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A LITERATURE REVIEW ON HOW CAVE HYENAS AND HUMANS CONFLICTED AND CO-EXISTED

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Abstract

This study aims to make a comprehensive analysis of the competition between cave hyenas (Crocuta crocuta spelaea/Crocuta spelaea) and humans (Homo neanderthalensis & Homo sapiens) in Europe during the Pleistocene epoch through a literature review. Initially, a total of thirty-six papers had been collected, which were, over time, narrowed down and eliminated to twenty-nine relevant sources, which have all been considered for this study. The sources focus on the chronological distribution and genetic identity of cave hyenas, the overlap of hominin/lithic remains with those of cave hyenas at faunal assemblage sites and the possibility of mutual predation and territorial attacks. Most cases show alternating use of cave sites by hyenas and humans; despite their significant niche overlap, direct encounters are only possibilities in carnivore/hominin modified faunal assemblages—there are no such documented cases. Due to the process of fossilisation, it is unfeasible for other parts of their known habitats to be considered. Therefore, all inferences and conclusions on the level of competition between the two species has been based on the assessment of faunal assemblages in caves.

Keywords*: Competition, faunal assemblage, bone modification, cave hyenas, humans.*

Introduction

Cave hyenas and humans were two of the few top-order predators in Europe during the Pleistocene epoch. Cave hyenas were close relatives of modern spotted hyenas (*Crocuta crocuta*). The degree of their similarity to spotted hyenas is heavily debated across the literature. Originally discovered and described by Goldfuss in 1823, they were labelled *Hyaena spelaea*. Later studies placed them in the genus *Crocuta* and considered them to be a subspecies of the spotted hyena (*C. crocuta*). Hence their name was changed to *Crocuta crocuta spelaea*. Recent studies from the last 25-30 years have argued for the spotted hyena being a separate species, based on their significant dental and skeletal differences with the extant spotted hyena. Other studies have also used their difference genetic lineages and old separation as a point of contention (Westbury 2020). The exact classification of the cave hyena is beyond the scope of this paper, so they will henceforth be referred to as *Crocuta crocuta spelaea*. Neanderthals and cave hyenas co-existed in Europe since nearly 300,000 years ago, while anatomically modern humans (AMH) entered the continent as early as 50,000 years ago. Though the European steppes were sparse and unforgiving—switching between periods of intense frigidity to more temperate climates, i.e., glacials and interglacials, every 100,000 years or so—the ecosystem was rich and biodiverse. As top-order predators in the same environment, cave hyenas and humans shared many resources in common, such as prey species, territory and potential shelter. A severe natural limitation on all of these would inevitably lead to the rise of interspecific competition between the two species. This competition could take the form of both avoidance and encounters. Caves were areas that were favourable to both species for safety and settlement, whether for temporary refuge or for extended stays to raise offspring. The relatively stable temperatures and the humidity of cave

environments make them ideal for the preservation of organic material, which may eventually lead to fossilisation. Most studies on the animals of Pleistocene Europe use and rely on faunal assemblages found in several cave systems throughout the continent. The aim of this paper is to combine, analyse and summarise available evidence that teaches us about cave hyena-hominin interaction.

Literature Review

A literature review is a form of secondary research that aims to summarise and/or analyse published works on a particular topic. This study is strictly a literature review. No empirical evidence was obtained through experimentation or field work. Only peer-reviewed, published sources have been used for the collection and assessment of information. Google Scholar was the main resource used for this study. The method of this study can be divided into the following stages: collection of sources, examination of sources, categorisation and prioritisation, and inferences and findings.

Collection of sources

The first step for the collection of sources was to enter a key word/phrase on Google Scholar. In my case, the key phrase was "cave hyenas." The displayed results primarily consisted of studies that discussed the classification, chronological distribution and population history of the cave hyena. In addition, there were papers on the diet or psychology of cave hyenas, or skeletal analyses at specific sites. These studies were important to learn about the background of cave hyenas—their anatomy and how they interacted with their environment during their existence on Earth. The next entry was "competition between cave hyenas and humans" and the available results included research articles discussing the relationship between carnivores and humans based on faunal assemblages at specific sites, along with a few of the results from the previous search. Many of the results were also irrelevant but similar research papers or extracts from reference books. The third key phrase, the simplest way of phrasing what I was looking for, was "cave hyenas and humans," which yielded the same results, but with a few more that were not previously visible or available. Lastly, to identify cases of potential attacks on Neanderthals by hyenas, it is important to be able to distinguish between postmortem (after death) and perimortem (at or near the time of death) bone damage on human remains with hyena modification. Hence, I searched for articles on this topic.

