UNIVERSITAT ROVIRA I VIRGILI

MODELIZACIÓN DE LA DISPONIBILIDAD DE RECURSOS TRÓFICOS PARA LAS POBLACIONES PALEOLÍTICAS DE CAZADORES-RECOLECTORES.

Guillermo Rodríguez Gómez

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La reconstrucción de las redes tróficas del pasado es esencial para evaluar el papel que desempeñó *Homo* en los paleoecosistemas del Pleistoceno europeo. En este trabajo se aplica un modelo matemático basado en la Matriz de Leslie, que proporciona estimaciones de los recursos cárnicos disponibles para los consumidores secundarios en una paleocomunidad, entre los que se encontrarán los homininos. Con los recursos disponibles se estiman las poblaciones de consumidores secundarios sostenibles en el paleoecosistema, reconstruyendo la comunidad de macromamíferos del paleoecosistema. El modelo se ha aplicado a yacimientos del Pleistoceno Inferior tardío y del Pleistoceno Medio, a nivel local en la Sierra de Atapuerca y en yacimientos Europeos a nivel continental. Los resultados obtenidos llevan a pensar que el humano del Pleistoceno Inferior tardío e inicios del Pleistoceno Medio era dependiente de la composición y estructura de la paleocomunidad para estar presente en ellas.

Modelización de la disponibilidad de recursos tróficos para las poblaciones paleolíticas de cazadores-recolectores

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UNIVERSITAT ROVIRA I VIRGILI

DEPARTAMENTO
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Modelización de la disponibilidad de recursos tróficos para las poblaciones paleolíticas de cazadores-recolectores

TESIS DOCTORAL
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UNIVERSITAT ROVIRA I VIRGILI

Tarragona

2015

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HACEN CONSTAR,

que el presente trabajo titulado "Modelización de la disponibilidad de recursos tróficos para las poblaciones paleolíticas de cazadores-recolectores", que presenta Guillermo Rodríguez Gómez para la obtención del título de Doctor, ha sido realizado bajo nuestra dirección en el Centro Nacional de Investigación sobre la Evolución Humana (CENIEH) de Burgos, dentro del Programa de Doctorado del Departamento de Historia e Historia del Arte de la Universitat Rovira i Virgili de Tarragona, y que cumple con los requisitos para poder optar a la Mención Europea.

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La presente Tesis Doctoral ha sido financiada por el Ministerio de Ciencia e Innovación (MICINN) y por el Ministerio de Economía y Competitividad (MINECO) del Gobierno de España con la ayuda BES-2010-033410 del Subprograma de Formación Personal Investigador (FPI), perteneciente a los proyectos CGL2009-12703-C03-01 (El Pleistoceno de la Sierra de Atapuerca: Geología, Paleontología, Paleobiología y Paleoeconomía de las poblaciones humanas IV) y CGL2012-38434-C03-02 (El Pleistoceno y Holoceno de la Sierra de Atapuerca (Burgos, España): Geología, Paleoecología y Paleobiología de homínidos). Durante el desarrollo de la Tesis Doctoral se disfrutó de ayudas para la realización de estancias en el *Natural History Museum* de Londres (EEBB-I-12-03857), en el *Research Centre at Senckenberg Forschungsinstitut* de Fráncfort del Meno (EEBB-I-13-07054) y en la *Universidad de Málaga* (EEBB-I-14-07930).

La tesis ha sido desarrollada en el Centro Nacional de Investigación sobre la Evolución Humana (CENIEH).

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Durante el desarrollo de la Tesis Doctoral se ha participado en la realización de diferentes estudios publicados en revistas y libros de ámbito nacional e internacional:

Jesús Rodríguez; Jesús A. Martín González; Idoia Goikoetxea; **Guillermo Rodríguez Gómez**; Ana Mateos (2010) Mammals, ecological barriers and the distribution of *Homo* in early Pleistocene Europe. *Communication on Contemporary Anthropology*. 4, pp. 140-142.

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Además, durante el desarrollo de la Tesis Doctoral se ha participado en la presentación de trabajos a congresos nacionales e internacionales:

Jesús Rodríguez; Jesús A. Martín-González; Idoia Goikoetxea; **Guillermo Rodríguez-Gómez**; Ana Mateos. Mammals, ecological barriers and the distribution of *Homo* in early Pleistocene Europe. *International Meeting of First Human Settlements in Eurasia*. Shangai, China. Del 8 al 10 de octubre de 2010. Comunicación oral.

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Guillermo Rodríguez-Gómez; Jesús A. Martín-González; Ana Mateos; Jesús Rodríguez. Competition Indexes to compare environmental conditions for secondary consumers between different faunal assemblages. *XVII World UISPP Congress*. Burgos, España. Del 1 al 7 de septiembre de 2014. Comunicación oral.

Tienes hasta los vinos tristes aunque reflejes charanga
Tienes la vida en Irlanda aún malviviéndola aquí
Tienes amigos cien mil ya sean de estudio o parranda
Tienes frente de uvas pasas, de genio sin descubrir
De caballero gentil tienes el don y las hadas
aunque guardas telarañas que no cazan su botín
Tienes vacío el jardín del amor más la esperanza
debes alimentar con savia tu árbol veceño de abril:
Y aunque siembres perejil de nimia flor umbelada
no desdeñes madrugadas con aromas a jazmín.
¡Hazme caso y ve por ir al huerto de rosas vanas
que a veces entre sus ramas hay prendido un potosí!

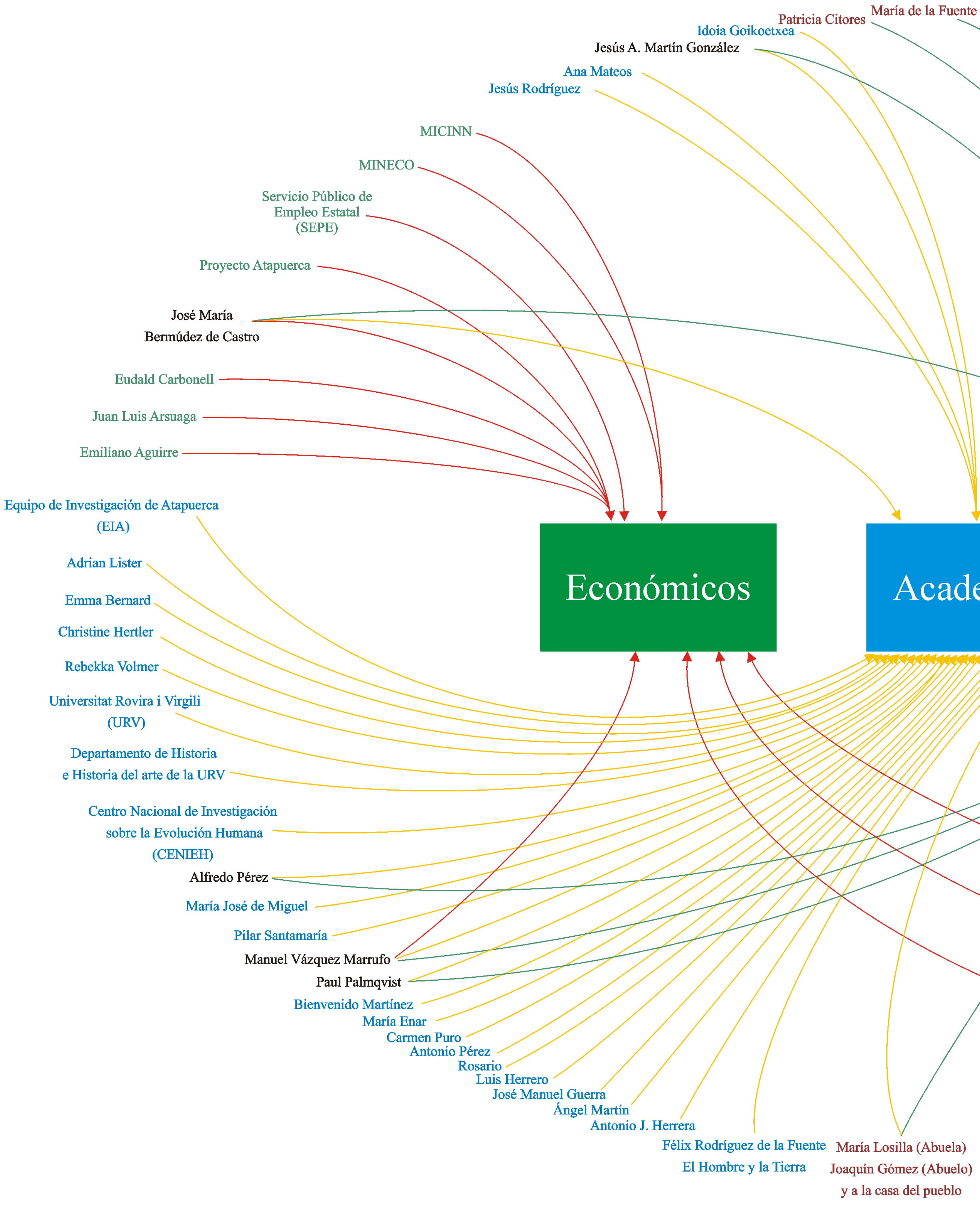
A Guille

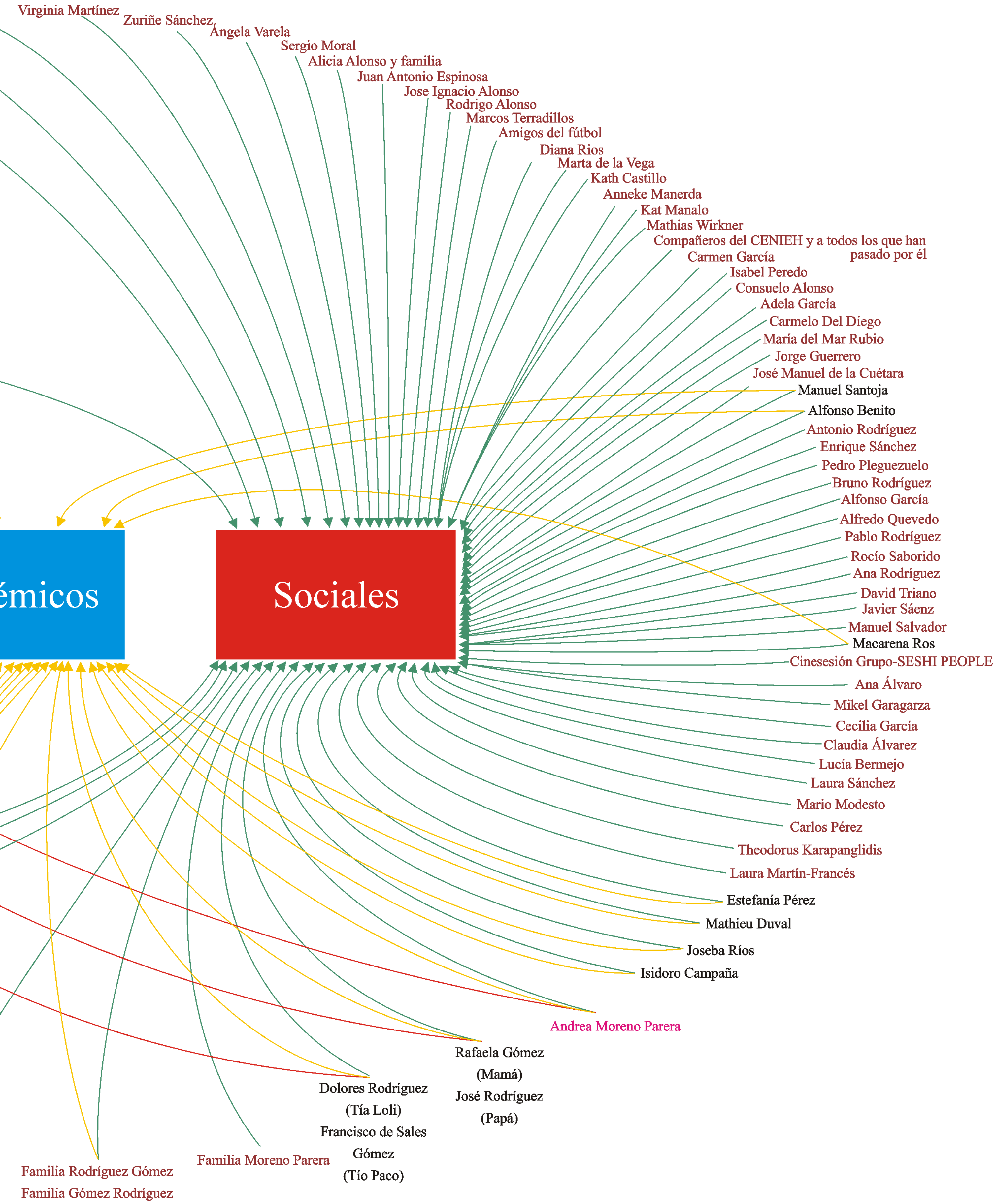
David Triano Mejías

Agradecimientos

Creo que en mi vida he tenido mucha suerte, y espero seguir teniéndola, porque para poder llegar a alcanzar el más alto nivel de titulación académica no sólo es suficiente con lo que pone uno o una, sino que hay que rodearse de muchas manos, al menos para que no sea un trago difícil. En mi caso puedo decir que la mayor parte del tiempo ha sido de disfrute y en ello han participado muchas personas. Tratándose de una tesis sobre recursos tróficos, se podría decir que me he alimentado de ellas para llegar a obtener el objetivo de la tesis doctoral. Podría clasificar los apoyos y ayudas que he recibido en económicos, académicos y sociales. Desde esta perspectiva se podría hacer el ejercicio de representar los apoyos y ayudas como una red trófica, en el que cada elemento del sistema aportaría según su naturaleza económica, académica o social. Como homenaje, en cuanto a la síntesis, al Profesor Doctor Felipe Cortés de la Universidad de Sevilla, se ha representado la "*red trófica*" de esta tesis doctoral en la **Figura Agradecimientos**. A parte de esta figura, me gustaría agradecer por un lado a mi familia, a mis padres y a mis hermanos (Jorge, Javier, Gonzalo, Alberto y Marta), por haber sido el mejor caldo de cultivo y, por otro lado, a Andrea por haber sido y ser imprescindible.

Figura Agradecimientos. Representación gráfica de los agradecimientos en la que se expresan mediante flechas el sentido y tipo de aportación o apoyo en el desarrollo de la tesis doctoral, diferenciándolos según su naturaleza económica (flechas rojas), académica (flechas amarillas) y social (flechas verdes). Se mantiene el mismo grosor en las flechas con el fin de no producir agravios comparativos.

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Marta de la Vega
Kath Castillo
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Kat Manalo
Mathias Wirkner
Compañeros del CENIEH y a todos los que han pasado por él
Carmen García
Isabel Peredo
Consuelo Alonso
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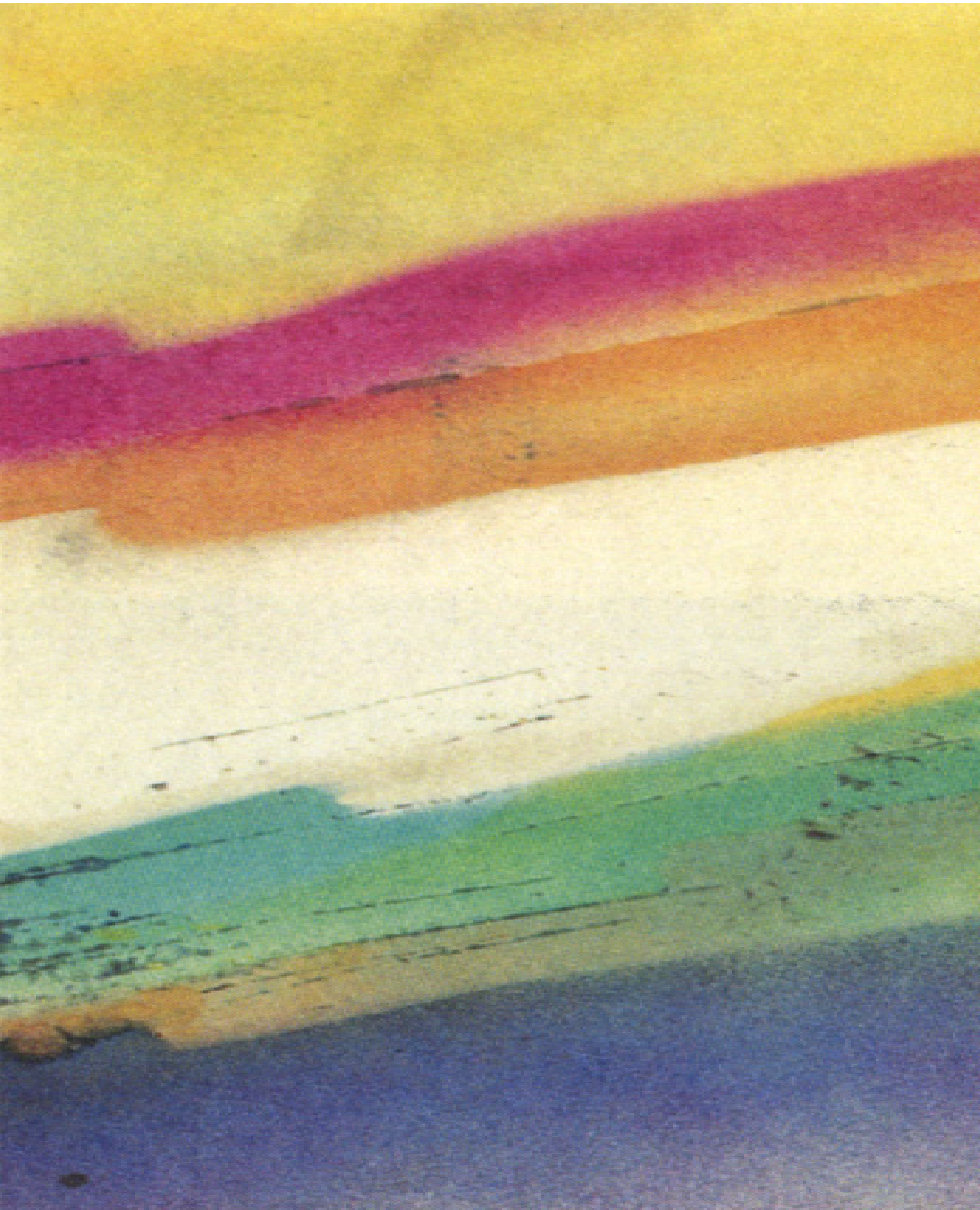
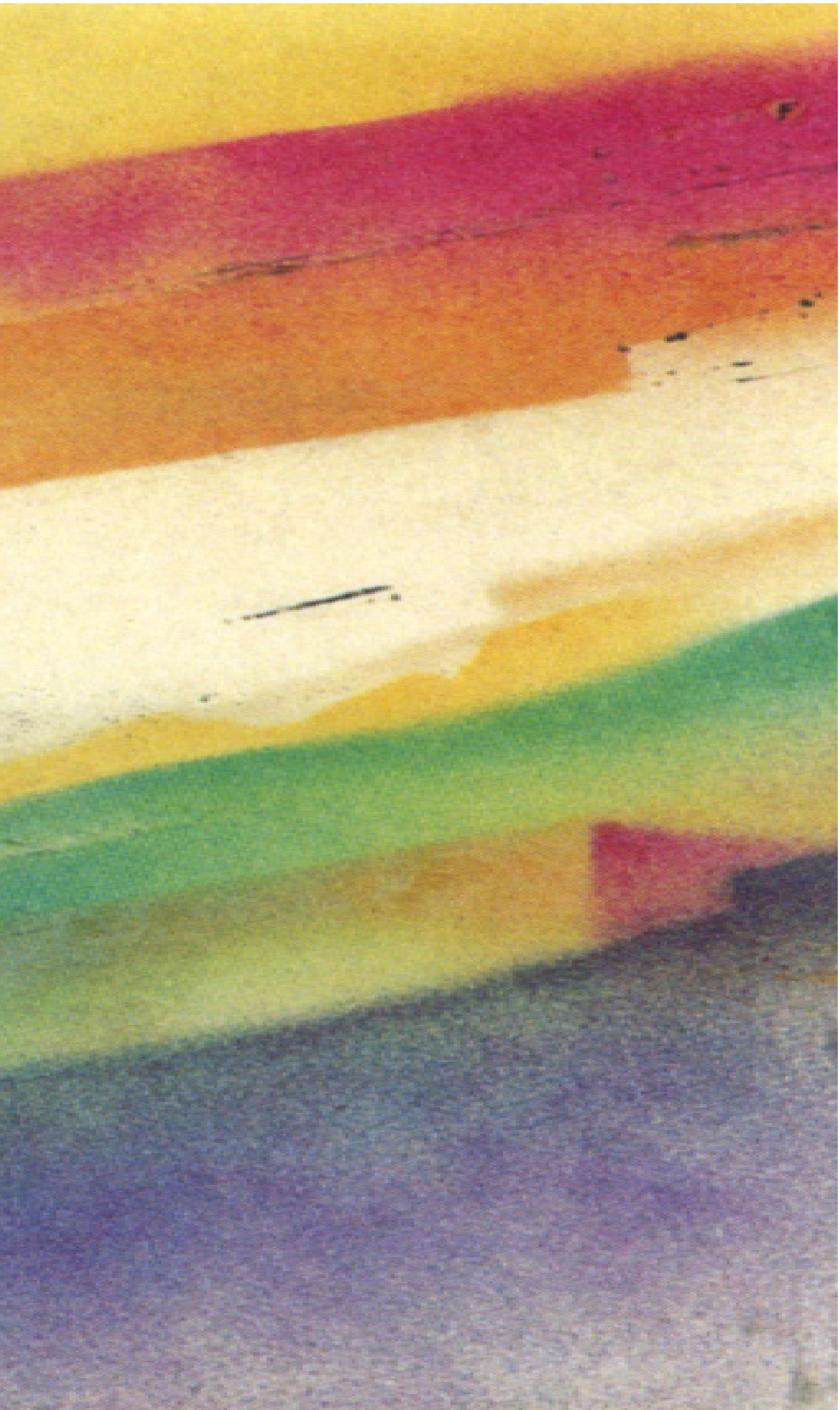
A mis padres, Rafi y José

Índice





Abstract / Resumen

En lás páginas anteriores:
Cuadro sin título de la serie *Tropical screens*. Autor: Gonzalo Rodríguez Gómez.

Abstract

The resources availability is one of the main constraints for the survival and dispersal of organisms. In the case of the European Pleistocene hominins, the ungulates would be one of the essential trophic resources. The abilities of hominins to obtain meat resources in their environmental would be conditioned by the prey abundance, their ecological capacities and the intensity of competition with carnivores for this resource type. The reconstruction of past food webs is essential to assess the role of *Homo* in these European Pleistocene paleoecosystems. Studies about food webs are essential to quantify and analyze the relationships and dynamics among the species of an ecosystem. The application of this type of studies to paleontological data could provide very relevant information such as the availability of resources for secondary consumers or the competition intensity among them. In this work a mathematical model based on the Leslie Matrix is applied. This model provides estimations of the available meat resources for secondary consumers (TAB) in a paleocommunity. The sustainable secondary consumer populations in the paleoecosystem are estimated from the available biomass (TAB) by distributing the TAB according to their prey preferences and their energetic requirements. Thus, a representation of the macromammal community of the paleoecosystem is obtained. To evaluate the state of the secondary consumer community, their access to resources and how they fulfill their requirements, a number of competition indexes or satisfied requirement indexes were developed, that allow comparison among local faunal assemblages of different chronology and localization. The model has been applied with different perspectives to know more about the role of the genus *Homo* in the Pleistocene ecosystems and as the results of these applications were used to improve and develop it. On the one hand, it was applied to study the state of the paleoecosystem represented at the TD6-2 level of the Gran Dolina site at the Sierra de Atapuerca because it is a very important level in the socioeconomic study of the Early Pleistocene European settlers due to its chronology and its richness in human fossils. On the other hand, the competition inside the secondary consumers guild was compared among two periods, the Early and Middle Pleistocene, to study whether that competition could explain the scarcity of evidences of human presence in the Middle Pleistocene with respect to the Early Pleistocene. This study was carried out at a local scale, comparing the TD6-2 level (Early Pleistocene) with the TD8 level (Middle Pleistocene) of the Gran Dolina site. Finally, the analyses were changed from the local to the continental scale to study the competition in the European paleoecosystems of the later Early and Middle Pleistocene. Results of these analyses showed a very important resource richness in the TD6-2 level that was enough to support the communtity of secondary consumer present in the taphocenosis, including *Homo antecessor* and might additionally support a large felid species not present in the fossil assemblage. On contrary, the TD8 level did not show enough resources to support the secondary consumers at their maximum densities, as in TD6-2, showing a higher competition degree for the meat resources. It was proposed that the degree of competition might explain the lack of human presence in the TD8 ecosystem. When the model was applied at a continental scale, the competition degree seemed to lose relevance from the point of view of human presence, being lower the competition degree in the Middle Pleistocene ecosystems than in the Early Pleistocene ecosystems, opposite result that shown at a local scale. The differences between the results obtained at local and continental scales could be due to different dynamics in the Gran Dolina site at the Sierra de Atapuerca, with respect to the other sites analyzed at a continental scale, or to differences between the two analyses types. The procedure of the analyses at a continental scale could mask up specific dynamics of the paleocommunities at a local scale that could result from different competition intensities for meat resources. From an ecological perspective, it could be interpreted from the results presented here that humans experimented difficulties to access meat resources during

the Early Pleistocene and the early Middle Pleistocene, being their presence conditioned by the structure and composition of the paleocommunities. From the Middle Pleistocene onwards, with a more complex technology (Acheulean) and social structure, the ecological constraints for humans might become weaker, resulting in a demographic explosion, as it has suggested by some authors.

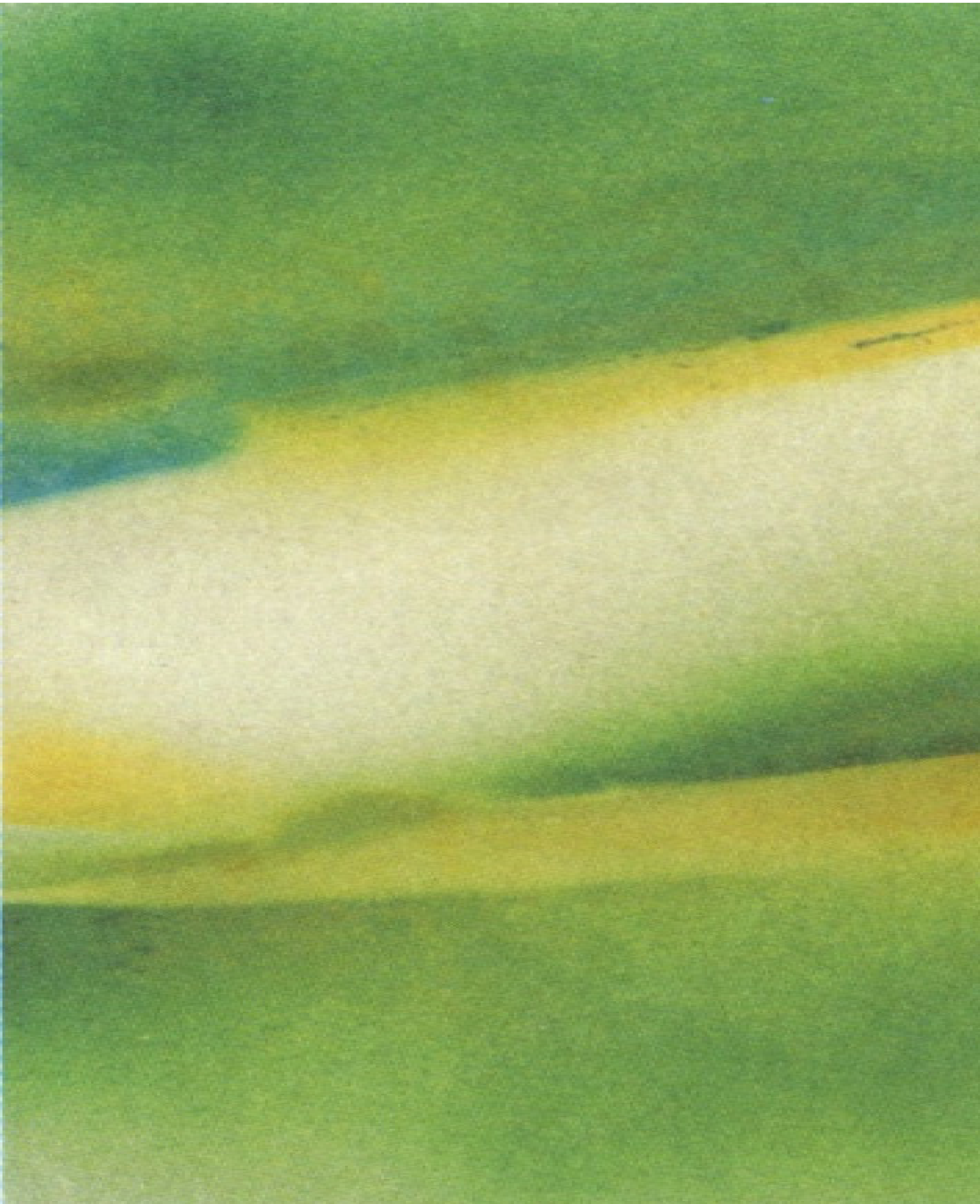
The model applied in these studies is a useful tool to evaluate roughly the state of the community of secondary consumers in an ecosystem and it provides relevant information to know the role of hominins in the Pleistocene ecosystems. The utility of the model shown by its application notwithstanding, it would require additional refinements to improve its resolution and to obtain results that might provide a more accurate approach to the niche that occupied by *Homo* in the Pleistocene paleoecosystems. Some aspects like the estimations of populations densities, or modeling the secondary consumer populations may be improved, as well as the study of the composition and configuration of communities, to include factors that might affect the presence or absence of species in the community lake spatial and habitat exclusions and inclusions.

Resumen

La disponibilidad de recursos es uno de los principales limitantes para la supervivencia y dispersión de los organismos. En el caso de los homininos del Pleistoceno en Europa, los ungulados serían uno de los recursos tróficos esenciales. La capacidad de los homininos de obtener recursos cárnicos de su ambiente estaría condicionada por la abundancia de presas, sus capacidades ecológicas y la intensidad de la competencia con carnívoros por esos recursos. La reconstrucción de las redes tróficas del pasado es esencial para evaluar el papel que desempeñó *Homo* en estos paleoecosistemas del Pleistoceno europeo. El estudio de las redes tróficas busca cuantificar y analizar las interacciones y dinámicas que se producen entre las especies de un ecosistema. La aplicación de este tipo de estudio a datos paleontológicos puede aportar información muy relevante como la disponibilidad de recursos para los consumidores secundarios o la intensidad de la competencia entre ellos. En este trabajo se aplica un modelo matemático basado en la Matriz de Leslie, que proporciona estimaciones de los recursos cárnicos disponibles para los consumidores secundarios (TAB) en una paleocomunidad. A partir de la biomasa disponible, se estiman las poblaciones de consumidores secundarios que se podrían sostener en el paleoecosistema, distribuyendo la TAB según las preferencias por determinados tipos de presas y según sus requerimientos energéticos. Así se obtiene una representación de la comunidad de macromamíferos del paleoecosistema. Para poder valorar su estado, el acceso a los recursos y cómo cubrían los requerimientos la comunidad de consumidores secundarios,

se desarrollaron unos índices de competencia o satisfacción de requerimientos con los que se puede comparar entre conjuntos faunísticos de diferente cronología y localización. El modelo se ha aplicado con diferentes perspectivas para conocer más sobre el papel del género *Homo* en los ecosistemas del Pleistoceno y, como fruto de estas aplicaciones, se han ido aportando ideas para su mejora y desarrollo. Por un lado, se aplicó para conocer cómo era el estado del paleoecosistema del nivel TD6-2 del yacimiento Gran Dolina de la Sierra de Atapuerca, ya que es un nivel muy importante en el estudio socioeconómico de los pobladores europeos del Pleistoceno Inferior por su cronología y riqueza de restos fósiles humanos. Por otro, se comparó la competencia en las comunidades de consumidores secundarios entre dos periodos, Pleistoceno Inferior y Medio, para estudiar si esta competencia podía explicar la escasez de evidencias de presencia humana en el Pleistoceno Medio respecto al Inferior. Este estudio se planteó a nivel local, comparando el nivel TD6-2 (Pleistoceno Inferior) con el nivel TD8 (Pleistoceno Medio) de Gran Dolina. Por último, desde la escala local se pasó a la escala continental y se estudió la competencia en paleoecosistemas europeos del Pleistoceno Inferior tardío y en los del Pleistoceno Medio. Los resultados de estos análisis mostraron una riqueza de recursos muy importante en el nivel TD6-2 que permitía sostener a la comunidad de consumidores secundarios presentes en la tafocenosis, incluido *Homo antecessor* e, incluso, pudiendo soportar una especie de gran félido no presente en la comunidad. Por otro lado, el nivel TD8 no mostraba una cantidad de recursos capaz de soportar a los consumidores secundarios con densidades máximas como en TD6-2, teniendo mayor grado de competencia por los recursos cárnicos. Se propuso que este grado de competencia podía explicar la falta de presencia humana en el ecosistema. Al aplicar el modelo a escala continental, el grado de competencia parecía perder relevancia al analizar la presencia humana, siendo menor el grado de competencia en los paleoecosistemas del Pleistoceno Medio que en los del Pleistoceno Inferior, resultado opuesto al obtenido a escala local. La diferencia de los resultados obtenidos a escala local y a escala continental puede deberse a una dinámica distinta en el yacimiento Gran Dolina de la Sierra de Atapuerca, con respecto a la del resto de yacimientos analizados continentalmente, o a la diferencia del tipo de análisis. El procedimiento del análisis a nivel continental podría enmascarar dinámicas específicas de las paleocomunidades a escala local que sí podrían obedecer a una diferente intensidad de competencia por los recursos cárnicos. Se puede interpretar a partir de los resultados, desde una perspectiva ecológica, que los humanos durante el Pleistoceno Inferior y comienzos del Medio, tenían dificultades para hacerse con recursos cárnicos, existiendo un condicionamiento de su presencia según la estructura y composición de las paleocomunidades. A partir del Pleistoceno Medio, con una tecnología (Achelense) y estructura social más compleja, los condicionamientos ecológicos podrían haberse hecho más débiles para los humanos, dándose una explosión demográfica, como han sugerido algunos autores.

El modelo aplicado en estos estudios es una herramienta útil para evaluar, a grandes rasgos, el estado de la comunidad de consumidores secundarios de los ecosistemas y aporta una información relevante para conocer el papel que desenvolvían los homininos en los ecosistemas durante el Pleistoceno. Pese a la utilidad observada al aplicarlo, el modelo requeriría algunos refinamientos para incrementar el grado de resolución y obtener resultados que posibilitaran una perspectiva más precisa del nicho que ocupaba *Homo* en los paleoecosistemas pleistocenos. Aspectos como las estimaciones de las densidades o la modelización de las poblaciones de consumidores secundarios deberían ser más desarrollados, así como el estudio de las composiciones y configuraciones de las comunidades, para contemplar parámetros que podrían afectar a la presencia o ausencia de especies, como la exclusión y la inclusión espacial o/y de hábitats.



Introducción

En lás páginas anteriores:
Cuadro sin título de la serie *Tropical screens*. Autor: Gonzalo Rodríguez Gómez.

Capítulo 1.- Introducción

1.1.- Marco ecológico

La disponibilidad de recursos en el medio ambiente influye sobre las capacidades de supervivencia de las especies y puede condicionar los movimientos migratorios. Entre los recursos que deben estar en el medio para que se desarrolle una especie se encuentran los recursos tróficos, necesarios para el crecimiento y mantenimiento de los individuos. A lo largo de la evolución del linaje humano, el ambiente o marco ecológico en el que los humanos desarrollaron sus actividades, tuvo una importante influencia en su supervivencia por lo que su estudio puede aportar una información relevante para entender sus organizaciones paleoeconómicas, su fisiología, demografía o evolución cultural.

Muchas sociedades cazadoras-recolectoras actuales tienen una alta dependencia de los recursos animales (Cordain et al., 2000) y se considera que para los primeros pobladores humanos europeos la carne era también un recurso trófico relevante. Estudios con poblaciones actuales de cazadores-recolectores muestran que el consumo de fuentes animales representa entre un 30 y un 60% de su dieta (Jenike, 2001; Leonard et al., 2007). Algunos autores asumen que los grandes mamíferos, o macromamíferos, eran una fuente de alimento común para los homininos durante el Pleistoceno Inferior (por ejemplo Binford, 1981; Binford, 1985; Gaudzinski y Roebroeks, 2000; Marean, 1989; Roebroeks, 2001; Speth, 2010) (ver Figura 1.1) aunque, por otra parte, McNabb (2007) defiende que apenas se encuentra información para apoyar una relevancia del consumo de pescado y aves en la dieta humana en este periodo. En el yacimiento Sima del Elefante de la Sierra de Atapuerca, en Burgos, se registran evidencias de consumo de tortugas en el Pleistoceno Inferior (Blasco et al., 2011), aunque debieran de considerarse como un comportamiento excepcional. Algunos autores defienden que el consumo de pequeñas presas se hace común, al menos, a partir del inicio del Paleolítico Medio, desde hace aproximadamente 200 ka (Klein y Scott, 1986; Stiner, 2001; Stiner, 2005; Stiner y Tchernov, 1998). Existen tanto en Europa Occidental como en Oriente Medio, yacimientos del Pleistoceno Inferior y Medio en los que se evidencia que los homininos consumían pequeñas presas, como por ejemplo en Gesher Benot Ya´aqov, en Israel, datado en aproximadamente 750 ka, en el que se registra el consumo de especies de medio acuático como cangrejos y peces (Alperson-Afil et al., 2009); en la Sierra de Atapuerca (Burgos, España) y en Cueva Bolomor (Valencia, España) (Blasco et al., 2013; Huguet et al., 2013), con evidencias de consumo de aves, peces, pequeños mamíferos y reptiles. La caza de grandes mamíferos está registrada en África en 1,8 Ma (Millones de años) (Bunn y Pickering, 2010) y en Europa el acceso primario a los cadáveres es evidente alrededor de 1,3 Ma en Fuente Nueva-3 (Orce, Granada, España) (Espigares et al., 2013), y en la Sierra de Atapuerca alrededor de 1,2 Ma (Carbonell et al., 2008; Rodríguez et al., 2011) y 0,9 Ma (Díez et al., 1999; Parés et al., 2013a; Saladié et al., 2011).

Siendo la relación entre los primeros pobladores humanos europeos y los macromamíferos tan estrecha, el análisis de estas relaciones podría ofrecer información sobre la dispersión europea del género *Homo*. Kahlke (2009) asume que la inestabilidad climática del Epivillafranquiense (1,2-0,9 Ma) (ver Figura 1.1) favoreció el primer asentamiento de homininos en Europa. Por otra parte, Made y Mateos (2010) defienden que la aparición de paisajes abiertos y ecosistemas con predominio de la vegetación herbácea favorecería la dispersión de los consumidores primarios, a partir del cambio de la frecuencia de los ciclos climáticos de la Tierra. Se pasó de ciclos de aproximadamente 41 ka (miles de años) a ciclos de 100 ka. Estos cambios de ciclo debidos a que la oblicuidad del eje de la Tierra toma menor relevancia que en el periodo anterior, tienen efecto sobre el clima aproximadamente entre 725-650 ka (Head y Gibbard, 2005), ocurriendo próximos en el tiempo a la inversión geomagnética

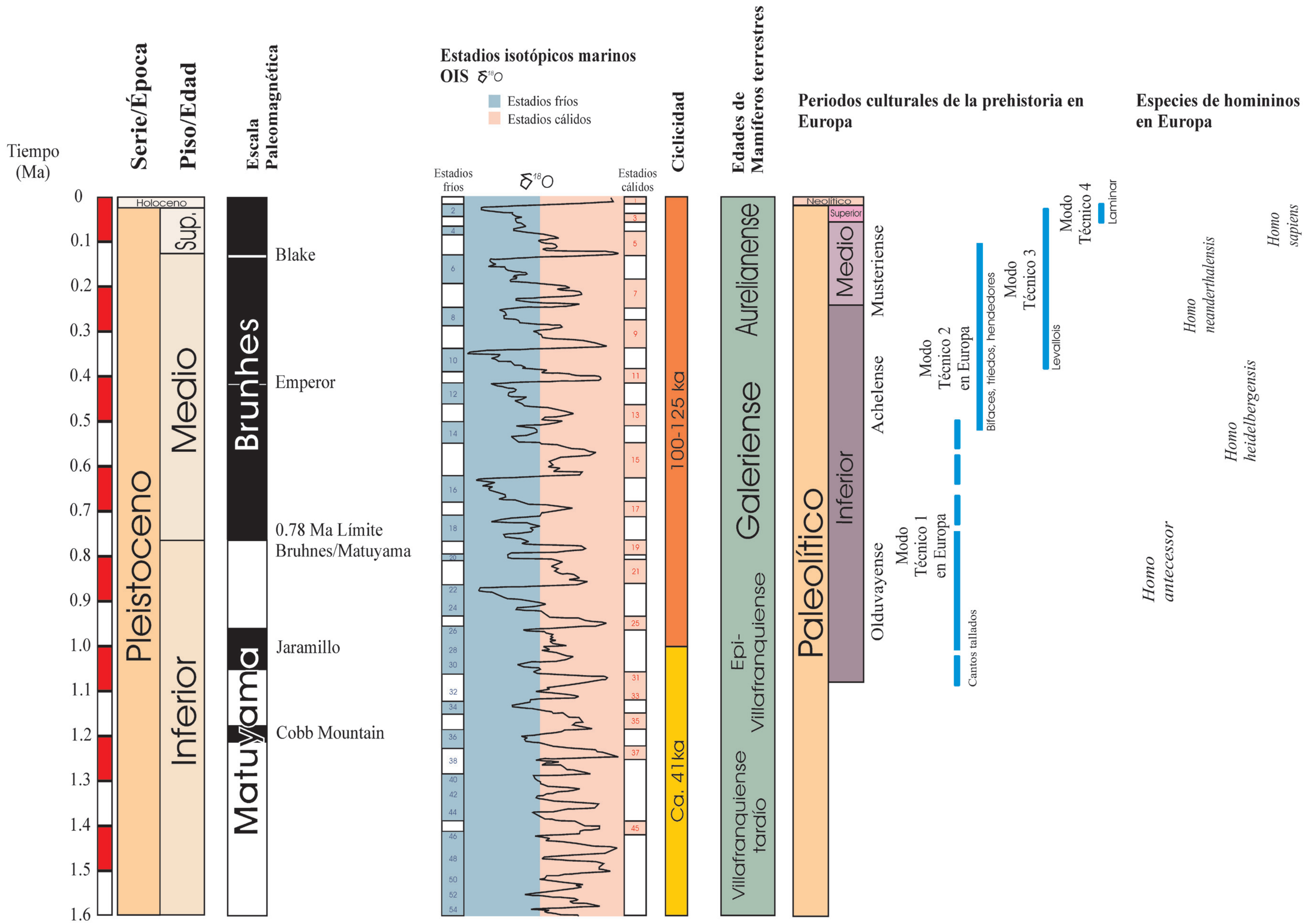


Figura 1.1.- Tabla Cronoestratigráfica del Pleistoceno en Europa. A partir de Silva et al. (2009), Palombo (2010), y Kahlke et al. (2011).

Matuyama-Brunhes (780 ka) (McNabb, 2007) (Figura 1.1). Sin embargo, según los estudios de Berger y colegas (Berger et al., 1999; Berger y Loutre, 1991) no está claro que los cambios climáticos que se observan al inicio del Pleistoceno Medio sean consecuencia exclusivamente de cambios en parámetros orbitales, teniendo que contar con la relevancia de la concentración de CO_2 atmosférica (Ruddiman, 2003) y con la reducción global de la temperatura (Zachos et al., 2001). Con los cambios de las condiciones climáticas (Head y Gibbard, 2005; Maslin y Ridgwell, 2005; Schneider y Root, 1998; Shackleton, 1995), ocurridos durante la denominada *Mid-Pleistocene Revolution* o Revolución de mitad del Pleistoceno (MPR) (Berger y Jansen, 1994; Maslin y Ridgwell, 2005), las especies de grandes mamíferos migrarían con la apertura de los paisajes, surgiendo cambios en las configuraciones de los ecosistemas. Es posible entonces que los homininos se trasladaran junto con esta fuente de recursos (Made, 2013; Made y Mateos, 2010). Una visión alternativa al efecto de estos cambios sobre las faunas la ofrece Palombo (2013), defendiendo que los grandes mamíferos no migrarían en oleadas sino que lo harían de forma independiente, cada especie en función de su tolerancia al medio y su flexibilidad etológica, no estando la dispersión humana correlacionada directamente con estas migraciones ni con los cambios climáticos.

Teniendo en cuenta que los macromamíferos tenían una importante presencia en la dieta humana durante el Pleistoceno, las capacidades de los homininos para obtener recursos del ambiente tendrían que haber estado condicionadas por la abundancia de presas, por sus características ecológicas y por la intensidad de competencia con carnívoros por esos recursos cárnicos. La disponibilidad de recursos y la competencia con los carnívoros ha sido propuesta, de forma repetida, como factor limitante clave para las poblaciones europeas de homininos (Arribas y Palmqvist, 1999; Martínez-Navarro y Palmqvist, 1996; Palombo, 2007; Palombo, 2010; Rodríguez et al., 2012; Turner, 1992). Palombo (2010) propone que la competencia con los grandes carnívoros por las presas o por la carroña pudo haber retrasado la expansión de *Homo* por Europa durante el Pleistoceno Inferior, porque esas primeras poblaciones no tendrían un suficiente desarrollo tecnológico para hacer frente a sus posibles competidores, aunque el registro de los humanos pobladores de la Sierra de Atapuerca durante el Pleistoceno Inferior parece apoyar que éstos tenían estrategias de subsistencia desarrolladas que permitirían sobrevivir y mantener de forma continua su ocupación en Europa (Huguet et al., 2013). Otros autores proponen que las poblaciones humanas en este periodo podrían haber tenido una gran dependencia del carroñeo de carcasas de ungulados debido, precisamente, a la alta competencia con carnívoros (Arribas y Palmqvist, 1999; Martínez-Navarro y Palmqvist, 1996; Turner, 1992). Sin embargo, la competencia por la carroña sería también muy alta por la presencia de la hiena gigante de rostro corto (*Pachycrocuta brevirostris*) en los complejos faunísticos europeos del Pleistoceno Inferior (Madurell-Malapeira et al., 2010; Palombo, 2010). Por otra parte, otros investigadores defienden que la abundancia de carroña sería muy alta y, por tanto, la competencia por ella baja, debido a que los tigres diente de sable (por ejemplo, *Megantereon*) no estarían capacitados para aprovechar con eficacia todos los recursos disponibles de los cadáveres de sus presas (Arribas y Palmqvist, 1999; Marean, 1989; Martínez-Navarro y Palmqvist, 1995; Palmqvist et al., 1996; Palmqvist et al., 2005; Palmqvist et al., 2007; Turner, 1992). De esta forma, como observan Espigares et al. (2013), el consumo secuencial de la carroña dejada por los dientes de sable pudo permitir la convivencia entre hiena gigante de rostro corto (*Pachycrocuta brevirostris*) y los homininos.

Como consecuencia de la MPR (Revolución de Mitad del Pleistoceno) se produce un cambio en las comunidades de mamíferos en Europa que conlleva la aparición de nuevos carnívoros, la extinción de otros como *Pachycrocuta brevirostris* y el incremento de riqueza de especies de herbívoros (e.g. Azanza et al., 2004; Cuenca-Bescós et al., 2005; Palombo, 2007; Palombo, 2010; Rodríguez et al., 2004; Turner, 1992; Turner et al., 2008). *Pachycrocuta brevirostris* probablemente competía intensamente con *Homo* por la carroña, mientras que los grupos de licaones, las panteras (*Panthera gombaszoegensis)* y pumas (*Puma pardoides*), entre otros (Madurell-Malapeira et al., 2010; Palombo, 2010), serían importantes competidores por la caza. Los cambios faunísticos a comienzos del Pleistoceno Medio pudieron permitir un mejor acceso a la carroña que en el periodo anterior ya que, unido a un desarrollo de armas y equipos de herramientas más efectivos, pudieron facilitar la dispersión de *Homo* a través de Europa (Palombo, 2010; Rodríguez et al., 2012). Por otra parte, se cree que con estos cambios en la composición de las comunidades se produjo una reducción en la cantidad de recursos susceptibles de ser consumidos como carroña, ya que, desaparecerían los tigres dientes de sable, principales generadores de carroña (Arribas y Palmqvist, 1999; Marean, 1989; Martínez-Navarro y Palmqvist, 1995; Palmqvist et al., 1996; Palmqvist et al., 2005; Palmqvist et al., 2007;

Turner, 1992) y aparecerían otros grandes félidos como el león (*Panthera leo*) y el leopardo (*Panthera pardus*) que aprovecharían con mayor eficacia las presas cazadas (Turner et al., 2008). Siendo menor la cantidad de carroña en el medio desaparecería ese nicho ecológico que explotaban los homininos y se incrementarían las dificultades y la competencia para acceder a los recursos cárnicos (Palmqvist et al., 2011). Arribas y Palmqvist (1999) sugieren que el cambio en la composición de la comunidad de carnívoros, con la sustitución de dientes de sable por panterinos, pudo forzar a los homininos a desarrollar mejoras conductuales y tecnológicas que llevaron a configurar herramientas del complejo tecnológico Achelense o Modo 2, más efectivas que el Olduvayense o Modo 1 (Figura 1.1). Tanto Jiménez-Arenas et al. (2011) como Santonja y Pérez-González (2010) proponen como explicación alternativa la sustitución de las poblaciones de *Homo antecessor* por una nueva especies de hominino inmigrante, *Homo heidelbergensis*, que traería consigo el Complejo Tecnológico Achelense o Modo 2. En los siguientes párrafos se trata el intenso debate paleoantropológico sobre la continuidad o discontinuidad de las poblaciones humanas en Europa durante la transición del Pleistoceno Inferior al Medio.

Según el registro fósil, los primeros humanos que poblaron Europa lo hicieron durante el Pleistoceno Inferior (Arzarello et al., 2007; Bahain et al., 2007; Carbonell et al., 2008; Despriée y Gageonnet, 2003; Despriée et al., 2006; Duval et al., 2012a; Duval et al., 2012b; Duval et al., 2011; Martínez et al., 2010; Moncel, 2010; Parés et al., 2013a; Parfitt et al., 2010; Rodríguez et al., 2011; Toro-Moyano et al., 2013; Voinchet, 2002). Esas primeras incursiones se pudieron deber a diferentes causas (cambios climáticos, migraciones de especies de mamíferos, presiones demográficas, competencias interespecíficas, barreras biogeográficas, cambios en las estructuras de las comunidades) que modificarían la disponibilidad de recursos en el medio y presionarían a los humanos a desplazarse a nuevos territorios (Arribas y Palmqvist, 1999; Jiménez-Arenas et al., 2011; Kahlke et al., 2011; Made, 2013; Made y Mateos, 2010; Palombo, 2010; Palombo, 2013). Parece que *Homo antecessor* descrito en el nivel TD6 de Gran Dolina de la Sierra de Atapuerca (Arsuaga et al., 1999; Carbonell et al., 1995; Carretero et al., 1999; Fernández-Jalvo et al., 1999; Lorenzo et al., 1999), habitó Europa Occidental al menos entre el Subcron Jaramillo y el Límite Matuyama-Brunhes. Hay evidencias más antiguas como los restos de la Sima del Elefante de la Sierra de Atapuerca (Carbonell et al., 2008) clasificados como *Homo* sp. y los de Barranco León (Toro-Moyano et al., 2013) (pero ver Muttoni et al., 2015; Muttoni et al., 2013). Además de por los restos humanos, la presencia humana se constata por las evidencias arqueológicas en yacimientos del Pleistoceno Inferior en Europa Occidental: Fuente Nueva 3 (Duval et al., 2012a; Duval et al., 2012b), Barranco León (Toro-Moyano et al., 2013), Vallparadís (Martínez et al., 2010) (pero ver también Madurell-Malapeira et al., 2012), Sima del Elefante y Gran Dolina (Rodríguez et al., 2011) en España; Pirro Nord (Arzarello et al., 2007), y Ca´Belvedere di Monte Poggiolo (Bahain et al., 2007) en Italia; Le Vallonet (de Lumley et al., 1988), Bois-de-Riquet (Bourguignon et al., en prensa; Crochet et al., 2009), Saint-Hilaire-la Gravelle (Despriée y Gageonnet, 2003; Voinchet, 2002) y Pont de Lavaud (Despriée et al., 2006) en Francia; Happisburgh (Parfitt et al., 2010) en Reino Unido; Untermassfeld (Parés et al., 2013b) y Dorn-Dürkheim 3 (Fiedler y Franzen, 2002) en Alemania. Desde el punto de vista tecnológico, estos yacimientos pueden considerarse como Complejo Tecnológico Olduvayense o Modo 1 (Barsky et al., 2013; Mosquera et al., 2013). A final del Pleistoceno Inferior, hay yacimientos con industria lítica que presentan características de un Modo 1 tardío o un pre-Achelense (Barsky y de Lumley, 2010; Barsky et al., 2013; Moncel et al., 2013; Mosquera et al., 2013; Santonja y Pérez-González, 2010; Scott y Gibert, 2009; Vallverdú et al., 2014; Walker et al., 2013), aunque algunas dataciones son discutibles (Jiménez-Arenas et al., 2011). Hace aproximadamente 0,6-0,5 Ma, se registra una expansión de la presencia humana y un incremento en los registros arqueológicos caracterizados como achelenses plenos o pertenecientes al Complejo Tecnológico Modo 2. En este intervalo de tiempo, se incrementa de forma significativa el número de yacimientos y empiezan a ocuparse con continuidad latitudes septentrionales (por ejemplo, Mania y Vlcek, 1999; Roberts y Parfitt, 2000; Thieme, 1997) por poblaciones humanas que ya definen cultural y paleoantropológicamente el Pleistoceno Medio europeo (Bermúdez de Castro y Martinón-Torres, 2013; Dennell et al., 2011; Doronichev y Golovanova, 2010; Jiménez-Arenas et al., 2011; Ollé et al., 2013). Un reflejo del cambio cultural son los hogares conservados en Europa con edades próximas a 400 ka (Terra Amata, Beeches Pit, Schöningen o Bilzingsleben) (Mosquera et al., 2013; Roebroeks and Villa, 2011).

A partir de las evidencias arqueológicas, algunos investigadores defienden que se produjo una discontinuidad de la ocupación humana de Europa durante la transición del Pleistoceno Inferior al Medio (Jiménez-Arenas et al., 2011; Moncel, 2010; Moncel et al., 2013; Mosquera et al., 2013; Santonja y Pérez-González, 2010; Vallverdú et al., 2014). Otras hipótesis proponen la existencia de diferentes oleadas de migración en Europa durante el Pleistoceno Inferior (Agustí et al., 2009; Bermúdez de Castro et al., 2013; Carbonell et al., 2010; Made y Mateos, 2010; Mosquera et al., 2013; Muttoni et al., 2010; O´Regan et al., 2011; O'Regan, 2008; Palombo, 2010; Palombo, 2013). Otros autores defienden que hubo periodos de contacto intermitente y de aislamiento entre las poblaciones euroasiáticas durante el Pleistoceno Inferior (Bermúdez de Castro y Martinón-Torres, 2013), y durante el Pleistoceno Medio (Dennell et al., 2011). En el debate de la temprana ocupación de Europa, como se comentó anteriormente, algunos investigadores apoyan una sustitución de las poblaciones de *Homo antecessor* por individuos de una especie de hominino africana que traería consigo la tecnología Achelense o Complejo Tecnológico Modo 2 (Jiménez-Arenas et al., 2011; Santonja y Pérez-González, 2010). Mosquera et al. (2013) sugieren una despoblación a nivel continental en el intervalo de tiempo entre 0,9 y 0,5 Ma, ya que las evidencias de presencia humana en Europa Occidental son escasas en este periodo. Concretamente, los homininos habrían habitado la Sierra de Atapuerca de forma continuada desde el Pleistoceno Inferior a excepción de este intervalo entre 0,9 y 0,5 Ma, primero con *Homo antecessor* y después de ese intervalo con las poblaciones de la Sima de los huesos. Sin embargo, existen evidencias de presencia humana en Europa Occidental entre los estadios isotópicos OIS 18 y OIS 16 (aproximadamente entre 0,7 y 0,6 Ma, respectivamente) (Figura 1.1), con restos de industria lítica recuperados en la cuenca del río Loire (Despriée et al., 2011) y en la Caune de l´Arago (Barsky and de Lumley, 2010) en Francia.

1.2.- Una aproximación paleoecológica al poblamiento humano de Europa durante el Pleistoceno

El conocimiento de la disponibilidad de recursos tróficos para las poblaciones paleolíticas, de la estructura de las redes tróficas y de la composición de carnívoros y herbívoros dentro del ecosistema, es esencial para los estudios de paleofisiología de homininos y paleodemografía (Mateos, 2004) así como para entender la organización paleoeconómica y la evolución cultural de estas sociedades (Arribas y Palmqvist, 1999; Croitor y Brugal, 2010; Palombo, 2010; Turner, 1992). El estudio de las estrategias de supervivencia y los modelos de obtención de recursos permite entender los modos de vida de las poblaciones humanas, contextualizando el aprovechamiento potencial de sus entornos así como las relaciones intra e intergrupales y las interespecíficas. La estimación cuantitativa de la oferta y la demanda de biomasa de consumidores primarios podría aportar una información interesante para el análisis de los ecosistemas pleistocenos, pudiendo profundizar en el análisis del papel desarrollado por los humanos en estos ecosistemas y su relación con los componentes bióticos y abióticos.

Los estudios teóricos y descriptivos de la arquitectura y funcionamiento de las redes tróficas tiene una larga tradición en Ecología (por ejemplo Cohen, 1977; May, 1983; Owen-Smith y Mills, 2008; Pascual y Dunne, 2006). En Paleoecología, se emplean herramientas cuantitativas para evaluar las dinámicas tróficas en las paleocomunidades (Alroy, 1999; Bermúdez de Castro et al., 1995; Croitor y Brugal, 2010; Choquenot y Bowman, 1998; Dennell et al., 2008; Fariña, 1996; Hemmer, 2004; Hertler y Volmer, 2008; Mithen, 1993; Nogués-Bravo et al., 2008; Palmqvist et al., 2003; Palmqvist et al., 1996; Palombo y Mussi, 2006; Raia et al., 2007; Rodríguez et al., 2012; Turner, 2009; Vizcaíno et al., 2010; Vizcaíno et al., 2004). Esta aproximación puede ser útil para abordar temas de debate sobre la evolución humana y el papel de los homininos en su paleoecosistema, como por ejemplo, las posibles implicaciones humanas en la extinción de megafauna al final del Pleistoceno Superior (Alroy, 1999; Choquenot y Bowman, 1998; Mithen, 1993; Nogués-Bravo et al., 2008) o para estudiar las dinámicas tróficas de las paleocomunidades y así poder entender las relaciones entre los mamíferos en esas comunidades (por ejemplo Bermúdez de Castro et al., 1995; Fariña, 1996; Hertler y Volmer, 2008; Palmqvist et al., 2003; Rodríguez et al., 2012; Vizcaíno et al., 2010; Vizcaíno et al., 2004).

Carbone y Gittleman (2002), estudiando especies actuales en diferentes ecosistemas, observaron que existía una relación entre la biomasa de presas y la biomasa de carnívoros relacionando qué biomasa de presas es necesaria para mantener a un carnívoro de un determinado tamaño y así, poder evaluar el estado de la comunidad de carnívoros en un ecosistema dado. Este tipo de relación ha sido aplicada a paleocomunidades miocenas, pliocenas y pleistocenas (Bermúdez de Castro et al., 1995; Fariña, 1996; Meloro y Clauss, 2012; Palombo, 2010; Vizcaíno et al., 2010; Vizcaíno et al., 2004). En estos estudios, para estimar la biomasa de presas y de depredadores se toma la lista de fauna de los yacimientos, se le asigna a cada especie un papel como depredador o como presa y se estima su tamaño corporal (peso) y número de individuos.

Con esos valores para todas las especies se multiplica el peso de los individuos de la especie por el número de individuos obteniendo así la biomasa de la población de esa especie. Para conocer la biomasa de todas las presas se sumaría la biomasa de las poblaciones de cada especie de presa. De igual forma se haría para estimar la biomasa de depredadores con especies de este grupo. Este tipo de análisis se basa en la relación biomasa de presas y biomasa de depredadores, y nos da una información a gran escala del ecosistema. Para tener una mayor resolución habría que reducir la escala y estudiar las relaciones específicas dentro de la paleocomunidad, teniendo que conocer con más precisión la estructura de la red trófica. Normalmente, no se

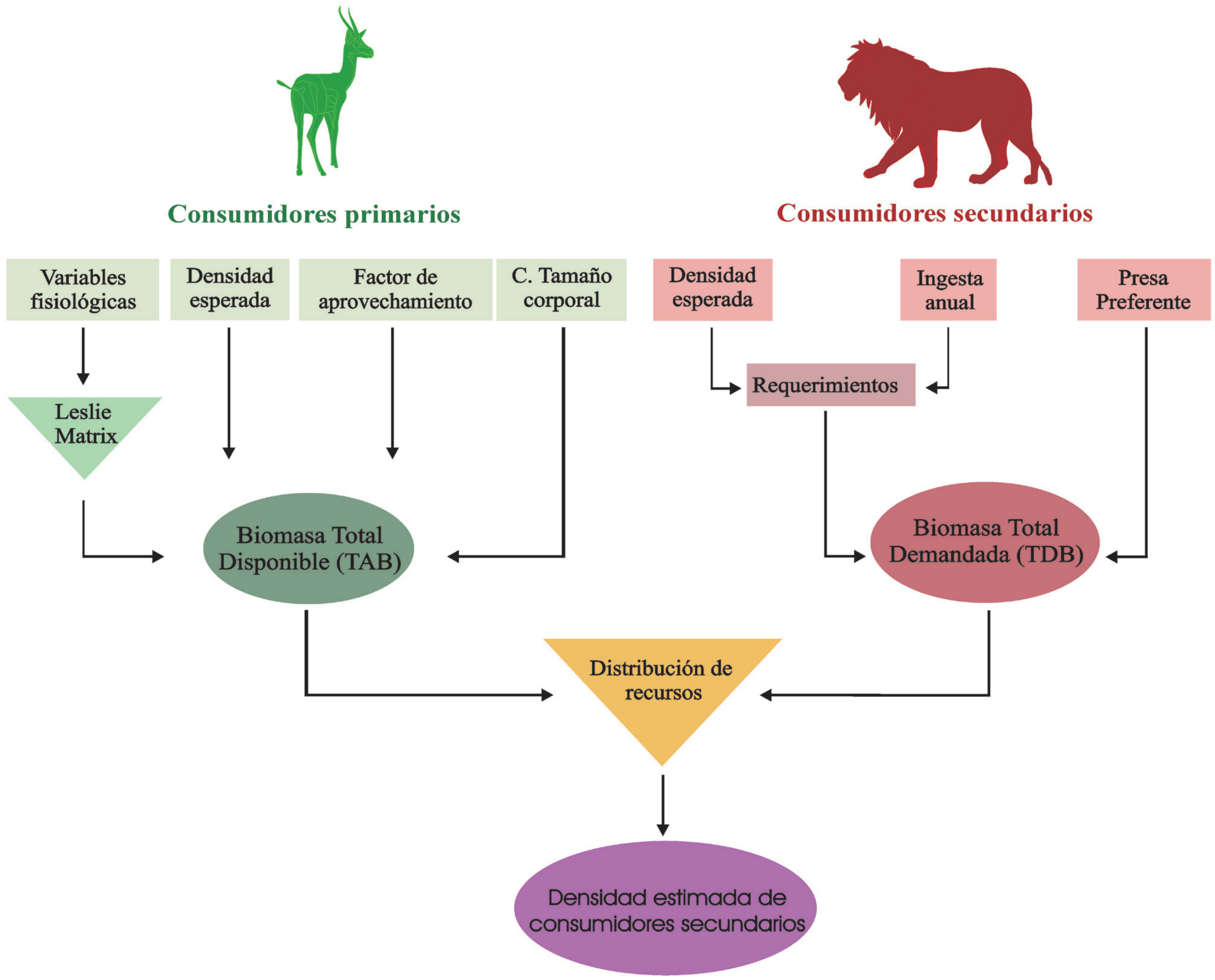


Figura 1.2.- Diagrama de flujos mostrando los componentes del modelo aplicado para evaluar la disponibilidad de recursos tróficos disponibles y la competencia en la comunidad de consumidores secundarios (modificado a partir de Rodríguez-Gómez et al., 2014a; Rodríguez-Gómez et al., 2014b; Rodríguez-Gómez et al., 2013a).

consideran las preferencias de depredación de los carnívoros ni sus habilidades para cazar ni las características de las presas. Si estos factores fueran tenidos en cuenta se podría aumentar la resolución de estos estudios de dinámicas tróficas de las paleocomunidades. Un refinamiento para estudiar el grado de competencia se muestra en el trabajo de Hertler y Volmer (2008) sobre el ecosistema de Java durante el Pleistoceno, en el que aplican el método de estimación del tamaño preferido de presas para cada carnívoro desarrollado por Hemmer (2004).

Los estudios a nivel local permiten alcanzar una mayor resolución, ya que la información disponible permite estimaciones más precisas de las preferencias de depredación (Feranec et al., 2010; García et al., 2009) y el funcionamiento de los ecosistemas (Palmqvist et al., 2003; Palmqvist et al., 2008). Por contra, estudios a nivel global o continental permiten encontrar propiedades generales de los sistemas (Carbone et al., 1999; Meloro y Clauss, 2012).

1.3.- Bases que subyacen en la metodología empleada

La presente tesis doctoral forma parte de una línea de investigación, desarrollada por los grupos de Paleofisiología y Paleoecología del CENIEH (Centro Nacional de Investigación sobre la Evolución Humana), que pretende modelizar la disponibilidad de recursos tróficos que podían tener las poblaciones de cazadores-recolectores durante el Pleistoceno. Tomando como punto de partida los yacimientos de la Sierra de Atapuerca se pretendía simular, mediante estimaciones cuantitativas, el ecosistema en el los homininos desarrollaron su vida. Para ello era necesario desarrollar una metodología con la que poder abarcar este objetivo.

Bermúdez de Castro y colaboradores (1995) intentaron llevar a cabo una estimación de los recursos disponibles para las poblaciones de cazadores-recolectores que habitaron la Sierra de Atapuerca en el Pleistoceno Medio. Basándonos en esa idea, nuestro equipo desarrolló un modelo (Figura 1.2) que contemplase los factores que consideramos claves para profundizar en las relaciones interespecíficas de las comunidades de macromamíferos en Europa:

1.- la biomasa de consumidores primarios disponibles para los consumidores secundarios o Biomasa Total Disponible (TAB, *Total Available Biomass*)

2.- la demanda de biomasa por parte de la comunidad de los consumidores secundarios en condiciones óptimas o Biomasa Total Demandada (TDB, *Total Demanded Biomass*)

3.- el reparto efectivo de la biomasa disponible entre los consumidores secundarios.

De esta forma, podríamos conocer la biomasa que podían tener disponible las poblaciones de cazadores-recolectores paleolíticos y qué comunidad de consumidores secundarios podía sostener la paleocomunidad. Las estimaciones se realizan tomando como unidad de tiempo el año y no se tiene en cuenta la estacionalidad de los recursos en el medio.

