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# Food Web Structure during the European Pleistocene

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Several models that have been proposed for explaining human evolution involve human-carnivore relationships. Reconstructing the structure and functioning of past food webs is, therefore, essential for evaluating the assumptions and conclusions of these models. Here we present a preliminary attempt to reconstruct the structure of some Pleistocene food webs from the Iberian Peninsula and to compare them with recent food webs from several regions and environments. The present work is a first step towards the reconstruction of past food web dynamics and is aimed at gaining a better understanding of the role of humans in past food webs. Our analysis was restricted to mammals weighing more than 10 kg because they constitute the portion of the food web that allegedly included hominins. Predator-prey interactions for fossil species pairs are inferred from their body sizes, evidence from the fossil record and behavioural information from close living relatives. The number of potential prey per predator in Pleistocene and recent food webs is compared, and the relationship between the number of secondary consumers and the standing biomass of primary consumers, estimated using allometric relationships, is investigated. Pleistocene food webs show a distinctive architecture, with a relatively large number of secondary consumers and a small number of primary consumers. In addition, the size distribution of primary consumers also differs between recent and Pleistocene food webs. Our results point to high intraguild competition during the Pleistocene, especially during the Early Pleistocene, which may have conditioned resource availability for Paleolithic hunter-gatherer populations.

***Keywords:*** FOOD WEBS, PLEISTOCENE, STANDING MASS, CARNIVORE GUILD



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## Introduction

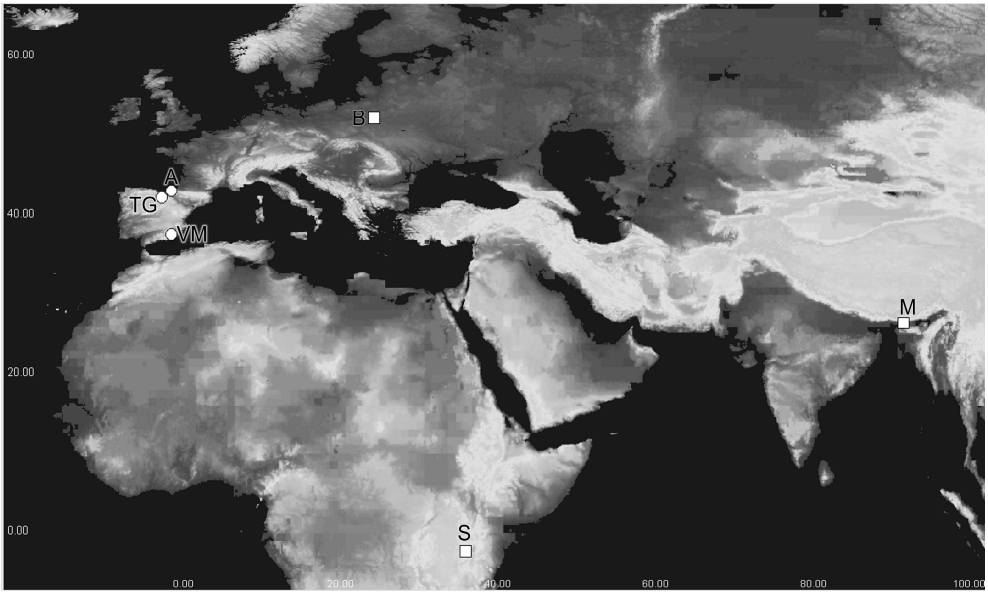
Trophic resource availability data are essential for understanding hominin dispersals and their roles in Pleistocene ecosystems. It is generally accepted that animal resources were essential for Pleistocene hominins in Europe (Hublin & Richards, 2009; Roebroeks, 2001). Most of the recent hunter-gatherer societies worldwide have a high reliance (>50%) on animal foods (Cordain *et al*., 2000). Speth (1989), Speth & Spielmann (1983) and Milton (2000) report that hominins might have been forced to live on animal matter, including its fats. Studies on recent hunter-gatherer populations indicate that meat consumption represents between 30% and 60% of their intake (Jenike, 2001; Leonard & Robertson, 1994). Although it is still a controversial topic, many authors assume that large mammals were a common meat resource for hominins since the Early Pleistocene (e.g., Binford 1981, 1985; Gaudzinski & Roebroeks, 2000; Marean, 1989; Moigne & Barsky, 1999; Roebroeks, 2001; Speth, 2010). Large mammals were a resource that hominins had to share with the entire guild of large carnivores, and thus, the guild structure conditioned the access probabilities of hominins to meat resources (Turner, 1992). According to Palombo (2010), the trophic dynamics of mammal palaeocommunities could have delayed human expansion in Europe during the Early Pleistocene. Several authors argue that the first European human populations were displaced by large predators, and therefore, they had to rely on the scavenging of ungulate carcasses (Arribas & Palmqvist, 1999; Martínez-Navarro & Palmqvist, 1996; Turner, 1992). The description and theoretical study of food web architecture and functioning has a long tradition in ecology (e.g., Cohen, 1977; May, 1983; Owen-Smith & Mills, 2008; Pascual & Dunne, 2006). Several studies that focused on carnivore guild structure and predator-prey relationships in Pleistocene communities have been published (Croitor & Brugal, 2010; Dennell *et al*., 2008; Hemmer, 2004; Hertler & Volmer, 2008; Palmqvist *et al*., 1996; Palmqvist *et al*., 2008; Palombo & Mussi, 2006; Raia *et al*., 2007; Turner, 2009), but the architecture of the entire food web, or at least of the portions of the food web that involve large mammals, have rarely been considered. The aim of this work is to study the architecture of some representative Pleistocene food webs, to understand their singularities and identify significant changes through time. We selected three food webs from the Iberian Peninsula that corresponded to three Pleistocene periods and compared them with some representative recent food webs (Figure 1). This is a first step towards understanding the effects that changes in food web architecture through time may have had on resource availability for hominins.

