

Investigating Middle Palaeolithic subsistence: zooarchaeological perspectives on the potential character of hominin climate refugia in Greece

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ABSTRACT: It has long been proposed that during Pleistocene climatic perturbations the Balkan peninsula sustained refugial areas for fauna, flora, and potentially, hominins. In this study, we explore Middle Palaeolithic subsistence at the peninsula's southern end, Greece, and discuss how the evidence contributes to our understanding of the region's character as a refugium. We present new data from the recent reanalysis of the fauna from Asprochaliko rockshelter and the ongoing zooarchaeological investigations at Lakonis Cave 1 and compare them with published analyses from Klissoura Cave 1. We employ taxonomic abundance and diversity indices, as well as mortality profiles, to investigate hominin prey choice. Additional taphonomic observations provide further information on carcass exploitation. We examine changes in the faunal composition of the three sites in an attempt to identify the extent to which climate might have influenced resource availability and diversity in the region, stimulating resource intensification or diversification processes. Our results suggest that Middle Palaeolithic hominins consistently acquired high-ranked prey through time. However, interregional differences in resource exploitation indicate that local topography and microclimate mediated prey choice and availability. Copyright © 2021 The Authors. *Journal of Quaternary Science* Published by John Wiley & Sons Ltd.

KEYWORDS: Greece; Middle Palaeolithic; Subsistence; Zooarchaeology

Introduction

The climatic instability of the Pleistocene exerted its influence on European ecosystems and impacted the demography and distribution of many species. During glacial stages, the advance of the Eurasian ice sheets rendered the climatic conditions of mid-latitude Europe less hospitable for thermophilic taxa (Van Andel and Tzedakis, 1996). Palaeoecological and phylogeographic studies document tree population crashes in Central and Eastern Europe, as well as major range shifts of vegetal zones; mainly the contraction of temperate tree taxa south of the permafrost during glacial maxima (Bennett *et al.*, 1991; Médail and Diadema, 2009; Tzedakis *et al.*, 2013; Van Andel and Tzedakis, 1996). Scholars have suggested similar demographic patterns for vertebrates and invertebrates associated with temperate forest biomes (Hewitt, 1999, 2000; Randi, 2007; Taberlet *et al.*, 1998). The negative effects of glacial conditions on environmental productivity and resource availability of habitats indirectly influenced the size and range of Middle Palaeolithic (MP) hominin populations, who either responded to the environmental changes with behavioural adaptations, such as increased mobility, or faced local extinction (Bradtmöller *et al.*, 2012; Finlayson and Carrión, 2007; Hublin and Roebroeks, 2009). In this context, the concept of glacial refugia broadly describes areas that facilitated the survival of flora and fauna during cold periods and acted as sources for post-glacial recolonisation (Hewitt, 2001; Stewart *et al.*, 2010). Such refugia were fundamental for

the maintenance of European biodiversity and, subsequently, the persistence of past human populations.

In Europe, the 'traditional' refugia hypothesis focused on the southern peninsulas as the main biodiversity havens during full-glacial times (Bennett *et al.*, 1991; Hewitt, 1999; Stewart *et al.*, 2010; Taberlet *et al.*, 1998). In the southernmost part of the Balkan Peninsula, Greece has offered a relatively rich MP archaeological record (Tourloukis and Harvati, 2018), as well as a wealth of palaeovegetational data. Pollen sequences from four sites in north, northwest and central Greece indicate different local vegetational responses to climatic cooling events within the region. The studies suggest that arboreal vegetation persisted locally in the Ioannina basin and the surroundings of Lake Prespa in northwestern Greece even during extreme stadial events, whereas a severe decline in tree populations was observed in Kopais, central Greece, and Tenaghi Philippon, eastern Macedonia (Panagiotopoulos *et al.*, 2014; Tzedakis *et al.*, 2004). Further evidence is reported from the phytolith analysis at the archaeological site of Theopetra in Thessaly, where glacial conditions have been associated with very low frequencies of arboreal plants and increased aridity (Tsartsidou *et al.*, 2015).

The palaeoenvironmental context for southern Greece is less well-established. A recent anthracological study at Klissoura 1 in the Peloponnese describes the persistence of open almond (*Amygdalus* sp.) woodland after marine isotope stage (MIS) 5e, reflecting overall arid conditions. During colder periods, drought-tolerant juniper (*Juniperus* sp.) parkland dominated the landscape. However, the continuous presence of deciduous oak (*Quercus* sp.) vegetation during the Pleniglacial and the late glacial hints

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at milder conditions that allowed the survival of temperate tree populations in the area (Ntinou, 2020).

In contrast to northern and central Greece, the influence of the climatic oscillations on vegetation was less severe in the western and southern part of the country (Tzedakis *et al.*, 2004). The presence of temperate tree populations during cold episodes follows the east–west precipitation gradient of the region, indicating that humidity was a major factor for the survival of tree populations. The highest precipitation regimes are found to the west of the Pindus mountain range, while the eastern part of mainland Greece is generally drier due to the rain shadow effect. The intraregional climatic heterogeneity and diverse topography of the region presumably resulted in the formation of small refugial areas. Genetic studies on modern fauna identify evidence for population bottlenecks during the Pleistocene and trace multiple centres of genetic differentiation within Greece for several species, including wild boar (Alexandri *et al.*, 2017), brown hare (Kasapidis *et al.*, 2005), red deer (Karaïskou *et al.*, 2014) and stone marten (Tsoupas *et al.*, 2019). Geographically localised lineages, likely the result of population isolation due to habitat fragmentation, could be traced to the Peloponnese (Kasapidis *et al.*, 2005; Tsoupas *et al.*, 2019) and western mainland Greece (Alexandri *et al.*, 2017; Kasapidis *et al.*, 2005), as well as north and northeastern Greece (Kasapidis *et al.*, 2005; Tsoupas *et al.*, 2019).

