

Comparative ecology and taphonomy of spotted hyenas, humans, and wolves in Pleistocene Italy

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Abstract

In Late Pleistocene Italy, spotted hyenas competed in certain niche dimensions with wolves and in other dimensions with Paleolithic humans. Spotted hyenas of the Italian peninsula consumed essentially the same ungulate species as Paleolithic humans did, and both of these predators depended heavily on bone marrow. Wolves tended to consume more hillside-adapted ungulates in the same area and period, suggesting some spatial separation of the three predators according to topography. There is complete overlap in the prey age groups commonly harvested by spotted hyenas and wolves, but pronounced differences between this pair of predators and Paleolithic humans of the Middle and Upper Paleolithic periods; from the narrow perspective of ungulate exploitation, Middle and Upper Paleolithic humans were quite similar. Taken together, there is good evidence for niche separation among the three ungulate predators during the Late Pleistocene in Italy. The intensity of bone transport to and modification at dens by hyenas varied greatly with circumstance and prey body size, indicating that prey size must be carefully controlled in comparisons of predator behavior. Populations of wolves and humans appear to have expanded toward the end of spotted hyenas' tenure on the Italian peninsula, and disappearance of the spotted hyenas from Eurasia may be best explained by rapid transformations of ecosystem structure associated with global warming after 13 KYA.

Key words

Taphonomy, zooarchaeology, cave sites, spotted hyenas (*Crocota crocuta*), wolves (*Canis lupus*), Paleolithic humans, Italy.

INTRODUCTION

When I first undertook comparisons of Pleistocene hominid and carnivore niches a decade and one-half ago, the subject seemed rather marginal to archaeology, possibly signaling imminent defection to paleontology. Since then taphonomic approaches concerned with site formation processes have bridged these fields, often in surprising ways, and made accessible insights once entirely out of scientific reach on hominid ecology and coexistence with other bone-collecting and bone-modifying predators. This presentation is a retrospective of research on the niches occupied by spotted hyenas, wolves, and Paleolithic humans in west-central Italy during the Late Pleistocene, the boundaries of which reveal behavioral information about such close neighbors in the food web. The conclusions offered here have grown from studies conducted by the author between 1985-1992, the details and methods for which appear in earlier publications (STINER, 1991a, b, 1992, 1994, 2002a). In the present circumstances, it is worth the risk of scholarly repetition, at least in summary form, in order to place the findings alongside data from the exciting new studies of hyena-collected faunas that appear in this volume. In this way scholars may advance toward comparisons across large areas of the Old World. I shall

focus on cave sites, where Paleolithic humans once lived and carnivores made their dens—mainly Buca della Iena, Grotta Guattari, Grotta dei Moscerini, Grotta di Sant'Agostino, and Grotta del Fossellone (Fig. 1). In addition to comparisons of sympatric predators in Italy, the Pleistocene data are considered against variation in the contents of modern den assemblages created by today's modern hyenas and wolves. Only the most recent issues of methodology that may affect perceptions of predator behavior are addressed so that I may concentrate on issues of behavioral ecology. The dimensions of predator niches to be compared are prey species eaten, bone processing and transport behaviors, predator-prey relations as reflected by ungulate mortality patterns, and shelter use. Finally, some thoughts are offered as to why hyenas disappeared from Europe after 14-11,000 years ago (14-11 KYA), where wolves and humans continued to flourish.

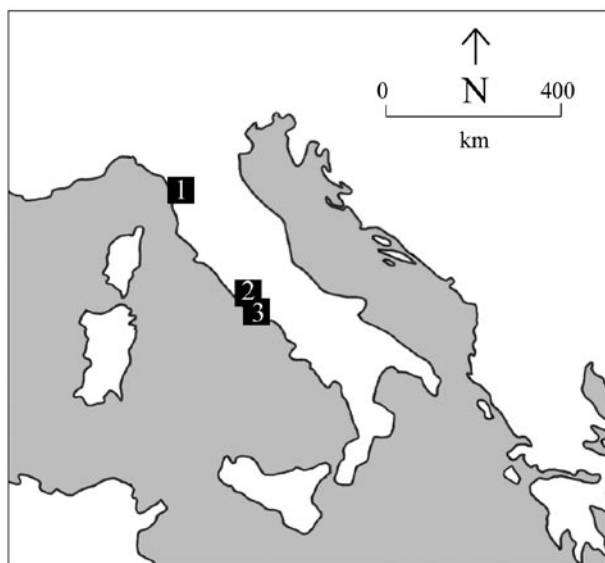
BACKGROUND AND TAPHONOMIC SIGNATURES

Hyenas frequently visited natural caves and rock overhangs on the Mediterranean Rim, using some of them as dens in which to raise their young, others

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only as short-term shelters. The paleontological record of Pleistocene spotted hyenas of west-central Italy is intermingled with Paleolithic human occupations in caves, less commonly with bear hibernation or wolf

Fig. 1: Distribution of the Italian sites discussed in the text: Area 1 - Buca della Iena; Area 2 - Grotta Guattari, Grotta del Fossellone; Area 3 - Grotta di Sant'Agostino, Grotta dei Moscerini.



den occupations (STINER, 1994). But first a word or two on what defines a carnivore den fauna: most diagnostic are the remains of cubs, obvious gnawing damage on the bones collected there in the cases of wolves and hyenas, and large quantities of coprolites (latrines) in the case of hyenas. Seldom, however, does one find “pure” occupations by one carnivore species in low elevation cave sites in Italy. Hyena or wolf signatures either dominate or, alternatively, are scant and represent only brief visitations to a cave, with remarkably little in between. A few stone artifacts often turn up in what are essentially hyena and wolf den deposits, indicating either disproportionate palimpsest accumulations, or artifact transport by sediment sheet flow (VILLA & SORESSI, 2000).

Heavy gnawing damage and other indications of carnivore activity are prevalent in the den assemblages discussed here, suggesting that hyenas or wolves were the dominant bone collectors and modifiers (STINER, 1994: 108-127). In four of the six layers (I3-6) in Buca della Iena, for example, the indications of hyena activity are overwhelming, and there are few if any traces of human activity in the form of artifacts or burned bone (Table 1). Because all materials from this site were retained by the excavators and examined by the author, it is possible to assess thoroughly the issues of skeletal representation and damage patterns. Though less completely recovered, other hyena-collected and wolf-collected assemblages from Grotta di Sant'Agostino (SX, S4), Grotta Guattari

Table 1: Damage frequencies and related information for Late Pleistocene assemblages collected principally or exclusively by spotted hyenas or wolves.