## Materials and Methods

### *Samples*

Three Local Faunas (LFs) from the Iberian Peninsula and three recent faunas from different continents were selected to explore predator-prey relationships throughout the Pleistocene. The three Pleistocene Local Faunas selected are Venta Micena, Atapuerca-Galería IIa/IIb and Amalda V and they represent typical palaeoecomunities of the Early, Middle and Late Pleistocene, respectively. In addition, these LFs include a large number of both primary and secondary consumers

*Figure 1. Map of sites and recent localities. A= Amalda Cave, TG= Atapuerca Galería, VM= Venta Micena; S= Serengeti N.P., M= Manas N.P.; B= Bialowieza N.P.*




relative to other Iberian faunas from the same period. Thus, they are assumed to be among the more complete assemblages available for their respective time periods. Regarding the recent communities, they have been selected to obtain a representative sample of different biomes from areas with rich carnivore faunas, in order to compare the patterns observed in the palaeocommunities with their recent counterparts. For this reason, we extracted the faunal lists for an East African savannah, the Serengeti National Park (Tanzania), a tropical deciduous forest, the Manas National Park (India) and a temperate deciduous forest, the Bialowieza National Park (Poland), from the Man and the Biosphere Fauna Database (UNESCO Man and the Biosphere Program, MAB); Information Center for the Environment (University of California, Davis, http:// ice.ucdavis.edu). Species lists for the Pleistocene Local Faunas were obtained from published sources (Table 1); however, because our analyses focused on large mammals, only species weighing more than 10 kg have been included in our dataset. Thus, we excluded from both the recent and fossil faunas any carnivore species whose diets are based mainly on small mammals, such as the small mustelids, the Viverridae and some felids such as *Catopuma temminckii*. We also excluded the cave bear *Ursus spelaeus*, whose diet was based on plants. Hominins were not included in the analyses for methodological reasons. Our approach was to investigate food web architecture without including them and to then discuss their possible roles in those networks.

*Food web reconstruction*

Predator-prey interactions for recent species were obtained from several published sources, including Nowak (1999), Ewer (1998), Smith & Xie (2008) and Wilson & Mittermeier (2009), among others. Some interactions, not reported in the literature, were inferred on the basis of prey size relative to predator size and behavioural information about both species. Predator-prey interactions for fossil species were inferred in a similar way, after reviewing published inferences on the behaviour of fossil predators obtained from morphofunctional, taphonomic, isotopic and actualistic approaches. As detailed below, graphical representations of predator-prey relationships in recent and past communities were determined based on Owen-Smith & Mills (2008). Prey species were classified into six body mass categories (10-45 kg; 45-90 kg; 90-180 kg; 180-360 kg; 360-1,000 kg and >1,000 kg).

*Predatory Behaviour of the Pleistocene carnivores*

The evidence available for inferring the behaviour of the large carnivores present in the three Pleistocene Local Faunas (LFs) considered in this work is reviewed below, and the potential prey species for each predator in the LFs are discussed.

Four canid species are present in the three Pleistocene LFs: *Canis lupus*, *Canis mosbachensis*, *Cuon alpinus* and *Lycaon lycaonoides* (Table 1). Canids usually have variable diets, including several degrees of omnivory. Extant grey wolves (*C. Lupus*) may be considered a hypercarnivorous canid with extremely variable prey preferences. Ungulates are its main food resource when they are present (Ansorge *et al*., 2006; Sillero-Zubiri, 2009), with small ungulates being the preferred prey. Roe deer represent 60% of the consumed biomass in Germany, and they are preferred over red deer and young wild boars (Ansorge *et al*., 2006). However, pack hunting allows grey wolves to kill larger ungulates such as red deer, bison, moose and horse (Garrott *et al*., 2007; van Duyne *et al*., 2009). Large cervids (red deer, moose) are negatively selected, but preyed upon if there is a scarcity of smaller prey, while *Bison bonasus* is not preyed upon in Europe (Okarma, 1995). Conversely, large ungulates seem to be their principal prey in North America (Milakovic & Parker, 2011). Concerning fossil populations, isotopic evidence from the Valdegoba Cave suggests that aurochs were part of the diet of Pleistocene wolves and that *Castor fiber* was not a common prey at this locality (Feranec *et al*., 2010). Thus, the diet of the grey wolf seems to be highly adapted to the availability of resources in the environment. Pack hunting allows wolves to kill large ungulates, but they may also survive by feeding on smaller species. Consequently, we assume that Pleistocene wolves consumed small and medium sized ungulates such as *Hemitragus bonali*, *Dama clactoniana* and *Rupicapra rupicapra* preferentially, and large ungulates such as *Cervus elaphus* and *Equus ferus* in smaller proportions.

An omnivorous diet similar to the extant coyote (*Canis latrans)* has been inferred for *Canis mosbachensis* on the basis of morphofunctional analyses (Palmqvist *et al*., 1999), an interpretation that is also supported by isotopic analyses (Palmqvist *et al*., 2003). Extant coyotes are opportunistic social predators that eat invertebrates, small mammals, ungulates and even some fruits. Large mammals are usually consumed as carrion, but ungulates, especially fawns, are also hunted

(Sillero-Zubiri, 2009). In a study of 30 radio-collared individuals, Turner *et al*. (2011) found that deer represented only 9.1% of their diet, while *Microtus sp.* represented 65%. Based on these data, we consider that small-sized ungulates were present in the diet of *Canis mosbachensis*, although in a very low proportion.

*Cuon alpinus* is also a hypercarnivorous canid. Living dholes are group hunters that prey upon medium-sized and large ungulates and occasionally eat carrion (Sillero-Zubiri, 2009). Their preferred prey in Bhutan are *Cervus unicolor* (130-270 kg), *Muntiacus muntjak* (20-28 kg) and *Sus scrofa* (31-38 kg) (Wang & Macdonald, 2009). However, studies in the Mudumalai Sanctuary provide evidence that *Cervus unicolor* and *Axis axis* fawns are highly preferred to the adults (Venkataraman *et al*., 1995). *Axis axis* (45-85 kg) and *Sus scrofa* provide 65% of the biomass consumed by dholes in Bandipur (Andheria *et al*., 2007). Taking into account the behaviour of extant dholes, *Cuon alpinus europaeus* most likely preferred prey in the 10-45 kg weight range (*Capreolus capreolus*, *R. rupicapra*), although cooperative hunting allowed them to kill larger prey effectively. Species in the 45-90 kg range (e.g., *Capra pyrenaica*, *Axis porcinus*, *Melurcus ursinus*), and even in the 90-180 kg range (*Cervus elaphus*, *Hemitragus bonali*, *Dama clactoniana*), were also likely killed, especially young and physically depleted individuals. Carrion was most likely also eaten.