Regarding the archaeological record, most of the MP sites are concentrated in Epirus, while site clusters have also been observed in Mani, western Peloponnese. Middle Palaeolithic find-spots are sparse in the rest of the region, with the

exception of the Late MP temporary camps or kill-sites along the Pineios River (Runnels and van Andel, 1999) and the nearby cave of Theopetra in Thessaly, on the eastern side of the Pindus mountain range (see Tourloukis and Harvati, 2018) for a detailed overview of the Greek Palaeolithic record). Site distribution in the region is certainly affected by research biases; however, this pattern of hominin occupation might also reflect a preference for biodiversity sanctuaries, as well as a propensity for maintaining settlements in areas with higher humidity and nearby bodies of fresh water (Tourloukis and Harvati, 2018).

Based on the proposed existence of multiple microrefugia for fauna and flora in mainland Greece, our goal with this paper is to examine the role of these areas in sustaining MP hominin populations during extreme environmental shifts. We hypothesise that if climatic conditions significantly reduced environmental productivity, as suggested by the aforementioned studies, we would recognise behavioural responses, visible in the faunal record, within the ‘putative’ refugia. Specifically, these responses would manifest as traces of resource intensification, triggered either by a reduction in prey encounters on a local scale or by the contraction of surrounding hominin populations in these areas. To investigate the topic, we analyse the faunal record of three MP sites, located within potential refugial sub-regions in Greece, that date to between 100 k and 40 k BP: Lakonis 1, Klissoura Cave 1 and Asprochaliko (Fig. 1). We examine prey abundance and diversity, carcass-processing intensity, and the targeted hunting of different age cohorts of animals, in order to determine whether climatic conditions

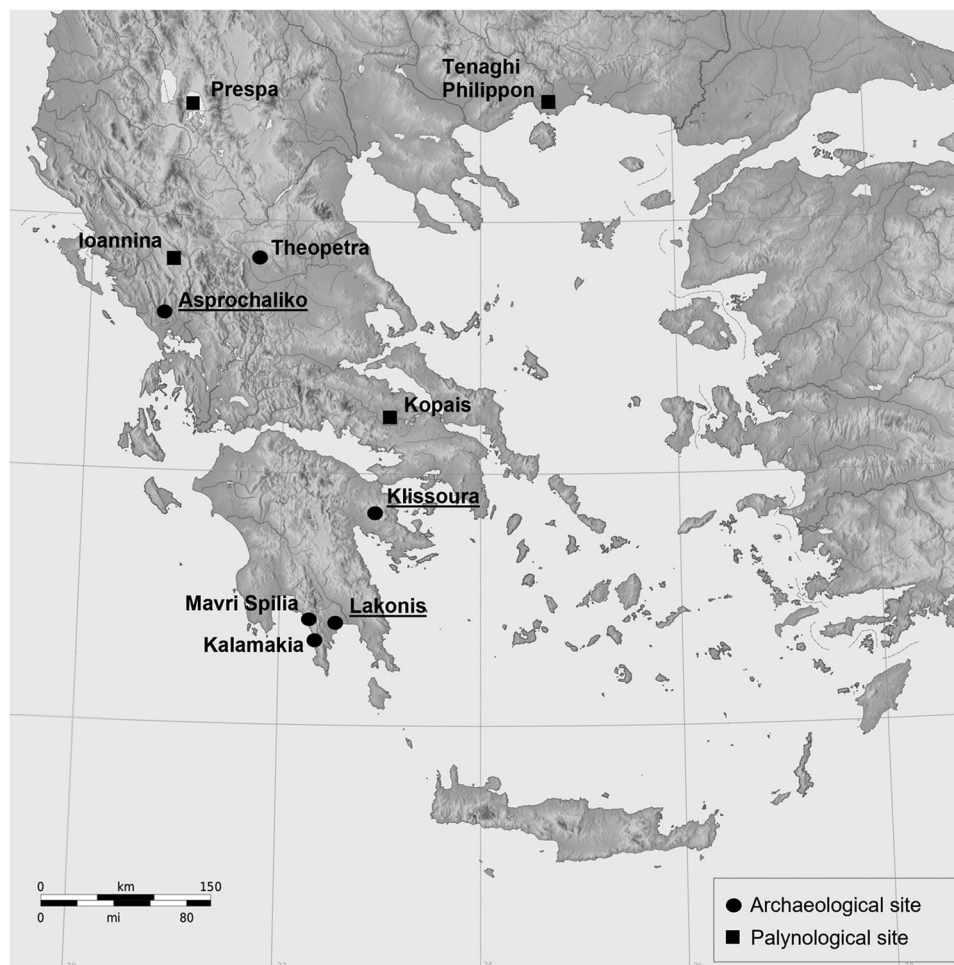


Figure 1. Map of Greece showing the main palynological and archaeological sites mentioned in the text.

or other factors explain fluctuations in hominin subsistence strategies and discuss how the evidence contributes to our understanding of the region's function as a hominin refugium.

Background

In spite of the abundance of MP localities in Greece, only a handful of sites have yielded animal bones from this period and provide some zooarchaeological information. In this study, we present results from three recently analysed sites, Lakonis 1 and Klissoura 1 caves, and Asprochaliko rockshelter. A summary of the dates and technological characteristics of each site can be found in Table 1.

Lakonis 1 is located on the east coast of the Mani Peninsula in the southern Peloponnese. Excavations at the site took place between 1999 and 2010 and archaeologists recovered a series of lithostratigraphic units numbered from the top downwards (I–IV). Accelerator mass spectrometry dates based on cultural materials recovered from well-defined hearths have placed Unit I between 39.640 ± 1000 ^{14}C a BP and 43.335 ± 1800 ^{14}C a BP (Panagopoulou *et al.*, 2004). The lower Unit IV likely formed during MIS 4 and represents the site's initial occupation phase. This attribution is based on U/Th dates that place the underlying beach conglomerate (Unit V) preliminarily to MIS 5a. Cultural remains from the site include a rich Levallois Mousterian lithic industry, in addition to a unique terminal MP or Initial Upper Palaeolithic (IUP) technocomplex, as well as a Neanderthal lower third molar from Unit Ia (Panagopoulou *et al.*, 2004; Starkovich *et al.*, 2018a).