Site and level	Lithic artifacts	Ungulate NISP	Cones %	Burning %	Tool marks %	Gnawed %
<i>Spotted hyenas :</i>						
Moscerini M5	127	430	3	2	<<1	15
Guattari G0	2	849	1	0	0	50
Guattari G1	240	615	2	0	0	44
Buca d. Iena I1-2	35	105	2	0	0	40
Buca d. Iena I3	33	36	0	0	0	11
Buca d. Iena I4	46	77	0	0	0	22
Buca d. Iena I5	0	102	5	0	0	18
Buca d. Iena I6	0	299	1	0	0	52
<i>Wolves :</i>						
Sant'Agostino S4	212	134	5	0	8	19
Sant'Agostino SX	0	473	0	0	<1	17

Source: STINER, 1994: 131.

Note: Damage frequencies are percentages of ungulate NISP.

(G0-1), layer group M5 of Grotta dei Moscerini, and Grotta del Fossellone also provide valuable information. The frequency of gnawing damage in carnivore dens varies a great deal, but is usually in excess of 10% of the total number of identifiable macromammal specimens (NISP), in sharp contrast to the $\leq 2\%$ typical of cultural accumulations of the same period. Low frequencies ($\leq 3\%$) of “cone” fractures – that is, compression fractures on compact bone that retain partial herzian cone morphology – are typical of hyena- and wolf-imposed damage to ungulate remains in the Italian and other den assemblages examined. Humans generate similar fractures with hammerstones at much higher frequencies during marrow processing, usually well over 6% in ungulate faunas. The difference in cone fracture frequencies between the assemblages generated by humans and large carnivores is explained by mechanical differences in how humans and large carnivores process bones of equivalent size: humans use stone hammers, whereas hyenas and wolves must expended far more energy in the form of direct compression in the jaws to produce the same kind of fracture.

Many hyena and wolf den faunas are rich in both ungulate and carnivore species, and the assemblages may display high ratios of *large* carnivores in particular (Table 2). Although there are no hard and fast rules on this point, high frequencies of large-bodied carnivore remains in den faunas contrasts with the situation in most human-collected faunas of the Middle and Upper Paleolithic (STINER, 1994, but see STINER *et al.*, 1996 on cave bears).

Much of this richness in carnivores ($>10\%$) appears to be the result of inter- and intraspecific competition. The ratio may be enriched by scavenging and infant mortality in the resident, reproducing species. Where long accumulation times and bioturbation are involved, time-averaged palimpsests (representing multiple, separate occupation events) may further enrich the array of carnivore species represented in den assemblages.

COMPARISONS OF UNGULATE PREDATOR NICHES

Prey Species

The main prey of spotted hyenas, wolves, and humans in Late Pleistocene Italy were red deer (*Cervus elaphus*), aurochs (*Bos primigenius*), horse (*Equus caballus*), roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), wild boar (*Sus scrofa*), and ibex (*Capra ibex*). Spotted hyenas consumed horses somewhat more often than did Paleolithic humans, but there are no very significant statistical differences in prey species or proportions eaten by these two predators where they coexisted (STINER, 1992). A preference for lowland habitats is suggested by the slight bias to horses and the near absence of ibex in the hyena diets (see also VERESCHAGIN & BARYSHNIKOV, 1984). Wolf diets were quite different in the same localities, with heavy reliance on slope-dwelling ibex and roe deer.

Table 2: NISP frequencies of ungulate and carnivore remains and species richness in Late Pleistocene faunal assemblages collected principally or exclusively by spotted hyenas or wolves.

Site and level	% Carnivore NISP	N Carnivore species	% Ungulate NISP	N Ungulate species
<i>Spotted hyenas :</i>				
Moscerini M5	30	5	70	6
Guattari G0	11	4	89	9
Guattari G1	11	4	89	6
Buca d. Iena I1-2	44	4	56	7
Buca d. Iena I3	72	5	28	6
Buca d. Iena I4	63	6	37	8
Buca d. Iena I5	56	6	44	9
Buca d. Iena I6	41	3	59	9
<i>Wolves :</i>				
Sant'Agostino S4	21	5	79	7
Sant'Agostino SX	20	5	80	6

The possibility that the perceived bias toward large-bodied ungulates in the carnivore den assemblages is a product of more complete consumption of smaller ungulate bones cannot be wholly excluded, but the prey profile observed in Italy is consistent with the prey body size range typical of recent spotted hyenas, human hunter-gatherers, and wolves. Wolves' greater focus on ibex and roe deer in Italy may have lowered the probability of competitive interference with hyenas and Middle Paleolithic humans. It is interesting that the wolves and spotted hyenas seem to display negative abundance relations over time, with wolf populations expanding in the region as hyenas disappeared (STINER, 1994).

Prey Age Selection

Variation in prey age selection by spotted hyenas in Late Pleistocene Italy is indistinguishable from patterns documented for modern African spotted hyenas (STINER, 1990, 1994). They are cursorial predators with a well-defined tendency to produce "attritional" or U-shaped mortality patterns while hunting common prey species, whether feeding on red deer, aurochs, and equids in Italy or antelopes and zebra in sub-Saharan Africa; prime-adult prey are notably under-represented relative to the structure of a living population (Fig. 2). Wolves have a similar relationship with prey populations both now and in the past, making the observed differences in wolves' major prey species in Pleistocene Italy significant. The U-shaped prey mortality patterns generated by hunting spotted hyenas and wolves stem from the way in which they isolate individual prey and chase them, often over long distances. These generalizations do not ignore the existence of exceptions but instead describe the broader patterns in predator behavior and ecology. Significant as well are observations that non-confrontational scavenging of larger ungulate carcasses is more likely to result in an old-age bias in modern den assemblages (e.g., TILSON *et al.*, 1980; STINER, 1994), although this is not particularly visible in the Late Pleistocene Italian cases, where there was a heavy emphasis on hunted prey by spotted hyenas and wolves.

The spotted hyenas and wolves of Pleistocene Italy contrasted greatly with Paleolithic humans with respect to prey age selection, as humans tended to hunt adult animals in the prime of life (Fig. 2). Evidence of this kind of niche separation emerged by at least the late Middle Pleistocene (STINER, 2002a; n.d.). The separation between hominids/spotted hyenas vs. wolves on prey species emphasis, but hominids vs. wolves/hyenas on prey age selection adds up to composite distinctions in their respective predatory niches. Thus there is evidence of limiting similarity or niche separation among the three predators in the time frame and area encompassed by this study. The same properties do not distinguish

effectively between Middle and Upper Paleolithic adaptations, however; other behavioral dimensions must be considered for this purpose (STINER, 1994, 2002a).

