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Mean body size estimation in large mammals and the computation of biomass in past ecosystems: An application to the Pleistocene sites of Orce and Sierra de Atapuerca (Spain)

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ABSTRACT

Estimates of adult body mass are usually considered as equivalent of mean population body size in most studies of ancient mammals. However, given that any population is composed in part of subadult individuals, this approach overestimates the mean population body mass and biomass.

KEY WORDS

Body mass, Weibull model, macromammals, paleoecosystems, carrying capacity, on-crop biomass.

MOTS CLÉS

Masse corporelle, modèle de Weibull, macromammifères, paléoécosystèmes, capacité de charge, biomasse "on-crop".

For this reason, more realistic estimates of mean population body mass should be used. In this paper, we: 1) test five different proxies of population mean mass; and 2) estimate the total prey biomass in the paleoecosystems from the Orce and Atapuerca sites as an approach for estimating their carrying capacity. Our results for past ecosystems support the use of survival profiles derived from the Weibull model (SPW), as they show values in better agreement with those of extant populations. They also estimate higher carrying capacities for the faunal assemblages of Orce than for those of Atapuerca. We suggest that the environmental conditions of Orce could have played an important role in the first peopling of Europe.

RÉSUMÉ

Estimation de la taille moyenne des grands mammifères et calcul de la biomasse dans les écosystèmes du passé : une application aux sites pléistocènes de l'Orce et de la Sierra de Atapuerca (Espagne).

Les estimations de la masse corporelle des adultes sont généralement considérées comme équivalentes à la masse corporelle moyenne de la population dans la plupart des études paléocéologiques des mammifères anciens. Cependant, étant donné que toute population est composée en partie d'individus subadultes, cette approche surestime la masse corporelle et la biomasse moyennes de la population. C'est pourquoi il convient d'utiliser des estimations plus réalistes de la masse corporelle moyenne de la population. Dans cet article, nous : 1) testons cinq différentes approximations de la masse corporelle moyenne de la population ; et 2) estimons la biomasse totale des proies dans les paléoécosystèmes des sites d'Orce et d'Atapuerca comme approche pour estimer leur capacité de charge. Nos résultats pour les écosystèmes passés soutiennent l'utilisation des profils de survie dérivés du modèle de Weibull (SPW), car ils montrent des valeurs en meilleur accord avec celles des populations existantes. Ils estiment également des capacités de charge plus élevées pour les assemblages fauniques de l'Orce que pour ceux de l'Atapuerca. Nous suggérons que les conditions environnementales de l'Orce pourraient avoir joué un rôle important dans le premier peuplement de l'Europe.

INTRODUCTION

Although the concept of carrying capacity is complex, it is widely used in life sciences (Sayre 2008). Among biologists, it covers a wide focus, from the molecular to the ecological level (see review in Chapman & Byron 2018). In a broad review, Sayre (2008) defined four basic uses of the concept of carrying capacity: 1) a characteristic of artificial elements or systems; 2) a property of species and natural systems; 3) *K*, the ceiling of population size; and finally; 4) the number of humans that the Earth can sustain.

According to the third definition, *K* refers to the logistic function defined by Verhulst in 1838 (see Bacaër 2011):

EQUATION 1

$$\frac{dN}{dT} = rN (1 - N/K),$$

where *N* is the number of individuals, *T* denotes time, *r* is the intrinsic rate of growth, and *K* is the maximum population size (i.e., the upper limit of population growth).

When applied to paleoecological studies, obtaining accurate estimates of biomass for past ecosystems is key for determining their predator-prey relationships and trophic dynamics of their food webs (Bermúdez de Castro *et al.* 1995; Fariña 1996; Palmqvist *et al.* 2003; Vizcaíno *et al.* 2004, 2010; Barnosky 2008; Marín Arroyo 2010; Palombo 2010, 2016; Meloro & Clauss 2012; Rodríguez-Gómez *et al.* 2012, 2013, 2014a, b, 2016a, b, 2017a, b, c; Volmer & Hertler 2016; Domingo *et al.* 2017; Rodríguez & Mateos 2018).

Explicitly or implicitly, these papers use the concept of carrying capacity under the third definition of Sayre (2008), with *K* as the intrinsic growth limit of a population after long-term environmental stability. However, some authors use the term on-crop biomass as an alternative to carrying capacity in order to refer to the biomass sustained by a paleoecosystem (e.g. Palmqvist *et al.* 2003; Vizcaíno *et al.* 2004, 2010; Palombo 2016). In this study, we consider both concepts as synonymous and use the term carrying capacity as equivalent to the biomass of prey species that an ecosystem can support, as proposed by Coe *et al.* (1976).

ABBREVIATIONS

Ma million years ago or megaannum.

Faunal assemblage parameters

A fossil assemblage;
MNI minimum number of individuals;
MPR Mid-Pleistocene Revolution;
NISP numbers of identified specimens;
SC numerical codes assigned in this study for identifying each species.

Population dynamics parameters

D population density;
MPBM population body mass;
T_r population turnover rate.

Approaches for estimating population biomass

ABM adult body mass;

AFBM adult female body mass;
 ¾AFBM three quarters of adult female body mass;
 SPW survival profiles-Weibull.

Sierra de Atapuerca sites

G Galería;
 TD Gran Dolina;
 TE Sima del Elefante.

Orce sites

BL Barranco León;
 FN-3 Fuente Nueva-3;
 VM Venta Micena.

POPULATION BIOMASS AND CARRYING CAPACITY OF PAST ECOSYSTEMS

There are two basic methodologies for estimating the maximum number or biomass of organisms that an ecosystem can support in the long term: 1) to consider the fossil record as an actual reflection of past ecosystems (e.g. Volmer & Hertler 2016; Domingo *et al.* 2017); and 2) to use the abiotic and biotic attributes (e.g. soil nature and composition, topography, climate, ecology) of past ecosystems inferred from the information locked in the fossil record for delivering these estimates (e.g. Fariña 1996; Palmqvist *et al.* 2003; Rodríguez-Gómez *et al.* 2013; Rodríguez *et al.* 2014). When the preservational completeness of the record is high, it can be considered as a reliable picture of ancient communities, as occurs in the case of the bone assemblages generated in some extant communities (e.g. Western & Behrensmeyer 2009; Miller 2011, 2012). In these cases, the estimates of minimum number of individuals (MNI) can be assumed to reflect the proportion of the living individuals of those species that inhabited in the past ecosystem and these numbers can be used as proxies for population densities in the long term. However, MNI counts tend to underestimate the abundance of common species and to overestimate the abundance of rare ones in those assemblages of small size; in such cases, it is more reliable to estimate species abundances using the numbers of identified specimens (NISP) of each species (Arribas & Palmqvist 1998). Moreover, apart from estimating taxonomic richness and community structure, NISP counts allow studying prey selection and provide information on the abundance of past resources (Stiner 1992; for the use of NISP values for juveniles and adults as evidence of prey selection in Venta Micena, see Palmqvist *et al.* 1996).

Once species abundances are estimated, the biomass of past populations and communities can be computed if body mass estimates are available for the individuals. However, in many cases the information of the fossil record is taphonomically biased, which makes it impossible to consider the relative abundances of the species preserved in a site as proportional to those shown in the original ecosystem. Damuth (1982) showed that the relative abundance of each species in a fossil assemblage (A) depends on its mean population density (D) in the paleocommunity and its population turnover rate (T_r). A number of studies (e.g. Western 1979, 1980; Damuth

1981, 1987, 1991; Calder 1982, 1984; Peters 1983) have shown that population density (i.e., number of individuals per unit area) scales inversely and allometrically to the -0.75 power of species body mass (M): $D = K_1 * M^{-0.75}$. In contrast, several parameters related to population turnover rate (e.g. birth rate, duration of postnatal growth, or reciprocal of life expectancy at birth) scale with a slope close to -0.3 : $T_r = K_2 * M^{-0.3}$. As a function of both equations, the original abundance (A) of bones of those species present in a fossil assemblage is determined by: $A = DT_r = K_1 * M^{-0.75} * K_2 * M^{-0.3} = K_3 * M^{-1.05}$, with a 95% confidence interval for this slope that ranges between -0.8 and -1.3 (Damuth 1982). It should be noted that these scaling relationships relate to the species of a given trophic level (e.g. herbivores), as population density decreases for a given body size as trophic level increases (which results in changes in the Y-intercept). In this way, if the slope that relates species abundances with species masses in a fossil assemblage for a given trophic level is included within this interval (-1.05 ± 0.25), this would mean that the composition of the assemblage did not experience significant taphonomic bias with respect to the original paleocommunity (i.e., community structure was preserved during fossilization; this analysis is usually made with ungulates, given their greater abundance in most fossil sites). In contrast, a value for the slope departing from the confidence interval would indicate that the relative frequencies of species do not fit the size/abundance relationship of recent communities. This would suggest the bias of the assemblage by taphonomic processes or other factors (e.g. sampling or curating errors; see Damuth 1982; Arribas & Palmqvist 1998). In most cases, the departure from the mass/abundance relationship expected results from differences in the size of species. The reason is that, apart from differences in the preservation potential of compact vs. spongy bones or rounded vs. elongated and/or flattened bones (see review in Arribas & Palmqvist 1998), the body size of a species (and of its skeletal elements) is one of the factors with greatest influence on the fossilization potential of terrestrial vertebrates (Behrensmeyer *et al.* 1979; Behrensmeyer & Dechant-Boaz 1980; Damuth 1982). The reason is that the bones of large-sized species use to be more resistant to physico-chemical weathering (e.g. exposure to sun radiation, salt precipitation, changes in relative humidity, etc.) and destruction by biotic agents (e.g. trampling by ungulates, carnivore gnawing, root growth, etc.) due to their lower outer surface to inner volume ratio. Damuth (1982) proposed a correction factor (d_i) for estimating this loss of information during the time the bones were exposed on the surface before burial in the sediment: $d_i = 0.68 * \log(M_m/M_i)$, where " M_i " is the mass estimated for species "i" and " M_m " is the mass of the largest species identified in the assemblage. In this way, the amended original abundance (A^*_i) of each species can be estimated as: $\log(A^*_i) = \log(A_i) + d_i$. Following this procedure, if the slope of the least-squares regression of $\log(A_i)$ on $\log(M_i)$ is close to -1.05 , this would mean that the main loss of information during the taphonomic history of the assemblage was due to the greater destruction of the skeletal remains

of those species of smaller body size, which biased their representation in the fossil assemblage. This was evidenced in the taphonomic analysis of the large mammals' assemblage from Venta Micena in Orce (Arribas & Palmqvist 1998).

The population densities of species in the original community (i.e., number of individuals per unit area) can be estimated using allometric equations like those proposed by Damuth (1981):

EQUATION 2

$$\log(D) = a (\log M) + b,$$

where a is the slope and b is the intercept of the least-squares regression of \log_{10} transformed values of population density (D , individuals per km^{-2}) on mean adult body mass (M , in g). Damuth (1981, 1993) published several equations for different trophic levels and ecosystem types. This provides an indirect way for obtaining individual numbers for the species preserved in the site. Once the species abundance is known, estimates of the population biomass of each species can be obtained multiplying their body mass by their number of individuals (Cyr & Pace 1993):

EQUATION 3

$$B_i = M_i \times D_i,$$

where B_i is the population biomass of species i , M_i is its mean body mass, and D_i is its population density. This approach has been used in a number of papers for estimating the population biomass of mammalian species in past ecosystems, considering the sum of all population biomasses as the carrying capacity of the paleocommunity (e.g. Bermúdez de Castro *et al.* 1995; Fariña 1996; Palmqvist *et al.* 2003; Vizcaíno 2004, 2010; Barnosky 2008; Marín Arroyo 2010; Meloro & Clauss 2012; Palombo 2016). However, it should be noted that the body mass of extinct species is often estimated from skeletal remains of adult specimens (see Damuth & MacFadden 1990). In the papers cited above, the adult body mass of each species was used to estimate its population biomass, using the mean body mass estimated for the adult individuals as a proxy of population body mass. This procedure tends to overestimate the population biomass, as a fraction of the population is composed of sub-adult individuals with lower body masses than the adults. Moreover, in a number of ungulate groups (e.g. ruminants with cranial appendages such as bovids and cervids), the males are usually greater than the females and their remains are usually better preserved in the sites thanks to the presence of anatomical structures that are well mineralized and have greater fossilization potential, such as the bovid horn-cores in the large-sized males. A good example of this is the site of Oued Sarrat (c. 0.7 Ma) in Tunisia, which records the earliest appearance of *Bos primigenius*. In this site, only bull remains have been determined (Martínez-Navarro *et al.* 2014b). Similarly, in the site of Venta Micena, Orce (see below), the estimates of minimal numbers of individuals for the medium-sized deer *Metacervoceros rhenanus* based on antler bases (only present in the males) are greater than those based on teeth (Martínez-Navarro 1991; Palmqvist *et al.* 1996). Therefore, it would be more realistic to calculate the mean body mass of the population in order to estimate with greater accuracy the

population biomass. In the case of extant ecosystems, this can be addressed if population structure is known. For doing so, the average body mass of each age class and the proportion of individuals per age class must be considered. Thus, we can multiply both parameters, as in the Cyr and Pace's equation (equation 3 in this paper). However, this is difficult to achieve in extant communities of large mammals. Schaller (1972) used as an approach the "three-quarters of the weight of an average adult female times the number of animals to obtain the biomass figure for a species". Owen-Smith (1988) applied also this method in a study on the effects of body mass on ecological parameters. Similarly, Hayward *et al.* (2007) used it for estimating the carrying capacity of several African communities. Furthermore, Hatton *et al.* (2015) used adult female body mass as a proxy for population body mass. In the field of paleontology, however, it is difficult to use these proxies for those species with a low degree of sexual dimorphism, and especially in those taxa which are not abundantly preserved in the fossil record of each site.