Klissoura 1 is located in the northeastern Peloponnese. The site was discovered during a comprehensive survey of the area directed by Curtis Runnels in 1988–1990 (Koumouzelis *et al.*,

2001). Subsequent excavations revealed Mesolithic, Upper Palaeolithic and MP deposits. The sequence includes seven Upper Palaeolithic layers, including a transitional Uluzzian technocomplex and an exceptional Aurignacian component. The latter contains an anthropogenic rock-lined structure, as well as 50 clay-lined hearths, which to date are the earliest in the world (Karkanis *et al.*, 2004). Six MP stratigraphic horizons, containing Mousterian lithic industries were deposited between MIS 5 and 3, with the older units (XXa–XXb, XVIII–XIX and XIV) attributed to warm phases of MIS 5 and the younger units to MIS 4/3 (Starkovich, 2014). Optically stimulated luminescence (OSL) dating places the latest MP phase to 45.150 ka BP, while the earliest horizons were deposited between 123 and 110 ka BP (Ntinou, 2020).

The site of Asprochaliko is located in Epirus, northern Greece, in a narrow gorge, on the right bank of the Louros River and overlooking the Louros Valley. It was discovered during the survey programme conducted by E. Higgs and S.I. Dakaris from 1962 to 1967. Excavations took place between 1964 and 1966. The first reports mention the recovery of 35,000 lithic artefacts from a 1.5 m-wide trench during the test excavation, and the existence of at least four Palaeolithic layers. Higgs (1965) described an Upper Palaeolithic layer containing lithic industries with backed-bladelets, burins and shouldered points. Below that, he defined the 'micro-Mousterian' level containing small Mousterian points and scrapers, followed by an underlying Levallois Mousterian industry (Basal Mousterian) with side-scrapers, D-scrapers, Levallois flakes and tortoise cores (Higgs, 1965). Later analytical efforts were organised by the British Archaeological School, the University of Cambridge and the University of Southampton between 1979 and 1981. Geoff N. Bailey and colleagues revisited the stratigraphy of the site and initiated new studies on the cultural remains, including a brief faunal

Table 1. Summary of techno-typological characteristics, stratigraphic attributions and dating by site.

Layer	Date (ka)	Industry
Klissoura		
VIII	45.10 (± 3.35) ¹	Mousterian – side scrapers common.
X	N/A	
XI–XIV	46.55 (± 5.55) –75.03 (± 6.25) ¹	Mousterian – end scrapers common, high proportions of blades and bladelets. Mousterian points especially common.
XV–XVII	82.49 (± 6.0) –91.15 (± 6.89) ¹	
XVIII–XIX	92.84 (± 7.65) ¹	
XXa–XXb	95–110 ¹	
Lakonis		
Unit I	39.64 (± 1.0) –43.33 (± 1.8) ²	Levallois and prismatic core reduction – blades & bladelets together with Levallois bidirectional points (Ia: IUP).
Unit II	N/A	
Unit III	N/A	Levallois – blanks, blades, laminar flakes and elongated Levallois points common. Scrapers of all types. (Ib–III: MP).
Unit IV	N/A	
Unit V	85.6 (± 13.7) –174.0 (+146.0) (–56.0) ³	sterile
Asprochaliko		
14 (R2–4) & 9 (R41–62)	>39.9 ⁴	Mousterian with pseudo-Levallois points.
16 (R2–4) & 11 (R41–62)	N/A	Levallois Mousterian with blade-like flakes. Lateral scrapers common.
18–19 (R2–4) & 12–17 (R41–62)	98.5 (± 12.0) ⁵	

¹ OSL dates (1 σ errors). Source: Ntinou (2020).

² Radiocarbon dates. Source: Panagopoulou *et al.* (2004).

³ Uranium-series dates. Source: Panagopoulou *et al.* (2004).

⁴ Radiocarbon dates. Source: Bailey *et al.* (1983).

⁵ Thermoluminescence date. Source: Huxtable *et al.* (1992).

analysis (Bailey *et al.*, 1983). As for the chronological framework, analysts have placed the early Mousterian at approximately 100 ka. Thermoluminescence dating on burnt flint provided a mean date of 98.5 ka for Layer 18 (Bailey *et al.*, 1992; Huxtable *et al.*, 1992), while radiocarbon dates from charcoal set a *terminus ante quem* of 39.900 ¹⁴C a BP for the Upper Mousterian layer (Bailey *et al.*, 1983).

Materials and methods

Our research compares material from a recent reanalysis of the faunal remains from Asprochaliko rockshelter (ER) in north-west Greece with the zooarchaeological collection from Klissoura Cave 1 (BMS) and an ongoing analysis of Lakonis 1 (BMS) in southern Greece. We analysed the three sites using the same methods and coding system (after Stiner, 2005).

The MP faunal component from Asprochaliko currently includes 1076 identified specimens, sampled from the collection housed at the Archaeological Museum of Ioannina. Excavators recovered the specimens from rectangles 2, 3 and 4 of the western trench and 41, 42, 51 and 52 of the eastern excavation. The selection of the units was based on the stratigraphic and contextual integrity of the samples, following the excavators' field notes. We examined the materials by stratigraphic unit, based on the scheme proposed by Bailey and colleagues (1983) and followed their division of the units into three phases. The lower Basal Mousterian (BM) incorporates layers 18 and 19 from the western trench and their corresponding layers 12, 15 and 17 from the eastern trench. This is followed by the upper Basal Mousterian, which refers to Layer 16 in the western trench and 11 in the eastern trench. The youngest MP layer is the Upper Mousterian (UM), which includes material from Layer 14 in the western trench and 9 in the eastern trench. Specimens that did not correspond to the aforementioned layer segregation or had been attributed to transitional contexts were excluded from this study.