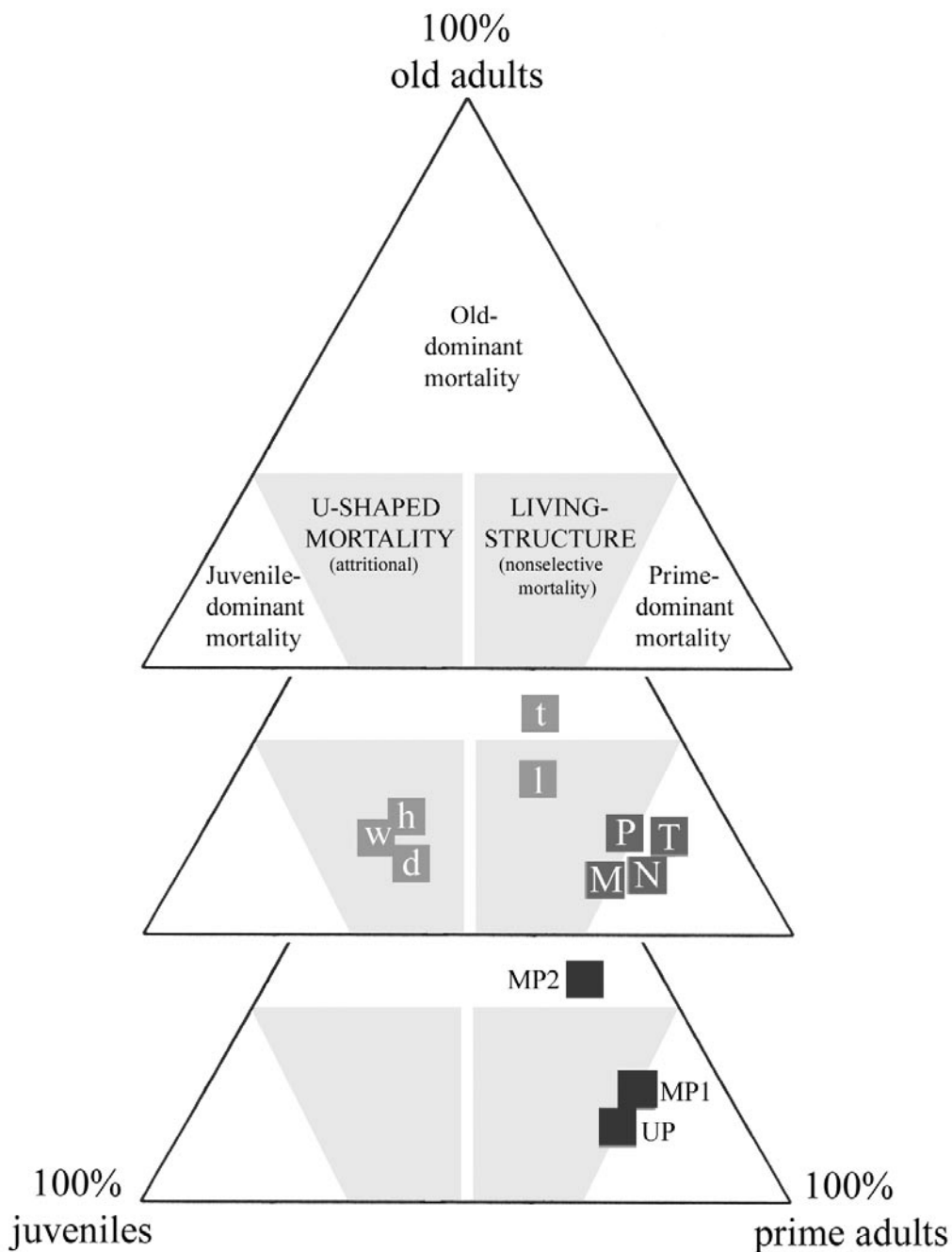
Bone Processing

The extent to which hyenas chewed up bones was a good deal less than has been reported for some modern captive animals. Punctures, tooth drag marks, and salivary rounding are common on bones in the Italian den sites, but "tubes" (long bones lacking both ends) are few (STINER, 1994, 2002b). Gnawing by wolves at Grotta di Sant'Agostino (layers SX, S4) also is highly visible, but the extent of damage falls well short of the total destruction of skeletal elements. MNE counts (minimum number of skeletal elements) based on long bone shaft features and the more abundant of the two ends of long bones are about the same in completely recovered assemblages from Buca della Iena and Middle and Upper Paleolithic assemblages of the same region. These results contrast markedly with what MAREAN & KIM (1998) report for the Middle Paleolithic fauna from Kobeh Cave in Iraq, wherein long bone shaft MNEs are said to be up to eight times as abundant as either end due to hyena activities at the site.

In Situ Bone Attrition vs. Evidence for Food Transport

Body part profiles in shelter faunas potentially yield information on the circumstances in which carcasses were acquired by predators, provided that *in situ* attrition of bones or archaeologists' recovery practices have not further biased the anatomical content of an assemblage. Because of demonstrable correlations to prey densities on landscapes and a predator's emphasis on hunting vs. scavenging in modern contexts (STINER, 1991a), prey body part representation in transported bone assemblages should be informative about predator behavior in the past. There has been much concern recently, however, about how density-mediated bone destruction, whether from gnawing or chemical decomposition, and MNE estimation techniques may distort archaeologists' perceptions of prey body part profiles in prehistoric sites. The Italian cave sediments are rich in calcite and related minerals, and the macroscopic appearances of the bones suggest little in the way of chemical dissolution (*sensu* STINER *et al.*, 2001). Thus the greater taphonomic concern is possible *in situ* attrition caused by biological agencies, particularly spotted hyenas and large canids. The extent of ravaging is thought by most zooarchaeologists to be conditioned by variation in the mineral or structural "density" of bone tissues (*sensu* LYMAN, 1984, 1991), particularly the contrast between compact and cancellous (spongy) macrostructures. Currently there is much

Fig. 2: Mean values for ungulate mortality patterns created by various human and nonhuman predators. Means are based on the percentages of juvenile, prime adult, and old adult prey in multiple death assemblages, grouped by predator agency and plotted in tripolar format (from STINER, 1990, 1994). Shading represents natural variation in the age structure of living ungulate populations and thus also nonselective mortality patterns (right panel); mortality patterns caused by attritional factors, such as disease, accidents, and malnutrition (left panel). Predators that ambush their prey ([t] tigers & [l] lions) tend to be non-selective with respect to age. Cursorial or long-chase hunters, such as [h] spotted hyenas, [w] wolves, and [d] African wild dogs, instead tend to produce attritional mortality patterns that overlap almost completely with those caused by nonviolent factors. The corners of this graph represent strong biases toward the designated prey age groups. Humans, from the Middle Paleolithic through recent times, tend to generate mortality patterns in ungulate prey that are slightly to strongly biased in favor of prime adult animals. Open circles represent various Holocene human cultures (Paleoindian/Archaic [p], Mississippian farmers [m], Nunamiut Eskimo [n], trophy hunters in modern game parks [t]). MP¹ is the mean for most Middle Paleolithic hunted faunas (250 KYA to 32 KYA) and closely resembles that for the Upper Paleolithic (UP). MP² refers to a handful of esoteric cases from coastal Italy, dominated nearly exclusively by the head parts of old adult prey, apparently obtained by scavenging, and coinciding with small-scale marine shellfish exploitation.