1.3.1.- TAB (Biomasa Total Disponible)

Para estimar la Biomasa Total Disponible o TAB, que sería la biomasa de consumidores primarios utilizable por los consumidores secundarios, tenemos en cuenta la estructura de la población y el perfil de mortalidad, la densidad de individuos de cada especie de consumidores primarios, el factor de aprovechamiento de cada cadáver y la variación de masa corporal a lo largo de la ontogenia de un individuo. En nuestros análisis empleamos sólo la parte del ecosistema compuesta por los macromamíferos, especies de mamíferos de más de 10 kilogramos, porque engloban las especies que podrían tener relevancia para las poblaciones de cazadores-recolectores como fuente de recursos, como competidores o como potenciales depredadores (Owen-Smith y Mills, 2008; Roebroeks, 2001).

En los estudios que relacionan biomasa de presas y biomasa de depredadores se asume una relación directa entre estos dos parámetros, como nos sugiere el trabajo de Carbone y Gittleman (2002). Sin embargo, las diferentes especies de una comunidad presentan valores promedio de tamaño adulto muy diferentes entre sí. En una misma paleocomunidad, como la del nivel TD6-2 de Gran Dolina en la Sierra de Atapuerca, habría *Mammuthus meridionales* adultos que pesarían de media 6.252 kg y castores (*Castor fibe*r) con un peso de 19 kg. Además, dentro de una misma especie también se observa una gran variación de tamaño según la edad de los individuos. Por ejemplo, *Equus altidens* pesaría en promedio al terminar su primer año de vida 70 kg, al segundo año 164 kg, al tercer año 276 kg y a partir del cuarto 306 kg (pesos estimados por edad a partir de los estudios de Millar (1977) y Case (1978)). Teniendo en cuenta que el tamaño corporal de las presas es el principal factor de selección para los depredadores (Carbone et al., 1999; Levinton, 1982; Radloff y Toit, 2004), podemos encontrar ecosistemas en los que los depredadores no puedan acceder a los consumidores primarios de mayor tamaño (evolución de las presas para evitar a los depredadores (Rodríguez et al., 2012; Stanley, 1973; Yoshida, 2006)). En esos ecosistemas, la relación entre biomasa de presas y biomasa de depredadores no expresaría la relación real entre estos grupos, siendo demasiado simplista, ya que se observarían menos depredadores de lo esperado al considerar la biomasa total de consumidores primarios. Por otra parte, hay depredadores que no podrían acceder a consumidores primarios de categorías de tamaño grande pero podrían acceder a subadultos de esas especies. Si en un paleoecosistema estuvieran presentes dos especies como el *Equus altidens* y el guepardo europeo (*Acinonyx pardinensis*), podríamos pensar que el guepardo se alimentaría de otra presa ya que el peso promedio de *Equus altidens* es de 306 kg, peso que estaría fuera del preferido por el guepardo, que se encontraría entre 45 y 90 kg (Rodríguez et al., 2012). Sin embargo, a lo largo de la ontogenia de *Equus altidens* los individuos alcanzarían pesos dentro del rango de presa preferidas por el guepardo, en el primer (70 kg) y segundo año (164 kg). Dada la importancia del tamaño corporal como principal factor de selección y para tener una perspectiva más cercana a la realidad, se consideró que había que implementar en el modelo:

- las diferentes categorías de peso, teniendo en cuenta los tamaños de los individuos y no el peso medio de la especie.
- las preferencias de los consumidores secundarios por cada categoría de peso.

Para esto, clasificamos la biomasa de consumidores primarios disponible para los secundarios (TAB) en diferentes categorías de peso (10-45 kg; 45-90 kg; 90-180 kg; 180-360 kg; 360-1.000 kg; >1.000 kg) siguiendo las categorías definidas por Rodríguez et al. (2012). Posteriormente, se asignó a cada categoría un porcentaje de preferencia de depredación por cada especie de consumidor secundario (TDB) (ver por ejemplo, Table 2 del Capítulo 3) (Rodríguez-Gómez et al., 2013b).

Como las poblaciones varían en estructura y tamaño a lo largo del tiempo, era necesario considerar una estimación de la estructura de la población. En el modelo asumimos que las fluctuaciones que sufre una población a lo largo del tiempo se producen alrededor de un valor promedio. Nuestra asunción se fundamentaba en que, de acuerdo al Teorema central del límite,

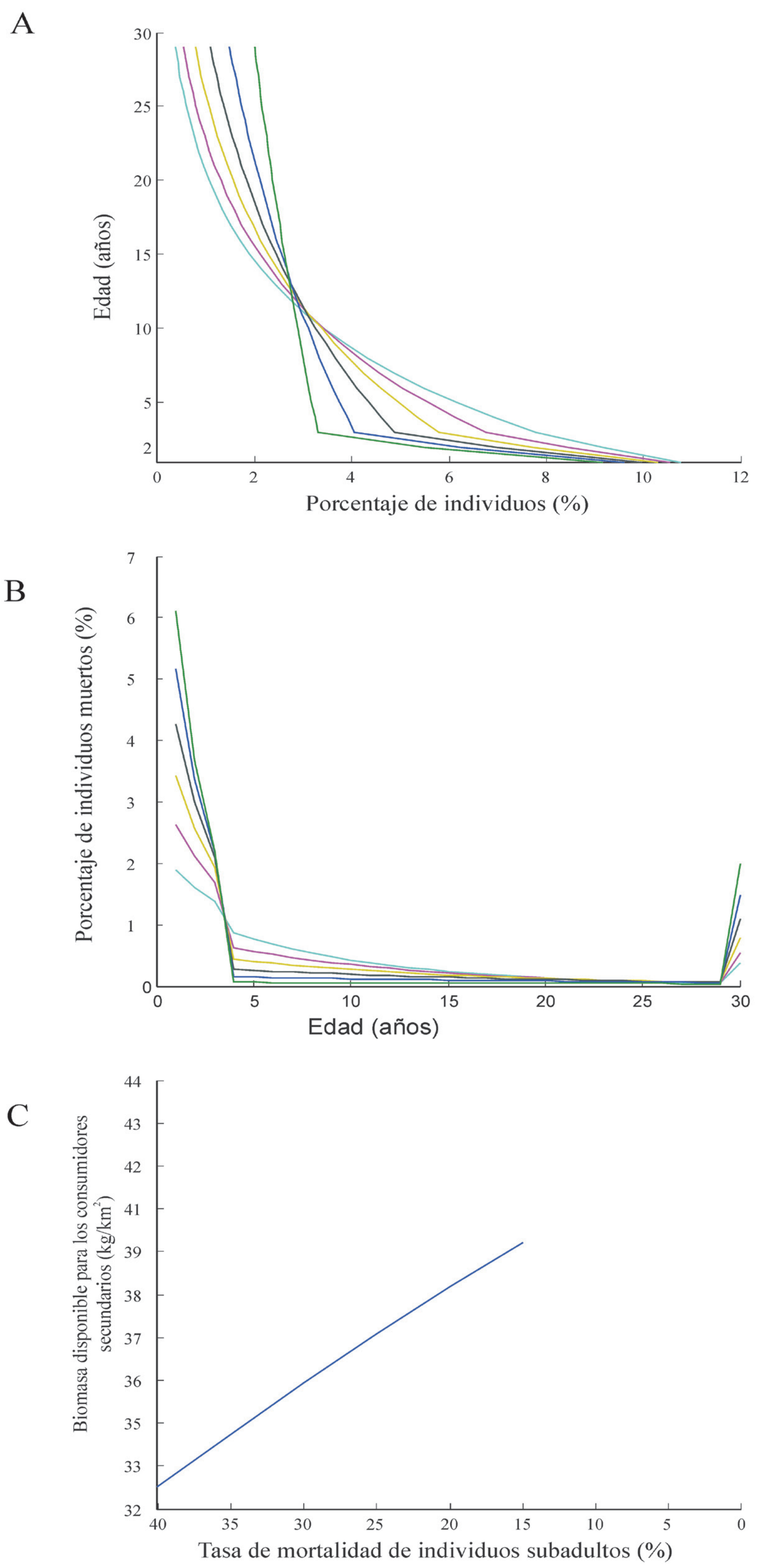


Figura 1.3.- Representación gráfica del perfil de población (A), el perfil de mortalidad (B), y la biomasa disponible para los consumidores secundarios (C) para diferentes tasas de mortalidad en subadultos para la especie *Equus altidens*. En los perfiles de población y mortalidad, cada línea se corresponde con una solución dada por el modelo para una tasa de mortalidad subadulta. El porcentaje de individuos muertos en el perfil de mortalidad representa el porcentaje de individuos de la población que mueren en cada edad *i*.

si una variable es resultado de la interacción de muchas variables aleatorias, aquella convergerá a una distribución normal y, por tanto, a la larga, las variaciones convergerán a la media. Esta asunción es aceptada en estudios de dinámica de poblaciones (por ejemplo, Owen-Smith, 2010). Para obtener una estructura de la población y unos perfiles de mortalidad promedio usamos la Matriz de Leslie (Leslie, 1945; Leslie, 1948). Esta Matriz se emplea en dinámica de poblaciones para representar la estructura de la población en diferentes momentos y describir sus oscilaciones. En nuestro caso, limitamos la Matriz de Leslie para que nos proporcione la estructura promedio de la población, introduciendo dos condiciones:

1.- La población debe ser estable, es decir, el tamaño de la población debe ser constante con el paso del tiempo.

2.- La población debe ser estacionaria, es decir, la estructura de edades de la población se debe mantener constante.

Con esto, la salida de la Matriz nos daría una estructura promedio de las oscilaciones poblacionales (Figura 1.3 A). Para conseguir estas salidas, debemos introducir valores de entrada como la longevidad de la especie, el tamaño promedio de los individuos en cada categoría de edad, la fertilidad en cada categoría de edad (número de crías promedio en un intervalo de tiempo), la edad en la que se alcanza la madurez sexual y la tasa de crecimiento para cada especie. La Matriz de Leslie está desarrollada considerando sólo la porción de la población que son hembras. En nuestro caso, al no tener datos de relación de machos y hembras, se decidió emplear una relación 1:1, es decir, consideramos que la estructura de la población de machos es idéntica a la de las hembras y que la relación de sexos es también igual. Esta práctica es habitual en la modelización de las dinámicas de poblaciones y se aproxima a la que se observa en la mayoría de especies actuales (Cicognani et al., 2000; Hutchins et al., 2003; Massei et al., 1997; Nowak, 1999; Woodd, 1999). En los perfiles de mortalidad (Figura 1.3 B) se expresan los individuos de cada clase de edad que no pasan a la siguiente edad. Se consideran las muertes sin tener en cuenta la causa (depredación, enfermedad o accidente). Para obtener los perfiles, se aplicaron diferentes tasas de mortalidad a las clases de edades subadultas, tasas de mortalidad que podrían soportar estas poblaciones. De esta forma obtendríamos diferentes perfiles de población y mortalidad según estas tasas, cumpliendo las condiciones impuestas de estabilidad y estacionaridad.

Para cumplir con el objetivo de estimar los recursos del medio disponibles para los consumidores secundarios, además de obtener los perfiles de la población que cumplieran con las condiciones anteriores de estacionaridad y estabilidad, debemos seleccionar aquellos en los que las tasas de mortalidad de los individuos que no han alcanzado el tamaño adulto (subadultos) sean mayores que la de los individuos que sí la han alcanzado (adultos), ya que lo contrario no sería sostenible a largo plazo (Gaillard et al., 2000).

Con los perfiles de población tendríamos los de mortalidad y con ellos sabríamos cómo está compuesta la población. Para tener una salida en biomasa (Figura 1.3 C), habría que multiplicar esta estructura por el número de individuos de la población en el ecosistema. En nuestro caso, trabajamos con paleoecosistemas, por lo que no tenemos datos reales del número de individuos que formaban las poblaciones. En yacimientos formados a partir de un evento catastrófico, se podría llegar a obtener las proporciones de la abundancia de especies, pero seguiría sin ser un censo. Para introducir un valor de densidad se emplean ecuaciones alométricas que relacionan el tamaño promedio de los individuos adultos de una especie con diferentes parámetros que pueden ser fisiológicos, como el número de crías por camada, o ecológicos, como la densidad. Nos basamos en los trabajos de Damuth (1981) para la estimación de la densidad de los consumidores primarios. Seleccionamos aquella ecuación descrita para climas de bosques mixtos templados europeos:

$$\log(D) = -0{,}79 \cdot \log(m) + 4{,}33$$

donde la D es la densidad de la población o número de individuos por kilómetro cuadrado (ind/km^2) y la m es el peso corporal en gramos.

Al introducir la estructura de la población tendríamos una mayor resolución de cómo son los individuos de la población. Si sumásemos toda la masa de los individuos del ecosistema tendríamos la biomasa de la comunidad de consumidores primarios en el ecosistema, también denominada “*on crop biomass*” o “*standing mass*”. Esta biomasa no podría ser utilizada en su totalidad por los consumidores secundarios, porque si fuera así las poblaciones de consumidores primarios se extinguirían y, con ellas, las de los consumidores secundarios. Los consumidores secundarios podrían alimentarse de un porcentaje de esta biomasa. Este porcentaje es estimado a partir de los perfiles de mortalidad obtenidos con el modelo. Estos perfiles de mortalidad serían los que harían sostenibles a las poblaciones a lo largo del tiempo y se traducen en la cantidad de individuos de cada clase de edad que debieran morir por año para mantener a las poblaciones estables. La biomasa que estaría disponible para los consumidores secundarios de una comunidad se obtendría como la suma de biomasa de todos los individuos de las especies de consumidores primarios muertos. Por tanto, combinando el promedio de individuos muertos sostenibles por clase de edad y el promedio de la masa corporal por clase de edad junto con la densidad de la población estimada, se obtiene la biomasa de salida sostenible del ecosistema (TBO o *Total Biomass Output*). Hay partes de la TBO que no pueden ser aprovechadas como recurso alimentario, como cuernos y cornamentas, huesos (salvo por algunos cánidos, hiénidos y homininos), pelaje y piel. Por esta razón, se aplica a lo anterior un factor de corrección, el *Factor de aprovechamiento* (*wastage factor*) (Viljoen, 1993). Al aplicar este factor, se obtiene como salida la Biomasa Total Disponible (TAB) que sería el promedio de la biomasa de consumidores primarios que estaría disponible para los consumidores secundarios en el paleoecosistema. La TAB no fue definida hasta que se realizó el análisis del Capítulo 4 por lo que en el Capítulo 3 se utilizó de forma equivalente el parámetro TBO al parámetro TAB.

1.3.2.- TDB (Biomasa Total Demandada)

La estimación de la Demanda Total de Biomasa (TDB) es un proceso más sencillo que el de la estimación de TAB en el modelo ya que no se introducen las estructuras de edades de las poblaciones de consumidores secundarios. Para estimar los requerimientos de una población se estiman los requerimientos de un individuo y el número de individuos de la población. Los requerimientos de un individuo se calculan a partir de la ecuación alométrica de Farlow (1976):

$$\log I = (0{,}69686 \pm 0.01276) \log (m) + 0{,}27747 \; ; \; r^2 = 0{,}96758; \; F_{1:100} = 2.984{,}773$$

siendo I la ingesta o requerimientos en kilocalorías por día (kcal/día) y m el peso en gramos. Un individuo de la especie *Acinonyx pardinensis* de 60 kg (60.000 g) tendría una ingesta diaria de 4.657 kcal/día, que al año serían 1.699.944 kcal.

El número de individuos de la población, se calcula por otra ecuación alométrica proporcionada por Damuth (1993):

$$\log(D) = -0{,}64 \cdot \log(m) + 2{,}23$$

donde D es la densidad de la población o número de individuos por kilómetro cuadrado (ind/km^2) y m es el peso corporal en gramos. Al multiplicar la densidad por la ingesta o requerimientos individuales, se obtendrían los requerimientos de la población (kcal/km^2*año). En el caso del *Acinonyx pardinensis* se estima una densidad de 0,15 individuos por km^2, siendo la demanda de la población de 252.591 kcal/km^2*año.

A través de las evidencias paleontológicas, los estudios de paleodietas basados en isótopos y la etología de especies actuales relacionadas filogenéticamente con las especies fósiles, se han atribuido a los consumidores secundarios unas preferencias por las diferentes categorías de tamaño corporal de consumidores primarios. Los requerimientos de cada población de cada especie se reparten según sus preferencias y así se obtendría la Biomasa Total Demandada (TDB), que sería la biomasa requerida por los consumidores secundarios por categoría de tamaño corporal en condiciones ideales (para más detalles, ver Rodríguez-Gómez et al., 2013b).

Tabla 1.1.- Porcentajes de depredación o consumo preferente (PD) de carnívoros en el paleoecosistema de TD8. Se expresa a partir de PD la relevancia de cada categoría de peso corporal de consumidores primarios en la dieta de cada especie de carnívoro. Cuanto mayor valor, mayor importancia. La suma de las filas es 100. Un valor de 0 indica que la especie de carnívoro no consume en esa categoría.

	Categorías de peso corporales (kg)					
Especies	**10-45**	**45-90**	**90-180**	**180-360**	**360-1.000**	**>1.000**
Canis mosbachensis	17	17	17	17	17	17
Crocuta crocuta	21	32	26	11	5	5
Lynx sp.	75	25	0	0	0	0
Ursus sp.	17	17	17	17	17	17
Panthera gombaszoegensis	6	6	31	38	19	0
Hyaena sp.	17	17	17	17	17	17

Tabla 1.2.- Reparto de la demanda de las poblaciones de consumidores secundarios (kcal/km^2*año) entre las categorías de peso de los consumidores primarios, siguiendo los Porcentajes de depredación o consumo preferente (PD) de carnívoros en el paleoecosistema de TD8.

	Categorías de peso corporales (kg)					
Especies	**10-45**	**45-90**	**90-180**	**180-360**	**360-1.000**	**>1.000**
Canis mosbachensis	6.677	6.677	6.677	6.677	6.677	6.677
Crocuta crocuta	45.866	68.799	57.333	22.933	11.467	11.467
Lynx sp.	14.868	4.956	0	0	0	0
Ursus sp.	3.995	3.995	3.995	3.995	3.995	3.995
Panthera gombaszoegensis	14.039	14.039	70.196	84.235	42.117	0
Hyaena sp.	27.155	27.155	27.155	27.155	27.155	27.155

Tabla 1.3.- Porcentaje de Presión de Depredación (PPP) de las poblaciones de consumidores secundarios en las categorías de peso de los consumidores primarios del paleoecosistema de TD8. La suma de las columnas es 100. Un valor de 0 indica que la especie de carnívoro no consume en esa categoría.

	Categorías de peso corporales (kg)					
Especies	**10-45**	**45-90**	**90-180**	**180-360**	**360-1.000**	**>1.000**
Canis mosbachensis	6	5	4	5	7	14
Crocuta crocuta	41	55	35	16	13	23
Lynx sp.	13	4	0	0	0	0
Ursus sp.	4	3	2	3	4	8
Panthera gombaszoegensis	12	11	42	58	46	0
Hyaena sp.	24	22	16	19	30	55

Supongamos que tenemos un paleoecosistema como el del nivel TD8 del yacimiento Gran Dolina, en la Sierra de Atapuerca. Estaban presentes las siguientes especies de carnívoros: *Canis mosbachensis*, *Crocuta crocuta*, *Hyaena* sp., *Lynx* sp., *Panthera gombaszoegensis* y *Ursus* sp. Se les asigna unos porcentajes de depredación (PD) o consumo de carne en las diferentes categorías de peso de los consumidores primarios (Tabla 1.1). Teniendo en cuenta estos porcentajes, se reparten los requerimientos de la población (ver Table 5 del Capítulo 4) (Rodríguez-Gómez et al., 2014b) según sus preferencias por cada categoría de peso. Por ejemplo, la población de *Canis mosbachensis* demanda 40.062 kcal/km^2*año y tiene la misma preferencia (PD o Porcentaje de Depredación) por todas las categorías de tamaño ya que se asume que sólo consumiría grandes mamíferos en forma de carroña. Para obtener su perfil de demanda de recursos se dividiría la demanda total entre las seis categorías de peso, requiriendo por categoría 6.677 kcal/km^2*año. En el caso del *Lynx* sp., sus requerimientos se repartirían sólo en las dos primeras categorías ya que se asume que no consumiría carroña, requiriendo 14.868 y 4.956 kcal/ km^2*año en la primera y segunda categoría, respectivamente. En la Tabla 1.2 se muestra cómo quedarían repartidos los requerimientos de los carnívoros por clase de peso. A continuación, se suman las demandas de todas las especies en cada categoría de peso de consumidores primarios y se obtiene la demanda total en cada categoría. Con esto se calculan los Porcentajes de Presión de Depredación (PPP o *Proportional Predation Pressure*), para conocer qué porcentaje de la biomasa de consumidores primarios en cada categoría iría a cada especie de consumidor secundario (Tabla 1.3). Si una especie sólo depreda sobre una categoría de tamaño, su intensidad de depredación sobre esa categoría es mayor en proporción a la de las demás especies que tengan preferencias por más categorías ya que el 100% de sus requerimientos tendrían que ser extraídos de esa categoría. Por otra parte, ante una situación de igualdad de preferencia por una categoría, con idénticos porcentajes de preferencia, aquella especie con más requerimientos consume mayor cantidad de biomasa de esa categoría (ver Rodríguez-Gómez et al., 2013b).

1.3.3.- Reparto de la TAB entre los consumidores secundarios

La distribución de la TAB entre los consumidores secundarios se realiza atendiendo a los Porcentajes de Presión de Depredación (PPP) que, como se ha indicado anteriormente, dependen de los requerimientos de las especies de consumidores secundarios, de sus capacidades depredadoras y de sus preferencias por las diferentes categorías de tamaño corporal de las presas (PD). En la Tabla 1.4 se puede observar cómo se repartiría la TAB entre los consumidores secundarios. Se permite consumir hasta un máximo de kcal/km^2*año definido por los valores de la Tabla 1.2, para cada especie de consumidor secundario en cada categoría de peso de consumidor primario. La TAB que supere ese consumo máximo, estaría disponible para todos los consumidores secundarios en una segunda ronda de reparto, en la que se considerarían de nuevo los PPP definidos en la Tabla 1.3. Si una población de una especie alcanza sus requerimientos totales deja de consumir y se rehacen los PPP teniendo en cuenta sólo las especies que no han alcanzado sus requerimientos totales. Se termina de distribuir la TAB cuando ésta tiene un valor igual a 0 ó cuando todos los consumidores secundarios alcanzan sus requerimientos totales. De esta forma, sólo consideramos un techo o valor umbral de consumo para cada población de las especies que conformaban los paleoecosistemas.

Tabla 1.4.- Distribución de consumo de TAB (Biomasa Total Disponible) (kcal/km^2*año) entre las diferentes especies de consumidores secundarios de la paleocomunidad de TD8.

	Categorías de peso corporales (kg)					
Especies	**10-45**	**45-90**	**90-180**	**180-360**	**360-1.000**	**>1.000**
Canis mosbachensis	7.527	6.313	2.931	4.741	2.785	5.053
Crocuta crocuta	51.702	65.045	25.168	16.282	4.783	8.677
Lynx sp.	16.760	4.686	0	0	0	0
Ursus sp.	4.503	3.777	1.754	2.836	1.666	3.023
Panthera gombaszoegensis	15.825	13.273	30.815	59.804	17.567	0
Hyaena sp.	30.610	25.674	11.921	19.280	11.327	20.550

1.3.4.- Índices de competencia entre los consumidores secundarios

Buscando comparar los recursos disponibles para las poblaciones de consumidores secundarios en diferentes paleoecosistemas, se han empleado diferentes índices para estimar el estado de los paleoecosistemas. Además de la relación entre la biomasa de consumidores primarios y la de secundarios (ratio presa-depredador), que es un índice tradicional para evaluar los ecosistemas (Carbone y Gittleman, 2002; Meloro y Clauss, 2012; Palombo, 2010; Rodríguez-Gómez et al., 2012; Rodríguez et al., 2012), se han empleado otros índices. Estos índices intentan estimar el grado de satisfacción de los requerimientos de los consumidores secundarios en relación a unos niveles esperados, o cómo se cubre la demanda de esta comunidad, partiendo de la biomasa que le ofertan los consumidores primarios. Se utilizan dos índices generales, uno en el que se mide cómo se alcanza el número esperado de consumidores secundarios y, en el otro, cómo se alcanza la biomasa esperada de consumidores secundarios. Estos índices se presentan en el Capítulo 4 (PLoS ONE) (Rodríguez-Gómez et al., 2014b) y en el Capítulo 5 (Rodríguez-Gómez et al., Enviado). Si en condiciones ideales la comunidad de carnívoros alcanza 100 individuos por kilómetro cuadrado y al hacer nuestro análisis la biomasa de consumidores primarios sólo es capaz de sostener a 50 individuos, se está cubriendo la mitad de la demanda. En otro paleoecosistema en el que se pudiese sostener hasta 70 individuos, los consumidores secundarios satisfarían mejor sus requerimientos que en el paleoecosistema anterior, alcanzando el 70% de los requerimientos de la comunidad. Este primer índice es denominado como Índice de Competencia Global (GCI o *Global Competition Index*). Para tener en cuenta no sólo el número de individuos sino la biomasa de consumidores secundarios, estimamos la biomasa esperada de consumidores secundarios en condiciones óptimas, en las que se sostiene al máximo número de individuos. Se estima como la suma de biomasa de cada población de cada especie multiplicando el número de individuos esperados por la biomasa promedio de los individuos. Como en el índice anterior, relacionaríamos la biomasa de consumidores secundarios obtenida a partir de los consumidores primarios del paleoecosistema con la biomasa que se obtendría en condiciones ideales. De esta forma se sabría el grado en el que se están satisfaciendo la demanda de la comunidad de consumidores secundarios. A este índice lo denominamos Índice de Competencia Global de Biomasa (GCIB o *Global Competition Index Biomass*).

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Objetivos

En lás páginas anteriores:
Cuadro sin título de la serie *Tropical screens*. Autor: Gonzalo Rodríguez Gómez.

Capítulo 2.- Objetivos

Como objetivo general, la presente tesis pretende obtener una cuantificación de los recursos tróficos que tendrían disponibles las poblaciones de cazadores-recolectores durante el Pleistoceno, y evaluar cómo pudo afectar a la dispersión de esas poblaciones en este periodo. Para ello, se ha empleado la metodología descrita en la introducción, en la que se integran las especies de macromamíferos de los paleoecosistemas, consideradas el recurso cárnico más relevante para estas poblaciones humanas, y se estudian las relaciones en las redes tróficas tejidas en los mismos. El modelo se aplica al registro fósil para obtener información del entorno en el que se encontraban los homininos y se pretende entender qué papel podían desempeñar en él. Para ello, se plantearon tres objetivos específicos:

2.1.- Aplicación del modelo al nivel TD6-2 del Pleistoceno Inferior del yacimiento de Gran Dolina de la Sierra de Atapuerca (Burgos, España)

Con este objetivo se pretende testar si existía un nicho en las paleocomunidades europeas para unos homininos que consumiesen una proporción relevante de carne en su dieta. Se ha seleccionado el yacimiento Gran Dolina de la Sierra de Atapuerca, específicamente el nivel TD6-2, porque son considerados un nivel y un yacimiento clave para resolver cuestiones paleoeconómicas de las poblaciones que habitaron Europa hace aproximadamente 1 Ma (Saladié et al., 2011 y referencias en este trabajo). En el nivel TD6 se han encontrado restos de homininos junto con una gran riqueza de artefactos líticos y fauna (Carbonell et al., 2005; Carbonell et al., 1995; Rodríguez et al., 2011), por lo que ofrece una información suficiente y precisa para conocer los hábitos nutricionales y culturales de esta población de homininos, así como la fauna con la que convivieron.

Este estudio se publicó en un artículo en la revista *Journal of Human Evolution*, volumen 64, páginas de la 645 a la 657, titulado “Modeling trophic resource availability for the first human settlers of Europe: The case of Atapuerca TD6” (Rodríguez-Gómez et al., 2013). Este artículo conforma el tercer capítulo de esta tesis doctoral.

2.2.- Aplicación del modelo a escala local para el estudio de la continuidad de las poblaciones humanas, comparando entre paleoecosistemas. Niveles TD8 y TD6-2 del yacimiento de Gran Dolina de la Sierra de Atapuerca (Burgos, España)

Después del análisis del nivel TD6-2, se planteó aplicar el modelo en otro nivel de la Sierra de Atapuerca para saber si esas condiciones eran una excepción en la Sierra o, si por el contrario, eran habituales. En los yacimientos de la Sierra de Atapuerca existe un amplio registro de presencia humana a lo largo de su secuencia, pero no es continua. Se ha constatado una falta de evidencias de poblamiento humano en el intervalo de tiempo entre 0,9 y 0,5 Ma (Mosquera et al., 2013). Asumiendo que la Sierra estaría despoblada en ese periodo, planteamos la posibilidad de que se debiera a la competencia por los recursos. Para comprobar esta hipótesis, aplicamos el modelo para estimar qué población de consumidores secundarios se podría soportar y, en comparación con TD6-2, si los consumidores secundarios tendrían mayores dificultades para alcanzar sus requerimientos en este periodo. Como representante de este intervalo seleccionamos el nivel TD8 de Gran Dolina por su riqueza en fauna. Además de analizar la paleocomunidad registrada en TD8, planteamos una hipotética paleocomunidad de TD8 con humanos, que no se registran en este nivel, para simular su estado y el grado de competencia que hubiesen soportado.

Este trabajo se publicó en un artículo de la revista *PLoS ONE*, volumen 9, número 7, páginas e101938, con el título "Discontinuity of human presence at Atapuerca during the early Middle Pleistocene: A matter of ecological competition?" (Rodríguez-Gómez et al., 2014). Este artículo se corresponde con el cuarto capítulo de esta tesis doctoral.

2.3.- Aplicación del modelo a escala continental para el estudio de la continuidad de las poblaciones humanas

Una vez aplicado el modelo para estudiar recursos tróficos para los carnívoros de los paleoecosistemas a escala local en Atapuerca, se planteó la hipótesis de que la posible escasez de yacimientos en Europa en el intervalo de 0,9 a 0,5 Ma se debiese a un incremento del grado de competencia entre los carnívoros de ese momento. En esta aproximación se pasa de un análisis a escala local a otro a escala continental. Para ello se seleccionan yacimientos en Europa de un periodo de tiempo comprendido entre 1,1 y 0,2 Ma que presenten una riqueza suficientemente abundante para poder considerarlos representativos de la comunidad de macromamíferos y se evalúa el grado de competencia entre los consumidores secundarios, incluyendo a los humanos, mediante diferentes índices. Se ha dividido el análisis en tres intervalos de tiempo: primer intervalo entre 1,1 y 0,8 Ma; segundo intervalo entre 0,8 y 0,5 Ma y tercer intervalo entre 0,5 y 0,2 Ma. De esta forma se agrupan los yacimientos y se comparan para testar la hipótesis.

Este trabajo ha sido enviado a la revista *Palaeogeography, Palaeoclimatology, Palaeoecology*, con el título "Ecological competition and community structure as limiting factors of human presence in Europe during the Early and Middle Pleistocene". Conforma el quinto capítulo de esta tesis doctoral.

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Modeling trophic resource availability for the first human settlers of Europe: The case of Atapuerca TD6

En lás páginas anteriores:
Cuadro *Paisaje de Agosto*. Autor: Gonzalo Rodríguez Gómez.

Capítulo 3.- Modeling trophic resource availability for the first human settlers of Europe: The case of Atapuerca TD6

Artículo publicado en la revista *Journal of Human Evolution*, en el volumen 64, desde la página 645 a la 657.

Journal of Human Evolution 64 (2013) 645–657

Contents lists available at SciVerse ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Modeling trophic resource availability for the first human settlers of Europe: The case of Atapuerca TD6

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ARTICLE INFO

Article history:
Received 15 June 2012
Accepted 24 February 2013
Available online 28 March 2013

Keywords:
Palaeolithic
Hunter–gatherers
Mathematical models
Homo antecessor

ABSTRACT

Food resource availability strongly influences the survival opportunities of all organisms. The effect of animal food resource availability on the survival and dispersal of hominin populations is hotly debated. In this article, we present a mathematical model that provides estimations of the maximum and minimum available resources for secondary consumers in a palaeocommunity. This model provides insights into the intensity of competition and the available niche space for hominins in Europe during the early Galerian (1.2–0.8 Ma). Published data from the Atapuerca TD6 assemblage were used in combination with the model to investigate trophic dynamics and resource availability for a *Homo antecessor* population 800,000 years ago. The effect on our results of the possible presence at Atapuerca of some large carnivores not recorded in the fossil assemblage is also evaluated. Results indicate the existence of a rich ecosystem at Atapuerca at the end of the Early Pleistocene. Secondary production was abundant enough to maintain a hunter–gatherer population and a rich carnivore guild more diverse than that recorded in the TD6 assemblage. Based on these results, the practice of cannibalism by *H. antecessor* cannot be explained by a long-term scarcity of resources. High food availability at TD6 implies a low to moderate level of competition for resources between carnivores and humans. According to this interpretation, an empty niche for a highly carnivorous omnivore existed in Europe during the early Galerian, and it was successfully exploited by *Homo*.

Introduction

The tempo, mode and conditioning of the earliest human settlement in Europe during the Pleistocene are hotly debated (e.g., Moncel, 2010; Palombo, in press). Trophic resource availability is one of the main constraints for the dispersal of any species, and there are several reasons to consider meat as a key resource for Early Pleistocene hominins. Most recent hunter–gatherer societies have a high reliance on animal food (Cordain et al., 2000), and it is generally accepted that animal resources were also essential to Pleistocene hominins in Europe (Roebroeks, 2001; Hublin and Richards, 2009). Studies of recent hunter–gatherer populations show that animal resource consumption represents between 30% and 60% of their nutritional intake (Jenike, 2001; Leonard et al., 2007). Although no consensus has been reached, Speth and Spielmann (1983), Speth (1989) and Milton (2000) agreed that hominins could have been forced to live on animal matter including fat, and most researchers assume that large mammals were a common source of meat for hominins during the Early Pleistocene (e.g., Binford, 1981, 1985; Marean, 1989; Gaudzinski and Roebroeks, 2000; Roebroeks, 2001; Speth, 2010). Large mammal hunting has been documented in Africa at 1.8 Ma (millions of years ago) (Bunn and Pickering, 2010), and in Europe primary access to carcasses is evident at Atapuerca, 0.8 Ma (Díez et al., 1999; Saladié et al., 2011). In summary, meat and fat were key resources for Pleistocene hunter–gatherer populations even if meat represented only 30% of their diet, as observed in some recent hunter–gatherers.

The ability of hominins to obtain animal resources from their environment is conditioned by the abundance of prey, their ecological characteristics, and the intensity of the competition with carnivores for these resources. Thus, several authors have linked the survival opportunities of the first European hominins to their ability to compete with carnivores. Palombo (2010) proposed that competition for prey or carrion with large carnivores, including *Pachycrocuta brevirostris* (short-face hyaena), *Megantereon whitei*

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http://dx.doi.org/10.1016/j.jhevol.2013.02.007

and *Homotherium latidens*, could have delayed human expansion in Europe during the Early Pleistocene because the first *Homo* populations in Europe lacked weapons to successfully confront such formidable opponents. Accordingly, several authors proposed that the Early Pleistocene European human populations would have relied on the scavenging of ungulate carcasses in such adverse conditions (Turner, 1992; Martínez-Navarro and Palmqvist, 1996; Arribas and Palmqvist, 1999). However, it has also been proposed that competition for carcasses was very strong in the Early Pleistocene because of the presence of the large and aggressive giant hyaena *P. brevirostris* in the European Faunal Complex (Palombo, 2010). However, some authors highlight the abundance of scavengeable food in the European Early Pleistocene ecosystems, assuming that sabertooths left a large amount of food at a kill because machairodontines hunted large ungulates and were ill-adapted to break bones (Turner, 1992; Arribas and Palmqvist, 1999). In addition, the dental characteristics of *M. whitei* have been taken as evidence of the inability of this sabertoothed cat to effectively clean the meat from the bones of their prey (Marean, 1989; Martínez-Navarro and Palmqvist, 1995; Palmqvist et al., 1996, 2005, 2007; Arribas and Palmqvist, 1999).

With the turnover at the beginning of the Middle Pleistocene, *Pachycrocuta* and other large carnivores became extinct (Turner, 1992). It has been suggested that the appearance of new carnivores in Europe like *Crocuta crocuta* and the progressive increase in herbivore richness enabled human populations to compete more effectively for carcasses and promoted the expansion of *Homo* throughout Europe (Palombo, 2010; Rodríguez et al., 2012). An alternative explanation is the replacement of *Homo antecessor* populations by a new immigrant hominin species (*Homo heidelbergensis*) with a more advanced technology: the Acheulean (Jiménez-Arenas et al., 2011).

Thus, two factors should be taken into account to evaluate food resource availability for early Palaeolithic hunter–gatherers: 1) the amount of biomass that can be extracted from the populations of large herbivores, and 2) the intensity of competition within the carnivore guild for those resources. Quantification of the trophic relationships within mammalian palaeocommunities may help to evaluate competition strength in past ecosystems and provide estimations of resource availability for ancient human populations. Quantitative studies of the trophic dynamics of palaeocommunities have been used by palaeoecologists to understand trophic relationships in mammalian palaeocommunities from the Miocene (Vizcaíno et al., 2010) and the Pleistocene (Fariña, 1996), and to evaluate the effects of extinctions and faunal turnover on ecosystems functioning during the mid-Pliocene (Vizcaíno et al., 2004). This approach has also been applied to the Early Pleistocene palaeocommunity of Venta Micena (Palmqvist et al., 2003) and the Middle Pleistocene hunter–gatherer populations at Sierra de Atapuerca (Bermúdez de Castro et al., 1995).

The aim of this work is to model palaeocommunity trophic relationships and to obtain quantitative estimates of resource availability for the first European human settlers, in order to understand their role in the palaeocommunity and how this role conditioned their dispersal opportunities. In particular, we aim to test whether there was niche space in the European palaeocommunities for a hominin with a relevant proportion of meat in its diet. Given the key role of animal food in the human diet, we assume that only as members of the carnivore guild were hominins able to maintain high population densities and effectively disperse throughout the continent. We selected the TD6 assemblage from the Atapuerca Gran Dolina site because it has been considered as a key sample in resolving several palaeoeconomic issues related to the populations that inhabited Europe approximately 1 Ma (Saladié et al., 2011 and references therein). This is the single European site from this period where hominin remains have been found together with abundant faunal remains and a rich collection of lithic artifacts. Thus, the TD6 assemblage provides both biological information about the first European settlers and evidence of their nutritional and cultural activities. We developed a model using Leslie (1945, 1948) matrices, a tool currently used in population dynamic studies, to refine previous approaches (see above). A main contribution of our model is that it provides a representation of the age structure of primary consumer populations and a distribution of the available biomass in body size categories. This allowed us to evaluate the effect of several predation pressure intensities on available biomass and to better estimate biomass availability for each secondary consumer. Thus, our model provides insights into competition for resources among secondary consumers, and the survival opportunities in southern Europe at the end of the Early Pleistocene for a hominin with a significant meat component in its diet. In this way, the hypothesis that human expansion through Europe was limited at this time by resource availability may be tested.

Materials and methods

The TD6 'Aurora stratum' assemblage

The Sierra de Atapuerca includes several archaeological and palaeontological sites, dating from the Early Pleistocene to the Holocene, which have been excavated since 1981 (Carbonell et al., 1999a). For a detailed description of the geology of Sierra de Atapuerca see Parés and Pérez-González (1999) and Pérez-González et al. (2001). The Gran Dolina (TD) site is a cave infill 18-m thick with a stratigraphic sequence of 11 stratigraphic units, named TD1–TD11 from bottom to top (Gil, 1997; Parés and Pérez-González, 1999; Pérez-González et al., 2001). Parés and Pérez-González (1999) interpreted the palaeomagnetic reversal at the limit between the TD7 and TD8 layers as the Matuyama–Brunhes boundary. The TD6 unit has a reversed polarity that has been interpreted as post-Jaramillo (0.990–0.780 Ma) (Parés and Pérez-González, 1999; Pérez-González et al., 2001). Radiometric dating of ungulate teeth by ESR/U–Th indicated an average age between 780 and 875 ka (thousand years) for TD6 and an age of 731 ± 63 ka for the 'Aurora Stratum' (TD6-2) (Falguères et al., 1999). The TD6 unit has been attributed to OIS 21 or 19 by Falguères et al. (1999) and Cuenca-Bescós and García (2007), although Berger et al. (2008) correlated it to OIS 25 based on thermoluminescence (TL) dates. A recent study by Moreno-García (2011) using ESR on quartz provided a range of 0.80 and 0.88 Ma for the TD6 unit.

TD6 is known for its so-called 'Aurora Stratum', corresponding to the stratigraphic subunit TD6-2 (Bermúdez de Castro et al., 2008) with a huge assemblage of human fossils attributed to *H. antecessor*, Mode 1 stone tools (Carbonell et al., 2010b) and abundant faunal remains (Carbonell et al., 1995, 2005; Rodríguez et al., 2011).

TD6 has been interpreted as a consumption site (Díez et al., 1999) where the entire operative chain has been recorded (Carbonell et al., 1999b). Zooarchaeological analyses show that humans had primary and immediate access to the majority of the remains present at the site (Díez et al., 1999; Saladié et al., 2011). With regard to prey selection, most ungulate individuals at TD6 weighed between 300 kg and 1000 kg (Saladié et al., 2011). Prey selection and primary or early access to the carcasses in competition with other predators has been interpreted as a sign of the degree of social cohesion in the individuals of these human groups (Rosell, 2001; Huguet, 2007; Saladié, 2009).

The faunal list for TD6 was obtained from Rodríguez et al. (2011). Our analysis was restricted to mammal species of more than 10 kg because they would have been important for a hunter–gatherer population as a main meat resource, as competitors or as potential predators (Roebroeks, 2001; Owen-Smith and Mills, 2008), as evidenced by the TD6 assemblage itself (Díez et al., 1999; Saladié et al., 2011). There are ten primary consumer species in TD6 weighing more than 10 kg: *Eucladoceros giulii*, *Bison* cf. *voigtstedtensis*, *Castor fiber* (beaver), *Cervus elaphus* (red deer), *Dama vallonetensis*, *Equus altidens*, *Mammuthus* sp., *Stephanorhinus etruscus*, *Sus scrofa* (wild boar) and *Ursus dolinensis*. This last species is considered to be an omnivore, and in this study, it was included as both a potential prey and a potential predator. Four large predators were identified in the TD6 assemblage: *Canis mosbachensis*, *C. crocuta* (spotted hyaena), *Lynx* sp. and *U. dolinensis*. The small canid *Vulpes praeglaciadis* was not included in the analyses because its diet was likely composed of small mammals, invertebrates and some carrion and fruits, all of which contribute to the diet of the recent red fox (Seebeck, 1978).

We also consider the possible presence at Atapuerca 0.8 Ma of two other large predators that were not recorded in the TD6 assemblage but that were common in the Iberian fauna at the end of the Early Pleistocene. The sabertooth *Homotherium* was present in Europe until the end of the Middle Pleistocene, according to Turner and Antón (1997), or until the Late Pleistocene, according to Reumer et al. (2003). Remains of this species have been recorded at Gran Dolina in the Early Pleistocene level TD5 and the Middle Pleistocene level TD10-3 (Rodríguez et al., 2011). Although it was not recorded at TD6, the European jaguar *Panthera gombaszoegensis* is another felid that could have been present at Atapuerca. This species appeared in Europe approximately 1.8 Ma and became extinct approximately 0.4–0.5 Ma (Turner and Antón, 1996). Furthermore, it is present in the lower levels of Gran Dolina (Rodríguez et al., 2011). Thus, we repeated our analyses including one or both large felids as members of the predator guild to evaluate the effect of their possible presence on our results.

Physiological variables

Estimations of body mass of the species present in TD6 were taken from Rodríguez (1997). The following physiological variables are used in the population dynamic models and in estimations of resource utilization by carnivores (see below): body mass for adult, body mass for neonates, litter size, breeding interval, age at reproductive maturity, growth rate and lifespan (see SOM, Tables S1 and S2). For species with living representatives, such as *S. scrofa* and *C. fiber*, the values of these physiological variables were taken directly from the literature. For species without living representatives, the values reported in the literature for closely related living species of similar body mass were used (e.g., *Equus zebra* was used as an analog for *E. altidens*). In the cases of *E. giulii*, *B.* cf. *voigtstedtensis*, *D. vallonetensis*, *Mammuthus* sp., *S. etruscus* and *U. dolinensis*, which lack closely related living species of similar size, we computed a least square regression equation for each physiological variable on mean body weight using data for species in the same family (see further details in SOM, Table S3). Recent *C. elaphus* populations exhibit a wide latitudinal variation in body size; thus, least square regression equations were also used to estimate the physiological parameters for this species. Growth rate was set as the mean of the estimates provided by the allometric equations from Millar (1977) and Case (1978). The computed growth rates were used to estimate average body weight of individuals in subadult age classes. For the subsequent analyses, subadults were defined as individuals that have not reached adult body size. Fecundity (a), defined as the number of female offspring per female, was computed as the number of litters per year multiplied by the litter size and divided by two, assuming that only half of the newborns are females.

The model

Population structure We modeled the average population dynamics of the ten primary consumer species in the TD6 assemblage to estimate the prey biomass available to secondary consumers per year (Biomass Output). In the model, each primary consumer population at time t is assumed to be discrete and age-structured ($X_t = [x_1^t, \ldots, x_n^t]$), with dynamics defined by a Leslie (1945, 1948) model

$$X_{t+1} = \begin{bmatrix} a_1 & a_2 & \cdots & a_n \\ b_1 & 0 & \cdots & 0 \\ \vdots & \ddots & \ddots & \vdots \\ 0 & \cdots & b_{n-1} & 0 \end{bmatrix} X_t$$

where a_i is fecundity, the per capita number of female offspring and b_i is the proportion of individuals that survives from age class i to age class $i + 1$. The number of individuals of age class i that died each year, whatever the cause (predation, illness or accident), is given by $1 - b_i$. The interval between age classes is one year. The matrix is denoted as Leslie Matrix (L). The value of a_i is obtained by combining information on litter size, breeding interval and age at reproductive maturity, as explained above (see SOM, Table S4). Leslie models consider entire populations as being composed of females. Thus, for physiological variables, we used values for the females of each species. Moreover, we assumed that the age structure of males was the same as that obtained for females (Woodd, 1999) using the Leslie model to find the structure of the entire population and the maximum biomass that may be extracted from it.

Population structure changes through time following the dynamics defined above. This complex system has many degrees of freedom. Thus, several of the possible solutions may make the population collapse or increase indefinitely beyond reasonable limits. The goal of the model is not to describe all of those oscillations or possibilities, but to find out the situations that make the population sustainable over time. Two additional conditions should be introduced to obtain an age structure that makes the primary consumer population sustainable over time: 1) the population should be stable (i.e., the population size should be constant from year to year), and 2) the population should be stationary (i.e., the age structure should be constant from year to year). Thus, the structure of the population at time t should be equal to the structure of the population in the next year (time $t + 1$), or $X_t = X_{t+1}$ for all t. These conditions yield the structure of an ideal population that intends to represent the long-term average structure of the real population. The structure of the population (X_t) should then be the eigenvector associated with the eigenvalue $\lambda = 1$, or $X_{t+1} = L \cdot X_t$.

Classical results (Brauer and Castillo-Chávez, 2010) show that the eigenvector associated with the eigenvalue λ, with a first-age value of 1, is

$$\overline{v} = \left[1, \frac{b_1}{\lambda}, \frac{b_1 b_2}{\lambda^2}, \ldots, \frac{b_1 \ldots b_{n-1}}{\lambda^{n-1}}\right]$$

The restriction that makes $\lambda = 1$ is found by writing the characteristic equation of L (Brauer and Castillo-Chávez, 2010)

$$a_1 + a_2 b_1 + a_2 b_1 b_2 + \cdots + a_n b_1 \ldots b_{n-1} = 1$$

Moreover, this restriction can be interpreted as the condition that makes the population stable and it occurs when the net reproduction rate (NRR) is equal to 1.

Accordingly, a stable and stationary population should fit the identity in the above equation and have the following form:

$$X_t = [1, b_1, b_1 b_2, \ldots, b_1 \ldots b_{n-1}]$$

The main goal of the model is to estimate the maximum biomass that can be sustainably extracted every year from the population of a primary consumer, thereby satisfying the constraints for a stable and stationary population. The annual biomass (in kg) represented by all dead individuals of the ith age class can be expressed as

$$(1 - b_i) \cdot v_i \cdot m_i$$

where m_i is the average mass of an individual of the ith age class and v_i is the proportion of individuals in the population that belong to the ith age class. Further, $1 - b_i$ represents the mortality rate of the ith age class. For subadult age classes, body mass is obtained from body weight at birth and growth rate (See SOM, Tables S1 and S2). The Biomass Output of the species is the biomass (in kg) represented by all dead individuals of all age classes for a given period of time

$$\sum_{i=1}^{n-1} (1 - b_i) \cdot x_i \cdot m_i$$

Finally, the maximum Biomass Output of a single population of primary consumer can be expressed as

$$\max_{0 \le b_i \le 1} \left\{ \sum_{i=1}^{n-1} (1 - b_i) \cdot x_i \cdot m_i \right\} \Big/ \text{with } (a_1 + a_2 b_1 + a_3 b_1 b_2 + \cdots + a_n b_1 \ldots b_{n-1} = 1)$$

Therefore, the survival rate values (b_1 to b_{n-1}) for each age class that maximize the biomass of dead individuals while keeping the population stable and stationary through time are identified. The values of b_i should be in the interval 0–1. Trivial solutions are produced because a maximum exists when the mortality rate of subadults is 0 and all individuals die during the first-age class of adulthood when they reach their maximum body weight. To correct this behavior, a new condition is introduced: the fractions of individuals that survive from age class i to age class $i + 1$ during the subadult period are equal. Thus, the model assumes that subadult mortality is constant for all subadult age classes. Analogously, the fraction of individuals that survive from age class i to age class $i + 1$ is also constant during the adult period, although it is not necessarily equal to the value obtained during the subadult period. If adulthood is reached in the kth period, these conditions can be formally expressed as follows:

$$b_1 = b_2 = \cdots = b_{k-1} \text{ and } b_k = b_{k+1} = \cdots = b_{n-1}$$

It is well known that mortality rates are not constant in real populations neither during the subadult nor during the adult phases, but this assumption is necessary in order to keep the model simple. In addition, assuming a constant mortality rate during adulthood does not affect our results (Biomass Output) since individuals in all adult age classes are assigned the same average body weight. However, since the higher subadult mortality typically occurs during the first year of life (Gaillard et al., 2000) and decreases as the calf grows older (and heavier), assuming a constant mortality rate equal to the average mortality during the subadult phase produces an overestimation of the Biomass Output. Simulations have been performed to evaluate the possible amount of this overestimation and it seems to be moderate (about 5–10%).

With this modification, the maximum Biomass Output is obtained with an unrealistically young population in which all individuals die during adulthood. To find a more realistic description of the population structure, we forced the death of young individuals while keeping the population stable over time. This is implemented in the model by changing the region in which the algorithm searches for the values of b_i for the subadult age classes and the restriction

$$0 \le b_i \le 1, i = 1, \ldots, k - 1$$

was replaced with the restriction

$$1 \le b_i \le b_i^{\max}, i = 1, \ldots, k - 1$$

where $b_i^{\max}$ variables take values from 1 to 0. An analysis of the sensibility of the population structure and the Biomass Output for a period of time (one year) is then performed. The method searches for solutions for different values of $b_i^{\max}$, starting with a $b_i^{\max} = 1$ and decreasing the value in 0.05 increments during each iteration until a critical value of $b_i^{\max}$ that makes the population unstable is identified. This means that the subadult age classes are stressed by increasing mortality rates and the population structure ages until a subadult mortality rate is reached that makes the population unstable. This enables the identification of several population structures that make the population stable and stationary. The results obtained in this way are filtered by removing those solutions in which subadult survival is higher than adult survival, since this situation is never observed in natural populations (Gaillard et al., 2000).

The result of this procedure may be resumed as

$$b_i^{\max} \ge b_1 = \ldots = b_{k-1} \ge b_k = \ldots = b_{n-1}$$

However, because the model solutions are not dependent on population size, an estimate of population density (see below) is needed to estimate the maximum Biomass Output ($BM_{\max}$). The mean body mass of a species was used to estimate the maximum biomass that can be extracted from the population, assuming a male to female ratio of approximately 1 for all species (Massei et al., 1997; Nowak, 1999; Woodd, 1999; Cicognani et al., 2000; Hutchins et al., 2003) and a similar population structure for males and females. Biomass Output values expressed in kg were converted to kcal using a conversion factor of 1.5 kcal/g (see Górecki, 1975; Banse and Mosher, 1980).

The model was written and executed in Matlab R2009b.

Population density Density estimates were obtained from allometric equations that relate population density to mean body weight. However, the prevailing opinion is that the global size–density relationship represents the maximum upper boundary on local abundance, or ecological density, rather than a mean value (Blackburn and Gaston, 1997; White et al., 2007). Several proxies indicate a temperate climate for TD6, with a landscape similar to that of a present-day Holarctic forest (Rodríguez, 1997; García-Antón, 1998; Cuenca-Bescós et al., 1999; Burjachs, 2002), while the abundance of *Celtis* seeds suggests Mediterranean conditions (Rodríguez et al., 2011). Thus, primary consumer population densities were estimated using the equation provided by Damuth (1981) for primary consumers in a European mixed temperate forest

$$\log(D) = -0.79 * \log(m) + 4.33$$

where D is population density in number of ind/km^2 and m is the body mass expressed in g. Using this method, the population densities for recent species were found to be congruent with field data available for them (e.g., Grubb, 1981; Laurie et al., 1983; Penzhorn, 1988; Hillman-Smith and Groves, 1994; Nowak, 1999; Granados et al., 2001; Rosell et al., 2001; Hutchins et al., 2003; Fernández-Llario, 2008; Leslie and Shaller, 2009; Carranza, 2011).

The equation provided by Damuth (1993) for African flesh-eaters was used to estimate the population density of carnivores

$$\log(D) = -0.64*\log(m) + 2.33$$

This equation has been previously used to estimate the population densities of fossil carnivores (Fariña, 1996; Vizcaíno et al., 2004, 2010). Damuth (1993) also provides equations to estimate carnivore density in Holarctic environments. However the estimates obtained using those equations are unreliable, likely because of the small sample size used to compute them and the scarcity of large carnivores in Europe and North America in the present. Conversely, the equation for African carnivores also produces population density estimates that are congruent with available data for recent species from a wide range of environments (Bekoff, 1977; Seymour, 1989; Larivière and Walton, 1997; Nowak, 1999; Hutchins et al., 2003; Haas et al., 2005). In the case of *U. dolinensis*, the equation for carnivores was used instead of the equation for primary consumers because it predicts more accurately population densities of recent bear species (DeMaster and Stirling, 1981; Pasitschniak-Arts, 1993; Larivière, 2001). The resources available for *H. antecessor* are estimated as the biomass remaining after all carnivores fulfill their nutritional requirements. It should be noted that this is just a methodological procedure, and it does neither imply that *Homo* necessarily accessed meat resources as a scavenger, nor that it was a less able competitor. Sustainable hominin population densities were computed on the basis of these available resources to illustrate the suitability of the Atapuerca environment for a hunter–gatherer population. The diet composition and nutritional requirements of *H. antecessor* were assumed to be similar to those of recent hunter–gatherer populations. Meat represents between 30% and 60% of the diet of recent hunter–gatherers (Jenike, 2001; Leonard et al., 2007), although according to Binford (2001), the percentage of meat in a diet is extremely variable (see Table 1). Mean daily requirements of 3000 kcal per individual were assumed, following Eaton et al. (1997).

Intake rate The carnivore intake rate was estimated using the equation reported by Farlow (1976)

$$\log I = 0.69686\log(m) + 0.27747; r^2 = 0.96758;$$
$$F = 2984.773; 1100\ df; p < 0.01$$

where I is the intake rate in kcal per day and m is the body mass expressed in g. The estimates obtained from this equation are within the range of values reported in the literature for several recent carnivores (Mech, 1974; Bekoff, 1977; Currier, 1983; Tumlison, 1987; Pasitschniak-Arts, 1993; Mills and Hofer, 1998; Nowak, 1999) (see SOM, Tables S5 and S6). Some adjustments were done for each secondary consumer according to its inferred dietary preferences. *Canis mosbachensis* is considered an omnivorous canid on the basis of morphofunctional and isotopic evidence (Palmqvist et al., 1999, 2003), similar in diet to extant coyotes (Rodríguez et al., 2012). By analogy with the coyote, it is estimated that large mammal flesh represented only 20% of the energetic requirements of *C. mosbachensis* and that it was mostly consumed as carrion. The spotted hyena, *C. crocuta*, is able to exploit bone marrow thanks to their bone crashing abilities, a food resource not available to other carnivores. Data on bone marrow content of ungulate carcasses provided by Blumenschine and Madrigal (1993) and Outram and Rowley-Conwy (1998) show that this resource represents around 2% of the total energy that a spotted hyaena could obtain from a carcass. Thus, we assumed that about 2% of the total energetic requirements of hyaenas were satisfied with bone marrow and, consequently, the energetic requirements of spotted hyaenas were reduced by a factor of 0.02. Diet of the TD6 lynx (*Lynx* sp.), was likely similar to that of the recent Iberian lynx (*Lynx pardina*) (Rodríguez et al., 2012), whose preys are in the range of 0.5–80 kg (Delibes, 1980). Small ungulates like *Dama dama* may represent up to 15% of its diet from October to February but only a 5% or 10% on a year basis (Delibes, 1980; Beltrán et al., 1985; Rodríguez, 2008). Red deer fawns are rarely consumed (Delibes, 1980; Beltrán et al., 1985; Rodríguez, 2008). Since the TD6 lynx was slightly larger than the recent Iberian lynx, it is assumed that species between 10 kg and 90 kg represented 10% of its diet. *U. dolinensis* was likely omnivorous. Possibly fish was an important component of its diet, as suggested for the Venta Micena bear on the basis of isotopic evidence (Palmqvist et al., 2008). The diet of *U. dolinensis* was assumed to include only 10% meat based on data from recent European brown bears, since meat proportion in the diet of European brown bears (*Ursus arctos*) is in the range 9–15% (Parde and Camarra, 1992; Bocherens et al., 2004).

Table 1
Population densities and food resource use observed in recent hunter–gatherer populations (Binford, 2001).

Group	Area	Density (ind/km^2)	Gathering (%)	Hunting (%)	Fishing (%)
Punan	29.6	0.118	65	30	5
Siberian Eskimo	274.9	0.047	1	30	60
Guayaki-Ache	28.7	0.0348	30	62	10
Efe	47	0.1596	88.2	11	0.8
Hadza	25	0.24	60	40	0
!Kung	110	0.066	67	33	0
G/Wi	180	0.0293	55	45	0
Mardudjara	226	0.0075	70	30	0
Kiowa	280	0.014	20	80	0
Caribou Inuit	2365	0.003	0.1	55	44.9
Nunamiut Inuit	249	0.0096	0.1	89	10.9
Polar Inuit	731	0.0041	0.01	30	69.99

Predation pressure Primary consumer species were classified into six body size classes (see Rodríguez et al., 2012): 10–45 kg (first category); 45–90 kg (second category); 90–180 kg (third category); 180–360 kg (fourth); 360–1000 kg (fifth category); >1000 kg (sixth category). Each dead individual of a primary consumer species was assigned to one of these size classes according to its body mass at the age of death. For example, bison (*B.* cf. *voigtstedtensis*) that died during adulthood were included in the 360–1000 kg interval, but subadults were included in the 45–90 kg size category if they died during the first year of life and in the 180–360 kg if they died during the second year. Thus, the Biomass Output of each species was distributed among six size classes. Subsequently, the Biomass Outputs of all primary consumer species were added to obtain a Total Biomass Output (TBO), which was also distributed according to size classes. Total Biomass Output was distributed among secondary consumers following the procedure described below. For active hunting species, the optimum and maximum sizes of their prey are related to the size of the predator (Carbone et al., 1999; Radloff and Toit, 2004). Thus, we inferred the prey size preferences of each predator on the basis of the behavior of their living relatives (Table 2) (Rodríguez et al., 2012). Preference of the predator for a body size category is represented by the percentage that this size category is supposed to represent in its diet. If a predator is unable to kill prey in a given size category and it does not consume carrion, a percentage of predation (PD) of 0 is assigned to it in that category. For example, *C. crocuta* is assumed to prefer prey in the 90–180 kg size class, a PD of 0.35 was assigned for this category and lower percentages were assigned for the remaining body size categories (Table 2). A detailed discussion on the prey preferences

Table 2
Preferences (PD) of the TD6 carnivores plus *Homotherium latidens* and *Panthera gombaszoegensis*.

	Body size range (kg)					
	10–45	45–90	90–180	180–360	360–1000	>1000
Canis mosbachensis	0.17	0.17	0.17	0.17	0.17	0.17
Crocuta crocuta	0.10	0.25	0.35	0.20	0.05	0.05
Lynx sp.	0.75	0.25	0.00	0.00	0.00	0.00
Ursus dolinensis	0.17	0.17	0.17	0.17	0.17	0.17
Homotherium latidens	0.05	0.05	0.15	0.40	0.30	0.05
Panthera gombaszoegensis	0.05	0.05	0.30	0.40	0.20	0.00

The scores represent the relative importance that animals in each body size category have in the carnivore's diet. The sum of the scores in a row is 1. A score of 0 means no consumption of mammals in that body size category.

of Early Pleistocene predators is provided in Rodríguez et al. (2012). In the cases of *U. dolinensis* and *C. mosbachensis*, which are assumed to obtain most of their meat resources by scavenging, all body size categories are assigned the same percentage.

TBO was distributed among *c* (number of carnivores) secondary consumers as follows: let TBO_i be the Biomass Output in the *i*th prey size category, i.e., $\mathrm{TBO} = [\mathrm{TBO}_1 \ldots \mathrm{TBO}_6]$, and IN_j the total intake requirements of the *j*th predator for a given and fix population density. Thus, $\mathrm{IN} = [\mathrm{IN}_1, \ldots, \mathrm{IN}_c]$.

The total requirements of all carnivore populations present in the community may be obtained as

$$\sum_{j=1}^{c} \mathrm{IN}_j$$

The preference of the *j*th carnivore for the *i*th prey body size category is represented as PD_{ij} and it may be interpreted as the proportion of carnivore *j*'s diet represented by the *i*th body size category. Vectorial notation can be used in order to simplify

$$\mathrm{PD} = \begin{bmatrix} \mathrm{PD}_{11} & \cdots & \mathrm{PD}_{1c} \\ \vdots & \ddots & \vdots \\ \mathrm{PD}_{61} & \cdots & \mathrm{PD}_{6c} \end{bmatrix}$$

Note that the columns of this matrix are distributions, thus the sum of the columns is equal to 1.

The amount of biomass demanded by the *j*th carnivore population from the *i*th body size category (D_{ij}) is thus obtained as

$$D_{ij} = \mathrm{IN}_i \cdot \mathrm{PD}_{ij}$$

The total amount of biomass demanded by the *c* carnivore populations from the *i*th body size category (TI_i) is obtained as the sum of the requirements of all carnivores

$$\mathrm{TI}_i = \sum_{j=1}^{c} D_{ij} = \sum_{j=1}^{c} \mathrm{IN}_i \cdot \mathrm{PD}_{ij}$$

Vector TI is then defined as $\mathrm{TI} = \mathrm{IN}' \cdot \mathrm{PD} = [\mathrm{TI}_1, \ldots, \mathrm{TI}_c]$.

Proportional Predation Pressure of the *j*th carnivore species in the *i*th body size category (PPP_{ij}) represents the relative amount of biomass demanded by a carnivore species from a body size category. It is calculated as the proportion of the total amount of biomass demanded from a prey body size category by all carnivores that corresponds to the requirements of a single carnivore species

$$\mathrm{PPP}_{ij} = D_{ij}/\mathrm{TI}_i \text{ for } i = 1, \ldots, 6, j = 1, \ldots, c$$

$$\mathrm{PPP}_{ij} = \begin{bmatrix} \dfrac{D_{11}}{\mathrm{TI}_1} & \cdots & \dfrac{D_{1c}}{\mathrm{TI}_1} \\ \vdots & \ddots & \vdots \\ \dfrac{D_{61}}{\mathrm{TI}_6} & \cdots & \dfrac{D_{6c}}{\mathrm{TI}_6} \end{bmatrix}$$

PPP_{ij} incorporates intraguild competition in the model, since the amount of resources obtained by a carnivore species depends on the number and characteristics of its competitors.

Distribution of resources among carnivores proceeds as follows. A first approximation to the amount of resources distributed to the *j*th predator from the *i*th category (BC_{ij}) is obtained multiplying the available resources in the *i*th body size category (TBO_i) by the Proportional Predation Pressure of the *j*th carnivore in the *i*th category (PPP_{ij})

$$\mathrm{BC}_{ij} = \mathrm{TBO}_i \cdot \mathrm{PPP}_{ij}; \quad \text{for } i = 1, \ldots, 6, j = 1, \ldots, c$$

However, if a carnivore species is assigned more biomass than demanded in this step, this amount is recalculated and set equal to the amount of biomass demanded in that size category. Formally

$$BC_{ij} = \min\{\mathrm{TBO}_i \cdot \mathrm{PPP}_{ij}, D_{ij}\}$$

The total amount of resources obtained by the *j*th carnivore species (BC_j) is given by

$$\mathrm{BC}_j = \sum_{i=1}^{6} \mathrm{BC}_{ij}$$

Some body size categories may still contain biomass after the distribution has been completed for all secondary consumers, while some carnivore species may have not completed their requirements. Thus, the remaining resources should be re-distributed among those secondary consumers that have not fulfilled their energetic requirements. In this way, we simulate the fact that carnivores are able to change their prey preferences according to prey availability and intraguild competition.

Remaining resources in the *i*th body size category after the first distribution round has been completed (RTBO_i) are computed as

$$\mathrm{RTBO}_i = \mathrm{TBO}_i - \sum_{j=1}^{c} \mathrm{BC}_{ij}$$

RTBO_i is distributed among the secondary consumers following the same procedure described above, although including only those species for which $\mathrm{BC}_j < \mathrm{IN}_i$. This is an iterative process that ends when all secondary consumers fulfill their requirements ($\mathrm{BC}_j = \mathrm{IN}_i$ for all carnivores) or when the entire resources have been consumed ($\mathrm{RTBO}_i = 0$ for all categories). PPP_{ij} and PD_{ij} are recalculated every iteration taking into account only the carnivore species which have not fulfilled their requirements and the prey body size categories with remaining resources.

At the end of the process, the distribution of resources assigned to a carnivore species from the six prey size categories may be markedly different from the proportions set at the initial conditions, although a secondary consumer is never allowed to obtain resources from a prey size category if it was initially considered unable to obtain resources from it ($\mathrm{PD}_{ij} = 0$).

Wastage factor Carnivores cannot consume and metabolize the entire biomass of a carcass, so a 'wastage factor' was introduced in our calculations (Farlow, 1976) to represent the proportion of the primary consumer body mass that can actually be consumed by predators, excluding non-edible tissue. Viljoen (1993) provides estimations of the amount of edible meat on carcasses of herbivores of different body sizes as follows: <50 kg, 80% edible; 50–150 kg, 75% edible; 151–250 kg, 70% edible; 251–500 kg, 65% edible; >500 kg, 60% edible; and in the case of buffalo and hippopotamus, 55% edible. These wastage factors were used by Rapson and Bernard (2007) to study the diet of lions in a recent ecosystem. Wastage factors from Viljoen (1993) were adapted to our body size categories as follows: 10–45 kg, 80% edible; 45–90 kg, 75% edible; 90–180 kg, 75% edible; 180–360 kg, 70% edible; 360–1000 kg, 60% edible; and >1000 kg, 55% edible.