The analysis of the remains from Lakonis 1 is still in progress, so the results we present here are preliminary but representative

for the purposes of the analyses we are conducting. We have identified 2362 specimens from the cave's four cultural units, though due to a small sample size (number of identified specimens, or NISP=22) we exclude Unit III from our discussion. Since the goal of this work is to investigate subsistence practices more broadly, we combine contexts representing different activity areas that we have previously considered separately (Starkovich *et al.*, 2018a). Finally, we use published data from Klissoura Cave 1 (Starkovich, 2017), which we analysed in near-entirety. Here, we include approximately 9000 identified specimens from the site's MP horizons.

Taphonomic overview

A wealth of taphonomic observations exist for the three accumulations. We present only a brief overview of the conditions, for the sake of brevity and thematic relevance (Table 2); however, detailed taphonomic observations for the three sites do exist (Roditi, 2019; Starkovich, 2011, 2017; Starkovich *et al.*, 2018a). The remains were examined under 13–20× magnification using a hand-held magnifier and taphonomic markers were established following criteria from Behrensmeier (1978), Fisher (1995), Haynes (1983) and Stiner (2005). The surface preservation of the Asprochaliko and Klissoura materials seems relatively good, with a low degree of weathering overall. All three assemblages demonstrate high rates of fragmentation. Low abundance of carnivore remains and low percentages of carnivore surface modifications indicate that none of the three sites were used as carnivore dens (Tables 2 and 3). Meanwhile, we observed high frequencies of anthropogenic damage, in the form of cut marks, percussion marks and green fractures at Klissoura and Asprochaliko. These types of damage are significantly lower at Lakonis, though this is mostly because of extreme fragmentation due to the brecciated deposits of the site and excavation methods (Starkovich *et al.*, 2018a). However, high frequencies of burning attest to the anthropogenic origin of the material.

Following Stiner (2005), we conducted a simple test of density-mediated attrition on the Asprochaliko and Lakonis

Table 2. Summary of taphonomic data by layer for taxonomically identifiable and non-identifiable remains from Asprochaliko rockshelter and Lakonis 1 cave.

Taphonomic marker	Asprochaliko rockshelter						Lakonis 1 cave							
	UM		BM (upper)		BM (lower)		Unit I		Unit II		Unit III		Unit IV	
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Human-induced damage														
Cut marks	50	18.32	151	27.86	93	62.00	88	0.89	17	1.30	0	0.00	19	1.82
Percussion marks	2	0.73	9	1.66	3	2.00	NA	NA	NA	NA	NA	NA	NA	NA
Burning	9	3.30	38	7.01	31	20.67	6494	65.77	901	68.88	87	49.71	176	16.87
Carnivore-induced damage														
Tooth marks	1	0.37	3	0.55	2	1.33	9	0.09	3	0.23	0	-	12	1.15
Digestion	0	0.00	0	-	0	-	0	-	0	-	0	-	0	-
Rodent	1	0.37	0	0.00	1	0.67	0	-	0	-	0	-	0	-
Post-depositional damage														
Weathering	11	4.03	17	3.14	9	6.00	39	0.39	1	0.08	2	1.14	69	6.62
Root etching	3	1.10	27	4.98	4	2.67	2	0.02	0	-	0	-	0	-
Trampling	0	0.00	1	0.18	1	0.67	0	-	0	-	0	-	0	-
Chemical deterioration	2	0.73	5	0.92	4	2.67	11	0.11	1	0.08	0	-	5	0.48
Oxidation	1	0.37	15	2.77	7	4.67	720	7.29	12	0.92	0	-	0	-
Breakage														
Green fracture	83	30.40	218	40.22	81	54.00	405	4.10	69	5.28	1	0.57	149	14.29
Percussion notch	11	4.03	35	6.46	12	8.00	13	0.13	4	0.31	0	-	3	0.29
No fracture	170	62.27	289	53.32	56	37.33	9456	95.77	1235	94.42	174	99.43	891	85.43
Total NISP	273	100.00	542	100.00	150	100.00	9874	100.00	1308	100.00	175	100.00	1043	100.00

BM: Basal Mousterian; NISP: number of identified specimens; UM: Upper Mousterian.

Table 3. Taxonomic frequencies by layer for Asprochaliko rockshelter and Lakonis 1 cave, expressed in NISP and MNI.

Taxon	Asprochaliko rockshelter						Lakonis 1 cave							
	UM		BM (upper)		BM (lower)		Unit I		Unit II		Unit III		Unit IV	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Ungulate														
Extra-large ungulate	1	NA	9	NA	0	NA	44	NA	5	NA	2	NA	15	NA
Rhinoceros (<i>Dicerorh. kirchbergensis</i>)	0	0	5	1	0	0	0	0	0	0	0	0	0	0
Aurochs (<i>Bos primigenius</i>)	3	1	8	1	2	1	2	1	1	1	0	0	6	1
Large ungulate	20	NA	41	NA	11	NA	96	NA	8	NA	1	NA	29	NA
<i>Equus</i> sp.	0	0	0	0	1	1	5	1	4	1	0	0	0	0
Red deer (<i>Cervus elaphus</i>)	27	2	47	2	10	1	1	1	0	0	0	0	3	1
Wild boar (<i>Sus scrofa</i>)	16	1	4	1	2	1	9	1	4	1	0	0	10	1
Medium ungulate	75	NA	206	NA	70	NA	962	NA	195	NA	14	NA	442	NA
Fallow deer (<i>Dama dama</i>)	48	3	74	2	8	1	144	4	31	2	4	1	96	2
Ibex (<i>Capra ibex</i>)	7	1	3	1	10	1	0	0	1	1	0	0	0	0
indet. Caprine	11	NA	16	NA	0	NA	0	NA	0	NA	0	NA	0	NA
Small ungulate	9	NA	40	NA	13	NA	2	NA	0	NA	0	NA	2	NA
Roe deer (<i>Capreolus capreolus</i>)	12	3	13	1	1	1	0	0	0	0	0	0	0	0
Chamois (<i>Rupicapra rupicapra</i>)	4	1	1	1	0	0	0	0	0	0	0	0	0	0
Carnivore														
Large carnivore	0	NA	2	NA	0	NA	2	NA	0	NA	0	NA	0	0
Brown bear (<i>Ursus arctos</i>)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyena (<i>Hyaen sp.</i>)	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Leopard (<i>Panthera pardus</i>)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Wolf (<i>Canis lupus</i>)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Small carnivore	0	NA	1	NA	0	NA	0	NA	0	NA	0	NA	1	NA
Eurasian lynx (<i>Lynx lynx</i>)	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Red fox (<i>Vulpes vulpes</i>)	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Stone/Pine marten (<i>Martes foina</i>)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Wild cat (<i>Felis silvestris</i>)	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Small mammals														
European hedgehog (<i>Erinaceus europaeus</i>)	1	1	0	0	0	0	0	0	0	0	0	0	0	0
European hare (<i>Lepus europaeus</i>)	0	0	4	1	0	0	0	0	0	0	0	0	1	1
Rodent	5	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA
Bird														
Large bird	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA
Medium bird	0	NA	3	NA	0	NA	2	NA	0	NA	0	NA	3	NA
Small bird	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA
Reptile														
Tortoise (<i>Testudo graeca</i>)	4	1	14	1	0	0	46	1	101	1	1	1	0	0
Amphibian														
Frog (<i>Rana sp.</i>)	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Fish														
indet. Fish	0	NA	0	NA	0	NA	1	NA	0	NA	0	NA	0	NA
Total	244	15	492	13	129	8	1317	10	350	7	22	2	609	7