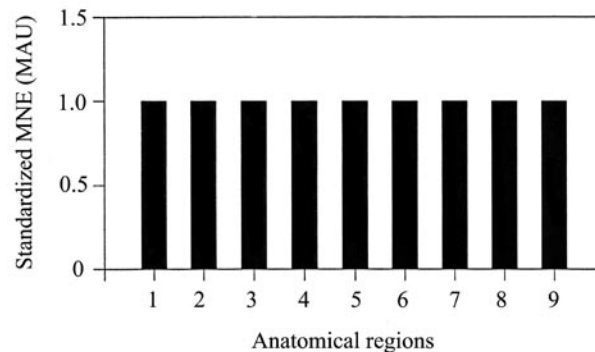
variation in the working definitions of skeletal density, the structural scale at which resistance of destruction is modeled, and the anatomical standards used as controls (compare LAM *et al.*, 1998, 1999; LYMAN, 1991, 1994; MAREAN & KIM, 1998).

My approach to identifying biases in body part representation in Pleistocene ungulate faunas circumnavigates variation in mineral density in the skeleton (STINER, 2002b). The MNE for each skeletal member of a given taxon is estimated from the most common morphologically unique “portion” or feature represented in a faunal assemblage. The technique differs from most others in focusing primarily on one common level of mineralization across the entire skeleton – compact bone – or estimating MNE values. Compact bone is the most widely distributed of macrostructure classes in vertebrate skeletons, with the partial exception of the vertebral column. End (epiphyseal) and shaft features of limb elements both are considered in the construction of MNE counts used in this study (e.g. Buca della Iena), unless incomplete recovery by excavators prohibits this (Guattari, Sant’Agostino, Moscerini); limb shafts lacking diagnostic features were discarded but all limb ends systematically retrieved by the excavators at the latter sites. Yet even this concern about past recovery practices is alleviated by the profiling technique (STINER, 2002b). For the skull, only bony portions are used for the comparisons to post-cranial MNEs; mature tooth enamel is much denser than any kind of bone tissue and thus not appropriate for this application (STINER, 1991a, 1994: 240-5).

The profiles are based on a simplified array of nine anatomical regions: (1) the horn/antler set, (2) head, (3) neck, (4) the rest of the axial column including the ribs and pelvis, (5, 6) upper and lower front limbs, (7, 8) upper and lower rear limbs, and (9) feet. The MNE counts for each region are standardized relative to the number of the same element types present in one complete skeleton [standardized MNE (STINER, 1991a), or BINFORD’s MAU (1981)]. If complete animals were transported to a shelter by a predator, and potential biases from density-mediate attrition are properly controlled, the values for all anatomical regions of prey bodies will be equal (Fig. 3). Species-specific and ungulate body size groups are pooled in the calculations to increase sample sizes and in recognition of the fact that some elements and portions of elements are more diagnostic of species or genera than are others.

The conceptual basis for this profiling technique is well supported by LYMAN’s (1984, 1985, 1991) and other’s (reviewed by LYMAN, 1994) estimates of variation in mineral density. Figure 4 shows the relation between my MNE profiling method and the potential impact of differences in bone mineral density as measured for similar taxa via photon densitometry. Data on deer are presented, but relative differences in bone mineral density in the skeleton are similar among artiodactyl and

Fig. 3: Expected body part profile if all skeletal parts of ungulate prey are present (and preserved) in a faunal assemblage.



perissodactyl species (LAM *et al.*, 1999; LYMAN, 1994). The chances for reduced recognizability and thus bias in MNE estimates are about the same for heads and major limb bones; a F-ratio indicates that there are no major differences among pooled cranial, limb, and foot regions ($n=32$, $r^2=0.27$, $p=0.124$) (STINER, 2002b). Upper front limbs and foot bones have a somewhat lower probability of preservation than heads and other limb regions (Table 3b), but these are minor differences (Table 3a). The risks of over-interpretation in this anatomical profiling technique actually center on the vertebral column, which is not crucial to the presentation below. Head, horn/antler, and limb regions will be used to create anatomical indexes for the inter-assemblage comparisons.

Moving on to the predator-collected assemblages, Figure 5 illustrates general patterns of variation in body part profiles of medium-sized ungulates collected by six kinds of predators in shelters or excavated den sites of modern and Pleistocene age (STINER, 1991a, 1994; data sources are BINFORD, unpublished; BRAIN, 1981; BUNN, 1983; HENSCHER *et al.*, 1979; HILL, 1980; MILLS & MILLS, 1977; SKINNER *et al.*, 1986; on striped and brown hyenas, SKINNER *et al.*, 1980; SKINNER & VAN AARDE, 1991). The relative balance between head and limb parts seems to reflect basic differences in how food is acquired and the degree of food dispersion in the environment. Striped and brown hyenas are obligate scavengers; wolves are principally hunters.

Of special importance for understanding food acquisition strategies of the ungulate predators for these data is the relative abundance of cranial and major limb bones, examined here as the anatomical index, $(H+H)/L$. It is the sum of horn/antler MNE and head MNE, divided by the total MNE for major limb elements, excluding phalanges. In a wide range of modern cases involving three hyena species and wolves, anatomically balanced representation of horns/antlers and heads relative to limb bones reflects access to relatively complete carcasses, obtained mainly via hunting (or artificial supplements

Fig. 4: Ranges and mid-points of variation in bone structural density for nine anatomical regions of the artiodactyl skeleton, using STINER's (1991) profiling method and LYMAN's (1994) photon densitometry data for deer.