Results

Populations and mortality profiles

The Leslie matrix-based model provides a number of solutions for each primary consumer species that represent different population structures under varying levels of subadult mortality rates. Figure 1 presents the solutions that make the populations of *S. scrofa*, *D. vallonetensis* and *Mammuthus* sp. stable. The population profiles (Fig. 1 top row) show the typical structure, with a high percentage of young individuals and progressively decreasing numbers of individuals in older age classes (see also SOM, Fig. S1). Each line in the graphs represents the population structure for a different level of subadult mortality. *Sus scrofa* and *Mammuthus* sp. represent two extreme cases corresponding to highly different life history strategies, while *D. vallonetensis* represents an intermediate case. *Sus scrofa* is an *r*-selected species characterized by a high rate of reproduction, which may experience great variations in subadult mortality rates without large effects in its population structure. Conversely, *Mammuthus* is a paradigmatic example of a *k*-selected species, with a population structure that varies markedly at different levels of subadult mortality. Although each line in Fig. 1 represents an age structure that makes the population stable at a subadult mortality rate, only four lines are visible for *S. scrofa* because many solutions overlap. Thus, the model is highly resilient (i.e., resistant to changes) to variations in the subadult mortality rate of *S. scrofa*. The remaining seven species show population structure solutions similar to those of *D. vallonetensis* (*A. giulii*, *B.* cf. *voigtstedtensis*, *C. elaphus*, *S. etruscus* and *U. dolinensis*) or *Mammuthus* sp. (*C. fiber* and *E. altidens*).

The mortality profiles obtained from the model (Fig. 1 middle row) serve as the basis for calculations of the amount of biomass available for predators at different levels of subadult mortality (Fig. 1 bottom row). Mortality profiles are expressed as the percentage of individuals in a population that are removed from each

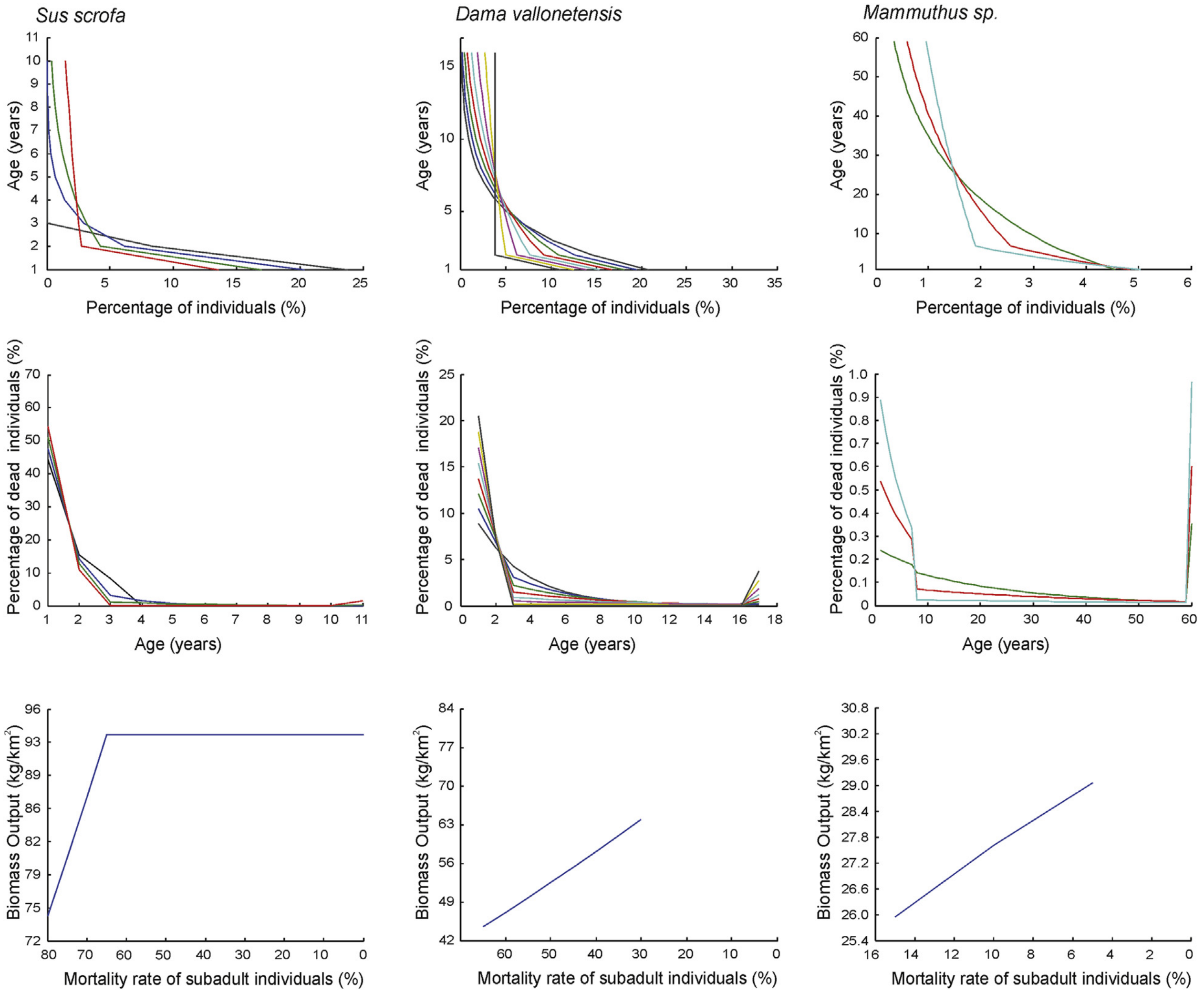

Figure 1. Graphical representation of population profiles (top row), mortality profiles (middle row) and Biomass Output available for secondary consumers (bottom row) at different subadult mortality rates for three representative species: *Sus scrofa*, *Dama vallonetensis* and *Mammuthus* sp. Each line represents the solution of the model for a different level of subadult mortality. Note, the scales of the *y*-axes are different for each species. The percentage of dead individuals in the mortality profiles represents the percentage of individuals in the population that died at age *i*.

age class during a year. The mortality peaks in the oldest age class of *Mammuthus* sp. and some other cases (see SOM, Fig. S2) are methodological artifacts that result from the model design. However, this does not alter the results because the biomass obtained from an adult individual is independent of its age at death. Again, the aforementioned life history strategies may also be identified in the mortality profiles. *D. vallonetensis* and *S. scrofa* may sustain high subadult mortality rates in comparison to *Mammuthus* sp. (Fig. 1, middle row). The *S. scrofa* population fits the premises of stability and stationarity, even when 55% of the individuals in the population die at the age of one year (Fig. 1), which corresponds to a subadult mortality rate of 80%. Conversely, for *Mammuthus* sp. the maximum subadult mortality rate that makes the population stable is 15%, and in this case only 0.9% of the individuals in the population die at the age of one year.

Combining the mortality profiles obtained in the previous step with the mean body size per age class and the estimated population density of the species, the Biomass Output can be computed. Fig. 1 (bottom row) shows the Biomass Output in kg for each species (see SOM, Fig. S3) at different levels of subadult mortality. As expected, the biomass available for secondary consumers decreases as the subadult mortality rate increases. The maximum value of Biomass Output is obtained when the subadult mortality rate is low. Different life history strategies produce different patterns of Biomass Output variation in relation to the subadult mortality rate (Fig. 1, bottom row). In the case of *S. scrofa*, the amount of biomass obtained is notably constant for subadult mortality rates between 0% and 80% before falling abruptly; *D. vallonetensis* and *Mammuthus* sp. show significantly different patterns. The values of subadult mortality rate obtained here are in agreement with published data for natural populations (Ueckermann, 1972; Focardi et al., 1996; Woolley et al., 2008; Saragusty et al., 2009).

Total Biomass Output

The maximum and minimum Biomass Output levels from a primary consumer population correspond to the minimum and maximum subadult mortality rates, respectively, that contribute to a stable population (see Table 3). If all primary consumer populations sustain maximum subadult mortality rates, TBO is 457,693 kcal/km^2. Conversely, if the subadult mortality rate is the lowest for all primary consumer species, TBO rises to 583,638 kcal/km^2. The difference between these two extremes is approximately 126,000 kcal/km^2 or 22% of the maximum value. Interestingly, the distribution of TBO among the six body size categories is markedly affected by the rate of subadult mortality (Fig. 2). Increased subadult mortality produces a strong decrease of Biomass Output in the 45–90 kg and 180–360 kg body size categories and increases Biomass Output in the 10–45 kg category. The lowest Biomass Output in the 360–1000 kg category occurs when subadult mortality rate is minimum because only juvenile rhinos and *Mammuthus* are included in this body size category. These results demonstrate the importance of including the age structure of primary consumer populations in our model because prey body size is a key factor for prey selection by most predators. Consequently, the distribution of Biomass Output along the primary consumer size categories strongly affects resource availability for active hunters.

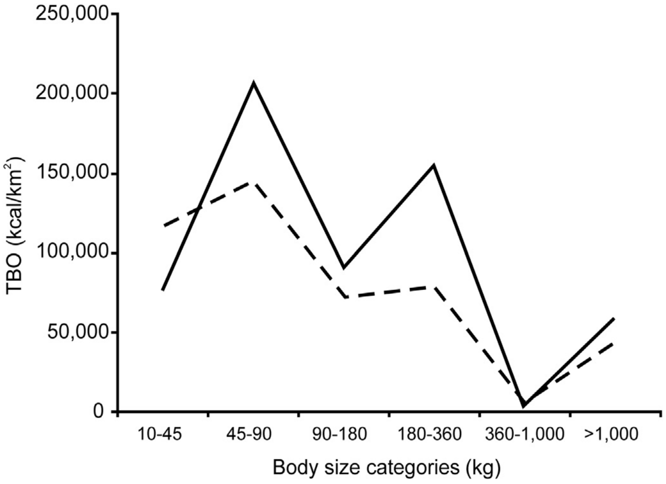

Figure 2. Biomass Output distributed among six body size categories (see text), for the maximum subadult mortality rate for all primary consumer species (dashed line) and a subadult mortality equal to 0 (solid line).

Table 3
Maximum and minimum Total Biomass Output (TBO) in kcal/km^2 year distributed along the six body size categories.

	Body size range (kg)						Total
	10–45	45–90	90–180	180–360	360–1000	>1000	
Maximum							
TBO	116.333	144.635	71.638	78.142	4.529	42.415	457.693
Minimum							
TBO	76.083	206.110	89.796	153.216	1.487	56.945	583.638

Maximum TBO is obtained when subadult mortality rate is minimum, while minimum TBO is obtained when all populations sustain the maximum possible subadult mortality, while simultaneously fitting the premises of stability and stationary.

Requirements of the secondary consumers

The nutritional requirements and sustainable densities of the TD6 secondary consumers plus *H. latidens* and *P. gombaszoegensis* are shown in Table 4. The estimated requirements were obtained by multiplying the annual caloric intake required by an average individual by the estimated population density. These estimates represent the kcal necessary to maintain a carnivore population at its ecological density. In the case of *H. antecessor*, the requirements of a population with the highest density observed in recent hunter–gatherers (Table 1) are shown for comparison. The estimated carnivore densities also tend to reflect maximum abundance. Table 4 shows the results of the distribution of TBO among secondary consumers according to the procedure explained in the Methods section. Three different scenarios were considered. In the first, only the species recorded in the TD6 assemblage were included. In the second, *H. latidens* was added to the predator guild and in the third, both *H. latidens* and *P. gombaszoegensis* were added. Because the requirements of *H. latidens* and *P. gombaszoegensis* are similar, the case in which the jaguar was included and the sabertooth was omitted is not shown. These three scenarios were evaluated for maximum and minimum TBO (i.e., the cases with low subadult mortality and maximum subadult mortality, respectively).

In the first scenario, all carnivores are able to satisfy their annual requirements for both the maximum and minimum TBO (Table 4). And the remaining resources are sufficient to maintain a high population density of hunter–gatherers (compare with data in Table 2). In the worst situation, with the minimum TBO and large herbivores representing 60% of the human nutritional intake, the remaining resources would support a population density of 0.23 ind/km^2. In the second scenario, in which a sabertooth was included in the TD6 carnivore guild, although it has not been recorded in the fossil assemblage, *H. antecessor* population is not sustained when the TBO is at a minimum (Table 4). When the

Table 4
Sustainable densities of secondary consumers in three different scenarios (see text) for maximum and minimum Total Biomass Output (TBO).

Species	Density (ind/km^2)	Requirements (kcal/km^2 year)	Total intake (kcal/km^2 year)	Not satisfied requirements (kcal/km^2 year)	Sustainable density (ind/km^2)
Scenario 1. Without large felids					
Minimum TBO					
Canis mosbachensis	0.34	40,808	40,808	0	0.34
Crocuta crocuta	0.13	217,864	217,864	0	0.13
Lynx sp.	0.30	20,621	20,621	0	0.30
Ursus dolinensis	0.05	24,054	24,054	0	0.05
Homo antecessor	0.24	157,680–78,840	–	–	0.23–0.47
Maximum TBO					
Canis mosbachensis	0.34	40,808	40,808	0	0.34
Crocuta crocuta	0.13	217,864	217,864	0	0.13
Lynx sp.	0.30	20,621	20,621	0	0.30
Ursus dolinensis	0.05	24,054	24,054	0	0.05
Homo antecessor	0.24	157,680–78,840	–	–	0.43–0.85
Scenario 2. With one large felid					
Minimum TBO					
Canis mosbachensis	0.34	40,808	35,498	5310	0.29
Crocuta crocuta	0.13	217,864	203,621	14,243	0.12
Lynx sp.	0.30	20,621	20,621	0	0.30
Ursus dolinensis	0.05	24,054	21,003	3052	0.05
Homotherium latidens	0.07	234,164	182,132	52,032	0.06
Homo antecessor	0.24	157,680–78,840	–	–	0.00
Maximum TBO					
Canis mosbachensis	0.34	40,808	40,808	0	0.34
Crocuta crocuta	0.13	217,864	217,864	0	0.13
Lynx sp.	0.30	20,621	20,621	0	0.30
Ursus dolinensis	0.05	24,054	24,054	0	0.05
Homotherium latidens	0.07	234,164	234,164	0	0.07
Homo antecessor	0.24	157,680–78,840	–	–	0.07–0.14
Scenario 3. With two large felids					
Minimum TBO					
Canis mosbachensis	0.34	40,808	28,905	11,903	0.24
Crocuta crocuta	0.13	217,864	152,649	65,215	0.09
Lynx sp.	0.30	20,621	20,621	0	0.30
Ursus dolinensis	0.05	24,054	17,038	7016	0.04
Homotherium latidens	0.07	234,164	115,986	118,178	0.04
Panthera gombaszoegensis	0.08	231,070	122,493	108,577	0.04
Homo antecessor	0.24	157,680–78,840	–	–	0.00
Maximum TBO					
Canis mosbachensis	0.34	40,808	33,219	7590	0.28
Crocuta crocuta	0.13	217,864	186,926	30,938	0.11
Lynx sp.	0.30	20,621	20,621	0	0.30
Ursus dolinensis	0.05	24,054	19,581	4474	0.04
Homotherium latidens	0.07	234,164	169,792	72,371	0.05
Panthera gombaszoegensis	0.08	231,070	161,499	69,571	0.06
Homo antecessor	0.24	157,680–78,840	–	–	0.00

Estimated density of carnivores (ind/km^2), nutritional requirements (kcal/year), total intake (kcal/year), not satisfied requirements (kcal/year) and sustainable density (ind/km^2). Total intake is defined as the biomass (in kcal) consumed by the species after dividing TBO among the secondary consumers, taking into account the distribution of TBO in body size categories (Table 3) and the carnivore preferences (Table 2). The annual energy requirement of a *Homo antecessor* population with a density of 0.24 ind/km^2 is shown for comparison. This is the maximum density recorded for recent hunter–gatherers (see Table 1). Sustainable density is the result of multiplying total intake by the requirements of an average individual.

maximum TBO is considered, all species may coexist, and the sustainable *H. antecessor* population density is 0.07 ind/km^2 for a diet of 60% meat and 0.14 ind/km^2 for a diet of 30% meat. Introducing the jaguar in the carnivore guild, which is also absent from the TD6 fossil assemblage (third scenario), reduces the population densities of other predators and excludes the possibility of sustaining a human population. Thus, the coexistence of two large felids at TD6 with *H. antecessor* was not possible with the minimum or the maximum TBO (Table 4).

Discussion

The approach presented in this work refines the methods previously used to study palaeocommunity trophic dynamics (Bermúdez de Castro et al., 1995; Fariña, 1996; Palmqvist et al., 2003; Vizcaíno et al., 2004, 2010). The model based on Leslie matrices enables estimations of the Total Biomass Output by primary consumer body size classes. This is a significant improvement because most predators select their prey by body size. Thus, using crude values of TBO fails to reflect that not all biomass is equally available for all predators. Moreover, our model produces a Biomass Output distribution by primary consumer body size and accounts for the age at death of primary consumers. These refinements permit a more precise analysis of the trophic dynamics and energy fluxes of palaeocommunities. Application of the model to the TD6 assemblage offers an estimation of trophic resource availability at Atapuerca 0.8 Ma. Overall, our results suggest that the ecosystem could provide enough resources to sustain both a rich carnivore guild and a hunter–gatherer population. The four large carnivores recorded at TD6 had enough resources to maintain high population densities. Moreover, although large felid remains have not been identified in the TD6 assemblage, our simulation shows that there was an available niche in the Atapuerca ecosystem for an additional top predator, either a jaguar or a sabertooth. However the simultaneous presence of hominins and two large felids at Atapuerca would not be sustainable.

The lack of resources for a human population in the scenario with a large felid and minimum Biomass Output should be considered in the context of the model. The expected densities of carnivores used in Table 4 should be interpreted as maximum ecological densities (White et al., 2007). Thus, a scenario with lower densities and predators coexisting with a hunter–gatherer population is reasonable. In addition, the maximum and minimum TBO values obtained from the model are the extremes of the possible values for this variable. The actual value was likely somewhere in between these two extremes. Thus, the sustainable human population density would also be an intermediate value between the estimates obtained for the cases of maximum and minimum Biomass Output. Future refinement of the model by limiting the possible population structures of the primary consumers could help to decrease the size of this interval.

In general, the sustainable population densities obtained with our model (Table 4) agree with values observed in nature. Lynxes can be found in densities ranging from 0.01 to 0.38 ind/km^2 (Nowak, 1999), and the sustainable density from our model is 0.30 ind/km^2, although certainly mammals weighing more than 10 kg were likely a secondary resource for lynxes. The calculated density for *C. crocuta* ranges between 0.09 and 0.13 ind/km^2, while recorded population densities for recent spotted hyenas range from 0.003 to 0.24 ind/km^2 (Mills and Hofer, 1998; Nowak, 1999). The calculated sustainable density for *H. latidens* is also similar to the value observed for the Asian *Panthera leo* (Caro, 1999).

In the case of *P. gombaszoegensis*, the estimated natural density is 0.08 ind/km^2, while the model results are between 0.04 and 0.06 ind/km^2, within the range observed for large felids. For example, the observed ranges are 0.02–14.2 ind/km^2 for *P. leo* (Haas et al., 2005), 0.027–0.04 ind/km^2 for *Panthera tigris*, 0.035–0.04 ind/km^2 for *Panthera pardus* and 0.04–0.12 ind/km^2 for *Panthera onca* (Nowak, 1999).

The ability of Early Pleistocene *Homo* populations to successfully compete with carnivores has been strongly debated (Turner, 1992; Arribas and Palmqvist, 1999; Roebroeks, 2001; Antón et al., 2005; Croitor and Brugal, 2010; Palombo, 2010). However, the result of competition depends not only on the ability of the competitor species to obtain the resource but also on resource abundance. Competition will be low if resources are abundant. Assuming that the proportion of meat in the diet of *H. antecessor* was similar to the value observed in recent hunter–gatherer populations (30–60%), our results suggest that the Atapuerca population had enough resources for long-term survival (Table 4). Secondary production was high enough to sustain population densities between 0.07 and 0.85 ind/km^2. The upper boundary of this interval is much higher than the values observed for recent hunter–gatherer populations, while its lower boundary is around the mean for recent populations (Table 2). The Hadza people, a modern-day group of hunter–gatherers, have the highest density at 0.24 ind/km^2 (Table 2). These results should not be interpreted as an estimation of the actual densities attained by the hominin population at Atapuerca; rather, they are only an estimation of the highest possible density given the single limiting factor of animal food resources. The population of Atapuerca likely had a density closer to the minimum value obtained (0.07 ind/km^2), a value well within the range observed for recent hunter–gatherers, than to the maximum. In summary, our main conclusion is that the game resources at Atapuerca were sufficient to sustain a human population over time, even with a carnivore guild that included a large felid not recorded in the TD6 assemblage. Only an extremely high predation pressure on subadults of all primary consumer species would make the long-term coexistence of humans and sabertooths, or jaguars, impossible.

Cannibalism and its causes, frequency and cultural implications are highly controversial topics of *H. antecessor* behavior at Atapuerca. According to the evidence available from the TD6 assemblage, *H. antecessor* individuals were consumed by other humans more than 780 ka (Fernández-Jalvo et al., 1996, 1999). Detailed microstratigraphic and sedimentological analyses suggests that the TD6-2 accumulation does not represent a single event and thus, cannibalism is interpreted as a recurrent behavior of this hominin population (Bermúdez de Castro et al., 2008; Carbonell et al., 2010a). Abundance of trophic resources in the Atapuerca territory during this period is usually argued against a nutritional explanation for this behavior and in support of interpretations that link *H. antecessor* cannibalism to cultural practices (Fernández-Jalvo et al., 1999; Bermúdez de Castro et al., 2006; Carbonell et al., 2010a; Saladié et al., 2012). However, this is the first time that resources available at TD6 for a hominin population are quantitatively evaluated. The results obtained herein indicate that, in the long term, animal food scarcity was not a problem for the human population at Atapuerca 0.8 Ma. Thus, if *H. antecessor* consumed other humans regularly, it was not a response to a sustained need to complement its diet. However, as explained in the Methods section, our model simulates the long-term average conditions at Atapuerca, and it does not provide information about short-term oscillations around those average conditions. Thus, our results do not rule out the possibility of a single and short starvation episode as the trigger for cannibalistic behavior. Though, as stated above, it is unlikely that the TD6 assemblage would represent a single and short-termed event.

The results shown herein may serve to evaluate how resource availability and intraguild competition might affect the distribution of hominins in Europe during the Early Pleistocene. The first human settlers entered Europe about 1.6 Ma, although they were unable to cross parallel 45° N until 1.2 Ma, coinciding with a reorganization and homogenization of the European mammalian faunas (Rodríguez et al., in press). It is widely recognized that intraguild competition was high in European communities during the late Villafranchian (1.6–1.2 Ma) but it decreased markedly at the early Galerian (1.2–0.8 Ma) (Raia et al., 2007; Croitor and Brugal, 2010). Accordingly, as proposed by several authors (Turner, 1992; Martínez-Navarro and Palmqvist, 1996; Arribas and Palmqvist, 1999; Palombo, 2010), survival opportunities for hominins were low in the late Villafranchian if they relied on meat as a main food resource. It has been proposed elsewhere that the faunal change occurred in Europe around 1.2 Ma relaxed intraguild competition and, likely, increased survival opportunities for hominins (Rodríguez et al., 2012). Our results support this interpretation. Intraguild competition was low at Atapuerca in the early Galerian, with a carnivore guild composed of *C. mosbachensis*, *U. dolinensis*, *C. crocuta* and *Lynx* sp. plus *H. antecessor*. Moreover, intraguild competition would have been moderate, even if a not recorded early Galerian large felid was present. Even in that scenario *H. antecessor* could have had relatively high population densities. Thus, our results are in agreement with a low to moderate intraguild competition and the existence of a niche for a carnivorous *Homo* in Europe during the early Galerian. The situation was likely very different during the late Villafranchian, with a richer carnivore guild and high competition for resources (Rodríguez et al., 2012) which may help to explain why evidence of human presence in Europe older than 1.2 Ma is so scarce.

Croitor and Brugal (2010) propose that the first European hominins occupied the ecological niche of a true omnivore, forced by their inability to effectively compete with the Villafranchian carnivores, and that the predominantly carnivorous human behavior evolved during the Middle Pleistocene when humans joined the carnivore guild as an additional social hunter. Although our results are based in the analysis of a single site, they evidence that the niche for a highly carnivorous *Homo*, with up to 60% of animal food in its diet, already existed in the early Galerian at Atapuerca. The study of other sites of similar age will show how frequent this ecological niche was in the early Galerian mammalian communities throughout Europe.

Another interesting feature of our approach is that it allows testing the effect of including additional members in the carnivore guild, as shown here with the jaguar and the sabertooth. The results of such a manipulation could provide clues to interpret the absence of a carnivore in a fossil assemblage as a result of competitive exclusion. In our case, competitive exclusion is not a valid explanation to the absence of a large felid species in the TD6 community, since our results show enough resources to sustain a carnivore guild that would include a large predator like that. However, if the addition of a new species produces a carnivore guild that cannot be sustained with the available resources, the absence of that species from the record is likely due to its real absence in the community (not to the incompleteness of the record). In this last case, provided that the added species is a common member of the regional fauna during the period under consideration, competitive exclusion would arise as a plausible explanation for the absence. This reasoning may be used to investigate competitive exclusion between carnivores and hominins, a hotly debated topic in relation to human dispersions in the Pleistocene.

Conclusions

Mathematical modeling of palaeocommunity trophic dynamics is a useful tool for investigating food resource availability for Palaeolithic populations. Our model determines the age structures that make the populations of primary consumers stable, the average biomass that can be sustainably extracted in the long term and its distribution in body size categories. Our results support the interpretation of a rich ecosystem at Atapuerca at the end of the Early Pleistocene that boasted a level of secondary production sufficient to maintain a well diversified guild of secondary consumers including a human population. This result suggests that the cannibalism identified in the TD6 assemblage cannot be explained as the result of a long-term scarcity of resources for the hominin population. Meat resources were high and competition moderate to low at Atapuerca TD6, suggesting that the niche for a highly carnivorous *Homo* already existed in Europe during the early Galerian. By reconstructing the geographical variation in food resource availability at the continental scale we will be able to understand how this factor influenced human distribution in the past.

Acknowledgments

We are grateful to P. Palmqvist, and the Associate Editor for their useful comments and suggestions. The suggestions and criticisms from an anonymous reviewer helped us to improve previous versions of the manuscript. An anonymous editor from Elsevier's Language services improved the English of the original manuscript. This research was funded by the MICINN project, CGL2012-38434-C03-02. G. Rodríguez-Gómez is the beneficiary of a pre-doctoral FPI Grant from the Spanish MICINN. Fieldwork at Atapuerca sites was funded by the Junta de Castilla y León.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2013.02.007.

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Discontinuity of Human Presence at Atapuerca during the Early Middle Pleistocene: A Matter of Ecological Competition?

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Capítulo 4.- Discontinuity of Human Presence at Atapuerca during the Early Middle Pleistocene: A Matter of Ecological Competition?

Artículo publicado en la revista *PLoS ONE*, volumen 9, número 7, páginas e101938.

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Discontinuity of Human Presence at Atapuerca during the Early Middle Pleistocene: A Matter of Ecological Competition?

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Abstract

Increasing evidence suggests that the European human settlement is older than 1.2 Ma. However, there is a fierce debate about the continuity or discontinuity of the early human settlement of Europe. In particular, evidence of human presence in the interval 0.7–0.5 Ma is scarce in comparison with evidence for the previous and later periods. Here, we present a case study in which the environmental conditions at Sierra de Atapuerca in the early Middle Pleistocene, a period without evidence of human presence, are compared with the conditions in the previous period, for which a relatively intense human occupation is documented. With this objective in mind, the available resources for a human population and the intensity of competition between secondary consumers during the two periods are compared using a mathematical model. The Gran Dolina site TD8 level, dated to 0.7–0.6 Ma, is taken as representative of the period during which Atapuerca was apparently not occupied by humans. Conditions at TD8 are compared with those of the previous period, represented by the TD6-2 level, which has yielded abundant evidence of intense human occupation. The results show that survival opportunities for a hypothetical human population were lower at TD8 than they were at TD6-2. Increased resource competition between secondary consumers arises as a possible explanation for the absence of human occupation at Atapuerca in the early Middle Pleistocene.

Citation: Rodríguez-Gómez G, Mateos A, Martín-González JA, Blasco R, Rosell J, et al. (2014) Discontinuity of Human Presence at Atapuerca during the Early Middle Pleistocene: A Matter of Ecological Competition? PLoS ONE 9(7): e101938. doi:10.1371/journal.pone.0101938

Editor: David Caramelli, University of Florence, Italy

Received January 6, 2014; **Accepted** June 12, 2014; **Published** July 23, 2014

Funding: This research was funded by the MINECO project, CGL2012-38434-C03-02, CGL2012-38434-C03-03, CGL2012-38358 and CGL-BOS-2012-34717. G. Rodríguez-Gómez is the beneficiary of a predoctoral FPI Grant from the Spanish MICINN. The fieldwork at the Atapuerca sites was funded by the Junta de Castilla y León. R. Blasco is a Beatriu de Pinós postdoctoral scholarship recipient from Generalitat de Catalunya and was co-financed by the European Union through Marie Curie Actions, FP7. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

The current paleoanthropological scenario shows an increasingly complex human population dynamic for the Pleistocene period. Some phenomena, such as migrations, replacements of species and abandonment of territories with unfavourable conditions for human colonization, seem to have played significant role in the evolution of the genus *Homo*. From this perspective, one of the most interesting subjects is the continuity or discontinuity between the hominins of the Early and Middle Pleistocene in Western Europe and the origin of the Neandertal lineage [1]. This topic has been treated from different perspectives and by different disciplines. Several authors have proposed the existence of migration waves during the Early Pleistocene taking into account different evidence [2–13]. Bermúdez de Castro and Martinón-Torres [14] suggest a theoretical evolutionary scenario for the Early Pleistocene based on isolation processes and intermittent contacts between the Eurasian populations, as previously proposed by Dennell et al [15] for the Middle Pleistocene. According to their hypotheses, the hominins from Eurasia lost contact with Africa after the first *Out of Africa* because of the formation and evolution of significant biogeographical barriers between the two continents, such as the Negev desert [16,17]. From this point forward, Eurasian populations followed an independent evolutionary process in which the same phenomena of climatic and geographical barriers caused periods of disconnection between some regions [13,18]. Apparently, these frontiers mainly affected the European populations, producing alternating episodes of isolation with population fluxes and refluxes. This dynamic seems to have also occurred during the Middle Pleistocene and may help to explain some significant changes that occurred in Western Europe during this period. An alternative explanation relates human dispersal in Europe to climate change [12] and links the permanence of humans Oldowan technology in Europe to faunal continuity, and specifically to the presence of the sabertooth *Megantereon whitei*, a hypercarnivorous predator which, presumably, provided hominins with large amounts of scavengable carcasses [13]. Arribas and Palmqvist [13] suggest that there was isolation between Europe and Africa between 1.8 Ma until 0.6 Ma, when Achelean populations expanded from Africa into Western Europe.

Currently, human settlement during the Early Pleistocene is represented in Western Europe by a short list of sites, such as Fuente Nueva 3 [19,20], Barranco León [21], Vallparadís [22,23] but see also [24], Sima del Elefante and Gran Dolina in Spain [25], Pirro Nord [26] and Ca'Belvedere di Monte Poggiolo [27] in Italy, Le Vallonet [28], Saint-Hilaire-la Gravelle [29,30] and Pont de Lavaud [31] in France, Happisburgh [32] in England and Untermassfeld [33] and Dorn-Dürkheim 3 [34] in Germany. The site of Pakefield (England), which dates to the beginning of the Middle Pleistocene (0.7 Ma) [35], can also be considered in this list. Lézignan le Cèbe, in southern France, has been proposed as one of the oldest sites documenting human occupation in Europe [36], but this interpretation is controversial. Technologically, all of these archaeological locations can be classified as Oldowan Technological Complexes or Mode 1 [11,37]. *Homo antecessor*, described from level TD6 of Gran Dolina, seems to have inhabited this area at least between the Jaramillo Subchron and the Matuyama-Brunhes Boundary [38]. Human remains older than the Jaramillo Subchron have been found at Sima del Elefante (1.2 Ma) [39] and Barranco León (1.4 Ma) [21], but see also Muttoni et al. [40]. Unfortunately, these fossil remains do not meet enough taxonomic criteria to establish possible relationships with other species such as *H. antecessor* and to describe the human scenario at this early time. In the absence of other data, these fossils have been classified as *Homo* sp. [21,38].

Mosquera et al. [11] postulated a general continuity in the hominin occupation of Sierra de Atapuerca with the exception of a gap between 0.9 and 0.5 Ma at the Gran Dolina site, based on the archaeological evidence. These authors suggest that this depopulation was not a local phenomenon but a European event. During this period, evidence of human presence is scarce in Western Europe. Although no human remains have been recovered between OIS18 and OIS16, some isolated lithic assemblages have been dated to the beginning of this period, such as those found at the Middle Loire River Basin [41] and at Caune de l'Arago [42] in France. In contrast, the number of archaeological sites increases significantly in approximately 0.6–0.5 Ma, revealing new palaeoanthropological and cultural features that mark the European Middle Pleistocene [12,43,44]. New lithic assemblages with early Acheulean industries seem to appear in Western Europe at the end of the Early Pleistocene ([11] and reference therein) although the dates of some sites are debatable [12]. In any case, Acheulean technology arrived in Europe around or before 0.6–0.5. Ma. The new settlers, with full Acheulean Mode 2 technology, occupied the European landscapes intensely at this time, as shown by the increasing number of sites. The sparsely populated northern latitudes began to be systematically occupied. Examples of this phenomenon can be found at Boxgrove in England [45], and at Bilzingsleben [46] and Schöningen [47] in Germany. Interestingly, the oldest European hearths have been dated to approximately 400 ka (Terra Amata, Beeches Pit, Schöningen or Bilzingsleben) [11,48]. The hominin fossil evidence is currently the focus of an intense debate concerning the evolutionary relationships of the Early and Middle Pleistocene European hominins [1,15,49–53] and references therein.

Given the shortage of sites and the sparse anthropic evidence from the beginning of the European Middle Pleistocene, three possible scenarios may be considered. In the first scenario, a discontinuity occurred between the Early and Middle Pleistocene human populations, and thus, Europe was almost depopulated at this time. Alternatively, if continuity between the Early and Middle Pleistocene human populations occurred, the scarcity of evidence might be explained by a contraction of the human populations as a response to adverse environmental conditions. In this latter case, the Early Pleistocene hominins would have survived in some refuges where the environment remained more consistent and eventually evolved into the new Middle Pleistocene forms, both anatomical and culturally. A third possible scenario is that the Early Pleistocene human populations survived in some refuges from OIS18 to OIS14 but were eventually substituted by the Acheulean immigrants approximately 0.5 Ma. Alternatively, it could be argued that the scarcity of evidence of human presence is just a consequence of the low completeness of the fossil record. Although this possibility may not be definitively ruled out, the scarcity of lithic record in this period, in comparison to the previous one, is striking, since stone tools are abundantly produced by humans and they have a high probability of being preserved in the archaeological record.

Here, we focus on the critical period 0.7–0.5 Ma to test whether the lack of evidence of human presence is related to adverse ecological conditions during this period. Resource availability and competition with carnivores have been repeatedly proposed as key limiting factors for Early Pleistocene European hominin populations [4,13,54–59]. Thus, a key question is whether resource availability was lower in the period between OIS18 and OIS12 than at the end of the Early Pleistocene. Rodríguez-Gómez et al. [60] presented a model to study predator-prey relationships and estimate resource availability on a local scale. This model is used here to test the hypothesis that the absence of human settlement was coincident with a period of low resource availability.

The Gran Dolina site in the Sierra de Atapuerca (in northern Spain) provides a unique opportunity to test this hypothesis on a local scale. This site has a long stratigraphic sequence that dates from the Jaramillo Subchron to the end of the Middle Pleistocene. Evidence of human presence at Sierra de Atapuerca before and after the critical period 0.7–0.5 Ma has been registered at different sites and stratigraphic levels. Human settlement in the 1.2–0.7 Ma period is documented at the TE9 level at Sima del Elefante, and the TD3-TD4 and TD6 levels at Gran Dolina, while the GII, GIIIa, GIIIb units of Galería, the TD10-2 and TD10-1 levels of Gran Dolina and the Sima de los Huesos site document human settlement during the period 0.5–0.25 Ma [61–64]. The interval between OIS18 and OIS16 (roughly from 0.7 to 0.5 Ma) is represented at Atapuerca by the TD7, TD8 and TD9 levels of Gran Dolina, all of which lack evidence of human presence in the Atapuerca area [25]. This archaeological gap in Atapuerca has been discussed taking as a perspective the technological evidence [11,43]. The TD8 level provides the richer faunal assemblage of this period at Atapuerca [62,63]; thus, it has been selected for the study of this critical period.

The aim of this study is to compare competition intensity and resource availability at Atapuerca during the period for which evidence of human presence is lacking, represented by the TD8 assemblage, with the conditions at the end of the Early Pleistocene, represented by the TD6-2 assemblage, a period of intense human occupation at Atapuerca. We introduce in this analysis an index of intraguild carnivore competition to compare the changes in the local conditions between these two periods. These data will provide us which information about the main features of the palaeoecosystem and the survival opportunities for a hypothetical human population at the Sierra de Atapuerca during this period.

Materials and Methods

The Atapuerca Gran Dolina TD8 Level

The Sierra de Atapuerca is located 15 km east of Burgos, in the north of the Iberian Peninsula. This Cretaceous limestone massif has various cavities filled with well-stratified Pleistocene sediments, known from south to north as Sima del Elefante (TE), Galería (G) and Gran Dolina (TD). These sites have been excavated since 1981 by Atapuerca Team with permission of the Consejería de Cultura y Turismo de la Junta de Castilla y León. Gran Dolina (TD) (3°31′08 W, 42°21′09 N; UTM coordinates: X = 457279, Y = 4689172) is a cavity approximately 18 m in height that was filled with Lower and Middle Pleistocene sediments. Its stratigraphic sequence was initially divided into 11 stratigraphic levels (TD1-TD11 from bottom to top) and revised in subsequent studies; e.g., [25].

The TD8 level was formed by a succession of brecciated flows of red lutites with boulders and gravels [65]. Its sedimentation is composed of overlapping cones with main vertexes at the north of the site. The vertical positions of these vertexes and their proximity to the roof suggest a small entrance into the cave during the TD8 formation. The ESR and U-series dates taken from the middle part of the sedimentary deposit suggest an average age of 600 kyr (602±52 kyr) [63]. The result obtained by TL from one sample collected at the base of TD8 correlates with the Matuyama-Brunhes boundary when the range of error is taken into account (820±140 kyr) [62]. From an archaeological perspective, evidence of human presence was not documented at TD8, as noted above. It might be argued that the small entrance and the general conditions (humidity and darkness) of the cave prevented a continuous access by a hypothetical human population, although the evidence available is not conclusive on this respect.

Taking into account the species of carnivores recovered at the TD8 level (see below) and the taphonomic characteristics identified in the faunal assemblage (e.g., tooth-mark dimensions), hyena is proposed as the main agent responsible for the ungulate accumulations [66]. However, a certain degree of variability with respect to those features traditionally used to define carnivore dens can be observed at TD8 (e.g., an absence of immature carnivore remains, a low proportion of coprolites, few marks related to the end stages of carnivore consumption, the absence of an attritional age profile and large quantities of whole bones and epiphyses) (see [67]). According to Blasco et al. [66], this variability seems to be the result of a combination of several types of dwellings (dens and refuges) and the occasional access of other carnivores during the formation of the TD8 deposit.

The TD8 Faunal assemblage

The faunal list for TD8 was obtained from Rodríguez et al. [25], Blasco et al. [66], and van der Made [68]. We restricted our analysis to mammal species of weighing more than 10 kg because these include the main sources of meat and fat, as well as the main potencial competitors and predators of a hunter-gatherer population [69,70]. This size interval includes small to medium-sized predators such as the lynx that may prey on small ungulates that are potentially important in a human diet. Rodríguez [71] provides estimations for the body mass of the mammal species identified at Gran Dolina based on the few fossils available at that time and using allometric equations. However, excavation of Gran Dolina in subsequent years increased the fossil sample from TD8. Gran Dolina TD8 site contains 899 remains that belong to mammal species of more than 10 kg. No specific permits are required for this study, which complied with all relevant regulations. The current regulation is Decreto 37/2007, 25th of April 2007, Junta de Castilla y León Cultural Heritage (BOCyL 79, 25/05/2007). The material revised is temporary housed at Institut Català de Paleoecologia Humana i Evolució Social (IPHES) at Tarragona (Spain). This research is under the frame of the Research Project CGL2012-38434-C03-02 from Spanish MINECO. The specimen numbers are provided in (Table S1).

Thus, we analysed the entire TD8 fossil assemblage and reviewed the body size estimations provided by Rodriguez [71], recalculating the body masses with allometric equations [72] when new data were available. There are eleven primary consumer species in TD8 weighing more than 10 kg: *Bison voigtstedtensis, Cervus elaphus* (red deer), *Dama vallonetensis, Equus altidens, Eucladoceros giulii, Hippopotamus* sp., *Macaca* sp., *Megaloceros solilhacus, Stephanorhinus etruscus, Sus scrofa* (wild boar) and *Ursus* sp. The bear, *Ursus* sp., is considered to be an omnivore, and in this study, it was included as both a potential prey and a potential predator. Five large predators were identified in the TD8 assemblage: *Canis mosbachensis, Crocuta crocuta* (spotted hyaena), *Hyaena* sp. (considered analogous to striped hyaena), *Lynx* sp., *Panthera gombaszoegensis and Ursus* sp. The small canid *Vulpes* sp. was not included in the analyses because its diet was presumed to be composed of small mammals, as discussed by Rodríguez-Gómez et al. [60]. The families Viverridae and Mustelidae were also excluded because their diets are also based mainly on small mammals. The TD8 fossil assemblage lacks adequate elements to estimate the body masses of *Hippopotamus* sp., *Hyaena* sp., *Macaca* sp., *Megaloceros solilhacus*, *Panthera gombaszoegensis* and *Sus scrofa* using allometric equations. Thus, for these species, we used the body masses provided by Rodríguez [71] and Blasco et al [66], except for *Hippopotamus* sp., for which the body mass for *Hippopotamus* gr. *H. antiquus* provided by Mazza and Bertini [73] was used. The body masses used are shown in Table 1.

Although we lack evidence of human presence at TD8, *Homo* sp. has been included in the analyses as a hunter-gatherer to estimate competition and resource availability for a hypothetical human population living in Atapuerca at that time. We assume for *Homo* sp. the same trophic behaviour inferred for *Homo antecessor* in the TD6-2 assemblage. Hunting has been interpreted as the main food procurement strategy at TD6-2 [74,75], although other Early Pleistocene sites like Fuente Nueva-3 evidence a predominantly scavenging behaviour of early *Homo* [55].

Thus, we analysed the distribution of resources between secondary consumers for two different scenarios and examined the effects of these different configurations of the TD8 paleoecommunity: 1) a TD8 assemblage and 2) a TD8 assemblage + *Homo* sp.

Rodríguez Gómez et al. [60] used a mathematical model to quantify the resources available for a human population in the ecosystem represented at TD6-2. TD6-2 is another level at the Gran Dolina site, lately dating to approximately 0.9 Ma [61]. This level has yielded abundant faunal remains [25,76,77] and Mode 1 stone tools, together with a large assemblage of human fossils attributed to *Homo antecessor* [8]. The study by Rodríguez-Gómez et al. [60] on the TD6-2 assemblage, suggests the existence of a rich environment, abundant in trophic resources for a hominin population, at Atapuerca at the end of the Early Pleistocene.

To make the results for TD6-2 and TD8 directly comparable we also ran the model for TD6-2, including *Homo antecessor* as a secondary consumer, because it was not included in [60]. Two different levels of animal food in the diet of *Homo* were tested to represent either a diet with a low (30%, H_{min}) or high (60%, H_{max}) meat component. In addition, we included two scenarios for TD6-2, adding a large felid to its carnivore guild, although none was recorded in the fossil assemblage. Thus, we repeated our analyses,

Table 1. Estimated body masses of the species in the TD8 assemblage.

Species	Estimated Body Mass (kg)
Bison voigtstedtensis	397
Cervus elaphus	163
Dama vallonetensis	84
Equus altidens	324
Eucladoceros giulii	360
Hippopotamus sp.	2,225
Megaloceros solilhacus	383
Macaca sylvanus	18
Stephanorhinus struscus	1,400
Sus scrofa	85
Ursus sp.	282
Canis mosbachensis	12
Crocuta crocuta	75
Hyaena sp.	50
Lynx sp.	10
Panthera gombaszoegensis	90

Weights of *Hyaena* sp., *Macaca* sp., *Megaloceros solilhacus*, *Panthera gombaszoegensis* and *Sus scrofa* were taken from Rodríguez [71] and Blasco et al [66].
To *Hippopotamus* sp. weight was taken from [73].
doi:10.1371/journal.pone.0101938.t001

including *Homotherium latidens* as a member of the TD6-2 predatory guild, to evaluate the effect of its possible presence on our results, as explained in Rodríguez-Gómez [60].

The model

We investigated the distribution of resources, primary consumer biomass, among secondary consumers in different scenarios. On the one hand, it is necessary to estimate resource availability, i.e., the biomass of primary consumers available to secondary consumers or total available biomass (TAB). On the other hand, the requirements of secondary consumers (TBD) should also be estimated (Figure 1) [78]. A summary description of the model components is provided below; for a detailed formal description of this model see Rodríguez-Gómez et al. [60]. The model was written and executed in Matlab R2009b.

Total Available Biomass

Our model was developed on the basis of the assumption that all of the variations in population size and composition may be taken as oscillations around a mean value that is constant through time-an assumption that is widely accepted in population dynamics studies [79]. We represented the average long-term condition of every population using a Leslie Matrix [80,81]. Leslie Matrices are used in population dynamics to represent a population structure at different times and to describe its oscillations (Figures 1 and 2A). We sought the Leslie Matrix that represented the average structure over time by introducing two additional conditions:

1. - The population should be stable (i.e., population size should be constant from year to year).
2. - The population should be stationary (i.e., the age structure should be constant from year to year).

Input data are physical and physiological variables (adult body mass, body mass at birth, litter size, breeding interval, age at reproductive maturity, growth rate and lifespan) that are species specific. For species with living representatives, such as *Sus scrofa* and *Cervus elaphus*, the values of these physiological variables were taken directly from the literature. For species without living representatives, the values reported in the literature for closely related living species of similar body mass were used (e.g., *Equus zebra* was used as an analogue for *Equus altidens*). For species defined to genus level such as *Macaca* sp., we used values for species of similar size, as *Macaca sylvanus*. In the cases of *Bison voigtstedtensis*, *Dama vallonetensis*, *Eucladoceros giulii*, *Hippopotamus* sp., *Stephanorhinus etruscus* and *Ursus* sp., which lack closely related living species of similar size, we computed a least square regression equation for each physiological variable with respect to mean body weight using data for species in the same family; see further details in Supplementary Material, Table S3 in [60].

The population profiles obtained from this model for every primary consumer population provide estimates of the average sustainable biomass output by age classes, which were eventually translated into body size intervals. Biomass output by age interval was obtained from the annual mortality rates obtained from the Leslie Matrix (Figure 2B). Each dead individual of a primary consumer species was assigned to one of six size categories according to its average body mass at the age of death: 10–45 kg, 45–90 kg, 90–180 kg, 180–360 kg, 360–1,000 kg or >1,000 kg (see [57]). The biomass made available for secondary consumers by each single primary consumer population was obtained as the sum of the biomass of all dead individuals (Figure 2C).Total biomass output (TBO) was obtained as the sum of the biomass outputs in each size category from each primary consumer population (Figure 1). The distribution of sustainable TBO by size category is an important feature of the model, because prey body size is a main selection factor for predators [82–84]. With this treatment of the data it is then possible to represent features such as the hunting of sub-adults in species with very low adult mortality rates and very low predation at the adult stage, such as rhinos and hippos. This model may overestimate TBO because it

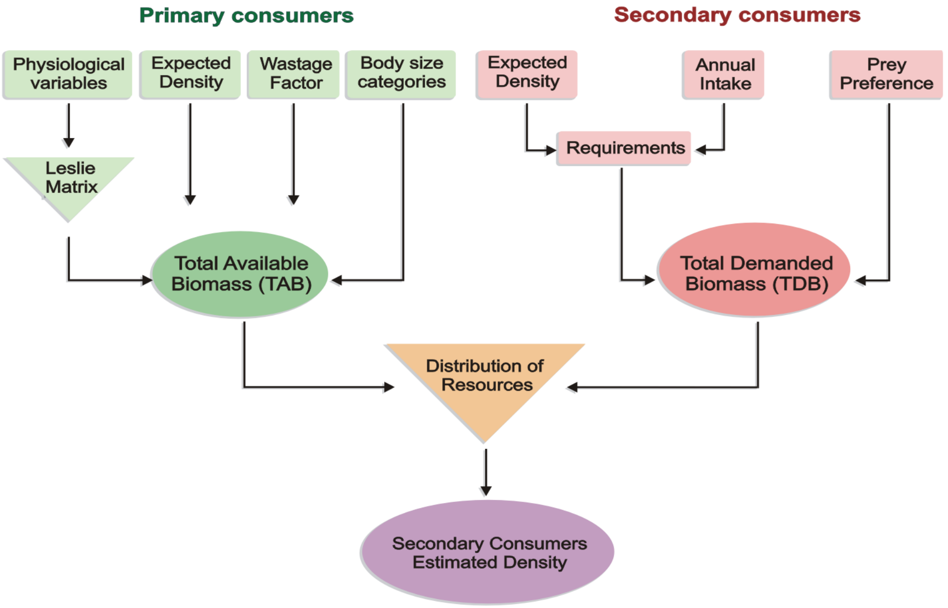

Figure 1. Flow diagram showing the components of the model used to evaluate trophic resource availability and intraguild competition (modified from [78]**).**
doi:10.1371/journal.pone.0101938.g001

considers that all the available biomass was consumed exclusively by mammals. The role of other secondary consumers, like vultures is not been considered in the model, although we acknowledge its relevance in actual ecosystems. There is not way to estimating the amount of TBO consumed by non-mammalian secondary consumers in the past, but it is reasonable to assume that it was similar in both levels (TD6-2 and TD8), an assumption that strengthens the null hypothesis of the absence of ecological differences between both assemblages.

Only female individuals are represented in a Leslie Matrix. Thus, we assumed the sex ratio was equal to 1:1, that the population profile was the same for males and females and that the survival rate was equal for both sexes. A further assumption is that the sub-adult survival rate should be lower than the adult survival rate [60].

The model solutions are not dependent on population size: thus, an estimate of population density is needed to estimate the sustainable biomass output. Mediterranean taxa dominate the TD8 pollen spectrum [25]; thus, we used the equation provided by Damuth [85] to estimate the density of primary consumers in a European mixed temperate forest:

$$\log(D) = -0.79 * \log(m) + 4.33$$

where D is the population density in number of individuals per square kilometre and *m* is the body mass in grams.

Combining the mortality profiles obtained from the Leslie Matrix with the mean body size per age class and the estimated population density of the species, the sustainable biomass output can be computed. Because a carcass includes a variable amount of non-edible tissues (horns, bones, hide, etc.), this sustainable biomass output cannot be fully used by secondary consumers. The percentage of non-edible TBO is represented in the model by a size-specific "wastage factor" [86]. Once this percentage has been subtracted, the final amount of biomass available to secondary consumers or total available biomass (TAB) is obtained. TAB is also distributed by body mass classes (Figure 1).

Our model yields several population profiles for each species, corresponding to different mortality rates. We selected extreme values with maximum and minimum pressure on sub-adults (or maximum and minimum mortality rates) that produce minimum and maximum TAB levels, respectively (TAB-m and TAB-M, respectively). We limited the results to those solutions for which sub-adult mortality rates were higher than adult mortality rates because this is the pattern usually observed in natural populations [87].

Total Demanded Biomass (TDB)

Carnivore-demanded resources should be estimated as a first step in evaluating resource distribution among secondary consumers. The carnivore intake rate was estimated using the equation reported by Farlow [88]:

$$\log I = 0.69686 \log(m) + 0.27747;$$

$$r^2 = 0.96758;\ F_{1;100} = 2{,}984.773;\ p < .01$$

where *I* is the intake rate in kcal per day and *m* is the body mass in grams. Some adjustments were made for each secondary consumer according to its inferred dietary preferences. Taking the coyote as an analogue, we estimated that large mammal flesh represented only 20% of the energetic requirements of *Canis mosbachensis* and that it was primarily consumed as carrion [57]. The spotted hyena, *Crocuta crocuta*, is able to exploit bone marrow thanks to its bone-crashing abilities. We assumed that approximately 2% of the total energetic requirements of the spotted hyaena were satisfied by bone marrow, and consequently, its energetic requirements were reduced by a factor of 0.02 [89,90]. In the case of *Hyena* sp., by analogy with the striped

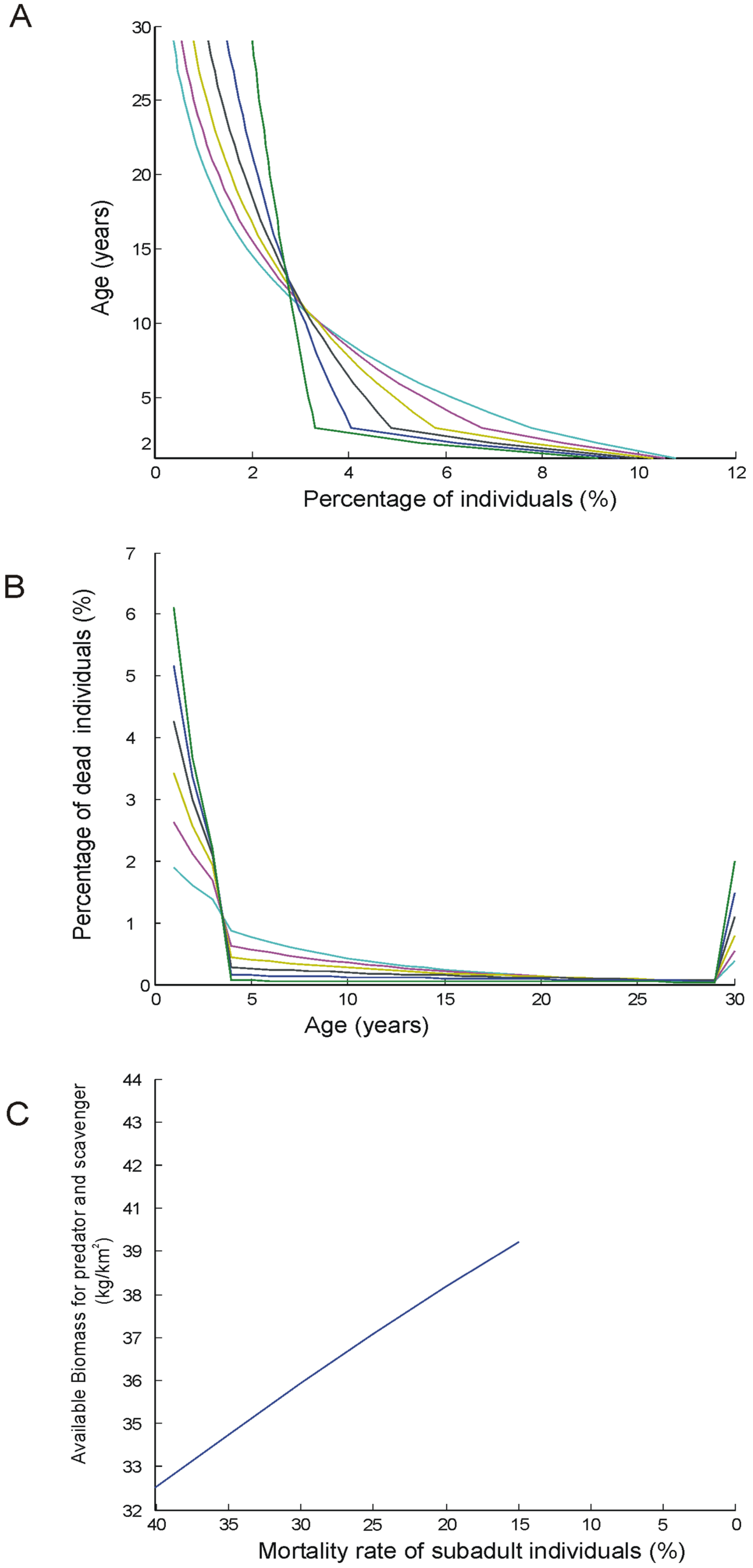
A
Age (years)
30
25
20
15
10
5
2
0
2
4
6
8
10
12
Percentage of individuals (%)
B
Percentage of dead individuals (%)
7
6
5
4
3
2
1
0
0
5
10
15
20
25
30
Age (years)
C
Available Biomass for predator and scavenger (kg/km²)
44
43
42
41
39
38
37
36
35
33
32
40
35
30
25
20
15
10
5
0
Mortality rate of subadult individuals (%)

Figure 2. Graphical representation of population profiles (A), mortality profiles (B) and biomass output available for secondary consumers (C) at different sub-adult mortality rates for *Equus altidens*. Each line represents the solution of the model for a different level of sub-adult mortality. The percentage of dead individuals in the mortality profiles represents the percentage of individuals in the population that died at age *i*.
doi:10.1371/journal.pone.0101938.g002

hyaena, carrion of large mammals would represent approximately 75% of its diet; the remainder could be invertebrates, vegetable food and small vertebrates [91]. The diet of the TD8 lynx (*Lynx* sp.), was presumed to be similar to that of the recent Iberian Lynx (*Lynx pardina*) [57]. Thus, it was assumed that species between 10 and 90 kg represented only 5% of the lynx diet [92–94], lagomomorphs and other small mammals making up the bulk of its diet. Because *Ursus* sp. was likely to have been highly omnivorous, it was assumed that meat represented only 10% of its energetic requirements as in recent European brown bears (*Ursus arctos*) [95,96]. Likely, fish was also an important component of its diet as suggested by the nitrogen-isotope values obtained for the Venta Micena bears [97].

The annual energetic requirements of a carnivore population by km^2 are obtained multiplying the individual annual intake by the population density (Figure 1). The equation provided by Damuth [98] for African flesh-eaters was used to estimate the typical carnivore density:

$$\log(D) = -0.64 * \log(m) + 2.33$$

where D is the population density in number of individuals per square kilometre and m is the body mass in grams. In the case of *Ursus* sp., the equation for carnivores was used instead of the equation for primary consumers because it predicts the population densities of recent bear species more accurately [99–101].

The requirements of *Homo* sp. were estimated to be similar to those of recent hunter-gatherer populations, with a mean daily requirement of 3,000 kcal per individual [102]. The average body mass was considered to be 76 kg, based on pelvis and femur estimates for *Homo heidelbergensis* from the Sima de los Huesos site [103,104]. Studies of recent hunter-gatherer populations have shown that animal resource consumption represents between 30% and 60% of their nutritional intake [105,106]. Thus, we modelled *Homo* sp. as a species that meets 30% (H_{min}) or 60% (H_{max}) of its energetic requirements (3,000 kcal/day) by consuming the meat of large mammals. Population densities and diet compositions observed for recent hunter-gatherers populations are shown for comparison in Table 2 (extracted from [107]).

As in the case of TAB, TDB was distributed over the same six body size categories based on the inferred prey size preferences of each predator, on the basis of the behaviour of their living relatives (Table 3 and Figure 1) [57]. The preference of a predator for a body size category is represented by the percentage of predation (PD) that this size category was presumed to represent in its diet. If a predator was presumed to be unable to kill prey in a given size category and to not consume carrion, a PD of 0 was assigned to the predator in that size category.

Distribution of TAB between secondary consumers

The distribution of TAB between secondary consumers is based on the proportional predation pressure (PPP_{ij}) of each species in each body size category. PPP_{ij} represents the relative amount of biomass demanded by the *jth* carnivore species from the *ith* prey body size category and is calculated as the proportion of the total amount of biomass demanded from a prey body size category by all carnivores that corresponds to the requirements of a single carnivore species. PPP_{ij} incorporates intraguild competition in the model because the resources obtained by a carnivore species depends on the number and characteristics of its competitors. See a detailed formal description of resource distribution computation in Rodríguez-Gómez et al. [60].

To compare the different scenarios considered in our analysis, we generated two indices (SCI and GCI) that relate the estimated and expected (estimated from allometric equations [98]) secondary consumer densities.

Species competition index (SCI):

$$SCI_i = 1 - (Ds_i / Dx_i)$$

where Dx_i is the expected density for species i obtained from the allometric equation in Damuth [98]. Ds_i is the estimated density for species i and is obtained from our model.

Global competition index (GCI):

$$GCI = 1 - (\sum Ds / \sum Dx)$$

where $\sum Ds$ is the summation of estimated densities for all species and $\sum Dx$ is the summation of expected densities for all species.

These indices provide information about competition intensity in the ecosystem with regard to an ideal condition in which all species reach optimal densities. We assume that if the densities estimated from our model approach these thresholds densities, all species would fulfil needs with the have plenty of resources available to them. The SCI index shows to what degree a species fulfils its requirements in a given environment. GCI performs similarly but at the scale of the whole guild of secondary consumers guild. In both cases, however, if the estimated densities were closer to the expected densities or optimal ones, we considered that resources were abundant when compared with requirements (i.e. that competition is low). Conversely, if our model results indicate that the secondary consumers were able to coexist only at low densities, this would be so because there was a scarcity of resources in relation to requirements, which implies a high competition.

Results

Total Available Biomass

The minimum TAB, corresponding to the maximum sub-adult mortality rate, was 496,814 kcal/km^2*year (TAB-m), and the maximum TAB, corresponding to the minimum sub-adult mortality rate, was 643,968 kcal/km^2*year (TAB-M). TAB-m is 23% lower than TAB-M. In addition, the distributions of TAB-M and TAB-m by size category are different (Table 4 and Figure 3), mainly because TAB-m has more biomass in the first category (10–45 kg) than TAB-M. The reason for the different distribution is that both adults and sub-adults of *Macaca* sp. are present in this category and with a low sub-adult mortality rate, the biomass output of macaques is higher, increasing TAB in this size category. For the rest of species considered, adult and sub-adult individuals belong to different body mass categories, and biomass increases in larger body size categories as sub-adult mortality rate decreases. These results demonstrate the importance of including the age structure of primary consumer populations in the model, because the distribution of TAB in size categories is not homogeneous, and

Table 2. Population densities and food resource use observed in recent hunter-gatherer populations [107].

Group	Area	Density ind./km^2	Gathering%	Hunting%	Fishing%
Punan	29.6	0.118	65.00	30	5
Siberian Eskimo	274.9	0.047	1.00	30	60
Guayaki-Ache	28.7	0.0348	30.00	62	10
Efe	47.0	0.1596	88.20	11	0,8
Hadza	25.0	0.240	60.00	40	0
!Kung	110.0	0.066	67.00	33	0
G/Wi	180.0	0.0293	55.00	45	0
Mardudjara	226.0	0.0075	70.00	30	0
Kiowa	280.0	0.014	20.00	80	0
Caribou Inuit	2365.0	0.003	0.10	55	44.9
Nunamiut Inuit	249.0	0.0096	0.10	89	10.9
Polar Inuit	731.0	0.0041	0.01	30	69.99

doi:10.1371/journal.pone.0101938.t002

prey body size is a key factor in prey selection by most predators. Thus, the TAB of a prey size category is not equally available for all secondary consumers.

Requirements of the secondary consumers

The energy necessary to maintain the species of the TD8 carnivore guild (first scenario) at their ecological densities is 693,725 kcal/km^2*year (Table 5). This energy requirement exists if all species fulfil all of their expected requirements. The species with higher energetic requirements are *Crocuta crocuta* and *Panthera gombaszoegensis*, approximately 222,000 kcal/km^2*year each, or 32% of total requirements. Next is *Hyaena* sp., which accounts for approximately 160,000 kcal/km^2*year or 23% of the total. *Canis mosbachensis* accounts for approximately 40,000 kcal/km^2*year or 6% of the total. *Lynx* sp. and *Ursus* sp. account for approximately 20,000 kcal/km^2*year. However, these are estimates, and to establish whether all of the requirements of the secondary consumers are fulfilled, the distribution of TAB by size category and the prey preferences of the carnivores should be taken into consideration.

Comparing different scenarios and conditions

Two scenarios were considered for TD8: only the species in the TD8 assemblage and the TD8 assemblage plus *Homo* sp. In addition, we considered two other factors: TAB (TAB-m or TAB-M) and *Homo* sp. requirements (H_{min} or H_{max}). Thus, we had six different scenarios for TD8 (Table S2 and Figure 4). Comparing the scenarios, we found the worst case to be the hypothetical assemblage of TD8 with *Homo* sp. meeting 60% of its energetic requirements from meat (H_{max}) and TAB at a minimum (TAB-m). The scenario with less competition between secondary consumers occurs when TAB is at a maximum (TAB-M). As might be expected, the parameter with the greatest effect is TAB (Table 6 and Figure 4).

Distribution of resources

The distribution of resources in all scenarios yield viable ecosystems with regard to the minimun viable population density (MVPD) of the species involved, estimated using equations provided by Silva and Downing [108] (Table 6 and Figure 4). Nevertheless, it should be noted that the MVPD corresponds to

Table 3. Percentage of predation (PD) of the TD8 carnivores plus *Homotherium latidens* and *Homo* sp. by body mass category.