BM: Basal Mousterian; MNI: minimum number of individuals; NA: not applicable; NISP: number of identified specimens; UM: Upper Mousterian.

faunas to determine whether bone loss occurred at the site. We present cranial bone and tooth-based minimum number of element (MNE) values for skulls and teeth by layer, based on the premise that these elements should have entered the site together. We expect teeth, with their higher mineral content, to be preserved better than bone in cases where density-mediated factors impacted the faunal material. Previous work indicates that the fauna from Klissoura were not subjected to density-mediated biases, with the exception of Layer VIII (Starkovich, 2011). At Asprochaliko, the sample size is small, but the test demonstrates that teeth and cranial bones were equally well preserved in the Upper Mousterian, whereas the two Basal Mousterian layers have higher bone than tooth MNE counts. These results suggest that the assemblage has not undergone density-mediated destruction. Similarly, there is no evidence for *in situ* attrition in Units II and IV at Lakonis, where the ratio of tooth to cranial bone MNE is nearly even. Density-mediated attritional processes may have influenced the composition of the assemblage from Lakonis Unit I, as bony skull elements are underrepresented. However, it is possible that increased

fragmentation has rendered these portions unidentifiable (Table 4, Fig. 2).

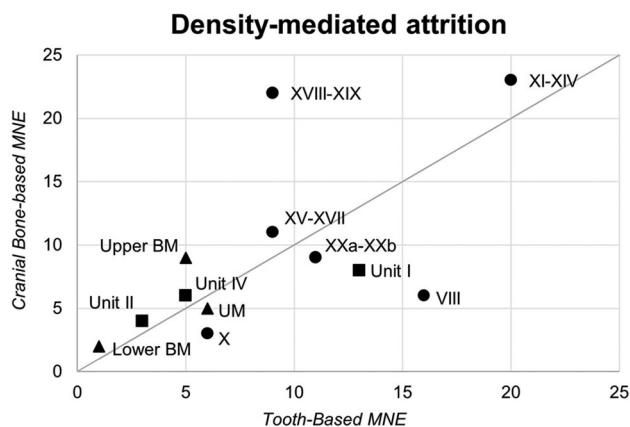
Identification and quantification

For the identification of the remains, we used the osteological comparative collection of the Malcolm H. Wiener Laboratory at the American School of Classical Studies at Athens, further aided by electronic manuals compiled by Mary C. Stiner and A. Blanco-Lapaz. For the analyses, we followed standard zooarchaeological methods and techniques (Grayson, 1984; Lyman, 1994, 2008; Reitz and Wing, 2008; Stiner, 1994, 2005). Our dataset includes all faunal remains that could be identified to skeletal element, considering landmarks on both long bone diaphysis and epiphyses. We identified specimens to the highest taxonomic level possible and, in cases where precise identification was not feasible, we assigned the remains to body size classes. We further collected taphonomic observations, including type of bone fracture and surface modifications.

Table 4. Tooth-based MNE to bone-based MNE for all ungulates by site and layer.

Layer	Tooth-based MNE	Cranial bone-based MNE	Tooth:bone MNE
Asprochaliko			
Upper Mousterian	6	5	1.20
Upper Basal Mousterian	5	9	0.56
Lower Basal Mousterian	1	2	0.50
Klissoura			
Layer VIII	16	6	2.67
Layer X	6	3	2.00
Layer XI–XIV	20	23	0.87
Layer XV–XVII	9	11	0.82
Layer XVIII, XIX	9	22	0.41
Layer XXa–XXb	11	9	1.22
Lakonis			
Unit I	13	8	1.63
Unit II	3	4	0.75
Unit IV	5	6	0.83

Note: Small sample size are in bold. MNE: minimum number of elements.

**Figure 2.** Comparison of the highest tooth-based minimum number of elements (MNE) to the highest bone-based MNE for crania and mandibles of all ungulates for Asprochaliko, Klissoura and Lakonis (data from Table 4).

We use NISP as the basic unit of quantification for measures of taxonomic abundance and diversity. To assess the frequency of skeletal elements, we further calculate the MNE. This unit is derived from NISP and provides a minimum estimate of the frequency of each body part within the assemblage by considering overlapping landmarks to represent different, individual specimens of an anatomical element (Lyman, 2008).