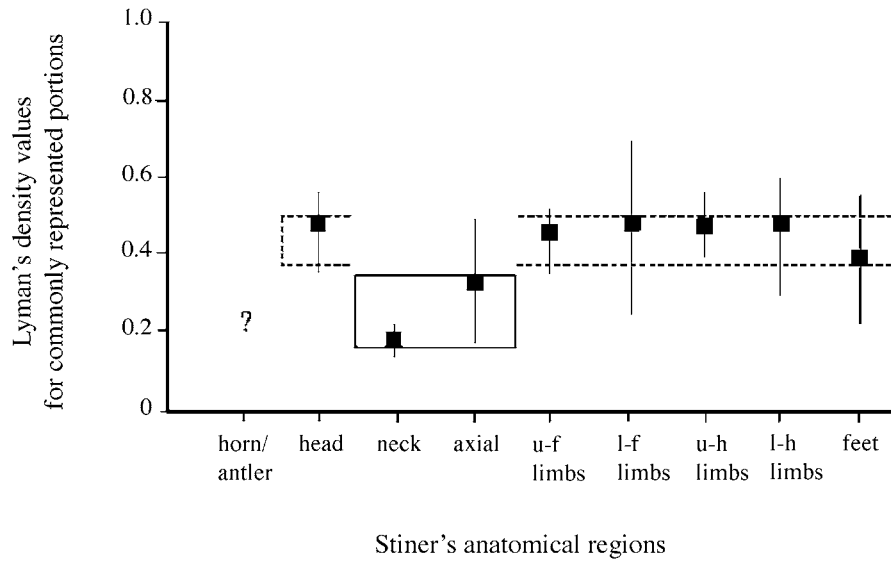


Table 3: Evaluation of differences in mean mineral density for the “portions of elements” most commonly used to estimate MNE by anatomical region, based on LYMAN's photon densitometry control data for deer.

a. Mean photon densitometry values by anatomical region:

anatomical region	N-portions considered	mean density	range	sd
head	5	0.52	0.09	
upper front limb	6	0.38	0.11	
lower front limb	6	0.54	0.13	
upper hind limb	3	0.42	0.14	
lower hind limb	7	0.52	0.18	
feet	5	0.36	0.12	

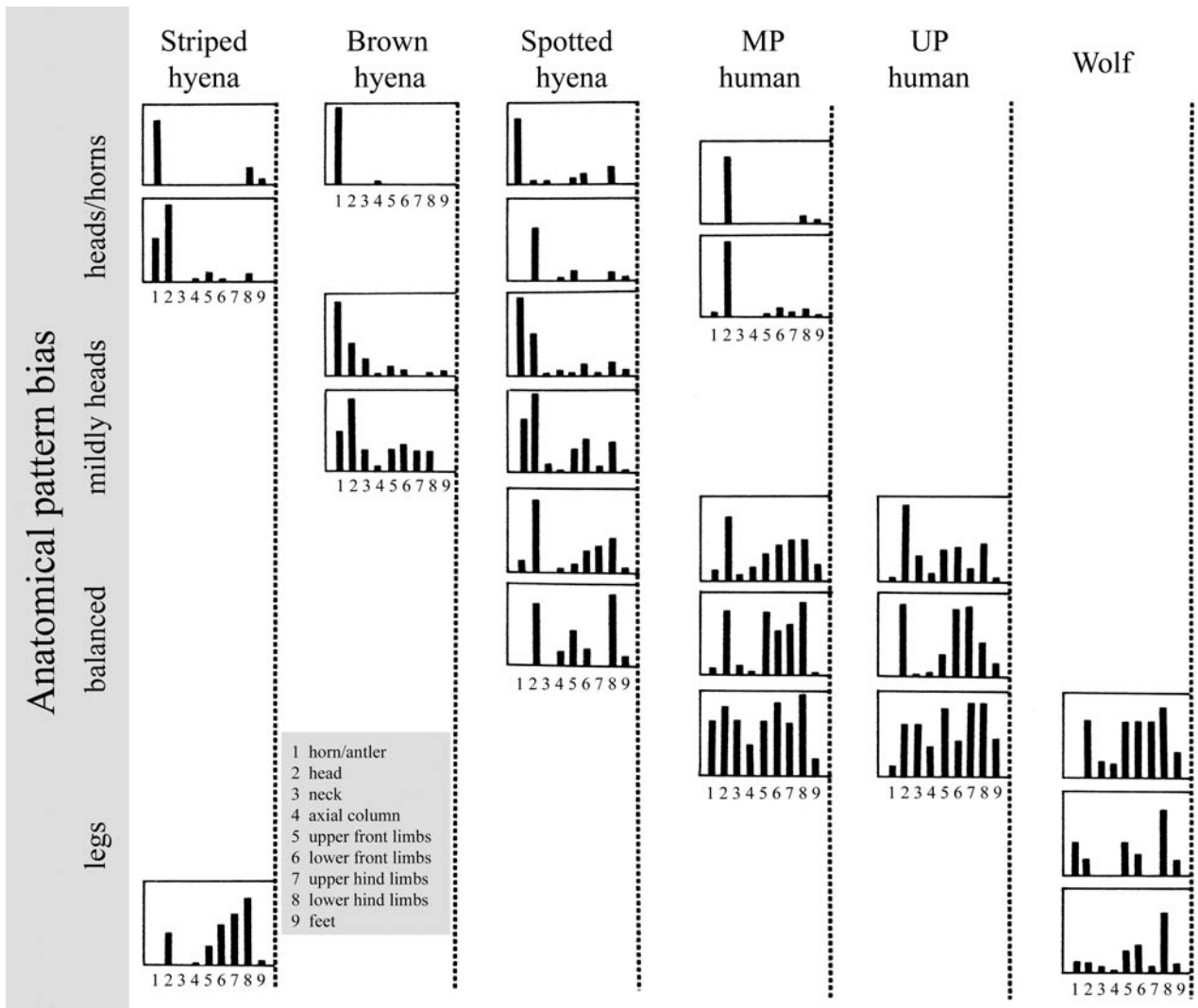
b. Statistical test of difference in mineral density among anatomical regions:

anatomical region pair	t	df	p	difference in means
head-upper front limb	2.251	9.0	0.051	0.138
head-lower front limb	-0.347	8.7	0.737	-0.023
head-upper hind limb	1.075	2.9	0.362	0.100
head-lower hind limb	-0.037	9.3	0.972	-0.003
head-feet	2.292	7.3	0.054	0.158

provided by biologists) (STINER, 1991a). These conditions also suggest a relatively concentrated food supply (KRUUK, 1972; MILLS, 1989). *Confrontational* scavenging simply produces the same signal as hunting in these contexts, because primary access to carcasses normally occurs by force. By contrast, a bias toward head and horn/antler parts and fewer elements transported per carcass source relates both to a higher component of *non-confrontational* scavenging and, more telling, a more dispersed food supply. The (H+H)/L index cannot provide fool-proof diagnoses of isolated assemblages. However, because it can be related to habitat variation in modern settings, it is useful for examining the habitual behaviors and ecology of prehistoric predators in the context of inter-assemblage comparisons.