Morphofunctional analyses carried out by Palmqvist *et al.* (1999) suggest that *Lycaon lycaonoides* was also a hypercarnivorous species. The closely related African wild dog (*Lycaon pictus*) may be taken as a recent analogue for the predatory behaviour of Early Pleistocene wild dogs. The following description is based on Hayward *et al*., (2006). Living wild dogs are social hunters which prefer prey within a bimodal body size range of 16-32 kg and 120-140 kg, likely reflecting the different efficiencies of solitary *versus* pack hunting individuals. A single wild dog, weighing 17-36 kg, may kill an adult female *Tragelaphus strepsiceros* weighing more than 120 kg; however, solitary hunters often kill smaller prey than do wild dogs hunting in packs. Scavenging has marginal importance in the diet of wild dogs. Isotopic analyses at Venta Micena indicate that horses and bovids in open environments were their preferred prey (Palmqvist *et al*., 2003). In a further analysis, Palmqvist *et al*. (2008) report *E. altidens* (58%), *Hemitragus albus* (30%) and *Pseudodama* sp. (12%) as the principal prey of the Venta Micena wild dogs. The abundance of medium-sized to large ungulates in the diet of the Venta Micena population suggests a high frequency of cooperative hunting.

Felids are highly specialised carnivorous mammals and the main predators in many recent communities, and they also played a key role in Pleistocene food webs. Six representatives of this family are present in the three Pleistocene LFs: *Homotherium latidens*, *Megantereon cultridens*, *Panthera leo*, *Panthera gombaszoegensis*, *Lynx* sp. and *Lynx pardinus spelaeus*.

The predatory behaviour of *Homotherium latidens* is a hotly debated topic. According to Antón & Galobart (1999) and Antón *et al*. (2004), *Homotherium* killed large prey, the size of a horse or a buffalo, with a canine shear-bite to the throat of the victim. In this way, they avoided the risk of tooth breakage. Group killing behaviour is inferred by Antón *et al*. (2005) on the basis of the clear adaptations in the head and neck for killing large prey,

*Table 1. Species lists for the three Pleistocene Local Faunas and three recent communities. Only mammals weighting more than 10 kg are included (Continue next page).*

| Fauna | Age | Secondary consumers | Primary consumers | References |
|---|---|---|---|---|
| Venta Micena | Early Pleistocene | *Canis mosbachensis*<br>*Homotherium latidens*<br>*Lycaon lycaonoides*<br>*Lynx sp.*<br>*Megantereon cultridens*<br>*Meles sp.*<br>*Pachycrocuta brevirostris*<br>*Panthera cf. gombaszoegensis*<br>*Ursus etruscus* | *Bison sp.*<br>*Bovini indet.*<br>*Equus altidens*<br>*Hemitragus albus*<br>*Hippopotamus antiques*<br>*Hystrix refossa*<br>*Mammuthus meridionalis*<br>*Praemegaceros verticornis*<br>*Praeovibos sp.*<br>*Pseudodama sp.*<br>*Soergelia minor*<br>*Stephanorhinus hundsheimensis* | (Arribas & Palmqvist, 1998; Duval *et al*., 2011; Martínez Navarro, 1992) |
| Atapuerca -Galería IIa/IIb | Middle Pleistocene | *Canis lupus*<br>*Cuon alpinus*<br>*Lynx pardinus*<br>*Meles meles*<br>*Panthera leo* | *Bison sp.*<br>*Cervus elaphus*<br>*Dama clactoniana*<br>*Equus ferus*<br>*Equus cf. hydruntinus*<br>*Hemitragus bonali*<br>*Homo sp.*<br>*Hystrix vinogradovi*<br>*Praemegaceros solilhacus*<br>*Stephanorhinus hemitoechus* | (Rodríguez *et al*., 2011) |
| Amalda V | Late Pleistocene | *Canis lupus*<br>*Cuon alpinus*<br>*Lynx pardinus*<br>*Panthera leo*<br>*Panthera pardus*<br>*Ursus spelaeus* | *Bos/Bison sp.*<br>*Capra pirenaica*<br>*Capreolus capreolus*<br>*Cervus elaphus*<br>*Equus ferus*<br>*Homo sp.*<br>*Rupicapra rupicapra*<br>*Sus scrofa* | (Altuna, 1992a, 1992b; Yravedra, 2003, 2006) |

on the one hand, and the relatively weak forelimbs, on the other hand, which made a single individual unable to subdue and retain a large prey individual in order to inflict the killing bite. Defence of the kill from the giant hyaena is also argued in favour of social behaviours in *Homotherium* (Antón *et al*., 2005). In addition, it has been proposed that *Homotherium* was specialised, or at least better adapted than lions, for killing proboscideans. This interpretation is based mainly on evidence from the North American Friesenhahn Cave (Marean & Ehrhardt, 1995), but see also Antón *et al*. (2005). Isotopic analyses carried out by Palmqvist *et al.* (2003) on material from Venta Micena suggest that juvenile *Mammuthus* were an important part of the diet of *Homotherium* at this locality, together with *Bison* sp. (52%) and *E. altidens* (38%) (Palmqvist *et al*., 2008). We consider *Homotherium* to be a top predator, and likely a group hunter, with a preferred prey size in the range of 90-360 kg, but able to kill prey up to 1,000 kg. Small ungulates were most likely negatively selected but preyed upon if available. Juveniles of the megafauna species are also considered to

