011) state that cave lions likely exhibited a similar lifestyle to modern lions, which might have meant that their more obvious position within the landscape meant that they were more easily visible to humans; therefore, it may well be the case that smaller cats were shyer and less frequently observed, as is the case in contemporary Europe. Alternatively, smaller species of felid may have posed little relevance to people, representing neither an indicator of viable food sources (such as carrion) nor threat to human life. Lion remains studied by Cueto et al. (2016) potentially evidence the use of decorative lion skins, suggesting a relationship with the lion remains that was not simply functional in nature. The nature of human relations with lions during this time is unclear, but it is suggested that their appearance in Upper Palaeolithic artistic motifs could evidence a close relationship with large felines; further evidence for this appears to be provided elsewhere in Europe by the Löwenmensch figurine from the Swabian Jura of Germany (ibid.).

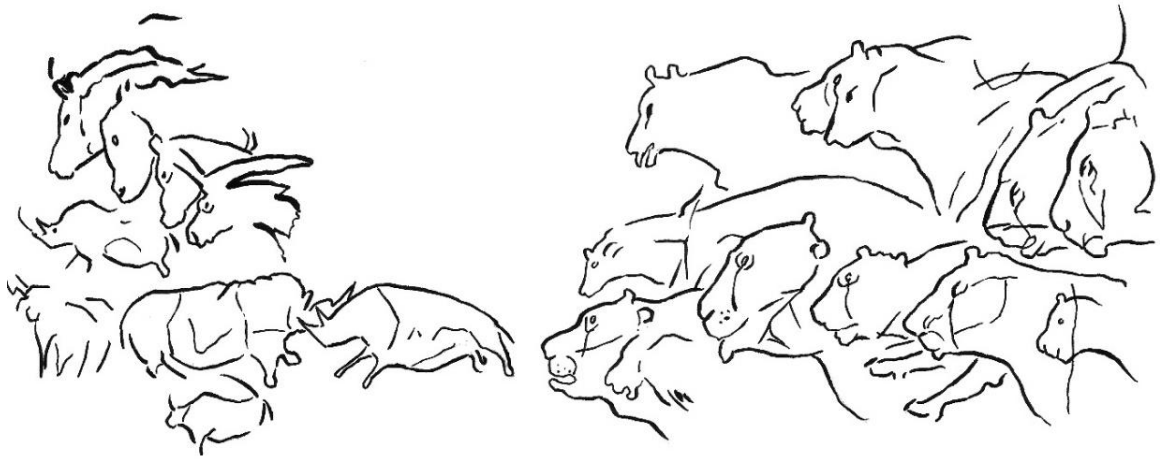

FIGURE 9: LION PANEL IN CHAUVET CAVE. ADAPTED FROM: BRADSHAW FOUNDATION

Across all sites examined in this study, there are no canine depictions aside from a wolf described from Altexerri by Mithen (1988), despite fossil evidence suggesting widespread populations of grey wolves and red foxes both within the study area and throughout Europe during the Late Pleistocene (Sommer & Benecke, 2005). Both widely-distributed canines are adaptable and readily inhabit the same area as humans, even into the modern day. There is also little evidence of canine representation outside of the study area, with only one depiction known from Font-de-Gaume cave, Dordogne, France, often suggested to represent a dog (Sykes et al. 2020) and a wolf's head from Les Combarelles, outlined by Kühn (1955). Despite their lack of representation in artwork, wolf remains are very common in archaeological sites throughout the late Pleistocene, with some considering this as evidence of human-canid association during the time that dogs were being domesticated (Pushkina & Raia, 2008).

Very few smaller carnivore taxa are represented. Canids such as the red fox and felids such as lynx and wildcat do not appear to have been priority species for depiction, despite fairly extensive late Pleistocene and Palaeolithic distributions within the study area (Sommer & Benecke, 2006). A similar story can be told for the Mustelidae, which demonstrate patchy but widespread distributions across Europe, encompassing the study area (Sommer & Benecke, 2004), but which are again only represented minimally, by a small representation of a stoat or weasel in Niaux cave, Ariège, France.

Human exploitation of small mammals such as rabbits for food is known throughout the Upper Palaeolithic, from the Aurignacian up until the Late Pleistocene–early Holocene boundary (Lloveras et al. 2016, Hockett & Bicho, 2000). The use of smaller game as food became more common than exploitation of large game at the end of the Pleistocene (Rillardon & Brugal, 2014), as a result of changing climate and habitat in Europe reducing the numbers of larger species. Despite rabbits constituting at least part of the European hunter-gatherer diet prior to this, the representation of lagomorphs is minimal, representing 0.1% of depictions. Following this pattern, it is unsurprising that representations of small mammals such as rodents and bats seem to be completely absent from Palaeolithic artwork, despite representing a large quantity of remains from Palaeolithic layers, such as those described by Cuenca-Bescós et al. (2008). It may be reasonably assumed that life for Palaeolithic humans was not devoid of encounters with micro-mammals, such as bats using caves and overhangs as roosts, but these encounters were not translated into artwork.

Birds did not represent a large proportion of representations (0.4%), and within the study area many of the birds described are non-specific, generally just being listed as 'birds' in inventories. Notable exceptions include the owl of Chauvet cave, and the great auks of Cosquer. Lloveras et al. (2020) lists 213 minimum individual fossil birds of 65 taxa from north-eastern Iberia; the number of birds decreases during the middle and upper Gravettian and Solutrean levels, but increases during the Magdalenian levels, potentially indicating fluctuating bird diversities in Iberia and corresponding to climatic and environmental changes during this time. Identifying bias for bird groups is significantly more difficult than for mammals, particularly when it comes to separating out species or genus groups, due to the high diversity of European birds when compared to megafaunal mammals.

Braun (2018) states that it is often not possible to generate an accurate identification beyond family level of birds from Palaeolithic art, unlike many species of larger mammals, which often look more distinct from one another. Nevertheless, in a preceding publication, McDonald (1994, p. 852) suggests that the same principles applied to other animals in general can also be applied to birds: owing to the reliance of Palaeolithic people on the keenness of the eye only, any bird which was represented had to have been "*quite large and to have had fairly distinctive plumage and/or certain behavioural characteristics which made it noteworthy*." Of the engravings identified to species level by McDonald (1994) many seem to be indicative of waterbirds: bittern, cormorant, great auk. While these identifications would seem to indicate a wetland or coastal habitat when taken at face value, the identifications are largely the opinion of the author and may represent bias towards certain groups and favour certain explanations.

Images of reptiles in the studied artwork are scarce, represented only by a single unspecified description from Llonín (Asturias) and – under the assumption that this determination is accurate – representing 0.03% of all represented works. Images of reptiles and amphibians are also exceedingly rare in Palaeolithic art in general. Among those identified from southern France and Spain are a carving of a lizard or salamander from Laugerie-Basse, Dordogne, France (Maury, 1913), and a carved tortoise or turtle from Le Roc-Saint-Cirq, Dordogne, France (Bougard et al. 2016). Elsewhere, several possible reptile or amphibian images are described from Germany. Three chelonian species are known from Europe during this time: the Hermann's tortoise (*Testudo hermanni*), the European pond turtle (*Emys orbicularis*) and the Mediterranean pond turtle (*Mauremys leprosa*); their presence is largely mediated by environmental factors (Bougard et al. 2016). Pleistocene herpetological fauna in Europe was largely stable, with only 4 of 76 species listed by Holman (1998) now extinct, but owing to the changing climate populations of reptiles and amphibians were likely only found around glacial refugia, which offered slightly warmer conditions. As stated by Bougard et al. (2016) reptiles and amphibians are largely reliant on climate due to their poikilothermy, although this does not mean that they are restricted only to warm climates: the European pond turtle is able to withstand cold winters, and was found in Britain during interglacial periods (Bougard et al. 2016). The example of the European pond turtle provides evidence for potential movement of other species too, such as cold-tolerant lizards (e.g. *Zootoca vivipara, Lacerta agilis*) and snakes (e.g. *Vipera berus*).