The relationship between (H+H)/L and foraging strategies of Pleistocene and modern large predators (humans, wolves, three species of hyena) is strongest for medium-sized ungulates, also the most common prey in most regions. Wolves produce leg biases most consistently, whereas spotted hyenas and Middle Paleolithic humans associate with the greatest diversity in anatomical patterns in ungulate prey. As demonstrated above, these phenomena cannot be explained by density-mediated bone attrition. It is interesting that the (H+H)/L values for the Italian cases cluster close to but somewhat short of perfect anatomical balance (Table 4), within the total range displayed by modern spotted hyenas but suggesting an emphasis on hunted meat; modern spotted hyenas routinely switch between scavenging and hunting of large mammals or displacing other large predators from fresh kills. The (H+H)/L values for small ungulates (e.g., roe deer) are about the same as for medium ungulates (Table 5), whereas Figure 6 shows a bias favoring legs

Fig. 5: The full extent of variation in anatomical patterns in medium ungulate remains collected at shelters by six ungulate predators (recent & Pleistocene), based on standardized MNE data for nine anatomical regions (from STINER, 1991a).



in three of the four large ungulate (aurochs & horse) samples available for comparison. HORWITZ (1998) in her study of modern striped hyena dens observes a similar relation between body part representation and prey body size.

The extent of bone destruction by carnivores is mediated by many factors. Food dispersion is one issue, because it affects the energetic balance between food transport and processing costs. The size and mass of skeletal parts is another factor, a matter of the relation between consumer body size and prey body size. Larger bones are more difficult to destroy, and Pleistocene and modern spotted hyenas tend(ed) to feed on large mammals 6-14 times their own body weight, and roughly an order of magnitude larger on average than domestic caprovines used in captive feeding experiments by MAREAN and

colleagues (MAREAN & SPENCER, 1991; MAREAN *et al.*, 1992). This could be the root of the discrepancy between experiment results and those for Pleistocene cave sites other than Kobeh Cave (HORWITZ, 1998; KLEIN & CRUZ-URIBE, 1998; KLEIN *et al.*, 1999; DELPECH, 1998; STINER, 1998, 2002b).

Many of the Late Pleistocene hyena-collected assemblages in Italy also display a conspicuous bias toward horn/antler parts, the most famous example being layers G0-1 of Grotta Guattari (STINER, 1991b, 1994: 257-260). Strong biases toward horn parts (HORN/L) are typical of modern spotted hyena dens (Table 4), slightly less but still prominent in the Pleistocene Italian dens, where deer antler occurs along with bovid horn cores. A few Middle Paleolithic ungulate faunas from Italy are dominated by head parts (Moscerini M2-M4,

Table 4: Summary data on anatomical representation for medium-sized ungulate prey collected by spotted hyenas or wolves in Late Pleistocene shelter sites in Italy and in modern den sites of other world regions.

Assemblage	Prey	tMNE	(H+H)/L	HORN/L	HEAD/L
MODEL (expected values):	~106	0.30	<0.10**	0.20	
<i>Spotted hyenas in Pleistocene Italy:</i>					
Buca d. Iena I1-4	red deer	44	0.81 +	0.64 +	0.18
Buca d. Iena I5-6	red deer	64	1.31 +	0.56 +	0.75 +
Guattari G0	red deer ^φ	186	0.77 +	0.19 +	0.58 +
Guattari G1	red deer ^φ	81	0.65 +	0.05	0.60 +
Moscerini M5	red deer ^φ	94	0.65 +	0.04	0.61 +
<i>Spotted and brown hyenas in modern Africa:</i>					
Timbavati	all spp.	135	4.31 ++	1.54 ++	2.77 ++
Kalahari '81	C II bovids	26	2.60 ++	1.40 ++	1.20 ++
Kalahari '81	C III bovids	49	2.20 ++	1.40 ++	0.80 +
Natab	C III bovids	40	0.67 +	0.58 +	0.08
Zimbabwe	wildebeest	12	1.67 +	0.00 –	1.67 ++
Amboseli	all spp.	~279	0.23 –	0.00 –	0.23
<i>Wolves in Pleistocene Italy:</i>					
Sant'Agostino S4	red deer ^φ	9	0.14 –	0.00 –	0.14 –
Sant'Agostino S4	ibex	25	0.12 –	0.00 –	0.12 –
Sant'Agostino SX	ibex	128	0.13 –	0.04 –	0.09 –
<i>Wolves in modern Alaska (North America):</i>					
WD1	caribou	93	0.05 –	0.01 –	0.03 –
WD2	caribou	25	0.18 –	0.00 –	0.18
WD3	caribou	20	0.17 –	0.08	0.08 –

Source: STINER, 1994: 253-254.

(MODEL) refers to the expected value for the major skeletal members in one complete artiodactyl skeleton; (~) estimate is for an artiodactyl skeleton. Observed value is (–) lower than, (+) higher than, or (++) much higher than the expected value. (tMNE) total minimum number of elements for all major skeletal members; ([H+H]/L) horn/antler plus head MNE divided by total limb MNE; (HORN/L) horn/antler MNE divided by total limb MNE; (HEAD/L) head MNE divided by total limb MNE.

**Varies with species, age, or sex; thus only the upper limit is provided for this ratio.

^φ Also includes fallow deer in low frequencies.

M6), but none displays a bias toward horns and antlers. Pronounced antler/horn biases appear to be an exclusively hyena signature, at least where and when antler was not an important raw material in human technology (e.g., some Upper Paleolithic cultures). This pattern no doubt is explained by the hyena's unique ability to digest hard skeletal structures.

HYENA AGE STRUCTURES AND DEN SITES

One reliable indication of den complexes in caves is

the presence of cubs among the hyena or wolf remains (Table 6). More than 70% of individual hyenas in Buca della Iena (I1-6), Grotta Guattari (G0-1), and Grotta del Fossellone are juveniles, based on premolar eruption and wear patterns (Fig. 7, 8). This is also true for the wolves in Sant'Agostino (Layers SX, S4; STINER, 1994: 316-331). In the case of spotted hyenas, the high volume and concentrations of coprolites indicate long-term den occupations. Likewise, the high numbers of young spotted hyenas in the Italian dens (Fig. 9) may suggest den sharing by clan females, as documented in some African cases today (KRUUK, 1972). Because of the extended

juvenile dependency (up to 2 years, KRUK, 1972) and den sharing by clan females, modern spotted hyenas have among the longest (collective) den occupancy periods of all carnivores, potentially spanning many years and excluding throughout that time occupations by other predators such as humans or wolves. Wolves' denning periods are very brief by contrast (e.g., EWER, 1973). In the Italian caves, slow turnover in hyena and hominid occupations seems more than anything to reflect changes

in the shape and size of the interior; as a cave gradually filled with sediments and vertical space declined, hyenas took over the cramped dark interiors.