Examination of sources

After I collected a total of thirty-seven sources, I read through all of them. In each paper, I highlighted points of information that may have been relevant to my study.

Categorisation and prioritisation

After being read through, two main categories were assigned to each paper: 'relevant' and 'irrelevant.' Some from the relevant category were placed into the 'important' subcategory.

Inferences and findings

A Microsoft Word document was created for my main findings and inferences. After each paper was read completely and thoroughly, the key points of information within, along with my own inferences, were recorded in the document.

Abbreviations and Acronyms

The following abbreviations and acronyms will be used herein:
ka – kiloannum; thousand years
BP – Before Present; 1950 is used as the 'present' year
C. c. spelaea – Crocuta crocuta spelaea; cave hyena

H. neanderthalensis – Homo neanderthalensis; Neanderthal
H. sapiens – Homo sapiens; modern human
AMH – anatomically modern humans
NISP – number of identified specimens
MNI – minimum number of individuals
MIS3 – Marine Isotopic Stage 3

Discussion

Most studies on carnivore-human interaction focus on the last 100,000 years, i.e., the last ice age. During this period, Europe was dominated by a steppe ecosystem. A wide variety of megafauna survived in this habitat. Among the top predators of this environment were the cave lion (*Panthera spelaea*), the cave bear (*Ursus spelaeus*), hominins (*Homo neanderthalensis*, *Homo sapiens*), cave hyenas (*Crocuta crocuta spelaea*) and the cave wolf (*Canis lupus spelaeus*). *H. neanderthalensis* and *C. c. spelaea* were frequent cave dwellers. These two animals, along with AMH, tended to use the outer sections of caves more than other animals, who would often occupy the deeper sections, e.g., *Ursus spelaeus, Ursus ingressus.* Caves could be used as dens by cave hyenas, short stops for mobile hominin groups, secure places to feed on hunted carcasses by large carnivores, hibernation sites for cave bears *(Ursus spelaeaus*, *Ursus ingressus)* and so on. Thus, caves play a central role in examining the competition between its occupant species.

Competition for shelter

At several cave sites across Europe, carnivores and hominins have been responsible for heavy accumulation of carcass bones, which end up as extensive faunal assemblages. The level of contribution by each animal to these assemblages can help one identify the primary occupants of a certain cave site. A high herbivore-carnivore NISP ratio indicates that the cave was used primarily by carnivores, which is the case with most studied caves. There is not much evidence for herbivore use, as most present in the assemblages were ungulates which were adapted to the steppe grasslands and sparse woodlands in the open air. A low herbivore-carnivore NISP ratio would either suggest that a certain type or carnivore used the cave regularly, or that a certain carnivore species was hunted and eaten quite frequently by another. Alternatively, a low herbivore-carnivore ratio could indicate that the cave was not significantly used by carnivores, if the NISP for both herbivores and carnivores are low. The first case is well-evidenced by the overwhelming presence of cave bears at certain sites. In Pleistocene Europe, cave hyenas mainly entered and occupied caves to scavenge the carcass remains left by other predators, such as hominins, as relatively safe spaces to consume their own kills, or for denning—to safeguard and raise their offspring. The presence of coprolites and hyena cub teeth, variation in cave hyena specimen ages, and diversity in herbivore specimens with digestive corrosion are characteristic signs that indicate the use of a cave site for a hyena den. On the other hand, hominins generally used caves as temporary refuges or stopovers. What cave hyenas and humans had in common was their preference for certain locations within cave systems. Both preferred areas close to the entrance, relative to other occupants, such as smaller carnivores or cave bears. However, relative to each other, they differed in their preference. Humans stayed closer to the entrance to receive enough light and ventilation while remaining under shelter. Hyenas occupied the dark interior for a greater degree of protection from other animals, especially when the cave was used as a den. Many sites show alternating usage of the same cave by hyenas and humans and a dense, recurring presence of one could have prevented the occupation of the other (e.g. Sophie's Cave).