3.3 IMPROVING THE RESULTS

Overall, the results indicate that there is a taxonomic bias towards medium and larger herbivorous species, capturing the diversity of species in these two groups well. There is also some depiction of larger predatory species, although the extent to which this represents the likelihood of predator encounters by humans is negligible. The faunal depictions differ by area too, such as higher diversity of depictions from French cave sites overall. Some patterns seem to be indicated by the results: for example, bovid depiction numbers increasing seems to result in a lack of deer depictions (or a lower number of deer drawings seems to correlate with a higher number of bovids). It is so far unclear whether these patterns correlate well with what people of the time were eating, but there is certainly an overlap between species which were hunted for food and species present in cave drawing panels. This is further complicated by the preservation of animal remains in caves which were also used by humans, as seen in Lloveras et al. (2020), Philippe & Fosse (2003), Fontana et al. (2006), Foucher et al. (2016), Cuenca-Bescós et al. (2009), López-García et al. (2011), Rufà et al. (2017).

The primary limitation of the approaches taken here are that they represent a small dataset, and could also not account for changes over time. Sorting the caves into time order (either to years BP or to stylistic period) would not have generated usable results due to the small number of sites corresponding to each time period, and an uneven distribution of caves over time. Many of the caves correspond to Solutrean and Magdalenian cultures, with uneven representation across all of the Upper Palaeolithic sub-periods. Additionally, some well-dated caves have incomplete inventory data, which may have generated inaccurate results if included as a complete set.

Separating the study into separate sub-periods and evaluating each in terms of artwork in conjunction with the cultural innovations such as lithics, clothing and ornamentation, would probably provide further clarity on how the production of cave art fitted into wider cultural developments. For example, the production of harpoons in

the Magdalenian period (Herrera & Garcia-Bertrand, 2018) may correlate to a greater number of fish depictions in artwork, something which can already be inferred from figures 4-6.

4. DISCUSSION

So far, we have examined bias evidenced by the number and percentages of animals drawn in a selection of French and Spanish Upper Palaeolithic cave sites. The results indicate that all sites demonstrate taxonomic bias towards medium and large herbivores, and exclusions of small taxa, even potentially in spite of smaller taxa representing a large part of everyday life. Upper Palaeolithic artwork at the sites in Asturias, Cantabria, and France have been compared to information about wider fossil biodiversity in those areas, indicating that these biases may have been deliberate.

The sections in this discussion are as follows. Ecology and Environmental Change, in which populations of Pleistocene animals and humans are examined and their ecological stability are outlined; Social Context and Sympathetic Magic, where the concepts of magical thinking and its place in human society (both prehistoric and contemporary) are considered. Finally, Spatial Context, where the physical environment of the cave in relation to rock art is examined, introduces more detailed ideas surrounding the magical thinking outlined earlier in the section, and also focuses on the inclusion of anthropomorphic figures seen with animals in certain caves.

Here, wider themes regarding the production and meaning of Upper Palaeolithic art will be explored, starting with the ecological foundations of late Pleistocene animal and human populations, extinctions and expansions, and the impact on human populations. The concepts of sympathetic or hunting magic are then introduced in greater detail, alongside the inclusion of anthropomorphic figures, and more contemporary analogies. The comparison of more recent examples lays a foundation for the study of common themes among groups of people, which in turn can help provide a framework from which theories about societies further back in time can be developed. Overall, the aims of the section are to develop ideas regarding human perspective in a changing environment.

4.1: ECOLOGY AND ENVIRONMENTAL CHANGE

Evidence from smaller species indicates that the effects of Palaeolithic environmental change were not felt equally by all organisms in western Europe, nor were they felt equally along different latitudes. Wilson & Veraguth (2010) conducted population genetics of the Broad-snouted pipefish (*Syngnathus typhle*) with the conclusion that post-glacial recolonisation had occurred in northerly and easterly population extremes, but not in southern ones, indicating that the effects of glaciation for *S. typhle* were not felt as strongly in southern climes. Evidence of strong endemic populations of smaller animals such as rodents (Bilton et al. 1998) in the Mediterranean with little evidence of post-glacial colonisation, and post-glacial colonisation of plant species such as *Arabidopsis thaliana* from the Mediterranean refuge (Sharbel et al. 2000) further supports the idea that population distributions of organisms across Europe during the late Pleistocene were unequal. Studies of late Pleistocene mammals (Sommer & Benecke, 2004, 2005, 2006) demonstrate that in smaller groups including mustelids, small felids and small canids, although population growth and expansion occurs throughout the Pleistocene, populations of these groups remain relatively stable. This pattern of gradual population change with underlying stability is visible for the badger (*Meles meles*), pine marten (*Martes martes*), wildcat, lynx, red fox, and wolf. All of these species were populous in the study area, and their populations were neither highly migratory nor consistently fluctuating throughout the Upper Palaeolithic. In Table 5, there is remarkable inclusion of nearly all members of certain groups (large and medium herbivores, 'megafauna') and near-exclusion of complete groups of others (small carnivores). The stability and abundance of smaller species suggests that their exclusion from Upper Palaeolithic artwork was not due to humans failing to encounter them.

European Pleistocene megafauna, in contrast, is characterised by its instability, a direct product of changing climatic conditions; many terrestrial large mammals had fluctuating population dynamics and eventually became extinct during this period, sometimes despite having survived previous glacial and interglacial changes (Stuart, 2005). Many others, such as bison, experienced increased instability as the climate began changing towards the end of the Pleistocene. Primarily ranging within the so-called 'great Pleistocene bison belt', which

stretched from southern to central and eastern Europe (Zver et al. 2021), by the end of the Pleistocene their range had contracted, being restricted to Asia by the Holocene (Zver et al. 2021). Other changes were occurring in the bison population too, with the assimilation of steppe bison and aurochs into what would later become the European bison. Distinct ecomorphs of bison were recorded in Pleistocene artwork such as those at Lascaux and Pergouset (Soubrier et al. 2016).