*Table 1. (See previous page).*

| Fauna | Biome | Secondary consumers | Primary consumers | References |
|---|---|---|---|---|
| Serengeti National Park | Savannah | *Acinonyx jubatus*<br>*Aonyx capensis*<br>*Caracal caracal*<br>*Civettictis civetta*<br>*Crocuta crocuta*<br>*Hyaena hyaena*<br>*Lycaon pictus*<br>*Panthera leo*<br>*Panthera pardus*<br>*Leptailurus serval* | *Aepyceros malempus*<br>*Alcelaphus buselaphus*<br>*Colobus guereza*<br>*Connochaetes taurinus*<br>*Damaliscus lunatus*<br>*Diceros bicornis*<br>*Equus burchellii*<br>*Gazella granti*<br>*Gazella thomsonii*<br>*Hippopotamus amphibius*<br>*Hippotragus equinus*<br>*Hystrix cristata*<br>*Kobus ellipsiprymnus*<br>*Loxodonta africana*<br>*Manis temminckii*<br>*Oreotraus oreotragus*<br>*Orycteropus afer*<br>*Ourebia ourebia*<br>*Papio hamadryas*<br>*Phacochoerus aethiopicus*<br>*Potamochoerus porcus*<br>*Raphicerus campestris*<br>*Redunca fulvorufula*<br>*Redunca redunca*<br>*Syncerus caffer*<br>*Sylvicapra grimmia*<br>*Taurotragus oryx*<br>*Tragelaphus scriptus* | Man and the Biosphere Fauna Database. UNESCO. Man and the Biosphere Program (MAB). Information Center for the Environment (University of California, Davis) http://ice.ucdavis.edu |
| Manas National Park | Tropical deciduous forest | *Arctictis binturong*<br>*Arctonyx collaris*<br>*Catopuma temminckii*<br>*Cuon alpinus*<br>*Neofelis nebulosa*<br>*Panthera pardus*<br>*Panthera tigris* | *Axis axis*<br>*Axis porcinus*<br>*Bos frontalis*<br>*Bubalus bubalis*<br>*Cervus duvaucelii*<br>*Elephas maximus*<br>*Melurcus ursinus*<br>*Muntiacus muntjak*<br>*Rhinoceros unicornis*<br>*Rusa unicolor*<br>*Sus scrofa* | |
| Bialowieza National Park | Temperate deciduous forest | *Canis lupus*<br>*Gulo gulo*<br>*Lynx lynx*<br>*Meles meles*<br>*Ursus arctos* | *Alces alces*<br>*Bison bonasus*<br>*Cervus elaphus*<br>*Capreolus capreolus*<br>*Castor fiber*<br>*Sus scrofa* | |

have been vulnerable to attack from *Homotherium*.

The other sabre-toothed cat, *Megantereon cultridens*, had teeth and forelimbs well adapted for taking medium-sized prey. Its strong body, large claws and sharp but fragile canines suggest that their prey were captured using a short rush, followed by pinning them down and killing them with a sudden slashing bite (Turner & Antón, 1998). *Megantereon* is considered to have been a solitary species specialised in ambush hunting in forest environments, especially in riparian forests (Antón *et al*., 2005). This interpretation is consistent with the evidence from isotopic analyses that suggest that *Megantereon* hunted browsing and mixed feeding cervids in a closed habitat (Palmqvist *et al*., 2003). Palmqvist *et al*. (2011) suggest that, based on the isotopic composition of tooth enamel, the main prey at Venta Micena were *Soergelia minor*, *Equus altidens* and *Praemegaceros verticornis*. With the evidence at hand, ungulates in the 90-360 kg body weight range were likely the preferred prey, and smaller ungulates (10-90 kg) the secondary prey. We consider it to be extremely unlikely that *Megantereon*, a solitary predator, was capable of killing prey heavier than 360 kg, i.e., more than 6 times its own weight.

Modern lions are certainly the best analogue for the predatory behaviour of Pleistocene *Panthera leo*. The sociability of lions allows them to kill very large prey during group hunting. Their cursorial abilities and social behaviour make them very efficient in open country, while their strong constitution also makes them good ambush hunters (Turner, 2009). Mean prey size is approximately 130 kg (correcting for age and sex of the prey), but almost half of their prey weigh approximately 70 kg, while 40% of the kills are approximately 220 kg and the rest correspond to large prey above 400 kg (Rapson & Bernard, 2007). Very large prey, such as rhinos (Brain *et al*., 1999) or young elephants, are opportunistically killed, while there is practically no limit for the smaller prey (Sunquist & Sunquist, 2009). Thus, we assume that Pleistocene lions killed mainly medium-sized and large ungulates (*C. elaphus*, *D. clactoniana*, *E. hydruntinus*, and juveniles of *Equus ferus*, *Bison* sp., *Bos* sp.), although smaller ungulates and juvenile megaherbivores (*Stephanorhinus hemitoechus*) were also taken sporadically.

The European jaguar *Panthera gombaszoegensis* is considered to be an ambusher, similar in behaviour to the modern jaguar. Isotopic evidence suggests that European jaguars preyed at Venta Micena on browsing ungulates in closed environments, in particular on *Praemegaceros verticornis* (43%), *Pseudodama* sp. (38%) and *Soergelia minor* (19%) (Palmqvist *et al*., 2008). Modern jaguars (the most proximate living biological relative of *P. gombaszoegensis*) inhabit a variety of forested habitats, from wooded savannahs to montane forests and gallery forests. Jaguars are often associated with rivers and swampy areas. They are non-selective hunters able to kill prey 3-4 times their own weight, whose diet tends to reflect the abundance of prey in the area (Sunquist & Sunquist, 2009). We consider the European jaguar to be a solitary ambush predator with a preferred prey size in the range of 90-360 kg, that was also able to kill species in the 360-1,000 kg body weight range, and that also sporadically hunted smaller ungulates.