Species	Body size range (kg)					
	10–45	45–90	90–180	180–360	360–1,000	>1,000
Canis mosbachensis	17	17	17	17	17	17
Crocuta crocuta	21	32	26	11	5	5
Homo sp.	24	29	19	14	10	5
Homotherium latidens	6	6	28	33	22	6
Hyaena sp.	17	17	17	17	17	17
Lynx sp.	75	25	0	0	0	0
Panthera gombaszoegensis	6	6	31	38	19	0
Ursus sp.	17	17	17	17	17	17

The scores represent the relative importance that animals in each body size category had in the carnivore's diet. The sum of the scores in a row is 1. A score of 0 indicates no consumption of mammals in that body size category.
doi:10.1371/journal.pone.0101938.t003

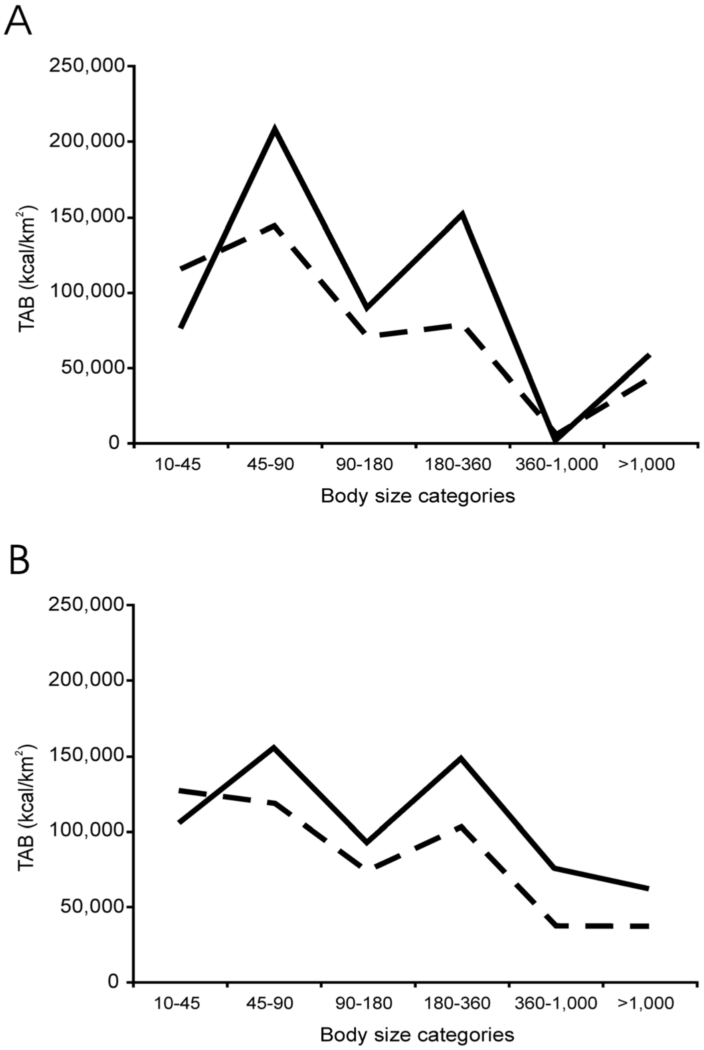

Figure 3. Biomass output distributed among six body size categories (see text). Dashed line: maximum sub-adult mortality rate for all primary consumer species or TAB-m; solid line: minimum sub-adult mortality rate (greater than or equal to the adult mortality rate) or TAB-M. A: TD6-2 available biomass; B: TD8 available biomass.
doi:10.1371/journal.pone.0101938.g003

populations living in extreme conditions and prone to extinction because MVPD is estimated on the basis of populations classified as "endangered", "vulnerable", or "close to extinction" by the IUCN [109].

With respect to the energy requirements met, mainly the species that satisfies a smaller percentage of its energy requirement in all cases is *Panthera gombaszoegensis* while *Lynx* sp. is the least affected by the competition for resources (Table S2). Even with the inclusion of *Homo* sp. all species reach viable densities, slightly higher when *Homo* sp. has minor requirements. We used as reference density for *Homo* sp. 0.24 individuals per square kilometre, the highest density observed in recent hunter-gatherers (Table 2). In the worst case, scenario with *Homo* sp. and TAB-m condition, *Panthera gombaszoegensis* met 49% of their requirements with 0.06 individuals per square kilometre; *Canis mosbachensis*, *Ursus* sp. and *Hyaena* sp. met 71% of their requirements with 0.24, 0.03 and 0.09 individuals per square kilometre, respectively; *Crocuta crocuta* met 61% of its requirements with a density of 0.08 individuals per square kilometre; and *Lynx* sp. met 81% of its requirements with a density of 0.38 individuals per square kilometre. *Homo* sp. met 60% of its requirements with a density of 0.15 individuals per square kilometre for TAB-m (see SCI in Table S2).

Comparison between TD8 and TD6-2

We take the conditions for the human groups inhabiting Atapuerca 900,000 years ago, represented by the TD6-2 assemblage, as a reference against which resource availability and competition between carnivores in TD8 may be compared (Figure 4). TAB varies in TD6-2 from a minimum of 457,693 kcal/km^2*year to a maximum of 583,638 kcal/km^2*year (see Table 3 in [57]), in both of which are below the respective values observed for TD8 (496,659 and 643,201 kcal/km^2*year, respectively). Moreover, in the TD6-2 assemblage, the maximum available resources (TAB-M) are higher than the maximum consumer requirements (TDB-M = 461,028 kcal/km2*year when

Table 4. Maximum and minimum total available biomass (TAB) in kcal/km^2*yr, distributed over the six body size categories for the TD8 assemblage.

Body size range (kg)						
	10–45	**45–90**	**90–180**	**180–360**	**360–1,000**	**>1,000**	**Total**

Body size range (kg)	10–45	45–90	90–180	180–360	360–1,000	>1,000	Total
TAB-M	106,512	155,722	92,136	149,351	76,849	62,630	643,201
TAB-m	126,928	118,768	72,589	102,942	38,128	37,304	496,659

The maximum TAB (TAB-M) is obtained when the sub-adult mortality rate is 0, while the minimum TAB (TAB-m) is obtained when all populations sustain the maximum possible sub-adult mortality rate while simultaneously satisfying the premises of stability and stationarity.

doi:10.1371/journal.pone.0101938.t004

Homo antecessor consumes more meat) and thus, all species are able to fulfil their requirements. Meat resources were high enough at TD6-2 to sustain the expected densities, even in excess (Table S3), except in the case of the most unfavourable scenario with TAB-m and the diet of *Homo antecessor* including a high amount of meat. Conversely, in the case of the TD8 assemblage, this does not occur, and TAB-M (643,201 kcal/km^2*year) is insufficient to satisfy the secondary consumers' requirements (TBD is equal to 689,279 kcal/km^2*year). Despite that TAB being lower in TD6-2 than in TD8, TD6-2-TAB meets the carnivores' requirements and TD8-TAB does not. This implies a higher degree of competition between secondary consumers in TD8 than in TD6-2. When the global competition indices are compared (Figure 4), we found that TD8 had a higher GCI than TD6-2, whether *Homo antecessor* is assumed to be highly dependent on animal resources (H_{max}) or not (H_{min}) for TAB-M condition but not for H_{max} with TAB-m. In addition, we evaluated two hypothetical scenarios: the TD6-2 assemblage with a large felid such as *Homotherium latidens* [60] and TD8 with *Homo* sp. In the hypothetical scenario of the TD6-2 assemblage with *Homotherium latidens* and TAB-m, TD8-GCI is similar to TD6-2-GCI with *Homo antecessor* consuming H_{min}. When *Homo antecessor* is considered to be more dependent on meat resources (H_{max}), TD6-2-GCI is slightly higher than TD8-GCI. However, if *Homo* sp. is included in the TD8 assemblage, both for H_{min} and H_{max} scenarios, competition increases to a level higher than observed in TD6-2 with *Homotherium latidens* (Figure 4 and Table 6). As it might be expected, the highest competition is observed when *Homo* is included in the TD8 assemblage with high meat consumption requirements (H_{max}). Under these conditions, GCI is 0.35 for TAB-m and greater than 0.2 for TAB-M (Figure 4 and Table 6). It is worth noting that the inclusion of *Homo* sp. and *Homotherium latidens* in TD8 and TD6-2 levels softens the differences between both macromammal guilds.

Discussion

Evidence of human presence in Europe during the period 0.5–0.7 Ma is very scarce. Although several European sites provide abundant evidence of human presence before and after this period, the European continent was apparently depopulated during the 0.5–0.7 Ma interval. The results presented here suggest that during this period, the environment was more hostile to a hominin population than it was previously. The Atapuerca environment was able to sustain the expected population densities of a diverse carnivore guild, including *Homo antecessor*, 0.9 Ma, as shown by the application of the model to the TD6-2 assemblage, even with the inclusion of a large felid not recorded in the fossil assemblage. In contrast, the higher values of the global competition index (GCI) obtained for TD8 in comparison to TD6-2 suggest an environment with a higher intraguild competition for resources at Atapuerca 0.6 Ma. Consequently, survival opportunities for *Homo* at Atapuerca would have been higher in the late Early Pleistocene than in the early Middle Pleistocene. Certainly the value of the population density obtained for *Homo* at TD8 is higher than the minimum viable population size (MVPS) for these species, according to the equation provided by Silva and Downing [108]. Nevertheless, the value of MVPD should be considered an absolute minimum and not an average for a sustainable population. For this reason, we focus our interpretation on the relative values of GCI in concluding that the conditions for a human population were worse at TD8 than at TD6-2 and that the Atapuerca environment was less suitable for a permanent human settlement at 0.6 Ma than at 0.9 Ma. These results support the

Table 5. Requirements of the secondary consumers in the TD8 assemblage plus *Homo* sp.

Species	W (kg)	D (ind/km^2)	Requirements (kcal/km^2/year)	Percentage requirement (%)	Percentage requirement with a less *Homo* sp. hunter (%)	Percentage requirement with a more *Homo* sp. hunter (%)
Canis mosbachensis	12	0.42	40,062	0.06	0.05	0.05
Crocuta crocuta	75	0.13	217,864	0.32	0.28	0.26
Lynx sp,	10	0.47	19,825	0.03	0.03	0.02
Hyaena sp,	50	0.17	162,932	0.24	0.21	0.19
Panthera gombaszoegensis	90	0.11	224,627	0.33	0.29	0.27
Ursus dolinensis	282	0.06	23,970	0.03	0.03	0.03
Homo sp. (30%)	76	0.24	78,840	-	0.10	-
Homo sp. (60%)	76	0.24	157,680	-	-	0.19

Two different levels of meat consumption were tested for *Homo* sp. In the first case, meat represents 30% of the energy intake, while in the second case, meat represents up to 60% of energy intake.
doi:10.1371/journal.pone.0101938.t005

hypothesis that the human absence from TD8 was related to a more hostile environment during this period at Atapuerca, characterised by a higher competition and less access to resources than in the previous period. These results support the interpretation of Blain et al. [110] that the Atapuerca area was not necessarily always a suitable place for human settlement.

The differences between TD6-2 and TD8 are due to different community structures. Cuenca-Bescós and García [111] and Cuenca-Bescós et al. [112] differentiate several faunal units (FU) in Gran Dolina and separate TD6-2 and TD8 assemblages into two different faunal units FU4 and FU5, respectively. FU4 is characterised by the presence of *Homo antecessor* and the large red-toothed shrew *Dolinasorex glyphodon*, and FU5 is considered the local range zone of *Microtus ratticepoide*s and *Blanus cinereus* [25,111,112]. With respect to large primary consumer mammals, it can be observed that the differences between TD6-2 and TD8 are reflected in *Castor fiber* and *Mammuthus* sp. which do not appear in the TD8 assemblage, and *Macaca* sp., *Megaloceros solilhacus* and *Hippopotamus* sp., which do not appear in TD6-2 assemblage. The rest of the species are equal in both assemblages. As *Castor fiber* and *Mammuthus* sp. are approximately equivalent in terms of biomass to *Macaca* sp. and *Hippopotamus* sp., respectively (because these species belong to the same body mass categories) the main change between both assemblages is the presence of *Megaloceros solilhacus*. This species provides biomass to the categories of 45 to 90 kg, 180 to 360 kg and 360 to 1,000 kg. As shown in Figures 3A and 3B, the patterns of biomass output distribution are different in both assemblages. In the TD8 assemblage, the fourth (180–360 kg) and fifth (360–1,000 kg) categories contain higher proportion of biomass than in TD6-2. TD8 presents a more balanced biomass distribution than TD6-2, with a trapezoidal form rather than a triangular form.

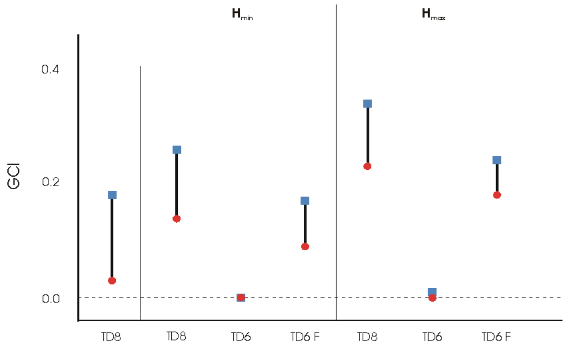

Figure 4. Graphical representation of the global competition index (GCI) for different scenarios. H_{min} denotes the scenarios that include human presence and assume low animal resource requirements for the human population, while H_{max} denotes the scenarios that include human presence and assume high animal resource requirements. TD8: TD8 assemblage; TD6: TD6-2 assemblage. TD6 F: TD6-2 assemblage plus *Homotherium latidens*. GCI takes values from 0 to 1, 0 being minimum competition and 1 being maximum competition. The solid circles represent the condition of maximum total available biomass (TAB-M). The solid squares represent the condition of minimum total available biomass (TAB-m). The black bars represent the range of values between TAB-m and TAB-M.
doi:10.1371/journal.pone.0101938.g004

The differences between TD6-2 and TD8 are larger for the secondary consumer group. *Canis mosbachensis*, *Crocuta crocuta*, *Lynx* sp. and *Ursus* sp. (*Ursus dolinensis* to TD6-2 level) are present in both assemblages. The TD8 level marks the last occurrence of *Canis mosbachensis* and *Crocuta crocuta* in the Gran Dolina sequence [112]. The main difference between TD8 and TD6-2 is the absence of *Homo antecessor* and the presence of *Panthera gombaszoegensis* and *Hyaena* sp. in the younger assemblage. *Panthera gombaszoegensis* is recorded at Atapuerca in the lower levels of Gran Dolina in TD3-TD4 and TD5 and also in Sima del Elefante in TE9 and TE12, all of which are older than 0.7 Ma [25]. If *Homo antecessor* were considered an effective hunter, the main difference between the TD6-2 and TD8 palaeoecosystems would be the presence of the scavenger *Hyaena* sp. In addition, it may be assumed that Middle Pleistocene human groups also used scavenging as a feeding strategy and were competitors of *Hyaena* sp., which might also be considered a partial ecological equivalent of *Homo*. In this interpretation, *Homo* would be replaced in the TD8 assemblage by two competitors: *Hyaena* sp. and *Panthera gombaszoegensis*. Alternatively, the absence of *Homo* may be interpreted as a key factor in determining the structure of the TD8 carnivore guild, allowing the presence of certain species that would be competitively displaced if a human population, absent for reasons other than competition, were

Table 6. Global competition index (GCI) for TD8 and TD6-2 assemblages and several hypothetical scenarios.

	TAB-m	TAB-M
TD8	0.19	0.04
TD8 H_{min}	0.27	0.14
TD6 H_{min}	0.00	0.00
TD6 F H_{min}	0.17	0.09
TD8 H_{max}	0.35	0.23
TD6 H_{max}	0.01	0.00
TD6 F H_{max}	0.24	0.18

TAB-m: minimum total available biomass; TAB-M: maximum total available biomass; H_{min}: meat represents 30% of the energy intake; H_{max}: meat represents 60% of the energy intake; F: scenario with a large felid such as *Homotherium latidens*.
doi:10.1371/journal.pone.0101938.t006

present in the area. In this alternative interpretation, the absence of human settlement at Atapuerca 0.6 Ma would not be the consequence but the cause of the community structure observed in the TD6-2 assemblage.

Although the results presented here suggest more adverse conditions in TD8 than in TD6-2 other possible explanations for the absence of hominins at TD8 should be considered. The Gran Dolina cave and its sedimentation dynamics constituted a favourable environment for the establishment of carnivore dens and shelters 0.6 Ma [66], but may not have been favourable for human access, unlike TD6-2, because the entrance into the cave was smaller during the deposition of TD8 [66]. The possible effect of an accumulation bias in the TD8 fossil assemblage against certain species should also be considered because the main accumulation agents were hyaenas [66]. Proboscideans were a common faunal element in the Iberian Peninsula during the late Early, Middle and Late Pleistocene [113], but their remains are rarely transported to dens and carnivore shelters, except maybe in the case of *Homotherium* [114,115]. However, because the secondary consumers present at TD8 were not able to prey on proboscideans, their presence at Atapuerca 0.6 Ma would have had little effect on the intensity of competition and thus would not affect our results. The hypothetical presence of the sabertooth *Homotherium latidens*, a large predator that has been recorded at Gran Dolina in level TD5 (Early Pleistocene) and in level TD10-3 (Middle Pleistocene) [25] would have significantly increased intraguild competition. Given that saberthooths were likely able to kill juvenile, and very old proboscideans [55,57], if both *Homotherium latidens* and a proboscidean species were present at Atapuerca 0.9 Ma, biomass output would have been increased in the heavier body mass categories, but little of this additional biomass could have been consumed by predators. The presence of a proboscidean would increase resource availability carrion, which would have reduced competition among scavengers. Conversely, competition between predators would be increased by the presence of a top predator like *Homotherium*. Thus, the presence of these species at Atapuerca in the early Middle Pleistocene would change the values of the results presented here, but not their meaning nor our interpretation.

With respect to the debate about the continuity or discontinuity of the peopling of Europe in the early Middle Pleistocene, the results presented here show that a discontinuity in hominin occupation existed at Gran Dolina that coincided with an increase in carnivore competition. According to this interpretation, at approximately 0.6 Ma the TD8 palaeoecosystem was not as favourable to maintaining a hominin settlement as it was at 0.9 Ma, and Atapuerca had no conditions that made it favourable as refuge for human populations, thus representing a "bottleneck" [49] to the human population at the Sierra de Atapuerca. Finlayson et al. [116] propose that *Homo* preferred mosaic landscapes and that homogeneous habitats were ignored by humans throughout the Palaeolithic. Although the Palaeolithic human groups were able to adapt to a wide range of environments [117], they required heterogeneous habitats [116]. If the Atapuerca palaeoecosystem were more homogenous 0.6 than 0.9 Ma, the absence of hominins at TD8 could be explained by their inability to settle homogeneous environments. With respect to vegetation, and according to Rodríguez et al. [25], TD8 presents a high dominance of Mediterranean taxa, while in TD6-2, Mediterranean taxa occur together with cold and dry adapted species, suggesting the existence of a mosaic habitat with areas of steppe vegetation. The preference of *Homo* for heterogeneous environments could indicate its inability to directly compete against specialist species, like open habitat cursorial predators [118], and its need for high environmental diversity to obtain resources using a generalist strategy.

It is likely, environmental conditions for *Homo* were better 0.9 Ma than in later periods, due to higher resource availability and less competition with other carnivores. A faunal turnover occurred in Europe at the beginning of the Middle Pleistocene [4,54,58], marked by the appearance of new carnivores and increased herbivore richness [4,57], that changed the structure of mammalian communities throughout Europe.

This dramatic change in the ecological scenario at the beginning of the Middle Pleistocene might be linked to the appearance in Europe of behavioral and technological improvements and innovations that increased the hunting abilities and survival opportunities of hominins. The use of fire for food processing improved the palatability and edibility of foods and increased energy gain [119]. Interestingly, both technology and hominin populations were completely different before and after the critical interval of the alleged European depopulation. Nevertheless, the subsistence strategies of human groups were successful in both the Early and Middle Pleistocene [120,121]. Roebroeks [67] suggests a demographic population increase and a human expansion in the Middle Pleistocene on the basis of the technological improvements that occurred during this time.

It is difficult to point towards a unique explanation for the absence of humans from TD8, but what can be said is that survival opportunities for a human population were worse at TD8 than at

TD6-2 because intraguild competition was higher. Nevertheless, it is necessary to take into account that the excavation of TD8 affected an area of only 24 m^2 [122]. It is expected that future excavation of a larger area of this level will provide more faunal remains and other evidence to shed light on the hominin population continuity or discontinuity debate.

The structure of the mammalian palaeocommunity and the intensity of competition in the predatory guild likely constrained human ecodynamics in the Pleistocene. This study provides a new avenue for evaluating the relative suitability of a palaeoenvironment for a human hunter-gatherer population, taking into consideration resource availability and competition intensity. Fossil assemblages with and without evidence of human presence may be compared providing a different way to approach the study of variations in human presence in the Palaeolithic. Although this approach does not provide information about the mechanisms that may have produced changes from one community structure to another, it quantifies changes in trophic relationships using the global competition index (GCI). Investigation of more European sites using a similar approach will help to test whether the apparent discontinuity in the peopling of Europe is related to more adverse environmental conditions or decreased survival opportunities at the beginning of the Middle Pleistocene (0.7−0.5 Ma), as suggested by the Atapuerca record, or whether other mechanisms are implicated.

Conclusions

The reconstruction of trophic relationships in palaeocommunities and the comparison of the intensities of intraguild competition, using the global competition index (GCI) presented here make it possible to evaluate the relative suitability of past ecosystems for hominins. Increased intraguild competition made conditions at Atapuerca more adverse for secondary consumers at 0.6 than 0.9 Ma. This increased competition is a possible cause of the apparent depopulation of the Atapuerca area in the early Middle Pleistocene. Nevertheless, more sites of this period should be studied with a similar approach to determine whether increased intraguild competition for resources played a role in changes in the distribution of *Homo* in Europe in the 0.5–0.7 Ma interval. Both sites with and without evidence of human presence should be compared to shed light on the fiercely debated question of the continuity *vs*. discontinuity of human occupation in Europe at the beginning of the Middle Pleistocene. This study demonstrates that mathematical modeling is a helpful tool in addressing this topic.

Supporting Information. Appendix B.

Table S1 Specimen Number.
(XLSX)

Table S2 Sustainable densities of the TD8 secondary consumers for six different scenarios (see text) for maximum and minimum total available biomass (TAB). Estimated density of carnivores (individuals per square kilometre), nutritional requirements (kilocalories per year), total intake (kilocalories per year), unsatisfied requirements (kilocalories per year), sustainable density (individuals per square kilometre), Species Competition Index (SCI). Total intake is defined as the biomass (in kcal) consumed by the species after dividing TAB among the secondary consumers, taking into account the distribution of TAB by body size category (Table 4) and the carnivore preferences (Table 3).
(DOCX)

Table S3 Sustainable densities of TD6-2 secondary consumers for eight different scenarios (see text) for maximum and minimum total available biomass (TAB). Estimated density of carnivores (individuals per square kilometre), nutritional requirements (kilocalories per year), total intake (kilocalories per year), unsatisfied requirements (kilocalories per year), sustainable density (individuals per square kilometre), Species Competition Index (SCI), Total intake is defined as the biomass (in kcal) consumed by the species after dividing TAB among the secondary consumers, taking into account the distribution of TAB by body size category (Table 4) and the carnivore preferences (Table 3).
(DOCX)

Acknowledgments

We are grateful to P. Palmqvist and the Academic Editor for their useful comments and suggestions on a previous version of this manuscript. An anonymous editor from Elsevier's Language services improved the English of the original manuscript. We also thank Estefanía Pérez Fernández for her suggestions and support in the revision of the manuscript. We are very grateful to the participants in the fieldwork and all of the members of the Atapuerca Research Team.

Author Contributions

Conceived and designed the experiments: AM J. Rodríguez. Performed the experiments: GRG. Analyzed the data: GRG AM J. Rodríguez. Contributed reagents/materials/analysis tools: JAMG. Wrote the paper: GRG AM JAMG RB J. Rosell J. Rodríguez. Discussion: GRG AM JAMG RB J. Rosell J. Rodríguez.

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Ecological competition and community structure as limiting factors of human presence in Europe during the Early and Middle Pleistocene

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Capítulo 5.- Ecological competition and community structure as limiting factors of human presence in Europe during the Early and Middle Pleistocene

Trabajo enviado a la revista *Palaeogeography, Palaeoclimatology, Palaeoecology*.

Submitted Manuscript

Ecological competition and community structure as limiting factors of human presence in Europe during the Early and Middle Pleistocene

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ARTICLE INFO

Keywords:
competition intensity
human presence
Europe
Early and Middle Pleistocene

ABSTRACT

Based on fossil remains and technological complexes recorded at archaeological sites, it has been proposed that the human presence in Europe during the late Early and the Middle Pleistocene was discontinuous. Moreover, several authors argue that competition for meat with other secondary consumers could have delayed human dispersal throughout Europe. In this work, we estimate the competition intensity among secondary consumer species in three periods (late Early, early Middle and late Middle Pleistocene) to evaluate the relevance of this factor in conditioning the discontinuity of the human occupation of Europe. The biomass available in a community for secondary consumers is estimated in this study using a mathematical model based on the Leslie Matrices and subsequently distributed among them according to their requirements and preferences for several size categories of primary consumer species. We develop several indexes to quantify the competition intensity among the secondary consumers. Moreover, we apply the traditional ratio of primary consumer biomass to secondary consumer biomass. These indexes are standardized; thus, it is possible to compare the competition intensity among different palaeoecosystems. The hypothesis to be tested is that the competition intensity was higher in the early Middle Pleistocene than in the late Early and in the late Middle Pleistocene, but this is not supported by our results. On the contrary, the lowest competition intensity is estimated to have occurred in the early Middle Pleistocene. This finding is observed due to an increase in large herbivore species and a decrease in secondary consumers in this period. It seems that these characteristics of the Early Pleistocene are different from those of the Middle Pleistocene because, generally speaking, the palaeoecosystems of the oldest period supported a higher competition intensity due to the configuration of the food webs during this period. A focus on food web structure and the intensity of the interactions among its components will be necessary to understand the role of the human populations in the Pleistocene palaeoecosystems.

1. Introduction

Assuming that large mammals were a relevant food source in the human diet during the Early Pleistocene (e.g. Binford, 1981; Binford, 1985; Gaudzinski and Roebroeks, 2000; Marean, 1989; McNabb, 2007; Roebroeks, 2001; Speth, 2010), the hominin ability to obtain meat was conditioned by prey abundance, ecological characteristics, and the intensity of competition with other carnivorous mammals for this trophic resource. The availability of resources and competition with carnivores have been repeatedly proposed as key limiting factors for the early European human populations (e.g. Arribas and Palmqvist, 1999; Madurell-Malapeira et al., 2010b; Martínez-Navarro and Palmqvist, 1996; Palombo, 2007; Palombo, 2010; Palombo, 2013; Rodríguez et al., 2012; Turner, 1992). Palombo (2010) proposed that competition with scavengers and/or predators could have delayed human expansion throughout Europe during the Early Pleistocene because the first European human populations had limited technological capabilities. In a recent work, Palombo (2014) noted that the changes in the structure of mammals´ paleocommunities and the enlarged prey spectrum played an important role in the success of the human settlement. Therefore, some scholars propose that human population in this time period were strongly dependent on the scavenging of ungulate carcasses (Arribas and Palmqvist, 1999; Espigares et al., 2013; Martínez-Navarro and Palmqvist, 1996; Turner, 1992). Stable populations of sabertooth felids most likely yielded a high amount of scavengeable food in the late Early Pleistocene, given their dental characteristics and killing capabilities (Arribas and Palmqvist, 1999; Marean, 1989; Martínez-Navarro and Palmqvist, 1995; Palmqvist et al., 1996; Palmqvist et al., 2011; Palmqvist et al., 2005; Palmqvist et al., 2007; Turner, 1992). The giant hyaena (*Pachycrocuta brevirostris*) was likely a powerful competitor for *Homo* in the search for carrion, whilst pack-hunting lycaons, *Panthera gombaszoegensis* and *Puma pardoides*, among others (Madurell-Malapeira et al., 2010b; Palombo, 2010), were strong hunting competitors. Climatic conditions changed at the early Middle Pleistocene transition (Maslin and Ridgwell, 2005; Schneider and Root, 1998; Shackleton, 1995) during the so called Mid-Pleistocene Revolution (MPR) (Maslin and Ridgwell, 2005). The MPR promoted the renewal of the mammalian faunal complex, with the appearance of new carnivores in Europe and a progressive increase of herbivore richness (e.g. Azanza et al., 2004; Cuenca-Bescós et al., 2005; Palombo, 2007; Rodríguez et al., 2004; Turner, 1992). Thus, it may be speculated that at this time *Homo* had a better access to carcasses than in the former period and that human weapons and tool kits became more effective, facilitating their dispersal across Europe (Palombo, 2010; Rodríguez et al., 2012). The eventual expansion of human populations in Europe during the Middle Pleistocene might be explained by a replacement of *Homo antecessor* populations with a new African hominin species with technological improvements (the Acheulean-Mode 2 technology) (Jiménez-Arenas et al., 2007; Jiménez-Arenas et al., 2011; Lordkipanidze et al., 2007; Santonja and Pérez-González, 2010). For Carbonell et al. (1999), the replacement of human populations was slow, initially with two coexisting technological modes (Mode 1 and Mode 2) in Europe. Carbonell et al. (2010) suggest that the Acheulean was spread throughout Eurasia, due to the demographic growth both in Near East and in Africa. For the local origin of the European Acheulean, see Molines and Moncel (2005). Whatever the causes and processes, the human expansion was evident around approximately 0.6-0.5 Ma when the number of archaeological sites significantly increased and the northern latitudes began to be frequently inhabited (e.g. Mania and Vlcek, 1999; Roberts and Parfitt, 2000; Thieme, 1997), showing different palaeoanthropological and cultural features that define the European Middle Pleistocene (Doronichev and Golovanova, 2010; Jiménez-Arenas et al., 2011; Ollé et al., 2013). However, although the Acheulean culture was undoubtedly established in Europe around 0.6-0.5 Ma, there are some lithic assemblages that exhibit early Acheulean or later Mode 1 features at the end of the Early Pleistocene (Barsky and de Lumley, 2010; Barsky et al., 2013; Moncel et al., 2013; Mosquera et al., 2013; Santonja and Pérez-González, 2010; Scott and Gibert, 2009; Vallverdú et al., 2014; Walker et al., 2013), although the age of some them is debatable (Jiménez-Arenas et al., 2011). Several researchers and studies defend a discontinuity in the human occupation of Europe during the Early to Middle Pleistocene Transition (Jiménez-Arenas et al., 2011; Moncel, 2010; Moncel et al., 2013; Mosquera et al., 2013; Santonja and Pérez-González, 2010; Vallverdú et al., 2014). Moncel (2010) suggests that the human occupation of Europe during this period was discontinuous and dependent on environmental factors and climate. The dependence of human populations on the ecological conditions during the Early Pleistocene has been repeatedly proposed and frequently related to the presence of saber-toothed cats, even relating the persistence of Mode 1 technology in Europe to the survival of these felids until the Middle Pleistocene (Arribas and Palmqvist, 1999; Jiménez-Arenas et al., 2011; Martínez-Navarro and Palmqvist, 1995; Martínez-Navarro and Palmqvist, 1996; Palmqvist et al., 2011). The existence of several migration waves into Europe during the Early Pleistocene has been proposed by several authors (Agustí et al., 2009; Bermúdez de Castro et al., 2013; Carbonell et al., 2010; Made and Mateos, 2010; Mosquera et al., 2013; Muttoni et al., 2010; O´Regan et al., 2011; O'Regan, 2008; Palombo, 2010; Palombo, 2013). Bermúdez de Castro and Martinón-Torres (2013) defend periods of isolation and intermittent contacts among the Eurasian populations during the Early Pleistocene, as was proposed by Dennell et al. (2011) for the Middle Pleistocene.

According to the hypothesis that human presence in Europe was conditioned by competition with carnivores (Arribas and Palmqvist, 1999; Martínez Navarro, 1992; Palombo, 2007; Palombo, 2010; Rodríguez et al., 2012), the discontinuity in human occupation during the Early and Middle Pleistocene transition could be explained by a high competition intensity among secondary consumers in this period. Rodríguez-Gómez et al. (2013) developed a quantitative model to estimate resources availability for secondary consumer species and to study predator-prey relationships. That model was applied, at a local scale, to study the large mammal palaeocommunity from the TD6 level of Gran Dolina site from the Sierra de Atapuerca (Spain). Human settlement is documented in Atapuerca between 1.2 to 0.9 Ma and between 0.5 to 0.25, but there is not evidence of human presence for the time period between 0.9 and 0.5 Ma (Mosquera et al., 2013). The same methodology was used to compare the competition intensity among secondary consumers at Atapuerca in two time periods, represented by the two Gran Dolina levels, namely, TD6, dated to 900 kyr ago and with human presence, and TD8, dated to some 600 kyr ago and without human presence. This methodology was used to evaluate competition intensity as a possible explanation for the discontinuity of human presence at a local scale (Rodríguez-Gómez et al., 2014b). These authors found that competition intensity was higher at TD8 than at TD6 and concluded that this could be a relevant factor in determining human occupation.

Our aim is to extend the analysis carried out in Rodríguez-Gómez et al. (2014b) to a continental scale to test whether variations in competition intensity and trophic resources availability acted as limiting factors for the human occupation of Europe. Our analysis focuses on three time intervals of the same duration: the oldest interval is roughly defined by the beginning of the Jaramillo Subchron and the Matuyama-Brunhes Boundary (1.1-0.8 Ma) and represents the period when population with Oldowan technology were well established in southern Europe (Carbonell et al., 2008; Toro-Moyano et al., 2013); the second interval (0.8-0.5 Ma) coincides with an apparent decrease in human presence in Europe; and the third interval (0.5-0.2 Ma) coincides with an expansion and increased intensity of human occupation at the continental scale. We compare the competition intensity in the European ecological communities among these three time periods using several indexes of intraguild competition to test whether the apparent depopulation of Europe from 0.8 Ma to 0.5 Ma may have been related to an increased difficulty in accessing trophic resources.

2. Materials

Information on European local faunal assemblages (LFAs) (longitude -10.00 to 45.00 degrees and latitude 30.00 to 55.00 degrees) dated to the late Early Pleistocene to late Middle Pleistocene (1.1-0.2 Ma) was compiled from published sources. Initially, a total of 93 LFAs from 69 localities with mammal species weighting more than 10 kg were selected. Because complete or nearly complete communities are required, the LFAs were filtered according to the number of prey and predator species in the assemblage. Only those LFAs with both a number of prey and carnivore species larger than the median for the 93 faunal assemblages (> 3 secondary consumer species and > 9 primary consumer species) were selected (Table S1 and S2). This criterion was reached by 34 LFAs distributed in three groups which correspond to the three time intervals: Interval 1, from 1.1 to 0.8 Ma; Interval 2, from 0.8 to 0.5 Ma; Interval 3, from 0.5 to 0.2 Ma. Thus, we have nine faunal assemblages in the first group, seven in the second and 18 in the third one (Figure 1 and Table 1).

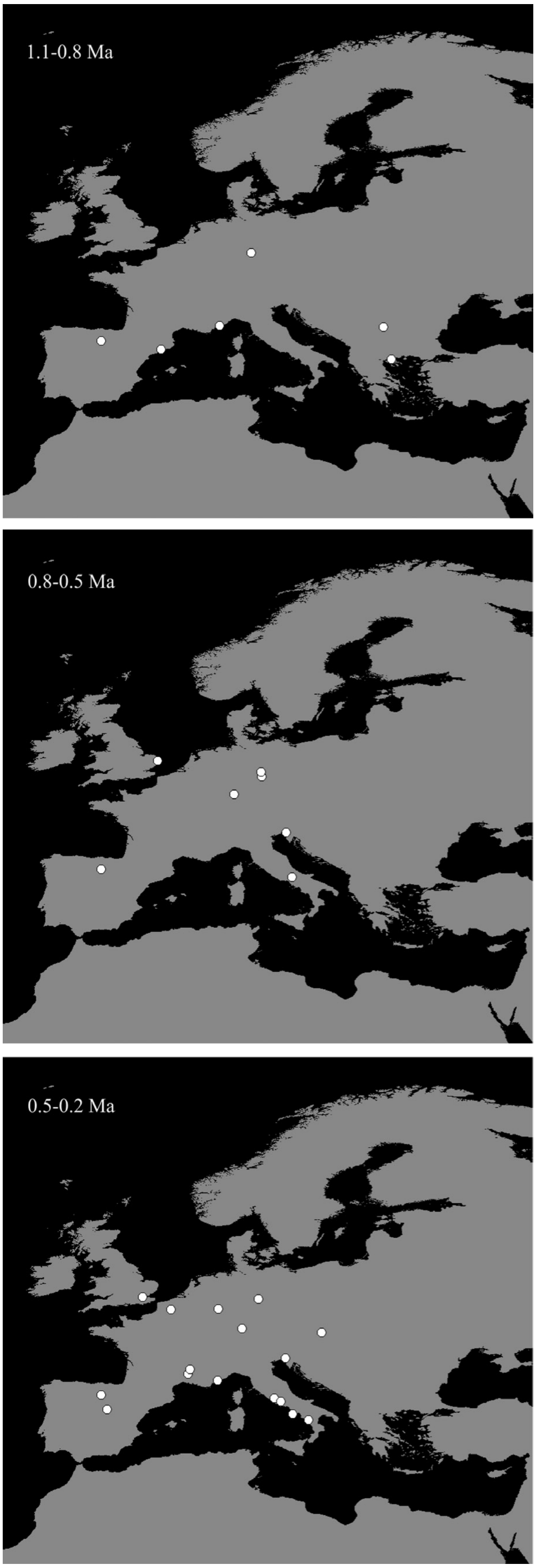

Figure 1. Geographical distribution of local faunas included in the analyses from interval 1.1 to 0.2 Ma. There are 10 local faunas for the Interval 1 (1.1-0.8 Ma) (top); 7 for the Interval 2 (0.8-0.5 Ma) (middle); and 18 for the Interval 3 (0.5-0.2 Ma) (bottom).

We reviewed all faunal lists and applied uniform taxonomic criteria (see Rodríguez et al., 2012 and references therein) to obtain a taxonomically consistent database. Our analysis was restricted to mammal species of more than 10 kg because they constitute the portion of the food web that allegedly included hominins (Binford, 1981; Binford, 1985; Díez et al., 1999; Gaudzinski and Roebroeks, 2000; Marean, 1989; Roebroeks, 2001; Saladié et al., 2011; Speth, 2010). Primary consumer species included in this study belong to the families Bovidae, Castoridae, Cercopithecidae, Cervidae, Elephantidae, Equidae, Hippopotamidae, Hystricidae, Rhinocerotidae, and Suidae. The secondary consumers belong to the families Canidae, Felidae, Hominidae, Hyaenidae, and Ursidae. The Family Mustelidae and the genus *Vulpes* were excluded because their diet is mainly based on small mammals (Carbone et al., 1999; Seebeck, 1978). Species in the genus *Ursus* were included in the analyses as both primary consumers and secondary consumers because they are considered omnivores (Bocherens et al., 2004; Parde and Camarra, 1992). Hominins were only considered only as secondary consumers.

To perform our analyses, it is necessary to estimate several physiological and life history parameters for every primary consumer species, namely, adult body mass, body mass at birth, litter size, breeding interval, age at reproductive maturity, growth rate and lifespan. In the case of secondary consumers, only adult body mass is required. We obtained values of these physiological variables for recent species from the PanTHERIA database (Jones et al., 2009). Values for the adult body mass of fossil species were obtained from the literature (Alberdi et al., 1995; Antón et al., 2005; Athanassiou, 2003; Breda and Marchetti, 2005; Brugal and Fosse, 2004; Carotenuto, 2009; Collinge, 2001; Crégut-Bonnoure and Dimitrijevic, 2006; Crégut-Bonnoure and Spassov, 2002; Crégut-Bonnoure and Tsoukala, 2005; Croitor and Brugal, 2007; Fostowicz-Frelik, 2008; Jones et al., 2009; Kahlke and Gaudzinski, 2005; Koufos et al., 1997; Lister and Stuart, 2010; Made, 1998; Made et al., In Press; Madurell-Malapeira et al., 2010a; Nowak, 1999; Palmqvist et al., 2003; Prado et al., 2004; Rodríguez, 1997; Weers, 1994). For species with living representatives and without body mass values, we took the values of the living populations. Sometimes, taxa were identified in the original source to the genus, subfamily or family level only. In these cases, we computed the mean adult body weight of the species present in Europe in that time interval in the corresponding taxonomic group (genus, subfamily or family). For example, the adult body mass of a taxon identified in a LFA as "Cervidae indet." is estimated as the mean body weight of the species in the Family Cervidae occurring in that period. In the case of *Homotherium* sp., the mean body mass of *Homotherium latidens* and *Homotherium crenatidens* is used (Antón et al., 2005; Brugal and Fosse, 2004). This procedure was used only for a 5% of the cases, defining "case" as the occurrence of a species in a LFA. A least square regression equation was computed for each primary consumer Family or Subfamily to estimate each physiological variable from the mean body weight (Table S3). The equation was computed only when data for at least four species in the family were available. Only those regression equations in which body mass explains more than 80% of the variance in the dependent variable were used. If body mass explains less than 40% of the variance, we took the median for the Family or Subfamily. If it explains between 40 and 80%, we took the median body weight for the species in the Family or Subfamily with a body weight similar to that of the species studied.

Table 1. Early and Middle Pleistocene faunal assemblages used in this study and distributed in three time intervals (see text) with locality codes (LC) assigned for this study. Number of species of primary consumers (N1) and secondary consumers (N2) macromammal species in each fossil assemblage are indicated. Ursids are considered in the first group (N1) to select faunal assemblage. HE shows if there is human evidence into the faunal assemblages.

LC	Locality	Layer	Longitude	Latitude	N1	N2	HE	References
1.1-0.8 Ma. Interval 1								
1	Apollonia-1 (Greece)	N/A	23.44	40.62	3	11	No	(Kostopoulos, 1997)
2	Atapuerca-Dolina (Spain)	TD3-TD4	-3.52	42.35	5	9	Yes	(Rodríguez et al., 2011)
3	Atapuerca-Dolina (Spain)	TD6 1-2	-3.52	42.35	4	10	Yes	(Rodríguez et al., 2011)
4	Grotte du Vallonnet (France)	III	7.47	43.77	7	12	Yes	(de Lumley et al., 1988)
5	Kozarnika (Bulgarian)	12	22.68	43.63	7	10	No	(Guadelli et al., 2005)
6	Kozarnika (Bulgarian)	13	22.68	43.63	5	9	Yes	(Guadelli et al., 2005)
7	Untermassfeld (Germany)	N/A	10.42	50.55	9	15	No	(Koenigswald and Heinrich, 1999)
8	Vallparadís (Spain)	Lower Unit	2.02	41.56	7	11	No	(Garcia et al., 2011; Madurell-Malapeira et al., 2014)
9	Vallparadís (Spain)	Middle Unit	2.02	41.56	8	11	Yes	(Madurell-Malapeira et al., 2014)
0.8-0.5 Ma. Interval 2								
10	Atapuerca-Dolina (Spain)	TD8	-3.52	42.35	5	11	No	(Rodríguez et al., 2011)
11	Isernia La Pineta (Italy)	N/A	14.22	41.60	3	12	Yes	(Palombo et al., 2000-2002)
12	Mauer (Germany)	N/A	8.82	49.33	7	14	Yes	(Koenigswald and Heinrich, 1999)
13	Pakefield/Kessingland (United Kingdom)	Rootlet bed	1.72	52.43	4	15	Yes	(Mosquera et al., 2013; Stuart and Lister, 2001)
14	Slivia (Italy)	N/A	13.66	45.76	4	17	No	(Montuire and Marcolini, 2002; Palombo et al., 2000-2002)
15	Sussenborn (Germany)	Hauptfauna	11.35	50.98	5	18	No	(Koenigswald and Heinrich, 1999)
16	Voigtstedt (Germany)	Lehmzone	11.32	51.40	3	14	No	(Koenigswald and Heinrich, 1999)
0.5-0.2 Ma. Interval 3								
17	Atapuerca-Dolina (Spain)	TD10-1	-3.52	42.35	4	9	Yes	(Rodríguez et al., 2011)
18	Atapuerca-Galería (Spain)	GIIb	-3.52	42.35	4	9	Yes	(Rodríguez et al., 2011)
19	Atapuerca-Galería (Spain)	GIII	-3.52	42.35	4	9	Yes	(Rodríguez et al., 2011)
20	Biache-Saint-Vaast (France)	Dépôts fluviatiles	2.96	50.31	3	13	Yes	(Palombo et al., 2003-2004)
21	Bilzingsleben II (Germany)	II	11.07	51.28	3	12	Yes	(Koenigswald and Heinrich, 1999; Mania and Vlcek, 1999)
22	Casal de' Pazzi (Italy)	N/A	12.53	42.02	3	9	No	(Palombo et al., 2000-2002; Palombo et al., 2005)
23	Cueva del Congosto (Spain)	A1	-3.02	41.00	5	12	Yes	(Arribas and Jordá, 1999)
24	Fontana Acetosa (Italy)	N/A	13.15	41.74	4	10	No	(Palombo et al., 2000-2002)
25	Grotta Lina (Italy)	N/A	15.75	40.00	4	10	No	(Barbera et al., 1995)
26	Grotte du Lazaret (France)	CII inf	7.25	43.70	4	14	Yes	(Valensi, 2009)
27	Heppenloch (Germany)	N/A	9.52	48.53	3	13	No	(Koenigswald and Heinrich, 1999)
28	Hundsheim (Germany)	N/A	16.93	48.13	7	9	No	(Koenigswald and Heinrich, 1999)
29	Orgnac 3 (France)	6	4.54	44.28	3	11	No	(Moncel et al., 2005)
30	Payre (France)	F	4.73	44.73	5	15	No	(Daujeard and Moncel, 2010)
31	Quisana-Certosa (Italy)	N/A	14.25	40.55	3	10	No	(Barbaro and Gliozzi, 1995)
32	Riparo di Visogliano (Italy)	Lower levels	13.60	45.77	3	9	Yes	(Abbazzi et al., 2000)
33	Swanscombe (United Kingdom)	Lower loam	0.32	51.42	3	14	Yes	(Ashton et al., 1994)
34	Wannenköpfe (Germany)	Wa1-Wa3	7.37	50.37	3	9	Yes	(Koenigswald and Heinrich, 1999)

3.-Methods

3.1.- The model

We investigate the distribution of meat resources, i.e., primary consumer biomass, among secondary consumers in the Pleistocene using a mathematical model that estimates the amount of primary consumer biomass available for the secondary consumers in a community (total available biomass, or TAB) and the requirements of secondary consumers (total demanded biomass, TDB) (Rodríguez-Gómez et al., 2014a). A summary description of the model components is provided below; for a detailed formal description of this model, see Rodríguez-Gómez et al. (2013). The model was written and executed in Matlab R2009b.

3.1.1 Total available biomass (TAB)

Our model was developed on the assumption that all of the variations in population size and composition may be taken as oscillations around a mean value that is constant through time, i.e., population fluctuations are randomly distributed above and below the value of this mean, an assumption that is widely accepted in population dynamics studies (Owen-Smith, 2010). We represented the average long-term condition of every population using a Leslie Matrix (Leslie, 1945; Leslie, 1948). Leslie Matrixes are used in population dynamics to represent a population structure at different times and to describe its oscillations. We conditioned Leslie Matrixes to obtain the average structure of a population that was stable (i.e., population size should be constant from year to year) and stationary (i.e., the age structure should be constant from year to year) over time.

The input data of the model are physical and physiological variables (adult body mass, body mass at birth, litter size, breeding interval, age at reproductive maturity, growth rate and lifespan) that are species specific. The population profiles obtained from this model for every primary consumer population provide estimates of the average sustainable biomass output by age classes, which were eventually translated into body size intervals. Biomass output by age interval was obtained from the annual mortality rates obtained from the Leslie Matrix. Each dead individual of a primary consumer species was assigned to one of six size categories according to its average body mass at the age of death: 10-45 kg, 45-90 kg, 90-180 kg, 180-360 kg, 360-1,000 kg or >1,000 kg (see Rodríguez et al., 2012). The biomass made available for secondary consumers by each single primary consumer population was obtained as the sum of the biomass of all dead individuals. Sustainable primary consumers´ biomass output was obtained as the sum of the biomass outputs in each size category from each primary consumer population.

Combining the mortality profiles obtained from the Leslie Matrix with the mean body size per age class and the estimated population density of the species, the sustainable biomass output (total biomass output, TBO) can be computed. A size-specific “wastage factor” is included in the model to account for the fact that a carcass includes a variable amount of non-edible tissues (horns, bones, hide, etc.), which are included in the TBO provided by the model. Thus, this percentage of non-edible biomass is substracted from the TBO to obtain the final amount of biomass available to secondary consumers or the total biomass or total available biomass (TAB), which is also distributed by body mass classes. See Rodríguez-Gómez et al. (2013) for the computational details.

The model yields several population profiles for each species, corresponding to different mortality rates. We selected extreme values with maximum and minimum pressure on sub-adults (or maximum and minimum mortality rates) that produce minimum and maximum TAB levels, respectively (TAB-m and TAB-M, respectively).

The model solutions are not dependent on population size: thus, we need to estimate the population density of each primary consumer species. We used the equation provided by Damuth (1981) for European mixed temperate forest ecosystems for all species included in this study:

$$\log (D) = - 0.79 * \log (m) + 4.33$$

where D is the population density in number of individuals per square kilometer and m is the body mass in grams.

3.1.2 Total demanded biomass (TDB)

Carnivore-demanded resources should be estimated as a first step in evaluating resource distribution among secondary consumers. The secondary consumer intake rate was estimated using the equation reported by Farlow (1976):

$$\log I = (0.69686 \pm 0.01276) \log(m) + 0{,}27747;\ r^2=0.96758;$$
$$F_{1,100}=2{,}984.773;\ p< .01$$

where I is the intake rate in kilocalories per day, and m is the body mass in grams. Some adjustments were made for some secondary consumers according to their inferred dietary preferences based on Rodríguez et al. (2012) and Rodríguez-Gómez et al. (2012) (Table 2). We estimated that large mammal flesh represented 20% of the energetic requirements of *Canis arnensis*, *Canis etruscus*, and *Canis mosbachensis*; 10% for *Lynx pardinus* and *Lynx* sp.; 80% for *Lynx issidorensis*; 98% for *Chasmaporthetes lunensis*, *Crocuta crocuta*, *Crocuta* sp., and *Pachycrocuta brevirostris* (because a 2% of the total requirements could be obtained from bone marrow); 75% for *Hyaena* sp.; 10% for *Ursus arctos*, *Ursus deningeri*, *Ursus dolinensis*, *Ursus etruscus*, *Ursus* sp., and *Ursus thibetanus*; and 1% for *Ursus spelaeus*. The requirements of genus *Homo* were estimated to be similar to those of recent hunter-gatherer populations, with a mean daily requirement of 3,000 kcal per individual (Eaton et al., 1997). The average body mass was considered to be 76 kg, based on pelvis and femur estimates for *Homo heidelbergensis* from the Sima de los Huesos site (Bonmatí and Arsuaga, 2005; Carretero et al., 2002).

The annual energetic requirements of a carnivore population per square kilometer are obtained multiplying the individual annual intake by the population density. The equation provided by Damuth (1993) for African flesh-eaters was used to estimate the typical carnivore density:

$$\log (D) = - 0.64 * \log (m) + 2.23$$

where D is the population density in number of individuals per square kilometre, and m is the body mass in grams. In the case of genus *Ursus*, the equation for carnivores was used instead of the equation for primary consumers because it predicts the population densities of recent bear species more accurately (DeMaster and Stirling, 1981; Larivière, 2001; Pasitschniak-Arts, 1993). The median for recent hunter-gatherers populations was taken as the population density of the genus *Homo* (Table 3).

Table 2. The guild of secondary consumers present in the European assemblages selected for this study (1.1 Ma and 0.2 Ma) with their body mass in kilogram and their requirements in kilocalories per square kilometre per year. Secondary consumers requirements were corrected according to their diet; this correction factor is multiplied by the total requirements for each secondary consumer. Last six columns represent the preference of each secondary consumer species for primary consumers in each size (see text). Preferences are expressed in percentages.

Order	Family	Genus	Species	Body mass (kg)	Requirements (kcal/km^2*year)	Correction factor	1Class	2Class	3Class	4Class	5Class	6Class
Carnivora	Canidae	*Canis*	*arnensis*	16	46,077	0.20	17	17	17	17	17	17
Carnivora	Canidae	*Canis*	*etruscus*	21	46,958	0.20	17	17	17	17	17	17
Carnivora	Canidae	*Canis*	*lupus*	43	246,599	1.00	12	18	29	35	6	0
Carnivora	Canidae	*Canis*	*mosbachensis*	23	47,184	0.20	17	17	17	17	17	17
Carnivora	Canidae	*Cuon*	*alpinus*	18	231,827	1.00	38	31	25	6	0	0
Carnivora	Canidae	*Cuon*	*priscus*	16	229,876	1.00	38	31	25	6	0	0
Carnivora	Canidae	*Cuon*	sp.	15	229,703	1.00	38	31	25	6	0	0
Carnivora	Canidae	*Lycaon*	*lycaonoides*	36	213,223	1.00	13	37	25	25	0	0
Carnivora	Felidae	*Acinonyx*	*pardinensis*	80	223,217	1.00	27	55	18	0	0	0
Carnivora	Felidae	*Homotherium*	*crenatidens*	150	269,229	1.00	0	11	21	26	32	11
Carnivora	Felidae	*Homotherium*	*latidens*	187	273,394	1.00	0	11	21	26	32	11
Carnivora	Felidae	*Homotherium*	sp.	169	271,418	1.00	0	11	21	26	32	11
Carnivora	Felidae	*Lynx*	*issiodorensis*	22	188,440	0.80	60	40	0	0	0	0
Carnivora	Felidae	*Lynx*	*pardinus*	14	22,825	0.10	75	25	0	0	0	0
Carnivora	Felidae	*Lynx*	sp.	18	23,228	0.10	75	25	0	0	0	0
Carnivora	Felidae	*Megantereon*	*cultridens*	63	253,450	1.00	6	19	25	31	19	0
Carnivora	Felidae	*Megantereon*	sp.	59	252,296	1.00	6	19	25	31	19	0
Carnivora	Felidae	*Megantereon*	*whitei*	56	251,256	1.00	6	19	25	31	19	0
Carnivora	Felidae	*Panthera*	*gombaszoegensis*	105	262,626	1.00	11	11	33	22	22	0
Carnivora	Felidae	*Panthera*	*leo*	170	271,586	1.00	14	29	24	19	10	5
Carnivora	Felidae	*Panthera*	*pardus*	63	253,310	1.00	55	27	18	0	0	0
Carnivora	Felidae	*Puma*	*pardoides*	38	213,880	1.00	38	31	25	6	0	0
Carnivora	Hyaenidae	*Chasmaporthetes*	*lunensis*	76	251,647	0.98	17	33	28	22	0	0
Carnivora	Hyaenidae	*Crocuta*	*crocuta*	65	248,922	0.98	15	30	25	15	10	5
Carnivora	Hyaenidae	*Crocuta*	sp.	64	248,654	0.98	15	30	25	15	10	5
Carnivora	Hyaenidae	*Hyaena*	sp.	44	161,752	0.75	17	17	17	17	17	17
Carnivora	Hyaenidae	*Pachycrocuta*	*brevirostris*	73	250,822	0.98	17	17	17	17	17	17
Carnivora	Hyaenidae	*Pliocrocuta*	*perrieri*	50	249,405	1.00	17	17	17	17	17	17
Carnivora	Ursidae	*Ursus*	*arctos*	260	27,974	0.10	17	17	17	17	17	17
Carnivora	Ursidae	*Ursus*	*deningeri*	475	29,173	0.10	17	17	17	17	17	17
Carnivora	Ursidae	*Ursus*	*dolinensis*	300	28,254	0.10	17	17	17	17	17	17
Carnivora	Ursidae	*Ursus*	*etruscus*	230	27,736	0.10	17	17	17	17	17	17
Carnivora	Ursidae	*Ursus*	sp.	203	27,496	0.10	17	17	17	17	17	17
Carnivora	Ursidae	*Ursus*	*spelaeus*	600	2965	0.01	17	17	17	17	17	17
Carnivora	Ursidae	*Ursus*	*thibetanus*	128	26,620	0.10	17	17	17	17	17	17
Primate	Hominidae	*Homo*	*antecessor*	76	108,405	0.45	24	29	19	14	10	5
Primate	Hominidae	*Homo*	*heidelbergensis*	76	108,405	0.45	24	29	19	14	10	5
Primate	Hominidae	*Homo*	sp.	76	108,405	0.45	24	29	19	14	10	5

Table 3. Population densities and food resource use observed in recent hunter-gatherer populations (Binford, 2001).

Group	Area	Density ind./ km^2	Gathering %	Hunting %	Fishing %
Punan	29.6	0.118	65.00	30	5
Siberian Eskimo	274.9	0.047	1.00	30	60
Guayaki-Ache	28.7	0.0348	30.00	62	10
Efe	47.0	0.1596	88.20	11	0,8
Hadza	25.0	0.240	60.00	40	0
!Kung	110.0	0.066	67.00	33	0
G/Wi	180.0	0.0293	55.00	45	0
Mardudjara	226.0	0.0075	70.00	30	0
Kiowa	280.0	0.014	20.00	80	0
Caribou Inuit	2365.0	0.003	0.10	55	44.9
Nunamiut Inuit	249.0	0.0096	0.10	89	10.9
Polar Inuit	731.0	0.0041	0.01	30	69.99

As in the case of TAB, TDB was distributed over the same six body size categories based on the inferred prey size preferences of each predator and based on the behaviour of their living relatives (Table 2) (Rodríguez et al., 2012). The preference of a predator for a body size category is represented by the percentage of predation (PD) that this size category was presumed to represent in its diet. If a predator was presumed to be unable to kill prey in a given size category and to not consume carrion, a PD of 0 was assigned to the predator in that size categories.

3.1.3 Distribution of TAB among secondary consumers

The distribution of TAB among secondary consumers is based on the proportional predation pressure (PPP_{ij}) of each species in each body size category. PPP_{ij} represents the relative amount of biomass demanded by the j^{th} secondary consumer species from the i^{th} primary consumer body size category and is calculated as the proportion of the total amount of biomass demanded from a prey body size category by all carnivores that corresponds to the requirements of a single carnivore species. PPP_{ij} incorporates intraguild competition in the model. See a detailed formal description of resource distribution computation in Rodríguez-Gómez et al. (2013).

3.2.- Analytic methods

To compare the different intervals considered in our analysis, we generated two indexes that relate the estimated and expected densities of secondary consumers.

Species competition index (SCI):

$$SCI_j = 1- (Ds_j / Dx_j) \qquad (1)$$

where Dx_j is the expected density for species j obtained from the allometric equation in Damuth (1993). Ds_j is the estimated density for species j and is obtained from our model. We obtain SCIs with TAB-m and TAB-M. The SCI index shows to what degree a species fulfils its requirements in a given environment.

Global competition index (GCI):

$$GCI = 1 - \left(\sum_{j=1}^{n} Ds_j \Big/ \sum_{j=1}^{n} Dx_j \right) \qquad (2)$$

Both indexes estimate to what degree secondary consumers satisfy their requirements according to their population densities. The SCI index shows to what degree a species fulfils its requirements in a given environment. GCI is similar to SCI, but its scale is at the level of the secondary consumers guild. We obtain a GCI for TAB-m and for TAB-M, GCI-m and GCI-M respectively.

Moreover, we also consider an index (GCIB) that relates the estimated and expect biomasses of secondary consumer species and provides information about the amount of secondary consumers in different palaeoecosystems.

Global competition index biomass (GCIB):

$$GCIB = 1 - \left(\sum_{j=1}^{n} Ds_j * W_j \Big/ \sum_{j=1}^{n} Dx_j * W_j \right) \qquad (3)$$

where W_j is the body mass of the j^{th} species. These indexes provide information about competition intensity in the ecosystem with regard to an ideal condition in which all species reach optimal densities. The closer the value of either index is to 1, the higher the competition among secondary consumers. Index values close to 0 indicate low competition. We obtained a GCIB for TAB-m and other for TAB-M, GCIB-m and GCIB-M respectively.

Finally, we also compute the ratio of primary consumer biomass/ secondary consumer biomass because it has been previously used by several authors (e.g. Meloro and Clauss, 2012; Palombo, 2010; Rodríguez-Gómez et al., 2012; Rodríguez et al., 2012). The ratio of primary consumer biomass to secondary consumer biomass (pB/PB) is based on population biomass (or standing crop), not the biomass output. The prey biomass (pB) is computed for *p* primary consumers (*p* varies from one local faunal assemblage (LFA) to another) and is distributed in the six body size categories (see above). The percentage of individuals (*PI*) of the i^{th} primary consumer species in the k^{th} body size category is represented as PI_{ki}. Vectorial notation can be used for simplification:

$$PI = \begin{bmatrix} PI_{11} & \cdots & PI_{1p} \\ \vdots & \ddots & \vdots \\ PI_{61} & \cdots & PI_{6p} \end{bmatrix}$$

Similarly to what was done with the for mortality profiles, we selected the extreme values of *PI*, corresponding to maximum and minimum pressure on sub-adults (or maximum and minimum mortality rates), that produce minimum and maximum population profiles referred to here as *PI*-m and *PI*-M, respectively.

PIki should be multiplied by the expected density (*Dxi*) to obtain the total number of individuals of the *i*th specie in the *k*th category. Dx_i is the expected density for primary consumer species *i* obtained from allometric equation by Damuth (1981). To obtain the biomass of the *i*th specie in the *k*th category (*pBki*), it is also necessary to multiply by the body mass of this specie in the *k*th category.

$$pB_{ki} = PI_{ki} * W_{ki} * Dx_i \text{ for } k = 1,\ldots, 6,\ i = 1,\ldots, p$$

The total biomass of all primary consumers present in each LFA may be obtained as:

$$pB = \sum_{k=1}^{6}\sum_{i=1}^{p} PI_{ki} \cdot W_{ki} \cdot D_{xi}$$

Thus, the ratio of primary consumer biomass to secondary consumer biomass (pB/PB) could be represented by the next equation:

$$\frac{pB}{PB} = \frac{pB}{\sum_{j=1}^{n}(Ds_j * W_j)} \qquad (4)$$

where the indexes to estimate secondary consumer biomass (Ds_j and W_j) are the same as before. The numerator represents the on-crop biomass of the paleoecosystem. The denominator is the sum of the estimated population density (Ds_j) of each secondary consumer multiplied by its body mass (W_j). We obtain two values of pB/PB for each LFA, one for *PI*-m (pB/PB-m) and other for *PI*-M (pB/PB-M).

To compare competition intensity in different time intervals, we used the non-parametric Mann-Whitney´s U test to detect differences in the median value of these four indexes. Similarly, Mann-Whitney´s U test was also used to test for differences in TAB and the TDB between time intervals.

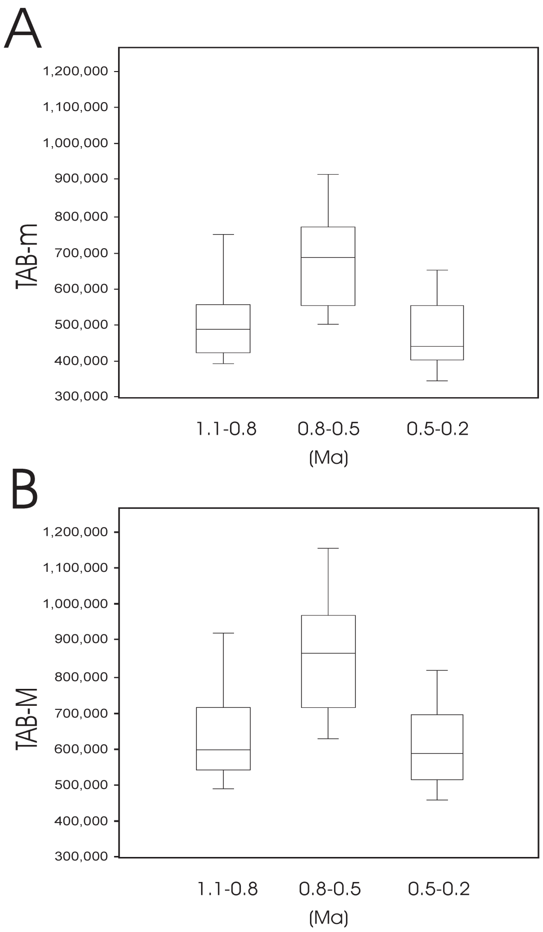

Figure 2. Boxplot representation of Total Available Biomass (TAB) values for the three intervals of this study, 1.1-0.8 Ma (Interval 1), 0.8-0.5 Ma (Interval 2) and 0.5-0.2 Ma (Interval 3) in kcal/km^2*year, in two scenarios: with minimum (A) and maximum (B) TAB in all assemblages.

4.- Results

We obtain minimum and maximum TAB in the three intervals of this study, the predator requirements in ideal conditions or expected requirements (TDB), and the TAB distribution among secondary consumers for each LFA. According to our results, the TAB was higher, on average, in the LFAs from the interval 0.8-0.5 Ma (Interval 2) than it was before or after this period, whether considering TAB-m or TAB-M (Figure 2 and Table 5). These differences are statistically significant (Table 6).

A gradual tendency towards a reduction in the requirements of secondary consumers (TDB) from the interval 1.1-0.8 Ma (1,086,000 kcal/km^2*year) to the intervals 0.8-0.5 Ma (860,000 kcal/km^2*year) and 0.5-0.2 Ma (640,000 kcal/km^2*year) is apparent (Table 5 and Figure 3), although the differences are not statistically significant (Table 6). This might be explained by a decrease in the number of secondary consumers and/or a change in the secondary consumer guild with the appearance of species with smaller meat requirements. The three intervals show a similar absolute minimum value of TDB approximately 350,000 kcal/km^2*year (Table 4). This is likely an artefact of our method because we selected sites with a minimum number of secondary consumers species. This tendency is not observed for the maximum values of TDB; the Interval 2 has a lower maximum TDB than the first and third intervals.

Concerning the competition indexes, GCI was significantly higher in the 1.1-0.8 Ma period than in the two younger intervals (Tables 5

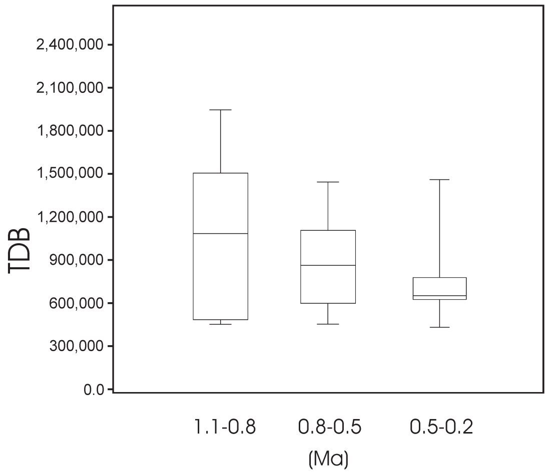

Figure 3. Boxplot representation of Total Demanded Biomass (TDB) values for the three intervals of this study, 1.1-0.8 Ma (Interval 1), 0.8-0.5 Ma (Interval 2) and 0.5-0.2 Ma (Interval 3) in kcal/km^2*year.

Table 4. Values for different parameters from each faunal assemblage are estimated by the model. TAB-m: Minimum Total Available Biomass; TAB-M: Maximum Total Available Biomass; TDB: Total Demanded Biomass; GCI-m: Global Competition Index with minimum TAB; GCI-M: Global Competition Index with maximumTAB; GCIB-m: Biomass Global Competition Index for minimum TAB; GCIB-M: Biomass Global Competition Index for maximum TAB; pB/PB-m: ratio primary consumer biomass to secondary consumer biomass for minimum primary consumer biomass; pB/PB-M: ratio primary consumer biomass to secondary consumer biomass for maximum primary consumer biomass.