Humans were not exempt from these changes, and experienced the same constraints as other species regarding environmental and ecological risks. The area encompassing modern-day southern France and north-eastern Spain was a large refugia for human populations during and after the LGM, with high rates of population growth within this area after the LGM contributing to the movement of groups beyond the refugium (Wren & Burke, 2019). Alongside the evidence suggested by Derex et al. (2013) regarding population size and complexity of culture, and the centring of both larger human populations and artistic centres in southern France and northern Spain, it can be suggested that innovations in artwork may have been directly impacted by human population dynamics in this area. Environmental instability is a direct product of changing habitat types as a result of changing climate. After the LGM (approx. 22,000 BP), the warming climate in Europe and Asia is thought to have generated an increase in forests, peat bogs, and lakes moving northwards from the south, and a subsequent decrease in tundra and steppe, particularly in Europe (Binney et al. 2017). This likely contributed to a decline in species which favoured the steppe environment, such as the keystone woolly mammoths and woolly rhinoceros, and an increase in smaller, more adaptable species including deer and small game. Other sources suggest a patchy distribution of steppe and forested areas, including directly around the LGM, which could have been controlled anthropogenically by humans, who at the time preferred semi-open habitats to hunt in (Kaplan et al. 2016). If there had been a steady transition between steppe and forest, this would likely have generated a driving force for human populations to adapt to both different game and different habitat types, favouring populations which were better adapted to cope with lifestyle changes. However, if habitats were anthropogenically controlled (e.g. with fire) as suggested by Kaplan et al. (2016) the relationship between humans and the environment becomes more complex, with anthropogenic impacts competing with natural climate change in the increase or reduction in biome types. The result for humans in both scenarios is an environment which becomes difficult to control and regulate, and which generates a selective pressure for humans to develop ways of expressing better-developed observational skills.

In order to physically produce cave paintings, the human brain must have the capacity to retain visual information regarding animals seen in the wild. Although species which were regularly hunted would have been readily viewed up close for butchery, many animal depictions seen on cave walls are in primarily natural positions and displaying wild behaviours, indicating that images were reproduced from observation of species in their natural habitats.

Folgerø et al. (2021) hypothesise that the Palaeolithic human brain's apparently superior capacity for such visual retention is comparable to modern-day savant syndrome, today seen in a small proportion of the human population who have superior visual memory and sometimes the ability to produce significantly above-average artwork. Since this condition is typically only expressed in a minority of the population (including autistic individuals and people with certain brain conditions) in the present day. Folgerø et al. (2021) suggest that archaic genes may play a part in the expression of the savant thinking mechanism, and intimate that better visual retention may have been suppressed by the rapidly-evolving complexity of language. The social shifts that occurred at the beginning of the Holocene (an increase in agriculture, coinciding with diminishing use of caves for artwork) may have provided the basis for such a scenario to occur. Additionally, physical anatomical differences resulting from Neanderthal genes, such as increased skull width, may also play a part in differences in visual perception (ibid.). These examples provide support for the hypothesis that the Palaeolithic human brain may have been able to process raw perception in the brain's memory, uninhibited by top-down processing of concepts as is seen in the majority of contemporary human brains (Folgerø et al. 2021). Comparing these theories with Derex et al.'s (2013) population dynamics implies that neurodiversity as a result of wider genetic admixture may have had benefits for Palaeolithic human populations, and also may have resulted in the ability of more individuals to produce similar and accurate artwork.

During the era of processual archaeology, the interpretation of the function of cave art shifted from sympathetic magic and cultural speculation to ecological function. As we have previously seen, interpretations before this had been complicated, steeped in the prejudices of nineteenth-century scholars. Cave art began to be examined in a way which assumed that it had to have a function. Art of animals was considered by some to be a map of useful information which viewers could read – such as a record of the population dynamics, tracks, and seasonality of game. Mithen (1988) theorised that even if the species depicted is not directly relevant to humans for consumption or danger, they may have been used as indicators of prey species or certain conditions. For example, depictions of carnivores in proximity to herbivores may be indicators of population health and dynamics of prey species, as they are able to support top predators. This theory seems to stand up well against the patterns highlighted so far in this thesis; there is indeed a bias towards medium and large herbivores. Examples, such as that of a Magdalenian-era woman from Saint-Germain-la-Rivière in southwestern France, indicate that large terrestrial herbivores were consumed as part of the human diet in at least some areas (Drucker & Henry-Gambier, 2005).

However, diet may not be the presiding factor in the inclusion of species depicted in caves. Although there is a distinct gap where smaller, less obvious species are concerned, their inclusion in lesser numbers is just as fascinating. For example, many depictions of birds in Palaeolithic art are unidentifiable, but those which are identifiable do not seem be of direct relevance. Great auks from Cosquer cave may have been hunted and consumed, but various depictions of owls from Chauvet and Les Trois-Frères leave more to the imagination, being neither harmful, of great culinary importance, nor particularly good indicators of predators or prey – if the behaviour of present-day Eurasian owls is still representative. If as Mithen (1988) states, carcass indicators were of significant importance as well as live game, then images of vultures and corvids might be expected to feature more heavily than they do. A sculpture of a lizard or salamander from Laugerie-Basse could be taken as an indicator species depending on the species represented, with lizards appearing from hibernation as a sign of spring or salamanders emerging just before wet weather, or partaking in seasonal breeding behaviour or colouration in spring or autumn.

It is perhaps more difficult to imagine the function of a small, enigmatic engraved cricket from Enlène and Les Trois-Frères (Fig. 14). Bégouën (1929) believed this cricket to be a "cave cricket" of the genus *Troglophilus*. However, in the same publication Bégouën admits that, having little entomological knowledge and consulting an entomologist for information, the genus is relatively uncommon in Europe. The idea that the cricket was a *Troglophilus* was based on speculation that the artist could have represented something which also inhabited cave mouths. There is a resemblance in the engraving to this genus, but the humped back, long ovipositor, and lack of wings are evocative of a number of cricket species.

FIGURE 10: CRICKET AND BIRDS ENGRAVED ON BISON BONE, FROM THE JUNCTION BETWEEN TROIS-FRÈRES AND ENLENE. AFTER BÉGOUËN (1929)

I believe this cricket better resembles a bush cricket (Tettigoniidae), an explanation which so far does not appear to have been suggested elsewhere. Esquer-Garrigos et al. (2019) analysed Pleistocene origins of chorusing in the western saddle bush-cricket (*Ephippiger diurnus*), a large species thought to inhabit glacial refugia ranges in southern France during the Pleistocene. The caves of Enlène and Les Trois-Frères are located within the Pleistocene range for this species, which was also thought to inhabit north-east Spain (Esquer-Garrigos et al. 2019). Large, colourful, and wingless, it fits both the morphology outlined in the carving, and inspires a thought-provoking idea regarding its inclusion with other fauna represented by artwork in the cave system. Around 14,000 years ago, the sea level began to rise as a result of glacial meltwater (Arntzen & Sá-Sousa, 2007). In this interglacial, as with others, temperature rise drove the expansion of refugia-restricted species and the contraction and extinction of cold-adapted ones. The humans of southern France were in a dramatic position during this time, bearing witness to the extinction of what would have been familiar species, and the subsequent arrival of new species. The situation of Enlène and Les Trois-Frères on the river Volp and their period of use (middle-Magdalenian, 13-14,000 years BP), coincides with the proposed expansion of *E. diurnus* via river valleys, 13,000 years ago (Esquer-Garrigos et al. 2019). Familiarity is a plausible explanation for the lack of drawings of largely sedentary species such as mustelids, canids, felids and smaller animals. More unusual species may have been noteworthy enough to record in artwork on the basis of them being new and unfamiliar.