Finally, the last felids present at the sites are lynxes. Lower Pleistocene lynxes are usually included in the species *Lynx issiodorensis*, which was larger than the

Middle and Late Pleistocene *L. pardinus* and similar in size to the recent European lynx (*L. lynx*) (Carotenuto, 2009). However, the lynx from Venta Micena, reported as *L.* aff. *issiodorensis* in Palmqvist *et al*. (2010) and *Lynx sp*. in Duval *et al*. (2011) had an estimated body weight of only 8-10 kg (Palmqvist *et al*., 2010), more similar to *L. pardinus* (Palmqvist *et al*., 2010) than to *L. lynx*. Eurasian lynxes (*Lynx lynx*) weigh 15-29 kg and prey on small ungulates in the 10-45 kg size range, although small mammals, lagomorphs in particular, are also present in their diet (Sunquist & Sunquist, 2009). In contrast, Iberian lynxes (*L. pardinus*) weigh 9-13 kg on average (Beltrán & Delibes, 1993), and their diet is composed almost entirely of lagomorphs and only very rarely includes small ungulates (Sunquist & Sunquist, 2009; Valverde, 1967). Isotopic evidence from Valdegoba (Feranec *et al*., 2010) confirms that ungulates were not a significant food resource for *Lynx pardinus spelaeus*, suggesting a diet similar to that of the modern Iberian lynx. Thus, for *Lynx* sp. from Venta Micena and for *Lynx pardinus spelaeus*, we assume a diet based on lagomorphs with the sporadic consumption of small ungulates in the 10-45 kg category.

The family Hyaenidae is represented in the three LFs selected by a single species: the giant hyaena, *Pachycrocuta brevirostris*. The spotted hyaena (*Crocuta crocuta*) is a common element of Middle and Late Pleistocene faunas, but it has not been identified in these assemblages. Turner *et al.* (2008) classify *P. brevirostris* as a member of Ecomorph Group 6, "fully developed bone crackers", and Arribas & Palmqvist (1998) concluded from their analysis of the Venta Micena assemblage that *P. brevirostris* fed largely on ungulates that had been preyed upon by other predators. Its short and strong legs were well adapted to carrying large pieces of carrion but they reduced the hyaena's cursorial capacities, making it unable to pursue and kill its own prey. Turner & Antón (1996) considered *P. brevirostris* to be a social, active scavenger that disputed the carcasses claimed by large felids, taking advantage of its large body size and group strength. The cooperative hunting of large ungulates was also considered possible, although not as the main activity. Based on study of the Venta Micena assemblage, Palmqvist *et al*. (2011) concluded that *Pachycrocuta* was a strict scavenger, or more precisely a specialised kleptoparasite, that stole the prey of sabertooths and other carnivores. Croitor & Brugal (2010) also considered *Pachycrocuta* to be a specialised scavenger that lived in open and highly productive environments. We agree with the widely accepted interpretation of *Pachycrocuta brevirostris* as a strict scavenger.

Living bears usually have an omnivorous diet, with fruits representing a high proportion of their consumed biomass. The main exceptions are the hypercarnivorous *Ursus maritimus*, the specialised herbivore *Ailuropoda melanoleuca* and the myrmecophagous *Melursus ursinus*. The proportion of meat in the diet varies between species and populations, but as a general rule, larger individuals include a higher proportion of meat in their diets. Scavenging is a common practice, but brown bears are also able to kill large ungulates such as moose, red deer, or reindeer, as both fawns and adults. In addition, the proportion of meat in the diet of brown bears is much higher in the Arctic than at lower latitudes, likely because plant resources are scarcer at high latitudes (Garshelis, 2009).

Two ursid species have been identified in the three LFs: *Ursus spelaeus* and *Ursus etruscus*. The cave bear (*Ursus spelaeus*) is generally considered to have been a largely vegetarian species. Cave bear tooth damage patterns suggest an abrasive diet based on nuts and tubers while the enamel isotope composition indicates a highly omnivorous diet and rules out any significant consumption of ungulates (Stiner *et al*., 1998). Thus, we exclude cave bears from our analyses.

The Early Pleistocene *Ursus etruscus* is here considered a "typical bear" with an omnivorous diet that likely included a high proportion of plant foods, at least in temperate environments. It is likely that ungulates in the 10-360 kg body weight range were sporadically hunted and that carrion was opportunistically consumed.

*Primary consumer biomass*

We estimated the biomass of primary consumers in each community using allometric relationships. The density of primary consumers was estimated using the equations provided by Damuth (1981) for different habitats:

$\log D = -0.79 * \log (W) + 4.59$ $r^2 = 0.85$ (1)

$\log D = -0.61 * \log (W) + 3.78$ $r^2 = 0.86$ (2)

$\log D = -0.79 * \log (W) + 4.33$ $r^2 = 0.94$ (3)

where D is the population density of individuals per sq. km. and W is the body weight in g. Equation 1 was obtained from data from a tropical grassland ecosystem from Sri Lanka, equation 2 from a woodland savannah (Transvaal lowveld from South Africa) and equation 3 from a mixed temperate forest in Poland (Damuth, 1981). Thus, we selected the equation from the most analogous environment for each case. Equation 1 was used to estimate densities in Manas National Park (India), equation 2 was used for Serengeti National Park and equation 3 for Bialowieza National Park and for the fossil communities. We tested two other equations for temperate ecosystems from the USA provided by Damuth (1981), a temperate grassland and an oak and chaparral ecosystem, but these equations were rejected because they produced very unreliable population density estimates.

The total primary consumer standing biomass (PSB) per square km was computed by multiplying the obtained densities with the mean body mass of the species and adding the results across prey species:

$$PSB = \sum_{i=1}^{n} W_i * D_i$$

where $W_i$ is the body mass of the *ith* species and $D_i$ is its population density.

*Graphical representations*

The relationships between predators and prey in the recent communities and in the Local Faunas where described using a graphical representation (Figure 2) based on Owen-Smith and Mills (2008). Prey are distributed in boxes by body size (see section 2.2); with the boxes delimited by dotted lines corresponding to prey body size categories not represented in the community. Predator species are distributed above and below the prey boxes, according to predation intensity, e.g., stronger predators (the best competitors)

appear above. Predator-prey interactions are represented by four arrows whose thicknesses represents the intensities of the interaction, i.e., the relative importance of prey from that size category in the diet of the predator. The thinnest arrows represent scavenging.