Prey abundance and diversity

To investigate dietary diversification, we examine changes in the proportion of small game versus large prey. Considering the reliance of Palaeolithic foragers on ungulate species through most of the Pleistocene, archaeologists have considered the inclusion of small, especially fast, game in hominin diets as a response to declining encounters with their preferred high-yield food sources (Stiner, 2004; Stiner and Munro, 2002; Stiner *et al.*, 2000). We use body-mass estimates as a criterion to sort large game into four size classes. We combine small game taxa (i.e., hares, game birds and tortoises) and further classify them into fast-moving and slow-moving groups, based on their evasion tactics. Finally, we use these features to rank the groups from highest to lowest, taking into consideration their nutritional return rates and costs of capture for hominin foragers (Table 5).

We examine local prey diversity by measuring taxonomic evenness for each site. High taxonomic diversity is characterised by the even distribution of specimens across all taxa and is often correlated with environmental heterogeneity (Starkovich *et al.*, 2018b). On the other hand, an uneven assemblage indicates low taxonomic diversity and the dominance of one taxon over the others. We measure taxonomic evenness using the reciprocal of Simpson's index. The index uses the formula $D = \sum p_i^2$, where p is the abundance of taxon i , and is expressed as $1/D$. The maximum value obtained corresponds to the total number of species in the assemblage, meaning that higher $1/D$ values indicate higher taxonomic diversity. To calculate $1/D$, we include specimens from the entire array of economic taxa, identified to the lowest taxonomic level possible, in this case species (Faith and Du, 2018; Lyman, 2008; Stiner, 2005).

Table 5. Taxa included in each prey category and their respective weight range and ranking. Weight ranges from (Silva *et al.*, 1995) and (Nowak, 1999).

Taxon	Weight range (kg)	Category	Ranking
Ungulates			
Aurochs (<i>Bos primigenius</i>)	500–1000	Very large ungulate	High
Wild boar (<i>Sus scrofa</i>)	50–350	Large ungulate	High
Red deer (<i>Cervus elaphus</i>)	75–340	Large ungulate	High
European wild ass (<i>Equus hydruntinus</i>)	200–260	Large ungulate	High
Fallow deer (<i>Dama dama</i>)	40–100	Medium ungulate	High
Alpine ibex (<i>Capra ibex</i>)	35–150	Medium ungulate	High
Chamois (<i>Rupicapra rupicapra</i>)	24–50	Small ungulate	High
Roe deer (<i>Capreolus capreolus</i>)	15–50	Small ungulate	High
Reptiles			
Mediterranean spur-thighed tortoise (<i>Testudo graeca</i>)	1–2 (+)	Small, slow moving	Medium
Small mammals			
European hare (<i>Lepus europaeus</i>)	1.3–7.0	Small, fast moving	Low
Birds			
Rock partridge (<i>Alectoris graeca</i>)	0.51–0.68	Small, fast moving	Low
Great bustard (<i>Otis tarda</i>)	10–16		

Carcass-processing intensity

The high-yielding marrow reserves of ungulate long bones are almost universally broken open at our study sites (e.g., Starkovich, 2017). Compared to these frequently exploited elements, ungulate phalanges have small marrow cavities. Therefore, they are considered as low-ranked resources, processed for the extraction of bone marrow only under conditions of high-ranked resource scarcity (Nagaoka, 2005). The marrow yields also differ between the three phalanges, with the terminal phalanx containing the smallest amount of bone marrow. We compared the occurrence of green split fractures between the three elements and used the proportion of unbroken ungulate phalanges as a proxy for increasing carcass-processing intensity. Hence, in this analysis, low percentages of complete feet elements, especially terminal phalanges, are perceived as potential indicators of resource stress.

Prey mortality

A pronounced selectivity towards prime adults characterises the hunting niche of Late Pleistocene hominins (Stiner *et al.*, 2009). The application of optimal foraging models has led researchers to hypothesise that this pattern likely stems from the predicted efforts of the foragers to maximise their caloric return rates by preferentially targeting prey with the highest caloric value, in this case adult individuals. This leads to the hypothesis that the elevated occurrence of juvenile ungulates in anthropogenic assemblages is associated primarily with the effects of increased hunting pressure in living populations, as well as with subsistence intensification, since the protein and fat deposits in young animals are significantly lower than in adults (Munro, 2009; Steele, 2003; Stiner, 1994, 2005).

We recorded tooth eruption and wear stages for ungulate species, following the standards from Hillson (2005), Severinghaus (1949), Payne (1973), Lowe (1967), Grant (1982) and Magnell (2006) for aurochs, fallow deer, ibex and chamois, red deer, and wild boar, respectively. Following Stiner (1990), we used the mandibular deciduous fourth premolar (dp4) and the fourth premolar (P4) to construct the age sequences for Klissoura and Lakonis, while for Asprochaliko we substituted the permanent fourth premolar with the mandibular third molar (M3) due to sample size restrictions. The lower M3 erupts at roughly the same time as the permanent P4 and thus its use should not constitute an obstacle in this analysis.

We followed the three-age division scheme described by Stiner (1990, 1994) and assigned each specimen to one of the three following categories – juveniles, prime adults and old adults. The boundary between juvenile and prime adult is considered the age at which the fourth deciduous premolar is shed, while the transition from prime adult to old adult is marked by advanced wear (i.e., more than half of the dental crown) on the permanent fourth premolar. We plotted profiles for all ungulate species and for fallow deer, the most common ungulate species at the three sites, in tripolar graphs. To minimise the effects of sample size bias, we used the programme from Weaver *et al.* (2011) that implements the likelihood-based approach with a 95% confidence interval. To aid the interpretation and ensure the comparability of our results, we superimposed the data onto both Stiner's zones (1990, 1994) and the more recently developed, taxon-specific zoning system by Discamps and Costamagno (2015), modified for fallow deer. We set the average potential ecological longevity at 12.5 years, as the lifespan of fallow deer in the wild ranges between 10 and 15 years (Geist *et al.*, 2004). At 16–18 months, male fallow deer reach physiological maturity and females reach sexual maturity (Chaplin and White, 1972).