If one purpose of Upper Palaeolithic artwork was to capture that which was becoming unfamiliar, uncommon, or scarce, an attempt to summon it back during times of ecological stress would be functional as a means to ensure group cohesion by planning for food or resources. The depictions of Rouffignac, dating to approx. 13,000 BP during the Magdalenian period (Lahlil et al. 2012) feature images of mammoths and rhinos – two species which were beginning to decline during the Magdalenian. Prior to this, during the Aurignacian and Gravettian the climate had already been changing, and the mammoth began to decline towards extinction around 14,000 years ago in western and central Europe (Drucker et al. 2015). While the mammoth populations of the Gravettian Dordogne were of some importance for raw material procurement, during the Gravettian and Magdalenian they were not particularly important in human diets (Drucker et al. 2015; Fosse et al. 2014) compared to smaller and easier prey species, highlighting an uneven distribution between supposed 'usefulness' and frequency of depiction. Fosse et al (2014) states that mammoths are unevenly distributed in cave art, with depiction frequencies having almost halved between the early Upper Palaeolithic (29 depiction sites) and the Magdalenian (14 depiction sites) – the authors conclude that the unequal distribution of mammoth art, as well as an increased frequency in mammoth imagery in portable art, represents exchange between different groups.

It could also be interpreted as being a response to declining populations of megaherbivores; small fragmentary populations of mammoths may have also existed during this period which were encountered and used by human groups, e.g. as scavenged remains from predator kill sites. However, on the opposing side of 'new and unfamiliar' is 'familiar but becoming scarcer', which may have been just as strong a motivation for wishing to represent an animal. From a sympathetic magic standpoint this could easily be interpreted as desire to increase their numbers through representation. However, humans are equally as drawn to things which are rare for non-religious purposes – rare and unusual (either through population decline or increase) may have been justification enough for depicting some of the creatures seen in cave art. This justification (that depictions of mammoths in Rouffignac is a response to declining mammoth populations) is also outlined by the work of Barkai and colleagues (Spikins, P. pers. Comm. 2022). Proboscideans were used as a food source for humans both during and prior to the Palaeolithic, and some suggestions argue that mammoth hunting is depicted in Rouffignac and El Pindal, with linear marks at Rouffignac representing spears and marks on a mammoth depiction at El Pindal representing a wound (Agam & Barkai, 2018). The potential for consideration of elephants (and their relatives) as other-than-human persons, suggests a more intimate dimension to their inclusion in art by Upper Palaeolithic humans (Agam & Barkai, 2018) as opposed to simply a multiplication of game suggested by other scholars.

Changing population dynamics would have been of direct interest to humans from an ecological and survival perspective, and the presence and absence of certain species in the surroundings would be noticed over a relatively short period of time. Attention to detail in the artwork may betray a sense of familiarity and

awareness of faunal change; the two ecomorphs of bison described by Soubrier et al. (2016) demonstrate not only the artists skill with accurate capture, but their attentive observational skills too – animals with changing morphological or behavioural features would not have gone unnoticed through several generations of people, nor would species' population decline and changing landscapes. Considering that there is no guarantee that the species represented in caves are fully representative of all species in artwork present at the time, it is possible that caves were simply one such instance of artwork which happened to be preserved, as described by Bahn (1995). There is a chance that common species were illustrated everywhere, but paintings made outside, or on more perishable materials such as wood, hide or bark, would have eroded faster and become lost.

Since the nature of human-animal interactions has always been complex, it is likely that complex explanations must be sought for the inclusion of specific species in many cases. The instance of canines in Palaeolithic art is one such testament. Mithen's (1988) theories offer a reasonable explanation for the scarcity of canine depictions: their presence in Palaeolithic art may only have been required when conducting certain behaviours, such as seeking out carcasses in the absence of large prey. However, details regarding the domestication of the dog, despite being possibly one of the most relevant and well-studied histories of human-associated mammals, are still relatively unclear. Estimates usually identify domestication as having occurred in the Upper Palaeolithic between 40,000 and 15,000 BP (Shipman, 2009) based on a combination of archaeological specimens and genetic analysis – within the timeframe of Palaeolithic artwork creation. In 1999, a set of footprints from Chauvet cave were discovered. These footprints were from a child seemingly accompanied by a canine, thought to be a dog by some researchers due to a shortened middle digit on the front paws (Shipman, 2009), although there is no way to ascertain whether the prints were made at exactly the same time. It is therefore interesting to note the apparent absence of wolves and dogs in Palaeolithic artwork, because these species were undoubtedly becoming closer and more integrated with human groups at this time than perhaps any other species had before. Shipman (2009) suggests that dogs may have already been considered extensions of the human family, and figures closer to home (such as humans and dogs) may have been forbidden to replicate in artwork, which elicits similar ideas of sympathetic magic as pioneered by earlier scholars. On the other hand, dogs or wolves may simply have been common enough that they did not need to be depicted – they weren't interesting or eye-catching enough.

To us in the twenty-first century, the fact of rapid climatic change and faunal extinction towards the end of the Pleistocene, particularly in Europe and the Americas, is common knowledge. The driving forces behind these changes, including glacial cycles, are well-understood, as is the relative position of the Earth in space and its relation to climatic changes. To our Palaeolithic ancestors, since the in-depth scientific knowledge of these processes would have been lacking without the modern technology to visualise it, all that would be noticeable over time would be the results of this climatic change, including changing flora and fauna and weather patterns. Within instances of rapid species changes, such as mammoth population reduction and the spread of saddleback bush crickets, these changes would likely have been noticeable within a generation in specific areas. The transition from large to small-game hunting occurred during the early Holocene, when climatic and social changes meant that small game was more optimal, but the rapidity of these changes would have ensured a relatively fast turnaround compared to the previous 20,000 years.

4.2, SOCIAL CONTEXT AND SYMPATHETIC MAGIC

The innate ability of humans to categorise objects in their surroundings, both literally and conceptually, is evidenced by the categorisation skills of children. The ability to mentally categorise certain things (such as animals, fruit, etc.) is a useful tool in human development, directly contributing to a sense of understanding and allowing us to make better sense of visual information (Bornstein & Arterberry, 2010). Human children demonstrate this ability, alongside the ability to modify mental categories for different objects, because it is adaptively beneficial – otherwise, a new response would have to be learned for every new object or situation (Bornstein & Arterberry, 2010). Moreover, both children and adults are able to apply flexibility to categorised subjects, depending on context or task (Bornstein & Arterberry, 2010). Our species' obsession with categorising things, perhaps best expressed in the science of taxonomy, may be intrinsic – it is undoubtedly beneficial for humans on an individual level to be able to quickly categorise a visual input and thus make a decision as to whether an object is beneficial, neutral, or potentially harmful. Some aspects of cave paintings, such as the

groupings of predatory species together in Chauvet cave, seem to hint at an early form of organisation – rather than place the predators with their associated prey, as has been previously suggested, in Chauvet cave in particular the predators are often grouped together, as seen in the Lion Panel and the Panther Panel (which groups a leopard and an assumed hyena, together with the outline of a bear). This seems to evidence the idea of not only increased levels of ecological understanding, but also the ability to organise species based on different factors – e.g. as being a threat to people. This may also be a contributing factor in the inclusion or exclusion of certain groups, such as the near exclusion of many small carnivores, rodents, reptiles, and invertebrates, although the exact nature of this categorisation still eludes detailed explanations.

Early on in the study of cave art, popular theories were largely utilitarian, with the interpretation that cave art was produced with the intention of influencing reality via sympathetic magic (Bradshaw Foundation, 2019). Ideas surrounding sympathetic magic have been well-studied, but are difficult to apply to Upper Palaeolithic art in more than a superficial way. However, since the properties of sympathetic magic are so widespread, it is necessary to examine them in detail, in order to examine their relevance to cave art.

