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Levantine overkill: 1.5 million years of hunting down the body size distribution

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ABSTRACT

Multiple large-bodied species went extinct during the Pleistocene. Changing climates and/or human hunting are the main hypotheses used to explain these extinctions. We studied the causes of Pleistocene extinctions in the Southern Levant, and their subsequent effect on local hominin food spectra, by examining faunal remains in archaeological sites across the last 1.5 million years. We examined whether climate and climate changes, and/or human cultures, are associated with these declines. We recorded animal abundances published in the literature from 133 stratigraphic layers, across 58 Pleistocene and Early Holocene archaeological sites, in the Southern Levant. We used linear regressions and mixed models to assess the weighted mean mass of faunal assemblages through time and whether it was associated with temperature, paleorainfall, or paleoenvironment (C3 vs. C4 vegetation). We found that weighted mean body mass declined log-linearly through time. Mean hunted animal masses 10,500 years ago, were only 1.7% of those 1.5 million years ago. Neither body size at any period, nor size change from one layer to the next, were related to global temperature or to temperature changes. Throughout the Pleistocene, new human lineages hunted significantly smaller prey than the preceding ones. This suggests that humans extirpated megafauna throughout the Pleistocene, and when the largest species were depleted the next-largest were targeted. Technological advancements likely enabled subsequent human lineages to effectively hunt smaller prey replacing larger species that were hunted to extinction or until they became exceedingly rare.

1. Introduction

Throughout the Pleistocene large mammals (and other vertebrates) went extinct while smaller ones mostly survived (Faith et al., 2018; Klein, 1984; Koch and Barnosky, 2006; Smith et al., 2018). Whether these size-selective extinctions were caused by *Homo sapiens* (Martin, 1984; Sandom et al., 2014; Smith et al., 2019a, b), sudden climatic events (Cooper et al., 2015, 2021; Louys and Roberts, 2020; Meltzer, 2020; Stewart et al., 2021), or both (Koch and Barnosky, 2006; Nogués-Bravo et al., 2008), has been debated for decades. Most studies, however, focused on the end of the Pleistocene and early Holocene, while earlier extinctions are seldom studied.

After recovering from the Cretaceous-Paleogene extinction, mean body size of the largest terrestrial mammals remained remarkably stable throughout the Cenozoic but declined in Africa during the Quaternary (Smith et al., 2018). This decline coincided with the emergence of the genus *Homo*. Smith et al. (2018) found that climate did not increase extinction risk for large mammals at any point during the Cenozoic (Smith et al., 2018). While the Late Pleistocene saw the extinctions of many large mammals globally, in Africa, mean mammal body mass started declining before the start of the Late Quaternary, possibly as a result of long-term hunting by early humans and finally by *Homo sapiens* (Smith et al., 2018). Some studies, however, propose that Early and Mid-Pleistocene extinctions are correlated with changes in climate or vegetation (Faith et al., 2018; Louys and Roberts, 2020; Potts et al., 2020). Large mammal extinctions started in Africa before the emergence of *Homo sapiens* but occurred in Australia and the New World following modern human colonization (Faith et al., 2018; Smith et al., 2019a, b; Wroe et al., 2013). However, declines in the

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abundance of large animals associated with early hominins have also been reported in European localities, spanning over one million years (Rodríguez et al., 2011; Yravedra, 2001).

The Southern Levant, situated between modern day southern Syria via Israel to Sinai, has a spatiotemporally dense and continuous Paleolithic archaeological record offering a unique opportunity to detect faunal changes, including those predating the appearance of *Homo sapiens* (Bar-Yosef, 1980; Stutz, 2014). It is thus a suitable model to test long-term changes in the body mass of mammalian assemblages, in view of paleoclimates and changing human lineages, to decipher whether climate and/or humans are responsible for animal body size declines. The excellent archaeological record can further illuminate whether size declines are observed since hominins first colonized the region, or whether they start with the emergence of *Homo sapiens* (Louys et al., 2021), or are concentrated in the last glacial and its aftermath. We tested whether the size, and size changes, in hominin prey through the Pleistocene and early Holocene were related to time, the prevailing human lineages and cultures, paleoenvironment, and temperatures.

2. Materials and methods

We searched for published data on fauna found in archaeological sites throughout the Southern Levant covering the last 1.5 million years (i.e. from the time of the first known archaeological site in Ubeidiya (Belmaker, 2006) to the beginning of agriculture ~10.5ka). We used all literature data available, from all Paleolithic (Pleistocene to Early Holocene) sites in the Southern Levant that provided data on faunal remains of at least three species, in the form of relative species abundance, and chronologies. Abundance data are in the form of number of identified specimens (NISP) and minimum number of individuals (MNI) when available.

Many archeozoological studies exclude certain faunal groups from their analyses (e.g., reptiles, carnivores, or birds). To ensure such practice does not bias our results, we verified, for each study, if the authors stated whether they excluded taxa from their analyses even though they were found at the site. This led to the exclusion of birds from our analyses as most studies did not analyze them even when remains were found, or simply reported them as ‘Aves’ and not specific species. We compiled two datasets: 1) for mammals, and 2) for mammals and reptiles. This was due to the large number of sites that chose to exclude reptiles from their analyses, and larger number of sites that excluded birds from their analyses despite them being present at the site. Since not all sources reported non-mammalian remains, the number of stratigraphic layers in the mammals and reptiles dataset is lower than in the mammal dataset. Layers were only excluded from the dataset of all species when it was specifically stated that only mammals were analyzed, and/or that other terrestrial vertebrates were found at the site, but no species-specific data were reported. We analyzed both datasets in order to test whether similar trends are observed across varying numbers of stratigraphic layers and species.