At 20 months most individuals have the full set of adult dentition (Bowen *et al.*, 2016). We define the juvenile/prime adult boundary at the average of 1 year and 7 months (19 months). In male individuals, senescence begins at the age of 9 years, leading to an abrupt increase in natural mortality (McElligott *et al.*, 2002). Additionally, a slight decline in the proportion of breeding females is observed in individuals aged between 9 and 10 years (San José *et al.*, 1999). This timeframe is in good correspondence with the estimated age of advanced dentition wear in Bowen *et al.* (2016). Hence, we set the prime/old boundary at 9 years.

Results

Prey abundance and diversity

The aggregation of taxa into prey categories indicates that all assemblages are dominated by large game. Medium ungulates are the predominant prey group throughout Klissoura's MP sequence, constituting over 80% of the assemblage in each layer (Fig. 3). This pattern can also be observed in Lakonis' Units I, II and IV (Fig. 4). The contribution of large ungulates appears limited in the faunal composition of the two sites, while small ungulates are almost absent in both assemblages. At Asprochaliko, medium ungulates comprise more than half of the faunal collection (Fig. 5). However, in comparison to the two Peloponnesian faunal samples, large taxa, and, to a lesser extent, small ungulates occur in higher frequencies. Finally, the percentage of extra-large ungulates remains small at all three sites. We observe a slight increase in the proportion of small game, specifically slow-moving taxa, in Lakonis Unit II and in Klissoura Layers XV–XVII, although the latter is of much smaller magnitude. The remains of small, fast-moving prey are scarce throughout our sample, although we note the presence of this group in comparatively higher proportions in Klissoura Layer XI–XIV.

We present results from the reciprocal of Simpson's index in Table 6. All species considered, taxonomic evenness is much higher at Asprochaliko, with 1/D values ranging between 3.74 and 4.22. At Klissoura, the highest value was obtained from Layers XV–XVII (1/D = 2.43), while the results of the analysis from the rest of the layers produced 1/D values between 1.20 and 1.66. We calculated similar results for the three MP Lakonis Units (1/D = 1.24–1.69, Table 6).

A closer look at selected prey categories provides further insights into species diversity. The evenness values for ungulates in the older Basal Mousterian phase and the Upper Mousterian layer of Asprochaliko (Table 6) demonstrate the even representation of four ungulate species in the assemblages, namely red deer, fallow deer, ibex and wild boar (Table 3). The more recent Basal Mousterian layer indicates the even representation of three species, red deer, fallow deer and roe deer. In the Lakonis and Klissoura sequences, ungulate evenness values are extremely low, reflecting the predominance of only fallow deer.

Carcass processing intensity

In the entire MP assemblage of Klissoura, the percentage of complete first phalanges is low, while second ungulate phalanges seem to be processed to some degree, especially in the younger MP layers (Table 7). On the other hand, the proportion of unopened terminal phalanges is fairly high overall. Nonetheless, we observe a statistically significant (Starkovich, 2017) increase through time in the processing of the latter, peaking in Layers XI–XIV (33%). Unfortunately, the sample sizes from Lakonis and Asprochaliko are relatively small, thus the results should be treated with caution.

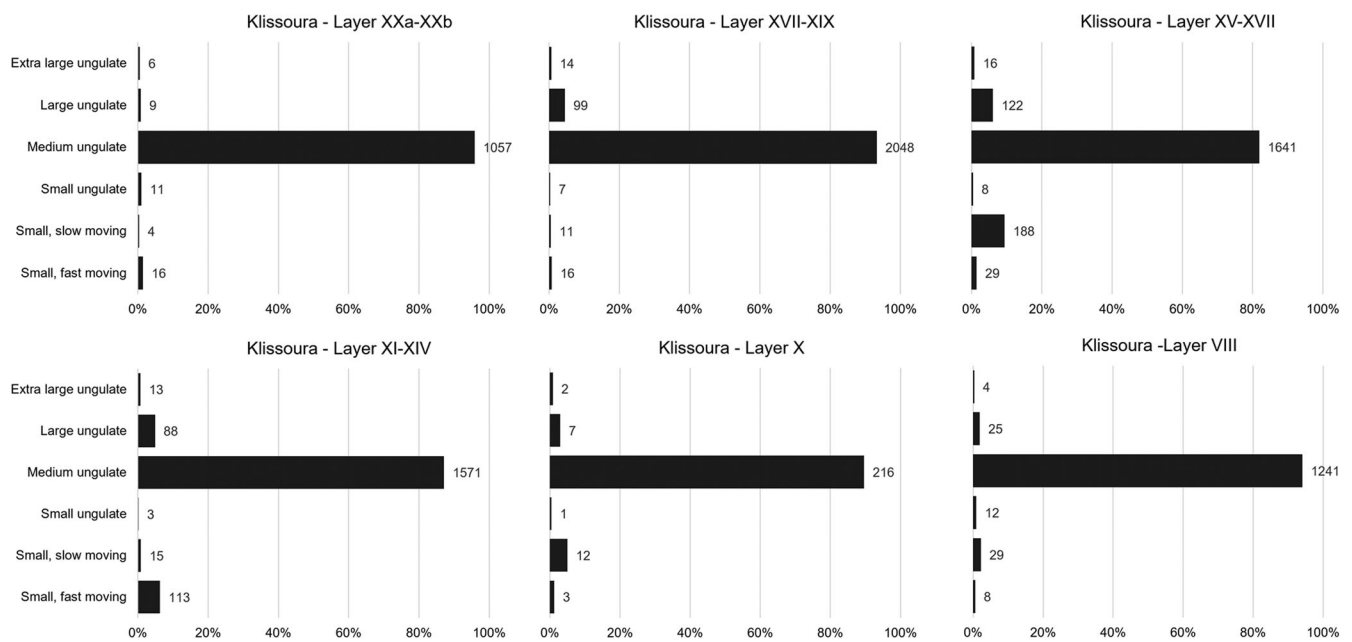


Figure 3. Relative abundance of major prey categories at Klissoura by layer. Values expressed in NISP %.