Competition for food

Cave hyenas and humans filled in highly similar ecological niches. One of the reasons for this is the large similarity in their diets. Many faunal assemblages are primarily modified by hyenas and

humans; thus, several criteria to distinguish human and hyena bone modification have been proposed over the years:

1. high carnivore-to-ungulate ratio
2. abundant carnivore modifications to bone surfaces
3. typical bone breakage (abundance of shaft cylinders)
4. high cranial-to-postcranial ratio
5. low representation of small hard bones
6. and U- or L-shaped age profiles
7. **Horn or Antler Over-Representation**

The type of modification also plays a significant role in discerning the agent responsible for its presence. Generally, cut marks are associated with lithic tools, which means human modification. The location of the cut marks is also an important factor; cut marks on long-bone shafts can be a result of separating flesh from bone, which human hunters often did, as they were not dedicated bone consumers like hyenas. Pits, fissures and punctures are characteristic of carnivore modification, and the largest punctures are often attributed to cave bears, hyenas or large felids (e.g. *Panthera spelaea*), and double arched punctures are specific to hyenas and felids. The greasy epiphyseal sections were particularly attractive to hyenas and other bone consumers due to its low density, which would provide easier and faster access to the nutrient-rich bone marrow within. Acidic corrosion of bones belonging to medium or large herbivores is a significant indicator of hyena modification as cave hyenas were the most prominent megafaunal bone consumers, supported by their highly specialised dentition. A notable intersection of their feeding habits and interaction with hominins was their tendency to scavenge Neanderthal corpses by digging up burials Additionally, during the first half of the MIS3 (late Middle Palaeolithic), prey choice greatly overlapped in southwest France and Italy: hyenas and humans both hunted bison and horse (*Equus ferus przewalskii*), the latter being a key prey species for cave hyenas. It is also evident that Neanderthals and hyenas consumed each other; specimens from both species display modifications attributable to each other. Whether they hunted each other or not can only be evidenced by perimortem bone modifications, or, from a more abstract point of view, cave painting depictions. Only one of either has been found.

Encounters

Hyenas and humans, with their significant niche overlap, were highly competitive, thus, encounters would likely result in dangerous conflict between individuals of either species. It can be inferred that they would have developed adaptations to avoid such a situation to the greatest extend possible, one of which could have been their alternating pattern of cave usage and preference for different areas within them. Nevertheless, encounters can be assumed to be inevitable between such prominent species within their ecosystem. Hyena teeth being on Palaeolithic necklaces suggests the possibility of them being hunted by hominins. The presence of perimortem puncture marks found on a cranial element of a juvenile Neanderthal from the Cova Negra in Spain is the only evidence found of a potential cave hyena attack, but the possibility of a simultaneous infliction by both canines belonging to a medium-sized carnivore with an inter-canine width of 17.74 mm is also considered. However, the size and depth of the puncture marks may be incompatible with the described inter-canine width. A carnivore with this inter-canine measurement would most likely not be able to create punctures of the size and depth observed in the specimen. Most encounters between hominins and cave hyenas probably occurred in the steppe plains or sparse woodlands, where hyenas hunted and scavenged like they currently do in the African savannah and sedimentary conditions were unfavourable for fossilisation. Changes in cave hyena dentition (mainly premolar) corresponding to transitions between glacial and interglacial periods show that hyenas were more adapted to hunting during the glacial periods (corresponding to increased metastyle length). Increased hunting as a result of constriction of food resources during the glacial periods indicates an increased chance of encountering hominins, due

to niche overlap; hominin encounters were probably more likely and frequent during the glacial periods where food was limited than during the interglacial periods where food was more available.

Conclusion

The nature and intensity of competition between carnivores such as cave hyenas and humans have recently been studied using notable novel methods. Caparrós et al., 2012 used path analysis to compare carnivores' influence on herbivore remains with Neanderthals', allowing an analysis of the competition between carnivores and Neanderthals. Faith, 2007 found an indirect correlation between bone density and levels of competition between carnivores. Under high levels of competition, there is no significant correlation between epiphyseal/near-epiphyseal survival and bone density. Thus, a strong correlation between epiphyseal abundance (in faunal assemblages) and bone density indicates a low level of competition because carnivores, primarily hyenas, can preferentially select low density portions. Though anatomically modern humans were the last ones standing, it would be erroneous to say that humans solely outcompeted cave hyenas. A rise in wolf contribution to faunal assemblages is contemporaneous with a decrease in the influence of cave hyenas. As the climate got warmer, the megafauna that the cave hyena preyed upon started to disappear and the hyena population moved towards the south, where they were outcompeted by wolves. The last cave hyena coprolite found is dated to 12,780 ka BP. More studies need to be conducted to gain a clearer understanding of the nature of the relationship between hominins and cave hyenas during the Pleistocene epoch.

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