In the case of extant communities, the best way to avoid these problems is to use the population structures of the constituent species or, alternatively, to obtain estimates of them from life tables. For instance, Coe *et al.* (1976) used population structures derived from the bibliography for quantifying the mean population biomass of large herbivores supported by a number of African ecosystems. However, the information used in this study for inferring the unit weights of several species was not enough for obtaining accurate estimates, as suggested by Mentis (1970). Moreover, these population structures were considered to represent situations distant from stability conditions (e.g. Laws 1966; Mentis 1970). In order to use this approach more accurately, decades of census data would be necessary. In such situation, life tables can be used as a proxy, because they are useful tools to deliver inferences on population ecology, including mortality profiles, life traits, population growth, and stability in the long term (Deevey 1947; Banfield 1955; Laws 1968; Caughley 1970a, b; Goddard 1970; Watson 1970; Corfield 1973; Sinclair 1974; Klein 1978; Ashby & Henry 1979; Attwell 1982; Melton 1983; Payne 1984; Simmons *et al.* 1984; Nesse 1988; Messier *et al.* 1988; Garrott & Taylor 1990; Dinerstein & Price 1991; Benton *et al.* 1995; Schwartz *et al.* 1998; Ha *et al.* 2000; Storz *et al.* 2002; Schindler *et al.* 2012). Life tables are built using census data obtained with direct or indirect methods. Some researchers have also used life tables for reconstructing fossil populations (Kurtén 1953a, b, 1954, 1983; Van Valen 1963, 1964, 1965; Voorhies 1969; Speth 1983; Frison 1984; Koike & Ohtaishi 1987; Muhlbachler 2003; Fernandez & Legendre 2003; Fernandez *et al.* 2006, 2017; Fernandez & Boulbes 2010; Monchot *et al.* 2012; Price *et al.* 2016). Once population structure is inferred from a life table, it is possible to estimate the mean body mass of the individuals in the community. However, it is not possible to apply this procedure to past ecosystems in which not enough information is available from the fossil record for constructing the life tables. In such cases, an alternative method is to reconstruct survival and mortality profiles of fossil populations. Leslie matrices

(Leslie 1945, 1948) are widely used to describe population dynamics in extant communities (Caswell 2000; Keyfitz & Caswell 2005) and can also be useful for obtaining the profiles of fossil populations. They have been used in a number of studies for: 1) analyzing the sustainability of past populations (Fernandez & Boulbes 2010; Monchot *et al.* 2012; Martín-González *et al.* 2016; Fernandez *et al.* 2017); 2) evaluating taphonomic biases (Domingo *et al.* 2017; Rodríguez-Gómez *et al.* 2017a); and even 3) estimating meat availability and competition intensity in carnivores and human populations of hunter-gatherers (Rodríguez-Gómez *et al.* 2013, 2014a, b, 2016a, b, 2017a, b; Domingo *et al.* 2017). Moreover, Martín-González *et al.* (2016) used the Weibull model, a parametrical survival model, to estimate the survival and mortality profiles of fossil populations, which allowed them to derive their age structure. Therefore, the use of these mathematical approaches to obtain survival curves and reconstruct the population structure of past species can be very useful when there is a lack of information on the fossil populations to reconstruct their life tables, or if such information is not reliable due to taphonomic biases.

The aim of this study is to test which method is better for estimating the population biomass and carrying capacity of past ecosystems. For doing so, we focus on the carrying capacity of prey species of large mammals. More specifically, in this study we pay special attention to the term M in the equation by Cyr & Pace (1993) (equation 3 in this study) and propose the use of population age structures derived from the Weibull model to estimate the mean mass of each species as a methodological innovation. In this way, the term D is not a target of this study (see equation 3) in order to avoid adding noise to our analyses. For evaluating our proposal, we compare five approaches that use different proxies of population body mass (see Material and methods section), three of them used also in other analyses. This comparison will allow to select the method more appropriate for future studies. The analyses will be performed at the species and community scales, in order to estimate the effects of each approach on both ecological levels. In addition, we will offer an example of the use of these methods to a number of assemblages preserved in different taphonomic contexts, modeling with them the human paleoecosystems for evaluating the influence of these approaches in the results obtained. For doing so, we have selected the faunal assemblages of several sites from Sierra de Atapuerca and Orce in Spain that are key to the study of human evolution in Western Europe during Early Pleistocene times. Moreover, we want to address with this analysis if the carrying capacity of the paleoecosystem was similar in these sites or, alternatively, if it played a relevant role in determining the first human settlements in Western Europe.

BACKGROUND ON THE SIERRA DE ATAPUERCA AND ORCE SITES

The Orce sites are placed in the Baza Basin, placed in eastern sector of the Guadix-Baza Depression, *c.* 150 km NE of the city of Granada (SE Spain). This basin was endorheic (*i.e.*, characterized by internal drainage) from latest Miocene to latest

Middle Pleistocene times (Viseras *et al.* 2005; García-Tortosa *et al.* 2008; García-Aguilar & Palmqvist 2011). The sediments from the lacustrine environments of the basin preserve huge assemblages of large mammals, some of them associated to lithic tools (Martínez-Navarro 1991; Martínez-Navarro & Palmqvist 1995; Martínez-Navarro *et al.* 1997; Arribas & Palmqvist 1998, 1999; Oms *et al.* 2000, 2011; Palmqvist & Arribas 2001; Palmqvist *et al.* 2005, 2011; García-Aguilar & Palmqvist 2011; Espigares *et al.* 2013, 2019; Toro-Moyano *et al.* 2013; García-Aguilar *et al.* 2014a, b, 2015; Ros-Montoya *et al.* 2017). Two archaeo-paleontological sites, Barranco León (BL) and Fuente Nueva-3 (FN-3), preserve skeletal remains of 18 species of large mammals associated with Oldowan (*i.e.*, Mode 1) lithic tools and the bones of large mammals unearthed in them document cut marks and percussion marks (Barsky *et al.* 2010, 2016; Espigares *et al.* 2013, 2019; Toro-Moyano *et al.* 2013). In the case of BL, a human deciduous tooth dated to *c.* 1.4 Ma is, at the moment, the earliest human fossil in Western Europe (Toro-Moyano *et al.* 2013). The stratigraphy of BL spans the middle terrigenous member and the upper silty calcareous member of the Baza Formation, dominated by limestones, sandstones, carbonate silts and dark mudstones. These sediments were deposited in a lacustrine system with an alternation of oligo- to mesosaline waters and the contribution of thermal waters (Turq *et al.* 1996; Anadón & Gabàs 2009; García-Aguilar *et al.* 2014a, b, 2015). The excavated layers of BL show sediments associated with a swampy environment, except level D (formerly named as BL5 by Arribas & Palmqvist 2002), which shows fluvial features and encloses most of the archaeological assemblage (Toro-Moyano *et al.* 2013). This level is divided in two sub-layers, D1 and D2 and the time elapsed in their deposition was very short, which indicates that the site was not time-averaged and cannot be considered as a palimpsest (Arribas & Palmqvist 2002; Toro-Moyano *et al.* 2013). In the case of FN-3, the semi-horizontal stratigraphy of this site shows three sedimentary cycles deposited in a lutitic-carbonate lacustrine to swampy environment, each with limestones at the top of the sequence separated by clays, fine sands and marly lutites. Subaerial pedogenesis is evident in all stratigraphic levels, including the archaeological ones. The fertile stratum comprises six layers, which group in two main archaeological levels: a Lower Level (layers 1-3) and an Upper Level (layers 4-6) (Turq *et al.* 1996; Martínez-Navarro *et al.* 1997; Espigares *et al.* 2013), which show no differences in the composition of their faunal assemblages and probably represent two events very close in time. The age of the fertile levels of BL and FN-3 has been estimated in 1.43 ± 0.38 Ma and 1.19 ± 0.21 Ma, respectively, using a combined approach based on biostratigraphy, magnetostratigraphy and electron spin resonance (ESR) applied to optically bleached quartz grains and fossil teeth (Duval *et al.* 2012; Toro-Moyano *et al.* 2013). In addition, an age of 1.50 ± 0.31 Ma has been derived for FN-3 based on cosmogenic nuclides (Álvarez *et al.* 2015). Another interesting site in the vicinity of the town of Orce is Venta Micena (VM). This site, which is slightly older (1.6-1.5 Ma) than BL/FN-3, does not preserve conclusive evidence of human presence. However, it has provided a rich

record of large mammals, with >24 000 skeletal remains of 21 species unearthed from an excavation area of *c.* 400 m² that show an excellent state of preservation (>90% of bones show weathering 0) and probably represent a single event of bone accumulation by the hyenas during few years at the surroundings of their denning site (Martínez-Navarro 1991; Palmqvist *et al.* 1996; Arribas & Palmqvist 1998; Palmqvist & Arribas 2001). The study of the Orce sites has contributed insightful inferences on a number of autecological and synecological aspects of the species of large mammals of Southern Europe during the Early Pleistocene and their paleocommunities (e.g. Martínez-Navarro & Palmqvist 1995, 1996; Turner & Antón 1996; Arribas & Palmqvist 1998, 1999; Palmqvist *et al.* 1999, 2002, 2003, 2008a, b, 2011; Espigares *et al.* 2013, 2019; García-Aguilar *et al.* 2014a, 2015). Moreover, these sites have been employed to model the ecological conditions before and after the first human arrival in Western Europe during the late Early Pleistocene (Rodríguez-Gómez *et al.* 2016a, 2017a).