The vast majority of archaeological sites we studied have been described as accumulated by hominins. The only clear exceptions to this are the site of Rantis Pitfall, and specific layers from sites accumulated by hyenas in Manot and Geula Caves (Marder et al., 2011; Monchot et al., 2012; Orbach and Yeshurun, 2021; Yeshurun, 2013). It was once argued that Ubeidiya and Gesher B'not Yaakov were not accumulated by hominins, but this is now known not to be the case following meticulous taphonomic studies (Gaudzinski, 2004; Rabinovich et al., 2008). Archaeological and ethnographic evidence suggests that the faunal assemblages accumulated by humans at such sites reliably reflect the relative abundance of human prey species in the environment in general (Bar-Yosef, 2004; Rendu et al., 2019), and specifically in the Southern Levant (Speth and Clark, 2006; Yeomans et al., 2017). Moreover, evidence suggests that hominins actively hunted large prey as opposed to passive scavenging (Domínguez-Rodrigo and Pickering, 2017; Yravedra et al., 2019). It was well within the abilities of early humans to hunt large animals (Agam and Barkai, 2018) and evidence suggests that large game were actively hunted throughout the Pleistocene (Bocherens, 2011; Bunn, 2019; Bunn and Pickering, 2010; Metcalfe, 2017; Nikolskiy and Pitulko, 2013). The high frequency of prime age individuals in the archaeological record of the region suggests active hunting (Speth and Clark, 2006; Stiner et al., 2009).

We calculated the weighted mean body mass of animal species in each stratigraphic layer by multiplying the mass of each species (Appendix 6) by its relative abundance (NISP), summed this across all species, and divided by the total NISP. We only collected data for animals weighing >400 g (the size of *Vormela peregusna*, the smallest mammal in our dataset). Thus, for example all amphibians were excluded, and only the largest reptiles (e.g., *Testudo graeca*, large snakes) as well as medium-sized and large mammals were included. Smaller species were often deposited by birds of prey (Avery and Andrews, 1991; Lev et al., 2020; Marín-Arroyo, 2013) and made up an insignificant proportion of the diets of early hominids (Ben-Dor and Barkai, 2020; Stiner, 2013). Body masses were recorded from the literature and from modern conspecifics from the Levant housed at the Steinhardt Museum of Natural History, Tel Aviv University. For remains only ascribed to genera we used the average body mass of all congenerics with known mass in our database. Remains identified as ‘likely *Bos primigenius*', were assigned to *Bos primigenius*. No body mass estimates are available for *Hippopotamus behemoth* from Ubeidiya, so we averaged the body mass of the larger *H. gorgops* and the smaller *H. amphibius*. If only one species was present from a certain genus throughout our dataset, then we attributed indeterminate remains in the archaeological record from the respective genus to this species (e.g., remains of *Bos* that were not identified to species were attributed to *Bos primigenius*, the only identified member of the genus in the database).

For each layer we recorded its date (Appendix 3) and techno-cultural complex (according to archaeological data, e.g., Acheulean, Mousterian, etc.). We further determined the hominin lineage that occupied each layer, either directly or according to the cultural association where no human remains were found. *Homo erectus* (sensu lato) is associated with Acheulean sites, *Homo sapiens* and *Homo neanderthalensis* with Mousterian sites, and *Homo sapiens* with all later sites. It is currently unknown which hominin lineage occupied the Acheulo-Yabrudian site of Qesem cave or the Mousterian site of Nesher Ramla (Hershkovitz et al., 2011, 2021). We attributed these two sites to *H. sapiens* or *H. neanderthalensis* since the dental remains from Qesem are reminiscent of both species and because Nesher Ramla is nonetheless a Mousterian site and it is debated if this specimen represents a new species of hominin (Hershkovitz et al., 2011, 2021). If a range of dates X was given to a site but not to the n layers within it, we treated all layers as spanning the same amount of time (x/n) and assigned the midpoint time to each layer. We coupled each layer with global oxygen isotope levels (δ^{18}O) from (Lisiecki and Raymo, 2005) as a proxy for temperature for the entire period studied. We further attributed to each layer 250,000 years or younger δ^{18}O and carbon isotope levels (δ^{13}C) obtained from speleothems in a local cave (Soreq; values are only available for this latter period (Bar-Matthews et al., 2003)). Oxygen isotope values from caves are indicative of rainfall (more negative values: higher rainfall) and carbon isotopes associated with C3 vs. C4 vegetation (lower values more C3 vegetation, higher values: more C4 plants)(Bar-Matthews et al., 2003). Data were available from another local cave (Peqiin) but there were long hiatuses in these data as opposed to the data from Soreq cave (Bar-Matthews et al., 2003). According to (Bar-Matthews et al., 2003), “There is a striking similarity between the oxygen and carbon isotopic profiles and the timing of the isotopic events in both caves”. We therefore only used the much denser sample from Soreq cave.

2.1. Data analysis

Data were organized and visualized using the ‘tidyverse’ package (Wickham, 2016) and analyzed in R (version 4.0.2). Since most sites had several stratigraphic layers, we repeated our analysis using archaeological sites as a random effect. Models with random effects were analyzed using the ‘lme4’, ‘lmertest’, and ‘MuMIn’ packages, and model selection was done using BIC from the ‘MuMIn’ package (Barton, 2018; Bates et al., 2007; Kuznetsova et al., 2017). Weighted mean body mass and date before present of each stratigraphic layer were log10-transformed to normalize residual distribution and reduce heteroscedasticity.