Faunal assemblages	TAB-m	TAB-M	TDB	GCI-m	GCI-M	GCIB-m	GCIB-M	pB/PB-m	pB/P-M
1.1-0.8 Ma. Interval 1									
Apollonia-1	548,298	715,763	485,773	0.23	0.29	0.20	0.25	302,048	315,004
Ata TD3-TD4	421,849	541,234	718,619	0.33	0.20	0.38	0.22	82,389	65,180
Ata TD6 1-2	487,612	596,629	455,993	0.00	0.00	0.00	0.00	74,538	74,780
Grotte du Vallonnet III	556,339	714,509	1,361,650	0.58	0.46	0.58	0.43	137,122	100,225
Kozarnika 12	391,803	488,212	1,504,834	0.74	0.69	0.73	0.65	149,400	113,356
Kozarnika 13	494,417	644,977	1,085,962	0.55	0.43	0.55	0.41	162,247	122,334
Untermassfeld N/A	751,117	920,475	1,950,235	0.56	0.49	0.61	0.51	149,938	119,679
Vallparadís Lower Unit	461,886	596,316	980,097	0.52	0.40	0.49	0.31	160,983	117,323
Vallparadís Middle Unit	461,886	596,316	1,313,752	0.65	0.55	0.62	0.48	153,549	111,042
0.8-0.5 Ma. Interval 2									
Ata TD8	501,915	627,928	771,209	0.26	0.16	0.32	0.17	111,573	90,273
Isernia La Pineta	553,723	715,142	455,240	0.07	0.00	0.02	0.00	99,754	96,365
Mauer N/A	632,850	774,520	1,445,539	0.55	0.45	0.56	0.44	120,602	94,218
Pakefield/Kessingland - Rootlet bed	772,387	970,064	875,512	0.11	0.00	0.12	0.00	171,428	150,081
Slivia N/A	688,247	866,598	862,091	0.17	0.00	0.19	0.00	169,350	136,231
Sussenborn - Hauptfauna	917,900	1,157,041	1,110,145	0.14	0.00	0.16	0.01	124,753	104,702
Voigtstedt - Lehmzone	710,431	881,349	603,060	0.00	0.00	0.00	0.00	110,749	110,338
0.5-0.2 Ma. Interval 3									
Ata TD10-1	393,060	516,352	677,314	0.30	0.22	0.36	0.21	98,453	80,280
Ata GIIb	441,228	587,534	634,642	0.34	0.26	0.28	0.11	143,941	114,136
Ata GIII	442,943	589,653	663,815	0.36	0.26	0.28	0.08	94,863	73,282
Biache-Saint-Vaast - Dépôts fluviatiles	546,823	684,058	683,736	0.19	0.02	0.15	0.01	90,119	76,455
Bilzingsleben II	555,363	668,580	654,086	0.14	0.02	0.13	0.01	111,889	99,181
Casal de´Pazzi - N/A	428,832	549,082	541,598	0.16	0.04	0.18	0.05	229,854	194,153
Cueva del Congosto - A1	624,556	769,347	884,809	0.22	0.09	0.28	0.13	83,287	68,663
Fontana Acetosa - N/A	413,039	550,840	623,888	0.31	0.09	0.32	0.10	143,993	107,542
Grotta Lina - N/A	416,123	519,267	1,051,356	0.59	0.49	0.53	0.42	102,487	82,238
Grotte du Lazaret - CII inf	531,526	704,017	662,078	0.21	0.14	0.10	0.06	90,403	86,172
Heppenloch N/A	562,909	693,979	780,950	0.26	0.14	0.21	0.05	93,042	76,524
Hundsheim N/A	404,585	509,193	1,466,469	0.72	0.65	0.71	0.62	156,462	117,154
Orgnac-3 6	476,600	596,319	575,493	0.10	0.00	0.15	0.00	70,964	60,199
Payre - F	652,355	815,582	1,052,429	0.32	0.23	0.29	0.14	107,663	88,020
Quisana-Certosa N/A	395,647	504,747	552,381	0.17	0.14	0.14	0.12	127,878	122,058
Riparo di Visogliano - Lower levels	383,655	464,105	433,684	0.11	0.00	0.11	0.00	60,331	53,318
Swanscombe - Lower loam	645,489	799,123	629,555	0.00	0.00	0.00	0.00	105,966	104,868
Wannenköpfe - Wa1-Wa3	345,590	459,996	629,555	0.43	0.26	0.38	0.21	118,914	93,702

Table 5. Median values of different parameters (see table 4) for the three time intervals considered in this study: 1 (1.1-0.8 Ma); 2 (0.8-0.5 Ma); 3 (0.5-0.2 Ma) with all faunal assemblages (Total), for faunal assemblages with human presence (With *Homo*) and for faunal assemblages without human presence (Without *Homo*).

Scenario	Parameter	1	2	3
Total	TAB-m	487,612	688,247	441,228
Total	TAB-M	596,629	866,598	587,534
Total	TDB	1,085,962	862,091	644,364
Total	GCI-m	0.55	0.14	0.24
Total	GCI-M	0.43	0.00	0.14
Total	GCIB-m	0.55	0.16	0.25
Total	GCIB-M	0.41	0.00	0.10
Total	pB/PB-m	149,938	120,602	106,814
Total	pB/PB-M	113,356	104,702	90,861
With *Homo*	TAB-m	487,612	632,850	486,377
With *Homo*	TAB-M	596,629	774,520	628,057
With *Homo*	TDB	1,085,962	875,512	644,364
With *Homo*	GCI-m	0.55	0.11	0.21
With *Homo*	GCI-M	0.43	0.00	0.12
With *Homo*	GCIB-m	0.55	0.12	0.22
With *Homo*	GCIB-M	0.41	0.00	0.09
With *Homo*	pB/PB-m	137,122	120,602	102,209
With *Homo*	pB/PB-M	100,245	96,365	89,937
Without *Homo*	TAB-m	505,092	699,339	422,478
Without *Homo*	TAB-M	656,039	873,974	549,961
Without *Homo*	TDB	1,242,465	816,650	702,419
Without *Homo*	GCI-m	0.54	0.15	0.29
Without *Homo*	GCI-M	0.44	0.00	0.14
Without *Homo*	GCIB-m	0.55	0.18	0.25
Without *Homo*	GCIB-M	0.41	0.01	0.11
Without *Homo*	pB/PB-m	155,461	118,163	117,771
Without *Homo*	pB/PB-M	118,501	107,520	97,781

and 6), both with TAB-m (Figure 4A) and with TAB-M (Figure 4B). Differences in GCI between the second and third intervals are not significant (Table 6). Similarly, GCIB was not significantly different in the second and third time intervals, but it was significantly higher in the LFAs from the 1.1-0.8 Ma interval (Figure 5A and 5B and Table 6). Thus, competition intensity between secondary consumer species to access meat resources was higher in the late Early Pleistocene than in the Middle Pleistocene, but it was similar in the 0.8-0.5 Ma and 0.5-0.2 Ma time intervals. The three intervals include some LFAs with very low competition intensity with the same absolute minimum value (0.0). Intervals 1 and 3 show LFAs with absolute maximum values higher than the second interval. In summary, the same pattern in GCI and GCIB along the three time intervals is observed for TAB-m and for TAB-M, although, as may be expected, with less competition when resources are more abundant (TAB-M).

The primary consumer biomass/secondary consumer biomass ratio (pB/PB) for *PI*-m (Figure 6A) shows a tendency to decrease along the Pleistocene (Table 5), although the differences are not significant (Table 6). With *PI*-M, the median values of pB/PB show the same pattern, but the differences are even smaller (Tables 5 and 6).

Considering the 34 LFAs selected for our study, *Homo* was present in 56% of them in the 1.1-0.8 Ma interval, in 42% of them from the 0.8-0.5 Ma interval and in 56% of them from the third interval. These values show a moderate reduction of *Homo* presence in Europe in the second interval. We explore the relationship between the presence of *Homo* in an LFA and the values of the competition indexes GCI and GCIB in the three time intervals in Figure 7 and Figure 8. The GCI and GCIB indexes both show a wide variation in the three intervals when all sites are considered, although the variation is smaller in the second interval. There are not significant differences in GCI or GCIB between the three intervals in the faunal assemblages with human presence. It is apparent, however, that the presence of *Homo* is not recorded in LFAs with a GCI higher than 0.65 in any time interval (Figure 7). Indexes for LFAs with human presence were similar in the three intervals. LFAs without *Homo* show values of GCI higher than 0.65 both in the Interval 1 and the Interval 3. In this subset, namely, LFAs without *Homo*, there are significant differences in GCI and GCIB with TAB-M between the first and second intervals, but there are not differences between the second and the third intervals.

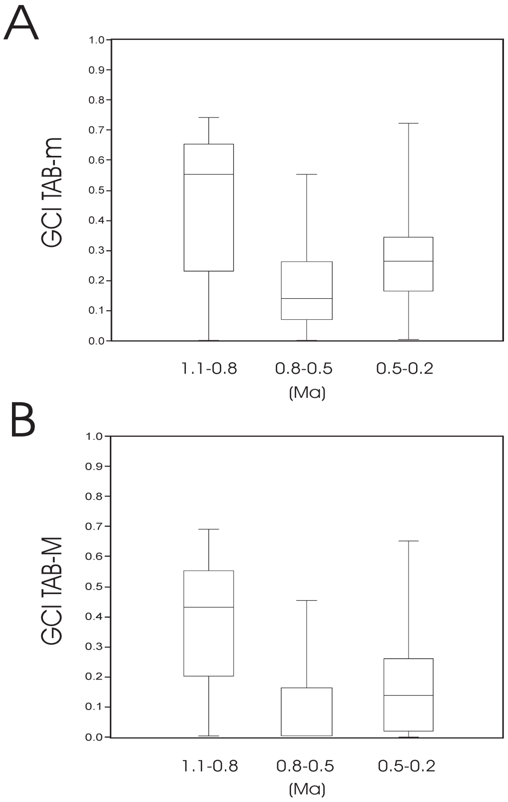

Figure 4. Boxplot representation of Global Competition Index (GCI) values for the three intervals of this study, 1.1-0.8 Ma (Interval 1), 0.8-0.5 Ma (Interval 2) and 0.5-0.2 Ma (Interval 3), in two scenarios: with minimum (A) and maximum (B) TAB in all assemblages. GCI takes the value is 0 when there are not competition between secondary consumers because all species reach their requirements. When GCI is 1, competition between secondary consumers species is highest.

5.- Discussion

Our results do not support the hypothesis that competition among secondary consumers was higher in the time interval between 0.8 to 0.5 Ma (Interval 2) than in the former (1.1-0.8 Ma) and later (0.5-0.2 Ma) intervals. On the one hand, the TAB (TAB-m and TAB-M) was higher in Interval 2 than in the other two intervals, and thus, there was more biomass available to secondary consumers. In contrast, the trophic requirements of secondary consumers (TDB) decreased trough time, being highest during the 1.1-0.8 Ma interval, although the differences are not statistically significant. On the other hand, the competition intensity is highest in the first interval and lowest in the second interval. The amplitude of the competition intensity could be a reflection of the diversity of palaeocommunity structures, and it is moderately higher in

Table 6. Exact p-values from U Mann-Whitney test of different parameters (see table 4) for the three time intervals of this study: 1 (1.1-0.8 Ma); 2 (0.8-0.5 Ma); 3 (0.5-0.2 Ma). These time intervals are compared two by two with this statistical test, i.e. 1-2 column corresponds to the comparison of a parameter of the first time interval with the second time interval. The p-values in bold show significant differences: *, p<0.05; **, p<0.01; ***, p<0.005.

Scenario	Parameter	1-2	1-3	2-3
Total	TAB-m	**8 (p=0.01093)***	66 (p=0.456)	**14 (p=0.001802)*****
Total	TAB-M	**9 (p=0.01565)***	64 (p=0.3966)	**12 (p=0.001024)*****
Total	TDB	23 (p=0.4079)	45 (p=0.06544)	46 (p=0.3198)
Total	GCI-m	**11 (p=0.02885)***	**40.5 (p=0.03618)***	38.5 (p=0.1448)
Total	GCI-M	**8.5 (p=0.0111)***	**34 (p=0.01371)***	34.5 (p=0.08149)
Total	GCIB-m	**11.5 (p=0.03199)***	**36 (p=0.01905)***	50 (p=0.4486)
Total	GCIB-M	**10 (p=0.02072)***	**27.5 (p=0.004446)*****	41 (p=0.1874)
Total	pB/PB-m	26 (p=0.6065)	44 (p=0.0595)	36 (p=0.1101)
Total	pB/PB-M	28 (p=0.7577)	49 (p=0.1061)	34 (p=0.08461)
With *Homo*	TAB-m	1 (p=0.07143)	24 (p=0.953)	4 (p=0.07692)
With *Homo*	TAB-M	**0 (p=0.03571)***	24 (p=0.953)	**3 (p=0.04895)***
With *Homo*	TDB	7 (p=1)	10 (p=0.07093)	10 (p=0.4476)
With *Homo*	GCI-m	4.5 (p=0.4643)	12.5 (p=0.1352)	12.5 (p=0.7168)
With *Homo*	GCI-M	4 (p=0.375)	13 (p=0.1542)	12 (p=0.6469)
With *Homo*	GCIB-m	5 (p=0.5714)	10 (p=0.0686)	14 (p=0.9406)
With *Homo*	GCIB-M	5 (p=0.5536)	9 (p=0.05062)	12 (p=0.6818)
With *Homo*	pB/PB-m	6 (p=0.7857)	19 (p=0.5135)	5 (p=0.1119)
With *Homo*	pB/PB-M	6 (p=0.7857)	19 (p=0.5135)	6 (p=0.1608)
Without *Homo*	TAB-m	4 (p=0.3429)	13 (p=0.6828)	**2 (p=0.01616)***
Without *Homo*	TAB-M	4 (p=0.3429)	12 (p=0.5697)	**2 (p=0.01616)***
Without *Homo*	TDB	5 (p=0.4857)	11 (p=0.4606)	13 (p=0.6828)
Without *Homo*	GCI-m	1 (p=0.05714)	9 (p=0.2828)	7 (p=0.1455)
Without *Homo*	GCI-M	**0 (p=0.02857)***	5.5 (p=0.08485)	6.5 (p=0.1152)
Without *Homo*	GCIB-m	1 (p=0.05714)	8 (p=0.2141)	10.5 (p=0.3899)
Without *Homo*	GCIB-M	**0 (p=0.02857)***	5 (p=0.06869)	8 (p=0.1899)
Without *Homo*	pB/PB-m	3 (p=0.2)	5 (p=0.07273)	13 (p=0.6828)
Without *Homo*	pB/PB-M	3 (p=0.2)	7 (p=0.1535)	12 (p=0.5697)

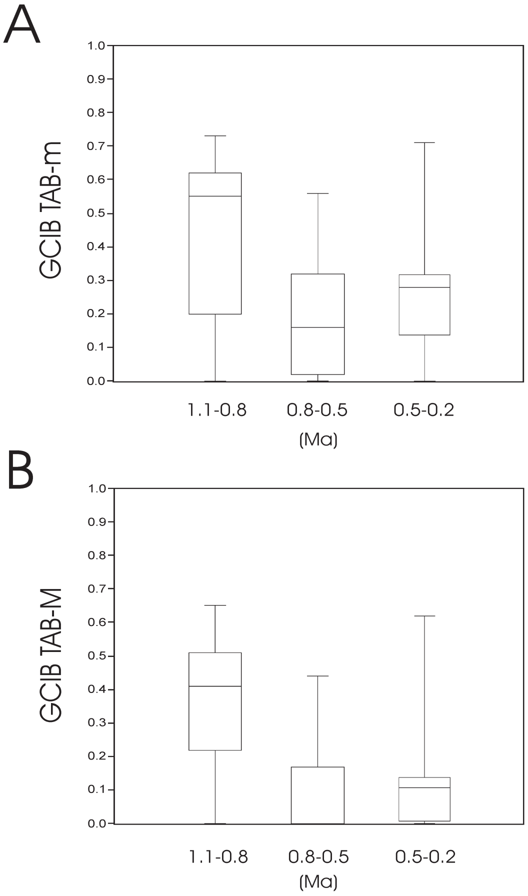

Figure 5. Boxplot representation of Global Competition Index Biomass (GCIB) values to three intervals of this study, 1.1-0.8 Ma (Interval 1), 0.8-0.5 Ma (Interval 2) and 0.5-0.2 Ma (Interval 3), in two scenarios, with minimum (A) and maximum (B) TAB in all assemblages. GCIB is equal to 0 when competition intensity is lowest and it is 1 when competition is highest.

the first than in the other two intervals. The second interval shows the lowest diversity of palaeocommunities, and it could be considered more homogeneous ecologically. The competition intensity in the secondary consumers guild during the late Early Pleistocene and the Middle Pleistocene seem to be characteristic of each period. Therefore, each time interval could have its own properties from the point of view of competition and ecological interactions.

Homo was only present in LFAs in which the secondary consumers satisfied at least half their requirements (GCI and GCIB less than 0.65). There was not faunal assemblages with competition intensity indexes (GCI and GCIB) higher than 0.65 and human presence. This threshold is represented by the Middle Unit from the Vallparadís site (Spain), although true human presence in this LFA is controversial (Garcia et al., 2013; Martínez et al., 2010) (but see Madurell-Malapeira et al., 2012). If the Middle Unit from Vallparadís is not considered, the threshold value for human presence would be GCI= 0.58, as in the level III from Grotte du Vallonnet (France). However, *Homo* was present in LFAs from the three time intervals, and our results suggest that there were not significant differences in competition intensity among LFAs with human presence from different time intervals. Therefore, human populations occurred in places under similar conditions during these periods.

On the other hand, in sites without human presence, competition indexes (GCI and GCIB) show significant differences between the first and second intervals considering the TAB-M, with dipolar scenarios: the first interval with very high competition intensity and the second interval with low competition intensity (Table 5 and Figure 7 and 8). With TAB-m, the differences between the two intervals are closer to being significant. Our results show that the first interval has a tendency towards high competition, and second and third intervals show a

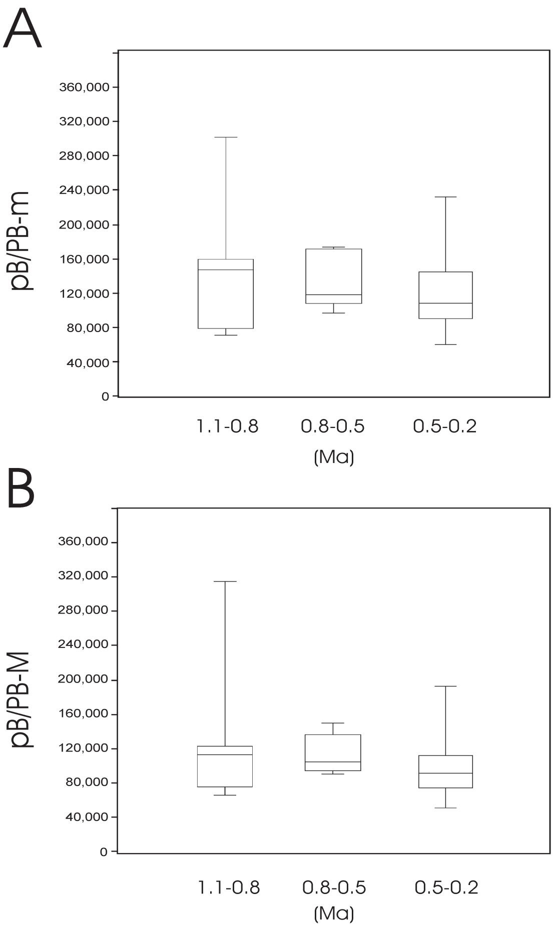

Figure 6. Boxplot representation of the ratio Primary consumer Biomass to Secondary Consumers Biomass (pB/PB) values for the three intervals of this study, 1.1-0.8 Ma (Interval 1), 0.8-0.5 Ma (Interval 2) and 0.5-0.2 Ma (Interval 3), in two scenarios: minimum biomass (A) and maximum biomass (B) in all assemblages. pB/PB is equal to 0 when competition intensity is lowest and 1 it is when competition is highest.

tendency towards lower competition (Figure 7 and 8). According to these results, we could consider *Homo* to be present in the three intervals only in ecosystems with moderate competition intensity, below a similar competition threshold, but it was not present in extreme conditions. Thus, *Homo* was able to successfully compete with other secondary consumers but in communities where competition was extremely high, exhibiting a remarkable adaptation capacity that was similar in the three studied periods. Extreme conditions would be represented by only two sites, one from the Early Pleistocene and the other one from the late Middle Pleistocene, namely, Kozarnika 12 from Bulgaria and Hundsheim from Germany. The latter site was excavated at the beginning of the twentieth century, and it no longer exists (Frank and Rabeder, 1998). It is a very rich assemblage with omnivorous, scavengers, and hypercarnivorous canids, felids, hyaenid and ursids. The probability exists that this assemblage was affected by the time-averaging phenomenon. In our sample, Hundsheim appears as an outsider for its time interval when considering competition intensity. If Hundsheim was removed from the sample, there would be no Middle Pleistocene site with a competition intensity comparable to the late Early Pleistocene sites. This could support an opposite tendency for the Early and Middle Pleistocene LFAs.

According to the pB/PB ratio, significant differences between intervals are not observed for any scenario (Total, *Homo* and Without *Homo*). This shows the low resolution of this index in comparison to the competition indexes, although it provides information on the proportion of primary to secondary consumers. A higher secondary consumer biomass per primary consumer biomass is indicated by a high pB/PB ratio. Note that this type of index considers the total biomass in the primary consumers guild, not the total available biomass to secondary consumers. Because the relationship between the population biomass and the available biomass is not necessarily direct, the pB/PB ratio should be analyzed with caution. According to our results, conditions were better for primary consumers in the third interval (0.5-0.2 Ma) because it has the lowest median value for the pB/PB ratio, whilst the first interval shows the highest value. However, we should take into account that some factors may distort the pB/PB ratio. The secondary consumer diet is one example. Some secondary consumer species (hypercarnivorous and strict scavengers) obtain all their trophic resources from species in our model, but other species fulfil only a part of their trophic requirements with large mammals and complete them with other resources, e.g., the lynx. These latter species increase the biomass of secondary consumers, although they partially rely on food resources others than large mammals, decreasing the ratio pB/PB and giving a wrong impression of the paleoecosystem performance. Another factor to be taken into account is the feed habits and killing capacities of the secondary consumers in relation to different body size categories of primary consumers. If a species cannot prey on a body size category, and there is available biomass remaining in that category, we obtain a ratio pB/PB higher than expected. This was likely the case in many Galerian communities because it is well known that herbivores increased in size during this period, and a significant number of primary consumer species were free, or almost free, of predators (Croitor and Brugal, 2010; Meloro and Clauss, 2012; Rodríguez et al., 2012). Another important factor is that the densities used in this type of study are considered maximum ecological densities. We use these densities in the model to obtain the threshold population biomass of secondary consumers. If all secondary consumers fulfil their requirements with *PI*-m, the ratio pB/PB will be necessarily higher with *PI*-M because the numerator increases but the denominator is kept constant. In our opinion, the complexity of this type of index invites a search for a simpler and more direct option. A ratio TAB/PB could provide a more reliable measure of the conditions for secondary consumers. Thus, the ratio pB/PB is not a good index to evaluate resources in LFAs.

In light of the results presented here, the discontinuity in the human occupation of Europe observed by Mosquera et al. (2013) on the basis of the scarcity of evidences of occupation and the apparent gap between the Mode 1 and Mode 2 technocomplexes in Europe cannot be explained by a higher competition in the palaeocommunities from 0.8 to 0.5 Ma. Moreover, when we take total LFAs initially considered (93 LFAs), including LFAs that did not meet the selection criteria (see Methods), 31 out of the 93 LFAs belong to the first interval, 12 to the second interval and 56 to the third interval. Evidence of human presence is recorded in this sample in 26% of the LFAs from the first interval, 25% of the LFAs from the second interval and 56% of the LFAs from the third interval. Thus, the relative frequency of human presence in LFAs is similar in the 1.1-0.8 MA and in the 0.8-0.5 Ma intervals, but the number of sites is markedly lower in Interval 2, being less than half in

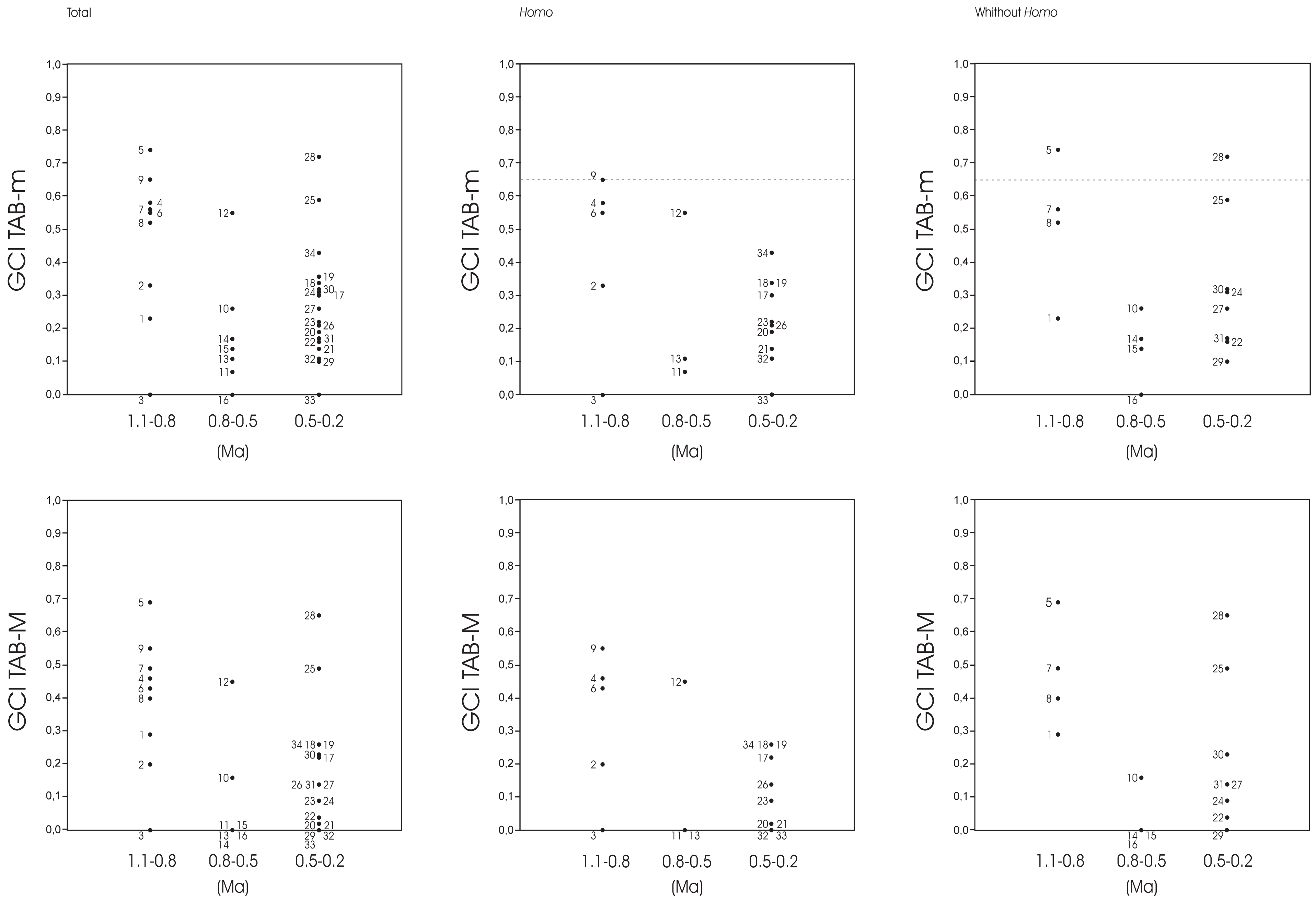

Figure 7. Graphical distribution of Global Competition Index (GCI) values in each LFA for the three intervals of this study, 1.1-0.8 Ma (Interval 1), 0.8-0.5 Ma (Interval 2) and 0.5-0.2 Ma (Interval 3), in two scenarios, with minimum (top) and maximum (bottom) TAB in all assemblages. First column (Total) contains all assemblages, second column (*Homo*) includes assemblages with evidence of *Homo* presence and third column (Without *Homo*) includes assemblage without evidence of *Homo* presence. GCI equal to 0 is the lowest competition intensity and 1 is the highest. Locality Codes (LC) used in the Table 1.

Interval 1. These figures show a reduction in the number of sites in the early Middle Pleistocene but not a reduction of human presence. This decrease may cause an underrepresentation of human occurrence in this periods (Rodríguez et al., In Press) and lead to misinterpretations.

A priori, both the local extinction and/or the demographic decrease of Middle Pleistocene humans may be caused by adverse conditions. Several theoretical scenarios may explain the observed pattern as it is discussed in Rodríguez-Gómez et al. (2014b). The first scenario is a discontinuity of human populations during the Early and Middle Pleistocene transition, which implies that Europe was uninhabited during this period. In the second scenario, a human population inhabited Europe continuously during the Early and Middle Pleistocene transition but with a severe contraction in population size during the 0.8-0.5 Ma interval and a retreat to some environmental refuges. Finally, a third possible scenario depicts human populations surviving in some refuges, but they were eventually substituted by a different human species arriving in Europe at approximately 0.5 Ma with a new technology. From a palaeocological point of view focused on macromammals and resource availability, two scenarios might explain human local extinction and/or demographic decrease by adverse conditions. In the first one, the competition among secondary consumers reached a high level in the 0.8-0.5 Ma interval across Europe. The human populations were unable to address this competition, and they became extinct. However, according to the results presented here, competition intensity was lower during the Middle Pleistocene than in the late Early Pleistocene, except for Hundsheim. Alternatively, changes in the configuration of palaeocommunities displaced human populations from many faunal assemblages, but they were able to survive in areas where the structure of the mammalian communities allowed them to successfully compete for resources.

With respect to changes in community configuration or food web structure, the limit between the first and second interval at 0.8 Ma roughly coincides with Matuyama-Brunhes boundary and the Mid-Pleistocene Revolution (Maslin and Ridgwell, 2005). Carrión et al. (2011) suggest a cyclic replacement of forested landscapes by open landscapes between 0.9 and 0.4 Ma coincident with the changes in climatic periodicity from 41 ka to 100 ka cycles. A faunal turnover also occurred in Europe at this time with the appearance of new carnivores and increased herbivore richness that modified the structure of mammalian communities (Palombo, 2007; Palombo, 2010; Palombo, 2013; Palombo, 2014; Rodríguez et al., 2012; Turner, 1992). Palombo (2013) concludes in her study that each mammal species varied its distribution and abundance according to its own environmental tolerances and ecological flexibility, each species could differ in the factors that trigged its dispersal. According to the results presented here, this turnover produced conditions more favourable to *Homo* from the point of view of meat resources, with a lower competition intensity and a better access to carcasses than in the former period. Surprisingly, these improved environmental conditions did not coincide with an increased presence of *Homo*. Human populations only increased and expanded much later, at approximately 0.5 Ma. It is also conceivable that other aspects of the human-fauna interactions not included in our analyses were limiting the viability of human population in this period.

A high biodiversity with many complex ecological interactions induces speciation, reduces extinction rates and may facilitate the support of biodiversity in an ecosystem (Bascompte et al., 2006; Ricklefs, 2010). The number of secondary consumer species was higher in the late Early Pleistocene than in the Middle Pleistocene, and perhaps this higher biodiversity induced specialization, made palaeocommunities more stable and allowed them to support higher levels of competition intensity. In contrast, the faunal turnover associated to the MPR induced the breakup of the existing relationships and perhaps made it more difficult for secondary consumers to enter in a Galerian paleocommunity and survive there. Moreover, the Galerian secondary consumers were more generalist than the Epivilllafranchian species (Croitor and Brugal, 2010), making their niches more prone to overlap and promoting territorial competition and spatial exclusion, as has been observed for recent cheetahs and wild dogs (Laurenson et al., 1995; Mills and Gorman, 1997). In any case, human populations overcame these difficulties between 0.5 and 0.2 Ma when they increased in numbers. Niche overlapping may be analyzed looking at the species that co-occur with *Homo* in the LFAs. Only six species did not show co-occurrences with *Homo* at any LFAs, but if analyzed at the genus scale, *Homo* coincided with all genuses (see Supplementary Material, Table S2) in at least one LFA. For this reason, we assume that the human niche did not overlap completely with any other genus. The flexibility and diversity of the human diet (omnivorous, scavenger and hypercarnivorous) and the lack of exclusion with other secondary consumers hampers a better knowledge of the role played by humans in these palaeoecosystems.

There are not enough Middle Pleistocene LFAs with high competition intensity to discuss in detail the relevance of the improvements in lithic technology in this period (Jiménez-Arenas et al., 2011; Mosquera et al., 2013). However, our results show that, considering ecological competition intensity, the Acheulian technology spread in Europe when environmental conditions were more favourable for secondary consumers (reduced competition). Moreover, human subsistence strategies were successful both with an Oldowan and with an Acheulian technology (Blasco et al., 2013; Huguet et al., 2013), but the last one coincided with demographic increase and range expansion (Roebroeks, 2001). Perhaps these technological improvements allowed humans to attain a higher performance with the same resources. Kahlke et al. (2011) suggest that improvements in hunting, gathering, food-processing techniques and other cognitive capacities supplied opportunities for subsistence and dispersal during late Early to early Middle Pleistocene interglacials. They suggest that technological innovation was along with unfavorable conditions, high seasonality and low levels of habitat variability because in stable environmental conditions, hominins could rely on traditional subsistence strategies rather than develop technological innovations, as Moncel also defends (2010). Our results show a more favorable conditions for secondary consumers in Interval 2 (0.8-0.5 Ma) than in Interval 1 (1.1-0.8 Ma). The earliest European Mode 2 appears at Barranc de la Boella (Spain) approximately 1.0 Ma (Vallverdú et al., 2014), but Mode 1 remained in Europe at least until around 0.61 Ma at Isernia La Pineta (Italy) (Coltorti et al., 2005; Mosquera et al., 2013; Peretto, 2006). Under the premise that hostile environments promote technological innovation, if the Acheulean appeared in Europe as a local innovation, it would be expected to appear during a period of high intraguild competition. Interestingly, intraguild competition was high during the late Early Pleistocene, when the late Mode 1 or early Mode 2 industries appeared (Barsky and de Lumley,

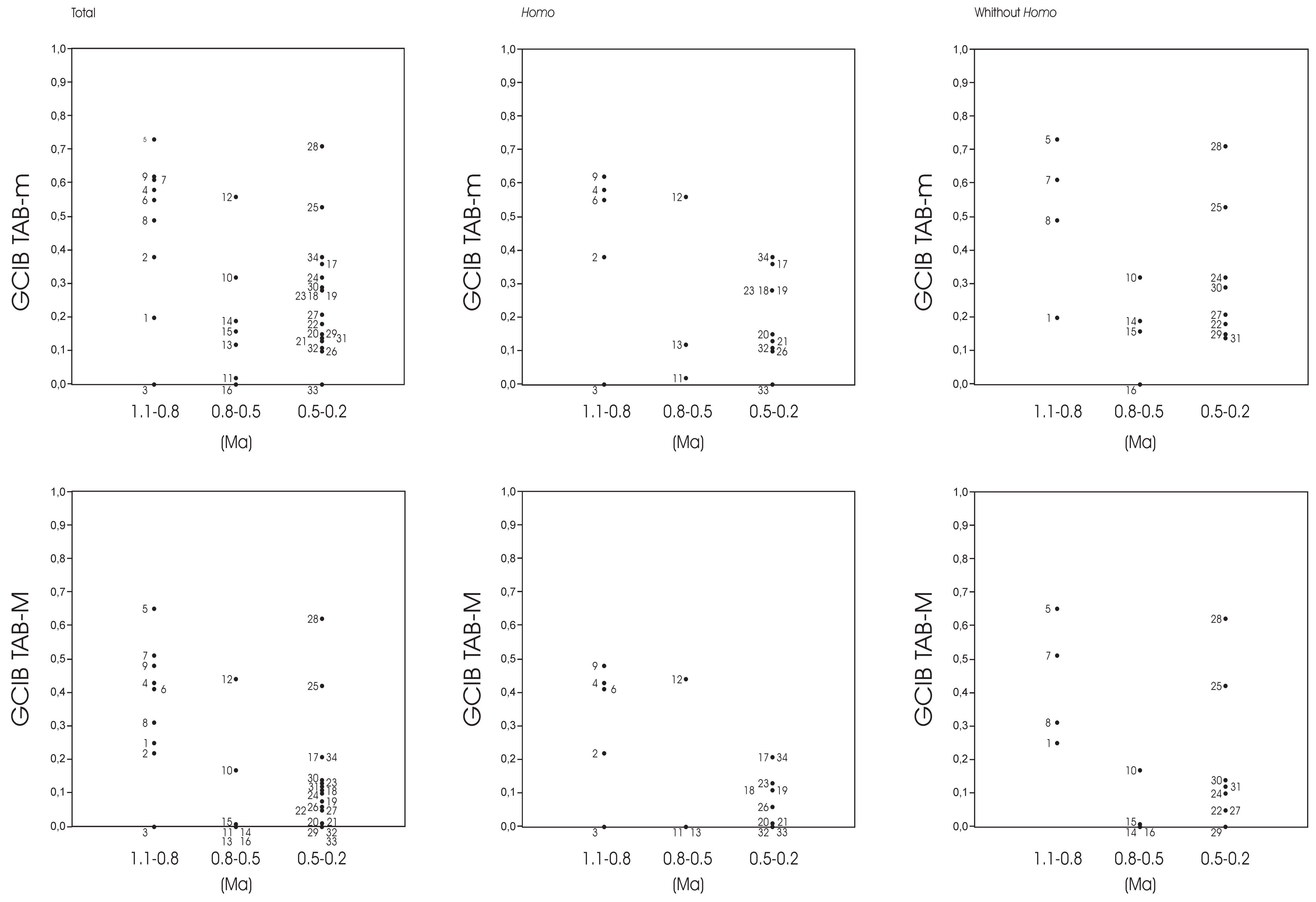

Figure 8. Graphical distribution of Global Competition Index Biomass (GCIB) values in each LFA for the three intervals of this study, 1.1-0.8 Ma (Interval 1), 0.8-0.5 Ma (Interval 2) and 0.5-0.2 Ma (Interval 3), in two scenarios, with minimum (top) and maximum (bottom) TAB in all assemblages. First column (Total) contains all assemblages, second column (*Homo*) includes assemblages with *Homo* evidence of presence and third column (Without *Homo*) includes assemblages without evidence of *Homo* presence. GCIB is equal to 0 when competition intensity is lowest and it is 1 when competition is highest. Locality Codes (LC) used in the Table 1.

2010; Barsky et al., 2013; Moncel et al., 2013; Mosquera et al., 2013; Santonja and Pérez-González, 2010; Scott and Gibert, 2009; Vallverdú et al., 2014; Walker et al., 2013). If the human occupation of Europe was continuous from 1.0 Ma to 0.5 Ma, these pre-Mode 2 technologies would be progressively developed into a full Mode 2 from 0.8 Ma to 0.5 Ma, as period of moderate intraguild competition. Otherwise, if the Acheulian evolved locally during the Middle Pleistocene, it was not triggered by harsh environmental conditions, at least with reference to intraguild competition. Finally, if the Acheulian arrived to Europe from overseas, as claimed by several scholars (e.g. Carbonell et al., 1999; Carbonell et al., 2010; Jiménez-Arenas et al., 2011; Santonja and Pérez-González, 2010), its appearance had nothing to do with the variations in intraguild competition. Carbonell et al. (2010) defend Acheulean or Mode 2 expansion across Europe due to demographic increase in Near East and Africa. The debate is still open, a review of the hypotheses about an African or local origin of the European Acheulean is provided by Molines and Moncel (2005). It is beyond the scope of this paper to support any of the three possible scenarios; our intention is only to provide their environmental background.

The results in the present study are in disagreement with those presented in Rodríguez-Gómez et al. (2014b). Applying the same methodology, it was shown that, at the local scale, the depopulation of the Sierra de Atapuerca area approximately 0.6 Ma coincided with a relatively high intraguild competition (Rodríguez-Gómez et al., 2014b). Studies at a local scale may provide information about the evolution of faunal assemblages in the long term, but analyses at the continental scale focus on average palaeocomunities. An average is a simplification, so there is a loss of information when it is applied to obtain a global perspective. From the continental point of view, competition does not appear to be a relevant factor to limit human presence in the early Middle Pleistocene. It would be desirable to combine analyses tracking the changes in intraguild competition both at the continental and local scales, although unfortunately, there are few local sequences such as Atapuerca that are long enough to apply this approach.

This study addresses the constraints imposed by the communities of large mammals to the human presence in the European Pleistocene from a palaeoecological point of view. We tried to describe with precision the role of humans in the palaeocommunities of the studied period. However, in understanding human behaviour during the Mid-Pleistocene Revolution, it is enough to know the limitations imposed to them by the availability of trophic resources. To obtain a more accurate view of the human niche in this period, it will be necessary to improve our knowledge of the interactions between species and/or food web structure in the palaeocommunities.

6.- Conclusion

In this study, we measure the intensity of intraguild competition as a limiting factor of human expansion across Europe and test whether the apparent scarcity of human evidences could be attributable to this factor. Early Pleistocene LFAs had a greater degree of competition than the Middle Pleistocene LFAs. This decrease of the competition intensity coincides with the decrease of human presence in Europe. It could be concluded that competition was not the main factor for that absence. It is noted that the *Homo* niche in Early Pleistocene palaeoecosystems does not completely overlap with any species because there is not complete exclusion between them. Perhaps food web configurations did not allow a settlement, as during the previous period. Culture and cognitive improvements in processing resources could have enabled population growth in the late Middle Pleistocene. To better define the role of *Homo* during the Pleistocene, it would be interesting to delve into palaeocommunity structures and the relationships among species in them.

Acknowledgements

We thank Professor Adrian M. Lister and the Natural History Museum of London for having permitted G. Rodríguez-Gómez to revise the Pleistocene macromammal material. The short stay to revise this material was funded with an Estancias Breves Grant (EEBB-I-12-03857) by the MINECO. This research was funded by the MINECO project CGL2012-38434-C03-02. G. Rodríguez-Gómez was the beneficiary of a predoctoral FPI Grant from the Spanish MICINN. An anonymous editor from Elsevier's Language services improved the English of the original manuscript. This research has also been carried out in the framework of the INQUA project 1403 "Modeling human settlement, fauna and flora dynamics in Europe during the Mid-Pleistocene Revolution (1.2 to 0.4 Ma)".

Role of funding Source

The Funding source had no involvement neither in study design, nor in the collection, analysis and interpretation of data.

Appendix C. Supplementary data.

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Discusión

En lás páginas anteriores:
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Capítulo 6.- Discusión

6.1.- La metodología

La Paleoecología tiene entre sus objetivos estudiar las interacciones en las comunidades del pasado por su interés en conocer las condiciones ambientales en las que se encontraban las especies. Las redes tróficas, sus estructuras y dinámicas, son centro de interés por su importancia para entender las interacciones que se establecían en aquellas paleocomunidades. El empleo de modelos matemáticos está permitiendo cuantificar esas interacciones y compararlas entre diferentes paleoecosistemas. La aproximación que se presenta en este trabajo emplea un refinamiento de los métodos utilizados anteriormente para el estudio de las dinámicas tróficas de las paleocomunidades (Bermúdez de Castro et al., 1995; Fariña, 1996; Palmqvist et al., 2003; Vizcaíno et al., 2010; Vizcaíno et al., 2004). De forma general, el refinamiento consiste en una mejora de la estimación de la biomasa de presas y en la forma de distribuir la biomasa de los consumidores primarios entre los secundarios.

6.1.1.- Fortalezas y potencialidades de la metodología

El método aplicado en los análisis de la tesis doctoral tiene varios aspectos destacables que refinan métodos anteriores:

- Utilización de perfiles de población para disminuir la sobreestimación de biomasa de consumidores primarios.
- Utilización de perfiles de mortalidad con los que cuantificar la biomasa extraída de las poblaciones.
- División en categorías de peso de los consumidores primarios para precisar el consumo de cada consumidor secundario.
- Posibilidad de estudiar el efecto en las paleocomunidades de especies no registradas en los yacimientos.
- Empleo de índices de competencia estandarizados.

La cantidad de biomasa de una especie en una comunidad puede ser calculada como la suma de la masa corporal de todos los individuos de la población de esa especie en la comunidad. Una forma de simplificar esta estimación es calcular el tamaño corporal promedio de la población y multiplicarlo por el número de individuos. En Paleoecología, la estimación de masas corporales de mamíferos suele hacerse a partir de restos de individuos adultos (Damuth y MacFadden, 1990), que se suelen usar para estimar la biomasa de una población (por ejemplo, en Bermúdez de Castro et al., 1995; Fariña, 1996; Meloro y Clauss, 2012; Palmqvist et al., 2003; Vizcaíno et al., 2010; Vizcaíno et al., 2004). Si se utiliza como promedio el peso del adulto se sobreestima la biomasa de la población al multiplicar por el número de individuos. Teniendo esto presente, se buscó refinar este aspecto empleando una herramienta como la Matriz de Leslie (Leslie, 1945; Leslie, 1948), aplicada habitualmente en dinámica de poblaciones. La Matriz de Leslie proporciona la estructura de la población a lo largo del tiempo usando como variables el número de individuos inicial, las clases de edad, la fertilidad, y las tasas de supervivencia y mortalidad de la población. En la metodología empleada en esta tesis doctoral se introducen unos condicionantes en la Matriz para obtener unos valores en los que las poblaciones serían estables y estacionarias, pudiendo considerarse los promedios de estructuras de la población a lo largo del tiempo. Desde un modelo dinámico, obtenemos un resultado dinámico-estático útil para el estudio de las poblaciones a largo plazo. Al aplicar la Matriz de Leslie, se obtienen los perfiles de población y de mortalidad por clases de edad. Esto introduce unas mejoras en los métodos empleados anteriormente ya que, por un lado, permite tener las proporciones de los individuos de cada clase de edad presentes en las poblaciones y, por otro, conocer los individuos de cada clase de edad que fallecerían, manteniendo a las poblaciones estables. Finalmente, conociendo los individuos que fallecen por clase de edad se puede estimar cuánta biomasa podría estar a disposición de los consumidores secundarios. Por tanto, esta implementación permite tener una visión más cercana a la realidad que al utilizar el peso promedio de los adultos y, además, proporciona información de cómo es la estructura promedio de la población en el tiempo, qué cantidad de individuos fallecerían por clase de edad y qué biomasa de consumidores primarios podría estar disponible en el medio para los consumidores secundarios.

En la Tabla 6.1, se pueden ver los resultados de aplicar las metodologías anteriores y la aplicada en la presente tesis doctoral, en una hipotética comunidad compuesta por tres especies de consumidores primarios: *Dama vallonetensis*, *Equus altidens*, y *Stephanorhinus etruscus*. La columna que encabeza el título *Biomasa Ecosistema (kg)* es la que se corresponde con las estimaciones de la biomasa de las poblaciones y del ecosistema a partir de las metodologías tradicionales, multiplicando el tamaño promedio adulto por la densidad. Las columnas encabezadas por *Categorías de tamaño (kg)*, corresponden a la estimación de la biomasa por la metodología utilizada en esta tesis doctoral. La columna encabezada con *Total* sería la comparable con la columna *Biomasa Ecosistema (kg)*. Las diferencias de valores entre una y otra

Tabla 6.1.- Comparativa de los resultados de biomasa del ecosistema obtenidos por metodologías clásicas y la metodología aplicada en esta tesis doctoral en una hipotética comunidad de consumidores primarios formada por tres especies: *Dama vallonetensis*, *Equus altidens*, *Stephanorhinus etruscus*. **La Masa Corporal Estimada (kg) para las especies fósiles es estimada por ecuaciones alométricas para restos de individuos adultos (Damuth y MacFadden, 1990). Las densidades son estimadas mediante la misma ecuación alométrica empleada en esta tesis (Damuth, 1981). En la columna encabezada como Biomasa Ecosistema (kg) (***On-Crop Biomass***), se realiza la estimación de la biomasa como en los estudios anteriores (Bermúdez de Castro et al., 1995; Fariña, 1996; Palmqvist et al., 2003; Vizcaíno et al., 2010; Vizcaíno et al., 2004). Las columnas encabezadas por Categorías de tamaño (kg), reflejan los resultados obtenidos al aplicar la metodología de la tesis doctoral. Biomasa de la población-Máxima: biomasa que alcanza la población con una mínima mortalidad sostenible de subadultos; Biomasa de la población-Mínima: biomasa que alcanza la población con una máxima mortalidad sostenible de subadultos.**

				Categorías de tamaño (kg)						
				10-45	45-90	90-180	180-360	360-1.000	>1.000	Total
Especie	Masa Corporal Estimada (kg)	Densidad (ind/km^2)	Biomasa Ecosistema (kg)	Biomasa de la población-Máxima (kg)						
Dama vallonetensis	84	3,47	291,14	22,14	190,84	0,00	0,00	0,00	0,00	212,98
Equus altidens	324	1,19	386,53	0,00	9,22	22,69	295,62	0,00	0,00	327,54
Stephanorhinus etruscus	1400	0,38	525,00	0,00	0,00	0,00	5,76	69,05	353,30	428,10
TOTAL			**1202,68**	22,14	200,06	22,69	301,38	69,05	353,30	**968,63**
Especie	Masa Corporal Estimada (kg)	Densidad (ind/km^2)	Biomasa Ecosistema (kg)	Biomasa de la población-Mínima (kg)						
Dama vallonetensis	84	3,47	291,14	24,68	192,34	0,00	0,00	0,00	0,00	217,03
Equus altidens	324	1,19	386,53	0,00	12,67	18,70	289,64	0,00	0,00	321,01
Stephanorhinus etruscus	1400	0,38	525,00	0,00	0,00	0,00	8,60	48,68	362,93	420,21
TOTAL			**1202,68**	24,68	205,01	18,70	298,24	48,68	362,93	**958,24**

son debidas al uso de los perfiles de población en la segunda. El uso de estos perfiles permite distribuir la biomasa de la población en diferentes categorías de peso y reducir la sobreestimación de biomasa que se produce al emplear el tamaño promedio de los adultos de cada especie.

El perfil de mortalidad permite distribuir a los individuos fallecidos de las especies de consumidores primarios por categorías de peso, diferenciando los subadultos de los adultos. Los subadultos son considerados los individuos que aún no han alcanzado el tamaño adulto. Siendo el tamaño de la presa un factor clave en la selección por los depredadores (Carbone et al., 1999; Radloff y Toit, 2004), la división por categorías de peso se consideró esencial para estudiar los recursos cárnicos disponibles para las poblaciones de consumidores secundarios y la competencia con otras especies. De esta forma, se puede cuantificar la biomasa que ingeriría cada población de cada especie de consumidor secundario teniendo en cuenta sus requerimientos energéticos y preferencias de consumo por cada categoría de peso corporal de los consumidores primarios. La Tabla 6.2 es un ejemplo de los resultados que se obtendrían en la paleocomunidad compuesta por las tres especies de consumidores primarios anteriores: *Dama vallonetensis*, *Equus altidens*, *Stephanorhinus etruscus.* El algoritmo desarrollado para este modelo permite distribuir la biomasa de forma dinámica y flexible entre las diferentes especies de consumidores secundarios, pudiendo consumir en las diferentes categorías de masa corporal según la oferta y la demanda. La demanda por categoría de peso corporal estaría condicionada por los hábitos alimenticios de cada especie, limitándose el acceso a categorías de peso de presas en las que no se concibe ese acceso. Esto se define a partir de las evidencias del registro fósil, de estudios isotópicos o por la conducta observada en especies actuales filogenéticamente próximas. El tratamiento de los datos empleado en metodologías anteriores no permitía este grado de resolución en la distribución de los recursos del medio, ya que se trataba la biomasa disponible de igual forma para todos los depredadores. Esta implementación permite un análisis más preciso de las dinámicas tróficas y de los flujos energéticos de las paleocomunidades.

Para los estudios que constituyen la tesis doctoral (Capítulos 3, 4 y 5), sólo se consideraron los perfiles extremos de las poblaciones, con la máxima y mínima mortalidad que podrían soportar las clases subadultas, manteniéndose las poblaciones estables y estacionarias. Se asumió que en este intervalo debían de haberse encontrado las estructuras de las poblaciones modelizadas. Las estructuras intermedias han sido descartadas en estos estudios pero pueden proporcionar información interesante para otras perspectivas y trabajos, no planteados hasta el momento. Si se pudiese concretar más sobre las tasas de mortalidad de los subadultos, se podría precisar más en la biomasa de salida de las especies. En estos análisis se tomó una postura conservadora, seleccionando los valores extremos.

Además de los refinamientos con respecto a los métodos tradicionales, otra potencialidad del método aplicado es la de poder incluir en las paleocomunidades especies que no están registradas en los conjuntos fósiles y analizar el efecto de su hipotética presencia en la paleocomunidad. Ha sido aplicado en los estudios de los Capítulos 3 (Rodríguez-Gómez et al., 2013) y 4 (Rodríguez-Gómez et al., 2014). Esto puede permitir, entre otras cosas, poder salvar sesgos tafonómicos. En el Capítulo 3 (Rodríguez-Gómez et al., 2013), se incluyeron *Homotherium latidens* y *Panthera gombaszoegensis* (jaguar europeo), especies comunes en las faunas ibéricas del Pleistoceno Inferior tardío pero que no están presentes en el nivel TD6-2 del yacimiento

Tabla 6.2.- Biomasa total de consumidores primarios disponible para los consumidores secundarios en kilogramos (kg) por categorías de peso, para una paleocomunidad compuesta por tres especies: *Dama vallonetensis*, *Equus altidens*, *Stephanorhinus etruscus*. **La Masa Corporal Estimada (kg) para las especies fósiles es calculada por ecuaciones alométricas para restos fósiles de individuos adultos (Damuth y MacFadden, 1990). Las densidades son estimadas mediante la misma ecuación alométrica empleada en los estudios de esta tesis (Damuth, 1981). Biomasa Total Disponible Máxima (TAB-M) (kg): biomasa total disponible para consumidores secundarios cuando se produce una mínima mortalidad sostenible de subadultos; Biomasa Total Disponible Mínima (TAB-m) (kg): biomasa disponible para consumidores secundarios cuando se produce una máxima mortalidad sostenible de subadultos.**

			Categorías de tamaño (kg)						
			10-45	**45-90**	**90-180**	**180-360**	**360-1.000**	**>1.000**	**Total**
Especie	Masa Corporal Estimada (kg)	Densidad (ind/km^2)	Biomasa Total Disponible Máxima (TAB-M) (kg)						
Dama vallonetensis	84	3,47	6,97	56,55	0,00	0,00	0,00	0,00	63,53
Equus altidens	324	1,19	0,00	1,58	3,30	34,77	0,00	0,00	39,64
Stephanorhinus etruscus	1400	0,38	0,00	0,00	0,00	0,67	6,41	32,91	39,99
TOTAL			6,97	58,13	3,30	35,44	6,41	32,91	**143,16**
Especie	Masa Corporal Estimada (kg)	Densidad (ind/km^2)	Biomasa Total Disponible Mínima (TAB-m) (kg)						
Dama vallonetensis	84	3,47	16,04	27,57	0,00	0,00	0,00	0,00	43,61
Equus altidens	324	1,19	0,00	5,07	7,48	20,27	0,00	0,00	32,82
Stephanorhinus etruscus	1400	0,38	0,00	0,00	0,00	2,58	14,60	15,35	32,54
TOTAL			16,04	32,64	7,48	22,85	14,60	15,35	**108,97**

Gran Dolina. *Homotherium latidens* habitó Europa hasta el final del Pleistoceno Medio, según Turner y Antón (1997), y hasta finales del Pleistoceno Superior, según Reumer et al. (2003). *Panthera gombaszoegensis*, apareció en Europa aproximadamente hace 1,8 Ma y se extinguió hace aproximadamente entre 0,4 y 0,5 Ma (Turner y Antón, 1996). Pese a no estar presentes ninguno de estos dos grandes félidos en el nivel TD6-2, sí que lo están en niveles inferiores y superiores de Gran Dolina (Rodríguez et al., 2011). Con la inclusión de estas especies en el análisis de TD6-2, se pretendió saber si la riqueza de consumidores primarios de este paleoecosistema permitía, además de soportar máximas densidades de los consumidores secundarios registrados en el nivel, hacerlo con poblaciones de estas especies de dientes de sable, no registradas en este nivel pero que podían haber estado presentes por cronología. Los sesgos tafonómicos son más probables con especies de consumidores secundarios que de primarios porque presentan, por lo general, densidades más bajas (Hutchins et al., 2003; Jones et al., 2009; Nowak, 1999) y conductas que limitan la presencia de otros consumidores secundarios, como la exclusión espacial (Laurenson et al., 1995; Mills y Gorman, 1997). En Saladié et al. (2014) se propone que la cueva en ese momento (TD6-2) serviría como un refugio de los cazadores-recolectores para el consumo de presas, fuera del alcance y la competencia con los carnívoros. De esta forma, en este nivel se podía haber producido un sesgo tafonómico de los restos de carnívoros. Con el método aplicado en la tesis doctoral, además de poder evaluar composiciones hipotéticas de paleoecosistemas, se permite superar los sesgos tafonómicos en las acumulaciones fósiles, pudiendo considerar especies que se encontraban en los paleoecosistemas pero que no han quedado registradas en los yacimientos.

En este estudio sobre el nivel TD6-2 (Rodríguez-Gómez et al., 2013), no se introducía inicialmente a *Homo antecessor* en la paleocomunidad hasta que todas las demás especies habían cubierto sus necesidades. Esta ausencia se justifica con el fin de evitar interferencias asumiendo inicialmente el papel de los homininos en el ecosistema bien como carroñeros o bien como cazadores. No obstante, las evidencias apuntan a que tenían un acceso primario a las presas (Díez et al., 1999; Saladié et al., 2011). Esto no implica exclusivamente la opción de la caza, sino que podrían practicar el cleptoparasitismo, aunque su acceso a los cadáveres tendría que ser temprano por las limitaciones de su sistema digestivo (Espigares et al., 2013).

En el Capítulo 4 (Rodríguez-Gómez et al., 2014), se incluyó una población de *Homo* sp.

en el nivel TD8 de Gran Dolina, en el que no hay evidencias de presencia humana. Con esto, se quería estudiar si el grado de competencia que alcanzaría la comunidad de consumidores secundarios era tan alto como para justificar su ausencia en el registro fósil. Por tanto, la metodología aplicada, además de superar los sesgos tafonómicos, permite extraer información y abordar trabajos de paleoecología en yacimientos en los que hay evidencias de la presencia del ser humano y en los que no lo hay. Es tan valiosa la información de condiciones en las que estaban presentes como en las que no estaban. Su ausencia puede dar información sobre las dispersiones de los distintos linajes humanos y de sus nichos ecológicos a lo largo de su evolución.

Con el fin de comparar las condiciones ecológicas de diferentes paleocomunidades, se han presentado varios índices que permiten estandarizar las comparaciones. Estos índices se centran en evaluar el grado de satisfacción de los requerimientos de las comunidades de consumidores secundarios para poder comparar qué condiciones tenían éstas en los diferentes complejos faunísticos fósiles. Las relaciones depredador-presa pueden ser empleadas como indicadores indirectos de la satisfacción o rendimiento que extraen los consumidores secundarios de los consumidores primarios. Como se discute en el Capítulo 5, este tipo de índice se consideró insuficiente para estimar la satisfacción de las comunidades y de las especies de consumidores secundarios. Por esta razón, se generaron otros índices en los que se podía tener una información más directa de la satisfacción de estos. Para ello fueron claves las implementaciones descritas anteriormente para estimar con precisión la biomasa de consumidores primarios efectiva que podrían consumir los consumidores secundarios. Como base de estos índices se consideró que las densidades estimadas por las ecuaciones alométricas (Damuth, 1981; Damuth, 1993) son densidades ecológicas máximas (White et al., 2007). Se esperaría que en condiciones óptimas los consumidores secundarios alcanzasen esas densidades máximas. En los análisis y en el modelo, estas densidades son consideradas densidades esperadas. Las densidades de los consumidores secundarios obtenidas como salidas del modelo son las densidades estimadas que serían sostenibles con los consumidores primarios. Con los índices del modelo se relacionan las densidades estimadas con las densidades esperadas (o densidades máximas). La relación entre las densidades estimadas y esperadas se traduce en el grado de satisfacción de los requerimientos de la comunidad de carnívoros. Cuanta más diferencia haya entre una y otra, peor alcanzarían sus requerimientos los consumidores secundarios y mayor sería la competencia por los recursos cárnicos. Cuanto más se aproximen, menor grado de competencia existiría en ese ecosistema ya que tendrían densidades más cercanas a la máxima. Uno de los índices relaciona únicamente las densidades estimadas y esperadas, obteniendo una estimación de hasta qué grado se alcanza el número de individuos esperados. Este tipo de índice se aplica a nivel de la comunidad de consumidores secundarios (GCI o Índice de Competencia Global) y a nivel de especie (SCI o Índice de Competencia de Especies). El otro índice introduce la biomasa de los carnívoros, lo que se traduce en hasta qué grado se alcanza la biomasa de consumidores secundarios esperada (GCIB o Índice de Competencia Global de Biomasa). Estos índices son unas herramientas útiles para comparar el estado de la comunidad de carnívoros entre diferentes yacimientos como se ha mostrado en los Capítulos 4 (Rodríguez-Gómez et al., 2014) y 5 (Rodríguez-Gómez et al., Enviado). Aportan a la clásica relación biomasa de presas-biomasa de depredadores (por ejemplo, Carbone y Gittleman, 2002; Meloro y Clauss, 2012; Palombo, 2010; Raia et al., 2007), una información complementaria de mayor grado de resolución para conocer las condiciones de la comunidad de consumidores secundarios. La relación de biomasa de presas-biomasa de depredadores puede dar una idea del estado y relaciones del ecosistema, pero también puede transmitir lecturas desvirtuadas porque depende mucho de las capacidades y comportamientos de los mamíferos de la comunidad. Por ejemplo, una hipotética comunidad formada por grandes mamíferos como elefantes, hipopótamos, rinocerontes, hiénidos carroñeros y guepardos, presentarían una ratio biomasa de presas-biomasa de depredadores que no se correspondería con la realidad, en cuanto a biomasa disponible y aprovechada. Los hábitos tróficos y las capacidades de los depredadores de esa comunidad simulada no les permitirían acceder a los grandes mamíferos salvo como carroña. Por esta razón, consideramos que lo más adecuado es tratar directamente sobre el grado de satisfacción de los requerimientos de los carnívoros. Al elaborar el modelo y los índices de competencia, éramos conscientes de que el umbral de satisfacción se basa en las densidades estimadas por medio de las ecuaciones alométricas y que éstas podrían estar introduciendo un error. Lo que se aporta con el modelo más que un reflejo de cómo era la comunidad es una estimación de la capacidad de carga de consumidores secundarios en los ecosistemas.

6.1.2.- Limitaciones o debilidades del método

Si bien se han introducido mejoras a metodologías empleadas previamente para cuantificar las relaciones entre los mamíferos en las paleocomunidades, el modelo tiene margen de mejora en varios parámetros que son tratados de forma simplista en este acercamiento:

- Estructura de la población correspondiente a los machos.
- Proporción de sexos en las poblaciones.
- Estimación de las densidades tanto de presas como de depredadores.
- Masa corporal por clase de edad de los consumidores secundarios.
- Estimación de requerimientos por clase de edad de los consumidores secundarios.
- Cuantificación de la biomasa consumida mediante un acceso primario y/o un acceso secundario.

En el modelo se asume que las estructuras de edades de machos y hembras en una población son simétricas. La Matriz de Leslie sólo contempla una población formada por hembras. Por esta razón, se tuvo que realizar esa asunción para tener una estimación de la población completa. Debería de aplicarse un factor corrector para modelizar la población de machos a partir del perfil de población de hembras, con perfiles de población y de mortalidad propios para los machos. De momento, esta cuestión no ha podido ser abarcada pero se espera implementarla en futuras versiones. Con esto, se podría refinar a su vez la proporción de sexos en la población que, aunque tiende a ser 1:1 en poblaciones actuales (por ejemplo, Cicognani et al., 2000; Hutchins et al., 2003; Massei et al., 1997; Nowak, 1999), pueden requerirse correcciones para determinadas especies. Por ejemplo, la población del gamo (*Dama dama*) en el Parque Nacional delle Casentinesi, Monte Falterona y Campigna (Italia), tenía una proporción de sexos de 1:1 (Cicognani et al., 2000); sin embargo, en California era de 100 hembras por 43 machos (1:0,43) (Wehausen y Elliott, 1982). Como sostienen Feldhamer et al. (1988), es habitual que se produzcan sesgos de la proporción de sexos hacia las hembras. También existen desviaciones de la proporción de sexos 1:1 en carnívoros. El león en África y Asia tiene una relación de 2,1 hembras por cada macho (1:0,48) (Haas et al., 2005).

Otro parámetro interesante es el de las densidades de las poblaciones de consumidores primarios y secundarios. La estimación del número de individuos de una población es una tarea difícil ya que, una misma especie en distintas localidades puede tener densidades muy diferentes. Por ejemplo, *Crocuta crocuta* presenta en zonas desérticas o semidesérticas de Sudáfrica, 3 individuos por grupo y, en sabanas de África del este, 54 individuos por grupo (Mills y Hofer, 1998). *Panthera leo* presenta en diferentes localidades un intervalo de densidad que va de 0,08 a 14,2 individuos por 100 kilómetros cuadrados (Haas et al., 2005). En el modelo aplicado en esta tesis doctoral, se estima el número de individuos en una población por medio de ecuaciones alométricas, diferenciando entre los consumidores primarios (Damuth, 1981) y los consumidores secundarios (Damuth, 1993). Según White et al. (2007) estas densidades estimadas debieran de ser consideradas como máximas ecológicas por lo que se podrían estar sobreestimando las biomasas de presas y, con estas, las de los depredadores. Sería necesario e interesante en un futuro intentar calibrar el método con datos de ecosistemas actuales, comparando estos con los obtenidos al emplear diferentes ecuaciones alométricas o utilizar otros acercamientos como el empleo de densidades medias de las especies, géneros o familias actuales. Esto nos permitiría evaluar y cuantificar la desviación del modelo con el fin de aplicar algún tipo de factor de corrección.

Otro aspecto que podría ser mejorado es el de las masas corporales por clase de edad. Éstas se estiman a partir de las ecuaciones de tasas de crecimiento de Millar (1977) y Case (1978). A partir de datos actuales podrían ajustarse estas estimaciones, pero la escasez de datos de este tipo no permite llevar a cabo esta mejora por el momento.

El modelo también podría incrementar su resolución en la cuantificación de la demanda de biomasa por los depredadores. En este caso, aplicamos una relación entre los requerimientos energéticos de los individuos adultos y la densidad. A priori, esto hace que sobreestimemos los requerimientos energéticos de la población ya que los individuos subadultos tendrían una demanda de cantidad de carne diferente. Sería conveniente introducir parámetros como los requerimientos de las hembras en periodo de gestación o lactancia y la de las crías en etapas iniciales de crecimiento y de desarrollo. La aplicación de la Matriz de Leslie a la población de consumidores secundarios podría ser un primer paso para abordar este refinamiento. Conseguir alcanzar este grado de resolución es una tarea de gran dificultad y se podrá abordar en un futuro.

En el estado actual de la aplicación del modelo se intenta distinguir las especies que actúan como cazadoras o como carroñeras. Esto se hace al definir la preferencia de los consumidores secundarios por las diferentes categorías de peso de los consumidores primarios. Para las especies carroñeras, se considera que se alimentan de todas las categorías de la misma forma, sin hacer distinción. Si existiera alguna limitación para generar carroña en un paleoecosistema, los carroñeros no habrían podido obtener todos los recursos potenciales y sus poblaciones habrían sido menores de las estimadas a través del modelo. Parece que en la Revolución de Mitad del Pleistoceno (MPR) (Maslin y Ridgwell, 2005), la producción de carroña se pudo ver mermada debido a los cambios en la comunidad de carnívoros en Europa durante este evento. Los carnívoros recién llegados aprovechaban mejor los recursos de las carcasas (Turner et al., 2008) de manera que ese nicho ecológico, explotado por los humanos, quedó muy afectado o desapareció (Palmqvist et al., 2011). Por tanto, en el modelo sería interesante diferenciar la cantidad de biomasa de los consumidores primarios que conseguirían los humanos con acceso primario y con acceso secundario.