As described in the Introduction, "The Golden Bough" by Frazer set about describing the laws and applications of sympathetic magic, with the two primary laws being the Law of Similarity (the image equals the object) and the Law of Contagion (contact between objects exchanges properties between them). Frazer was later criticised by Émile Durkheim for failing to differentiate the social concepts of magic and religion in his works (Vyse, 2014), but Frazer's theories were already popular, appealing to post-Darwin scholars with ideas surrounding social hierarchy, which saw some cultures as inferior to Europeans, and who thought sympathetic magic the product of a 'primitive' mind (Vyse, 2014). Similar theories were expounded by the Abbé Henri Breuil and Count Bégouën, who pioneered early studies of rock art. Ideas of sympathetic magic in cave art typically revolved around hunting, in which depictions of game species on cave walls would multiply their numbers and ensure the survival of the group in the future (Bradshaw Foundation, 2019), perhaps as an act of future planning and resource division. This reasoning certainly provides a logical ecological-survival explanation for the creation of rock art in the Palaeolithic, without considering more complex social functions. Palacio-Pérez (2010) states that ideas of this nature as an explanation for Palaeolithic art extend back to the mid-late 1800s, with researchers such as Breuil and Reinach expressing gratitude for the work of previous scholars. Reinach was of the opinion that carved batons (*bâtons de commandement*) (examples in Fig. 11) represented religious objects, a theory partially inspired by the aforementioned work of Frazer (1890) (Palacio-Pérez, 2010). This theory is also utilised by Davenport & Jochim (1988) who state that a stick present in the Shaft Scene of Lascaux (Fig. 13) could represent a totemic or religious object, similar to more recent examples used by Siberian shamans. Both of these examples, in both portable and wall art, encompass the idea that the artwork of prehistoric people may have had deeper meaning than simply observation-based sketching. In many cases, using comparison to contemporary examples appears to link the creation and existence of artwork with influence in the physical world.

FIGURE 11: EXAMPLES OF PERFORATED BATONS FROM LA MADELAINE, FRANCE

The presence of such beliefs in the more modern periods of history does not provide evidence that these beliefs were also present in the Upper Palaeolithic. However, comparisons such as these do suggest that the presence of magical thinking or belief in the supernatural – separate from religious practises – adds a dimension to human society which is not readily accessible without written or oral record. Beliefs surrounding animals, particularly predators or species otherwise capable of causing harm, have seemingly always inspired thoughts of the supernatural, possibly arising as a result of fear of the unknown. The environmental changes resulting in human population crashes and subsequent lifestyle changes after the LGM (Djindjian, 2016) coupled with the population changes of many species (such as mammoths, rhinoceros, bison and other mammals) during this timeframe certainly provide a highly uncertain environment for humans to live in. This environment is likely further complicated by the proximity of humans to predatory species such as wolves and large felines, two types of predator which pose particular threat to humans (Camarós et al. 2015). All of these factors create an environment in which magical thinking should thrive, if the examples presented by contemporary comparison represent a common state of the human mind.

This discussion has so far considered the artwork without its spatial context. Reviewing spatial relationships (of the art in the cave itself) is, however, particularly relevant to identifying potential functions of art in a social or cultural context. The study area encompasses sites which have paintings on the walls of cave interiors, as well as some associated portable artwork. Since the sites are composed of geological areas of preservation, it is not possible to say whether artwork also appeared outside caves on rocks and cliff surfaces, although this is fairly likely. Bahn (1995) highlights this fact, stating that the majority of Palaeolithic artwork would have been made outside the unusual environment of caves, with very limited examples from Europe providing evidence for this; similarly, the faunal composition within caves could be entirely different from that found in the open air. Evidence suggests that the spatial distribution of cave paintings may provide an insight into their ultimate meaning, although all theories should be examined in awareness of the fragmentary nature of the data and information.

The importance of spatial context can help to develop more detailed interpretations of cave art, particularly regarding images in which a modern visitor can envision a sense of organisation or place with. The Sorcerer of Trois-Frères (Fig. 14) is an unusual figure, often regarded as one of the most famous in cave art. It is somewhat difficult to argue against a more abstract explanation for some of the anthropomorphic figures seen in European cave art; the Sorcerer of Trois-Frères has been hypothesised to be a spirit or primitive 'god', as suggested by Campbell (1959), or a self-portrait, as believed by Kühn (Campbell, 1959), but there is no way to tell for certain. The shaft scene of Lascaux, containing another anthromorphic figure, this time with the head of a bird, is similarly situated in a small shaft at the back of the cave that only one person can reasonably enter at a time; access could have been restricted to one person only, or a group in succession. The contents of the scene appear to depict themes surrounding death or injury, which makes it difficult to imagine a purely social function, if the definitions of Durkheim and Malinowski are adhered to. Additionally, it is one of the rare individual pieces of Palaeolithic art which certainly seems reminiscent of a narrative or scene (Halverson et al. 1987) significantly more so than other 'compositions' which feature multiple individual figures. It is not possible to say for any of these instances whether any form of ritual was conducted around the images, or – if this was the case – whether outside equipment was brought in, as there is no direct evidence for either. It is also not possible to say whether some images were intended to be viewed by a single person only – for example, the shaman, magician, monster or spirit whose image the figure might represent. The basic ideas described by Kühn (1955, p. 98) of the Trois-Frères Sorcerer being "*sinister (…) even frightening*" may not be far off the intention of the artists.

The Sorcerer is situated in a chamber accessible only by a 'cat's hole' tunnel, in which a slim adult human can crawl along on their stomach for approx. 35m before entering the chamber (Campbell, 1959; Kühn, 1955). This figure is not alone on a wall, nor is it sandwiched in between figures as an equal (although other anthropomorphic figures do seem to be drawn as such); it is located in a small apse approximately 15 feet from the floor and outlined in black paint, the only figure in the chamber to be painted in this way (Campbell, 1959). To the modern eye, this seems evidence of particular importance, and that was certainly argued for by earlier scholars. Around it are a great number of animal engravings, interpreted by Campbell and Breuil as being 'presided over' by the figure (Campbell, 1959). In this context, the drawing assumes a different identity on the cave wall, potentially rendering the entire chamber as one scene. Kühn (1955, p. 100) provides a highly interesting and detailed account of this image, from the access tunnel to the nature of the portrait, which he describes (alongside other artwork) as arousing in the viewer "*either anxiety or terror*" at the concept of viewing the art, but not understanding the artists' intentions. The Lascaux 'shaft scene' occupies a similar niche in the cave, inside a narrow shaft which requires equipment such as a rope or ladder to enter. Discovery of the remains of a small lamp at the bottom of this shaft indicates that viewing was limited to a small field of vision. The physical limitations surrounding both of these images inspire a more interpretive explanation; some areas of caves may only have been accessible to people in restricted numbers, or one at a time, and the potential for physical discomfort in reaching the images suggests that a response to the artwork is elicited by these factors. In both Campbell and Kühn's accounts of seeing the Trois-Frères figure they describe the Sorcerer in context, as opposed to just as an isolated drawing; the experience of viewing this figure seems just as much to do with the setting and the 'journey' to reach it, as seeing the portrait itself.