2.2. Global temperature models

We tested whether temperature (in the form of global marine δ^{18}O levels) and temperature changes (differences in δ^{18}O between successive layers, Appendix 4) affected the mean body mass within assemblages over time using four models. 1. A regression of mean body mass on temperature (δ^{18}O levels). 2. A regression of mass change (the differences in mean body mass between consecutive stratigraphic layers according to their dates) on temperature changes (difference in δ^{18}O between the same layers). 3. Mass change (as in model #2) on absolute temperature change (the absolute value of the difference in temperature between the same layers, regardless of its direction). 4. Absolute mass change on absolute temperature change (as in model #3).

2.3. Local paleoenvironmental models

We used multiple linear regression models in order to test whether weighted mean body mass changed with time, δ^{18}O values (global and from local Soreq cave), or δ^{13}C values. Data were analyzed with global δ^{18}O values (Lisiecki and Raymo, 2005) for the entire period, but since isotope data from the local cave were only available for the past 250ka, we analyzed the association between local isotope values and body size for this period separately, in addition to the other analyses. In these analyses we only used sites dated with exact methods and minimal possible range (<4ka) in order to assess a possible relationship with local rainfall (using local oxygen isotopes as indices) and vegetation (carbon isotopes) during this period, alongside date and global marine oxygen isotopes (a proxy for temperature, Appendix 10). We obtained one dataset on locally sampled marine oxygen isotopes as a proxy for temperature spanning 325ka (Emeis et al., 1998). However, we could not use this dataset because it contains too many hiatuses: we could only ascribe isotope values to 12 out of the 80 layers in this time frame. We are unaware of other local datasets containing proxies for paleotemperatures. We removed one stratigraphic layer from this analysis: the site of Shishan Marsh (Appendix 10) because both oxygen and carbon isotope values for it have extremely high statistical leverage, and the datum is an extreme statistical outlier. We used model selection procedures in order to analyze local climate, running modes with all local and global isotopic predictors (as well as time) and progressively removing the predictor variables with the highest p-values. We reported R^2, BIC, and p values of all predictor variables (Table 1).

2.4. Type of site

Fauna can vary significantly based upon the type of site (open-air, cave, rock shelter, terrace) where the species were sampled (Enloe, 2006; Griggo, 2004; Klein, 1978; Smith et al., 2019a, b). Specifically, caves are thought to have been used for smaller-bodied fauna as carcasses would need to be carried back to caves, whereas open-air sites could represent the kill sites, preserving all species (Bocherens, 2009, 2011; Thompson and Henshilwood, 2011). In order to confirm that the type of site (cave, open-air, rock shelter, or terrace) did not influence our results we used a linear regression with site type as an additional predictor. We did this in order to ensure that body size declined in all types of sites in the region, and that changes in mean body mass of faunal assemblages reported here, do not simply represent changes in the frequency of types of sites.

2.5. Hominin species

We evaluated whether different sized fauna is associated with different hominin lineages throughout our study period using multiple linear regressions and controlling for hominin lineages. We note, however, that not all sites can be confidently associated to a specific hominin lineage, and there was possibly significant

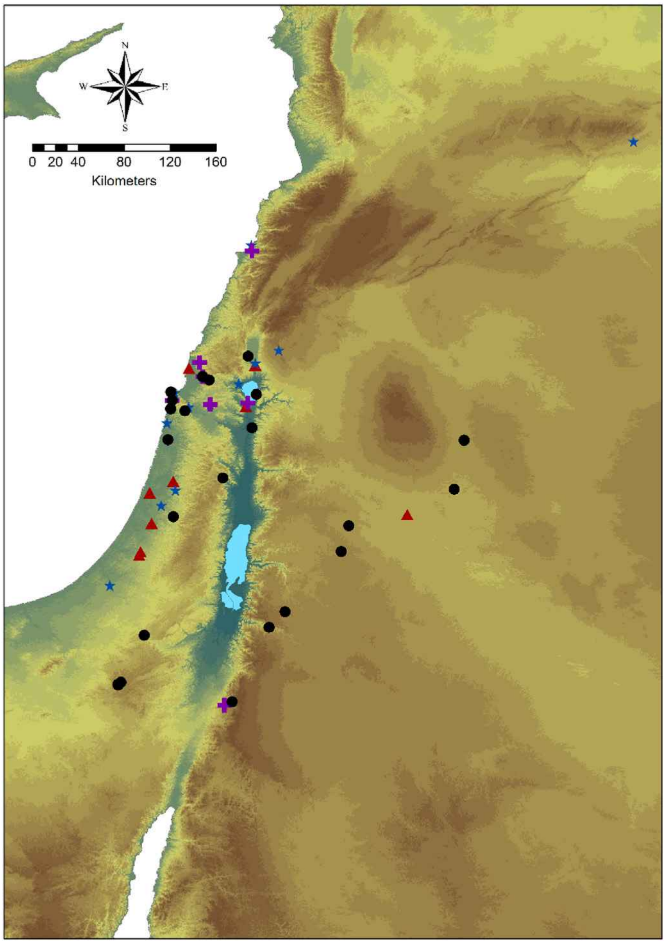

Fig. 1. All archaeological sites analyzed in this study organized by period. Lower Paleolithic: red triangles; Middle Paleolithic: blue stars; Upper Paleolithic: purple crosses; Epipaleolithic: black dots (Coordinates are in Appendix 11). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

temporal overlap between different hominid lineages. We also measured the relative frequency of larger vs. smaller prey species acquired by different human lineages (Appendix 5).