The numbers of potential prey for each carnivore species (PPrey) have been computed based on the inferred preferences of the carnivores and the body sizes of the primary consumers that are present in the local fauna. Mean, maximum and minimum PPrey were computed for each Local Fauna as proxies for the strength of predation pressure and for resource competition. In addition, the number of secondary consumers was plotted against the estimated total primary consumer biomass (PSB) in order to quantify resource availability.

## Results

Although there is a wide gradient of food web complexity from the simplest case (Bialowieza National Park) to the most complex webs (Serengeti National Park and Venta Micena), some general rules emerge from Figure 2:

1) Prey in the 45-90 and 90-180 kg body size classes always support the highest intensity of predation pressure.
2) Prey above 1,000 kg are only predated by one or two species and always at very low intensity.
3) The top predator is always a large felid, the only exception being in the food web from Bialowieza National Park, where prey of 45-90 kg and of more than 1,000 kg are absent.

Recent food webs present wider variations in complexity than do Pleistocene food webs, from the most complex example (Serengeti) to the simplest one (Bialowieza). Concerning the Pleistocene food webs, the most complex one is Venta Micena, while the Middle (Atapuerca-Galería IIa/IIb) and Late Pleistocene (Amalda V) food webs are significantly simpler.

All body size categories of prey are represented, both in the Serengeti food web and in the Early Pleistocene one. However, small ungulate diversity (<180 kg) is much lower at Venta Micena than in the Serengeti, while the numbers of large and very large prey are very similar in both communities. This is especially interesting because the three body size categories that fall between 10 and 180 kg are those that support the highest predation pressure in the Serengeti food web. Moreover, the number of predators is even larger at Venta Micena than in the Serengeti but they do not concentrate their pressure on the smallest prey (Figure 2). Manas National Park, with an equal number of primary consumers than Venta Micena, although they are more homogenously distributed in size categories, supports a carnivore guild with half the number of species as the Early Pleistocene food web. The Middle Pleistocene food web from Atapuerca-Galería IIa/IIb, with nine primary consumers and without any species in the second body size category (45-90 kg) has the same number of predators as in Manas National Park. Amalda V represents the more impoverished Pleistocene food web with no prey in the 180-360 kg and >1,000 kg size categories. The number of primary consumers in the Amalda V food web is the same as in Bialowieza National Park but the predator guild is much more complex. The Bialowieza National Park food web is dominated by only two predators: the grey wolf, which focuses on medium-sized and

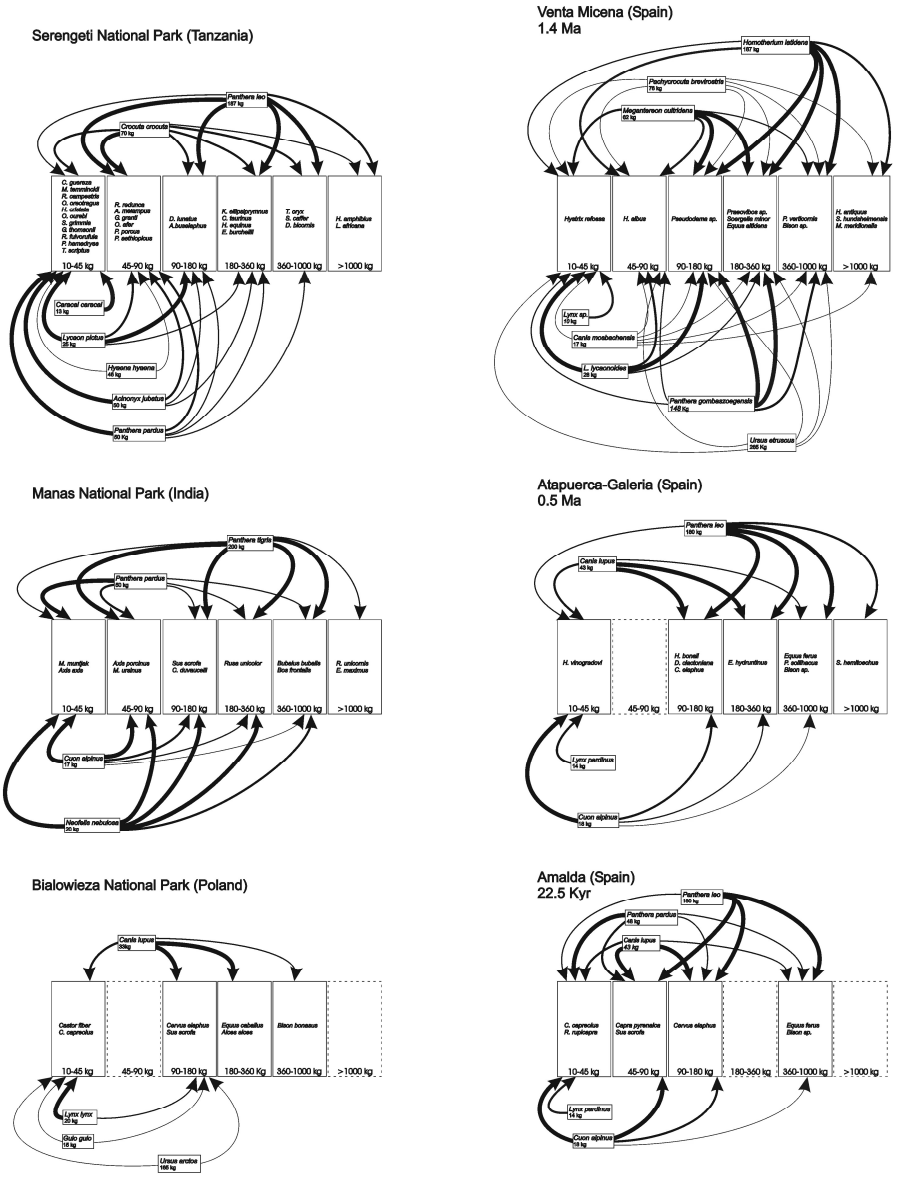



*Figure 2. Predator-prey interactions in some recent and fossil communities. Arrow thickness is proportional to the significance of the prey in that size category to the diet of secondary consumers. There are four categories of thickness, the narrowest one being restricted to scavengers. Body size categories are shown on the bases of the boxes. Empty boxes (no primary consumers in that size category) are marked with discontinuous contour lines. The dominant predators (best competitors) are shown above the boxes and weaker competitors below.*

large prey, and the European lynx, which relies on small ungulates. In contrast, four predators (dhole, grey wolf, lion and leopard) distribute their pressure throughout the four size categories in the Amalda V food web (Figure 2).