The Sierra de Atapuerca cave sites are located at *c.* 15 km east of the city of Burgos (NW Spain). The sedimentary infillings of this karst system have been dated between the Early Pleistocene (*c.* 1.2 Ma) and the Holocene (Arsuaga *et al.* 1997; Carbonell *et al.* 1999a, b, 2008; Carretero *et al.* 2008; Vergés *et al.* 2008; Rodríguez *et al.* 2011; Ollé *et al.* 2013). These sites preserve exceptional paleoanthropological records and have provided remains of up to four different human species: *Homo sp.*, *H. antecessor* Bermúdez de Castro Arsuaga, Carbonell, Rosas, Martínez & Mosquera, 1997, *H. heidelbergensis/neanderthalensis* Schoetensack, 1908/ King, 1864, and *H. sapiens* Linnaeus, 1758 (Arsuaga *et al.* 1997; Bermúdez de Castro *et al.* 1997, 1999; Carbonell *et al.* 1995, 2005, 2008; Carretero *et al.* 1999, 2008, 2012). In addition, those of Early Pleistocene age preserve rich faunal assemblages associated to Oldowan artifacts, as in the case of the Orce sites (Carbonell *et al.* 1995, 2005, 2010; Made 1999, 2013; Rodríguez *et al.* 2011; García-Medrano *et al.* 2014). Specifically, analysis of the stone tools has documented the whole operative lithic chain (Carbonell *et al.* 1999a), the consumption by hominins of a varied diet (Blasco *et al.* 2011, 2013; Huguet *et al.* 2013), their early access to ungulate carcasses (Díez *et al.* 1999; Saladié *et al.* 2011) and the oldest evidence of human cannibalism (Fernández-Jalvo *et al.* 1996; Fernández-Jalvo *et al.* 1999; Saladié *et al.* 2012). An area named as Trincheras del Ferrocarril in Atapuerca has three cavities filled with Pleistocene sediments: Sima del Elefante (TE), Galería (G) and Gran Dolina (TD) sites. The TE site is a cave with a 16 m thick sequence of sediments, which is divided into 16 stratigraphic units, named TE7 to TE21 from bottom to top, and whose lower units (TE7 to TE16) are dated as Early Pleistocene (1.2-0.78 Ma), whereas its upper ones (TE17 to TE21) dated to the Middle and Late Pleistocene (0.78-0.25 Ma) (Rosas *et al.* 2006; Carbonell *et al.* 2008; López-García *et al.* 2011; Rodríguez *et al.* 2011; Arnold & Demuro 2015). The G site is a cave sedimentary infilling 17 m thick that shows six lithostratigraphic units, named GI to GIV from bottom to top and dated to 0.50-0.25 Ma (Berger *et al.* 2008; Rodríguez *et al.* 2011; Falguères *et al.* 2013; Demuro *et al.* 2014).

Finally, the TD site is a cave with a 25 m thick sedimentary infilling that can be divided in 11 stratigraphic units, named TD1 to TD11 from bottom to top and dated to 1.2-0.25 Ma. Levels TD1-TD6 belong to the Early Pleistocene and TD7-TD11 to the Middle Pleistocene (Falguères *et al.* 1999, 2013; Berger *et al.* 2008; Rodríguez *et al.* 2011; Arnold & Demuro 2015; Moreno *et al.* 2015; Campaña *et al.* 2016; Campaña Lozano 2018; Álvarez-Posada *et al.* 2018; Duval *et al.* 2018; Parés *et al.* 2018).

MATERIAL AND METHODS

Data from 21 species of large mammals, including seven bovids (*Aepyceros melampus* Lichtenstein, 1812, *Connochaetes taurinus* Burchell, 1823, *Hemitragus jemlahicus* Smith, 1826, *Kobus ellipsiprymnus* Ogilby, 1833, *Ovis dalli* Nelson, 1884, *Rupicapra rupicapra* Linnaeus, 1758 and *Syncerus caffer* Sparman, 1779), three cervids (*Capreolus capreolus* Linnaeus, 1758, *Cervus elaphus* Linnaeus, 1758 and *Rangifer tarandus* Linnaeus, 1758), one hippo (*Hippopotamus amphibius* Linnaeus, 1758), one suid (*Phacochoerus aethiopicus* Pallas, 1766), two equids (*Equus burchellii* Gray, 1824 and *Equus caballus* Linnaeus, 1758), two rhinocerotids (*Diceros bicornis* Linnaeus, 1758 and *Rhinoceros unicornis* Linnaeus, 1758), two cercopithecids (*Macaca nemestrina* Linnaeus, 1758 and *Papio cynocephalus* Linnaeus, 1758), one elephantid (*Loxodonta africana* Blumenbach, 1797), and two large sized rodents (one castorid: *Castor canadensis* Kuhl, 1820; and one sciurid: *Marmota flaviventris* Audubon & Bachman, 1841) were collected (Table 1). We selected these species because they show stable populations with growth rates that are approximately stationary (Deevey 1947; Banfield 1955; Laws 1968; Caughley 1970a, b; Goddard 1970; Watson 1970; Spinage 1972; Corfield 1973; Sinclair 1974; Klein 1978; Ashby & Henry 1979; Attwell 1982; Melton 1983; Payne 1984; Simmons *et al.* 1984; Messier *et al.* 1988; Garrott & Taylor 1990; Dinerstein & Price 1991; Benton *et al.* 1995; Schwartz *et al.* 1998; Ha *et al.* 2000; Storz *et al.* 2002; Schindler *et al.* 2012). As this research line is aimed to reconstructing the population dynamics of Pleistocene large mammals, we made this selection of species, independent of their actual geographic distribution, because we consider that the size of their populations fluctuates around an average value over time, being represented by stable and stationary age structures (Martín-González *et al.* 2016, 2019; Rodríguez-Gómez *et al.* 2013, 2014a). Five databases were used to define the life-history traits of these species, including their body mass, fertility and longevity (Owen-Smith 1988; Nowak 1999; Hutchins *et al.* 2003; Magalhães & Costa 2009; Jones *et al.* 2009) (Table 1). The five approaches use the average adult body mass or the average adult females body mass as reference. Adult body mass was calculated as the geometric mean of the mass values provided for each species in the references cited above. In the case of females, when the references provided a range of values for a given species, including males and females, adult female body

TABLE 1. — List of extant species modeled in this study with their life traits, obtained from different databases (Nowak 1999; Hutchins *et al.* 2003; Magalhães & Costa 2009; Jones *et al.* 2009). Body masses in kilograms (kg), age at first birth and longevity in years. Abbreviations: **ABM**, adult body mass; **AFBM**, adult body mass; **SC**, numerical codes assigned in this study for identifying each species. See Appendix 3 for species.

Order, Family	Species	Mean ABM (kg)	Mean AFBM (kg)	Age at first birth (y)	Litter size	Litters per year	Neonate body mass (kg)	Longevity (y)	SC
Artiodactyla									
Bovidae	<i>Aepyceros melampus</i>	52.55	41.54	2.00	0.98	1.00	5.24	18	1
	<i>Connochaetes taurinus</i>	203.06	145.94	2.00	0.98	1.00	18.04	22	2
	<i>Hemitragus jemlahicus</i>	51.91	39.57	2.00	1.01	1.00	2.70	22	3
	<i>Kobus ellipsiprymnus</i>	204.39	155.10	4.65	1.00	1.00	12.00	20	4
	<i>Ovis dalli</i>	71.65	51.27	2.00	1.22	1.00	3.50	16	5
	<i>Rupicapra rupicapra</i>	36.25	29.86	3.75	1.00	1.00	2.25	22	6
	<i>Syncerus caffer</i>	700.00	514.22	4.00	1.08	0.57	39.84	30	7
Cervidae	<i>Capreolus capreolus</i>	24.50	17.76	2.00	1.79	1.00	1.21	17	8
	<i>Cervus elaphus</i>	224.18	155.50	2.72	1.09	0.90	8.26	27	9
	<i>Rangifer tarandus</i>	105.17	68.45	2.69	2.00	1.00	5.49	20	10
Hippopotamidae	<i>Hippopotamus amphibius</i>	1536.00	1071.00	4.00	1.00	0.52	40.20	55	11
Suidae	<i>Phacochoerus aethiopicus</i>	100.00	47.00	2.00	3.20	1.00	0.69	19	12
Perissodactyla									
Equidae	<i>Equus burchellii</i>	280.00	213.08	3.50	1.00	0.95	32.27	40	13
	<i>Equus caballus</i>	350.00	277.71	3.50	1.00	0.67	37.90	57	14
Rhinocerotidae	<i>Diceros bicornis</i>	1112.50	868.83	5.62	1.00	0.35	35.00	47	15
	<i>Rhinoceros unicornis</i>	1846.83	1329.33	7.17	1.41	0.40	61.33	49	16
Primates									
Cercopithecidae	<i>Macaca nemestrina</i>	7.87	6.86	3.92	1.01	0.90	0.47	34	17
	<i>Papio cynocephalus</i>	15.69	14.14	5.50	1.01	0.55	0.71	45	18
Proboscidea									
Elephantidae	<i>Loxodonta africana</i>	4525.00	3677.61	9.50	0.84	0.20	105.00	80	19
Rodentia									
Castoridae	<i>Castor canadensis</i>	20.25	12.53	2.12	3.60	1.00	0.42	15	20
Sciuridae	<i>Marmota flaviventris</i>	3.50	2.48	2.00	4.66	0.80	0.03	8	21

mass was considered as the lowest value reported among the references. Species fertility was defined considering age at first birth, litter size, litters per year, age at last birth and maximum longevity. The main source for these values was the PanTHERIA database (Jones *et al.* 2009), because it compiles the highest amount of original references. In some cases, however, the information was complemented with data from AnAge (Magalhães & Costa 2009) (e.g. litters per year for *C. elaphus*, or longevity for *E. caballus*). Age at first birth for *K. ellipsiprymnus* and *C. canadensis* was estimated as the sum of female sexual maturity age and gestation time.

This study is based on three different analyses: 1) an analysis at a population scale, in which we evaluate the five methods used to estimate population carrying capacity; 2) an analysis at a community scale, in which we also apply the same proxies but at a higher scale; and 3) an analysis of past ecosystems for evaluating the contributions of our approaches and for comparing the carrying capacity conditions of the Orce and Sierra de Atapuerca sites as well as their role in the first humans settlements in Western Europe. The five methods compared for estimating population biomass in the analysis at a population scale were the following: 1) to consider the adult body mass (ABM) value of a species as an estimate of its mean population body mass (MPBM); 2) to consider adult female body mass (AFBM) as a proxy of MPBM; 3) to use three quarters of adult female body mass ($\frac{3}{4}$ AFBM); 4) to gather information from life tables (LT) as a procedure for estimating the actual

body mass of age-structured populations; and 5) to use survival profiles derived from the Weibull model (SPW, Survival Profiles-Weibull) for estimating the mean mass of individuals in age-structured populations. The SPW approach uses only part of the outputs of the Weibull model, the survival profiles, to reconstruct the population structure. For this reason, we refer this approach as SPW instead of the Weibull model. The LT approach was considered as a reference of actual values of recent population to evaluate the other approaches.

In the analysis at a population scale, we estimated population biomass as a function of population density and mean individual mass in the population. We used population densities of one individual for comparing these approaches, which means that in the case of ABM, AFBM and $\frac{3}{4}$ AFBM the population body mass corresponds to the estimate of individual body mass used. In the case of age-structured populations (LT and SPW), we estimated the population biomass (B) considering the distribution of individuals per age classes in fractions of unity, which can be expressed as follows:

EQUATION 4

$$B = \sum_{i=1}^n R_i \times M_i \times D, \quad i = 1, \dots, n,$$

where R_i is the proportion in fractions of unity of the individuals of age i that are present in the population, M_i is the mean body mass of the individuals that belong to this age class and D is population density, equal to 1 in this analyses.

TABLE 2. — Species composition of twenty hypothetical ecosystems (A-T) used in the analysis at a community scale. We used four approaches in this study to estimate community biomass: adult body mass; three quarters adult female body mass; life tables; and survival profiles-Weibull. See Appendix 3 for species.

Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
<i>Aepyceros melampus</i>	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Connochaetes taurinus</i>	1	1	0	0	1	0	0	0	0	1	1	0	1	1	0	1	1	1	0	0
<i>Hemitragus jemlahicus</i>	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	0	1	1	1	1
<i>Kobus ellipsiprymnus</i>	1	1	1	1	1	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0
<i>Ovis dalli</i>	0	1	0	1	1	0	1	0	1	0	0	1	0	1	0	1	0	1	0	1
<i>Rupicapra rupicapra</i>	1	1	1	1	0	1	0	0	0	0	1	1	1	1	1	0	0	0	0	0
<i>Syncerus caffer</i>	0	0	0	0	1	0	1	1	1	1	0	0	0	0	1	1	1	1	1	1
<i>Capreolus capreolus</i>	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0
<i>Cervus elaphus</i>	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1
<i>Rangifer tarandus</i>	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
<i>Hippopotamus amphibius</i>	1	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0
<i>Phacochoerus aethiopicus</i>	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0
<i>Equus burchellii</i>	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0
<i>Equus caballus</i>	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1
<i>Diceros bicornis</i>	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0
<i>Rhinoceros unicornis</i>	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1
<i>Macaca nemestrina</i>	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
<i>Papio cynocephalus</i>	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0
<i>Loxodonta africana</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Castor canadensis</i>	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
<i>Marmota flaviventris</i>	1	1	0	0	1	0	0	0	0	1	1	0	1	1	0	1	1	1	0	0

Therefore, in the first, second and third approach (i.e., ABM, AFBM and 3/4AFBM, respectively) we assume that the whole population is represented by only one age class (i.e., $R_i = 1$ in these cases). As noted above, M_i is the mean adult body mass of each species in the first approach (ABM), the body mass of adult females in the second (AFBM) and third (3/4AFBM), and the age structure from life tables in the fourth (LT). In the latter, R_i was estimated as follows:

EQUATION 5

$$R_i = \frac{X_i}{\sum_{i=1}^n X_i}, \quad i = 1, \dots, n,$$

where X_i is the number of individuals from each age class. After applying equation 4, we obtain the population biomass for a population consisting of one individual. The fifth approach (SPW) takes the perspective of the fourth for estimating population biomass, but it is based on the survival profiles derived from the Weibull model (Survival Profiles-Weibull) (see Martín-González *et al.* 2016, 2019), using fertility data to construct survival profiles. Given that this mathematical approach allows to obtain different survival profiles for stable and stationary populations, the mean population body mass generated from them is used. For estimating M_p , the mean body mass for individuals in each subadult age class was obtained from body mass at birth, adult body mass and growth rate following Zullinger *et al.* (1984):

EQUATION 6

$$M(t) = A \times e^{-e^{-K(t-1)}},$$

where A is the asymptotic mass (i.e., the adult body mass, ABM), $M(t)$ is the mass (g) at age t , K is the growth rate constant (days⁻¹), and I is the age at the inflection point (days). K is related to the mass of adults by the equation:

EQUATION 7

$$\log(K) = -0.901 - 0.302 \times \log(M)$$

The average mass for each age class was estimated as the geometric mean of the two most extreme values within each age range.

The five approaches provide mean population body masses for populations with densities of one individual. However, we use the mean population body mass of each species in the analysis at a community scale for reconstructing the hypothetical composition of an ecosystem (Table 2). In this case, densities of one hundred individuals are considered for all species ($D = 100$), in order to compute with numbers that are easier to understand. Five outputs for each hypothetical ecosystem according to the body mass proxy used (i.e., ABM, AFBM, 3/4AFBM, LT or SPW) were obtained. Community biomass was estimated by summing the mean population biomass of each species that appeared in the ecosystem configuration (Table 2). In the previous analyses, population biomass was estimated for populations with only one individual. In this way, these values equaled the mean population body mass. In the case of populations with densities of 100 individuals, following equations 4 and 5 we computed their population biomass by multiplying the mean population body mass by 100. Information from two life tables were available for several species, including *H. jemlahicus*, *O. dalli*, *R. tarandus*, *C. taurinus*, and *S. caffer* (see Results section). In these cases, we took the highest values of mean population body mass as inputs for computing the carrying capacity of the prey community in the analyses. In this way, we assumed a more conservative position by considering those values that were closer to the ABM approach, which is the one traditionally used in paleontology.

Finally, we carried out a third analysis where we recreated the past ecosystems of the rich faunal assemblages preserved in the sites of Orce and Sierra de Atapuerca for estimating their carrying capacity. The sites were selected because they

TABLE 3. — Faunal assemblages from the sites of Orce and Sierra de Atapuerca modeled in this study, with the estimates of population body mass and density for their species. Adult body mass (ABM) values were taken from Meloro *et al.* (2007), Jones *et al.* (2009) and Rodríguez-Gómez *et al.* (2016a, 2017a, c). Average population body masses were estimated with survival profiles obtained from the Weibull model (SPW), using life traits as inputs. Estimates of life traits were taken from Rodríguez-Gómez *et al.* (2017c). Densities (in individuals per square kilometer) were computed with the equation from Damuth (1981) (see text). Orce sites abbreviations: VM, Venta Micena; FN-3/BLD, Fuente Nueva, level 3, and Barranco León. Sierra de Atapuerca sites abbreviations: G, Galería; TD, Trincheras Dolina; TE, Trincheras Elefante. Abbreviations: x, species identified in each faunal assemblage; a, Martínez-Navarro 1991, Martínez-Navarro & Rook 2003, Martínez-Navarro *et al.* 2015; b, Duval *et al.* 2012, Toro-Moyano *et al.* 2013, Álvarez *et al.* 2015; c, Carbonell *et al.* 2008, Arnold & Demuro 2015; d, Moreno *et al.* 2015, Álvarez-Posada *et al.* 2018; e, Arnold & Demuro 2015; f, Duval *et al.* 2018; g, Moreno *et al.* 2015; h, Falguères *et al.* 1999; i, Falguères *et al.* 1999, Berger *et al.* 2008; j, Falguères *et al.* 2013; k, Falguères *et al.* 2013, Demuro *et al.* 2014; l, López-García *et al.* 2011, Rosas *et al.* 2006. See Appendix 3 for species.

Species	ABM (kg)	SPW (kg)	D (ind/km ²)	Dating (Ma)																
				c. 1.60 ^a	c. 1.50–1.2 (FN-3) ^b	c. 1.4 (BL) ^b	c. 1.22 ^c	1.22 – 0.90 ^c	c. 1.10 – 0.85 ^d	c. 0.85 ^e	c. 0.900 – 0.800 ^f	c. 0.79 ^g	c. 0.60 ^h	c. 0.43 ^h	c. 0.42 – 0.24 ⁱ	c. 0.39 – 0.31 ⁱ	0.36 – 0.31 ^k	0.27 – 0.22 ^k	0.28 – 0.21 ^k	0.350 – 0.250 ^l
				FN-3/	TD3-	TD6														
				VM	BL	TE9	TE14	TD4	TD6-3	1-2	TD7	TD8	TD10-3	TD10-2	TD10-1	GIIa	GIIb	GIII	TE19a-e	
<i>Ammotragus europaeus</i>	135	89	2.38		x															
<i>Bison schoetensacki</i>	631	405	0.70												x					x
<i>Bison</i> sp. Atapuerca	410	276	0.99										x	x		x	x	x		
<i>Bison</i> sp. Orce	450	320	0.92	x	x															
<i>Bison</i>	400	275	1.01			x	x	x	x	x		x								
<i>voigtstedtensis</i>																				
Bovidae indet. Orce	25	20	9.03	x																
<i>Hemibos</i> aff. <i>gracilis</i>	300	205	1.27	x																
<i>Hemitragus albus</i>	75	54	3.79	x	x															
<i>Hemitragus bonali</i>	96	66	3.12													x	x	x		
<i>Praeovibos priscus</i>	692	369	0.66								x									
<i>Praeovibos</i> sp.	315	191	1.22	x																
<i>Soergelia minor</i>	225	142	1.59	x																
<i>Arvernoceros giulii</i>	276	187	1.35					x		x		x								
<i>Capreolus priscus</i>	52	37	5.07											x	x					
Cervidae indet. Atapuerca	252	173	1.46			x														
Cervidae indet. Orce	25	20	9.03	x																
<i>Cervus elaphus</i>	163	117	2.05					x		x		x	x	x	x	x	x	x		x
<i>Dama clactoniana</i>	110	81	2.80										x	x	x	x	x	x		x
<i>Dama vallonnetensis</i>	84	64	3.47			x	x	x	x	x	x	x								
<i>Megaloceros giganteus</i>	646	398	0.69																	x
<i>Metacervoceros rhenanus</i>	95	71	3.14	x	x															
<i>Praemegaceros solilhacus</i>	383	253	1.05									x				x	x	x		
<i>Praemegaceros verticornis</i>	400	261	1.01	x	x															
<i>Hippopotamus antiquus</i>	3200	2015	0.20	x	x		x						x							
<i>Sus scrofa</i>	85	22	3.43			x	x		x	x		x								
<i>Equus altidens</i>	350	272	1.12	x	x	x	x	x	x	x	x	x								
<i>Equus ferus</i>	564	429	0.77										x			x	x	x		x
<i>Equus hydruntinus</i>	210	172	1.68											x		x	x	x		
<i>Equus suessenbornensis</i>	565	452	0.77		x															
<i>Stephanorhinus etruscus</i>	1400	1084	0.38				x	x	x	x	x	x								
<i>Stephanorhinus hemitoechus</i>	1400	1084	0.38										x	x	x	x	x	x		x
<i>Stephanorhinus hundsheimensis</i>	1000	801	0.49	x	x															
<i>Macaca</i> sp.	18	15	11.70			x						x								
<i>Mammuthus meridionalis</i>	6000	4486	0.12	x	x															
<i>Mammuthus</i> sp.	6040	4506	0.12			x				x										
<i>Castor fiber</i>	22	14	10.00					x		x										
<i>Hystrix refossa</i>	20	13	10.77		x			x		x										
<i>Hystrix</i> sp.	15	10	13.52	x																

TABLE 4. — Population body masses (in kg) of extant species estimated from the four approaches of this study (see text). Abbreviations: **ABM**, adult body mass; **¾AFBM**, three quarters adult female body mass; **LT**, life tables; **SPW**, survival profiles-Weibull; **%AFBM/ABM**, percentage of population body mass estimated by the proportion of adult female body mass in relation to the average body mass of adult individuals; **%¾AFBM/ABM**, percentage of population body mass estimated by the proportion of three quarters adult female body mass in relation to the average body mass of adult individuals; **%LT/ABM**, percentage of the mean population body mass estimated by life tables in relation to the average adult body mass of adult individuals; **%SPW/ABM**, percentage of the mean population body mass estimated by survival profiles-Weibull in relation to the average body mass of adult individuals. See Appendix 3 for species.

Species	%AFBM/					Life tables	%LT/ABM	SPW	%SPW/ABM
	ABM	AFBM	ABM	¾AFBM	%¾AFBM/ABM				
<i>Aepyceros melampus</i>	53	43	81	32	61	45	85	42	79
<i>Connochaetes taurinus albojubatus</i>	203	165	81	123	61	156	77	146	72
<i>Connochaetes taurinus taurinus</i>	203	165	81	123	61	153	75	146	72
<i>Hemitragus jemlahicus</i>	52	35	68	26	51	41	79	40	76
<i>Hemitragus jemlahicus</i>	52	35	68	26	51	44	85	40	76
<i>Kobus ellipsiprymnus</i>	204	170	83	127	62	125	61	155	76
<i>Ovis dalli</i>	72	48	67	36	50	56	78	51	72
<i>Ovis dalli</i>	72	48	67	36	50	62	86	51	72
<i>Rupicapra rupicapra</i>	36	33	92	25	69	30	82	30	82
<i>Syncerus caffer</i>	700	500	71	375	54	511	73	514	73
<i>Syncerus caffer</i>	700	500	71	375	54	567	81	514	73
<i>Capreolus capreolus</i>	25	22	88	16	66	17	70	18	72
<i>Cervus elaphus</i>	224	200	89	150	67	191	85	155	69
<i>Rangifer tarandus</i>	105	98	93	73	70	90	86	68	65
<i>Rangifer tarandus</i>	105	98	93	73	70	80	76	68	65
<i>Hippopotamus amphibius</i>	1536	1350	88	1013	66	1254	82	1,071	70
<i>Phacochoerus aethiopicus</i>	100	76	76	57	57	56	56	47	47
<i>Equus burchellii</i>	280	279	100	209	75	239	85	213	76
<i>Equus caballus</i>	350	300	86	225	64	271	77	278	79
<i>Diceros bicornis</i>	1113	996	90	747	67	844	76	869	78
<i>Rhinoceros unicornis</i>	1847	1600	87	1200	65	1644	89	1329	72
<i>Macaca nemestrina</i>	8	8	99	6	75	7	88	7	87
<i>Papio cynocephalus</i>	16	12	76	9	57	15	93	14	90
<i>Loxodonta africana</i>	4525	2800	62	2868	63	3696	82	3,678	81
<i>Castor canadensis</i>	20	18	90	14	67	15	73	13	62
<i>Marmota flaviventris</i>	4	3	80	2	60	2	70	2	71

TABLE 5. — Estimates of on crop biomass (kg/km²) obtained for 20 hypothetical ecosystems using the four approaches of this study (see text and Table 2). Abbreviations: **ABM**, adult body mass; **AFBM**, adult female body mass; **¾AFBM**, three quarters adult female body mass; **LT**, life tables; **SPW**, survival profiles-Weibull. We considered that all species in these ecosystems had densities of 100 individuals per square kilometer (see text).