Otro aspecto que podría ser interesante implementar, de forma directa o indirecta, es la influencia de la composición (desde un punto de vista etológico de cada especie) y la estructura de la paleocomunidad. Aspectos como la limitación a ciertos tipos de hábitats, estrategias de caza (de persecución o al acecho), comportamientos de exclusión espacial o de hábitat, de dependencia o simbiosis, no están incluidos en el modelo y sólo pueden discutirse de forma indirecta. Estos factores pudieron influir en la manera en que las poblaciones de cazadores recolectores paleolíticas accedían a los recursos cárnicos. La inclusión de la arquitectura de las paleocomunidades en futuras versiones del método podría suponer un aporte relevante en debates como el de la continuidad o discontinuidad de la presencia humana en Europa durante el Pleistoceno. El incremento del grado de resolución mediante estos refinamientos posibilitará visualizar, con más detalle del que se ha visto hasta ahora, el nicho que ocuparon los homininos en los paleoecosistemas del Pleistoceno y entender su relación con los recursos del medio.

Pese a que el modelo presenta aspectos que pueden ser refinados, consideramos que lo avanzado hasta el momento permite dar una visión general del funcionamiento de los ecosistemas pasados y, específicamente, de las redes tróficas de mamíferos. Una muestra de su potencia son los estudios llevados a cabo con su aplicación a escala local y continental, en los yacimientos de la Sierra de Atapuerca y en el continente europeo respectivamente (Capítulos 3, 4 y 5).

6.2.- Aportaciones a los debates sobre la presencia humana en Europa durante el Pleistoceno

Una vez desarrollada por el grupo de investigación la metodología para estimar los recursos cárnicos disponibles para las poblaciones de cazadores recolectores pleistocenos, se planteó su aplicación en aspectos relevantes para la evolución humana en Europa. De forma general, lo que se quería analizar eran los posibles efectos de la disponibilidad de recursos cárnicos en las poblaciones humanas del Pleistoceno. Más concretamente, la influencia de la competencia por los recursos cárnicos con otros consumidores secundarios en la expansión humana por Europa durante este periodo (Arribas y Palmqvist, 1999; Martínez-Navarro y Palmqvist, 1996; Palombo, 2007; Palombo, 2010; Rodríguez et al., 2012; Turner, 1992), y en la continuidad de la presencia de sus poblaciones en éste continente hasta el Pleistoceno Medio tardío (Agustí et al., 2009; Arribas y Palmqvist, 1999; Bermúdez de Castro et al., 2013; Gómez-Robles et al., 2013; Jiménez-Arenas et al., 2011; Made y Mateos, 2010; Moncel, 2010; Moncel et al., 2013; Mosquera et al., 2013; Muttoni et al., 2010; O´Regan et al., 2011; O'Regan, 2008; Palombo, 2010; Palombo, 2013; Santonja y Pérez-González, 2010; Vallverdú et al., 2014). Se podrían dividir las propuestas según su escala de análisis: escala local y escala continental. Los estudios de escala local se centraron en paleoecosistemas de la Sierra de Atapuerca y los de escala continental, en paleoecosistemas europeos.

6.2.1.- Escala local

El yacimiento Gran Dolina de la Sierra de Atapuerca es un interesante conjunto para este tipo de análisis ya que su secuencia abarca desde el Pleistoceno Inferior tardío o Epivillafranquiense (TD3-4-5) hasta el Pleistoceno Medio tardío (TD10-1) (Rodríguez et al., 2011). Las evidencias humanas están presentes a lo largo de la secuencia salvo en el intervalo de tiempo que abarca aproximadamente entre 0,9 y 0,5 Ma (Mosquera et al., 2013), que se corresponde con los niveles TD7, TD8 y TD9 (Rodríguez et al., 2011).

Los análisis llevados a cabo en el nivel TD6-2 muestran un paleoecosistema muy rico en recursos cárnicos para la comunidad de consumidores secundarios registrados (Rodríguez-Gómez et al., 2014; Rodríguez-Gómez et al., 2013). En los escenarios que contemplaban sólo los consumidores secundarios registrados en el nivel, estos alcanzaban las densidades máximas esperadas, consumiendo totalmente el porcentaje en sus dietas de carne de grandes mamíferos. *Homo antecessor* podía alcanzar densidades por encima de su densidad máxima esperada (24 individuos por 100 km^2). Siendo este el paleoecosistema de la Sierra en ese momento, se podía decir que era un ambiente con recursos cárnicos suficientes para sostener de forma óptima a la comunidad de consumidores secundarios del nivel TD6-2. Incluso al incluir una población de una especie de gran félido (*Homotherium latidens*), existían recursos suficientes para que todos los carnívoros alcanzasen densidades altas, incluido el gran félido. En esas condiciones, la población humana que se podría haber soportado habría tenido una densidad algo menor al del escenario anterior. La razón por la que no aparece *Homotherium* en el nivel, no podría deberse a una escasez de recursos, si es que se encontraba en ese periodo en el ecosistema de la Sierra. La capacidad de recursos del paleoecositema de TD6-2 permite descartar que el canibalismo registrado en este nivel por parte de *Homo antecessor* (Fernández-Jalvo et al., 1999; Fernández-Jalvo et al., 1996), se pudiese deber a la escasez de recursos cárnicos. Probablemente se debía a la competencia intraespecífica (Carbonell et al., 2010a). Este análisis nos refleja que el marco ecológico que envolvía a *Homo* en este momento de la Sierra de Atapuerca mostraba una importante riqueza de recursos cárnicos.

Después del nivel TD6-2, se aplicó este tipo de análisis en el nivel TD8 del yacimiento Gran Dolina. Se tomó este nivel TD8 como representante de los paleoecosistemas del periodo en el que no se han hallado evidencias de presencia humana en la Sierra (entre 0,9 y 0,5 Ma). El objetivo era saber si los recursos cárnicos eran menores en este periodo que en el correspondiente a TD6-2 y esto podía explicar la ausencia de evidencias de la presencia humana en este nivel. El nivel TD8 mostró una riqueza de fauna comparable a la del nivel TD6-2, con una comunidad de carnívoros similar pero en la que faltaba *Homo* y estaban presentes un carroñero como *Hyaena* sp. y un hipercarnívoro como *Panthera gombaszoegensis* (jaguar europeo). En el análisis se comparan los niveles TD6-2 y TD8 con la misma perspectiva incluyendo a *Homo* en el reparto de recursos cárnicos disponibles en la paleocomunidad, a diferencia del trabajo anterior. Como resultado del análisis se observa que la disponibilidad de recursos cárnicos para los consumidores secundarios era menor en el ecosistema de TD8 que en el de TD6-2. Existía mayor competencia en la comunidad de carnívoros de TD8 que en la de TD6-2, siendo comparable a la del escenario de la comunidad del nivel TD6-2 en la que se le añadía un gran félido. En otro escenario hipotético, en el que se incluyó una población humana a la comunidad de TD8, el análisis mostró que se habrían alcanzado niveles de competencia considerablemente mayores que los de TD6-2. Estos resultados apoyan la idea de que la competencia por la carne con la comunidad de carnívoros y por el acceso a ella eran factores relevantes. El grado de competencia por esta clase de recursos pudo bloquear la presencia de *Homo* en la paleocomunidad de TD8. Como se comentó anteriormente, al observar la composición de las dos paleocomunidades estudiadas, las diferencias relevantes entre las estructuras de ambas paleocomunidades residían en la presencia de *Homo antecessor* en TD6-2, y la de *Panthera gombaszoegensis* e *Hyaena* sp. en TD8. Aunque el acercamiento no proporciona información sobre los mecanismos que podrían haber producido estos cambios de estructura de una a otra, a partir de los resultados del grado de competencia (GCI), se puede proponer que la presencia de *Homo* en el paleoecosistema de TD8 podía haberse visto impedida por la presencia de estas dos especies. Considerando a las poblaciones humanas del Pleistoceno Inferior como omnívoros, que no podrían competir con los carnívoros del Villafranquiense de forma efectiva (Croitor y Brugal, 2010), se propuso en el Capítulo 4 (Rodríguez-Gómez et al., 2014) que su ausencia en el registro del nivel TD8 se debía a un posible solapamiento de nichos con *Panthera gombaszoegensis* e *Hyaena* sp., que lo excluirían del ecosistema. De esta forma, se planteaba un papel de *Homo* con dificultades para competir, pudiendo estar presente en paleoecosistemas con una competencia relativamente baja por los recursos cárnicos. También se expone una hipótesis alternativa a los resultados en el análisis del Capítulo 4 (Rodríguez-Gómez et al., 2014), en la que se defiende que el cambio en la estructura de la comunidad de carnívoros de TD8 con respecto a la de TD6-2, se debiera precisamente a la ausencia de *Homo*. La ausencia de los humanos en la Sierra de Atapuerca hace 0,6 Ma podría ser la causa del cambio observado en la estructura de la comunidad y no la consecuencia. En esta hipótesis la competencia con otros consumidores secundarios no sería el motor de la ausencia humana en este momento, pudiendo responsabilizar a las condiciones ambientales, como la mayor homogeneidad vegetal en el paleoecosistema de TD8 (Rodríguez et al., 2011) o a los cambios en las estructuras de las comunidades de grandes mamíferos (Palombo, 2010; Rodríguez et al., 2012).

6.2.2- Escala continental

Con el estudio a nivel continental se pretendía analizar el efecto de la disponibilidad de recursos cárnicos para las poblaciones humanas en los paleoecosistemas europeos, del Epivillafranquiense al Galeriense. Se pretendía comprobar si la hipótesis de la discontinuidad de las poblaciones humanas en Europa durante la transición entre el Pleistoceno Inferior y Medio podía tener un apoyo al analizar el grado de competencia por los recursos cárnicos. Los resultados de este análisis mostraron que, a escala continental, existía una diferencia en el grado de competencia por los recursos cárnicos disponibles para los consumidores secundarios entre el Pleistoceno Inferior tardío y el Pleistoceno Medio. Se observaba mayor competencia en el primer periodo que en el segundo. Se ha sugerido que la discontinuidad de las poblaciones humanas se debió producir en el Pleistoceno Medio temprano y, según nuestros análisis, las condiciones para acceder a los recursos cárnicos eran mejores que en el periodo anterior. El alto grado de competencia que llegan a soportar las paleocomunidades del Epivillafranquiense en comparación con las del Galeriense muestra una diferencia en las propiedades entre estos periodos que podrían influir en la composición de las comunidades de macromamíferos en ambos y, de esta forma, en la presencia humana en Europa durante el Pleistoceno Medio.

Desde una perspectiva global, se han propuesto como motores de la posible ausencia humana al inicio del Pleistoceno Medio los cambios en factores ecológicos o climáticos (Arribas y Palmqvist, 1999; Kahlke, 2009; Made, 2013; Made y Mateos, 2010; Martínez-Navarro y Palmqvist, 1995; Martínez-Navarro y Palmqvist, 1996; Palombo, 2007; Palombo, 2010; Rodríguez et al., 2012; Turner, 1992). En ecosistemas actuales se ha observado la influencia de parámetros ecológicos en las propiedades de los ecosistemas como, por ejemplo, la relación directa entre la biomasa de presas con la productividad primaria (McNaughton et al., 1989) y con la riqueza de especies (Fritz y Duncan, 1994), o el control de las poblaciones de grandes herbívoros por la productividad primaria y de las de pequeños herbívoros por el tamaño de los depredadores (Fritz et al., 2011; Sinclair, 2003). En las paleocomunidades de la transición del Pleistoceno Inferior al Medio, se observa una tendencia al aumento del tamaño de las presas y a la reducción de la riqueza de especies de carnívoros capaces de cazar grandes mamíferos (Croitor y Brugal, 2010; Kostopoulus et al., 2007; Palombo y Mussi, 2006; Prado et al., 2004; Radloff y Toit, 2004; Raia et al., 2007; Rodríguez et al., 2004; Rodríguez et al., 2012; Stanley, 1973; Yoshida, 2006). En esta transición se producen sustituciones faunísticas (Palombo, 2007; Palombo, 2010) que al modificar las composiciones y arquitecturas de las comunidades pudieron llegar a provocar cambios en sus propiedades como, por ejemplo, la extinción de nichos para grandes carroñeros especialistas (Palmqvist et al., 2011). La configuración, la intensidad y la relevancia de las interacciones entre especies en un ecosistema proporcionan propiedades a este. Cuanto más rica es una comunidad y mayor complejidad de redes interespecíficas tiene, mayor efecto de tamponamiento se ejerce ante condiciones desfavorables, reduciéndose las tasas de extinción (Ricklefs, 2010). Con las modificaciones en las comunidades de macromamíferos en la transición entre el Pleistoceno Inferior y Medio se podrían provocar roturas en las redes de interacciones y hacer que no se pudiese soportar una riqueza de especies de carnívoros similar en el Pleistoceno Medio que en el Inferior. Entre las modificaciones que podían facilitar estos cambios en las estructuras de las comunidades se puede considerar la sustitución de los consumidores secundarios por otros con un perfil más generalista, propio de ecosistemas con climas inestables como los presentes en el comienzo del Pleistoceno Medio (Rodríguez et al., 2012). El solapamiento de nichos que ocurriría con consumidores más generalistas podría reducir las posibilidades de acoger tanta riqueza como en periodos anteriores con carnívoros especialistas. Los humanos del Pleistoceno, con comportamientos omnívoros (Croitor y Brugal, 2010), podrían sufrir la entrada de consumidores secundarios que solapasen su nicho, como se propuso en el análisis del nivel TD8 (Rodríguez-Gómez et al., 2014). Nuestros resultados continentales indican que había más competencia por los recursos cárnicos en el Pleistoceno Inferior tardío que en el Medio temprano y, sin embargo, el número de yacimientos con presencia humana era menor en el segundo periodo que en el primero (Moncel, 2010). Con este escenario, se defendió en Rodríguez-Gómez et al. (Enviado) (Capítulo 5) que la competencia por los recursos cárnicos no fue el factor más relevante para la presencia humana en Europa en el Pleistoceno Medio, y que la estructura y la composición de los ecosistemas podían haber jugado un papel más relevante. Sin existir variación significativa en el grado de competencia por los recursos cárnicos entre paleoecosistemas del Pleistoceno Medio temprano y del tardío, se produce un incremento de la presencia humana en Europa (por ejemplo, Mania y Vlcek, 1999; Moncel, 2010; Roberts y Parfitt, 2000; Roebroeks, 2001; Thieme, 1997). El incremento de la presencia humana de este periodo coincide con la aparición del Achelense o Modo 2 (Doronichev y Golovanova, 2010; Jiménez-Arenas et al., 2011; Ollé et al., 2013). Según se propuso en el Capítulo 5, esta tecnología más eficiente que el Modo 1, junto con una mejor organización social y crecimiento demográfico, llevarían a la expansión por Europa a partir de mitad del Pleistoceno Medio (Carbonell et al., 2010b).

Una reinterpretación de los resultados obtenidos en el Capítulo 5 es llevada a cabo en la sección 6.3 de este capítulo, en el que se extiende esta discusión y se intenta dar una lectura global de los resultados obtenidos.

6.2.3- Análisis a escala local frente al análisis a escala continental

Las diferencias entre los resultados obtenidos en los análisis a escala local y continental pueden ser debidas al tratamiento realizado en ambos tipos de estudios. En el caso del análisis a escala local, el grado de resolución es mucho mayor que a escala continental. El acceso al material de una paleocomunidad es más sencillo que al de varias y es posible aplicar la información registrada en éste, para evaluar la paleocomunidad con sus especificidades. Cuando se comparó entre los paleoecosistemas de los niveles de TD6-2 y TD8, se consideraron diferencias intraespecíficas entre ambos como por ejemplo los pesos de *Dama vallonetensis*. En el tratamiento a escala continental, se consideran los mismos valores para una especie en todo el continente pese a que es conocido que pueden existir diferencias latitudinales y longitudinales. Esto resta precisión en el análisis pero lo agiliza, ya que, la revisión de todo el material de las localidades empleadas en el estudio es muy complicada y, en muchas ocasiones, no existe material adecuado para estimar los pesos corporales de las especies con suficiente fiabilidad para todos los conjuntos faunísticos.

En el estudio a escala continental se agruparon los yacimientos por intervalos de tiempo porque se consideró que era el factor principal para agrupar los conjuntos faunísticos. Tal vez, una división más regional y temporal pueda llevar a observar otras tendencias que se ven difuminadas con la escala de este estudio. Si se pudiesen realizar estudios con diferentes yacimientos con la resolución del análisis a escala local se podría tener una visión más precisa, pudiendo llegar a conclusiones generales más rotundas. La falta de secuencias largas, que abarquen varios cientos de miles de años, impide realizar análisis de este tipo para estudiar localmente la presencia humana en Europa a lo largo del Pleistoceno.

La manera de afrontar el problema de los sesgos tafonómicos también diferencia a los análisis de escala local y de escala continental. En los análisis locales, la manejabilidad de los datos permite plantear diferentes posibles composiciones de los paleoecosistemas y, con ellos, intentar superar los sesgos tafonómicos. Como se comentó en secciones anteriores, en el análisis del nivel TD6-2 (Capítulo 3) (Rodríguez-Gómez et al., 2013) se incluyeron dos hipotéticos escenarios con dos grandes félidos (*Homotherium latidens* y *Panthera gombaszoegensis*) que pudieron estar presentes en el ecosistema de la Sierra de Atapuerca en esa época, ya que están presentes en esas cronologías en Europa (Reumer et al., 2003; Turner y Antón, 1996; Turner y Antón, 1997). En el Capítulo 4 (Rodríguez-Gómez et al., 2014), se tuvo en cuenta la propuesta de ausencia de evidencias humanas en el registro del nivel TD8 de Gran Dolina debida a que el acceso de la cueva podría ser pequeño, siendo favorable para la entrada de la especie de carnívoro (hiénido) que ejerció como agente acumulador pero no para los humanos (Blasco et al., 2011b). Para evitar este posible sesgo tafonómico, y comprobar el grado de competencia en la comunidad de consumidores secundarios, se incluyó un escenario que consideraba una población humana en el ecosistema que correspondería con este nivel (Rodríguez-Gómez et al., 2014). En este análisis, también se apunta la posibilidad de que no hubiesen quedado registrados en este nivel TD8 restos de proboscídeos u otro gran félido (*Homotherium latidens*). Con la metodología empleada se podrían haber incluido en otro escenario hipotético. En el estudio a escala continental, en el que se empleaba una cantidad importante de faunas locales (34 Faunas Locales (LFA o *Local Faunal Asseamblage*)), cada una con una composición ecológica diferente, se consideraba irrealizable un modo de proceder similar a los análisis a escala local. Para minimizar los sesgos se seleccionaron de un total de 93 LFAs. El criterio de inclusión era que tuviesen una composición de consumidores primarios y secundarios por encima de la mediana y se consideró que aquellos que cumplían este criterio representaban la fauna de sus paleoecosistemas (Capítulo 5). Por otro lado, al analizar por grupos en intervalos de tiempo, se esperaba que los posibles sesgos tafonómicos se difuminasen, teniendo una visión promedio de los recursos cárnicos disponibles en el ambiente y de la competencia entre los consumidores secundarios.

Se puede tratar de elaborar una interpretación del nicho ecológico que ocupaban los homininos desde el final del Pleistoceno Inferior al final del Pleistoceno Medio con los estudios realizados para esta tesis doctoral, pero han de tenerse en cuenta los tipos de análisis realizados y las diferencias entre ellos. La visión a escala local puede aportar una información que no se vislumbre a escala continental y no coincidir en sus conclusiones con esta, y viceversa.

6.3.- Nicho ecológico humano de Europa durante el Pleistoceno: recursos cárnicos

Como fue comentado en la Introducción, el objetivo general de la tesis doctoral era medir la disponibilidad de recursos para poblaciones humanas pleistocenas, analizar cómo podía afectar en la dispersión y poblamiento de Europa, y entender qué papel podían desempeñar en sus paleoecosistemas. Sirviendo de premisas en el modelo, se suponía que la disponibilidad de recursos cárnicos para los humanos dependía de:

- los recursos potenciales que podía haber en el medio en forma de consumidores primarios.
- la competencia con otros consumidores secundarios.
- las habilidades de los humanos para acceder a esos recursos.

En los análisis que componen esta tesis doctoral, se han tratado los recursos potenciales y la competencia por los recursos como propiedades generales de los paleoecosistemas, y las habilidades por acceder a los recursos en función de las preferencias de consumo de cada especie de consumidor secundario por cada tipo de presa.

Tanto a escala local como continental existe menor cantidad de recursos cárnicos, potencialmente disponibles, para los consumidores secundarios (TAB) en el final del Pleistoceno Inferior que al inicio del Pleistoceno Medio. Al final del Pleistoceno Medio se reducirían los recursos disponibles con respecto al periodo anterior (ver capítulos 3, 4 y 5).

En cuanto a la competencia en la comunidad de consumidores secundarios, no se observan coincidencias entre los análisis a escala local y a escala continental. A escala local en el yacimiento Gran Dolina se observa un incremento en el grado de competencia en la comunidad de consumidores secundarios del Pleistoceno Medio con respecto a la del Pleistoceno Inferior. A escala continental, se observa mayor grado de competencia en el final del Pleistoceno Inferior que durante el Pleistoceno Medio, siendo la competencia por los recursos similar entre el inicio y final en este último periodo (Pleistoceno Medio). La existencia de mayor grado de competencia en el nivel del Pleistoceno Medio (TD8) que en el del Inferior (TD6-2) se origina por el cambio en la estructura de la comunidad, posiblemente por la MPR (Maslin y Ridgwell, 2005), proponiéndose como posible causa de la falta de evidencias de presencia humana en la Sierra de Atapuerca en aquel periodo (TD8). Esta hipótesis basada en el grado de competencia podría ser correcta a nivel local aunque a nivel continental no se pueda apoyar porque los resultados hallados son opuestos a los de a nivel local. Hay que considerar que, con respecto a otros conjuntos faunísticos europeos del Pleistoceno Inferior, la Sierra de Atapuerca tuvo unos paleoecosistemas con un grado de competencia muy bajo (ver Capítulo 5). A partir de los resultados obtenidos con el estudio a escala continental se trató de dar una interpretación, desde el punto de vista paleoecológico, a la hipotética discontinuidad de la presencia humana en la Europa del inicio del Pleistoceno Medio (Jiménez-Arenas et al., 2011; Moncel, 2010; Moncel et al., 2013; Mosquera et al., 2013; Santonja y Pérez-González, 2010; Vallverdú et al., 2014). Ya que los recursos disponibles para los consumidores secundarios en el inicio del Pleistoceno Medio eran mayores que en el Epivillafranquiense, y la competencia menor, se planteó la hipótesis de que no se debiera a la disponibilidad de los recursos cárnicos, si no a otros aspectos independientes de los recursos del medio. Como en el caso de la hipótesis alternativa para explicar la ausencia de evidencias humanas en el nivel TD8, en Rodríguez-Gómez et al. (Enviado) (Capítulo 5) se propuso la posibilidad de que un cambio en las estructuras de las paleocomunidades del Pleistoceno Medio llevase a excluir a las poblaciones humanas de algunas paleocomunidades, pudiendo existir procesos de exclusión de hábitat o espacial, como en el caso de los perros salvajes y los guepardos (Laurenson et al., 1995; Mills y Gorman, 1997). Numerosos autores defienden que en el Epivillafranquiense se produjo un cambio en las comunidades de carnívoros que estuvo relacionado con la llegada de *Homo* a Europa (Arribas y Palmqvist, 1999; Martínez-Navarro y Palmqvist, 1996; Palombo, 2010; Turner, 1992; Turner, 1999). Rodríguez et al. (2012) consideran que fue el cambio en la estructura y arquitectura de las comunidades de carnívoros la que permitió esa primera dispersión humana por Europa. En el Capítulo 5 se realizó un análisis sencillo con el que se quería conocer si existía una exclusión entre *Homo* y alguna especie o género concreto. El análisis descartó este tipo de exclusión ya que aparecían humanos en al menos un paleoecosistema con todos los géneros y casi todas las especies. Sin embargo, la simplicidad de este análisis y la complejidad de los comportamientos de exclusión no pueden descartar esta hipótesis, para ello habrían de aplicarse otros modelos. Tal vez un análisis como el realizado por Rodríguez et al. (2013), pero enfocado en la Transición entre el Pleistoceno Inferior y Medio, podría proporcionar información más válida para esta cuestión.

Además de los hipotéticos comportamientos de exclusión para con los humanos que podrían explicar los resultados obtenidos en el análisis a escala continental, habría que tener en cuenta los comportamientos de inclusión. Con esto nos referiremos a las habilidades de los humanos para acceder a los recursos. En los análisis de los Capítulos 4 y 5 se incluye a la población humana con el perfil de consumo que se registra en el nivel TD6-2 de Gran Dolina (Saladié et al., 2011). Según los estudios de Saladié y colaboradores (2011; 2014) en el nivel TD6-2, se considera que los humanos accedieron primariamente a los recursos cárnicos siendo los carnívoros los que tendrían un acceso secundario. Otros investigadores defienden que pese a que el acceso a los recursos cárnicos durante el Pleistoceno Inferior fuera primario, se debía de realizar por cleptoparasitismo (Espigares et al., 2013), defendiendo Palmqvist et al. (2011) la dependencia de la carroña de esas primeras poblaciones humanas en Europa. Turner et al. (2008) sostienen que durante el Pleistoceno Medio se produjo la sustitución de grandes félidos, como los dientes de sable, por modernos félidos que rendían mejor provecho de sus presas. Esto llevó a una pérdida de recursos carroñeables llegando a desaparecer este nicho trófico explotado por el hombre (Palmqvist et al., 2011). Con la pérdida de este nicho trófico se elevarían las competencias en otros, lo que llevaría a otro escenario ecológico, que provocaría la extinción de la hiena gigante de rostro corto (*Pachycrocuta brevirostris*), por su tamaño y su alta especialización anatómica, derivada de su perfil de carroñero estricto, forzando a *Homo* a explotar otros nichos (Palmqvist

Representación de una escena de transporte de una presa cazada por humanos del Pleistoceno Inferior. Ilustración de Gonzalo Rodríguez Gómez.

et al., 2011). Los cambios en la composición de los carnívoros pudieron forzar a los humanos a mejorar conductual y tecnológicamente para competir con aquellos (Arribas y Palmqvist, 1999). Como se comentó anteriormente, a mediados del Pleistoceno Medio, tiene lugar un incremento en el número de yacimientos con evidencias de presencia humana coincidiendo con la aparición del Achelense o Modo Tecnológico 2 (por ejemplo, Doronichev y Golovanova, 2010; Jiménez-Arenas et al., 2011; Mania y Vlcek, 1999; Moncel, 2010; Ollé et al., 2013; Roberts y Parfitt, 2000; Roebroeks, 2001; Thieme, 1997). Según los resultados del Capítulo 5, el grado de competencia es similar a lo largo del Pleistoceno Medio, no existiendo diferencias significativas entre el periodo inicial y el final. A nivel continental y, teniendo en cuenta lo anterior, podría plantearse que los humanos tuvieran una alta dependencia de los carnívoros para conseguir acceder a los recursos cárnicos durante el final del Pleistoceno Inferior e inicios del Pleistoceno Medio, hasta la aparición del Achelense o Modo tecnológico 2. Las mejoras tecnológicas y sociales del Modo 2 (Carbonell et al., 2010b) pudieron permitir una independencia de los otros consumidores secundarios para acceder a los recursos cárnicos, como apuntaban Arribas y Palmqvist (1999), y la expansión por Europa. Carbonell et al. (2010b) defienden que el Modo 2 se expandió por Europa debido a un incremento demográfico en Próximo Oriente y en África, mientras que otros investigadores apoyan que sería una sustitución de las poblaciones de *Homo antecessor* por individuos de una especie de hominino africana, *Homo heidelbergensis*, la que traería consigo la tecnología Achelense o Complejo Tecnológico Modo 2 (Jiménez-Arenas et al., 2011; Santonja y Pérez-González, 2010). Las estrategias de subsistencia por parte de los humanos fueron eficientes tanto con la tecnología Olduvayense como con la Achelense (Blasco et al., 2013; Huguet et al., 2013), aunque es con el Achelense con el que se produce un incremento demográfico y una mayor expansión (Roebroeks, 2001). Por los resultados obtenidos a nivel continental, se puede proponer que los humanos con tecnología pre-Achelense podrían estar presentes en paleoecosistemas del Pleistoceno Inferior tardío, que presentaban una alta competencia por los recursos cárnicos, y Medio temprano, pero tal vez obtendrían la carne principalmente a través del carroñeo que presentaría un bajo grado de competencia. Esta interpretación sugiere que la carroña tendría un papel muy importante en el nicho trófico humano, como se defiende para los humanos que poblaron Orce en el Pleistoceno Inferior (Espigares et al., 2013; Palmqvist et al., 2011), muy dependientes de otros consumidores secundarios. Esta es una interpretación dada a los resultados obtenidos en el análisis a escala continental, desde un punto de vista exclusivamente paleoecológico, sin tener en cuenta el posible efecto de otros parámetros. Aunque, hay que tener en cuenta que varios estudios de zooarqueología y tafonomía muestran evidencias de actividades de caza por los homininos europeos del Pleistoceno Inferior (Díez et al., 1999; Gaudzinski, 2004; Saladié et al., 2011).

A escala local, según los resultados de los capítulos 3 y 4 los humanos están presentes en la Sierra de Atapuerca cuando existe una abundancia de recursos cárnicos tan importante como para mantener a la población de consumidores secundarios con densidades máximas (TD6-2) pero no cuando no llegan a cubrir todos sus requerimientos (TD8). La alta cantidad de recursos cárnicos de un paleoecosistema como el del nivel TD6-2, debida a la baja competencia entre los consumidores secundarios, podría permitir a los humanos acceder a estos. Sin embargo, un incremento en la competencia podría reducir el acceso, haciendo insostenible a la población humana (Rodríguez-Gómez et al., 2014). La riqueza de los yacimientos de la Sierra de Atapuerca ha permitido dar unos perfiles socioeconómicos de los humanos que la habitaron en el Pleistoceno Inferior (Bermúdez de Castro et al., 2006; Bermúdez de Castro et al., 1995; Blasco et al., 2011a; Carbonell et al., 2010a; Carbonell et al., 1999; Fernández-Jalvo et al., 1999; Huguet, 2007; Huguet et al., 2013; Rodríguez et al., 2011; Saladié, 2009; Saladié et al., 2011; Saladié et al., 2014). Se considera que estos humanos tenían un comportamiento altamente oportunista, por el consumo variado de fuentes animales que incluyen mamíferos de diferentes tallas, aves y reptiles (Blasco et al., 2011a; Huguet et al., 2013; Rodríguez et al., 2011), y que su acceso a estos era primario (Saladié et al., 2011; Saladié et al., 2014). El acceso primario unido a la diversidad de recursos que consumían apoyan la idea de un control de los recursos del medio por la población humana, situándolos en lo más alto de la pirámide trófica (Huguet

Representación de una cueva utilizada por los humanos para refugiarse de los carnívoros durante el Pleistoceno Inferior en la Sierra de Atapuerca. Ilustración de Gonzalo Rodríguez Gómez.

et al., 2013; Saladié et al., 2014). Además, el transporte y la caza de animales muestra un grado de cooperación social (Saladié et al., 2011). Pese a este perfil de especie dominadora, se constata la ausencia de presencia humana en la Sierra de Atapuerca en un intervalo de tiempo entre 0,9 y 0,5 Ma (Mosquera et al., 2013). Un estudio reciente, considera que el nivel TD6-2 actuaba tanto como campamento base para los humanos como de refugio para evitar competir con los carnívoros (Saladié et al., 2014). La flexibilidad en las estrategias de subsistencia de las poblaciones humanas en la Sierra de Atapuerca es interpretada como una fortaleza de la especie (Huguet et al., 2013; Saladié et al., 2014) pero podría ser interpretada también como una incapacidad para la especialización en explotar un recurso concreto eficientemente, teniendo que diversificarse. La flexibilidad o capacidad de adaptarse a las condiciones ambientales es una fortaleza conductual porque puede sobreponerse a cambios en la disponibilidad de recursos del medio pero puede mostrar una falta de especialización, al no poder explotar eficientemente el medio. La aparición de poblaciones humanas con mejoras cognitivas, en estrategias de caza, en técnicas de procesamiento de los alimentos (Kahlke et al., 2011), con una tecnología más eficiente como la Achelense, junto con mejoras en la organización social (Carbonell et al., 2010b), pudieron llevar a un control efectivo de los recursos del medio. En la paleocomunidad del nivel TD6-2 de Gran Dolina, la hiena manchada (*Crocuta crocuta*) es el gran carnívoro registrado en el nivel. Esta especie en la actualidad tiene un comportamiento flexible que le permite acceder a la carne desde un perfil de cazador estricto hasta como uno de carroñero estricto (Cooper et al., 1999; Henschel y Skinner, 1990; Mills y Hofer, 1998; Palmqvist et al., 2011). En el hipotético escenario de una población humana carroñera, esta especie debiera de haber proporcionado las carcasas que consumían los humanos en el paleoecosistema de TD6-2. Según un reciente estudio (Pobiner, 2015), en el que se analizaron las carcasas de las que se alimentaron (5 de mamíferos mayores de 115 kg), cuando la hiena manchada actual se encuentra en grupos de menos de 10 individuos, en menos de un 30% de los huesos dejaron algún resto de carne, teniendo que en más del 70% de los huesos no se encontró ningún resto de carne. En el caso de las carcasas de mamíferos de menos 115 kg, no se halló ningún resto de carne. Según los resultados de este estudio, se podría considerar que los restos que se podrían encontrar en las carcasas de las que se habrían alimentado las hienas manchadas podrían haber aportado alguna cantidad de carne a las poblaciones humanas de Atapuerca, pero no serían su única vía si el porcentaje de la carne en su dieta era de entre un 30 y un 60 % (Jenike, 2001; Leonard et al., 2007). Además de *Crocuta crocuta*, la paleocomunidad de TD6-2 podría haber contado con un tigre dientes de sable (Rodríguez-Gómez et al., 2013), que podría haber generado carcasas accesibles para *Homo* como las observadas en Fuente Nueva-3 (Espigares et al., 2013). Si los humanos del nivel TD6-2 hubiesen sido carroñeros, las especies de tigres dientes de sable serían buenas candidatas para ser las productoras de este tipo de sustento para los humanos. Según el perfil de consumo de presas, tanto *Homotherium latidens* como *Panthera gombaszoegensis* (jaguar europeo) presentarían unos perfiles de consumo con el foco de la categoría de presas preferentes desplazada hacia pesos más altos que los de la hiena manchada y el *Homo antecessor* (ver Table 2 del Capítulo 5) por lo que, tampoco se podría defender que alguna especie de tigres dientes de sable hubiese surtido a los humanos del nivel TD6-2 de la Sierra de Atapuerca de carroña. Según la hipótesis de un humano carroñero, en el nivel TD8 la hiena manchada podría competir con la hiena rayada (*Hyaena* sp.) por las carcasas que generaría el jaguar europeo, dejando pocos recursos para el aprovechamiento por las poblaciones humanas de la Sierra de Atapuerca en este periodo. Intentando conjugar la hipótesis propuesta a escala continental de la inclusión de los humanos en los paleoecosistemas europeos del Pleistoceno Inferior por estrategias carroñeras, la baja cantidad de recursos cárnicos que no aprovecharían las hienas manchadas de los cadáveres, junto a las evidencias encontradas de consumo por parte de los humanos en el nivel TD6-2, sugerirían que su acceso primario (Díez et al., 1999; Saladié et al., 2011) debía de ser a las presas recién abatidas por grandes depredadores como los dientes de sable o, incluso, las propias hienas, a semenjanza de lo registrado en Fuente Nueva-3 (Espigares et al., 2013).

No pudiendo defenderse que los humanos en la Sierra de Atapuerca durante el Epivillafranquiense y el inicio del Galeriense fuesen exclusivamente dependientes de la carroña, y volviendo a lo que se comentaba anteriormente de un humano con un comportamiento flexible y oportunista (Blasco et al., 2011a; Huguet et al., 2013; Rodríguez et al., 2011) pero no dominador del ecosistema, se podría proponer como hipótesis que los humanos sobrevivían por sus capacidades adaptativas pero que su diversificación de la explotación de los recursos del medio mostraría su incapacidad de especializarse y dominar el ecosistema, lo que conllevaría la imposibilidad de excluir a otros consumidores secundarios cuando tuviesen que competir por recursos similares. Los cambios en las estructuras de las comunidades que se produjeron con la MPR pudieron provocar rupturas en procesos de inclusión, como la explotación del nicho de carroña comentado anteriormente, y provocando procesos de exclusión como se propuso para explicar la ausencia de *Homo* en el paleoecosistema de TD8 (Capítulo 4) (Rodríguez-Gómez et al., 2014). Apoyando esta imagen de unos humanos poco dominadores de sus ecosistemas, Finlayson et al. (2011) defienden la preferencia de *Homo* por paisajes mosaico más que por paisajes homogéneos, que fueron ignorados por los humanos a través del Paleolítico, pese a que los grupos humanos fueron capaces de habitar una amplia variedad de medios (Carrión et al., 2011). La preferencia de *Homo* por ecosistemas heterogéneos podría indicar su incapacidad para competir directamente frente a especialistas y su necesidad de ambientes diversos para obtener los recursos usando estrategias generalistas (Rodríguez-Gómez et al., 2014).

Representación de una escena de canibalismo por la especie *Homo antecessor*. Ilustración de Gonzalo Rodríguez Gómez.

Como se comentó al inicio de esta sección, el acceso a recursos cárnicos por parte de los humanos, dependía de los que pudiese haber disponibles a partir de las poblaciones de consumidores primarios, de la competencia por ellos con los consumidores secundarios y de las habilidades de los humanos para su acceso. Poniendo el foco sobre el comportamiento caníbal registrado en el nivel TD6-2, se asume habitualmente que esta fue una estrategia recurrente en la lucha por el territorio con otros humanos (Bermúdez de Castro et al., 2006; Carbonell et al., 2010a; Saladié et al., 2012; Saladié et al., 2014). Se descarta la posibilidad de un canibalismo por escasez de recursos cárnicos, como propuso Turner (1999), dada la riqueza del registro de fauna de este nivel (Bermúdez de Castro et al., 2006; Carbonell et al., 2010a; Fernández-Jalvo et al., 1999; Huguet et al., 2013; Saladié et al., 2012). En los análisis llevados a cabo en esta tesis doctoral, se cuantifican los recursos cárnicos de la población humana en el nivel TD6-2 mostrando una comunidad excepcionalmente rica en este tipo de recursos. Pero la riqueza de recursos en el ecosistema no quiere decir que los humanos pudiesen acceder a ellos. Sería interesante en futuras reevaluaciones de este comportamiento plantear si las habilidades de los humanos permitían acceder a la riqueza del ecosistema en estos momentos.

La metodología utilizada no es suficiente para estudiar el efecto de las composiciones y estructuras de las paleocomunidades, como los mecanismos de inclusión y exclusión, ni tampoco para estudiar los mecanismos que influyeron en las tendencias evolutivas, como las de la Revolución de Mitad del Pleistoceno (MPR) (Maslin y Ridgwell, 2005). Sería necesario avanzar en metodologías que permitieran analizar estos aspectos de las paleocomunidades, para abordar con mayor profundidad la definición del nicho ecológico que habrían ocupado los homininos durante el Pleistoceno en Europa.

6.4. Referencias

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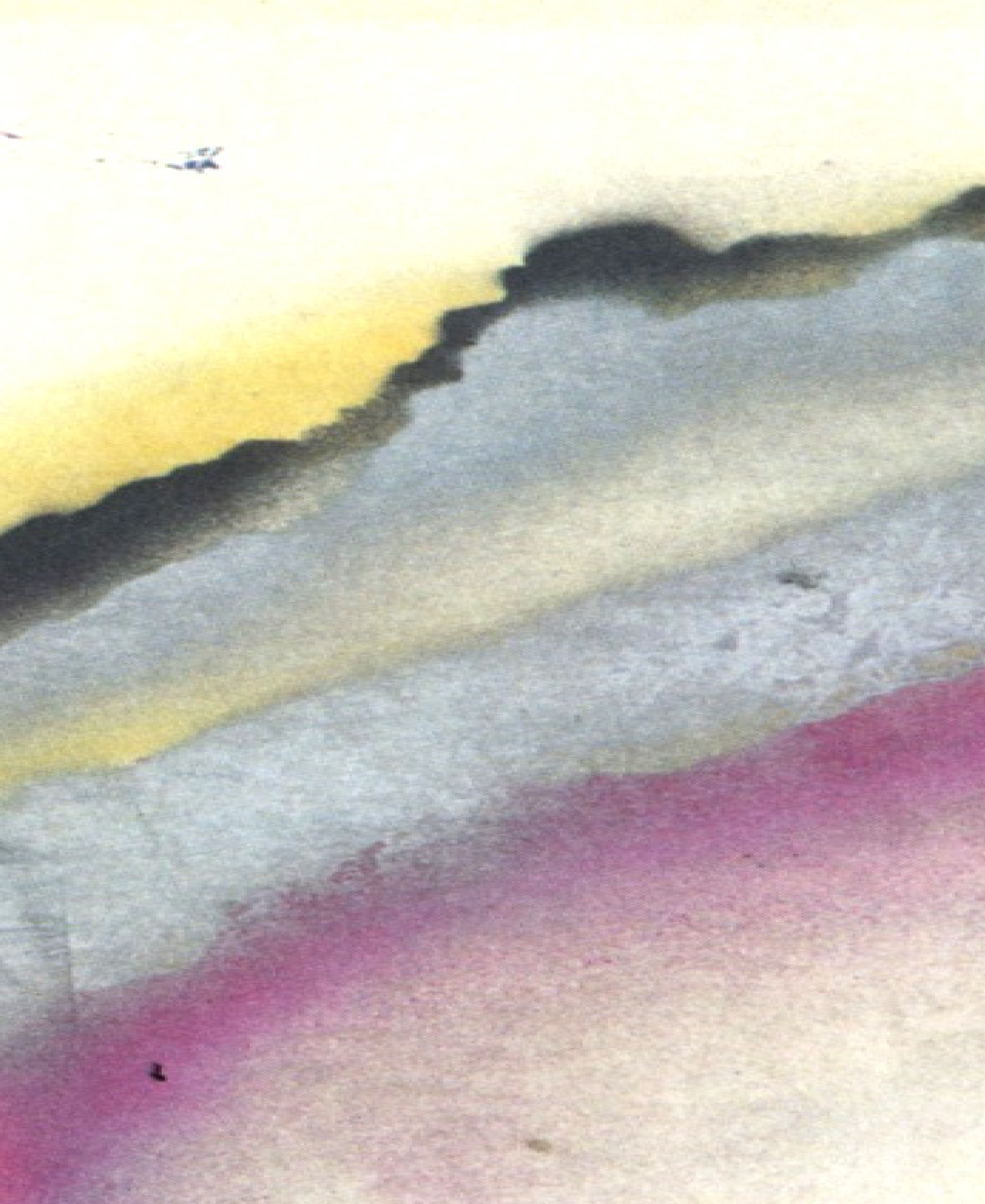


Conclusions/Conclusiones

En lás páginas anteriores:
Cuadro sin título de la serie *Tropical screens*. Autor: Gonzalo Rodríguez Gómez.

Chapter 7.- Conclusions

The application of mathematical models to the study of the trophic dynamics of paleocommunities has been shown as a useful tool to investigate the meat resources availability for the hunter-gatherer Paleolithic populations. This availability and the competition for resources condition the opportunities of survival and they represent some of the main drivers for the dispersal of species. The application of models for describe the human paleoecology may provide relevant information to characterize the role played by humans in the paleocommunities.

The methodology applied in this PhD thesis, was developed by the research groups of Paleophysiology and Paleoecology at CENIEH (National Research Centre on Human Evolution) located in Burgos. This methodology was designed to analyze the trophic relationships among the primary and secondary consumers in the Pleistocene macromammal paleocommunities, applying it in this PhD thesis to analyze the sustainability of the human populations according to their access to meat resources in those paleocommunities. The methodology assumes that the access to the meat of macromammals by the humans depends on the abundance of primary consumers, the human abilities and preferences, and on the competition with others secondary consumers for the primary consumers. For this PhD thesis, the model was applied at a local scale in two stratigraphic levels from Gran Dolina site at the Sierra de Atapuerca (TD6-2 and TD8) and at a continental scale in European sites dated between 1.1 and 0.2 millions of years

(Ma). Results obtained with these analyses led to the following conclusions:

1.- The applied methodology has shown to be a useful tool to characterize the macromammal paleocommunity and to reflect the sustainability of the human populations and other secondary consumers (see Section 6.1.1). It allows to use population and mortality profiles of primary consumers to recreate the paleoecosystems and to study the effect on the paleocommunities of the inclusion of species not recorded in the fossil assemblages.

2.- The methodology allows comparing the degree of satisfaction of the requirements of secondary consumers in different paleoecosystems through different standardized indexes. These have permitted to compare the paleocommunities at local and continental scales. The resolution of these indexes allowed dealing with hypotheses as the discontinuity and dispersal of human populations across Europe due to the increase of competition with other secondary consumers during the Pleistocene.

3.- The Sierra de Atapuerca ecosystem was very rich 900,000 years ago (TD6-2). Results obtained for the community of large mammals of the TD6-2 level show a paleoecosystem very rich in meat resources provided by the guild of primary consumers. This allowed secondary consumers to reach their maximum expected densities and, even, to support secondary consumer populations not present in the fossil record of this level, i.e. populations of the saber-tooth tiger *Homotherium latidens*.

4.- The richness in meat resources of the TD6-2 paleoecosystem, quantified by the application of the methodology, supports that humans of this level, attributed to the *Homo antecessor* species, practiced cannibalism although there were abundant meat resources in the environment. Since the methodology applied here analyses the paleocommunities at a broad time scale, it is not possible to exclude the existence of punctual events of scarcity of resources, but the cannibalism is recurrent at this level.

5.- At the beginning of the Middle Pleistocene there was absence of human presence at the Sierra de Atapuerca. When the methodology was applied to the TD8 level, to represent this period, and the results compared with the results for the TD6-2 paleocommunity, representing the Early Pleistocene, it was proposed that the degree of competition for meat resources among the secondary consumers could block the presence of *Homo* in the TD8 paleocommunity. This supports the image of *Homo* as bad competitor, and its exclusion from the TD8 paleoecosystem by the overlapping of niches with other secondary consumers.

6.- The analysis at a continental scale in Europe did not coincide with the results obtained at a local scale at the Gran Dolina levels. The competition for meat resources among secondary consumers was higher in the Early Pleistocene than in the Middle Pleistocene. This factor appeared as relevant for the discontinuity in human presence at local scale at the beginning of the Middle Pleistocene, but it was not significant at the continental scale.

7.- In the continental analysis, *Homo* does not seem to suffer spatial or habitat exclusion by other genus, thus, there is not complete overlapping of niches. This factor cannot be considered the reason for the hypothetical decrease of human presence in the Middle Pleistocene.

8.- The faunal turnovers of the MPR (Mid-Pleistocene Revolution) might be part of the explanation for the discontinuity in the human presence. Initially, when the composition and architecture of the food web changed, the dispersal of the human populations in the Middle Pleistocene paleoecosystems could became more difficult.

9.- Taking into account the previous point, it is proposed that both exclusion and inclusion behavior could be the driver of the hypothetical human discontinuity.

10.- As general hypotheses, it is proposed that the high competition for meat resources in the Early Pleistocene, joint together with the difficulties to compete in this conditions, could led humans to an opportunistic and flexible behavior. When carrion yielded by the saber-tooth tigers of this period was abundant, it allowed a scavenger behavior for humans due to the low competition for this resources with other secondary consumers. After the MPR, there were changes in the communities and humans could survive in the ecosystems thanks to their flexible behavior. Together with this, their presence could be affected by their inability to integrate in the communities, decreasing their populations. The improvements in the processing of resources due to cultural and cognitive developments that appeared with *Homo heidelbergensis* could permit the demographic expansion observed at the mid of the Middle Pleistocene through a higher control of the environment.

Capítulo 7.- Conclusiones

La aplicación de modelos matemáticos al estudio de las dinámicas tróficas de las paleocomunidades se ha mostrado como una metodología útil para investigar la disponibilidad de recursos cárnicos para las poblaciones cazadoras-recolectoras paleolíticas. Esta disponibilidad y la competencia por ellos condicionan las oportunidades de supervivencia y representan uno de los motores principales de las dispersiones de las especies. La aplicación de modelos que describan la paleoecología humana puede aportar información relevante para conocer cuál era el papel de los humanos en sus paleocomunidades.

En esta tesis doctoral, se ha aplicado una metodología desarrollada por los grupos de investigación de Paleofisiología y Paleoecología del CENIEH (Centro Nacional de Investigación sobre la Evolución Humana) en Burgos. Esta metodología fue diseñada para analizar las relaciones tróficas entre los consumidores primarios y secundarios de paleocomunidades de macromamíferos del Pleistoceno, aplicándola en esta tesis doctoral para analizar la sostenibilidad de las poblaciones humanas según su acceso a recursos cárnicos procedentes de esta comunidad. La metodología contempla que el acceso de los humanos a carne de macromamíferos dependía de la abundancia de consumidores primarios, de las capacidades y preferencias humanas y de la competencia con otros consumidores secundarios por estos. Para esta tesis doctoral, el modelo fue aplicado a escala local en dos niveles estratigráficos del yacimiento Gran Dolina de la Sierra de Atapuerca (TD6-2 y TD8) y a nivel continental en yacimientos europeos de entre 1,1 y 0,2 millones de años (Ma). Los resultados alcanzados con estos análisis llevan a las siguientes conclusiones:

1.- La metodología aplicada ha mostrado ser una herramienta útil para caracterizar la paleocomunidad de macromamíferos y reflejar la sostenibilidad de las poblaciones humanas y de otros consumidores secundarios (ver sección 6.1.1). Permite utilizar perfiles de población y mortalidad de los consumidores primarios, con los que recrearlas en los paleoecosistemas y estudiar el efecto que hubiesen tenido en las paleocomunidades especies no registradas en los yacimientos.

2.- La metodología permite comparar los grados de satisfacción de requerimientos de los consumidores secundarios en diferentes paleoecosistemas a través de diferentes índices estandarizados. Estos han permitido comparar las paleocomunidades a escala local y continental. La resolución de estos índices posibilitó abordar hipótesis como la de la discontinuidad y dispersión de poblaciones humanas en Europa por el incremento de la competencia con otros consumidores secundarios durante el Pleistoceno.

3.- El ecosistema de la Sierra de Atapuerca era muy rico hace 900.000 años (TD6-2). Los resultados obtenidos en la paleocomunidad de grandes mamíferos del nivel TD6-2 muestran un paleoecosistema muy rico en recursos cárnicos provenientes de la comunidad de consumidores primarios. Estos permiten a los consumidores secundarios alcanzar densidades máximas esperadas e, incluso, sostener poblaciones de consumidores secundarios que no están en el registro fósil de este nivel como, por ejemplo, la del dientes de sable *Homotherium latidens*.

4.- La riqueza en recursos cárnicos del paleoecosistema de TD6-2, cuantificada a partir de la aplicación de la metodología, apoya que los humanos de este nivel, atribuidos a la especie *Homo antecessor*, practicaron el canibalismo a pesar de que existían abundantes recursos cárnicos en el medio. Como la metodología aplicada analiza las paleocomunidades en una amplia escala de tiempo, no se podrían excluir episodios puntuales de escasez de recursos aunque se haya planteado que el canibalismo sea recurrente en el registro de este nivel.

5.- En la Sierra de Atapuerca al inicio del Pleistoceno Medio hay ausencia de presencia humana. Al aplicar la metodología al nivel TD8, como representante de este periodo, y comparar los resultados con los obtenidos para la paleocomunidad de TD6-2, como representante del Pleistoceno Inferior, se postuló que el grado de competencia por los recursos cárnicos entre los consumidores secundarios pudo bloquear la presencia de *Homo* en la paleocomunidad de TD8. Esto apoyaría la imagen de un *Homo* que sería poco competitivo, con su exclusión del paleoecosistema de TD8 por solapamiento de nicho con otros consumidores secundarios.

6.- El análisis a escala continental en Europa no coincidió con el obtenido a escala local en los niveles de Gran Dolina. Las competencias por los recursos cárnicos entre los consumidores secundarios eran mayores en el Pleistoceno Inferior que en el Pleistoceno Medio. Este factor que aparecía como relevante a escala local para la discontinuidad humana al comienzo del Pleistoceno Medio, no era significativo a escala continental.

7.- En este análisis a escala continental no aparece exclusión de hábitat o espacial de *Homo* por ningún género, por lo que no hay un solapamiento completo de nichos. Este factor no puede ser considerado como la razón de una hipotética reducción de la presencia humana en el Pleistoceno Medio.

8.- Las sustituciones faunísticas de la MPR (Revolución de Mitad del Pleistoceno) podrían ser parte de la explicación de la discontinuidad de la presencia humana. Inicialmente, al modificarse la composición y arquitectura en las redes tróficas podría resulta difícil la dispersión de las poblaciones humanas en los paleoecosistemas del Pleistoceno Medio.

9.- Teniendo en cuenta el punto anterior, se plantea que tanto los comportamientos de exclusión como los de inclusión podrían ser motores de la hipotética discontinuidad humana.

10.- Se propone como hipótesis general que las altas competencias por los recursos cárnicos en el Pleistoceno Inferior, junto a las dificultades para competir en estas condiciones, llevarían a los humanos a un comportamiento oportunista y flexible. Cuando tenía lugar una abundancia de carroña producida por los tigres dientes de sable en este periodo, podría producirse un comportamiento carroñero de los humanos por la baja competencia que tenía este recurso frente a otros consumidores secundarios. Después de la MPR se producirían cambios en las comunidades y los humanos sobrevivirían en los ecosistemas por su flexibilidad de comportamientos. Unido a esto, se vería afectada su presencia, por sus debilidades para integrarse en las comunidades, reduciéndose sus poblaciones. Las mejoras en el procesamiento de los recursos por desarrollos culturales y cognitivos que aparecieron con la especie *Homo heidelbergensis* pudieron permitir la expansión demográfica observada a mediados del Pleistoceno Medio por un mayor control del medio.

Valoración y futuro

En lás páginas anteriores:
Cuadro *Nº2- Pareja de bailarines*. Autor: Gonzalo Rodríguez Gómez.

Capítulo 8.- Valoración del trabajo de tesis doctoral y líneas a abordar en el futuro

La tesis doctoral se planteó inicialmente para modelizar los recursos tróficos que tendrían las poblaciones de cazadores-recolectores paleolíticas. El interés de esta línea de trabajo es poder contextualizar a los humanos en los ecosistemas del pasado en los que desarrollaron sus vidas porque el marco ecológico tuvo que ser clave en la evolución humana. La modelización se focalizó en describir las relaciones tróficas de origen animal y, más concretamente, en los grandes mamíferos porque representan el recurso cárnico esencial durante el Pleistoceno. Por tanto, en la modelización quedaron fuera otras fuentes importantes de recursos como los de origen vegetal y otras pequeñas presas. De esta forma, la descripción que se llevó a cabo con la aplicación de la metodología desarrollada para modelizar los ecosistemas pasados representaba una porción importante de la dieta humana pero no completa. Se consideró que el humano cubriría totalmente sus requerimientos en otras fuentes para centrar el análisis en la competencia por los recursos cárnicos con otros consumidores secundarios, que se ha defendido en la literatura como uno de los más importantes condicionantes para las poblaciones humanas en este periodo.

La aplicación de esta metodología ha mostrado que es una herramienta interesante y útil para conocer las condiciones ecológicas en la que se desenvolvió la vida humana en Europa durante el periodo del Pleistoceno que engloba el Epivillafranquiense y el Galeriense. Probablemente sea también útil para aplicar en otros periodos de tiempo y con otros tipos de comunidades si se realizan los ajustes convenientes. Considerando que la metodología es mejorable, hay que mencionar que la estimación de los recursos cárnicos de los que podían valerse las poblaciones humanas del Pleistoceno no se había trabajado anteriormente con este grado de resolución (ver sección 6.1.1). La utilidad del método justifica que sea necesario seguir avanzando en su desarrollo y refinamiento. Para progresar en su precisión y reflejar de forma más real el comportamiento de los paleoecosistemas, podría ser útil trabajar en mejorar los siguientes aspectos (ver sección 6.1.2): estructura de la población de machos, proporción de sexos, estimación de densidades, masa corporal de la poblaciones de consumidores secundarios, requerimientos por clase de edad de los consumidores secundarios, cuantificación de la biomasa consumida con acceso primario y/o secundario, etc. Con el incremento en el grado de precisión se podrá analizar con más detalle la disponibilidad de recursos en los paleoecosistemas y la competencia por ellos.

La aplicación de la metodología empleada para modelizar los paleoecosistemas pasados ha aportado información sobre parte del nicho ecológico de las poblaciones de cazadores recolectores y con ella, las condiciones ecológicas en las que se encontraron con respecto a la fuente de carne y la competencia con otros consumidores secundarios. El empleo de esta herramienta ha permitido abordar hipótesis sobre el canibalismo en el nivel TD6-2 del yacimiento Gran Dolina de la Sierra de Atapuerca o sobre la ausencia de presencia humana en este yacimiento y en el continente europeo durante el inicio del Pleistoceno Medio. El grado de resolución ha permitido comparar las condiciones ecológicas en las que se hallaban diferentes conjuntos faunísticos y proponer hipótesis sobre sus diferencias o similitudes. Las posibilidades que brinda la línea de investigación de esta tesis doctoral sobre el conocimiento de aspectos relevantes en la evolución humana, como la relación con el medio y la interacción con otras especies, hace que sea necesario ampliar la inversión de trabajo y esfuerzo en ella.

La aplicación del modelo también ha generado nuevas cuestiones que no han podido resolverse en los análisis de la tesis doctoral. Una de estas cuestiones es la explicación de la ausencia humana en TD8. El análisis a escala local apuntaba a una ausencia debida al grado de competencia con otros consumidores secundarios por los recursos cárnicos, pero el análisis a escala continental mostraba que los humanos soportaban altos grados de competencia. Se propuso que a nivel local la ausencia de la presencia humana fuese debida a una exclusión por solapamiento de nichos con dos especies de consumidores secundarios en TD8, pero en el análisis continental no se observaba una exclusión específica, lo que no rechazaba una exclusión de las redes tróficas por sus estructuras. Para dar respuesta a esta cuestión será necesario trabajar en analizar procesos de exclusión e inclusión espacial, asi como en profundizar en los perfiles tróficos de los humanos durante el Epivillafranquiense y el inicio del Galeriense.

En el futuro, además de abordar los refinamientos metodológicos planteados anteriormente, sería interesante completar la modelización del nicho trófico humano. Para ello habría que incluir algunos parámetros en la modelización y especificar otros. Uno de estos sería precisar en la procedencia de los recursos en las dietas de los consumidores secundarios, es decir, especificar los porcentajes de carne en la dieta que procederían de cada especie de consumidor primario. También sería interesante incluir otros recursos de origen animal además de los recursos tróficos provenientes de los grandes mamíferos, no contemplados en ese conjunto, sobre todo para aplicar esta metodología en periodos más modernos, en los que se amplifica el abanico de recursos tróficos para los humanos. Por otra parte, para completar la visión del nicho trófico durante la evolución humana, los recursos tróficos de origen vegetal deberían ser tenidos en cuenta. Este tipo de recurso tiene y ha tenido un importante papel en la dieta humana a lo largo de su evolución. Al profundizar en la relación con la fracción vegetal de la dieta, se podrá caracterizar al completo el perfil trófico de estas poblaciones y, con ello, se podrán abordar aspectos relevantes de la evolución humana y completar la visión proporcionada con los análisis de esta tesis doctoral.

Appendix/Apéndices

En lás páginas anteriores:
Cuadro sin título, de la serie *Brut mementoes.* Autor: Gonzalo Rodríguez Gómez.

Appendix A.- Modeling trophic resource availability for the first human settlers of Europe: The case of Atapuerca TD6

Table S1. Data on living species used to estimate the values of some physiological variables in fossil species. For Families with data for more than two species (Cervidae, Bovidae, Ursidae and Rhinocerotidae) allometric equations relating average body weight of the species in kg (W), litter size (number of individuals) (Lt), average weight at birth in kg (Wb), age at reproductive maturity in years (RM), longevity in years (L) and breeding interval in years (BI) were obtained (Table S3).

Bovidae	**W**		**Lt**		**Wb (kg)**		**RM**		**L**		**BI**	
Bison bison	579	Meagher, 1986	1.0	Meagher, 1986	20.0	Meagher, 1986	3.0	Meagher, 1986	14	Meagher, 1986	1.0	Hutchins et al., 2003
Bison bonasus	700	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993	30.0	Nowak, 1999	3.0	MacDonald and Barret, 1993	22	MacDonald and Barret, 1993	1.5	MacDonald and Barret, 1993
Bubalus midorensis	300	Custodio et al., 1996	1.0	Nowak, 1999					25	Nowak, 1999	2.0	Custodio et al., 1996
Bos mutus	700	Leslie and Shaller, 2009	1.0	Leslie and Shaller, 2009	18.0	Geist, 1998	3.5	Leslie and Shaller, 2009	25	Nowak, 1999	1.0	Nowak, 1999
Syncerus caffer	700	Nowak, 1999	1.0	Hutchins et al., 2003	40.0	Nowak, 1999	4.8	Hutchins et al., 2003	30	Nowak, 1999	2.0	Hutchins et al., 2003
Bubalus bubalis	950	Hutchins et al., 2003	1.0	Hutchins et al., 2003			1.5	Hutchins et al., 2003	25	Nowak, 1999	2.0	Hutchins et al., 2003
Bos taurus	900	Hutchins et al., 2003										

Cervidae	**W**		**Lt**		**Wb**		**RM**		**L**		**BI**	
Hydropotes inermis	11	MacDonald and Barret, 1993	3.0	MacDonald and Barret, 1993	0.8	MacDonald and Barret, 1993	0.5	MacDonald and Barret, 1993	11	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993
Muntiacus reevesi	14	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993	0.8	MacDonald and Barret, 1993	19	MacDonald and Barret, 1993	0.6	MacDonald and Barret, 1993
Mazama americana	20	Hutchins et al., 2003	1.0	Hutchins et al., 2003	0.5	Nowak, 1999			14	Hutchins et al., 2003		
Capreolus capreolus	27	Hutchins et al., 2003	1.9	MacDonald and Barret, 1993	1.8	MacDonald and Barret, 1993	1.2	MacDonald and Barret, 1993	20	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993
Capreolus pygargus	43	Hutchins et al., 2003	1.0	Hutchins et al., 2003					3	Hutchins et al., 2003		
Cervus nippon	53	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993	3.0	MacDonald and Barret, 1993	1.4	MacDonald and Barret, 1993	15	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993
Dama dama	53	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993	4.5	MacDonald and Barret, 1993	1.3	MacDonald and Barret, 1993	16	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993

Table S1 (continued)

Odocoileus hemionus	65	Hutchins et al., 2003	2.0	Nowak, 1999	2.5	Nowak, 1999	2.0	Hutchins et al., 2003	6	Hutchins et al., 2003		
Odocoileus virginianus	81	Hutchins et al., 2003	1.0	MacDonald and Barret, 1993	2.5	MacDonald and Barret, 1993	2.0	MacDonald and Barret, 1993	15	MacDonald and Barret, 1993		
Cervus axis	88	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993	13.5	MacDonald and Barret, 1993	1.3	MacDonald and Barret, 1993	20	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993
Rangifer tarandus	90	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993	6.0	MacDonald and Barret, 1993	1.5	MacDonald and Barret, 1993	28	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993
Cervus eldii	120	Hutchins et al., 2003	1.0	Hutchins et al., 2003			1.5	Hutchins et al., 2003			1.0	Hutchins et al., 2003
Blastocerus dichotomus	125	Nowak, 1999	1.0	Nowak, 1999			1.0	Hutchins et al., 2003			1.0	Hutchins et al., 2003
Elaphurus davidianus	175	Nowak, 1999					2.5	Nowak, 1999	20	Nowak, 1999		
Cervus elaphus	203	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993	7.9	Geist, 1998	1.5	MacDonald and Barret, 1993	25	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993
Cervus unicolor	225	Nowak, 1999	1.1	Leslie, 2011	6.3	Leslie, 2011	1.1	Leslie, 2011			1.0	Leslie, 2011
Cervus duvaucelii	225	Hutchins et al., 2003									1.0	Hutchins et al., 2003
Cervus albirostris	230	Hutchins et al., 2003	1.0	Hutchins et al., 2003			3.0	Hutchins et al., 2003	19	Hutchins et al., 2003	1.0	Hutchins et al., 2003
Alces alces	443	MacDonald and Barret, 1993	2.0	MacDonald and Barret, 1993	13.5	MacDonald and Barret, 1993	2.0	MacDonald and Barret, 1993	27	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993
Castoridae	**W**		**Lt**		**Wb**		**RM**		**L**		**BI**	
Castor fiber	22	Rodríguez, 1997	2.7	MacDonald and Barret, 1993	0.4	Nowak, 1999	3.0	MacDonald and Barret, 1993	8	MacDonald and Barret, 1993	1.0	MacDonald and Barret, 1993
Elenphantidae	**W**		**Lt**		**Wb**		**RM**		**L**		**BI**	
Elephas maximus	4,060	Shoshani and Eisenberg, 1982	1.0	Shoshani and Eisenberg, 1982	110.0	Laursen and Bekoff, 1978	15.5	Shoshani and Eisenberg, 1982	60	Laursen and Bekoff, 1978	4.9	Shoshani and Eisenberg, 1982
Loxodonta africana	4,250	Laursen and Bekoff, 1978	1.0	Nowak, 1999	110.0	Nowak, 1999	14.0	Nowak, 1999	60	Nowak, 1999		

Table S1 (continued)

Equidae	**W**		**Lt**		**Wb**		**RM**		**L**		**BI**	
Equus zebra	310	Penzhorn, 1988	1.0	Nowak, 1999	25.0	Penzhorn, 1988	5,0	Penzhorn, 1988	30	Nowak, 1999	2,1	Penzhorn, 1988
Rhinocerotidae	**W**		**Lt**		**Wb**		**RM**		**L**		**BI**	
Dicerorhinus sumatrensis	800	Hutchins et al., 2003			23.0	Groves, 1972					4.0	Hutchins et al., 2003
Diceros bicornis	987	Hillman-Smith and Groves, 1994	1.0	Hillman-Smith and Groves, 1994	36.0	Hillman-Smith and Groves, 1994	7.5	Hillman-Smith and Groves, 1994	35	Hutchins et al., 2003	2.7	Hillman-Smith and Groves, 1994
Rhinoceros sondaicus	1,500	Hutchins et al., 2003			54.5	Nowak, 1999			50	Nowak, 1999		
Rhinoceros unicornis	1,688	Laurie et al., 1983	1.0	Laurie et al., 1983	71.0	Laurie et al., 1983	7.0	Hutchins et al., 2003	30	Hutchins et al., 2003	3.8	Hutchins et al., 2003
Cerantotheriun simun	2,000	Groves, 1972			48.5	Groves, 1972	7.0	Hutchins et al., 2003	40	Hutchins et al., 2003	2.5	Hutchins et al., 2003
Suidae	**W**		**Lt**		**Wb**		**RM**		**L**		**BI**	
Sus scrofa	70	Fernández-Llario, 2008	3.5	Fernández-Llario, 2008	0.8	Geist, 1998	0,9	Fernández-Llario, 2008	11	Fernández-Llario, 2008	1.0	MacDonald and Barret, 1993
Ursidae	**W**		**Lt**		**Wb**		**RM**		**L**		**BI**	
Ursus americanus	66	Larivière, 2001	2.5	Larivière, 2001	0.3	Nowak, 1999	5.0	Larivière, 2001	23	Larivière, 2001	2.5	Larivière, 2001
Ursus thibetanus	88	Nowak, 1999	2.0	Nowak, 1999			3.5	Smith and Xie, 2008	33	Nowak, 1999		
Ursus arctos	214	Hutchins et al., 2003	2.0	Hutchins et al., 2003	0.5	Nowak, 1999	5.5	Hutchins et al., 2003	30	MacDonald and Barret, 1993	3.0	Pasitschniak-Arts, 1993
Ursus maritimus	388	DeMaster and Stirling, 1981	1.7	DeMaster and Stirling, 1981	0.6	DeMaster and Stirling, 1981	6.5	DeMaster and Stirling, 1981	32	MacDonald and Barret, 1993	3.1	DeMaster and Stirling, 1981

Table S2. Physiological variables used in the models. W: average body weight of the species in kg; Lt: litter size (number of individuals), Wb: average weight at birth in kg; RM: age at reproductive maturity in years; L: longevity in years; BI breeding interval in years.