The same seems to be true of the so-called 'monsters' in Pergouset Cave (Lot, France), which is situated in a narrow, steep passage and contains images of apparently fantastical, unrealistic animals (Fig. 12). Lorblanchet & Sieveking (1997, p. 52) provide a comprehensive overview of monsters in Upper Palaeolithic art, correlating not only humanoid anthropomorphic figures such as those at Trois-Frères and Lascaux, but also composite animal figurines including "[in Trois-Frères] *one which is part deer, part bison and the other a deer drawn with fingered hands instead of hooved forefeet. There are two further composite animals in this cave, both bears, one with the head of a wolf and one with a bison's tail. Gabillou (Dordogne) has three human/animal figures (each with an animal head with horns, a human body and a tail) that are comparable to the Trois Freres sorcerer.*". They also highlight the peculiar 'unicorn' from Lascaux, which is entirely fictitious. The monsters of Pergouset are drawn on a sloping ceiling and are apparently based on real animals, with peculiar proportions, including a horse with a very long neck, and other exaggerated features (Lorblanchet & Sieveking, 1997). Being outside of the range of real animals, which we have already seen adhered to in cave paintings with remarkable accuracy, the inclusion of unreal animals rendered on cave walls, sometimes among realistic depictions of other animals, is also of

interest. Lorblanchet and Sieveking (1997) suggest that the ingestion of hallucinogenic substances, such as the fly agaric mushroom (*Amanita muscaria*) also used by contemporary Siberian tribes, is a plausible suggestion for the induction of visions which match the organisation seen at Pergouset. However, they also recognise the potential for imagination as motivation (Battersby, 1997) and even contemplate simply "bad drawing" ! (Lorblanchet & Sieveking, 1997). Horvath & Szakolczai (2017) take these ideas a step further, building on Lorblanchet's theory that the cave contains a creation myth and stating that there can be connections to the myth of Prometheus (about "*the human mastery of fire*"). This is not the first time that connections to Greek mythology have been inferred from cave art. It is mentioned in Kühn (1955, p. 92) that one of the sons of Count Bégouën had taken with him into the cave which would later be known as Trois-Frères, "*a ball of string with him as a precaution so that, like Theseus in the Labyrinth, he might find his way back again safely*". The fact that there was also a monstrous, horned humanoid figure depicted in this cave system (described by Lorblanchet & Sieveking , 1997, p. 52 as "*part brute, part human*") remains a curious coincidence.

FIGURE 12: A PANEL OF CREATURES FROM PERGOUSET. AFTER LORBLANCHET AND SIEVEKING (1997)

While the rock art of Indigenous groups (such as Indigenous Australians and Americans) lacks the specific context and therefore is not an exact parallel to the artwork of prehistoric "Europeans", it can provide some background to the creation of rock art and petroglyphs. However, it is pointed out by Halverson et al. (1987) that comparison to modern hunter-gatherer communities is typically restricted by environment: desert and sub-tropical cultures (such as Aboriginal Australians) are not comparable to ice-age humans, aside from shallow parallels. Similarly, even communities living in the same geographical areas display significant variation in culture, and culture is typically steeped in tradition (ibid.). Halverson et al (1987) state that drawing

comparisons to modern-day hunter-gatherer communities is functionally useless and possibly even misleading, with no intrinsic value. Under this assumption, hunting magic, sympathetic magic, and fertility-based theories have no substance, as there is no direct evidence for magical or religious connotation within the artwork (ibid.).

Insoll (2004), on the other hand, states that carefully-applied ethnographic interpretation using the explanations provided by modern people (who still have knowledge of rock art production) can certainly provide a differing perspective than the common interpretations of Western scholars. For example, the commonly-suggested Western interpretation of open-air North American rock art as representing trail markers or signs was disproven, and worldwide accounts regarding rock art often reflect a religious origin (ibid.). The themes of shamanistic or visionary works are also explored by North American Indigenous groups, with Insoll (2004) identifying a number of western North American groups as creating artwork with this function on both owned and communal sites. Lewis-Williams (2002) also discusses the concepts of vision quests and altered states of consciousness in *The Mind in the Cave*, which offers a psychological insight into the potential creation of cave art. The concepts of dreams or hallucinations being assigned different meaning and importance in different places and times certainly seem suggestive of some of the more abstract images drawn in caves. Delanoy et al. (2015) also identify the importance of caves as social constructions, as opposed to simply natural resources occasionally exploited by humans. In their cross-cultural examination, the artwork and spaces of Indigenous Australians (where meanings can be readily provided from living people) were compared to Chauvet cave. Sites are variously interpreted across Aboriginal Australia as being spaces where ancestors formed, with the importance of the artwork directly linked to the importance of the space itself (ibid.). This understanding has the potential to modify the way in which prehistoric painted caves elsewhere may be viewed, with limited attention previously focused on the caves without the artwork (ibid.). Archaeomorphological analysis has demonstrated that a number of features and objects in Chauvet cave were subject to anthropogenic movement or alteration, such as the geological 'Cactus' (featuring stone blocks organised around a central stalagmite, with subsequent Holocene stalagmites growing around) and the cave bear skulls, one of which is placed on a plinth (Fig. 8). The authors state that the focus on human-modified and culturally significant features should be on more than just cave art and explicit modification of small parts, instead focusing on the potential importance of the three-dimensional space as a whole. Lewis-Williams & Clottes (1998), suggest a shamanic reasoning behind the placement of images in caves, using comparison to more contemporary examples. – Europe's limestone caves constitute a physical representation of an 'underworld' which is often visualised by individuals who are hallucinating or in a trance-like state. While Lewis-Williams & Clottes (1998) are heavy in their comparison to modern-day cultures, they also argue that the psychology of altered states is universal, dictated by the human nervous system, and thus typically produces several base experiences:

- Feelings of flight or weightlessness, evocative of the sky.
- Feelings of constriction, or of being drawn into a vortex, evocative of underground tunnels.
- Projection of visions onto surfaces such as walls and ceilings.

They argue that these base experiences constitute enough evidence to be able to confidently assign them to the creation of European cave art; the context for the creation of cave art, they argue, is created by the interaction of the psychological experience with the physical landscape of the European karst. Caves are an 'underworld' in which animals metaphysically inhabit the spaces beyond the curves of the walls, and that shamans (who drew the artwork) sought to draw animals through the permeable membrane of the cave wall (Lewis-Williams & Clottes, 1998). Davenport & Jochim (1988) also drew comparisons between the bird on a stick present in the Lascaux shaft scene, and modern Siberian shaman's familiars. They also suggest that the schematic form of both anthromorph and bird are deliberately vague so as not to invoke too great a likeness to a particular person, particularly a powerful figure such as a shaman.

Another argument which supports this research can be found in Hodgson (2008), who states that states of mind common at population level in modern humans (such as extreme concentration, hunger, stress and sleep deprivation) can produce hyperimagery, which often takes the form of seeing animals. Hodgson's assertion that the images are often of extreme interest to the person experiencing them, occasionally being regarded as real, and that this experience in the life of Cro-Magnon humans would be more than enough to imprint a sense of importance on the image of an animal. Particular activities such as game hunting, which require concentration

(both on the target species and potential predators) and invariably result in mental fatigue, present a commonplace scenario under which such images could be generated. Under the right conditions, with trigger cues from phenomena such as shadows or stains on cave walls, the images from the original event are likely to be projected (Hodgson, 2008). Additional stressors, such as the potential for the presence of dangerous species such as lions or bears in caves also utilised by humans, would also generate a similar effect (ibid.). The idea of magic in a different sense can also be gleaned from this process; if the phenomenon of seeing animals which weren't there was considered significant, the importance could be renewed by visiting the site where it originally occurred, such as a cave (Hodgson, 2021) and thus, a magical connotation linked to the image of an animal could be re-experienced.