Hypothetical ecosystems	ABM	AFBM	¾AFBM	LT	SPW
A	809344	594694	446058	647766	628412
B	916910	679817	509901	754589	699826
C	635088	442964	332261	506510	506492
D	742654	528087	396103	613333	577906
E	882884	646168	484663	707708	681975
F	863058	636879	477697	718165	662877
G	682597	473029	354809	552069	543074
H	791082	561982	421524	654567	615787
I	851445	621459	466132	685540	661706
J	967363	715525	536681	797309	738960
K	663818	467789	350842	529079	525963
L	735479	522752	392064	611994	570982
M	802169	589359	442019	646426	621488
N	909735	674482	505861	753250	692902
O	627913	437629	328222	505170	499568
P	825403	590042	442532	681942	639014
Q	856189	626489	469867	692465	663126
R	963755	711612	533709	799289	734540
S	681933	474759	356069	551209	541206
T	789499	559882	419912	658033	612620

are very relevant for studying the earliest human settlements in Western Europe during the Early and Middle Pleistocene (Aguirre *et al.* 1987; Carbonell *et al.* 1995, 2008; Martínez-Navarro *et al.* 1997, 2014a; Made 1999, 2013; Arribas & Palmqvist 1999, 2002; Bermúdez de Castro *et al.* 1999, 2004;

Oms *et al.* 2000; Palmqvist *et al.* 2005, 2016; Espigares 2010; Rodríguez *et al.* 2011; Duval *et al.* 2012; Espigares *et al.* 2013, 2019; Toro-Moyano *et al.* 2013; Arsuaga *et al.* 2014) (see the Background section). We selected three faunal assemblages from the Orce sites: Venta Micena (VM), Fuente Nueva-3

(FN-3) and Barranco León (BL). From the Sierra de Atapuerca sites, we selected fourteen faunal assemblages: three from Trinchera Elefante (TE: TE9, TE14 and TE19a-e); eight from Gran Dolina (TD: TD3-TD4, TD6-3, TD6 1-2, TD7, TD8, TD10-3, TD10-2, and TD10-1) and three from Galería (G: GIIa, GIIb and GIII). These faunal assemblages were selected following the criteria of focusing on those sites that preserve remains of at least six species of artiodactyls, perissodactyls, proboscideans, and rodents of >10 kg (Table 3).

In order to analyze these Pleistocene assemblages, we only applied the ABM and the SPW approaches because the information available on the sites did not allow to use the other three (AFBM, $\frac{3}{4}$ AFBM and LT) because we have no estimates of adult female body size for all the species recorded and neither know their age-structures. For doing that, we summed the population biomass of all species in each site (Table 3), using equations 4 and 5. In the case of the ABM approach, we used for each species $R_i = 1$, M_i as the adult body mass and D_i as the population density of each species, which is estimated with Damuth's equation (1981) for European mixed temperate forests:

EQUATION 8

$$\log(D) = -0.79 \times \log(M) + 4.33; r^2 = 0.94,$$

where D is the population density (individuals/km²) and M is the mean adult body mass (in g). We used this equation instead of the one provided by Silva & Downing (1995) because it showed a better goodness-of-fit with the PanTHERIA values (Jones *et al.* 2009) according to a chi-square test (see the Appendices). Moreover, Damuth's equation provided higher density values, which are in better agreement with the concept of carrying capacity. In the case of the SPW approach, we also used Damuth's equation to obtain D for each species, but we estimated different values of R and W for each age class. In order to do that, we reconstructed survival profiles using life traits. We defined the life traits (i.e., fertility and other ecological aspects) of the species preserved, following the approach used in Rodríguez-Gómez *et al.* (2017c) and using the databases available for the recent species (Nowak 1999; Hutchins *et al.* 2003; Magalhães & Costa 2009; Jones *et al.* 2009). For those species with living representatives, we used the values of the living populations. When the species had not living representatives, we used least squares regression equations for each family or subfamily (see Rodríguez-Gómez *et al.* 2017c). We calculated the body mass values of the extinct species using information from Meloro *et al.* (2007), Jones *et al.* (2009) and Rodríguez-Gómez *et al.* (2013, 2014b, 2016a, 2017a, 2017c).

RESULTS

ANALYSES AT A POPULATION SCALE

Table 4 shows the estimated biomass of the populations analyzed. The second column provides the median value for the adult individuals of the species analyzed in this study, the third lists the values of adult female body mass, and the fifth shows

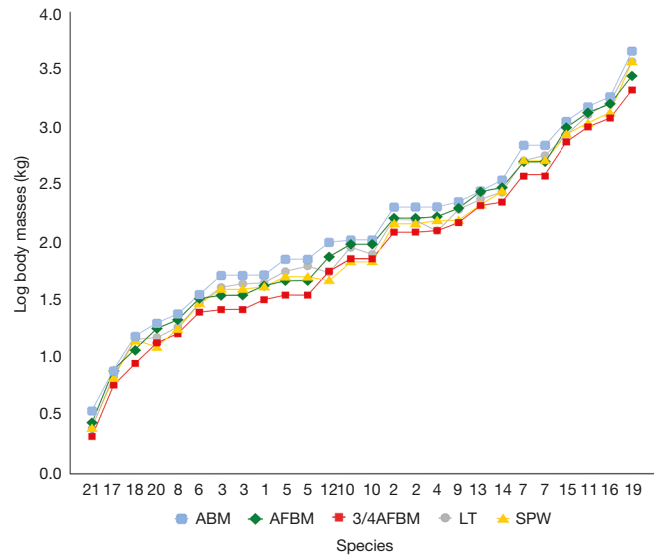


Fig. 1. — Estimates of population body masses in kilograms (kg) logarithmically (base 10) for the species analyzed in this study (see text and Table 1) using four approaches. Abbreviations: **ABM**, adult body mass; **AFBM**, adult female body mass; $\frac{3}{4}$ **AFBM**, three quarters of adult female body mass; **LT**, life tables; **SPW**, survival profiles-Weibull. Species have assigned codes between 1 and 21 for identifying them (see Table 1). In some cases, species had two values for the LT approach (*Hemitragus jemlahicus* Smith, 1826 (3), *Ovis dalli* Nelson, 1884 (5), *Rangifer tarandus* Linnaeus, 1758 (10), *Connochaetes taurinus* Burchell, 1823 (2), and *Syncerus caffer* Sparman, 1779 (7)). For these cases, the other approaches repeat values in the two occasions.

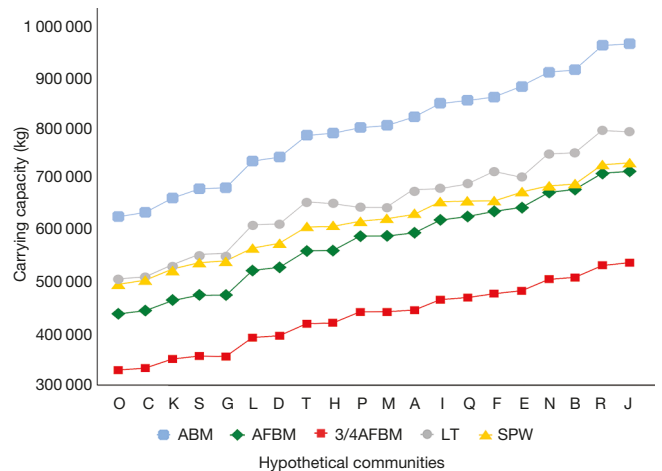


Fig. 2. — Carrying capacity in kilograms (kg) of different hypothetical ecosystems constructed with the 21 large mammals of this study (see Tables 1; 2). These carrying capacities were estimated using four approaches. Abbreviations: **ABM**, adult body mass; **AFBM**, adult female body mass; $\frac{3}{4}$ **AFBM**, three quarters of adult female body mass; **LT**, life tables; **SPW**, survival profiles-Weibull.

the $\frac{3}{4}$ values of adult female body mass following Schaller (1972). The seventh column provides the values of population body mass derived from life tables and the ninth those estimated with the SPW approach. Figure 1 is a graphical representation of these values at a logarithmic scale. Moreover, the fourth, sixth, eighth, and tenth columns of Table 4 show the differences in percentages between the use of ABM for estimating population body mass and those estimates

TABLE 6. — Statistics of the 20 hypothetical ecosystems (A-T) (see text and Table 2) tested in this study with four approaches. Abbreviations: **ABM**, adult body mass; **¾AFBM**, three quarters adult female body mass; **LT**, life tables; **SPW**, survival profiles-Weibull. *, denotes a statistically significant difference. Test statistic = 63.9808; *p*-value = 0.

Approach	Sample size	Average	Standard deviation	Coefficient of variation	Minimum	Maximum
ABM	20	799 916	104 791	13.10%	627 913	967 363
AFBM	20	577 770	88 030	15.24%	437 629	717 525
¾AFBM	20	433 346	66 025	15.24%	328 222	536 681
LT	20	653 321	90 571	13.86%	505 170	799 289
SPW	20	620 921	73 002	11.76%	499 568	738 960
Total	100	634 164	153 236	24.16%	328 222	967 363

One way ANOVA						
Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value	
Between groups	1.40121 × 10 ¹²	4	3.50302 × 10 ¹¹	47.83	0.0000*	
Within groups	6.95824 × 10 ¹¹	95	7.32447 × 10 ⁹			
Total (Corr.)	2.09703 × 10 ¹²	99				

Kruskal-Wallis test						
Approach	Sample size	Average rank	Contrast	Significance	Difference	+/- Limits
ABM	20	84.60	ABM - AFBM	*	42.60	25.7524
AFBM	20	42.00	ABM - ¾AFBM	*	71.05	25.7524
¾AFBM	20	13.55	ABM - LT	–	24.70	25.7524
LT	20	59.90	ABM - SPW	*	32.15	25.7524
SPW	20	52.45	AFBM - ¾AFBM	*	28.45	25.7524
			AFBM - LT	–	–17.90	25.7524
			AFBM - SPW	–	–10.45	25.7524
			¾AFBM - LT	*	–46.35	25.7524
			¾AFBM - SPW	*	–38.90	25.7524
			LT - SPW	–	7.45	25.7524

based on AFBM, ¾AFBM, LT, and SPW, respectively. As indicated before, the ABM approach is the one more used in paleontology for estimating carrying capacity. In our analyses, it showed the highest values, which were used as a ceiling for each species. In contrast, the ¾AFBM approach of Schaller (1972), Owen-Smith (1988) and Hayward *et al.* (2007) for African communities showed the lowest values in our case for most species. For this reason, we considered them as the floor values among the methodologies of our study. The AFBM, LT and SPW approaches provided values that overlapped in some cases each other. In the case of small-to-medium sized species, the values based on AFBM were generally higher than those derived from LT and SPW. In contrast, the AFBM estimates were lower than the LT ones in the case of the largest species (*S. caffer*, *R. unicornis*, and *L. africana*), with the exceptions of the black rhino (*D. bicornis*) and the hippo (*H. amphibius*). As a general trend, LT values were higher than SPW ones. However, there were also exceptions for other seven species (*M. flaviventris*, *C. capreolus*, *R. rupicapra*, *K. ellipsiprymnus*, *S. caffer*, *E. caballus*, and *D. bicornis*), which showed the opposite trend. In the case of *S. caffer*, the LT approach provided two values, one lower and one higher than the SPW value.

When we analyzed the mean differences among the approaches compared, taking as a reference the ceiling values provided by the ABM approach, the estimates were 18% lower for AFBM, 39% for ¾AFBM, 21% for LT and 27% for SPW (Table 4). The differences between the LT and AFBM approaches were of *c.* 5% for all species. In the comparison between LT and SPW they were of *c.* 6%. The mean value of AFBM (369.18) was the closest to the average value of all approaches (378.23),

SPW showing a value (367.65) which is very close to that of AFBM. A Kruskal-Wallis test showed no significant differences between the approaches (test statistic = 1.32989; *p* = 0.856284), which indicates that the methodologies compared do not differ at a population scale.

ANALYSES AT A COMMUNITY SCALE

Although the pattern of the analyses at a community scale was similar to the one found in those performed at a population scale, the differences among the proxies used for deriving biomass estimates were amplified (Table 5; Fig. 2). ABM and ¾AFBM showed the highest and lowest values, respectively, while AFBM, LT and SPW provided intermediate ones. However, LT showed higher values than SPW and AFBM. Thus, the results of LT were the closest to those of ABM, 18% lower on average, followed by SPW, AFBM and ¾AFBM (values 22%, 28% and 46% lower, respectively).