It might be expected that communities with a higher herbivore biomass will support a richer predator guild, although see Fritz *et al*. (2011). Figure 3 shows the relationship between the standing biomass of primary consumers (PSB) and predator richness. Although the sample size is too small to draw strong conclusions, the pattern exhibited by the three recent assemblages seems to support the existence of a positive relationship between prey biomass and predator richness. If this were the case, Amalda V and Venta Micena would show a large number of predator species relative to the estimated prey biomass (Figure 3).

Another singularity of the Pleistocene food webs is that, despite the fact that they are similar in complexity to the two more complex recent food webs (Serengeti National Park and Manas National Park), their numbers of potential prey per carnivore (PPrey) are moderate (Figure 4), although higher than in the recent European community (Bialowieza National Park). This difference is explained mainly by the lower species richness in the small size categories of the Pleistocene communities when compared with Manas National Park and Serengeti National Park.

## Discussion

The three Pleistocene food webs analysed here show remarkable architectural characteristics that make them different from the recent food webs used for comparison. Prey body size distribution is one of the main differences between the recent and Pleistocene food webs. In recent food webs, primary consumers with body sizes between 10 kg and 180 kg are always more abundant than are species weighing more than 180 kg (Figure 2), while the opposite is observed in the Early and Middle Pleistocene food webs represented herein. A possible explanation for these differences is a bias in the fossil record towards small ungulates, as suggested by Arribas & Palmqvist (1998) for the Venta Micena assemblage. Certainly, accumulation biases such as these are always difficult to rule out. However, the scarcity of small-sized ungulates during the Early and Middle Pleistocene is not observed at the scale of LFs only, as shown here, but also at the scale of the entire regional fauna of the western Mediterranean (see Figure 3 in Rodríguez et *al*., 2004). It is likely that both the Venta Micena and the Atapuerca IIa/IIb assemblages failed to record all of the small ungulate species that were present in the palaeocommunity. Nevertheless, this bias alone cannot explain the large differences in prey body size distribution observed between the recent and Pleistocene food webs. On the contrary, the high proportion of large prey species (>380 kg) is a distinctive characteristic of the European Pleistocene faunas, both at the local and at the regional scales, as already highlighted elsewhere (Rodríguez, 2001; Rodríguez *et al*., 2004). This characteristic is also reflected in the increased preference of the Pleistocene predators for the largest prey body size categories (Figure 2). This trend is well illustrated by the comparison between the Serengeti and Venta Micena food webs. While, in the Serengeti, the 10-45 kg and 15-180 kg categories support the highest pressure, the Early Pleistocene predators distributed their preferences in a more even fashion.

*Figure 3. Number of secondary consumers relative to primary consumer standing biomass (PSB) (N). VM: Venta Micena; TG: Atapuerca-Galería IIa/IIb; A: Amalda V; S: Serengeti National Park; M: Manas National Park; B: Bialowieza National Park.*

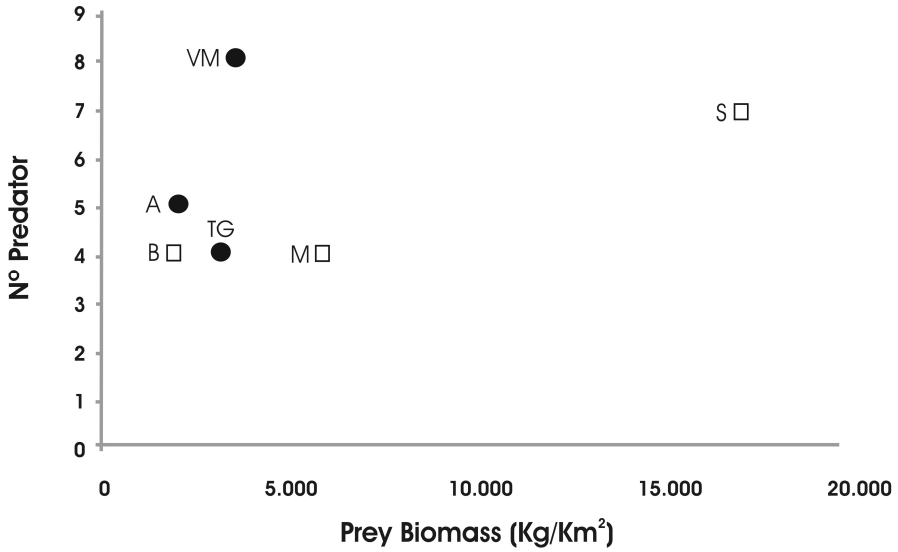
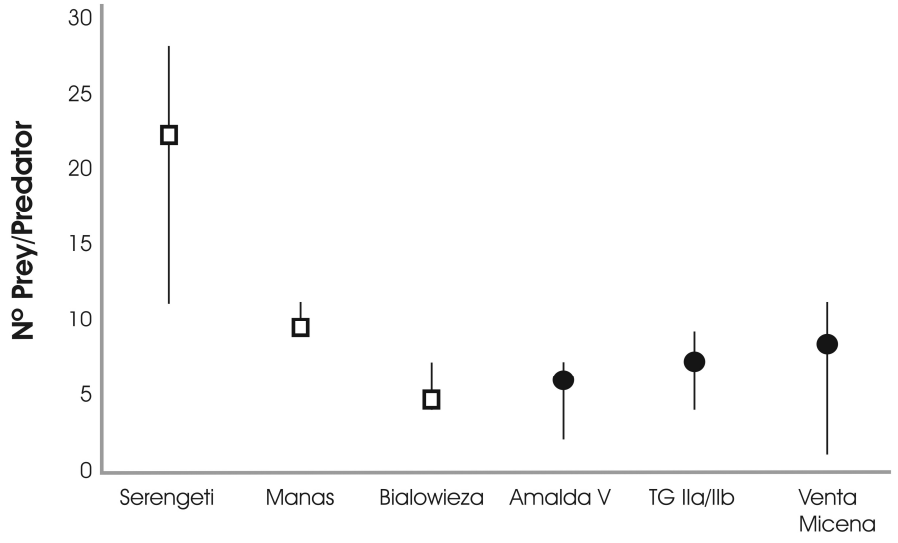