2.6. Additional sensitivity analyses

To test whether the use of NISP does not bias our results we compared weighted mean body masses calculated using the minimum number of individuals (MNI), to mean masses from the same layers calculated with NISP (Appendix 7 and 8). MNI has fallen out of favor with some archaeozoologists (Lyman, 2019), but we include this sensitivity analysis for the sake of being thorough as NISP and MNI likely bracket the true relative abundance (Lyman, 2018). We found that both data types yielded similar trends. We used NISP because it is much more commonly reported than MNI. Another model with mass based on NISP, only included layers for which we had direct dates (i.e., Electronic spin resonance (ESR) or thermoluminescence (TL) dating and not inferred from stratigraphy) and this analysis also yielded qualitatively similar results (Supplementary material, Appendix 9). We thus focus on the NISP analyses of all layers in the results and discussion.

3. Results

In total, we recorded 83 animal species that were accumulated by early humans across 133 stratigraphic layers from 58 archaeological sites spanning 1.5 million years before present (the earliest sites associated with humans known from the S. Levant) to 10,500 years before present (the end of the Paleolithic; Stutz, 2014, Fig. 1, Appendix 1 and 2). Weighted mean body mass across 133 stratigraphic layers (for all mammals) steeply declined with time (slope: -0.881 ± 0.055, on a log-log scale, $P < 0.001$, $R^2 = 0.67$; Fig. 2) but was unrelated to $\delta^{18}O$ levels (slope: -0.015 ± 0.081, $P = 0.86$). $\delta^{18}O$ levels alone were unrelated to weighted mean mass ($R^2 = 0.014$, slope: -0.189 ± 0.139, $P = 0.177$). An analysis with archaeological site as a random effect yielded similar results, with mass declining through time (slope: -0.821 ± 0.074, $R^2 = 0.85$, $P < 0.001$) and $\delta^{18}O$ an insignificant predictor (slope: -0.099 ± 0.072, $P = 0.17$).

Sequential differences in mean body mass between successive layers were not associated with differences in $\delta^{18}O$ (slope: 0.176 ± 0.107, $R^2 = 0.02$, $P = 0.104$) nor were they associated with absolute differences in $\delta^{18}O$ between the same layers (i.e., with temperature change regardless of its direction; $R^2 = 0.01$, slope: -0.111 ± 0.122, $P = 0.36$). Absolute differences in temperature were weakly associated with absolute differences in body mass (slope: 0.330 ± 0.085, $R^2 = 0.1$, $P < 0.001$). Models for all terrestrial vertebrates gave similar results: weighted mean body mass declined through time (n = 110 layers, slope: -0.975 ± 0.070, $R^2 = 0.65$) but was unassociated with temperature (slope: 0.081 ± 0.101, $P = 0.42$). The same holds true when archaeological site is used as a random effect (slope: -0.873 ± 0.094, $P < 0.001$, $R^2 = 0.81$) and $\delta^{18}O$ is insignificant (slope: -0.041 ± 0.090, $P = 0.65$). Differences in mean body mass between successive layers were not correlated with differences in temperature ($P = 0.42$, $R^2 = 0.01$, slope: 0.098 ± 0.121) and neither were absolute values of temperature differences ($P = 0.63$, $R^2 < 0.01$, slope: -0.066 ± 0.137). Absolute difference in temperature was weakly associated with absolute difference in body mass ($P = 0.014$, $R^2 = 0.05$, slope: 0.232 ± 0.093).