Table 6 shows the results of several statistical indexes and tests applied in this analysis. An ANOVA test showed that the differences between the means of the five approaches were statistically significant (*p* < 0.05). Figure 3 shows the results of an Analysis of Means Plots (ANOM) to compare among the mean values of the five proxies used in the analysis of community biomass. AFBM, LT and SPW provided mean values within the range between Under Decision Line (UDL) and Lower Decision Line (LDL), showing the Central Line (CL) that corresponds to the value 617 054 kg, the average of all approaches (Table 6). This analysis showed that, among the five approaches, SPW (620 921 kg) provided the closest value to the total average value or CL. A Kruskal-Wallis test

(Table 6) for analyzing differences among the outputs from the five approaches showed also that the difference among the medians was statistically significant at $p < 0.05$. In order to explore in further depth this result, we applied the Bonferroni procedure, which showed that several pair-wise comparisons were also significant at $p < 0.05$: ABM-AFBM, ABM- $\frac{3}{4}$ AFBM, ABM-SPW, AFBM- $\frac{3}{4}$ AFBM, $\frac{3}{4}$ AFBM-LT, and $\frac{3}{4}$ AFBM-SPW. These results indicate that the SPW approach provides outputs that are closer to the LT approach and that their values are the closest to the average values for all of the five approaches tested.

ANALYSES OF PAST ECOSYSTEMS

The analyses with the Orce and the Sierra de Atapuerca sites provided biomass estimates that are *c.* 20% higher using the ABM approach than those derived from the SPW approach, as happened in the analysis of the hypothetical recent ecosystems (Table 7). The mean biomass value for all these sites was 2921 kg/km² with ABM and 2070 kg/km² with SPW. There are relevant differences between the estimates of biomass for Orce and Atapuerca, as the former are higher than the latter with both approaches. The mean of the Orce sites was 4997 kg/km² with ABM and 3568 kg/km² with SPW. In contrast, the corresponding values for the Sierra de Atapuerca sites were 2645 kg/km² and 1871 kg/km², respectively. Venta Micena was the site from Orce with the highest biomass (5400 kg/km² for ABM and 3828 kg/km² for SPW), while TD7 was the site from Atapuerca with the lowest biomass (1663 kg/km² for ABM and 1175 kg/km² for SPW) (Table 7). If we focus exclusively on the sites of Atapuerca, TD8 shows the highest biomass (3850 kg/km² for ABM and 2618 kg/km² for SPW). It is worth noting that there are differences between these analyses and the previous ones with the hypothetical ecosystems (Table 5). The reason is that the biomass values obtained in the analyses of past ecosystems are presented in kg by km², but in the other analyses they did not refer to surface units. In order to compare both analyses, we should consider a surface of reference of *c.* 230 km² in the past ecosystems for obtaining values with a similar order of magnitude.

DISCUSSION

In any paleontological research, to know the numbers of individuals of each species and their biomass in communities allows contextualizing the role of species in them. Different authors have used the concept of on-crop biomass as an approach to calculate the biomass of large mammals in past ecosystems, based on the obtaining of estimates of population density and body mass for each species (e.g. Palmqvist *et al.* 2003; Vizcaíno *et al.* 2004, 2010; Palombo 2010, 2016). The on-crop biomass can be considered as an estimate of mean population biomass in the long term, because it is often assumed that the faunal assemblage unearthed from a site represents the average composition of the ecosystem during the interval of deposition of the assemblage. A similar approach has been applied to recent ecosystems with large mammals, in order

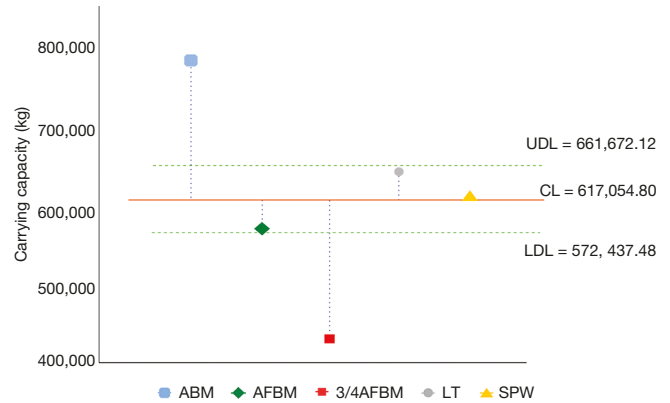


Fig. 3. — Analysis of means plots (ANOM) for comparing the means of carrying capacity (in kg) provided by the four approaches of our study: **ABM**, Adult Body Mass; **AFBM**, Adult Female Body Mass; **$\frac{3}{4}$ AFBM**, three quarters Adult Female Body Mass; **LT**, Life Tables; **SPW**, Survival Profiles-Weibull. Abbreviations: **CL**, Central Line; **LDL**, Lower Decision Line; **UDL**, Upper Decision Line.

to their management under stable conditions (Schaller 1972; Owen-Smith 1988; Hayward *et al.* 2007; Hatton *et al.* 2015). In these cases, community on-crop biomass was calculated from estimates of population density and body mass for species, with densities derived from census data and population body masses estimated as three quarters of the body mass of adult females in the case of Schaller (1972), Owen-Smith (1988) and Hayward *et al.* (2007), or as adult female body mass by Hatton *et al.* (2015). Hayward *et al.* (2007) used the concept of carrying capacity to refer to the community biomass (i.e., the biomass of an ecosystem sustainable in the long term). We consider that the concepts of on-crop biomass and carrying capacity can be used in a similar way in recent and past ecosystems. However, their application to past ecosystems is largely conditioned by the taphonomy of the fossil assemblages, which usually require the use of methods to calculate population body masses and densities.

We have presented and compared five approaches for estimating the carrying capacity of past ecosystems: ABM, AFBM, $\frac{3}{4}$ AFBM, LT, and SPW. Among these approaches, LT estimates were considered as a reference baseline, because their values came from real populations. However, we should keep in mind that our estimates assume sex ratios of 1:1 for all species. Although the sex ratio at birth is close to 1:1 in most species of large mammals (e.g. Caughley 1966; Grubb 1981; Laurie *et al.* 1983; Feldhamer *et al.* 1988; Fernández-Llario 2014), adult individuals use to be biased toward females (e.g. Attwell 1982; Laurie *et al.* 1983; Feldhamer *et al.* 1988; Carranza 2017). However, there are also populations with sex ratios of *c.* 1:1 for adults (e.g. Novak 1977; Grubb 1981; Attwell 1982; Woodd 1999; Cicognani *et al.* 2000). This assumption might bias our calculations, overestimating the biomass of the ecosystem (males use to be larger than females), but we consider that this bias can be assumed in the estimation of the carrying capacity of an ecosystem. Moreover, to consider a sex ratio of 1:1 for the adult individuals results in an easier computation of ecosystem biomass, which makes the approach more acces-

sible to other researchers. Therefore, we compared the four approaches with the results provided by LT to estimate their divergence from real data. We used AFBM in a similar way to Hatton *et al.* (2015) and used $\frac{3}{4}$ AFBM following the studies of carrying capacity in recent ecosystems of Schaller (1972), Owen-Smith (1988) and Hayward *et al.* (2007).

The estimates derived from $\frac{3}{4}$ AFBM at a community scale were *c.* 28% lower than the one obtained from LT. In the analyses at a population scale, the differences were *c.* 21% lower. These differences were significant when the whole ecosystem was considered (Tables 4; 6). The ABM approach was employed in order to compare the methodology usually employed in paleontology with the values derived from the LT approach. It showed the highest values among the different approaches (*c.* 21% and *c.* 18% higher than LT at a population and community scale, respectively; Tables 4; 5), although there were not significant differences neither at a population or at a community scale (Table 6). Finally, we propose the SPW approach as an alternative way to estimate the age structure of a fossil species, using the Weibull model to obtain this information (survival profiles) when it is not preserved in fossil record, as usually happens. The SPW approach showed the closest values to the LT approach (Tables 4; 5), *c.* 6% and *c.* 4% lower at a population and at a community scale, respectively, with values that overlapped in the analyses performed at a population scale (Fig. 1) and showing non-significant differences either at a population or at a community scale (Table 6). Moreover, the SPW approach provided values that are the closest to the mean of all approaches (Table 6; Fig. 3). Our results at a population scale show that the AFBM and SPW approaches exhibited the most similar values when all species are considered, even in those cases in which for some species the differences were as high as 24%. These results support the ABM approach with preference to the $\frac{3}{4}$ AFBM approach, because it shows fewer differences with the real data that represents the LT approach. However, there are differences of up to *c.* 35% between ABM and LT for some species, for example *K. ellipsiprymnus* (Table 4). In most cases, our results suggest that mean population body mass can be estimated as 79% of adult body mass (LT is 21% lower than ABM on average), but it should be considered that there were differences among the species and that our sample should be wider to extract a similar conclusion (Table 4). At a population scale, the lowest differences with LT were obtained for the AFBM approach (*c.* 5%), but AFBM was the third highest at a community scale. This inconsistency between the analyses was due to the estimates for the largest species, which showed relevant differences with the LT and SPW approaches. Thus, AFBM could be a useful proxy in recent ecosystems to estimate the mean body mass of a population of large mammals, except in the case of megaherbivores. However, this methodology can be only used when adult female body mass is known, something which is sometimes difficult to estimate from the fossil record. For this reason, we propose to use the SPW approach to estimate mean population body mass when the age structure of the population is not available or reliable, because this proxy provides the values that are

closer to real data both at population and community scales. We found the highest differences between SPW and LT for *R. tarandus*, being 23.9% lower with SPW than with LT in one of the two populations of this species analyzed (Table 4).

Regarding the results obtained for the paleoecosystems modeled in this study, we found differences between sites from Orce and Sierra de Atapuerca (Table 7). Specifically, the Orce paleoecosystems reached biomasses that were around two times higher than those estimated for the Sierra de Atapuerca ones. If we consider the faunal assemblages from Orce and Atapuerca as a continuous record of the Iberian Peninsula, this would indicate that an important change in the carrying capacity of the ecosystems took place between 1.5 and 1.2 Ma. However, no relevant faunal change has been documented in this period (Azanza *et al.* 2004; Rook & Martínez-Navarro 2010). Climatic conditions changed in the Early-Middle Pleistocene transition at *c.* 1 Ma (Shackleton 1995; Schneider & Root 1998; Maslin & Ridgwell 2005), which resulted in the renewal of the mammalian assemblages during the Mid-Pleistocene Revolution (MPR) (Maslin & Ridgwell 2005), when new carnivores appeared and herbivore richness increased in Europe (e.g. Turner 1992; Azanza *et al.* 2004; Rodríguez *et al.* 2004; Cuenca-Bescós *et al.* 2005; Raia *et al.* 2005, 2007; Palombo 2007; Meloro *et al.* 2007; Madurell-Malapeira *et al.* 2014). However, the paleoecosystems of Sierra de Atapuerca do not show the effects of the MPR, as they record no evidence of a continuous trend of increasing diversity towards the Early-Middle Pleistocene transition. Therefore, the differences of carrying capacity between the Orce and Atapuerca sites would reflect that the Orce ecosystems developed under exceptional conditions of biological productivity thanks to, among other parameters, the hydrothermal activity in the lacustrine systems of the Guadix-Baza Basin, which allowed a rich and well-diversified mammalian paleocommunity (García-Aguilar & Palmqvist 2011; García-Aguilar *et al.* 2014a; 2015) under moderate climate conditions (16.5°C, 750 mm) (Blain *et al.* 2011). According to Rodríguez *et al.* (2014), climate conditions in the Sierra de Atapuerca paleoecosystems (TE9, TE14, TD6-3, TD6 1-2, TD7, TD8, TD10-3, TD10-2, TD10-1, and TE19 levels) were more severe than in the Orce sites for temperature, with average values around 11.9°C, but they had higher values of rainfall (average of 900 mm per year), except TE19 level. Currently, researchers on climate change defend that the main limiting factors for primary production, in decreasing order of relevance, are water availability, temperature and solar radiation. Showing a positive trend, primary production is higher when the values of these climatic parameters are higher (Churkina & Running 1998; Nemani *et al.* 2003). In the equations of Rodríguez *et al.* (2014), temperature would be the most limiting factor to the carrying capacity of the paleoecosystems from Orce and Sierra de Atapuerca, as the estimates of paleoprecipitation provide the higher values of this parameter for both sites. Depending on the temperature, the lower values in the Sierra de Atapuerca would result in a lower primary production, which would lead to a lower carrying capacity for large herbivores than in Orce. Extant African ecosystems show a correlation between

TABLE 7. — Biomass of the faunal assemblages (in kilogram per square kilometer) from the Orce (Venta Micena (VM) and Barranco León/Fuente Nueva-3 (BL/FN-3)) and Sierra de Atapuerca (Trincheras Elefante (TE), Trincheras Dolina (TD); Galería (G)) sites. Biomass values computed from two approaches used in this study to estimate population biomass: Adult body mass (ABM) and survival profiles-Weibull (SPW) (see text). The results obtained with the approach used in Rodríguez *et al.* (2014) are also shown.