	W	Lt	Wb	RM	L	BI	**References**
Bison cf. voigtstedtensis	350	1	19.33	1.77	25	1.92	Custodio et al., 1996; Geist, 1998; Hutchins et al., 2003; Leslie and Shaller, 2009; MacDonald and Barret, 1993; Meagher, 1986; Nowak, 1999
Castor fiber	22	3	0.43	3.00	8	1.00	Hutchins et al., 2003; MacDonald and Barret, 1993; Nowak, 1999; Rodríguez, 1997
Cervus elaphus	163	1	5.92	1.76	20	1.02	Geist, 1998; MacDonald and Barret, 1993; Rodríguez, 1997
Dama vallonetensis	83	1	3.74	1.56	16	1.00	Geist, 1998; MacDonald and Barret, 1993; Rodríguez, 1997
Eucladoceros giulii	276	1	1.30	1,81	24	1.00	Geist, 1998; MacDonald and Barret, 1993; Rodríguez, 1997
Equus altidens	306	1	25.00	5.00	30	2.08	Nowak, 1999; Penzhorn, 1988; Rodríguez, 1997
Mammuthus sp.	6,040	1	110.00	15,50	60	4.88	Laursen and Bekoff, 1978; Rodríguez, 1997; Shoshani and Eisenberg, 1982
Stephanorhinus etruscus	2,050	1	86.34	7,50	40	2.50	Groves, 1972; Hillman-Smith and Groves, 1994; Hutchins et al., 2003; Laurie et al., 1983; Rodríguez, 1997
Sus scrofa	85	4	0.75	0,90	11	1.00	Fernández-Llario, 2008; Geist, 1998; MacDonald and Barret, 1993; Rodríguez, 1997
Ursus dolinensis	300	2	0.56	6,04	30	3.05	DeMaster and Stirling, 1981; Larivière, 2001; MacDonald and Barret, 1993; Nowak, 1999; Pasitschniak-Arts, 1993; Rodríguez, 1997; Smith and Xie, 2008

Table S3. Allometric equations used to estimate Litter size, Weight at birth, Reproductive maturity, Longevity and Breeding interval in fossil species.

	Bovidae	Cervidae	Rhinocerotidae	Ursidae
Litter size (number)				$y = 4.5619x^{-0.161}$; $R^2=0.74$
Average birth mass (kg)	$y = 7.2544e^{0.0028x}$; $R^2=0.76$	$y = -0.2473x^2 + 1.7232x - 1.737$; $R^2= 0.79$	$y = 0.0498x - 15.748$; $R^2=0.97$	$y = 0.1839\ln(x) - 0.4888$; $R^2=0.99$
Reproductive maturity (female)(years)	$y = -1E\text{-}05x^2 + 0.0137x + 0.5215$; $R^2=0.47$	$y = -0.2309x^2 + 1.1347x - 1.1353$; $R^2=0.55$		$y = 1.4329\ln(x) - 1.4225$; $R^2=0.80$
Longevity (years)	$y = 0.0004x^2 - 0.3497x + 98.331$; $R^2=0.80$	$y = 9.0678x^2 - 25.216x + 31.299$; $R^2=0.33$		$y = 16.492x^{0.1144}$; $R^2=0.32$
Breeding interval (years)	$y = -0.0013x + 2.375$; $R^2=0.28$	$y = -0.0889x^2 + 0.3869x - 0.4138$; $R^2=0.33$		$y = 0.3508\ln(x) + 1.0521$; $R^2=0.97$

Table S4. Model input data. Age intervals (Age), fecundity (a) defined as number of female offspring per female per age interval and mean body weigh of the individuals per age interval (W) in kg.

Bison cf. voigtstedtensis			*Castor fiber*			*Cervus elaphus*			*Dama vallonetensis*			*Equus altidens*			*Eucladoceros giulii*			*Mammuthus sp.*			*Stephanorhinus etruscus*			*Sus scrofa*			*Ursus dolinensis*		
Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W
1	0.0	70	1	0	9	1	0.0	38	1	0.0	24	1	0.0	67	1	0.0	55	1	0.0	508	1	0.0	254	1.0	0.2	22	1	0.0	54
2	0.1	181	2	0	21	2	0.1	105	2	0.2	65	2	0.0	164	2	0.1	153	2	0.0	1,358	2	0.0	632	2.0	1.8	66	2	0.0	162
3	0.3	302	3	1.35	22	3	0.5	160	3	0.5	83	3	0.0	274	3	0.7	251	3	0.0	2,263	3	0.0	1,053	3.0	1.8	85	3	0.0	267
4	0.3	350	4	1.35	22	4	0.5	163	4	0.5	83	4	0.0	306	4	0.7	276	4	0.0	3,169	4	0.0	1,263	4.0	1.8	85	4	0.0	300
5	0.3	350	5	1.35	22	5	0.5	163	5	0.5	83	5	0.0	306	5	0.7	276	5	0.0	4,074	5	0.0	1,900	5.0	1.8	85	5	0.0	300
6	0.3	350	6	1.35	22	6	0.5	163	6	0.5	83	6	0.2	306	6	0.7	276	6	0.0	4,979	6	0.0	2,050	6.0	1.8	85	6	0.0	300
7	0.3	350	7	1.35	22	7	0.5	163	7	0.5	83	7	0.2	306	7	0.7	276	7	0.0	5,884	7	0.0	2,050	7.0	1.8	85	7	0.3	300
8	0.3	350	8	1.35	22	8	0.5	163	8	0.5	83	8	0.2	306	8	0.7	276	8	0.0	6,040	8	0.1	2,050	8.0	1.8	85	8	0.3	300
9	0.3	350				9	0.5	163	9	0.5	83	9	0.2	306	9	0.7	276	9	0.0	6,040	9	0.2	2,050	9.0	1.8	85	9	0.3	300
10	0.3	350				10	0.5	163	10	0.5	83	10	0.2	306	10	0.7	276	10	0.0	6,040	10	0.2	2,050	10.0	1.8	85	10	0.3	300
11	0.3	350				11	0.5	163	11	0.5	83	11	0.2	306	11	0.7	276	11	0.0	6,040	11	0.2	2,050	11.0	1.8	85	11	0.3	300
12	0.3	350				12	0.5	163	12	0.5	83	12	0.2	306	12	0.7	276	12	0.0	6,040	12	0.2	2,050				12	0.3	300
13	0.3	350				13	0.5	163	13	0.5	83	13	0.2	306	13	0.7	276	13	0.0	6,040	13	0.2	2,050				13	0.3	300
14	0.3	350				14	0.5	163	14	0.5	83	14	0.2	306	14	0.7	276	14	0.0	6,040	14	0.2	2,050				14	0.3	300
15	0.3	350				15	0.5	163	15	0.5	83	15	0.2	306	15	0.7	276	15	0.0	6,040	15	0.2	2,050				15	0.3	300
16	0.3	350				16	0.5	163	16	0.5	83	16	0.2	306	16	0.7	276	16	0.1	6,040	16	0.2	2,050				16	0.3	300
17	0.3	350				17	0.5	163	17	0.5	83	17	0.2	306	17	0.7	276	17	0.1	6,040	17	0.2	2,050				17	0.3	300
18	0.3	350				18	0.5	163				18	0.2	306	18	0.7	276	18	0.1	6,040	18	0.2	2,050				18	0.3	300
19	0.3	350				19	0.5	163				19	0.2	306	19	0.7	276	19	0.1	6,040	19	0.2	2,050				19	0.3	300

Table S4 (continued)

Bison cf. voigtstedtensis			*Castor fiber*			*Cervus elaphus*			*Dama vallonetensis*			*Equus altidens*			*Eucladoceros giulii*			*Mammuthus sp.*			*Stephanorhinus etruscus*			*Sus scrofa*			*Ursus dolinensis*		
Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W
20	0.3	350				20	0.5	163				20	0.2	306	20	0.7	276	20	0.1	6,040	20	0.2	2,050				20	0.3	300
21	0.3	350				21	0.5	163				21	0.2	306	21	0.7	276	21	0.1	6,040	21	0.2	2,050				21	0.3	300
22	0.3	350										22	0.2	306	22	0.7	276	22	0.1	6,040	22	0.2	2,050				22	0.3	300
23	0.3	350										23	0.2	306	23	0.7	276	23	0.1	6,040	23	0.2	2,050				23	0.3	300
24	0.3	350										24	0.2	306	24	0.7	276	24	0.1	6,040	24	0.2	2,050				24	0.3	300
25	0.3	350										25	0.2	306				25	0.1	6,040	25	0.2	2,050				25	0.3	300
26	0.3	350										26	0.2	306				26	0.1	6,040	26	0.2	2,050				26	0.3	300
												27	0.2	306				27	0.1	6,040	27	0.2	2,050				27	0.3	300
												28	0.2	306				28	0.1	6,040	28	0.2	2,050				28	0.3	300
												29	0.2	306				29	0.1	6,040	29	0.2	2,050				29	0.3	300
												30	0.2	306				30	0.1	6,040	30	0.2	2,050				30	0.3	300
																		31	0.1	6,040	31	0.2	2,050						
																		32	0.1	6,040	32	0.2	2,050						
																		33	0.1	6,040	33	0.2	2,050						
																		34	0.1	6,040	34	0.2	2,050						
																		35	0.1	6,040	35	0.2	2,050						
																		36	0.1	6,040	36	0.2	2,050						
																		37	0.1	6,040	37	0.2	2,050						
																		38	0.1	6,040	38	0.2	2,050						
																		39	0.1	6,040	39	0.2	2,050						
																		40	0.1	6,040	40	0.2	2,050						
																		41	0.1	6,040									
																		42	0.1	6,040									
																		43	0.1	6,040									
																		44	0.1	6,040									
																		45	0.1	6,040									

Table S4 (continued)

Bison cf. voigtstedtensis			*Castor fiber*			*Cervus elaphus*			*Dama vallonetensis*			*Equus altidens*			*Eucladoceros giulii*			*Mammuthus sp.*			*Stephanorhinus etruscus*			*Sus scrofa*			*Ursus dolinensis*		
Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W	Age	a	W
																		46	0.1	6,040									
																		47	0.1	6,040									
																		48	0.1	6,040									
																		49	0.1	6,040									
																		50	0.1	6,040									
																		51	0.1	6,040									
																		52	0.1	6,040									
																		53	0.1	6,040									
																		54	0.1	6,040									
																		55	0.1	6,040									
																		56	0.1	6,040									
																		57	0.1	6,040									
																		58	0.1	6,040									
																		59	0.1	6,040									
																		60	0.1	6,040									

Table S5. Body size and published intake rates of some living carnivores

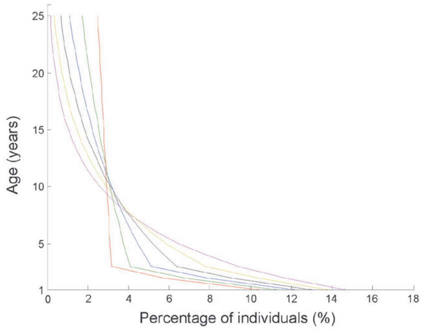
Species	**Body Size (kg)**	**References**	**Intake observed per year (kg/year)**	**References**
Canis latrans	15	Bekoff, 1977	219 (meat)	Bekoff, 1977
Canis lupus	33	Smith and Xie, 2008	912.5 - 2,299.5	Mech, 1974
Crocuta crocuta	70	Nowak, 1999	2-4	Mills and Hofer, 1998;Henschel and Tilson, 1988; Kruuk, 1972
Felis concolor	70	Currier, 1983	2.36-3.5	Currier, 1983
Lynx lynx	20	Tumlison, 1987	0.59-0.96	Tumlison, 1987
Panthera pardus	50	Smith and Xie, 2008	1,715.5	Odden and Wegge, 2009
Panthera tigris	200	Mazák, 1981	1,825 - 2,190	Mazák, 1981
Uncia uncia	50	Smith and Xie, 2008	730 - 1,095	Hemmer, 1972
Panthera leo	187	Nowak, 1999	1,788.5 - 4,142.75	Green et al., 1984; Kruuk and Turner, 1967; Stander, 1991

Table S6. Estimated body size and intake rate of fossil species

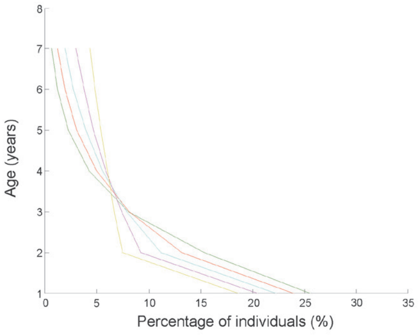
Species	Body Size (kg)	References	Intake estimated (kg)
Canis mosbachensis	16600	Rodríguez, 1997	0.22 (meat)
Crocuta crocuta	75000	Rodríguez, 1997	3.15
Lynx sp.	2000	Rodríguez, 1997	1.26
Panthera leo	156000	Rodríguez, 1997	5.25
Panthera gombaszoegensis	148000	Rodríguez, 1997	5.06
Homotherium latidens	187000	Rodríguez, 1997	5.96

Figure S1. Graphical representation of population profiles

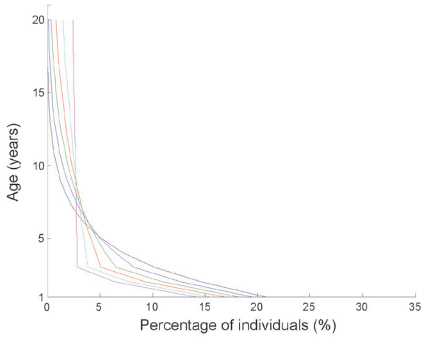
B. voigtedtensis



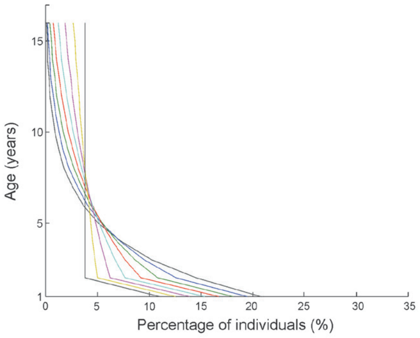
C. fiber



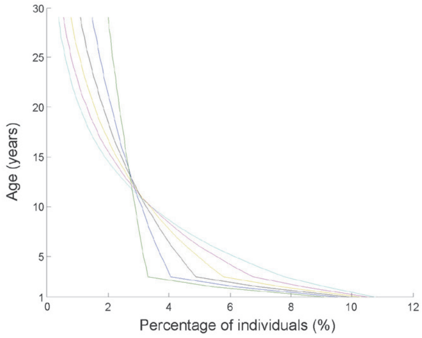
C. elaphus



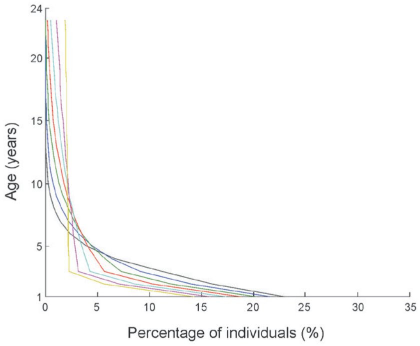
D. vallonetensis



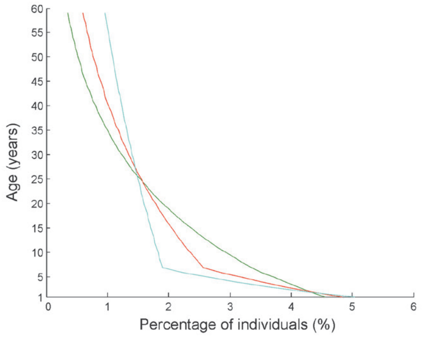
E. altidens



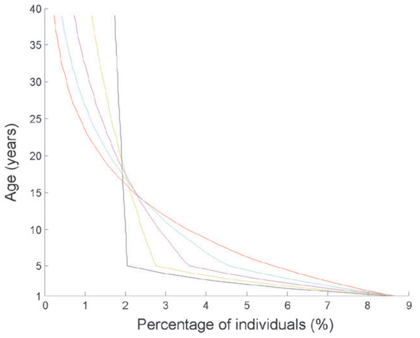
E. giulii



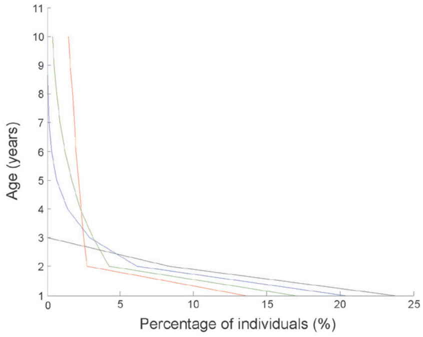
M. meridionalis



S. etruscus



S. scrofa



U. dolinensis

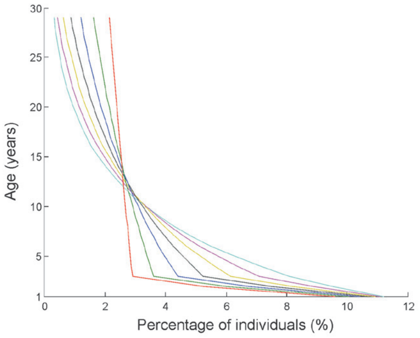


Figure S2. Graphical representation of mortality profiles

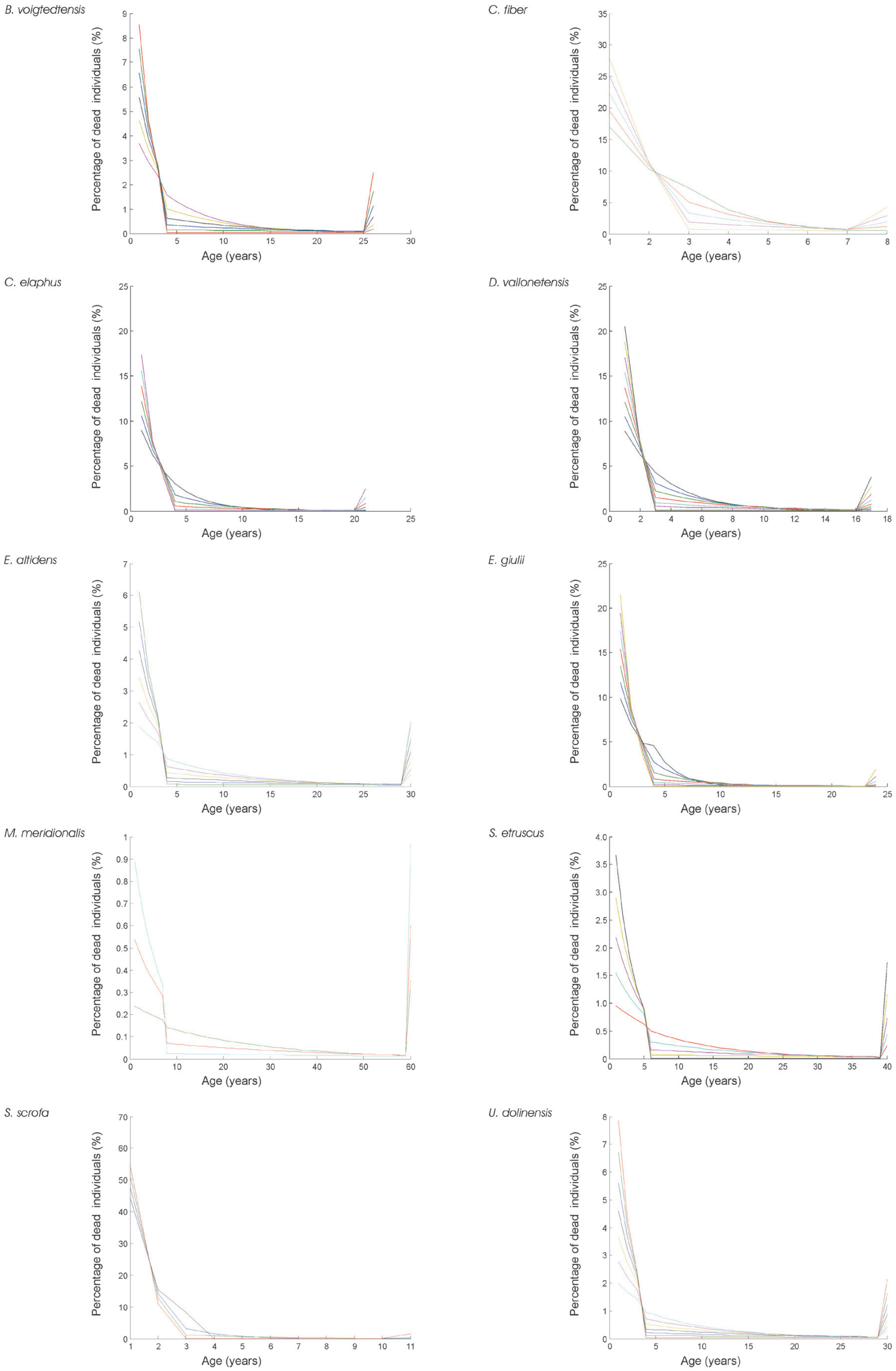
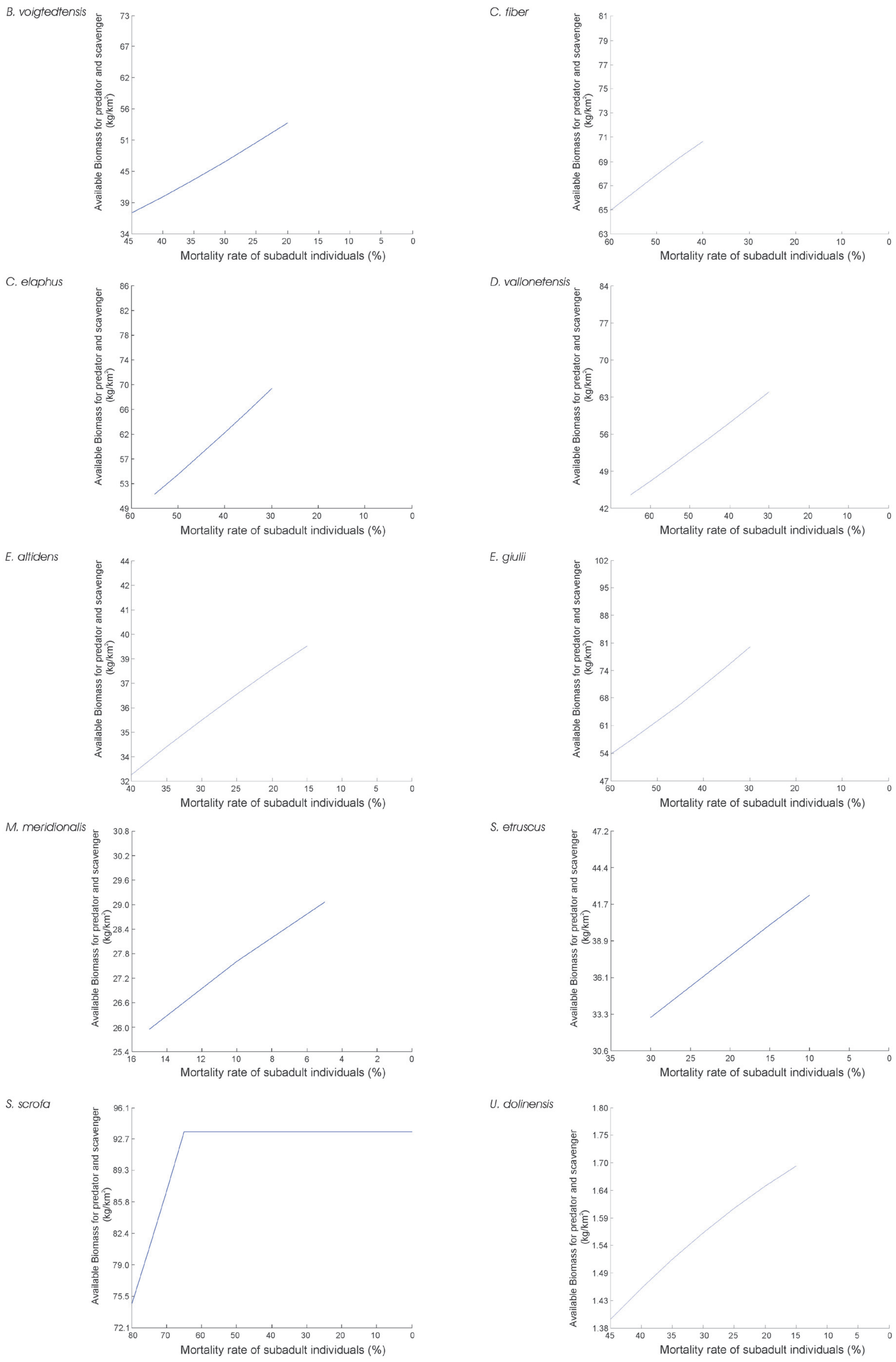


Figure S3. Graphical representation of Biomass Output



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Appendix B.- Discontinuity of Human Presence at Atapuerca during the Early Middle Pleistocene: A Matter of Ecological Competition?

Table S1 Specimen Number

Specimen Number	**Taxa**
ATA02 TD08b F11 n1	*Ursus* sp.
ATA04 TD08b G14 n28	*Ursus* sp.
ATA02 TD08b G15 n1	*Ursus* sp.
ATA05 TD08b G08 n1	*Sus scrofa*
ATA94 TD08 H16 n42	*Stephanorhinus etruscus*
ATA94 TD08 H16 n52	*Stephanorhinus etruscus*
ATA06 TD08b G03 n68	*Lynx* sp.
ATA06 TD08b G03 n98	*Lynx* sp.
ATA06 TD08b G04 n127	*Lynx* sp.
ATA06 TD08b G03 n117	*Lynx* sp.
ATA05 TD08b G08 n2	*Hyaena* sp.
ATA94 TD08 I16 n62	*Hippopotamus* sp.
ATA05 TD08b G03 n12	*Eucladoceros giulii*
ATA06 TD08b G04 n110	*Eucladoceros giulii*
ATA94 TD08 I17 n3	*Eucladoceros giulii*
ATA04 TD08b H05 n3	*Eucladoceros giulii*
ATA02 TD08a A01 n3	*Equus altidens*
ATA03 TD08b G06 n17	*Equus altidens*
ATA03 TD08b G06 n18	*Equus altidens*
ATA02 TD08b G07 n19	*Equus altidens*
ATA02 TD08b G07 n55	*Equus altidens*
ATA02 TD08b G08 n1	*Equus altidens*
ATA02 TD08b G08 n2	*Equus altidens*
ATA02 TD08b G09 n51	*Equus altidens*
ATA02 TD08b G10 n32	*Equus altidens*
ATA04 TD08b H06 n3	*Equus altidens*
ATA02 TD08b A01 n5	*Dama vallonetensis*
ATA05 TD08b E12 n11	*Dama vallonetensis*
ATA02 TD08b F09 n9	*Dama vallonetensis*
ATA02 TD08b F10 n14	*Dama vallonetensis*
ATA02 TD08b F11 n78	*Dama vallonetensis*
ATA02 TD08b F12 n60	*Dama vallonetensis*
ATA05 TD08b F13 n5	*Dama vallonetensis*
ATA06 TD08b G03 n5	*Dama vallonetensis*
ATA03 TD08b G03 n17	*Dama vallonetensis*
ATA05 TD08b G03 n17	*Dama vallonetensis*
ATA06 TD08b G03 n62	*Dama vallonetensis*
ATA06 TD08b G04 n83	*Dama vallonetensis*
ATA06 TD08b G04 n109	*Dama vallonetensis*
ATA06 TD08b G04 n126	*Dama vallonetensis*
ATA06 TD08b G04 n128	*Dama vallonetensis*
ATA03 TD08b G05 n26	*Dama vallonetensis*
ATA03 TD08b G05 n27	*Dama vallonetensis*
ATA03 TD08b G05 n57	*Dama vallonetensis*
ATA04 TD08b G06 n2	*Dama vallonetensis*

Table S1 (continued)

Specimen Number	**Taxa**
ATA02 TD08b G07 n31	*Dama vallonetensis*
ATA02 TD08b G07 n34	*Dama vallonetensis*
ATA02 TD08b G07 n39	*Dama vallonetensis*
ATA02 TD08b G07 n50	*Dama vallonetensis*
ATA02 TD08b G07 n54	*Dama vallonetensis*
ATA02 TD08b G07 n103	*Dama vallonetensis*
ATA02 TD08b G08 n3	*Dama vallonetensis*
ATA02 TD08b G08 n84	*Dama vallonetensis*
ATA02 TD08b G09 n11	*Dama vallonetensis*
ATA02 TD08b G09 n17	*Dama vallonetensis*
ATA02 TD08b G09 n34	*Dama vallonetensis*
ATA02 TD08b G10 n65	*Dama vallonetensis*
ATA02 TD08b G12 n22	*Dama vallonetensis*
ATA02 TD08b G12 n27	*Dama vallonetensis*
ATA02 TD08b G12 n33	*Dama vallonetensis*
ATA02 TD08b G12 n48	*Dama vallonetensis*
ATA02 TD08b G13 n17	*Dama vallonetensis*
ATA03 TD08b G15 n14	*Dama vallonetensis*
ATA05 TD08b H03 n17	*Dama vallonetensis*
ATA05 TD08b H03 n18	*Dama vallonetensis*
ATA06 TD08b H03 n32	*Dama vallonetensis*
ATA06 TD08b H03 n40	*Dama vallonetensis*
ATA06 TD08b H04 n9	*Dama vallonetensis*
ATA02 TD08b H08 n7	*Dama vallonetensis*
ATA02 TD08b H08 n22	*Dama vallonetensis*
ATA94 TD08 G17 n22	*Dama vallonetensis*
ATA94 TD08 H16 n39	*Dama vallonetensis*
ATA94 TD08 I17 n2	*Dama vallonetensis*
ATA06 TD08b G04 n77	*Crocuta crocuta*
ATA02 TD08b G07 n109	*Crocuta crocuta*
ATA02 TD08b G08 n25	*Cervus elaphus*
ATA02 TD08b G09 n39	*Cervus elaphus*
ATA02 TD08b G12 n9	*Cervus elaphus*
ATA05 TD08b H03 n63	*Cervus elaphus*
ATA94 TD08 G17 n4	*Cervus elaphus*
ATA94 TD08 H16 n32	*Cervus elaphus*
ATA06 TD08b G03 n64	*Canis mosbachensis*
ATA04 TD08b G05 n85	*Canis mosbachensis*
ATA02 TD08b F11 n58	*Bison voigtstedtensis*
ATA06 TD08b G03 n58	*Bison voigtstedtensis*
ATA06 TD08b G04 n36	*Bison voigtstedtensis*
ATA06 TD08b G04 n38	*Bison voigtstedtensis*
ATA02 TD08b G07 n91	*Bison voigtstedtensis*
ATA94 TD08 I16 n39	*Bison voigtstedtensis*

Table S2. Sustainable densities of the TD8 secondary consumers for six different scenarios (see text) for maximum and minimum total available biomass (TAB). Estimated density of carnivores (individuals per square kilometre), nutritional requirements (kilocalories per year), total intake (kilocalories per year), unsatisfied requirements (kilocalories per year), sustainable density (individuals per square kilometre), Species Competition Index (SCI). Total intake is defined as the biomass (in kcal) consumed by the species after dividing TAB among the secondary consumers, taking into account the distribution of TAB by body size category (Table 4) and the carnivore preferences (Table 3).

Scenario	Species	Density (ind/km2)	Requirements (kcal/year)	Total Intake (kcal/year)	Not satisfied requirements (kcal/year)	Sustainable Density (ind/km2)	SCI
TD8							
Minimum TAB							
	Canis mosbachensis	0.42	40,062	29,300	10,762	0.30	0.27
	Crocuta crocuta	0.13	217,864	169,425	48,439	0.10	0.22
	Lynx sp.	0.47	19,825	19,573	252	0.46	0.01
	Ursus dolinensis	0.06	23,970	17,531	6,439	0.04	0.27
	Panthera gombaszoegensis	0.11	224,627	141,669	82,957	0.07	0.37
	Hyaena sp.	0.17	162,932	119,162	43,770	0.12	0.27
Maximum TAB							
	Canis mosbachensis	0.42	40,062	38,553	1,510	0.39	0.04
	Crocuta crocuta	0.13	217,864	209,400	8,464	0.12	0.04
	Lynx sp.	0.47	19,825	19,724	100	0.46	0.01
	Ursus dolinensis	0.06	23,970	23,067	903	0.05	0.04
	Panthera gombaszoegensis	0.11	224,627	193,901	30,726	0.10	0.14
	Hyaena sp.	0.17	162,932	156,793	6,139	0.16	0.04
With *Homo* sp.							
Minimum TAB							
High Hunter							
	Canis mosbachensis	0.42	40,062	23.652	16.410	0,25	0,41
	Crocuta crocuta	0.13	217,864	133.680	84.184	0.08	0.39
	Lynx sp.	0.47	19,825	16.018	3.806	0.38	0,19
	Ursus dolinensis	0.06	23,970	14.151	9.819	0.03	0,41
	Panthera gombaszoegensis	0.11	224,627	114.568	110.059	0.06	0,49
	Hyaena sp.	0.17	162,932	96.191	66.741	0.10	0,41
	Homo sp,	0.24	157,680	98.399	59.281	0.15	0.38
Low Hunter							
	Canis mosbachensis	0.42	40,062	26.159	13.903	0.27	0.35
	Crocuta crocuta	0.13	217,864	150.134	67.730	0.09	0.31
	Lynx sp.	0.47	19,825	18.339	1.486	0.43	0.07
	Ursus dolinensis	0.06	23,970	15.651	8.319	0.04	0.35
	Panthera gombaszoegensis	0.11	224,627	124.796	99.830	0.06	0.44
	Hyaena sp.	0.17	162,932	106.388	56.545	0.11	0.35
	Homo sp.	0.24	78,840	55.193	23.647	0.17	0.30
Maximum TAB							
High Hunter							
	Canis mosbachensis	0.42	40,062	31.784	8.278	0.33	0.21
	Crocuta crocuta	0.13	217,864	164.814	53.050	0.10	0.24
	Lynx sp.	0.47	19,825	15.070	4.755	0.36	0.24
	Ursus dolinensis	0.06	23,970	19.017	4.953	0.04	0.21
	Panthera gombaszoegensis	0.11	224,627	161.380	63.246	0.08	0.28
	Hyaena sp.	0.17	162,932	129.265	33.668	0.13	0.21
	Homo sp.	0.24	157,680	121.872	35.808	0.19	0.23
Low Hunter							
	Canis mosbachensis	0.42	40,062	35.139	4.924	0.37	0.12
	Crocuta crocuta	0.13	217,864	181.972	35.891	0.11	0.16
	Lynx sp.	0.47	19,825	17.194	2.631	0.41	0.13
	Ursus dolinensis	0.06	23,970	21.024	2.946	0.05	0.12
	Panthera gombaszoegensis	0.11	224,627	177.767	46.860	0.09	0.20
	Hyaena sp.	0.17	162,932	142.908	20.025	0.15	0.12
	Homo sp.	0.24	78,840	67.198	11.642	0.20	0.15

Table S3. Sustainable densities of TD6-2 secondary consumers for eight different scenarios (see text) for maximum and minimum total available biomass (TAB). Estimated density of carnivores (individuals per square kilometre), nutritional requirements (kilocalories per year), total intake (kilocalories per year), unsatisfied requirements (kilocalories per year), sustainable density (individuals per square kilometre), Species Competition Index (SCI), Total intake is defined as the biomass (in kcal) consumed by the species after dividing TAB among the secondary consumers, taking into account the distribution of TAB by body size category (Table 4) and the carnivore preferences (Table 3).

Scenario	Species	Density (ind/km2)	Requirements (kcal/year)	Total Intake (kcal/year)	Not satisfied requirements (kcal/year)	Sustainable Density (ind/km^2)	SCI
TD6-2							
Minimum TAB							
High Hunter							
	Canis mosbachensis	0.34	40,808	40,276	532	0.33	0.01
	Crocuta crocuta	0.13	217,864	216,092	1,772	0.13	0.01
	Lynx sp,	0.30	20,621	20,621	0	0.30	0.00
	Ursus dolinensis	0.05	24,054	23,740	314	0.05	0.01
	Homo antecessor	0.24	157,680	156,072	1,608	0.24	0.01
Low Hunter							
	Canis mosbachensis	0.34	40,808	40,808	0	0.34	0.00
	Crocuta crocuta	0.13	217,864	217,864	0	0.13	0.00
	Lynx sp,	0.30	20,621	20,621	0	0.30	0.00
	Ursus dolinensis	0.05	24,054	24,054	0	0.05	0.00
	Homo antecessor	0.24	78,840	157,680	0	0.24	0.00
Maximum TAB							
High Hunter							
	Canis mosbachensis	0.34	40,808	40,808	0	0.34	0.00
	Crocuta crocuta	0.13	217,864	217,864	0	0.13	0.00
	Lynx sp,	0.30	20,621	20,621	0	0.30	0.00
	Ursus dolinensis	0.05	24,054	24,054	0	0.05	0.00
	Homo antecessor	0.24	157,680	157,680	0	0.24	0.00
Low Hunter							
	Canis mosbachensis	0.34	40,808	40,808	0	0.34	0.00
	Crocuta crocuta	0.13	217,864	217,864	0	0.13	0.00
	Lynx sp,	0.30	20,621	20,621	0	0.30	0.00
	Ursus dolinensis	0.05	24,054	24,054	0	0.05	0.00
	Homo antecessor	0.24	78,840	78,840	0	0.24	0.00
TD6 with *Homotherium latidens*							
Minimum TAB							
High Hunter							
	Canis mosbachensis	0.34	40,808	27,155	13,654	0.23	0.33
	Crocuta crocuta	0.13	217,864	163,664	54,200	0.10	0.25
	Lynx sp,	0.30	20,621	19,803	819	0.29	0.04
	Ursus dolinensis	0.05	24,054	16,006	8,048	0.04	0.33
	Homo antecessor	0.24	157,680	115,297	42,383	0.18	0.27
	Homotherium latidens	0.07	234,164	115,768	118,396	0.04	0.51
Low Hunter							
	Canis mosbachensis	0.34	40,808	34,753	6,055	0.29	0.51
	Crocuta crocuta	0.13	217,864	197,227	20,637	0.12	0.09
	Lynx sp,	0.30	20,621	14,882	5,739	0.22	0.28
	Ursus dolinensis	0.05	24,054	20,485	3,569	0.05	0.15
	Homo antecessor	0.24	78,840	139,127	18,553	0.21	0.12
	Homotherium latidens	0.07	234,164	177,164	57,000	0.05	0.24
Maximum TAB							
High Hunter							
	Canis mosbachensis	0.34	40,808	34,753	6,055	0.29	0.15
	Crocuta crocuta	0.13	217,864	197,227	20,637	0.12	0.09
	Lynx sp,	0.30	20,621	14,882	5,739	0.22	0.28
	Ursus dolinensis	0.05	24,054	20,485	3,569	0.05	0.15
	Homo antecessor	0.24	157,680	139,127	18,553	0.21	0.12
	Homotherium latidens	0.07	234,164	177,164	57,000	0.05	0.24
Low Hunter							
	Canis mosbachensis	0.34	40,808	38,143	2,666	0.32	0.07
	Crocuta crocuta	0.13	217,864	211,793	6,071	0.13	0.03
	Lynx sp,	0.30	20,621	16,775	3,846	0.24	0.19
	Ursus dolinensis	0.05	24,054	22,483	1,571	0.05	0.07
	Homo antecessor	0.24	78,840	75,832	3,008	0.23	0.04
	Homotherium latidens	0.07	234,164	192,817	41,347	0.06	0.18

Appendix C.- Ecological competition and community structure as limiting factors of human presence in Europe during the Early and Middle Pleistocene

Table S1. Primary consumer species present in the Early and Middle faunal assemblages. 0 = species do not present; 1= species present.

	Local Faunal Assemblages (LFAs)																																	
Primary consumers plus ursids	Apollonia-1	Ata TD3-TD4	Ata TD6 1-2	Grotte du Vallonnet III	Kozarnika 12	Kozarnika 13	Untermassfeld N/A	Vallparadís Lower Unit	Vallparadís Middle Unit	Ata TD8	Isernia La Pineta (Molise, Italy)	Mauer N/A	Pakefield/Kessingland - Rootlet bed	Slivia N/A	Sussenborn - Hauptfauna	Voigtstedt - Lehmzone	Ata TD10-1	Ata GIIb	Ata GIII	Biache-Saint-Vaast (Pas de Calais, France) - Dépôts fluviatiles	Bilzingsleben II	Casal de´Pazzi (Roma, Italy) - N/A	Cueva del Congosto (Guadalajara, Spain) - A1	Fontana Acetosa (Lazio, Italy) - N/A	Grotta Lina - N/A	Grotte du Lazaret - CII inf	Heppenloch N/A	Hundsheim N/A	Orgnac-3 6	Payre (Ardèche, France) - F	Quisana-Certosa N/A	Riparo di Visogliano - Lower levels	Swanscombe - Lower loam	Wannenköpfe - Wa1-Wa3
Arvernoceros dicranios	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Arvernoceros giulii	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arvenoceros veretschagini	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bison menneri	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bison priscus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0
Bison schoetensacki	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0
Bison sp.	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bison voigtstedtensis	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bos primigenius	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	1	0	0	1	0
Bos-Bison	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
Bovidae indet	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bovini indet.	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capra ibex	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Capra pyrenaica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Capreolus capreolus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	1	1	0	0	0	0	1	0
Capreolus cusanoides	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capreolus priscus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Capreolus sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Capreolus süessenbornensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caprinae indet.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Castor fiber	0	1	1	0	0	0	1	0	0	0	0	1	1	1	1	1	1	0	0	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0
Cervalces carnutorum	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cervalces latifrons	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cervidae indet.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cervus elaphus	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1
Cervus nestii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Coelodonta antiquitatis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Croizeros ramosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Dama clactoniana	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0
Dama dama	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0
Dama vallonetensis	0	1	1	1	0	0	1	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elephantidae indet.	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Elephas antiquus	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1	0	1	0
Elephas sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Equus altidens	0	1	1	0	0	0	1	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Equus apolloniensis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Equus ferus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	1	1	0	0	1	0	0	0	0	0	0	1	0
Equus hydruntinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Equus mosbachensis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0

Table S1 (continued)

	Local Faunal Assemblages (LFAs)																																	
Primary consumers plus ursids	Apollonia-1	Ata TD3-TD4	Ata TD6 1-2	Grotte du Vallonnet III	Kozarnika 12	Kozarnika 13	Untermassfeld N/A	Vallparadís Lower Unit	Vallparadís Middle Unit	Ata TD8	Isernia La Pineta (Molise, Italy)	Mauer N/A	Pakefield/Kessingland - Rootlet bed	Slivia N/A	Sussenborn - Hauptfauna	Voigtstedt - Lehmzone	Ata TD10-1	Ata GIIb	Ata GIII	Biache-Saint-Vaast (Pas de Calais, France) - Dépôts fluviatiles	Bilzingsleben II	Casal de´Pazzi (Roma, Italy) - N/A	Cueva del Congosto (Guadalajara, Spain) - A1	Fontana Acetosa (Lazio, Italy) - N/A	Grotta Lina - N/A	Grotte du Lazaret - CII inf	Heppenloch N/A	Hundsheim N/A	Orgnac-3 6	Payre (Ardèche, France) - F	Quisana-Certosa N/A	Riparo di Visogliano - Lower levels	Swanscombe - Lower loam	Wannenköpfe - Wa1-Wa3
Equus sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1
Equus steinheimensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Equus stenonis	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Equus suessenbornensis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Hemitragus bonali	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Hemitragus orientalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemitragus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Hippopotamus amphibius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Hippopotamus antiquus	0	0	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippopotamus sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Hystrix refossa	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hystrix sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Hystrix vinogradovi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptobos sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Macaca sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Macaca sylvanus	0	0	0	1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0
Mammuthus chosaricus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Mammuthus meridionalis	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Mammuthus primigenius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mammuthus sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Mammuthus trogontherii	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megacerini indet.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megaloceros boldrini	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megaloceros giganteus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	1	0
Megaloceros savini	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megaloceros sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ovibos moschatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ovis sp.	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pontoceros ambiguus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Praemegaceros pliotarandoides	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Praemegaceros solilhacus	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Praemegaceros verticornis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Praeovibos sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proboscidea indet.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Procamptoceras sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rangifer tarandus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Rhinocerotidae indet.	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rupicapra rupicapra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1
Soergelia brigittae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table S1 (continued)

Primary consumers plus ursids	**Local Faunal Assemblages (LFAs)** Apollonia-1	Ata TD3-TD4	Ata TD6 1-2	Grotte du Vallonnet III	Kozarnika 12	Kozarnika 13	Untermassfeld N/A	Vallparadís Lower Unit	Vallparadís Middle Unit	Ata TD8	Isernia La Pineta (Molise, Italy)	Mauer N/A	Pakefield/Kessingland - Rootlet bed	Slivia N/A	Sussenborn - Hauptfauna	Voigtstedt - Lehmzone	Ata TD10-1	Ata GIIb	Ata GIII	Biache-Saint-Vaast (Pas de Calais, France) - Dépôts fluviatiles	Bilzingsleben II	Casal de´Pazzi (Roma, Italy) - N/A	Cueva del Congosto (Guadalajara, Spain) - A1	Fontana Acetosa (Lazio, Italy) - N/A	Grotta Lina - N/A	Grotte du Lazaret - CII inf	Heppenloch N/A	Hundsheim N/A	Orgnac-3 6	Payre (Ardèche, France) - F	Quisana-Certosa N/A	Riparo di Visogliano - Lower levels	Swanscombe - Lower loam	Wannenköpfe - Wa1-Wa3
Soergelia elisabethae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Soergelia sp.	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stephanorhinus etruscus	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stephanorhinus hemitoechus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	1	0	0	1	1	0	1	1	1	0	1	0
Stephanorhinus hundsheimensis	0	0	0	1	0	0	0	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0
Stephanorhinus kirchbergensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	1	0
Stephanorhinus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Sus scrofa	0	0	1	0	0	0	1	0	0	1	1	1	1	1	1	1	0	0	0	1	1	1	1	0	1	0	1	1	1	1	1	1	1	0
Sus sp.	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Sus strozzii	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trogontherium cuvieri	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Ursus arctos	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	1	0	0	0	0
Ursus deningeri	0	0	0	0	1	0	0	1	1	0	1	1	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0
Ursus dolinensis	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ursus etruscus	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ursus sp.	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ursus spelaeus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0	1	1
Ursus thibetanus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table S2. Secondary consumer species present in the Early and Middle faunal assemblages. 0 = species do not present; 1= species present.

Local Faunal Assemblages (LFAs)

Secondary consumers	Apollonia-1	Ata TD3-TD4	Ata TD6 1-2	Grotte du Vallonnet III	Kozarnika 12	Kozarnika 13	Untermassfeld N/A	Vallparadís Lower Unit	Vallparadís Middle Unit	Ata TD8	Isernia La Pineta (Molise, Italy)	Mauer N/A	Pakefield/Kessingland - Rootlet bed	Slivia N/A	Sussenborn - Hauptfauna	Voigtstedt - Lehmzone	Ata TD10-1	Ata GIIb	Ata GIII	Biache-Saint-Vaast (Pas de Calais, France)	Bilzingsleben II	Casal de´Pazzi (Roma, Italy) - N/A	Cueva del Congosto (Guadalajara, Spain) - A1	Fontana Acetosa (Lazio, Italy) - N/A	Grotta Lina - N/A	Grotte du Lazaret - CII inf	Heppenloch N/A	Hundsheim N/A	Orgnac-3 6	Payre (Ardèche, France) - F	Quisana-Certosa N/A	Riparo di Visogliano - Lower levels	Swanscombe - Lower loam	Wannenköpfe - Wa1-Wa3
Acinonyx pardinensis	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Canis arnensis	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Canis etruscus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Canis lupus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	1	1	1	0	1	1	0	0	1	1
Canis mosbachensis	0	1	1	1	0	0	1	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0
Chasmaporthetes lunensis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crocuta crocuta	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	1	1	0	0
Crocuta sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Cuon alpinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Cuon priscus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cuon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Homo antecessor	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Homo heidelbergensis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Homo sp.	0	1	0	1	0	1	0	0	1	0	1	0	1	0	0	0	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	1
Homotherium crenatidens	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Homotherium latidens	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Homotherium sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyaena sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Lycaon lycaonoides	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lynx issidorensis	1	0	0	1	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lynx pardinus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0
Lynx sp.	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Megantereon cultridens	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megantereon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Megantereon whitei	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachycrocuta brevirostris	0	0	0	1	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Panthera gombaszoegensis	0	1	0	1	1	1	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Panthera leo	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	0	0	0	1	0	1	0	0	1	0	0	1	1
Panthera pardus	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0
Panthera sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Pliocrocuta perrieri	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Puma pardoides	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ursus arctos	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	1	0	0	0	0
Ursus deningeri	0	0	0	0	1	0	0	1	1	0	1	1	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0
Ursus dolinensis	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ursus etruscus	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ursus sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ursus spelaeus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0	1	1
Ursus thibetanus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table S3. Allometric regresions used to estimate Weight at birth in fossil species.

Order	Family	Subfamily	Neonate Body Mass (NBM) (kg)
Artiodactyla	Bovidae	Bovinae	$\log NBM = 0{,}8687 * \log(m) - 0{,}9904$
Artiodactyla	Bovidae	Caprinae	$NBM = 0{,}0278 * m + 1{,}1992$
Artiodactyla	Bovidae	Antilopinae	$\log NBM = 0{,}7982 * \log(m) - 0{,}7169$
Artiodactyla	Cervidae	Capreolinae	$NBM = -0{,}000004\ m^2 + 0{,}0442 * m + 0{,}2052$
Artiodactyla	Cervidae	Cervinae	$NBM = 0{,}1221 * m^{0{,}8391}$
Perissodactyla	Equidae		$NBM = 0{,}0002\ m^2 - 0{,}0816 * m + 36{,}946$

Apéndice D.- Food Web Structure during the European Pleistocene

Artículo publicado en la revista *Journal of Taphonomy*, volumen 10, número 3-4, páginas de la 165 a la 184, con fecha del año 2012.

PROMETHEUS PRESS/PALAEONTOLOGICAL NETWORK FOUNDATION (TERUEL)
Journal of Taphonomy
2012 *Available online at www.journaltaphonomy.com*
VOLUME 10 (ISSUE 3-4)

Food Web Structure during the European Pleistocene

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Journal of Taphonomy 10 (3-4) (2012), 165-184.
Manuscript received 15 March 2012, revised manuscript accepted 15 November 2012.

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

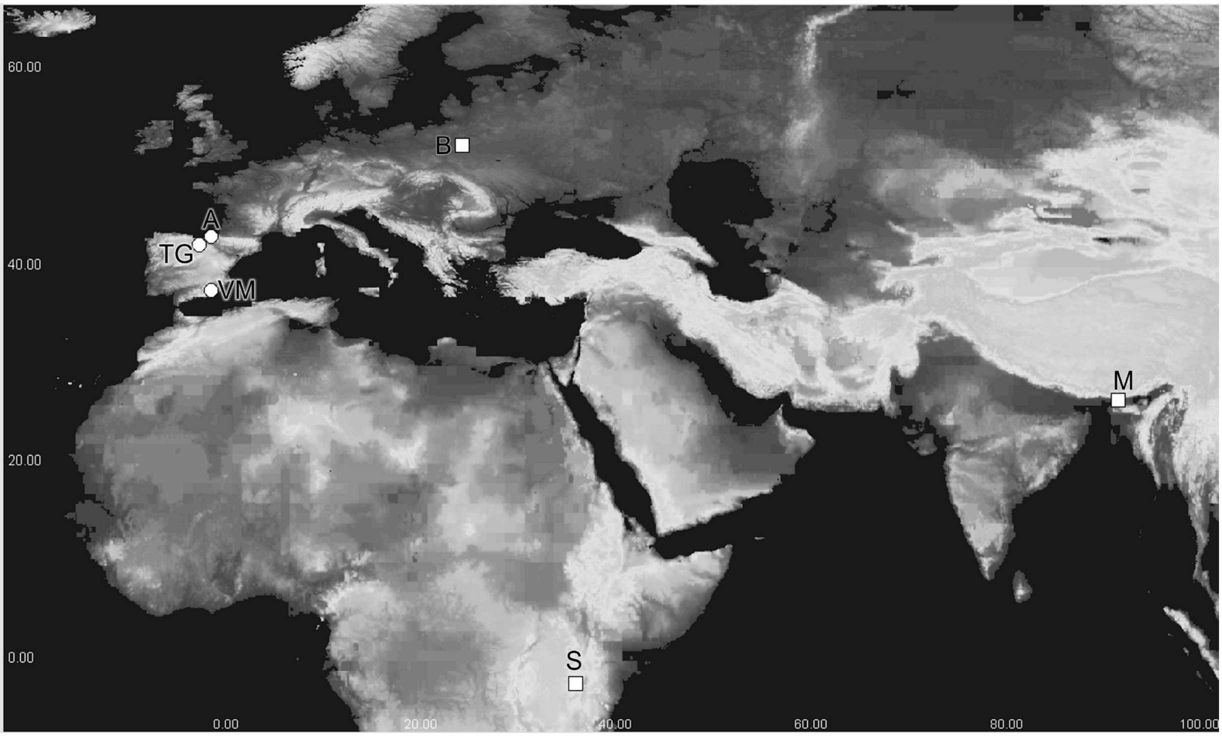
Trophic resource availability data are essential for understanding hominin dispersals and their roles in Pleistocene ecosystems. It is generally accepted that animal resources were essential for Pleistocene hominins in Europe (Hublin & Richards, 2009; Roebroeks, 2001). Most of the recent hunter-gatherer 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* *Homotherium latidens* *Lycaon lycaonoides* *Lynx sp.* *Megantereon cultridens* *Meles sp.* *Pachycrocuta brevirostris* *Panthera cf. gombaszoegensis* *Ursus etruscus*	*Bison sp.* *Bovini indet.* *Equus altidens* *Hemitragus albus* *Hippopotamus antiques* *Hystrix refossa* *Mammuthus meridionalis* *Praemegaceros verticornis* *Praeovibos sp.* *Pseudodama sp.* *Soergelia minor* *Stephanorhinus hundsheimensis*	(Arribas & Palmqvist, 1998; Duval *et al.*, 2011; Martínez Navarro, 1992)
Atapuerca -Galería IIa/IIb	Middle Pleistocene	*Canis lupus* *Cuon alpinus* *Lynx pardinus* *Meles meles* *Panthera leo*	*Bison sp.* *Cervus elaphus* *Dama clactoniana* *Equus ferus* *Equus cf. hydruntinus* *Hemitragus bonali* *Homo sp.* *Hystrix vinogradovi* *Praemegaceros solilhacus* *Stephanorhinus hemitoechus*	(Rodríguez *et al.*, 2011)
Amalda V	Late Pleistocene	*Canis lupus* *Cuon alpinus* *Lynx pardinus* *Panthera leo* *Panthera pardus* *Ursus spelaeus*	*Bos/Bison sp.* *Capra pirenaica* *Capreolus capreolus* *Cervus elaphus* *Equus ferus* *Homo sp.* *Rupicapra rupicapra* *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* *Aonyx capensis* *Caracal caracal* *Civettictis civetta* *Crocuta crocuta* *Hyaena hyaena* *Lycaon pictus* *Panthera leo* *Panthera pardus* *Leptailurus serval*	*Aepyceros malempus* *Alcelaphus buselaphus* *Colobus guereza* *Connochaetes taurinus* *Damaliscus lunatus* *Diceros bicornis* *Equus burchellii* *Gazella granti* *Gazella thomsonii* *Hippopotamus amphibius* *Hippotragus equinus* *Hystrix cristata* *Kobus ellipsiprymnus* *Loxodonta africana* *Manis temminckii* *Oreotraus oreotragus* *Orycteropus afer* *Ourebia ourebia* *Papio hamadryas* *Phacochoerus aethiopicus* *Potamochoerus porcus* *Raphicerus campestris* *Redunca fulvorufula* *Redunca redunca* *Syncerus caffer* *Sylvicapra grimmia* *Taurotragus oryx* *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* *Arctonyx collaris* *Catopuma temminckii* *Cuon alpinus* *Neofelis nebulosa* *Panthera pardus* *Panthera tigris*	*Axis axis* *Axis porcinus* *Bos frontalis* *Bubalus bubalis* *Cervus duvaucelii* *Elephas maximus* *Melurcus ursinus* *Muntiacus muntjak* *Rhinoceros unicornis* *Rusa unicolor* *Sus scrofa*	
Bialowieza National Park	Temperate deciduous forest	*Canis lupus* *Gulo gulo* *Lynx lynx* *Meles meles* *Ursus arctos*	*Alces alces* *Bison bonasus* *Cervus elaphus* *Capreolus capreolus* *Castor fiber* *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

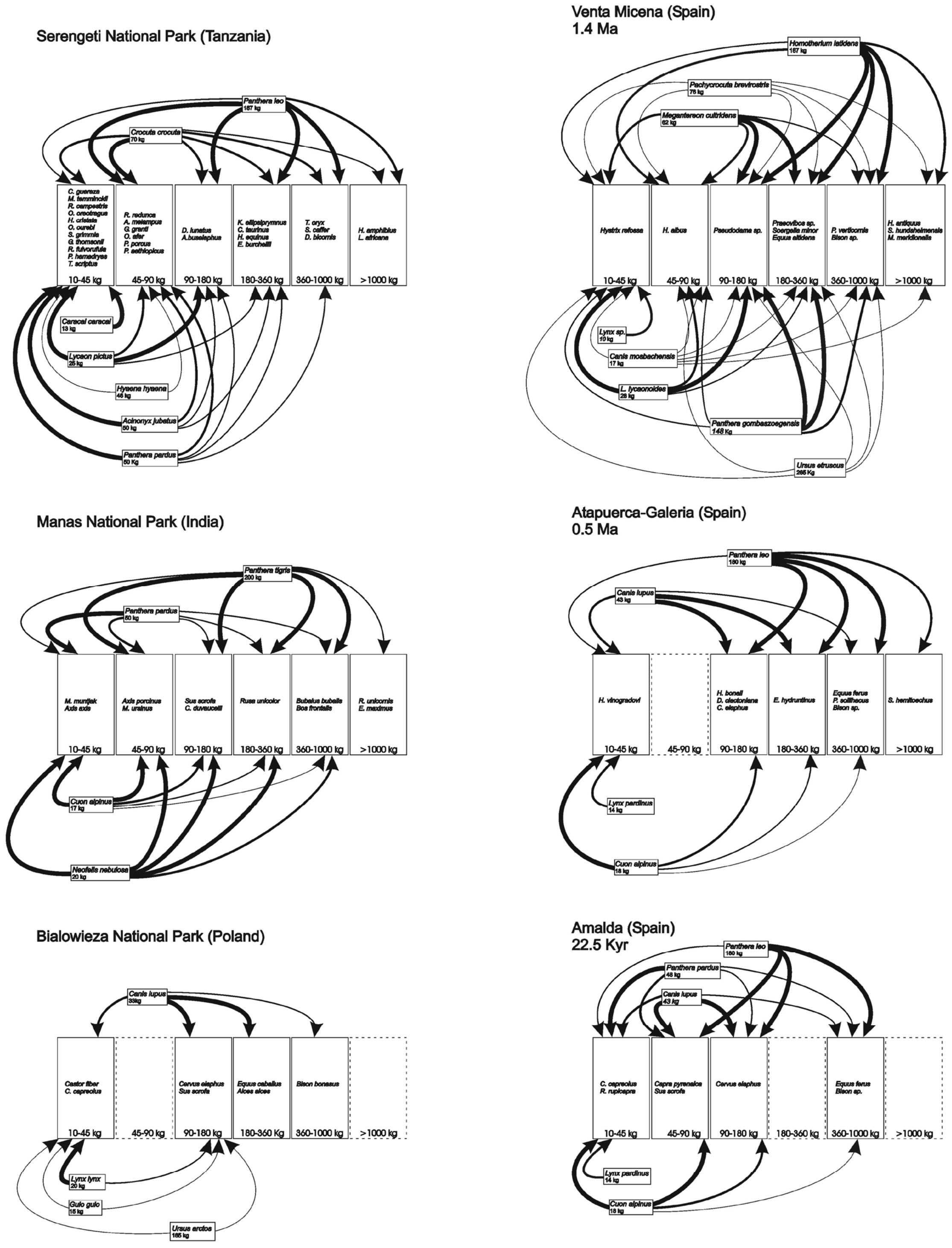


Figure 2. Predator-prey interactions in some recent and fossil communities. Arrow thickness is proportional to the significance of the prey in that size category to the diet of secondary consumers. There are four categories of thickness, the narrowest one being restricted to scavengers. Body size categories 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.

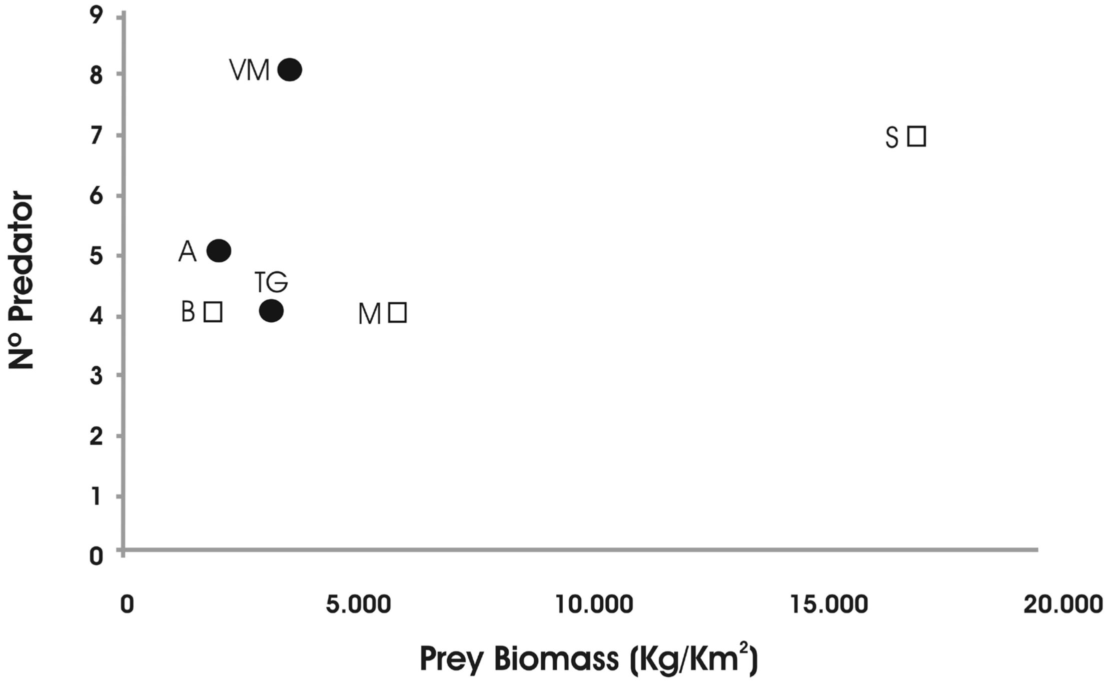
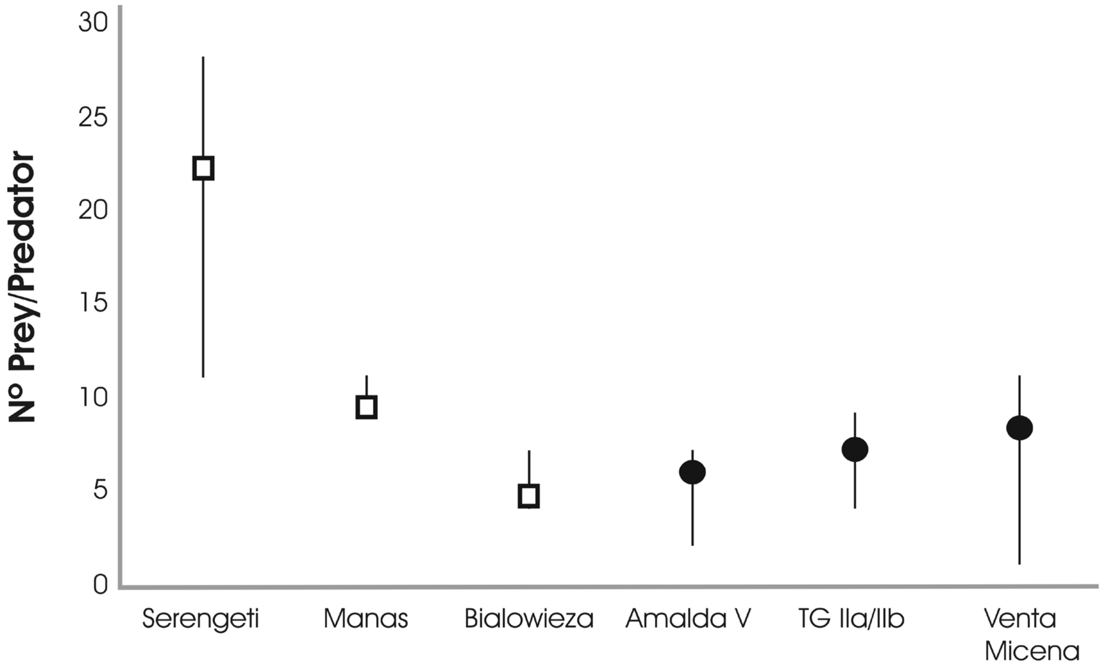


Figure 4. Number of potential prey per secondary consumer (N). Dots and squares represent the mean value and whiskers mark the maximum and minimum numbers of prey per carnivore in each community.



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.

Acknowledgments

We thank Jordi Rosell and Enrique Baquedano for organizing the International Congress “Hominid-Carnivore Interactions during the Pleistocene”. We are grateful to Christine Hertler for their useful comments and suggestions. We also thank also to the congress participants for the thought provoking discussion on some of the topics addressed here. An anonymous editor from Elsevier’s Language services improved the English of the original manuscript. This research was funded by the MICINN project, CGL2009-12703-C03-01. G. Rodríguez-Gómez is beneficiary of a pre-doctoral FPI Grant from the Spanish MICINN.

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Apéndice E. Recursos tróficos y poblamiento humano en el Pleistoceno Medio. Un estudio preliminar en el nivel TD8 de la Sierra de Atapuerca, Burgos

Este trabajo forma parte del Capítulo VII: Suelos y técnicas aplicadas a registros cuaternarios, del libro "El Cuaternario Ibérico: Investigación en el S. XXI", de la VIII Reunión de Cuaternario Ibérico, La Rinconada - Sevilla (2013).