Evidence for interspecific aggression and cannibalism is not easily distinguished in the den faunas, but gnawing damage on young hyena bones is likely to have been from conspecifics, including sibling cannibalism (e.g., KRUK, 1972). Piece-meal body part representation of carnivores other than hyenas in these sites (STINER, 1994) suggests that most or all of them were prey of the hyenas, a general indication of predator competition, and high carnivore species richness in the Italian Pleistocene assemblages (see Table 2) is consistent with this assessment.

While alternating predator occupations in caves are a widely repeated feature of Pleistocene faunal series, GAMBLE (1986) in his survey of species composition in Mediterranean sites demonstrates the eventual exclusion of large carnivore occupations from human sites following the Last Glacial Maximum. This shift may be linked to unprecedented demographic growth in human populations (STINER *et al.*, 2000), especially after about 14 KYA.

Table 5: Summary data on anatomical representation for small- and large-bodied ungulate prey collected by spotted hyenas in Late Pleistocene shelter sites in Italy.

Assemblage	tMNE	(H+H)/L
MODEL (expected values):	~106	0.30
Small Ungulates:		
Buca d. Iena I1-4	13	0.01 –
Buca d. Iena I5-6	11	0.80 +
Guattari G0-1	9	0.40
Moscerini M5	72	0.69 +
Large Ungulates:		
Buca d. Iena I1-4	37	0.09 –
Buca d. Iena I5-6	63	0.01 –
Guattari G0-1	113	0.45 +
Moscerini M5	18	0.01 –

Source: STINER, 1994: 255-256.

Note: Acronyms, symbols, and model as in Table 4. Small ungulates are dominated by roe deer; large ungulates by aurochs and horse.

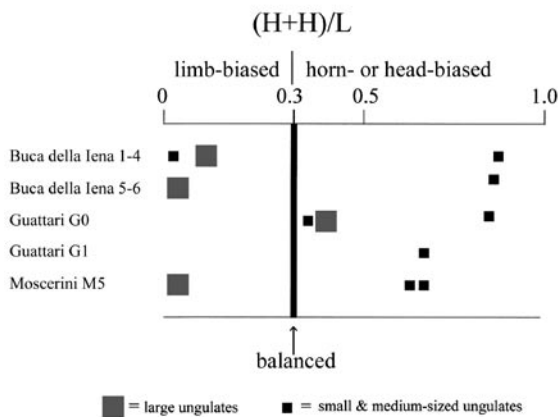
WHY DID SPOTTED HYENAS DISAPPEAR FROM EUROPE?

Recent paleontological finds in Spain, Italy, Georgia, and China suggest a late Early Pleistocene date of entry for hominids in Europe and Asia, along with the primitive hyena, *Pachycrocuta brevirostris*, and the sabre-toothed cat, *Megantereon whitei* (ARRIBAS & PALMQVIST, 1999; MARTÍNEZ-NAVARRO & PALMQVIST, 1995). TURNER (1984, 1985) and TCHERNOV (1992, 1994) suggest that early hominid incursions to Eurasia around the Early-Middle Pleistocene boundary were made possible by climate change and significant turnover in the membership of large mammal communities around that time. With subsequent climate cooling, hominids and spotted hyenas held fast to most of the regions they had colonized.

Table 6: Age structures of spotted hyena and wolf remains in the Italian cave sites.

Site	Dental element	MNI	% Juveniles	% Prime adults	% Old adults
<i>Spotted hyenas:</i>					
Guattari	dP ₃ -P ₃	6	73	27	0
Buca della Iena	dP ₃ -P ₃	12	71	29	0
Fossellone	dP ₃ -P ₃	11	72	27	0
<i>Wolves:</i>					
Sant'Agostino	M ₁	6	73	27	0

Fig. 6: Horn/head to limb ratios ((H+H)/L) for small, medium, and large ungulates in Pleistocene hyena dens of Italy.

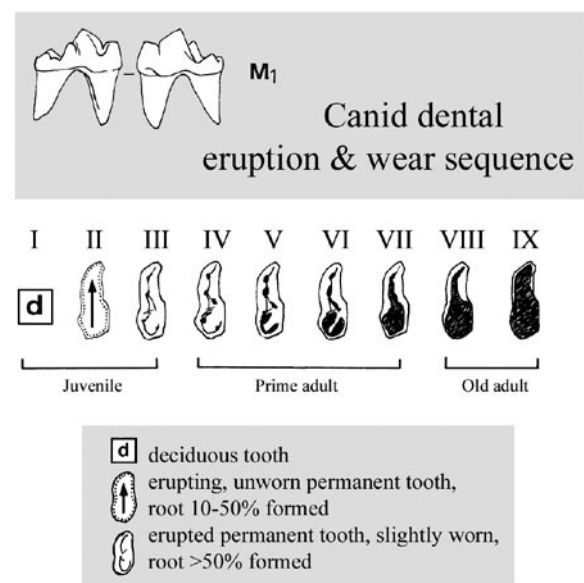


Oddly spotted hyenas disappeared from Europe, along with the cave bear, between 20-10 KYA (hyenas closer to 13-11 KYA, STUART, 1991). Though spotted hyenas are versatile animals in many aspects, some properties of the species appear less flexible, such as its affinity to open habitats and low altitudes (VERESHCHAGIN & BARYSHNIKOV, 1984). Spotted hyenas' heavy dependence on cervids on the Italian peninsula underscores the lack of modern analogs for the animal communities that dominated Eurasia during the Pleistocene. Yet other aspects of spotted hyena behavior are common to virtually all Pleistocene and modern variants, independent of regional differences in habitat and prey availability, and these properties may explain the hyena's eventual disappearance from Europe and Asia. With the decline of grasslands after 12.5 KYA (e.g., MADEYSKA, 1999), Europe may have experienced catastrophic loss of the kinds of habitats most suited to spotted hyenas, and a corresponding increase in mixed woodlands. Under these circumstances, spotted hyenas would have been inferior competitors to wolves, the latter being as much at home in forests as in open lands, and in highlands as in lowlands. This is also the period of wolf domestication in Eurasia, expanding the life space of *Canis* in close proximity to humans as well as in the wild.