Faunal assemblages	Faunal assemblage biomass from ABM (kg/km ²)	Faunal assemblage biomass from SPW (kg/km ²)	Carrying capacity from Rodríguez <i>et al.</i> (2014) (kg/km ²)
VM	5399.63	3827.82	18267.00
BL/FN-3	4594.20	3307.63	14459.00
TE9	2671.75	1842.21	7923.00
TE14	2530.85	1680.27	4982.00
TD3-TD4	2757.21	1987.31	—
TD6-3	1905.56	1286.59	8021.00
TD6 1-2	3763.60	2595.37	8021.00
TD7	1662.99	1175.25	7220.00
TD8	3850.29	2618.12	8021.00
TD10-3	2008.79	1478.82	8021.00
TD10-2	2624.89	1954.77	6452.00
TD10-1	2663.38	1966.97	6452.00
GIIa	2708.59	1948.35	—
GIIb	3061.50	2237.75	—
GIII	3061.50	2237.75	—
TE19a-e	2494.12	1766.00	4328.00

primary production, rainfall and the carrying capacity of the ecosystem (Phillipson 1975; Coe *et al.* 1976; Bell 1981; East 1984). The correlation between carrying capacity and rainfall is usually positive in all types of ecosystems up to *c.* 700 mm per year, when a change of trend is observed (Coe *et al.* 1976). Bell (1981) proposes that above 700 mm a negative trend in carrying capacity takes place in the ecosystems with low nutritious soils; however, the trend remains positive in those with highly nutritious soils. East (1984) made a similar analysis, observing that in soils with low nutrient levels, arid and moist savannas could be differentiated according to the density of large herbivores, and that in moist savannas with rainfall values above 1000 mm, only elephants, buffalos and hippopotamus were present. Thus, in addition to temperature, nutrient richness may have played a role in the differences between the carrying capacities that we estimate for Orce and Sierra de Atapuerca. Those areas with tectonic activity show more richness of soil nutrients, although less than volcanic areas (Bell 1981; East 1984). The record of hydrothermal events in the Orce deposits of the Guadix-Baza Depression originated from neotectonic movements and the mineral and geochemical components of the water ponds increased the richness of soil nutrients, which made these sites hotspots of biological diversity (García-Aguilar & Palmqvist 2011; García-Aguilar *et al.* 2014a, 2015). It would be interesting to compare in future studies the richness of nutrients found in the Orce and Sierra de Atapuerca paleoecosystems, in order to deduce whether the differences in carrying capacity between these sites could be also explained by this parameter.

A comparison between FN-3/BL and VM showed that the availability of meat in the paleoecosystem of Orce was lower when the human populations inhabited the area at *c.* 1.4 Ma than during the preceding period (Rodríguez-Gómez *et al.* 2016a, 2017a). This suggests that food limitations were not a limiting factor for hominin dispersal in the temperate latitudes of Europe. Furthermore, Rodríguez-Gómez *et al.* (2014b)

proposed that the habitability of the Sierra de Atapuerca paleoecosystems for humans was reduced by the competition with carnivores for meat resources during the early Middle Pleistocene, which is represented by level TD8 at Gran Dolina (*c.* 600 Ka; Falguères *et al.* 1999). The Gran Dolina site shows an almost continuous sequence, with periods of activation and inactivation of the cave between *c.* 1.2 and 0.25 Ma (Rodríguez *et al.* 2011; Campaña *et al.* 2016; Campaña Lozano 2018). In this sequence, the lower and upper levels evidence human occupation but in the intermediate levels, dated to the beginning of the Middle Pleistocene, there is an absence of hominin record (Mosquera *et al.* 2013). Rodríguez-Gómez *et al.* (2014b) compared the level of this interval of human absence that shows a more complete faunal record (TD8) with level TD6 1-2, which preserves the most complete palaeoanthropological record of the TD site, including the evidence of cannibalistic behavior (Fernández-Jalvo *et al.* 1996; Fernández-Jalvo *et al.* 1999; Saladié *et al.* 2012). They measured the level of competition intensity for meat among the members of the carnivore guild and found that it was higher in TD8 than in TD6 1-2. This led Rodríguez-Gómez *et al.* (2014b) to argue that one of the factors that could explain human absence was the competition with other carnivores. A subsequent study with more TD levels plus other levels from the Galería site (Rodríguez-Gómez *et al.* 2017b) suggested that although TD8 showed less competition intensity than these levels, if a hypothetical human population was included in the TD8 assemblage the intensity of competition in the paleoecosystem exceeded those of other levels. According to our results, TD8 is the assemblage of Atapuerca that shows the highest carrying capacity, followed by level TD6 1-2. This cannot support that the absence of humans from Atapuerca at this time was due to a lower capacity of the ecosystem to maintain the populations of prey species. However, it is possible that in the previous time period, represented by level TD7, the species that inhabited Atapuerca experienced a bot-

tleneck. This interpretation is justified by the fact that TD7 shows a lower carrying capacity, as deduced from the values of precipitation and average annual temperature (Rodríguez *et al.* 2014). Our results also support this view, as the carrying capacity of the TD7 assemblage is approximately half of those recorded immediately before and after it (TD6 1-2 and TD8, respectively). It is possible that a reduction of meat availability in the TD7 paleoecosystem would result in a non-sustainable rich carnivore paleoguild, which would influence the faunal composition of subsequent communities. Only two carnivore species are recorded at TD7: *Lynx* sp. and *Crocota crocuta* Erxleben, 1777 (Rodríguez *et al.* 2011). According to Campaña Lozano (2018), the sedimentary dynamics of this TD level would favor a flow of sediments from the interior towards the exterior of the cave. Under these circumstances, the cave would provide some access to the large mammals, which would trap in it, as suggested the fact that most bone elements are in anatomical connection or closely associated. For this reason, it should be taken into account that the taphonomic features of TD7 may show important biases, which suggests that the actual richness of the paleoecosystem was not recorded in the assemblage. If this interpretation holds, it would invalidate the proposal of TD7 as evidencing a bottleneck for the large mammals of Sierra de Atapuerca. The excavation at greater extent of this level will shed light on this issue. A comparison of the indexes of competition intensities among the secondary consumers in Orce and Atapuerca shows the highest values in FN-3/BL, followed by TD8 (Rodríguez-Gómez *et al.* 2016a, 2017a, b). If these values are compared with those obtained in an analysis at a global scale, VM shows more similarities with the sites of Atapuerca than with other European localities, but FN-3/BL are more similar to the Middle Unit from Vallparadís Estació (NE Spain) and level III from Grotte du Vallonnet (SE France), both with evidence of human presence (Rodríguez-Gómez *et al.* 2017c). Thus, despite the differences in carrying capacity observed in this study between the assemblages from Orce and Atapuerca, the community of large carnivores that they supported was similarly arranged, except for the paleoecosystems of FN-3/BL and TD6 1-2 (Rodríguez-Gómez *et al.* 2016a, 2017a, b). However, carnivore density may have been lower during the Early Pleistocene (Late Villafranchian) compared to the early Middle Pleistocene (Galerian) (see Rodríguez *et al.* 2012; Rodríguez-Gómez *et al.* 2012), which would mean lower competition intensity. According to these results, we can affirm that carrying capacity did not limit human presence in the Iberian Peninsula and that the highest estimates of carrying capacity for the Orce sites were probably key for the earliest human settlements in Western Europe.

Furthermore, we can compare the methodologies used for estimating the carrying capacity of the Sierra de Atapuerca sites, in which an approach with climate inferences has been previously applied (Rodríguez *et al.* 2014). In this study, carrying capacity values were obtained for several sites of Atapuerca using estimates of paleoprecipitation and mean annual temperature (MAT) derived from the analysis of the herpetofaunal assemblages (Blain 2009). Table 7 shows part

of the results of this study and also those obtained with the SPW and ABM approaches, together with the results for the three faunal assemblages from Orce (FN-3, BL and VM). FN-3 and BL are considered as a single site because they preserve assemblages of large mammals with the same composition (Martínez-Navarro *et al.* 2010; Rodríguez-Gómez *et al.* 2016a). Table 7 shows that the approach of Rodríguez *et al.* (2014) provided higher values of carrying capacity (twofold on average) than the SPW and ABM approaches for all the levels analyzed. Given that ABM shows higher values than SPW, its differences with the approach of Rodríguez *et al.* (2014) are smaller. Other similar approach performed by Rodríguez & Mateos (2018) provided estimates of ungulate carrying capacity at a global scale in the Iberian Peninsula, the Occitane-Provence region, the Apennine Peninsula, and the Balkan Peninsula for three-time periods: 1.60-1.07 Ma, 1.07-0.78 Ma, and 0.78-0.5 Ma. They compared their results with those from Palombo (2016), who used the ABM approach for estimating the carrying capacities of South-Western European paleoecosystems (the Iberian and Italian Peninsulas, and France). Rodríguez & Mateos (2018) obtained values that were similar to those of Palombo (2016) for these time periods, except for the Apennine Peninsula and France during the first part of the Middle Pleistocene. In the latter, the results of Palombo (2016) were noticeably higher. This contradiction is difficult to interpret, because Rodríguez & Mateos (2018) provided estimates of maximum carrying capacity while Palombo (2016) reported average values. Therefore, we must consider the possibility that Palombo (2016) overestimated the values of community biomass because she used the adult body mass of species as a proxy of their mean population body mass. For this reason, we remade her analyses using the SPW approach. For doing so, we took the faunal list from Palombo (2016) and used the values of body mass reported by Meloro *et al.* (2007), Jones *et al.* (2009) and Rodríguez-Gómez *et al.* (2016a, 2017a, c) for each species. According to Palombo (2016), community biomass increased between the early Galerian and the Aurelian. In contrast, our results support the opposite trend. It is worth indicating that Palombo (2016) included herbivores and carnivores in her estimates of carrying capacity. Although this precludes a direct comparison of her results with ours, she provided also the percentage of contribution of each group, which allows to discuss on the differences between both studies. As noted above, the differences detected could result from the body masses used in each study, but this should not be so relevant as for explaining the difference of trends observed. On the other hand, the trend reported by Palombo (2016) in the values for the Iberian Peninsula is closer to our results, although when we checked the faunal lists used for the sites of Orce and Sierra de Atapuerca we appreciated several differences with the faunal lists published previously for these sites (Pons-Moyà 1987; Martínez-Navarro 1991; Martínez-Navarro & Palmqvist 1995; Martínez-Navarro *et al.* 2010, 2015; Rodríguez 1997; Martínez-Navarro & Rook 2003; Palmqvist *et al.* 2005; Rodríguez *et al.* 2011; Ros-Montoya *et al.* 2012; Espigares *et al.* 2013, 2019; Toro-Moyano *et al.* 2013; Rodríguez-Gómez *et al.* 2014b, 2016a,

2017a; Boscaini *et al.* 2015; Medin *et al.* 2017). Therefore, the differences between the results of Palombo (2016) and Rodríguez & Mateos (2018) could result from discrepancies in the faunal composition of the assemblages as well as from computational mistakes.