With the presence of very recent research, a comparison of Lewis-Williams & Clottes' theory can be made with Folgerø et al. (2021)'s Superior Visual Retention Hypothesis. Would the presence of such a system, which retains visual information in a different manner to how many people in the modern day experience it, impact the way this information was processed in the imagination? Is there a chance that the way the Upper Palaeolithic human's "mind's eye" worked was different to how we perceive things (accounting for the scale of individual differences in perception) in the present? The presence of this different perception may mean that there may have been one or more additional dimensions to the experience of hallucinogenic or altered-consciousness states for people at the time.

The overall conclusion from the above is that critical thinking must be rigorously applied when developing ideas which are based on analogies using modern-day people as examples. The primary criticisms of sympathetic and hunting magic, and the use of visual phenomena, is that they are fundamentally unprovable at present, and rely on the comparison to the modern day. There is also very limited potential for recreating events which would generate comparative data. The inclusion of neurodiversity in the expansion of individual perception styles is an extremely interesting recent development, although some of the experiences detailed by Hodgson (2008, 2021) are common to much of the population. This new foundation of theories represents a logical next step from previous theories of hunting-magic and similar, and seem to provide a more plausible framework which bypasses cross-cultural differences and timescales.

FIGURE 13: THE SCENE IN THE SHAFT AT LASCAUX. ADAPTED FROM LEWIS-WILLIAMS (2002)

FIGURE 14: THE SORCERER OF TROIS-FRÈRES

The attempt to understand the abstraction of ideas which led to the production of cave paintings is conducted backwards. We are seeing the result of the environment which dictated that the painting were created, but we have little understanding of that environment, or of the thought or behaviour patterns which led to it. We find the animals painted on cave walls interesting, but the chimerical 'monsters' are more powerful, particularly when they appear alongside recognisable, drawn-from-life species. If the Superior Visual Retention hypotheses of Folgerø et al. (2021) is adhered to, then people of the Upper Palaeolithic may have had thought or imaginative patterns which we today might see as alien. We may not be able to comprehend the level of abstraction necessary to produce these images. Halverson et al. (1987) states that a shamanistic or otherwise abstracted function is easy to apply to depictions such as that from Trois-Frères, but that the same idea (of magic or shamanistic appearance) cannot be gleaned from images of animals alone. The idea of the figure 'presiding' over the animal depictions in the chamber certainly seems evocative from the positioning of the figure in an elevated position, but there the religious connotation seems to end – there are certainly no implicit abstracted ideas in the animals themselves at any location. It is tempting to think that, in the absence of written word, cave art could function by itself as a language able to communicate the lives of Palaeolithic people. However, it is far more likely that the 'function' of Palaeolithic artwork, assuming there was a concrete and standardised one, was only one facet of a complex web of social and interpersonal connection within a human group.

There have been two distinct lines of enquiry within this discussion. The first section discussed the relationships between animals and people within the environment of the late Pleistocene, particularly the notice human beings would have taken of changing animal populations. The second concerns the social and psychological mechanisms with which people understand the world, particularly in the assignment of supernatural properties to situations (and animals) which are outside their control. Ecology provides a physical basis for analysis, by examining the physical environment and the fossil record of the animals (and humans) which existed there.

It therefore can be asked: are there different functions for different cave paintings? The answer is almost certainly yes, although it is difficult, and potentially impossible, to disentangle them into specific categories. Leroi-Gourham categorised animals as being split into "male" and "female" based on species (for example, bison being distinctly female), a theory which takes a large step away from the information offered by the available

data (Halverson et al. 1987). Separating the anthropomorphic figures from the animal figures seems like a logical step to take, but given the potential for narrative structure with the wounded bison in the Lascaux Shaft Scene, and the positioning of the Trois-Frères Sorcerer 'over' the other paintings, it is possibly ignoring ideas of a more conceptual nature. Regardless as to the intention behind the anthropomorphic figures, what is undoubtable is that humans were using the appearance of animals to create these images, demonstrating that not only were they observing the animals themselves for accurate copies, they were also beginning to depict them in more imaginative ways.

As Derex et al. (2013) suggested, cultural innovation and maintenance can be a direct product of a large and relatively stable population, and group size can be key to the maintenance of population stability. However, stratigraphic and archaeological evidence indicates that after the Last Glacial Maximum came a human population crash, where the survivors were forced to adopt a Local Opportunistic Strategy lifestyle. This reduced their contact with other human groups, changed their subsistence from migratory herds and adopted opportunistic hunting (Djindjian, 2016). Population fragmentation during times of ecological stress may lead to population collapses (Derex et al. 2013) and thus larger, stable populations are needed for optimum function. The genetic refuges for humans in southern France and northern Spain, with frequent out-migration (Wren & Burke, 2019), seem to correlate strongly with the presence of more extensive and complex artwork within the area. The fundamentals of art began before the LGM, when human populations were still large, with plenty of mixing. However, the reason for further developing artistic techniques throughout this period of relative hardship may come down to other factors.

However, there were potentially more factors at play than simply the obtaining of food. The psychology behind the creation of some of the more unusual figures seen in cave art elude concrete, functional explanations, but that has not stopped speculative research. We have seen that the ideas of shamanic origins for many examples of Palaeolithic art are common, and have been explored in detail. The hallucinogenic theories of Lorblanchet & Sieveking (1997) and Lewis-Williams & Clottes (1998) coupled with the shamanic origins for the bird-headed figure in Lascaux by Davenport & Jochim (1988) suggest that ideas surrounding human perception and psychological motivation are just as intriguing as the contents of the cave art itself.

Evidence suggests that our ancestors may have possessed better visual retention skills than we generally possess today (Folgerø et al. 2021), which may have been responsible for the high degree of accuracy and attention to detail seen in animal depictions. Our natural proclivity for categorisation and taxonomic organisation is also implied in the arrangement of animal compositions. From this, it is likely that the presence or absence of particular species, as the climate and habitat changed, would have been readily noticeable within a few generations, representing new or reduced opportunities for survival. The use of cave art for recording game health and other crucial information, suggested by Mithen (1988), seems to be supported by population-level evidence. However, the idea of 'function' in cave art does not need to rely on the viewing of the artwork communicating important messages – the production of art could have functioned as a social bonding mechanism, either for survival via group cohesion, or simply as an enjoyable activity. A dynamic and changeable climate, coupled with ecological declines and changing landscapes, create an environment in which change is a certainty. Human sociality, intelligence, and a propensity for superstitious thought generate a powerful motivation to want to control the environment and resources to ensure population survival, and it is possible that artwork in caves was designed to achieve this purpose. While the invocation of sympathetic magic in cave art has its rightful criticisms, and should be examined with caution, evidence from more modern examples suggests that reliance on magical thinking during times of social stress is common and widespread, and may have had its roots, like religion, during the Upper Palaeolithic or earlier. However, this idea treads firmly into territory proposed by scholars such as Breuil, who remained convinced of a hunting-magic explanation for European cave paintings.