SUMMARY

The foraging conditions for ungulate predators – spotted hyenas, wolves, and Paleolithic humans – in Late Pleistocene Italy included a moderately concentrated food supply, and all three species relied heavily on hunted prey. Spotted hyenas and wolves of Pleistocene Italy displayed cursorial hunting patterns and did not differ substantially from modern representatives in this regard. Prey species selection by spotted hyenas and Paleolithic

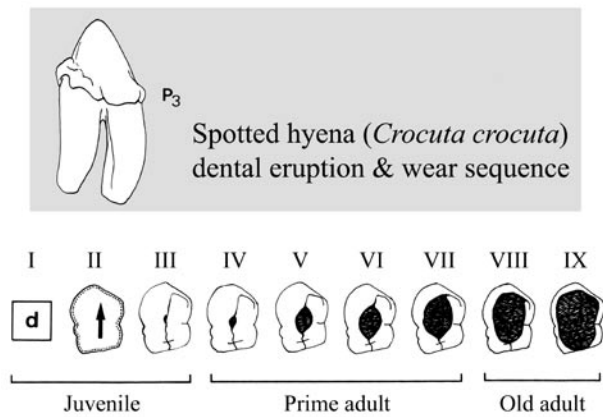
Fig. 7: Canid tooth eruption-wear sequence based on the M_1 , illustrated here for red fox (*Vulpes*) but applicable to *Canis*. The age stages are divided into nine cohorts, collapsible to three. The sequence begins with development of the deciduous tooth, followed by development and emergence of the permanent counterpart. The sequence ends with nearly complete destruction of the permanent tooth by occlusal wear. Note that this system makes no attempt to estimate real age in years for any cohort, nor does it assume that the cohorts are equal in duration; neither assumption is necessary for the age structure comparisons if the criteria are applied consistently (adapted from STINER, 1994, fig. 12.3).



humans overlapped greatly in Italy, less with wolves. The latter predator relied on more small ungulates on average, and more woodland and highland species than was typical of spotted hyenas or Middle Paleolithic humans; slope-dwelling species are common in some Upper Paleolithic faunas, however. There is a mild bias in favor of equids in the Italian hyenas' diet, perhaps due to the open settings where they preferentially hunted. In Italy hyenas transported bones to dens in appreciable quantities, as did wolves. Evidence of gnawing is widespread in these faunas, but the extent of *in situ* destruction of ungulate skeletal elements was limited. I find no evidence for extensive pilfering of bone from human sites in the Mediterranean Basin, nor habitually heavy and indiscriminant consumption of all limb ends in hyena dens.

Hyena-collected assemblages intercalate with those created by other large carnivores and Paleolithic humans in many Italian cave sites. Some wolf occupations are apparent but less common in Italian cave records overall. The phenomenon of alternating shelter occupations by

Fig. 8: Hyena tooth eruption-wear sequence based on the dP₃. Suitable with minor adjustments for the upper third premolar. Other information as in Figure 7 (adapted from STINER, 1994, fig. 12.6).



humans and non-human predators began at least 200-250 KYA in western Asia and Europe (e.g., BRUGAL & JAUBERT, 1991; GAMBLE, 1986; STINER, 1991b, 1994; STRAUS, 1982), coinciding with greater cave use by hominids overall. As noted by GAMBLE (1986), alternating use of caves by hominids, spotted hyenas, bears, and wolves was particularly common in the Mediterranean Basin, with many examples from Italy (e.g., BONFIGLIO *et al.*, 2000, 2001; GIACOBINI, 1990-91; PITTE & TOZZI, 1971; STINER, 1991b, 1994; WHITE & TOTH, 1991), France (e.g., BRUGAL & JAUBERT, 1991; VILLA & BARTRAM, 1996), Germany (e.g., GAMBLE, 1999), and western Asia (SPETH & TCHERNOV, 1998; and on recent hyena dens, see HORWITZ, 1998; HORWITZ & SMITH, 1988). In some cases, the spatial associations of artifacts and carnivore-collected materials resulted from the slope wash into natural traps (VILLA & SORESSI, 2000), but other cases clearly resulted from primary disposal on-site of materials by different predators at different times. Where hominid components are thin and ephemeral, carnivore components often are thick and easily recognized, and vice versa. The near disappearance of intercalated hominid- and carnivore-collected faunas on the Mediterranean Rim after the Last Glacial Maximum may be partly a product of declining hyena populations and increasing human populations, and more frequent re-use of places by humans.

Wolves may have quickly filled the niche vacated by spotted hyenas. Some researchers have suggested that wolves played a more direct role in squeezing hyenas out of Europe. Data points on this question are few, but in west-central Italy hyenas appear to be more abundant in the earlier paleontological records, whereas wolves are more abundant later. Certainly the spotted hyena was not pushed out of Europe by climate deterioration of the Last Glacial Maximum. They could have been displaced

Fig. 9: Juvenile spotted hyena mandibles from Grotta del Fossellone, Monte Circeo, in various stages of development.



by other ungulate predators (see also VERESHCHAGIN & BARYSHNIKOV, 1984), but the collapse of certain prey populations and associated carcass availability to scavengers may also have been a major factor. It is interesting that these changes had little if any deleterious effect on sympatric wolves or humans.

An end-member of Middle and Late Pleistocene ungulate predator guilds in Europe, spotted hyena populations began to shrink after roughly 20 KYA. They disappeared completely from this continent between 14-11 KYA (STUART, 1991:484), and earlier in some areas (VERESHCHAGIN & BARYSHNIKOV, 1984). The spotted hyenas' presence in Late Pleistocene animal communities of Eurasia was strongly felt prior to this time, and the paleontological records that they created in caves are widespread and abundant (KURTÉN, 1971: 207; PITTI & TOZZI, 1971; VILLA & BARTRAM, 1996; STINER, 1991b, 1994; BRUGAL & JAUBERT, 1991; VERESHCHAGIN & BARYSHNIKOV, 1984). Though versatile in many regards, spotted hyena adaptations may be less flexible in their affinity to open habitats and relatively low altitudes. With the fragmentation/decline of the vast Pleistocene grasslands and semi-open woodlands after about 12.5 KYA (e.g., MADEYSKA, 1999), spotted hyena populations may have suffered radical loss of habitat area and, in this

context, were unable to compete effectively with wolves and humans. As humans and canids became more closely locked in co-evolving relations in Eurasia, the once bold presence of spotted hyenas in cave records gave way to quiet disappearance.

ACKNOWLEDGMENTS

Many thanks to my Italian colleagues, A. SEGRE, E. SEGRE-NALDINI (Istituto Italiano di Paleontologia Umana), A. BIETTI (Università di Roma), P. CASSOLI, and A. TAGLIACCOZZO (Museo Pigorini) for their unflinching assistance in this long-term research project, and to the organizers, J.-P. BRUGAL and P. FOSSE, of the UISPP symposium dedicated to the memory of our friend and colleague, Philippe MOREL. This paper hardly lets on to the fact that, actually, Philippe and I always liked the bears a bit more than the hyenas, and it was on the subject of Pleistocene cave bears that we came to know one another well. A light went out when we lost Philippe, and I will miss him.

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