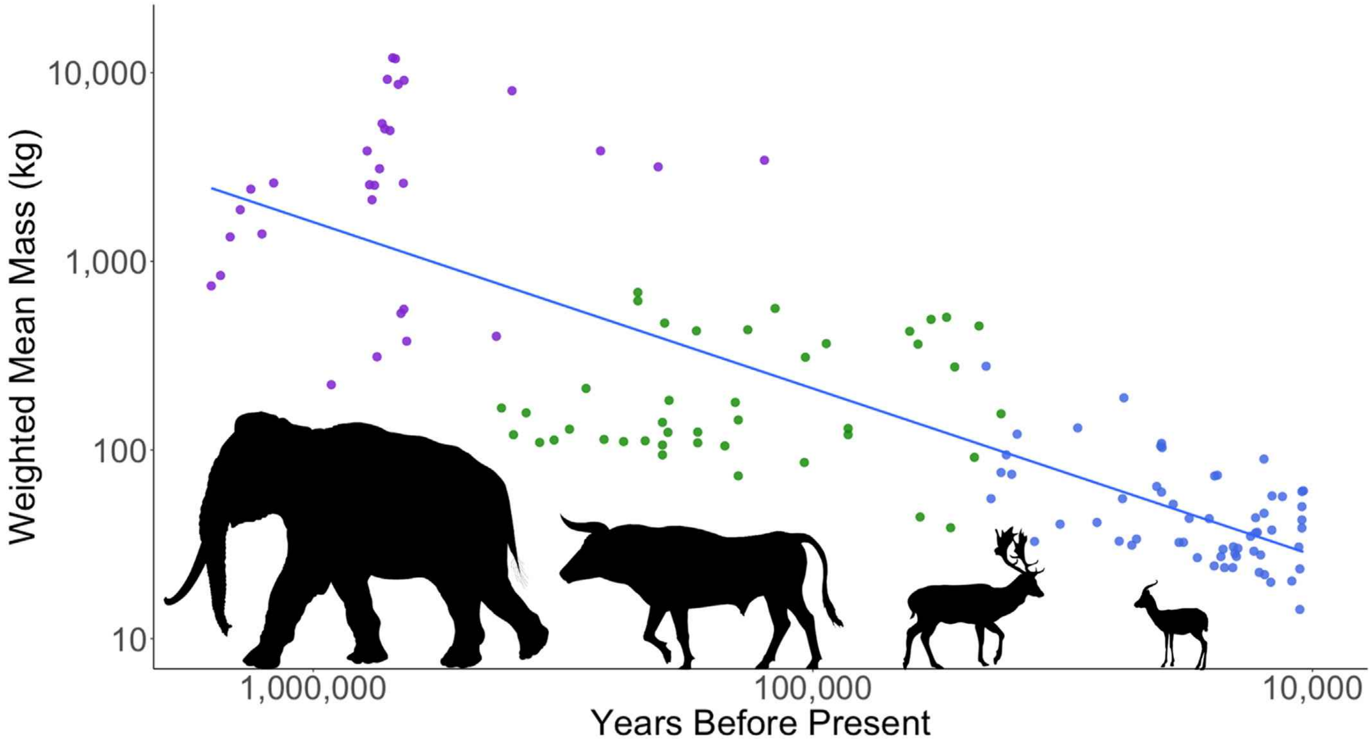

Fig. 2. Linear regression of log10 transformed weighted mean body mass (in kg) per stratigraphic layer as a function of time (log10 years before present). Results for datasets with all taxa, and only mammals are qualitatively the same (Supplementary material). Dots depict individual archaeological assemblages. Colors relate to the hominin lineages occupying the different sites. Human remains were found in a few sites; thus, the association of hominin lineages is in accordance with the archaeological culture and should not be regarded as definitive. Purple: *H. erectus* (sensu lato) of the Lower Paleolithic Acheulean, green: *H. neanderthalensis* and/or Archaic *H. sapiens* of the Middle Paleolithic Mousterian, blue: *H. sapiens* of the Upper and Epi Paleolithic. Silhouettes represent some of the most common animals at sites during corresponding periods. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The results indicate that subsequent human lineages hunted progressively smaller prey. Mean prey body sizes did not change linearly through time in sites associated with *H. erectus* (sensu lato; 31 layers). Likewise, time was not a significant predictor of mass across all 42 sites associated with either 'archaic *H. sapiens*', *H. neanderthalensis*, or an unknown Middle Pleistocene *Homo*. Mean mass declined strongly through time in sites known to be inhabited by modern *H. sapiens* (slope: -0.742 ± 0.232, $R^2 = 0.82$, n = 60 layers) (Supplementary Material).

3.1. *Local paleoenvironmental analyses*

We found marginally significant relationship between carbon isotopes from Soreq cave and body mass when time was an additional predictor, and a slight effect from global oxygen isotopes in one model when carbon isotopes were also used. In all other models we found no effect of oxygen isotopes (global or from Soreq cave, Table 1). The positive effect of $\delta^{13}C$ on weighted mean body mass indicates that more savanna-like environments (more C4 plants) were associated with higher prey mass. Although values were marginally significant, models with time alone (or mixed models with time and site alone) had lower BIC values than similar models that also included $\delta^{13}C$ as a predictor (Table 1).

3.2. *Size, time, and extinctions*

Although weighted mean body mass declined steadily and steeply over approximately 1.5 million years, proboscideans only went extinct in the region ~125,000 years ago (Pokines et al., 2019). Some argue that they disappeared in the region earlier, approximately 400ka (Barkai et al., 2017; Ben-Dor et al., 2011). The last remains of *Hippopotamus* were from 42,000ka (Monchot et al., 2012) though they may have re-entered the region after the end of the period we studied, only to go extinct again during the Iron Age (Horwitz & Tchernov, 1990) and of *Stephanorhinus* rhinos from 15,500 years ago (Stiner and Bar-Yosef, 2005). Extinctions of herbivores progressed from the largest to succesively smaller species, but mean body mass declined steeply prior to any extinction. Earlier size declines were therefore due to declines in the abundance of large animals (Fig. 3). The contribution of large mammals to overall biomass decreased with time (Fig. 3B).

3.3. *Type of site analysis*

Body size declined through time across all types of sites (Fig. 4). Open-air sites had on average larger mean mass of fauna, which declined faster than in caves (open-air: slope = −0.936 ± 0.054; caves: -0.498 ± 0.106; $P < 0.001$, model $R^2 = 0.77$). We combined the analysis of rock shelters and terraces due to their small sample size in the data (n terraces = 3, n rock shelters = 11). The mean mass of fauna in rock shelters and terraces declined through time as well (slope = −1.336 ± 0.501, $P = 0.008$). We thus confirm that decline in the mean mass of species was not the result of the types of sites sampled in this study.

Table 1
Comparison of models analyzing the effect of time,$\delta^{18}O$ (global and from cave) and$\delta^{13}C$ from Soreq cave on mean species body mass over the last 250ka years.

Predictors	Time slope	Time p value	Global$\delta^{18}O$ slope	Global$\delta^{18}O$ p value	Cave$\delta^{18}O$ slope	Cave$\delta^{18}O$ p value	Cave$\delta^{13}C$ slope	Cave$\delta^{13}C$ p value	R^2	BIC
Time + Global$\delta^{18}O$ + Cave$\delta^{18}O$ + Cave$\delta^{13}C$	−0.754 ± 0.077	<0.001	−0.215 ± 0.111	0.055	0.033 ± 0.072	0.654	0.051 ± 0.051	0.322	0.59	54.13
Time + Global$\delta^{18}O$ + Cave$\delta^{13}C$	−0.754 ± 0.077	<0.001	−0.186 ± 0.090	0.041	NA	NA	0.069 ± 0.033	0.039	0.59	49.97
Time + Cave$\delta^{13}C$	−0.761 ± 0.079	<0.001	NA	NA	NA	NA	0.029 ± 0.027	0.288	0.57	50.01
Time	−0.774 ± 0.078	<0.001	NA	NA	NA	NA	NA	NA	0.56	46.81
Time + Global$\delta^{18}O$ + Cave$\delta^{18}O$ + Cave$\delta^{13}C$ + Site as random effect	−0.610 ± 0.072	<0.001	0.082 ± 0.091	0.374	−0.062 ± 0.051	0.231	0.084 ± 0.035	0.022	0.90	49.73
Time + Cave$\delta^{18}O$ + Cave$\delta^{13}C$ + Site as random effect	−0.623 ± 0.073	<0.001	NA	NA	−0.031 ± 0.038	0.418	0.077 ± 0.035	0.035	0.89	43.05
Time + Cave$\delta^{13}C$ + Site as random effect	−0.628 ± 0.072	<0.001	NA	NA	NA	NA	0.056 ± 0.024	0.024	0.90	34.65
Time + Site as random effect	−0.666 ± 0.075	<0.001	NA	NA	NA	NA	NA	NA	0.88	29.55