G.T.P.E.Q.

VIII Reunión de Cuaternario Ibérico, La Rinconada - Sevilla (2013)

RECURSOS TRÓFICOS Y POBLAMIENTO HUMANO EN EL PLEISTOCENO MEDIO. UN ESTUDIO PRELIMINAR EN EL NIVEL TD8 DE LA SIERRA DE ATAPUERCA, BURGOS

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Abstract (Middle Pleistocene Trophic Resourcse and Human Settlement. A Preliminary Study of Atapuerca-TD8 Level, Sierra de Atapuerca, Burgos): *Mathematical modelling of palaeocommunity trophic dynamics is a useful tool for investigating food resource availability and intraguild competition. We use a mathematical model based on Leslie Matrices to obtain estimations of the available resources for secondary consumers. Although humans inhabited the Sierra de Atapuerca since more than one million years ago to the Neolithic, the evidence of human presence is not continuous over time. TD8 level of Gran Dolina site, about 600,000 years old, lacks any evidence of human presence. We analyze trophic resource availability for secondary consumers at TD8 to test the hypothesis that human absence coincides with low resource availability. Our results suggest an environment rich in trophic resources, able to sustain a rich guild of secondary consumers.*

Palabras clave: Poblaciones humanas, recursos tróficos, modelos matemáticos, interacción predador-presa
***Key words**: Human population, trophic resource, mathematical models, predator-prey relationship*

INTRODUCCIÓN

El estudio de redes tróficas busca cuantificar y analizar las interacciones que se producen entre las especies de un ecosistema. La aplicación de este tipo de estudio a datos paleontológicos puede aportar información muy relevante como la disponibilidad de recursos para los consumidores secundarios o la intensidad de la competencia entre los carnívoros. La disponibilidad de recursos tróficos es uno de los principales limitantes para la supervivencia y dispersión de cualquier especie. En el caso de los homininos del Pleistoceno de Europa, los recursos tróficos esenciales los constituían los ungulados (Roebroeks, 2001; Hublin y Richards, 2009).

Las habilidades de los homininos para obtener recursos animales del medio estaban condicionadas por la abundancia de presas, sus características ecológicas y la intensidad de la competencia entre los carnívoros por estos recursos. Con respecto a esto último, varios autores han vinculado las oportunidades de supervivencia de los primeros homininos europeos a sus habilidades para competir con los carnívoros (Turner, 1992; Martínez-Navarro y Palmqvist, 1996; Arribas y Palmqvist, 1999; Palombo, 2010).

Los dos factores principales que deberían ser tenidos en cuenta para evaluar la disponibilidad de recursos para los cazadores recolectores del Paleolítico inferior son: 1) la cantidad de biomasa que se puede extraer de las poblaciones de grandes herbívoros y 2) la intensidad de la competencia entre los carnívoros por esos recursos.

Los estudios cuantitativos de las dinámicas tróficas de las paleocomunidades se han empleado anteriormente para entender las relaciones tróficas en paleocomunidades del Mioceno (Vizcaíno, Bargo et al., 2010) y el Pleistoceno (Bermúdez de Castro, Díez Fernández-Lomana et al., 1995; Fariña, 1996; Palmqvist, Gröcke et al., 2003) y para evaluar los efectos de extinciones y de recambio de fauna sobre el funcionamiento del ecosistema durante el Plioceno medio (Vizcaíno, Fariña et al., 2004). Recientemente, Rodríguez-Gómez et al. (2013) han mostrado cómo se puede usar esta aproximación para evaluar la disponibilidad de recursos tróficos para una población de cazadores recolectores paleolíticos.

En la Sierra de Atapuerca se registran indicios de ocupación humana desde hace más de un millón de años hasta el Neolítico. Aunque, en ocasiones, se ha propuesto que esta ocupación fue continuada, el nivel TD8 de la Gran Dolina de la Sierra de Atapuerca, datado en unos 600.000 años, no muestra ninguna evidencia de presencia humana. Teniendo evidencias de ocupación humana en cronologías anteriores y posteriores, es interesante saber cuál podría ser la razón por la que no se registra presencia en esta época. En este trabajo se evalúa la hipótesis de que la ausencia se deba a la escasez de recursos tróficos para sostener una población humana. Para ello aplicamos un modelo matemático desarrollado a partir de la Matriz de Leslie para cuantificar los recursos tróficos del paleoecosistema.

MATERIALES Y METODOLOGÍA

FAUNA DE TD8

Se ha obtenido un listado de las especies de grandes mamíferos identificadas en TD8 de Rodríguez et al. (2011), Blasco et al. (2011) y van der Made (2012). Nuestro análisis se restringe a mamíferos de más de 10 kg porque estos eran la principal fuente de carne, competidores y potenciales depredadores de la población de cazadores-recolectores (Roebroeks, 2001; Owen-Smith y Mills, 2008). Las estimaciones de peso fueron obtenidas de Rodríguez (1997).

Hay 11 consumidores primarios en TD8 con un peso por encima de 10 kg: *Bison voigtstedtensis, Cervus elaphus*, *Dama vallonetensis, Equus altidens, Eucladoceros giulii, Hippopotamus sp., Macaca sp., Megaloceros solilhacus, Stephanorhinus etruscus, Sus scrofa y Ursus sp*. El oso (*Ursus sp.*) es considerado omnívoro y en este estudio se le trata tanto como consumidor primario como secundario. En TD8 hay 5 consumidores secundarios: *Canis mosbachensis, Crocuta crocuta*, *Hyaena sp.* (considerada análoga de la hiena rayada), *Lynx sp. y Ursus sp*. El pequeño cánido *Vulpes sp.* no ha sido incluido, ya que su dieta probablemente estaba compuesta básicamente por pequeños mamíferos, invertebrados, carroña y fruta, como el actual zorro rojo (Seebeck, 1978).

En nuestras simulaciones hemos incluido también en la comunidad de TD8 una población humana (*Homo sp.*) para evaluar si su presencia era sostenible en este ecosistema. Los requerimientos de *Homo sp.* fueron estimados en unas 3.000 kcal por individuo de promedio a partir de los datos de Eaton (1997), para poblaciones de cazadores-recolectores actuales. Otros estudios de poblaciones actuales de cazadores-recolectores muestran que el consumo de recursos animales representa del 30 al 60% de sus ingesta nutricional (Jenike, 2001; Leonard, Robertson et al., 2007).

EL MODELO

El modelo matemático utilizado ha sido explicado en detalle en otros trabajos (Rodríguez-Gómez, Martín-González et al., 2013; Rodríguez-Gómez, Martín-González et al., En prensa). Su objetivo es cuantificar los recursos tróficos del Pleistoceno y estudiar cómo se distribuyen entre los consumidores secundarios. El modelo presenta dos bloques principales: la estimación de los recursos disponibles para los consumidores secundarios, es decir, la biomasa de consumidores primarios o la Biomasa de Salida Total (TBO) (Total Biomass Output); y por otra parte, los requerimientos de los consumidores secundarios o Biomasa Demandada Total (TDB) (Total Demanded Biomass).

En la Figura 1 se puede ver un diagrama de flujos del modelo matemático empleado en el estudio. En la parte superior se muestran las diferentes entradas de datos del modelo y en la inferior la salida, que son las densidades de los consumidores secundarios que se estiman al realizar el reparto de los recursos disponibles para este grupo. Existen dos procesos, representados con triángulos, que representan lo verdaderamente novedoso del modelo. Por una parte, la aplicación de la Matriz de Leslie (Leslie, 1945; Leslie, 1948) para obtener los perfiles de mortalidad para cada especie de consumidores primarios y cuantificar la biomasa que puede ser extraída de cada población manteniéndola estable. Por otra parte, la distribución de recursos entre los consumidores secundarios, generando un reparto que considera la capacidad predatoria de estas especies, sus preferencias de presas y sus requerimientos o presiones de predación (Rodríguez-Gómez, Rodríguez et al., 2013).

Nuestro modelo no es dinámico, ya que pretende ser una aproximación a las condiciones medias del sistema en el tiempo. Asumimos que la estructura y la composición de las poblaciones oscilan alrededor de un valor medio, que se mantiene constante a lo largo del tiempo, asunción ampliamente aceptada en estudios de dinámica de poblaciones (Owen-Smith, 2010).

RESULTADOS

Los resultados muestran que se alcanza una TBO capaz de sostener densidades viables para todas las especies de consumidores secundarios del nivel TD8 de la Sierra de Atapuerca, en comparación con la Mínima Densidad de Población Viable (Minimun Viable Population Density) (MVPD) de Silva y Downing (1994). Las especies alcanzan densidades superiores a la MVPD, aunque no llegan a alcanzar la densidad esperada en función de su tamaño, estimada a partir de ecuaciones alométricas (Damuth, 1981; Damuth, 1993). No obstante, Blackburn y Gaston (1997) y White et al. (2007) defienden que los valores que generan las ecuaciones alométricas más que medias de densidad poblacional proporcionan una estimación de la máxima densidad posible para un mamífero de un peso dado. Sería necesario evaluar si la competencia entre los consumidores secundarios era lo suficientemente baja como para posibilitar que todos pudiesen convivir en la misma comunidad junto con una población humana ya que los valores de densidad obtenidos no nos pueden resolver esta cuestión.

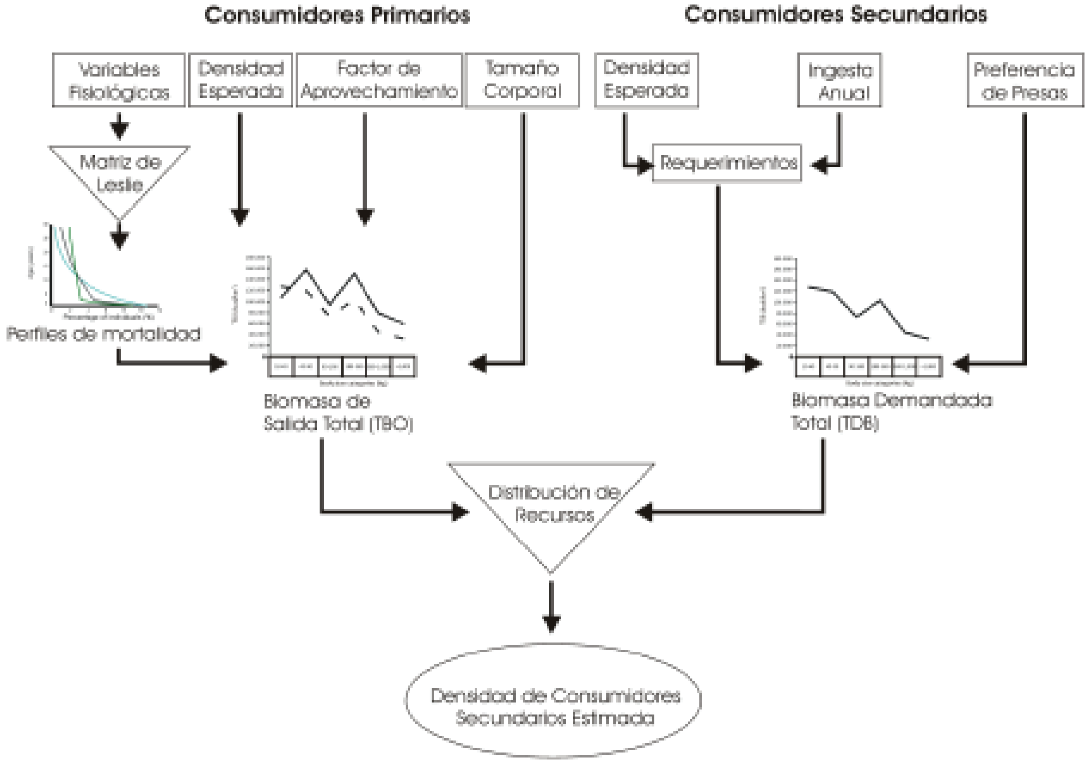

Figura 1. Diagrama de Flujo que muestra los componentes del modelo empleado para evaluar la disponibilidad de recursos tróficos y competencia entre consumidores secundarios.

CONCLUSIONES

La utilización de modelos matemáticos para simular dinámicas tróficas en paleocomunidades es una herramienta útil para investigar la disponibilidad de recursos tróficos para poblaciones paleolíticas. Nuestro modelo determina la biomasa que puede ser extraída de los consumidores primarios por parte de los consumidores secundarios y distribuye esa biomasa en relación a las capacidades y requerimientos de cada especie de consumidor secundario. Los resultados que obtenemos muestran que todos los consumidores secundarios alcanzan densidades por encima de la MVPD pero no alcanzan las densidades esperadas. *Homo sp.* muestra densidades viables para este paleoecosistema. En principio, se podría decir que bajo estas condiciones sería posible su existencia descartando que su falta de presencia se deba a escasez de recursos. No obstante, sería necesario profundizar en el grado de competencia entre consumidores secundarios para poder confirmar que los recursos del medio eran suficientes para que todos los consumidores secundarios pudiesen convivir incluyendo una población humana.

Agradecimientos: Esta investigación ha sido financiada por el proyecto del MINECO, CGL2012-38434-C03-02. G. Rodríguez-Gómez es beneficiario de una beca pre-doctoral FPI del MICINN. R. Blasco es beneficiaria de una beca post-doctoral Beatriu de Pinós-A procedente de la Generalitat de Catalunya y cofinanciada por la Unión Europea mediante las Acciones Marie Curie, FP7. Las campañas de excavación en los yacimientos de la Sierra de Atapuerca han sido financiadas por la Junta de Castilla y León.

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Apéndice F. Estudio de las redes tróficas europeas durante el Pleistoceno Temprano

Artículo publicado en la revista de divulgación científica *Chronica naturae*, número 3, páginas de la 19 a la 37, con fecha del año 2013.

Chronica naturae, 3: 19-37 (2013) G. Rodríguez-Gómez *et al.*

Estudio de las redes tróficas europeas durante el Pleistoceno Temprano.

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RESUMEN

Se han propuesto diferentes modelos de interacción entre humanos y carnívoros para explicar la evolución humana, para cuya evaluación es necesaria una reconstrucción de las redes tróficas del pasado y de sus dinámicas. En este estudio se analizan las faunas de la Europa mediterránea del Pleistoceno Temprano para conocer el papel que pudo tener el humano en las redes tróficas de este periodo y se comparan con comunidades actuales en espacios naturales. Nuestro análisis se restringe a mamíferos con pesos por encima de 10 kg. Analizamos la riqueza de especies de los diferentes ecosistemas y las interacciones entre los predadores y las presas. Nuestros resultados muestran que las redes del Pleistoceno tenían una estructura diferente a las actuales, con una distribución de tamaño de los consumidores primarios distinta en Pleistoceno Temprano y la actualidad. Se observa un incremento de competencia entre los carnívoros hacia mitad del Pleistoceno Temprano, al que le sigue un descenso de esta hasta alcanzar los niveles actuales. La reducción de competencia entre depredadores probablemente permitió la presencia de Homo con un papel más protagonista en las comunidades europeas.

Palabras clave: redes tróficas, megafauna, predador-presa, Pleistoceno, Europa.

INTRODUCCIÓN

La disponibilidad de recursos en el medio ambiente influye sobre las oportunidades de supervivencia de las especies y puede condicionar sus movimientos migratorios. Las especies del linaje humano, que reciben el término de homininos (Subfamilia Homininae), probablemente llegaron a Europa en el Pleistoceno Temprano (2.6-0.78Ma (Millones de años)) aunque no pudieron cruzar el paralelo 45ºN hasta hace 1.2Ma (ver Rodríguez *et al.*, 2011b). La región mediterránea por debajo del paralelo 45ºN, estuvo separada del resto de Europa durante el Pleistoceno Temprano por barreras biogeográficas y climáticas de intensidad variable (Rodríguez *et al.*, 2011b). A su vez, como argumentan Kostopoulus y colaboradores (2007), las tres penínsulas de la región mediterránea de Europa estuvieron separadas por barreras ecológicas y geográficas desde el Cenozoico (65Ma), aunque hubo conexión entre la península Italiana y la Balcánica durante la última glaciación (Michaux *et al.*, 2005).

Se acepta, de forma general, que los animales eran una fuente esencial de recursos para los homininos europeos del Pleistoceno (Hublin y Richards, 2009; Roebroeks, 2001). La mayoría de autores asumen que los grandes mamíferos proporcionaban carne y grasa a los grupos de homininos del Pleistoceno Temprano (Binford, 1981; 1985; Gaudzinski y Roebroeks, 2000; Hublin y Richards, 2009; Marean, 1989; Moigne y Barsky, 1999; Roebroeks, 2001; Speth, 2010). Los grandes herbívoros eran un recurso trófico que los homininos compartían con la comunidad de carnívoros y, de esta forma, la estructura del "guild" (gremio) de carnívoros condicionaba el acceso de los homininos a este recurso (Turner, 1992a). Según Palombo (2010), la dinámica trófica de las paleocomunidades de mamíferos durante el Pleistoceno Temprano pudo retrasar la expansión de los humanos por Europa. Varios autores argumentan que las primeras poblaciones humanas europeas estaban en desventaja por la competencia con los grandes depredadores y, por tanto, que el acceso a los consumidores primarios tenía que producirse mediante carroñeo (Arribas y Palmqvist, 1999; Martínez-Navarro y Palmqvist, 1996; Turner, 1992a). El estudio de las redes tróficas del Pleistoceno es una fuente de información esencial para evaluar todas estas hipótesis sobre las estrategias de supervivencia de los primeros europeos.

El estudio teórico y la descripción de las redes tróficas, su dinámica y arquitectura, tiene una larga tradición en Ecología (por ejemplo, Cohen, 1977; May, 1983; Owen-Smith y Mills, 2008; Pascual y Dunne, 2006). Sin embargo, aunque se han publicado diversos trabajos sobre la comunidad de carnívoros y las relaciones predador-presa en comunidades pleistocenas (Croitor y Brugal, 2010; Dennell *et al.*, 2008; Hemmer, 2004; Hertler y Volmer, 2008; Palmqvist *et al.*, 1996; Palombo y Mussi, 2006; Raia *et al.*, 2007; Turner, 2009) el estudio de la estructura completa de la red trófica de mamíferos raramente se ha tenido en cuenta.

El objetivo de este trabajo es estudiar las redes tróficas de la región sur de Europa, por debajo del paralelo 45ºN, durante el Pleistoceno Temprano y analizar las diferencias, si es que existían, entre las tres regiones peninsulares en este periodo, comparándolas con cuatro regiones actuales. Con ello, se pretende avanzar en el conocimiento de cuál era el papel que desempeñaba el humano en los ecosistemas del Pleistoceno Temprano e intentar aportar información del momento en el que el *Homo* deja de tener un papel secundario o marginal en el ecosistema y pasa a un primer plano.

MATERIALES Y MÉTODOS

El área de estudio es la región europea por debajo del paralelo 45ºN. Este área se ha dividido en tres regiones que coinciden aproximadamente con las tres penínsulas del sur de Europa: Región Sudoeste (SW) (entre las longitudes -10.00 y 4.00 grados) (Península Ibérica), Región Central (C) (entre 4.00 y 18.00 grados) (Península Italiana) y Región Sudeste (SE) (entre 18.00 y 40.00 grados) (Península Balcánica) (Figura 1 y Tabla 1). Se ha recopilado información sobre yacimientos paleontológicos dentro de cada región a partir de fuentes bibliográficas (ver Rodríguez *et al.*, 2012) asignándolos a uno de los tres periodos de tiempo en que puede dividirse el Pleistoceno Temprano: Villafranquiense medio (de 2.6 a 1.8 Ma), Villafranquiense tardío (de 1.8 a 1.2 Ma) y Galeriense temprano (de 1.2 a 0.78 Ma). La ubicación en cada periodo de tiempo se establece según las dataciones bioestratigráficas o numéricas proporcionadas por las fuentes originales.

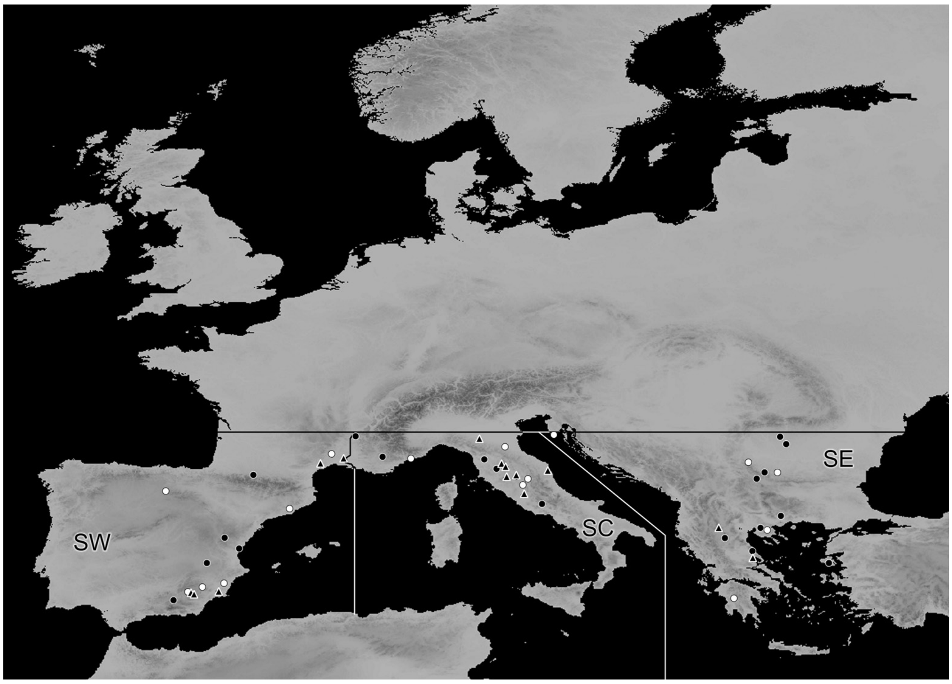

Figura 1. Área de estudio dividida en tres regiones: Sudoeste (SW), Central (SC) y Sudeste (SE) de Europa. Los yacimientos del Villafranquiense medio están marcados con círculos negros, los del Villafranquiense tardío con triángulos negros y los del Galeriense temprano con círculos blancos (Rodríguez *et al.*, 2012).

Tabla 1. Fauna Local del Pleistoceno Temprano del sur de Europa empleada en este estudio. PD:Base de Datos de Paleobiología a fechas del 16/04/2010. http://paleodb.org/

REGIÓN	EDAD	LOCALIDAD	LONGITUD	LATITUD	REFERENCIAS
Sudoeste del Mediterráneo (SW)	**Galeriense temprano**	Atapuerca-Sima del Elefante desde TE 08 a TE14	-3.52	42.35	Rodríguez *et al.*, 2011
		Atapuerca-Dolina TD3-TD4	-3.52	42.35	Rodríguez *et al.*, 2011
		Atapuerca-Dolina TD5	-3.52	42.35	Rodríguez *et al.*, 2011
		Atapuerca-Dolina TD6 1-2	-3.52	42.35	Rodríguez *et al.*, 2011
		Atapuerca-Dolina TD6-3	-3.52	42.35	Rodríguez *et al.*, 2011
		Durfort	3.95	43.98	PD
		Estrecho de Quipar	-1.88	38.04	Scott and Gibert, 2009
		Huescar-1	-2.50	37.77	PD
		Sierra de Quibas	-0.93	38.20	Montoya *et al.*, 2001; Montoya *et al.*, 1999
		Vallparadís 10-10c	2.02	41.56	Martínez *et al.*, 2010
	Villafranquiense tardío	Barranco León V	-2.43	37.71	Scott and Gibert, 2009
		Cueva Victoria	-1.18	37.85	Gibert *et al.*, 1999
		El Chaparral C1-C2	36.69	-5.39	Giles Pacheco *et al.*, 2011
		Fuente Nueva 1	-2.38	37.70	PD
		Fuente Nueva-3	-2.40	37.71	PD
		Lézignan-le-Cèbe	3.43	43.48	Crochet *et al.*, 2009
		Venta Micena	-2.38	37.73	PD
	Villafranquiense medio	Casablanca 1	-0.22	39.76	PD
		Fonelas P-1	-3.17	37.40	PD
		Montoussé 5	0.40	43.07	PD
		Puebla de Valverde	-0.91	40.21	Azanza *et al.*, 1997
		Valdeganga III	-1.68	39.13	Hernández-Fernández, 2004

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<< continuación

REGIÓN	EDAD	LOCALIDAD	LONGITUD	LATITUD	REFERENCIAS
Mediterráneo Central (C)	**Galeriense temprano**	Colle Curti	12.75	42.95	Palombo *et al.*, 2000-2002
		Grotte du Vallonnet III	7.47	43.77	de Lumley *et al.*, 1988
		Imola	11.71	44.35	Palombo *et al.*, 2000-2002
		Redicicoli	41.93	12.52	Raia *et al.*, 2009
		Torre di Picchio	12.49	42.65	Raia *et al.*, 2009
	Villafranquiense tardío	Capena	12.55	42.17	Palombo *et al.*, 2000-2002
		Casa Frata	11.57	43.55	Palombo *et al.*, 2000-2002
		Il Crostolo	10.56	44.63	Palombo *et al.*, 2000-2002
		La Sartanette	4.50	43.76	Palombo and Valli, 2003-2004
		Pietrafitta	12.21	42.99	PD
		Pirro Nord Combined	13.65	43.28	PD
		Selvella	11.76	42.93	PD
		Val di Chiana (arenas de la primera fase fluvial-lacustre)	11.73	43.41	Torre *et al.*, 1992 Palombo *et al.*, 2000-2002
	Villafranquiense medio	Casa Sgherri	10.80	43.77	Marcolini *et al.*, 2000
		Casino Lignite mine, nivel lacustre superior	11.33	43.32	PD
		Collepardo	13.36	41.76	Palombo *et al.*, 2000-2002
		Cornillet	6.20	43.91	Palombo and Valli, 2003-2004
		Costa San Giacomo	13.36	41.76	Palombo *et al.*, 2000-2002
		Saint-Vallier	5.02	44.81	PD
		Valle Catenaccio	13.36	41.76	Palombo *et al.*, 2000-2002
Sudeste del Mediterráneo (SE)	**Galeriense temprano**	Kozarnika 11c	22.68	43.63	Guadelli *et al.*, 2005
		Kozarnika 11d	22.68	43.63	Guadelli *et al.*, 2005
		Kozarnika 12	22.68	43.63	Guadelli *et al.*, 2005
		Kozarnika 13	22.68	43.63	Guadelli *et al.*, 2005
		Krimni	40.50	23.50	Koufos, 2001
		Kunino Lower Level	23.96	43.18	Palombo *et al.*, 2006
		Marathousa-Megalopolis	22.04	37.51	Palombo *et al.*, 2006
		Ravin Voulgarakis	23.50	40.60	Palombo *et al.*, 2006
		Sandalja-I	13.89	44.90	Kahlke *et al.*, 2011
	Villafranquiense tardío	Alikes	22.81	39.29	Palombo *et al.*, 2006
		Libakos	21.30	40.63	Palombo *et al.*, 2006
	Villafranquiense medio	Dafnero 1	21.59	40.17	Spassov, 2003
		Gerakarou	23.22	40.65	PD
		Sésklo	22.82	39.63	Athanassiou, 2003
		Slatina 2	24.37	44.43	PD
		Slivnitsa	23.02	42.87	PD
		Valea Roscai	24.09	44.78	PD
		Varshets	23.38	43.19	Spassov, 2003
		Vassiloudi	23.22	40.65	Palombo *et al.*, 2006
		Vatera	26.20	39.02	Palombo *et al.*, 2006
		Volakas	24.15	41.24	Palombo *et al.*, 2006

Se han revisado todas las listas de fauna aplicando un criterio taxonómico uniforme para obtener una base de datos con coherencia taxonómica. Hemos basado nuestra revisión en las realizadas por especialistas en la sistemática de los diferentes grupos (Alberdi *et al.*, 1998; Breda y Marchetti, 2005; Crégut-Bonnoure, 2007; Croitor, 2005, 2006a, b; Fostowicz-Frelik, 2008; Turner, 1992b; Turner *et al.*, 2008; van der Made y Mazo, 2003; Weers, 1994). Restringimos nuestro análisis a las especies de mamíferos con un peso mayor de 10 kg porque asumimos que estas especies constituyen la parte de las redes tróficas que tienen mayor influencia sobre los humanos. Los carnívoros incluidos pertenecen a las familias Canidae (cánidos como el lobo (*Canis lupus*) o el coyote (*Canis latrans*)), Felidae (felinos como el león (*Panthera leo*) y el jaguar (*Panthera onca*)), Hyenidae (como la hiena manchada (*Crocuta crocuta*) o la rayada (*Hyaena hyaena*)) y Ursidae (osos).

Las listas de especies de cada región, Fauna Regional (FR), se confeccionan a partir de las especies presentes en cada yacimiento y se agrupan por periodo de tiempo. Así se obtienen nueve conjuntos de fauna, tres regiones por tres periodos de tiempo. Si se registró en una Fauna Local (FL), fauna presente en un yacimiento en un intervalo de tiempo, una especie en el Villafranquiense medio y en el Galeriense temprano, se supuso que estaba presente también en el Villafranquiense tardío, aunque no haya sido registrada en ningún yacimiento de este periodo.

Las redes tróficas del Pleistoceno Temprano se compararon con las de cuatro regiones actuales: Este de África (E Afr.), Sudáfrica (S Afr.), Nordeste de América (NW A.) y Sudeste de Asia (SE A.). Se seleccionaron 25 Faunas Locales (FLs) actuales presentes en estas cuatro áreas, de extensión similar a las regiones pleistocenas estudiadas (Tabla 2 y 3, y Figura 2). La lista de especies para cada Fauna Regional fue obtenida a partir de las FLs al igual que se hizo para las regiones pleistocenas.

Figura 2. Las faunas del Pleistoceno han sido comparadas con faunas actuales de cuatro regiones. Los cuadrados negros representan las cuatro regiones: Noroeste de América (NW A.), Este de África (E Afr.), Sur de África (S Afr.) y Sudeste de Asia (SE A.). Los círculos blancos muestran la posición de los Parques Nacionales y Reservas utilizados en cada región como Faunas Locales (Rodríguez *et al.*, 2012).

Tabla 2. Las nueve Faunas Regionales del Pleistoceno Temprano y las cuatro actuales que se consideraron para realizar este estudio, clasificadas por regiones geográficas y datación (Rodríguez *et al.*, 2012).

REGIÓN	ÁREA	EDAD	FAUNA REGIONAL	CRONOLOGÍA (MA.)
Sudoeste del Mediterráneo	514.421	Galeriense temprano	SW Gal	1.2-0.78
		Villafranquiense tardío	SW lVil	1.8-1.2
		Villafranquiense medio	SW mVvil	2.6-1.8
Mediterráneo Central	202.761	Galeriense temprano	C Gal	1.2-0.78
		Villafranquiense tardío	C lVil	1.8-1.2
		Villafranquiense medio	C mVvil	2.6-1.8
Sudeste del Mediterráneo	683.782	Galeriense temprano	SE Gal	1.2-0.78
		Villafranquiense tardío	SE lVil	1.8-1.2
		Villafranquiense medio	SE mVvil	2.6-1.8
Este de África	604.463	Actual	E Afr.	-
Sur de África	545.945	Actual	S Afr.	-
Noroeste de América	550.033	Actual	NW A.	-

Tabla 3. Se utilizaron 25 localidades actuales en el análisis. MAB= Base de datos del Hombre y la fauna de la Biosfera. UNESCO. Man and the Biosphere Program (MAB). Information Center for the Environment (University of California, Davis) http://ice.ucdavis.edu.

REGIÓN		EDAD	FAUNA REGIONAL	CRONOLOGÍA (MA.)
Este de África	Amboseli	37.15	-2,39	MAB
	East Usambara	38.20	-4,45	Rodgers and Homewood, 1981
	Lake Manyara	35.60	-3,30	MAB
	Mount Kenya	37.19	0,10	Young and Evans, 1993
	Serengeti	35.10	-2,25	Swynnerton, 1958
	South Turkana	35.37	1,57	Coe, M, 1972.
Noroeste de América	Coram Biosphere Reserve	-113.79	48,24	MAB
	Craters of the Moon	-113.10	43,33	MAB
	Glacier	-113.50	48,37	MAB
	Grand Teton	-110.71	43,81	MAB
	Waterton	-113.50	49,60	MAB
	Yellowstone	-110.10	44,58	MAB
Sur de África	Kruger	31.24	-24,35	MAB
	Malolotjia Nature Reserve	31.30	-26,00	MAB
	Mlawula	32.00	-26,00	MAB
	Transvaal 38	28.15	-26,20	Rautenbach, 1978
	Transvaal 41	29.45	-23,15	Rautenbach, 1978
	Transvaal 42	27.15	-25,15	Rautenbach, 1978
	Transvaal 44	30.10	-23,15	Rautenbach, 1978
	Weenen Game Reserve	30.40	-28,70	Bourquin and Mathias, 1995
Sudeste de Asia	Bandhavgarh	80.77	23,39	MAB
	Mount Everest (Sagarmatha)	86.72	27,93	MAB
	Royal Chitwan	84.33	27,29	MAB
	Sanjay	81.37	23,77	MAB
	Simlipal	86.35	21,70	MAB

Clasificamos los consumidores primarios de acuerdo a las categorías de tamaño definidas por Andrews *et al.* (1979): D = 10-45 kg; E = 45-90 kg; F = 90-180 kg; G = 180-360 kg; H = 360-1.000 kg e I > 1.000 kg. Las presas preferidas por cada carnívoro se infirieron a partir de análisis publicados de datos morfofuncionales (a partir de aspectos anatómicos) y análisis isotópicos sobre especímenes fósiles (por ejemplo, Palmqvist *et al.*, 2003; Palmqvist *et al.*, 2008a). Esta información fue complementada con la proporcionada por estudios sobre la etología de las especies vivas de similar tamaño y filogenéticamente próximas. Describimos las preferencias de los predadores mediante el código P, S y N. P para las especies en la categoría de tamaño preferida o principal; S para las especies secundarias que se encuentran en categorías de peso por encima o por debajo de la preferida; y N para las categorías en las que no se alimenta la especie. Estudios con fauna actual evidencian que, en la práctica, no existe un límite inferior de tamaño corporal para las presas secundarias (Radloff y Toit, 2004), por lo que definimos todas las categorías de tamaño por debajo de la P como S. Como ejemplo del proceso que se ha llevado a cabo podemos ver la interpretación de las preferencias del tigre de dientes de sable (*Homotherium latidens*) presente en el yacimiento de Venta Micena en el Villafranquiense tardío. Según los análisis isotópicos llevados a cabo por Palmqvist *et al.* (2003) sobre fósiles del yacimiento de Venta Micena, el elefante meridional (*Mammuthus meridionalis*), probablemente en su etapa juvenil, representaba una parte importante de la dieta de este félido, junto con los bisontes (*Bison sp.*) (52%) y caballos (*Equus altidens*) (38%) (Palmqvist *et al.*, 2008b). Por tanto, consideramos que los intervalos de peso más importantes son los de las categorías G (180-360 kg) y H (360-1.000 kg) aunque probablemente los dientes de sable pudieran consumir también esporádicamente presas de más de 1.000 kg de peso. Asumimos que los ungulados más pequeños serían depredados ocasionalmente (para ver el proceso completo, ver Rodríguez *et al.*, 2012).

Construimos las redes tróficas a partir de esa información y las representamos como se muestra en la Figura 3 para el paleoecosistema de Venta Micena (Rodríguez-Gómez *et al.*, in press). Esta representación está basada en el trabajo de Owen-Smith and Mills (2008) y permite visualizar fácilmente la complejidad de las comunidades y los posibles focos de competencia. Las presas se distribuyen en cajas por tamaño corporal. Las cajas que aparecen con líneas discontinuas son aquellas que no contienen ninguna especie de ese tamaño corporal en ese ecosistema.

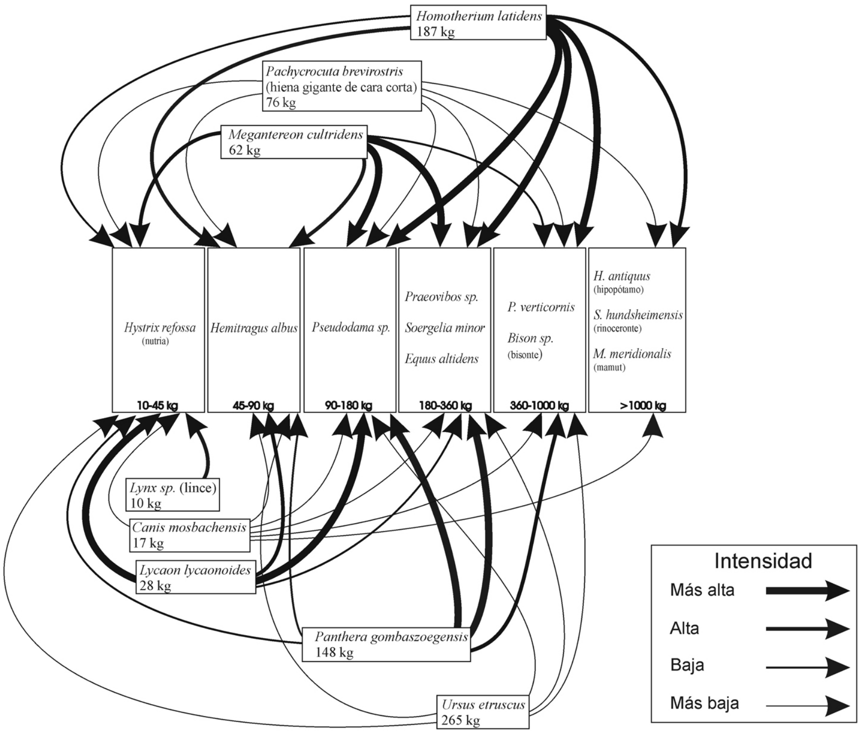


Figura 3. Interacciones predador-presa en la paleocomunidad de Venta Micena (Granada, España). El grosor de la flecha es proporcional a la relevancia de las presas de esa categoría de peso en la dieta del consumidor secundario. Se proponen cuatro categorías de grosor, la más fina se reserva para el carroñeo. Las categorías de tamaño corporal se muestran en las bases de las cajas. Los predadores dominantes (los mejores competidores) se disponen por encima de las cajas y los más débiles por debajo (Rodríguez-Gómez *et al.*, 2013 in press).

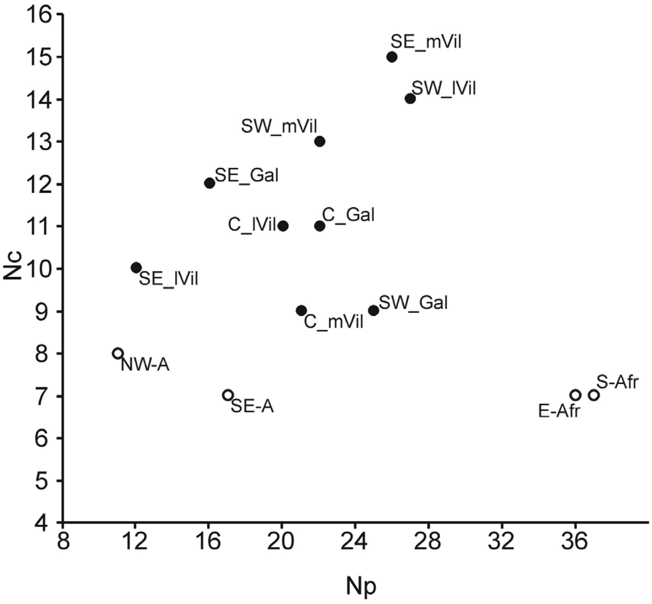
Los depredadores se sitúan por encima y por debajo de las cajas de presas ordenados por el peso del depredador. Los depredadores más fuertes (los mejores competidores) aparecen encima. Se representa la interacción predador-presa mediante flechas de cuatro grosores diferentes que simbolizan la intensidad de la interacción o importancia relativa de cada intervalo de tamaño corporal en la dieta del depredador. Las flechas más finas representan carroñeo.

Para cuantificar las presiones de predación y la competencia entre predadores utilizamos dos indicadores, NMP y MNMP. El Número de Predadores Principales (NMP) para cada consumidor primario es igual al número de carnívoros que tienen a esa especie como presa preferente. La Media del valor de NMP (MNMP) se emplea para estimar la intensidad de la competición entre predadores. No entran en el cálculo de MNMP aquellos consumidores primarios con NMP igual a 0, herbívoros exentos de predadores, ya que lo que se pretende es reflejar el grado en que los predadores comparten las presas, es decir, el grado de solapamiento de sus nichos.

RESULTADOS Y DISCUSIÓN

Las redes tróficas del Pleistoceno presentan una arquitectura diferente a las actuales. Las diferencias son tanto a nivel estructural como de riqueza del ecosistema. Las comunidades del Pleistoceno muestran un mayor número de especies de carnívoros y un número intermedio de especies de consumidores primarios con respecto a las actuales, siendo más abundantes en las redes africanas (S Afr. y E Afr.) y más pobres en la asiática (SE A.) y norteamericana (NW A.) (Figura 4).

Figura 4. Número total de carnívoros (Nc) y consumidores primarios (Np) en las Faunas Regionales del Pleistoceno y actuales. Círculos negros: FRs del Pleistoceno; círculos blancos: FRs actuales. Códigos como en la Tabla 2. (Rodríguez *et al.*, 2012).



Si se observa la distribución de tamaños de los consumidores primarios junto con la presión de predación por categoría de tamaño de las presas, se observan unas tendencias diferentes entre las comunidades del Pleistoceno Temprano y las actuales (Figura 5). Los patrones generales de las redes tróficas del Pleistoceno consisten en una baja proporción de consumidores primarios en las categorías de peso menores y una alta proporción en las categorías mayores y, a su vez, una importante presión de predación en las categorías de tamaño más pequeñas. Estos patrones son más marcados en las comunidades que se corresponden con el Galeriense temprano. En las comunidades actuales, como tendencia general, son más abundantes las presas de menor tamaño y la relación entre el número de presas y el número de carnívoros que se alimentan de cada categoría es más baja que en el Pleistoceno.

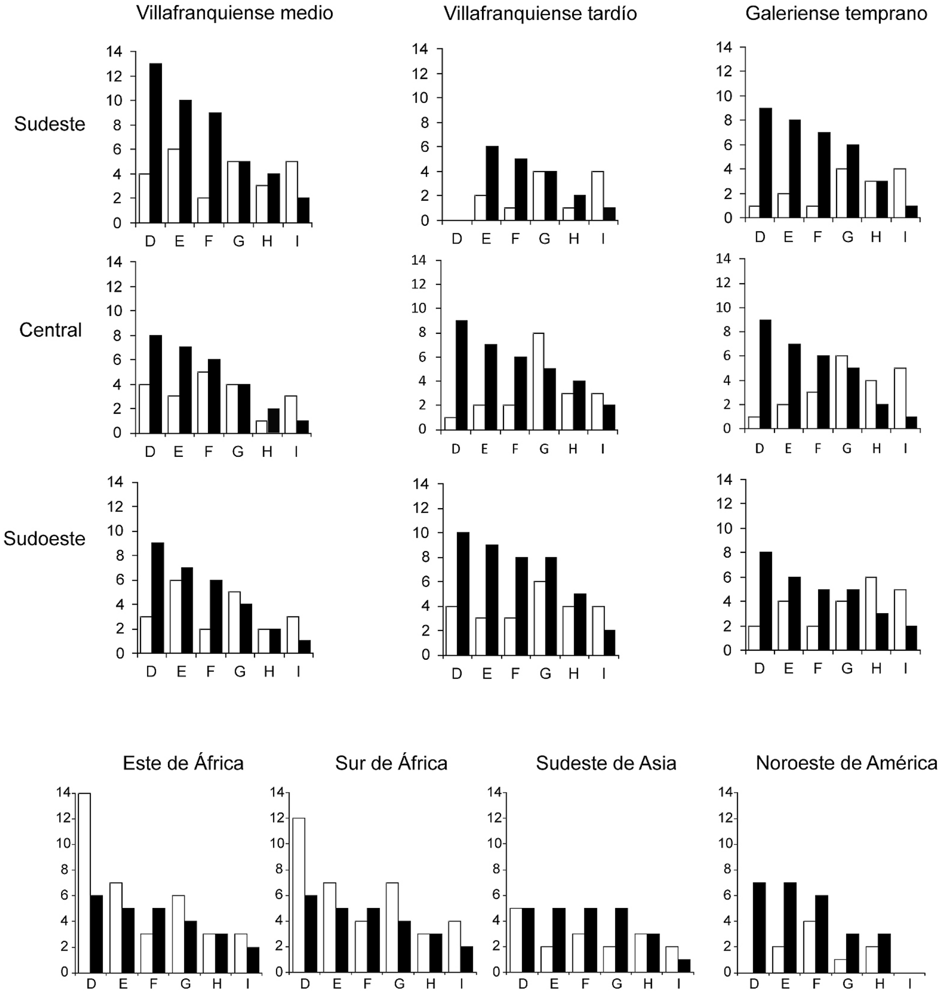


Figura 5. Interacciones predador-presa en Faunas Regionales actuales y fósiles. Las barras blancas representan el número de consumidores primarios por intervalo de tamaño corporal, las barras negras indican el número de depredadores capaces de cazar especies en ese intervalo de tamaño. Nótese que un mismo depredador puede cazar presas de diferentes categorías de tamaño. D=10–45 kg; E=45–90 kg; F=90–180 kg; G=180–360 kg; H=360–1000 kg; I>1000 kg. (Rodríguez *et al.*, 2012).

No obstante, dentro de estas redes actuales se observan diferencias importantes. Un factor que destaca sobre los demás es la alta abundancia de consumidores primarios de la categorías D (10-45 kg) y E (45-90 kg) en las comunidades africanas. En SE A. se observa una baja proporción de pequeños ungulados junto a una moderada aparición de megaherbívoros. En NW A. se da una alta proporción de ungulados de tamaño intermedio y no hay presencia de megaherbívoros de la clase I (>1.000 kg). La escasez de pequeños consumidores primarios en las comunidades del Pleistoceno podría deberse en parte a sesgos en el registro fósil, pero la abundancia de mamíferos de gran tamaño que se observa es incontrovertible, además de ser un aspecto que las diferencia de las redes actuales, como ya se apuntaba en trabajos previos (Rodríguez, 2004). En los ecosistemas actuales existe una amplia variación en la distribución de tamaños corporales de unas regiones biogeográficas a otras, que no está influenciada por factores medioambientales (Nieto *et al.*, 2005), sino por la extinción de megafauna ocurrida a finales del Pleistoceno. La megafauna aparece en muy baja proporción en los ecosistemas actuales mientras que su abundancia en el Pleistoceno Temprano debió tener profundos efectos en la estructura y dinámica de las redes tróficas, condicionando intensamente las capacidades de caza de los carnívoros (Carbone *et al.*, 1999; Levinton, 1982). Está ampliamente aceptado que el incremento de tamaño es una eficaz estrategia evolutiva para evitar a los depredadores (Stanley, 1973; Yoshida, 2006), que permite explicar el incremento de tamaño corporal en muchos linajes (Prado *et al.*, 2004).

Como se observa en las FRs del Pleistoceno Temprano el tamaño medio de las especies de consumidores primarios se fue incrementando desde el Villafranquiense medio hasta el Galeriense temprano (Figura 6). La diversidad de carnívoros capaces de cazar megafauna se incrementó en el Villafranquiense tardío pero decreció de nuevo en el Galeriense temprano, tanto en el suroeste (SW) como en el centro sur de Europa (SC). El balance energético entre ingesta y gasto es dependiente del tamaño corporal del carnívoro (Carbone *et al.*, 2007) y un "megadepredador" especializado en herbívoros de 1.000 kg o más habría sido muy vulnerable a las fluctuaciones en las poblaciones de sus presas. Croitor y Brugal (2010) han propuesto que la caza en grupo evolucionó en este periodo como una estrategia social de los grandes depredadores para poder cazar presas más grandes sin tener que incrementar su tamaño. Pero aunque los megaherbívoros (>1.000 kg) pudieron formar parte esporádicamente de las dietas de varios predadores, las especies más grandes no eran presas preferidas por ningún predador. La existencia de un elevado número de especies sin predadores implica que sus poblaciones no estaban reguladas por éstos, sino por la producción primaria (los recursos) y que los mecanismos reguladores "abajo-arriba" (bottom-up) cobraron más y más importancia al final de Pleistoceno Temprano, y posteriormente en el Pleistoceno Medio, como ya señalaron Raia *et al.*, (2007) para la Península Italiana.

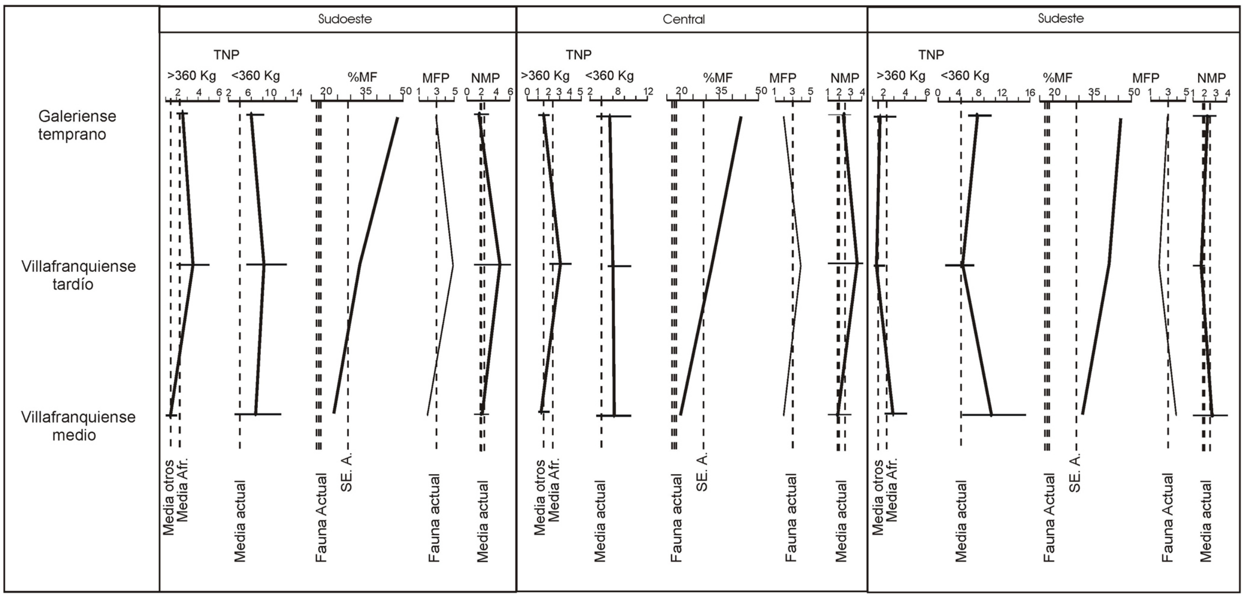


Figura 6. Cambios en la estructura de las redes tróficas durante el Pleistoceno Temprano en las Faunas Regionales (Sudoeste, Centro y Sudeste del Mediterráneo). El Número Total de Depredadores (TNP) considera al número de especies de carnívoros capaces de cazar megaherbívoros (>360 kg) o a consumidores primarios de tamaño medio o pequeño (<360 kg). Las barras representan el máximo y mínimo número de depredadores para una presa, mientras que las líneas conectan los valores medios. El Número de Depredadores Principales (NMP) representa al número de depredadores que comparten una presa preferida por todos ellos. La línea conecta los valores de la Media del Número de Depredadores Principales (MNMP), que es un índice de la competencia entre los carnívoros. Las barras representan la NMP máxima y mínima para un consumidor primario en esa FR. El porcentaje de megafauna (% MF) se define como la proporción de consumidores primarios que pesan más de 360 kg, y el número de depredadores capaces de cazarlos se indica por el MFP (Depredadores de Megafauna). Se muestran, además, los valores de todos los índices para las cuatro FRs actuales como referencia. (Rodríguez *et al.*, 2012).

Observando el índice de competencia entre depredadores (MNMP) se aprecia que en el Villafranquiense tardío y en las comunidades SW y SC, se produjo un incremento de la competencia respecto a la época anterior y un posterior descenso en el Galeriense temprano. La tendencia en las preferencias de los consumidores primarios hacia tamaños mayores, incrementó la competencia entre los depredadores por las categorías de peso intermedias. Los patrones observados en el Villafranquiense tardío para las Faunas Regionales (FRs) del SW y SC no se observan en la FR del SE, debido, probablemente, a que el registro fósil de esta última FR está muy incompleto. El Villafranquiense tardío en esta región está representado únicamente por dos yacimientos (Alikes y Libakos) que, además, muestran una baja diversidad específica (Figura 4).

El género *Homo* se dispersó por el sur de Europa a finales del Villafranquiense o principios del Galeriense (Bosinski, 2006; Carbonell *et al.*, 2010). Según los resultados que presentamos, la llegada de los humanos a Europa coincide con cambios importantes en la comunidad de carnívoros y en la estructura de las redes tróficas. Hay varios autores que apoyan una relación entre los cambios en la comunidad de carnívoros al final del Villafranquiense y la llegada de *Homo* (Arribas y Palmqvist, 1999; Martínez-Navarro y Palmqvist, 1996; Palombo *et al.*, 2010; Turner, 1992a). La alta competencia entre predadores durante el Villafranquiense tardío apoya la hipótesis de la existencia de un impedimento para la expansión de *Homo* durante este periodo. Croitor y Brugal (2010) sugieren que en un ambiente de alta competencia entre carnívoros, los homininos recién llegados sobrevivieron gracias a su versatilidad, adoptando una dieta fuertemente omnívora, no dependiente de la carne. Por otro lado, los estudios de la dieta de poblaciones actuales de cazadores-recolectores destacan la carne como una fuente de alimento clave para los mismos (Cordain *et al.*, 2000; Jenike, 2001; Leonard y Robertson, 1994). De momento no se han encontrado evidencias arqueológicas claras de las estrategias de subsistencia llevadas a cabo por los homininos durante el Villafranquiense tardío en el Sur de Europa. La escasez de yacimientos arqueológicos lleva a pensar que el papel de *Homo* en las redes tróficas era marginal. Entre las más antiguas evidencias encontradas se haya el nivel TE9 del yacimiento de la Sima del Elefante en la Sierra de Atapuerca (Burgos), datado aproximadamente en 1,2 Ma. El registro óseo y de industria lítica de TE9 apoya un comportamiento oportunista-generalista de estos grupos humanos, con un consumo de gran variedad de alimentos de origen animal entre los que se incluyen mamíferos de tamaño medio y pequeño, conejos, pájaros y tortugas (Blasco *et al.*, 2011; Rodríguez *et al.*, 2011a).

La competencia entre depredadores disminuyó al final del Villafranquiense y paralelamente aumentan las evidencias de actividad humana en este periodo. Es tentador pensar que *Homo* ocupó el nicho vacío de un predador especializado en megafauna. Su comportamiento social y capacidades de planificación hacen de los humanos buenos candidatos para cubrir la plaza vacante. Las evidencias arqueológicas disponibles para este periodo, siendo escasas, no pueden arrojar mucha luz sobre esta cuestión. No obstante, el registro fósil del nivel TD6-2 del yacimiento arqueológico de Gran Dolina en la Sierra de Atapuerca, acumulado por la especie *Homo antecessor* hace aproximadamente 0,8Ma (Falguères *et al.*, 1999; Moreno-García, 2011), muestra que las presas preferentes eran los herbívoros de tamaño pequeño y medio (Saladié *et al.*, 2011). Esta muestra sugiere que las presas prefridas por los pobladores europeos del Pleistoceno Temprano estaban entre los 90 y 360 kg, lejos por tanto de lo que se esperaría de un "megapredador".

CONCLUSIONES

Las redes tróficas del sur de Europa durante el Pleistoceno Temprano están caracterizadas por una alta riqueza de carnívoros junto con una distribución de tamaños corporales diferente de las observadas en ecosistemas actuales. La proporción de megafauna en el Villafranquiense medio es mayor que en el presente, incrementándose en el Villafranquiense tardío y reduciéndose en el Galeriense temprano. La competencia entre carnívoros se incrementa en el Villafranquiense tardío a niveles muy superiores a los observados en comunidades actuales, reduciéndose a valores similares a los actuales durante el Galeriense temprano. Estas características tuvieron importantes efectos sobre la dinámica de las redes tróficas del Pleistoceno Temprano.

En el Pleistoceno Temprano, el papel de los homininos en las redes tróficas como depredadores era probablemente marginal, mantendrían una dieta omnívora con un comportamiento oportunista. Este estilo de vida pudo limitar la expansión de sus poblaciones durante el Villafranquiense final como propuso Palombo (2010). La competencia entre carnívoros se redujo en el Galeriense temprano a niveles similares a los observados actualmente, *Homo antecessor* entró a formar parte de la comunidad predadora y fue capaz de expandir sus poblaciones.

AGRADECIMIENTOS

Querríamos agradecer a Andrea Moreno Parera, Estefanía Pérez Fernández, José Rodríguez Mellado y Enrique Sánchez Anguiano la revisión y los comentarios que han hecho para mejorar el texto. Este estudio ha sido financiado por el proyecto del MINECO, CGL2012-38434-C03-02. G. Rodríguez-Gómez es beneficiario de una beca predoctoral FPI del MICINN.

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Apéndice G. A New Mathematical Approach to Model Trophic Dynamics of Mammalian Paleocommunities. The Case of Atapuerca-TD6

Este trabajo forma parte del capítulo Part XXII: Recent Advances in Quantitative Methods Applied to Stratigraphy and Paleontology, del libro “Mathematics of Planet Earth. 15th Annual Conference of the International Association for Mathematical Geosciences”, publicado por Springer en la serie “Lectures Notes in Earth System Sciences.

A New Mathematical Approach to Model Trophic Dynamics of Mammalian Palaeocommunities. The Case of Atapuerca-TD6

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1 Introduction

Trophic resource availability is one of the main constraints for the survival and dispersal of any species and it is generally accepted that animal resources were also essential to Pleistocene hominins in Europe [1, 2]. The ability of hominins to obtain animal resources from their environment is conditioned by the abundance of prey, their ecological characteristics, and the intensity of the competition with carnivores for these resources. Thus, several authors linked the survival opportunities of the first European hominins to their ability to compete with carnivores [3–5]. Two main factors should be taken into account to evaluate food resource availability for early Palaeolithic hunter-gatherers: (1) the amount of biomass that can be extracted from the populations of large herbivores and (2) the intensity of competition within the carnivore guild for those resources. Quantitative studies of the trophic dynamics of palaeocommunities have been used by palaeoecologists to understand trophic relationships in mammalian palaeocommunities from the Miocene [6] and the Pleistocene [7–9] and to evaluate the effects of extinctions and faunal turnover on ecosystem functioning during the mid-Pliocene [10]. Here we present a model that quantifies trophic resource availability for secondary consumers in a large mammal community, simulates resource distribution among those consumers and provides information about the intensity of competition inside the carnivore guild. We show the application of our model to the TD6 assemblage from the Atapuerca Gran Dolina, Burgos, Spain.

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Lecture Notes in Earth System Sciences, DOI: 10.1007/978-3-642-32408-6_160,

2 The Model

Our aim is to investigate the distribution of resources, primary consumer biomass, among secondary consumers in different scenarios and evaluate if the last may they reach viable densities. In order to achieve this aim, we propose a mathematical model. It provides the estimation of the biomass of primary consumers available to secondary consumers, i.e. the Total Biomass Output (TBO). Moreover, it is necessary to estimate the requirements of secondary consumers or Total Demanded Biomass (TDB). A detailed description of this model is provided in Rodríguez Gómez et al. [11] (Fig. 1).

2.1 Total Biomass Output (TBO)

2.1.1 Input

Physiological Variables

Input data are physical and physiological variables (adult body mass, body mass at birth, litter size, breeding interval, age at reproductive maturity, growth rate and lifespan) which are species specific. The values of these physiological variables are taken from the literature or estimated through allometric equations.

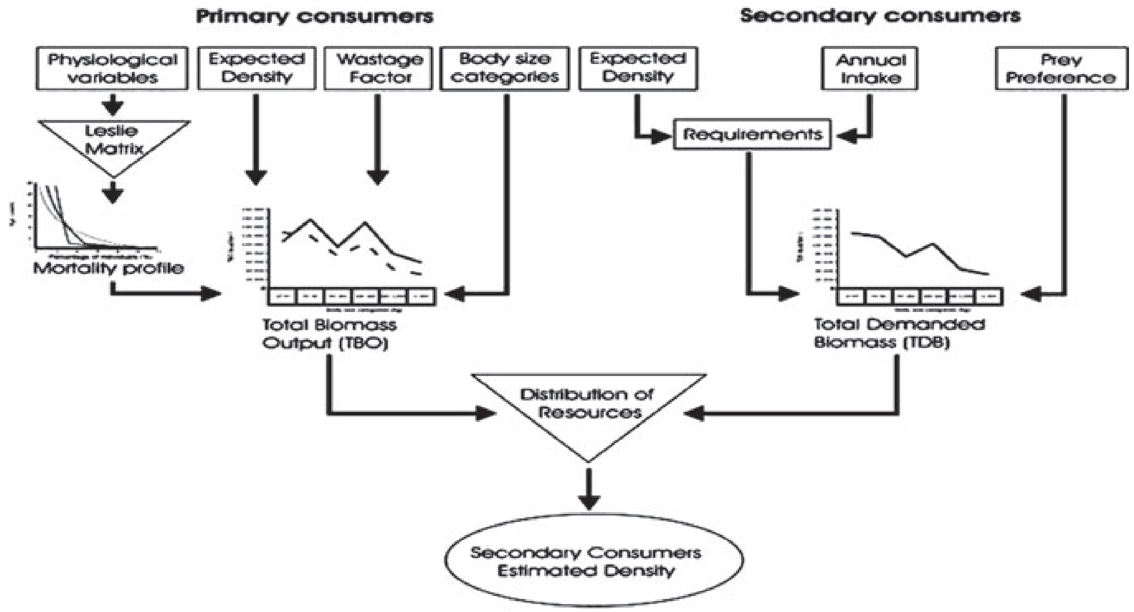

Fig. 1 Flow Diagram showing the components of the model used to evaluate trophic resource availability and intraguild competition

Expected Density

The model solutions are not dependent on population size, thus, an estimate of population density is needed to estimate the sustainable Biomass Output. Allometric equations are used to estimate primary consumers density e.g. [12–14].

Body Size Category

Each individual of a primary consumer species is classified into one of six body size categories according to its body mass at the age of death: 10–45, 45–90, 90–180, 180–360, 360–1,000, >1,000 kg see [15].

Wastage factor

We use the wastage factors from Viljoen [16] to account for the fact that a carcass includes a variable amount of non edible tissues (horns, bones, hide…).

2.1.2 Process: Leslie Matrix

Our model is developed under the assumption that all the variations in population size and composition may be taken as oscillations around a mean value that is constant through time, an assumption widely accepted in population dynamics studies [17]. We represent the average long term condition of every population using the Leslie Matrix [18, 19]:

$$X_{t+1} = \begin{bmatrix} a_1 & a_z & \cdots & a_n \\ b_1 & 0 & \cdots & 0 \\ \vdots & \ddots & \ddots & \vdots \\ 0 & \cdots & b_{n-1} & 0 \end{bmatrix} X_t \tag{1}$$

where a_i is fecundity, the per capita number of female offspring and b_i is the proportion of individuals that survive from age class *i* to age class *i*+1. The number of individuals of age class *i* died each year, whatever the cause is given by $1 - b_i$. The interval between age classes is one year and only female individuals are represented in a Leslie matrix. Leslie Matrix Inputs are physiological variables of section *Physiological Variables*. We assumed that sex ratio is equal to 1:1, that population profile is the same for males and females and that the survival rate is equal for both sexes. A further assumption is that sub-adult survival rate should be lower than adult survival rate [11].

Two additional conditions are introduced: (1) The population should be stable (i.e., the population size should be constant from year to year); (2) The population should be stationary (i.e., the age structure should be constant from year to year). These restrictions can be interpreted as the condition that makes the population structure stable and it occurs when the net reproduction rate (NRR) is equal to one.

The population profiles obtained from this model for every primary consumer population provide an estimation of the average sustainable biomass output by age classes (mortality profile), which are eventually translated into biomass per body size intervals. Total Biomass Output (TBO) is obtained as the sum of the biomass output in each size category from each primary consumer population.

2.1.3 Output

Combining the mortality profiles obtained in from the Leslie Matrix with the mean body size per age class, the estimated population density of the species and the wastage factor, the Total Biomass Output (TBO) is computed.

2.2 Total Demanded Biomass (TDB)

2.2.1 Input

Expected Density

Estimated using allometric equations e.g. [12–14].

Annual Intake

Carnivore intake rate was estimated using allometric equations e.g. [20].

Prey Preference

Six predation body size categories, equal to the primary consumer categories are defined and the preferences of each carnivore recorded: 10–45, 45–90, 90–180, 180–360, 360–1,000, >1,000 kg see [15].

2.2.2 Process: Requirements

The annual energetic requirements of a carnivore population by km^2 are obtained multiplying the individual annual intake by population density.

2.2.3 Output: Total Demanded Biomass (TDB)

Combining the Prey Preferences and the Requirements of each secondary consumer, Total Demanded Biomass (TDB) per body size categories is obtained.

2.3 Distribution of TBO Between Secondary Consumers

2.3.1 Input

Total Biomass Output (TBO) and Total Demanded Biomass (TDB) are the inputs for this process.

2.3.2 Process

Distribution of TBO between secondary consumers is based on the Proportional Predation Pressure (PPPij) of each species in each body size category. PPPij represents the relative amount of biomass demanded by the jth carnivore species from the ith prey body size category. It is calculated as the proportion of the total amount of biomass demanded from a prey body size category by all carnivores that corresponds to the requirements of a single carnivore species. See a detailed description of the computation of resource distribution in Rodríguez-Gómez et al. [11].

2.3.3 Output

This process provides estimated densities for the secondary consumers as output.

3 Application

We selected the TD6 assemblage from the Atapuerca Gran Dolina site (Burgos, Spain) (approximately 0.8 Ma.) because it has been considered as a key sample in resolving several palaeoeconomic issues related to the populations that inhabited Europe approximately one million years ago [21] and references therein. This is the single European site from this period where hominin remains have been found together with abundant faunal remains and a rich collection of lithic artifacts. Thus, the TD6 assemblage provides both biological information about the first European settlers and evidences of their nutritional and cultural activities.

We applied our model in TD6 to know if there was enough resources to maintain a stable human group in this ecosystem. Our results show that meat resources covered all secondary consumer requirements. Our results support the interpretation of a rich ecosystem at Atapuerca at the end of the Early Pleistocene that boasted a level of secondary production sufficient to maintain a well diversified guild of secondary consumers including a human population.

4 Conclusion

Mathematical modelling of palaeocommunity trophic dynamics is a useful tool for investigating food resource availability for Palaeolithic populations. Our model determines the age structures that make the populations of primary consumers stable, the average biomass that can be sustainably extracted in the long term and its distribution in body size categories. Thus, our model provides insights into competition for resources among secondary consumers. When the model is applied to the TD6 assemblage, the results suggest that resources were abundant enough to support the carnivore guild at maximum densities, i.e. it was a rich ecosystem for secondary consumers, including *Homo*.

Acknowledgments This research was funded by the MINECO project, CGL2012-38434-C03-02. G. Rodríguez-Gómez is the beneficiary of a pre-doctoral FPI Grant from the Spanish MICINN. Fieldwork at Atapuerca sites was funded by the Junta de Castilla y León.

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