Concerning the potential contributions of our study, from a theoretical point of view we must emphasize that it incorporates procedures not used previously for estimating the carrying capacity of both recent and past ecosystems, as well as for addressing the age structure of populations (LT and SPW approaches). Moreover, from a conceptual point of view we consider that the estimation of age structures is useful in itself, because they can provide estimates of population mean body mass that are closer to the real values than those considered previously, based on estimates of mean adult body mass or $\frac{3}{4}$ adult female body mass. In fact, a number of quantitative analyses of past ecosystems have been based on the mean body mass of adult individuals, estimated as the average of females and males (e.g. Bermúdez de Castro *et al.* 1995; Fariña 1996; Vizcaíno *et al.* 2004; Barnosky 2008; Vizcaíno *et al.* 2010; Meloro & Clauss 2012; Palombo 2016). For this reason, this study can be important in future analyses for addressing more clearly the concept of mean population body mass, as one of its major contributions is that the estimation of the age class structure of populations provides more accurate biomass values for ecosystems. Secondly, we offer an alternative way for estimating population biomass, the use of the SPW approach (using the Weibull model), which provides values that are closer to the average of all approaches (Fig. 3) and also very close to those from life tables (Tables 3; 5; Figs 1; 2). The SPW approach can be applied to those fossil species for which their life-history traits can be inferred from recent species. Moreover, life tables can only be reconstructed if the faunal assemblages unearthed from the sites show an outstanding completeness. For this reason, the SPW approach can be an alternative for estimating population profiles, which allows calculating the carrying capacity of an ecosystem as the biomass of the population sustainable in the long term. Those approaches that use climate parameters as paleoprecipitations or median annual temperature (e.g. Rodríguez *et al.* 2014; Rodríguez & Mateos 2018) estimate maximum values of carrying capacity of an ecosystem according to these parameters, independently from their biological composition. In our point of view, they are very interesting methodologically, but can be less precise than others that consider the actual species that inhabited the paleoecosystem. The reason is that annual rainfall and mean annual temperature are not good predictors of ungulate biomass, but factors that limit it (Rodríguez *et al.* 2014). Moreover, Blackburn & Gaston (1997) and White *et al.* (2007) considered that the allometric equations used to estimate population densities provide values that are close to the maximum ecological densities. Thus, we suggest as optimal the use of a biomass ceiling value in those cases in which all species have maximum densities estimated from allometric equations. In this way, this ceiling value would represent the maximum carrying capacity in the long term. However, the application of this approach to a fossil assem-

blage is very sensitive to the absence of record of species, which results in an underestimation of the carrying capacity of this paleoecosystem. For this reason, it is important to use these approaches keeping in mind the taphonomic biases and focusing only on those sites that show a well-preserved record. Otherwise, we should be aware of the limitations. In any case, the different methodologies that use climate parameters are complementary rather than alternative. According to our interpretation, the approaches like the one of Rodríguez & Mateos (2018) provide estimates of the maximum potential carrying capacity of an ecosystem, which depends on a number of factors that ultimately determine its faunal composition (e.g. biogeography, climate barriers or soil characteristics). For this reason, we suggest estimating community biomass using a similar perspective to the one provided by the SPW approach. Although it provides more precision compared to previous methodologies, which opens a new avenue for these studies, we are aware that it is not a panacea and should be improved in future developments.

Finally, we wish to emphasize that we have not used here the mathematical model of Rodríguez-Gómez *et al.* (2013, 2014a, b, 2016a, 2017a, b, c, 2020) and Domingo *et al.* (2017) to estimate the biomass available in the paleoecosystems. Given that this model uses mortality profiles instead of survival profiles, the SPW approach cannot be used to estimate the biomass available because it only considers the individuals that survive, not those that die. Therefore, it could be interesting to obtain average biomasses from mortality profiles with the Weibull model for each species, simplifying the methodology used in our previous studies.

CONCLUSION

The carrying capacity of a paleoecosystem is a useful concept for investigating the ecology of ancient communities. The body size of each species preserved in the fossil assemblage is usually a key parameter to estimate the carrying capacity of this paleoecosystem, but the age structure of fossil populations is not usually considered in this type of research. Our study analyzes different methods for estimating the mean body size of extinct taxa and tests them with the fossil sites from Orce and Sierra de Atapuerca. Our results show that the methodologies used previously tend to over- or underestimate the biomass of these communities. Depending on if data are available, we recommend using with preference the life tables (LT) in both recent and past ecosystems. The second alternative is the Weibull model (SPW), the third the use of the adult female body mass (AFBM) and the fourth the adult body mass (ABM). We rule out the method that uses the three quarters of adult female body mass ($\frac{3}{4}$ AFBM) because it provides results that differ significantly from real data. In contrast, those derived from the mean body mass of adult females are more precise at population scale. Finally, we suggest analyzing the ecosystems using those approaches that are more direct, because they are closer to real conditions. However, it is interesting to combine them with indi-

rect methods in order to get a better understanding of those aspects that determine the composition of past and recent ecosystems. Our analyses of the sites of Orce and Sierra de Atapuerca suggest that human presence in the Iberian Peninsula was not limited by carrying capacity during the Early Pleistocene. However, the ecological scenario was possibly more relevant for the earliest settlements, because the Orce sites show the highest carrying capacity values.

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APPENDICES

APPENDIX 1. — Damuth (1981) vs Silva & Downing (1995)

Our methodology was developed from different studies performed previously (Bermúdez de Castro *et al.* 1995; Fariña 1996; Palmqvist *et al.* 2003; Vizcaíno *et al.* 2004, 2010). All those works used Damuth’s equation (Damuth 1981). Thus, we can compare our results with those of previous works. Moreover, these equations are more specific for populations of primary consumers than those of Silva & Downing (1995). Furthermore, it is possible to compare the equations of Damuth (1981) and Silva & Downing (1995) with the density values of recent species of large primary consumers (>10kg) reported in the PanTHERIA database (Jones *et al.* 2009) (Appendix 2). Appendix 2 shows a high dispersion of densities for recent species of primary consumers, which indicates that the allometric equations of Damuth and Silva and Downing do not show a good adjustment to the density values reported for extant species. It appears that the approaches of Damuth and Silva and Downing overlap for the species of primary consumers with body masses (BM) higher than approximately 500 kg. However, the approach of Damuth shows higher values than the one of Silva and Downing for those species with masses ranging between 10 and 500 kg,

and the later seems to underestimate the population density of these species according to data in Jones *et al.* (2009) values. For this reason, the approach of Damuth is more interesting for estimating carrying capacities of paleoecosystems in order to know the maximum biomass that they can sustain.

We can test the goodness of fit of the equations of Damuth and Silva and Downing through the chi-squared statistic.

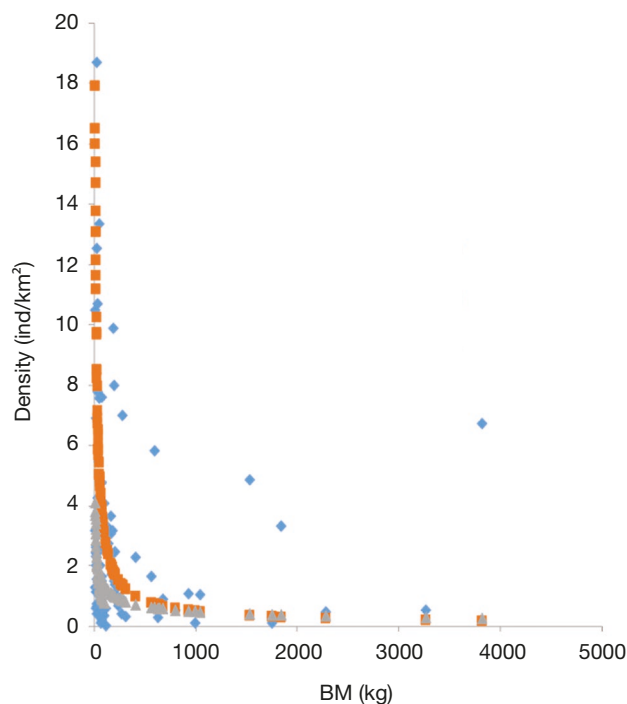
$$(\chi^2 = \sum_{i=0}^n \frac{(O_i - E_i)^2}{E_i})$$

The results are as follows:

Chi-squared statistic	Primary consumers (degrees of freedom 87)
Damuth’s equations	692.77
Silva and Downing’s equations	962.54

The equations of Damuth show a lower value (i.e., provide a better adjustment) of the chi-squared test than the ones of Silva and Downing for herbivore species. Given that, we considered that it is better justified to use the equations of Damuth than those of Silva and Downing.

APPENDIX 2. — Body masses (BM) of the species of primary consumers and their relationship with population density. Density of recent species by Jones *et al.* (2009) and estimated densities from allometric equation by Damuth (1981) and Silva & Downing (1995). Symbols: ◆, Jones *et al.* (2009); ■, Damuth (1981); ▲, Silva & Downing (1995).



APPENDIX 3. — Table of species.

Order, Family	Species	Autorship
Artiodactyla		
Bovidae	<i>Aepyceros melampus</i>	Lichtenstein, 1812
	<i>Ammotragus europaeus</i> †	Moullé, Echassoux & Martinez-Navarro, 2004
	<i>Bison schoetensacki</i> †	Freudenberg, 1910
	<i>Bison voigtstedtensis</i> †	Fischer, 1965
	<i>Connochaetes taurinus</i>	Burchell, 1823
	<i>Hemibos aff. gracilis</i> †	Qiu, 2004
	<i>Hemitragus albus</i> †	Moyá-Solá, 1987
	<i>Hemitragus bonali</i> †	Harlé & Stehlin, 1913
	<i>Hemitragus jemlahicus</i>	Smith, 1826
	<i>Kobus ellipsiprymnus</i>	Ogilby, 1833
	<i>Ovis dalli</i>	Nelson, 1884
	<i>Præovibos priscus</i> †	Staudinger, 1908
	<i>Rupicapra rupicapra</i>	Linnaeus, 1758
	<i>Soergelia minor</i> †	Moyá-Solá, 1987
	<i>Syncerus caffer</i>	Sparrman, 1779
Cervidae	<i>Arvernoceros giulii</i> †	Kahlke, 1997
	<i>Capreolus capreolus</i>	Linnaeus, 1758
	<i>Capreolus priscus</i> †	Soergel, 1914
	<i>Cervus elaphus</i>	Linnaeus, 1758
	<i>Dama clactoniana</i> †	Falconer, 1868
	<i>Dama vallonnetensis</i> †	De Lumley, Kahlke, Moigne & Moulle, 1988
	<i>Megaloceros giganteus</i> †	Robert, 1930
	<i>Metacervoceros rhenanus</i> †	Dubois, 1904
	<i>Praemegaceros solilhacus</i> †	Robert, 1830
	<i>Praemegaceros verticornis</i> †	Dawkins, 1872
	<i>Rangifer tarandus</i>	Linnaeus, 1758
Hippopotamidae	<i>Hippopotamus amphibius</i>	Linnaeus, 1758
	<i>Hippopotamus antiquus</i> †	Desmarest, 1822
Suidae	<i>Phacochoerus aethiopicus</i>	Pallas, 1766
	<i>Sus scrofa</i>	Linnaeus, 1758
Perissodactyla		
Equidae	<i>Equus altiden</i> †	Von Reichenau, 1915
	<i>Equus burchellii</i>	Gray, 1824
	<i>Equus caballus</i>	Linnaeus, 1758
	<i>Equus ferus</i>	Erxleben, 1777
	<i>Equus hydruntinus</i> †	Regalia, 1907
	<i>Equus suessenbornensis</i> †	Wüst, 1900
Rhinocerotidae	<i>Diceros bicornis</i>	Linnaeus, 1758
	<i>Rhinoceros unicornis</i>	Linnaeus, 1758
	<i>Stephanorhinus etruscus</i> †	Falconer, 1868
	<i>Stephanorhinus hemitoechus</i> †	Falconer, 1859
	<i>Stephanorhinus hundsheimensis</i> †	Toula, 1902
Primates		
Cercopithecidae	<i>Macaca nemestrina</i>	Linnaeus, 1766
	<i>Papio cynocephalus</i>	Linnaeus, 1766
Proboscidea		
Elephantidae	<i>Loxodonta africana</i>	Blumenbach, 1797
	<i>Mammuthus meridionalis</i> †	Nesti, 1825
Rodentia		
Castoridae	<i>Castor canadensis</i>	Kuhl, 1820
	<i>Castor fiber</i>	Linnaeus, 1758
Hystriidae	<i>Hystrix refossa</i> †	Gervais, 1852
Sciuridae	<i>Marmota flaviventris</i>	Audubon & Bachman, 1841