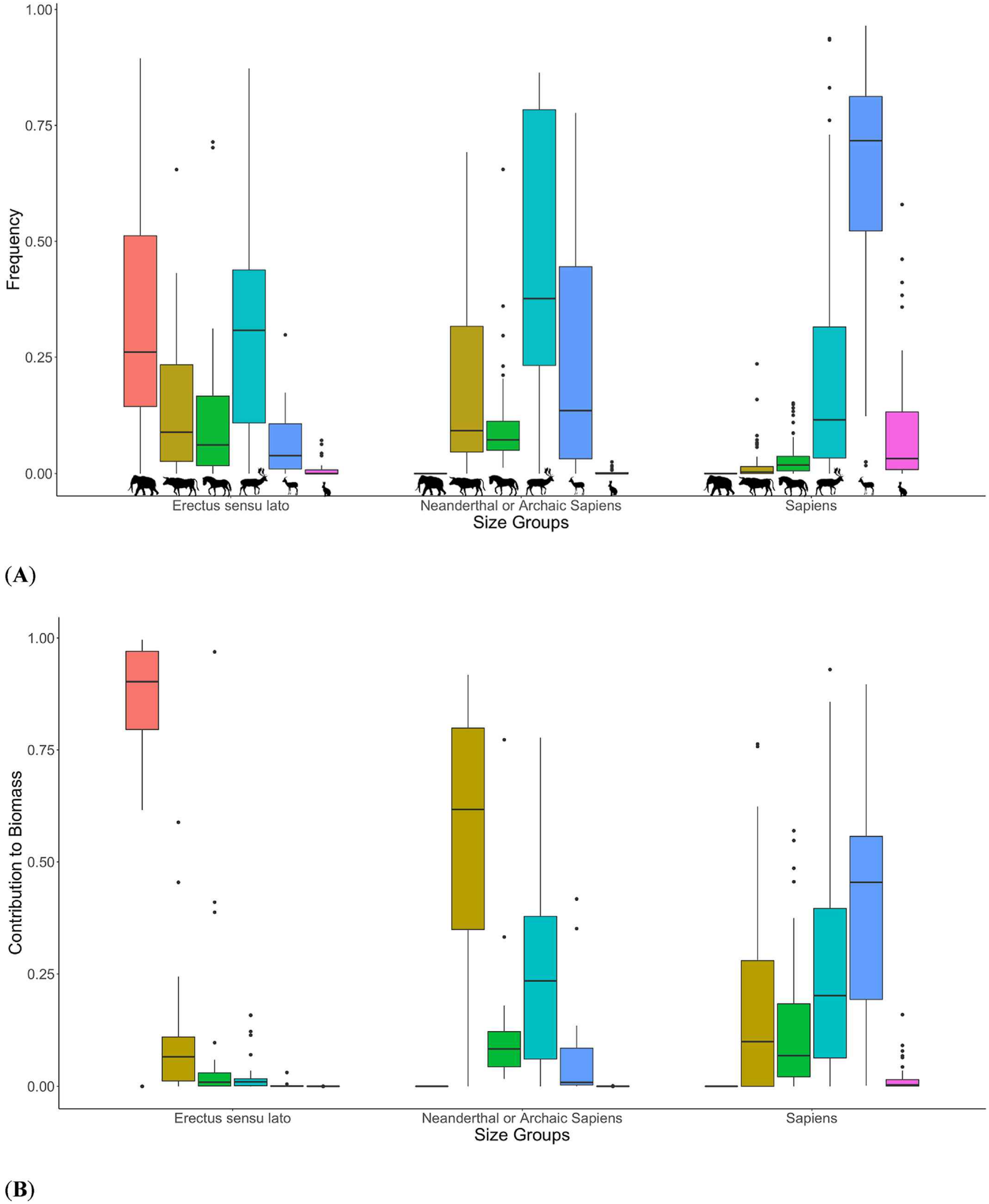

Fig. 3. Frequency of species divided into body size groups in the archaeological record and their contribution to total biomass. (**A**) The abundance of fauna (NISP per size class divided by total NISP) divided into different size groups across species of hominids: Red: >3125 kg; Yellow: 625–3125 kg; Green: 125–625 kg; Turquoise: 25–125 kg; Blue: 5–25 kg; Pink: 0.4–5 kg. (**B**) Percent of total biomass contributed by each size group across different species of hominid. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