*Figure 4. Number of potential prey per secondary consumer (N). Dots and squares represent the mean value and whiskers mark the maximum and minimum numbers of prey per carnivore in each community.*



The Late Pleistocene food web (Amalda V) is more similar to recent food webs in prey body size distribution. Nevertheless, an accumulation bias may also be present at Amalda V, but in the opposite direction. If we compare the faunal list from Amalda V with the regional fauna of the Cantabrian region at the end of the Late Pleistocene (Álvarez Laó, 2003), the species below 360 kg seem to be well represented. However, there are no megaherbivores represented at Amalda V, while at least *Coelodonta antiquitatis* and *Mammuthus primigenius* are present at other geographically close sites of similar age, such as Lezetxiki III (Altuna, 1972; Soto Barreiro, 2003) and Labeko Koba IV (Altuna & Mariezkurrena, 2000), respectively. If this were the case, the pattern of having a high proportion of large primary consumers would be a distinctive characteristic of the Pleistocene food webs under study here.

Carnivore richness is as high in the Pleistocene food webs as it is in the recent ones, or even higher. This fact, combined with the relative scarcity of primary consumers weighing less than 360 kg in the Pleistocene food webs, produces low primary/secondary consumer ratios (Figure 4). Consequently, the niches of Pleistocene carnivores overlapped more than do those observed in recent food webs because they competed for a reduced number of prey species, from 1 to 11 potential prey per carnivore in Pleistocene ecosystems, compared with 4 to 28 in recent ecosystems. As noted in Rodríguez *et al.* (2012), competition inside the predator guild was very high in southern Europe during the Early Pleistocene. The results shown here suggest that competition might have been intense during the entire Pleistocene. Another consequence of the low primary/secondary consumer ratios in the Pleistocene assemblages is that the richness of the carnivore guild is very high when compared with the estimated biomass of primary consumers (Figure 3). This is especially evident in the case of Venta Micena, but it is also observed in Amalda V, with less than 5,000 kg/km$^2$ for 8 and 5 secondary consumers, respectively, against approximately 18,000 kg/km$^2$ for 7 predators in Serengeti National Park. It should be noted, however, that two out of the eight carnivores present at Venta Micena (*Canis mosbachensis* and *Ursus etruscus*) were omnivorous and that they would exert a lower pressure on the populations of primary consumers. In comparison, there are seven carnivores at Serengeti and only one of them (*Hyaena hyaena*) might be considered omnivorous (Mills & Hofer, 1998), although carrion is the principal component of its diet (Holekamp & Kolowski, 2009). The high secondary consumer/PSB ratios at Venta Micena and Amalda V (<5,000 kg/km$^2$) are a paradox that can only be resolved in one of two ways. A possible solution to this paradox is that we have underestimated the primary consumer biomass, and this might have resulted from either an underestimation of primary consumer population density or from an underestimation of primary consumer species richness. As discussed above, a strong bias against primary consumers in the case of Venta Micena is not feasible, although a significant bias against megaherbivores might be present in the case of Amalda V. Underestimation of the population density of primary consumers is extremely unlikely because a general consensus exists that considers the estimates of population density obtained from the equations used here to be maximum or "ecological" densities (White *et al.*, 2007).

Alternatively, the low secondary consumer/PSB ratio might be indicating that carnivore population densities were lower in the Pleistocene palaeocommunities than those observed in recent communities. This

would explain how it was possible to maintain an extremely rich carnivore guild with a relatively low primary consumer standing biomass.

Results presented here suggest high competition levels inside the carnivore guild throughout the Pleistocene, especially in the case of the Venta Micena palaeocommunity (lower PSB than Manas National Park, with twice the number of secondary consumers). The inclusion of a hunter-gatherer population into any of these food webs would increase competition even more. It is known, however, that *Homo sp*. was present at Atapuerca-Galería IIa/IIb and at Amalda V but that they were not present at Venta Micena. These results support the hypothesis that high competition inside the carnivore guild during the Villafranchian delayed the expansion of *Homo* into Europe (Palombo, 2010; Rodríguez *et al*., 2012).

## Conclusion

The three Pleistocene food webs analysed exhibit a remarkable complexity, similar to that observed in the most complex recent food webs. The number of secondary consumers is similar in the Pleistocene and recent communities, while the ratio of potential prey per carnivore is lower in the Pleistocene assemblages than in recent tropical food webs. This led to a low prey biomass availability per predator species, especially for the Early Pleistocene Venta Micena community, that was most likely resolved by reducing carnivore population densities. The body size distribution of primary consumers is also a distinctive feature of the Pleistocene food webs, which likely had an effect on trophic web dynamics.

Although this analysis is only a first approach, our results suggest that predation pressure and predator competition were high during the Pleistocene. Further analysis using a larger database of recent and fossil assemblages may help to determine whether this pattern is due to biases in the selected fossil assemblages. If the pattern of high competition and high predation pressure remains after being tested with more data, it will constitute a new and significant challenge to the models of human subsistence during the European Pleistocene.

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