The results and discussion of this paper suggest that the particular style and execution of Upper Palaeolithic art was a product of a particular lifestyle and environment, directed by the fauna and external conditions which influenced the artists. What is undoubtable from the artwork was that humans at the time were able to observe the appearance and behaviour of species they shared their environment with, and translate this into stylised, accurate, and even full-colour images, painted in torchlight inside the depths of caves. Studying in greater detail

the animals present in Upper Palaeolithic art provides insights into their influence over the artists who recorded them, presenting a unique case study into prehistoric association between humans and animals.

5. CONCLUSION

This thesis aimed to evaluate the hypothesis that there were strong taxonomic biases in Upper Palaeolithic cave art with theories and ideas surrounding the production and social use of such art. It did this by examining the percentages of animals depicted in a group of geographically-close cave sites, before comparing them to the wider fossil record.

Using the extensive study of prehistoric cave paintings as a subject, literature was consulted to extract cave painting inventories, before the hypothesis could be tested. The hypothesis (H1) which was tested was that distinct taxonomic bias is demonstrated in European Palaeolithic art towards certain animal groups. This hypothesis could be considered proven with the data used for this thesis. The broadness of this hypothesis allows for the testing of two miniature hypotheses within the constraints of the data: whether geographical closeness of the caves resulted in greater similarity of depiction, and whether number of species depicted coincided with the number of individual drawings. For the first mini-hypothesis there was no correlation (-0.27), and for the second a weak positive correlation (0.67), indicating that while taxonomic bias did not seem to differ between separate groups of close-knit caves, caves with more drawings overall appeared to demonstrate a slightly higher number of species being drawn.

These correlations were calculated using the dataset that was available, and while providing some interesting implications, could be improved in future by adding more sites as clear data becomes available. Looking at species depicted in caves in comparison to the wider biodiversity of the area indicated that not only were specific taxonomic groups being completely omitted, some taxonomic groups had extensive coverage, such as medium-sized and large herbivores. Similarly, examining the percentages of each species depicted in each individual cave demonstrated some surprising insights, such as differing percentage compositions of species between northern Spain and southern France (such as a greater frequency of carnivores depicted in sites from the south of France). Spanish sites were dominated by deer and horses, whereas French sites were dominated by horses, mammoths and bison.

As suggested by Halverson et al. (1987), the idea of art for art's sake in the Palaeolithic is not as unusual as it may first sound. The idea that art has to have had an adaptive function in order to compete with other, perhaps more 'useful' activities is a popular one, and features in one of the hypotheses in this study – testing whether the species numbers increase if there are more individual paintings. The hypothesis used an adaptive basis as this theory, assuming that if the species depicted in cave art had some importance, that this importance would be conveyed first, with less important species being drawn later, when the primary choices had been fully expressed. As it stands, there was a weak positive correlation between these factors in this thesis. However, as Halverson et al. (1987) state, there is the possibility that art was a leisure activity in itself, rather than a competitive survival activity, the possibility exists that there was no direct functional advantage gleaned from the viewing of the artwork – it may not have expressed the state of game, as indicated by Mithen (1988), and it may not have expressed a religious or sympathetic magic-based function. The changing of the climate as a prompt for population-level species change which would have been noticeable to humans may have provided a similarly-powerful motivation for representing animals – interest in things which are rare, or novel. Lurking in the background is this theory: that Upper Palaeolithic artwork had no complex function, and was simply a pleasurable activity engaged in by prehistoric humans as we engage in creating things today, and that the biases identified here are the product of certain species catching our collective eye. Even if the art itself had no importance as a visual message, the production of the artwork as a social activity may have been just as important, and thus contained all the functional advantages necessary for the humans who produced it.

What can be inferred from all of these studies and findings is that there is no single theory of the 'function' of cave art which perfectly fits all available evidence; Upper Palaeolithic society was complex, and the combination of interacting factors alongside the particularly human ability and desire to control the external environment creates a scenario in which social cohesion may rely to a greater or lesser extent on religious or magical

thinking, as it did in early modern Europe. Such thinking is born of a need to understand the world around us. Pleistocene climate changes, particularly around the Last Glacial Maximum, resulted in population contraction of human groups, which in turn drove lifestyle changes in the smaller and more distantly-spaced human groups. This is further complicated by the fluctuation and extinction of many large mammal species which would have been of particular importance to humans. This uncertainty creates a perfect environment for the human mind to rely to a greater extent on magical thinking, in order to guarantee group resources in the face of difficult circumstances. This would certainly explain not only the large amount of art produced after the LGM and towards the end of the Pleistocene, during the Magdalenian period. Regardless of whether traditional game-hunting or supernatural thinking were majority factors in the production of ice age art, the result is near-universal: accurate and comprehensive representations of wildlife which was directly encountered in the world of Upper Palaeolithic humans. Using this style, examples of artistic license using these ideas also resulted in the inclusion of extraordinary, fictitious creatures, which may represent the beginnings of more abstract ideas about the world and how it can be manipulated and controlled.

These ideas have been influenced by the works of multiple authors, and it is extremely difficult to provide what could be described as an unbiased view of Palaeolithic cave art. Indeed, the subject of human history, artistic ability, palaeoenvironment and psychology are viewed through the lens of another human, and with a topic as subjective as human history it becomes easy to state that certain ideas are plausible or even probable, simply because a theory that fits has been hypothesised. Using the 31 sites processed here, there seems to be a bias towards large and medium-sized herbivores, with smaller taxa excluded either partially or fully. However, there are several hundred decorated cave sites in Europe, with many more examples of portable art, as well as a global richness in prehistoric art. The addition of other decorated cave sites in Europe would likely generate similar results in terms of species composition, although that would not necessarily bring us any closer to being able to determine the exact motivations of the artists. The inclusion Agam & Barkai (2018)'s ideas about intimate relations with proboscideans in their habitat, as well as the isolated instance of Bégouën (1929)'s cricket aligns well with my own ideas regarding faunal change as a motivator for artwork, although my own bias as somebody greatly interested in invertebrates, reptiles and amphibians prompts me to ask more about why these smaller groups are not included. What Bégouën interpreted as a cave cricket, I interpret as a bush cricket based on theories about the reduction or expansion of certain species, and yet Hodgson (2008) provides an equally plausible explanation of projected hyperimages (a common feature of which is seeing insects which aren't there). It is evident that the timespan of the Upper Palaeolithic, alongside changes in culture throughout, is highly complex, and it would be impossible for an individual to be able to understand the motivations of the Upper Palaeolithic artists without significantly more physical evidence. The limiting factor of preservation of cave systems eliminates the ability to study other forms of artwork – for example, on wood, hide, paper etc. which undoubtedly would have coexisted with drawings on stone and bone but which are now lost. However, the remaining artwork has always stood out to modern humans as a reminder of similarities between prehistoric humans and ourselves.

Overall, the success of identifying taxonomic bias in recorded Upper Palaeolithic art is matched by the complexity of factors which may have preceded this bias. The bias of the artists' depictions parallels the bias of those who try and understand the nature of Palaeolithic art: since each individual is a product of a complex environment, our interpretations of figurative representation are all likely to be different. The specific importance of certain species for prehistoric social groups and the interest taken in recording ecological change may elude specific scientific explanation, but examples of our relationship with wildlife, and the complexity of thought and sociality it can encourage, can be seen in most of human history, prompting speculation about how much we have really changed between the Upper Palaeolithic and today.

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