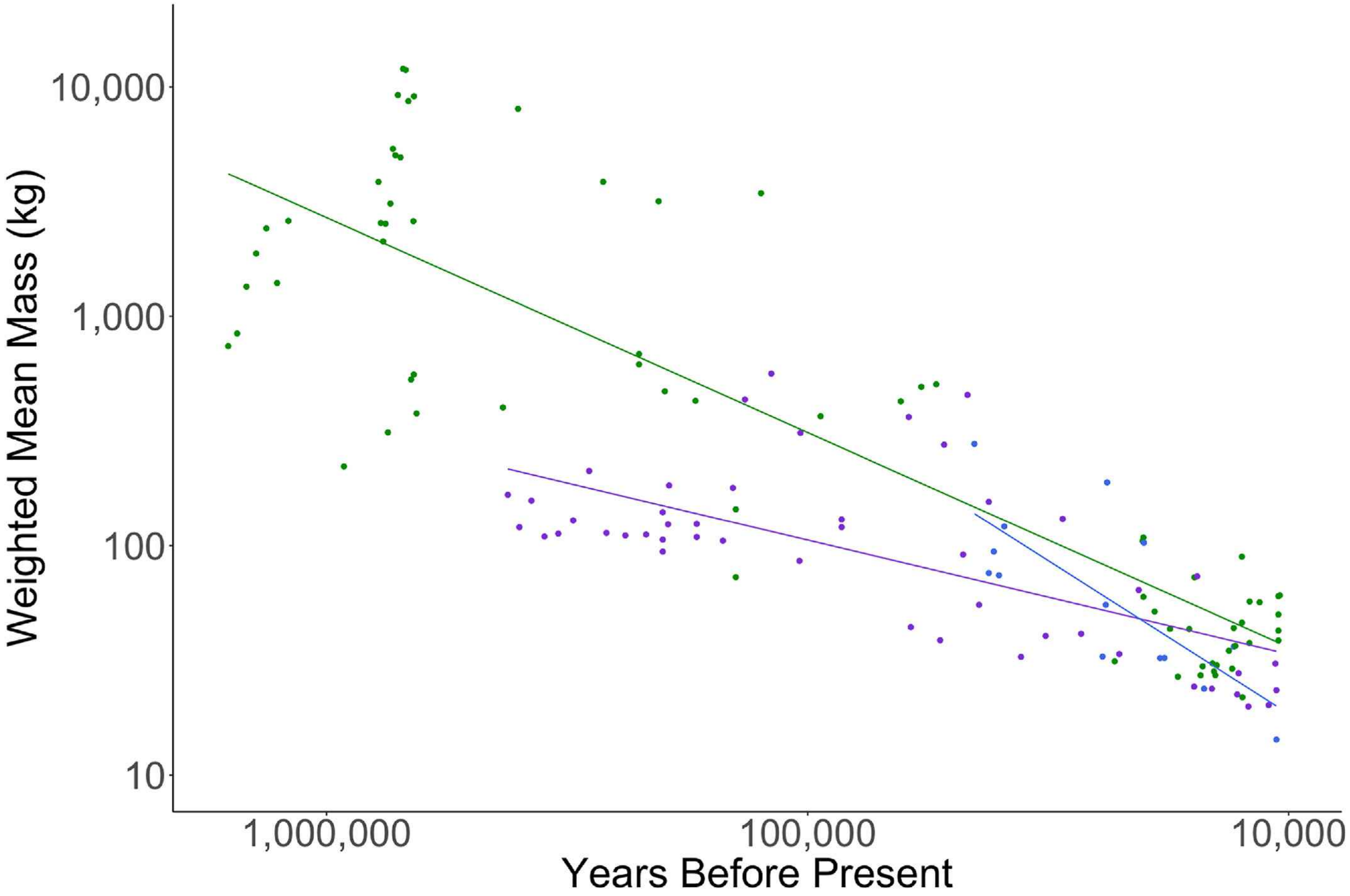

Fig. 4. Body mass through time using type of site as an additional predictor variable. Green: open-air, purple: caves, and blue: rock shelters and terraces. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

Animal prey weighted mean body mass within archaeological assemblages declined steadily in the Levant throughout the last 1.5 million years. We found no evidence that temperatures were linked to the size (or size change), and weak evidence for temperature changes (in either direction) being correlated with size of human prey over this period. In addition, paleorainfall was not a significant predictor, and vegetation was only a marginally significant predictor of mean body mass. The unidirectional, smooth nature of body mass declines against a background of well over a dozen glacial-interglacial cycles (Lisiecki and Raymo, 2005) suggests that climatic events were, if anything, a minor cause of decline. The decline is evident even within some sites spanning relatively long periods of time (e.g., Hayonim Cave and Kebara, Speth & Clark, 2006; Stiner and Bar-Yosef, 2005). Similar declines in the abundance of large animals throughout the Paleolithic have been reported from the Iberian Peninsula (Rodríguez et al., 2011; Yravedra, 2001). Yravedra (2001) for example, recorded ~400 stratigraphic layers from ~150 sites. He showed that in the Lower Paleolithic, large animals dominated the faunal assemblages (elephants, large bovids and horses) while the Middle Paleolithic was dominated by equids, cervids and large bovids. Finally, small prey predominated during the Upper Paleolithic along with the reduction in the abundance of large ungulates. Our work indicates that this phenomenon is perhaps more common than once appreciated.

Taphonomy is not enough to explain why a larger number of small species are found in more recent periods (as one could argue that they would not be preserved as well in earlier sites). First, if taphonomy were to blame then we would not expect to see a decline in larger animals as well. Second, there are more ‘small’ species of birds, reptiles, mammals and amphibians found and described in Ubeidiya, the oldest site in our dataset, than any other site (Haas, 1968; Tchernov, 1980) and small species are found throughout the entire period studied (Appendix 1,2). Moreover, the type of sites sampled do not affect our results as weighted mean mass declined across all site types (Fig. 4). We did find that open-air sites contained, on average, larger-bodied species than other types of sites. The use of caves increases abruptly during the Middle-Paleolithic, and earlier with the site of Qesem Cave (Appendix 1,2). We suggest that the decline of megafauna might have allowed for caves to be utilized more frequently as smaller prey (e.g., cervids or gazelles) could be more easily transported to caves than Proboscideans. Interestingly, we find that the mean mass of fauna in cave and open-air sites were essentially the same at the end of the Pleistocene (Fig. 4). We propose that faunal assemblages essentially reached their minimum threshold for mean body mass, making the difference in body mass between cave and open-air sites irrelevant.

Similar declines in the abundance of the largest species are well known in the most pervasive form of hunting today, fishing, in which “fishing down marine food-webs” refers to the decline of fisheries from large piscivorous fish, to smaller planktivorous fish, and eventually to small invertebrates (Pauly et al., 1998). We infer that hominins specifically targeted the largest species available (Ben-Dor & Barkai, 2020, 2021; Stiner, 2013) to extinction, or at least until they became too rare to significantly appear in the archaeological record. In the Lower Paleolithic (~1,500,000 to ~ 400,000 years ago), megaherbivores, specifically Proboscideans, made up a large portion of the diets of hominins in the Southern Levant (Fig. 3B). Later hominins (Ben-Dor and Barkai, 2021; Ben-Dor et al., 2011; Stiner and Bar-Yosef, 2005) hunted much smaller animals (Fig. 2). We did not find a strong connection between the reduction of mean body size through time and the extinction of large species. Rather, megaherbivores became scarcer and scarcer and mean weighted body mass continued to decline. This indicates that reduced abundance, and not extinction, explains most size declines.

Extinctions, however, certainly followed and the 10 largest species in our dataset all went extinct during the study period leaving the aurochs (*Bos primigenius*; 900 kg) as the largest species by the end of the period (it went extinct in the Southern Levant during the Iron Age, ~1200−586 BCE (Tsahar et al., 2009)). The largest extinct species (*Palaeoloxodon antiquus*), weighed 15 times as much (13.3 tons; Appendix 6). Humans progressively incorporated smaller prey when larger species were no longer available (Fig. 3A). Towards the end of the Pleistocene exploitation of small animals (*e.g.,* the tortoise *Testudo graeca* and the hare: *Lepus capensis*) increased steeply as larger game declined (Speth and Clark, 2006; Stiner et al., 2000). Small species were hunted throughout the period (Stiner and Bar-Yosef, 2005; Zaidner et al., 2014) but at lower frequencies in earlier sites (Fig. 3A).

Studies that aim to understand Pleistocene extinctions usually use the first and last occurrence of species (e.g., Belmaker, 2009; Faith and Surovell, 2009; Wroe et al., 2013). This makes it difficult to understand long periods of overlap between hominids and megafauna (Johnson et al., 2016). Using relative abundances enabled us to detect a gradual decline in large mammals which has before only been shown over relatively short (~10ka) periods of time (Davis et al., 1988; Munro et al., 2018; Rendu et al., 2019). Relative abundance of species in the faunal record can be used to determine if long periods of co-existence with hominids during the Quaternary (*e.g.,* Australia, Madagascar, or Southeast Asia (Hansford et al., 2018; Louys and Roberts, 2020; Trueman et al., 2005)) correspond with gradual declines of megafauna. We infer that long periods of temporal overlap with humans prior to extinctions do not necessarily indicate harmonious coexistence.

The evolution of larger brains, and the emergence of progressively sophisticated hunting tools (e.g., bow and arrow), did not allow humans to better exploit the largest prey taxa. We infer that humans shifted their focus from large game species as they became rare to smaller species because they no longer had a choice. We suggest that hunting smaller, not larger prey, required new technological advancements. Later techno-cultural advances were probably driven by the need to adapt to obtaining smaller prey (Ben-Dor and Barkai, 2021; Churchill, 1993) rather than enabling the hunting of even larger animals. Thus, better technology was the result of size declines rather than their cause. Reduction in large game availability in the Southern Levant has been linked to cultural transformations (Barkai et al., 2017; Ben-Dor et al., 2011) and the beginning of agriculture (Munro et al., 2018). In East Africa, the extinction of large species has been linked to the transition from the Acheulean to the Middle Stone Age and the possible appearance of *H. sapiens* (Potts et al., 2018, 2020). In America, the disappearance of megafauna has recently been associated with the replacement of the formative Clovis culture by later adaptation strategies (Waters et al., 2020). We provide strong support through the analysis of a dense archaeological record that decline of prey size led to technological advancements and not vice versa.

5. Conclusion

We did not find strong evidence to suggest that climate, climatic fluctuations, rainfall, or vegetation over the last 1.5 million years, influenced the size of animals hunted and consumed by humans. Rather, mean body size declined linearly on a backdrop of multiple glacial-interglacial cycles. New human lineages subsisted on smaller prey than their predecessors and used more advanced tools to cope with hunting smaller prey. We suggest that hominins were likely the leading cause of Pleistocene extinctions and reduced large-animal abundances in the region, and that humans hunted animals ‘down the body size distribution’ as we did not find similar evidence for steady environmental decline. The constant decline of mean body mass of species in the environment may have influenced hominin physiology, culture and technology as hunter gatherer societies needed to adapt to hunting smaller prey.

Data accessibility statement

All data are available in the supplementary material.

Author contributions

MB, RB, JD, SM conceptualized the study. SM, JD, RB, MB established the methods. JD, RB, and MB collected data. JD and SM performed analyses and visualized the results. JD wrote original draft and SM, RB, MB, JD reviewed and edited the writing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary data

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