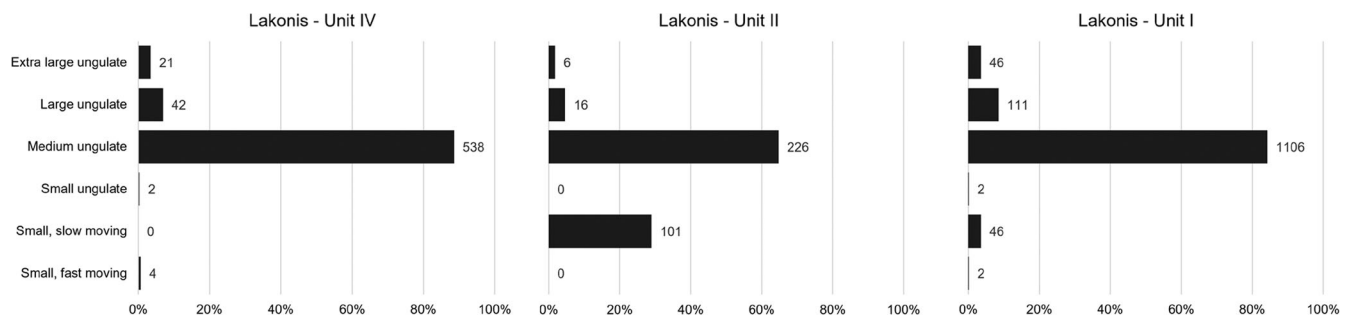


Figure 4. Relative abundance of major prey categories at Lakonis by unit. Values expressed in NISP %.

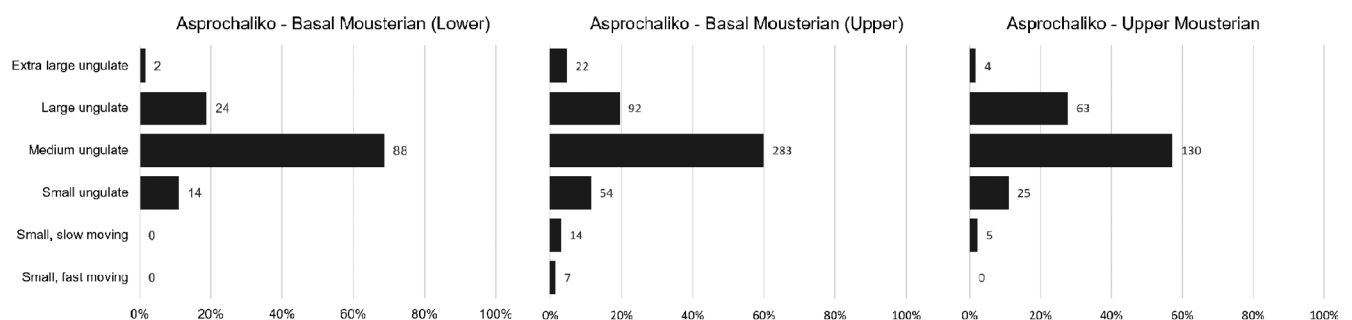


Figure 5. Relative abundance of major prey categories at Asprochaliko by unit. Values expressed in NISP %.

However, trends in phalanx processing like those of Klissoura are apparent in the assemblage from Lakonis. First and second phalanges appear to be opened systematically in all three units. Terminal phalanges remained largely unprocessed in the older layer (Unit IV), whereas in the younger layer (Unit I) all third phalanges were fractured. Finally, in the Asprochaliko sequence, first and second phalanges were occasionally opened, in contrast to the third phalanges, which are mostly found complete (Table 7).

Prey mortality

The age distribution of ungulates based on tooth wear and eruption stages is shown in Table 8. Due to the small sample

size, we combined specimens from different layers into younger and older MP units for each site. When we consider all species, prime adults constitute the largest proportion of the assemblages at all three sites (71–100%). A low percentage of juvenile animals (14–18%) is present in both younger and older Klissoura 1 units, and the Upper Mousterian of Asprochaliko. We recorded the occurrence of old individuals in the youngest MP of Asprochaliko and Lakonis, and the younger unit of Klissoura (9–25%). Mortality profiles for all ungulates combined are depicted in Fig. 6. Following Stiner's zoning system, all mean values plot within the prime-dominated region. Considering that the confidence interval contours largely overlap with the living structure portion of the graph, the mortality profiles could be interpreted as evidence

Table 6. Taxonomic evenness values by layer for Asprochaliko, Klissoura and Lakonis.

Layer	Total NISP	All 1/D	All N-taxa	Ungulate NISP	Ungulate N-taxa	Ungulate 1/D
Asprochaliko						
Upper Mousterian	122	4.22	9	117	7	3.90
Upper Basal Mousterian	175	3.74	11	156	9	3.06
Lower Basal Mousterian	34	4.22	7	34	7	4.22
Lakonis						
Unit I	207	1.87	5	161	5	1.24
Unit II	142	1.80	5	41	5	1.69
Unit IV	117	1.46	6	115	4	1.41
Klissoura						
Layer VIII	658	1.31	10	622	7	1.17
Layer X	133	1.66	7	118	5	1.32
Layer XI–XIV	997	1.54	13	870	7	1.20
Layer XV–XVII	892	2.43	13	655	7	1.47
Layer XVIII, XIX	887	1.51	13	862	8	1.43
Layer XXa–XXb	474	1.20	11	457	7	1.11

Note: Small sample size are in bold. NISP: number of identified specimens.

Table 7. Percentage of complete phalanges by site and layer.

Layer	1st Phalanx		2nd Phalanx		3rd Phalanx	
	MNE	% complete	MNE	% complete	MNE	% complete
Asprochaliko rockshelter						
Upper Mousterian	3	33.0	1	100.0	2	100.0
Basal Mousterian (Upper)	3	0.0	3	33.0	3	67.0
Basal Mousterian (Lower)	1	100.0	3	0.0	2	100.0
Klissoura Cave						
Layer VIII	21	4.8	7	0.0	9	55.6
Layer X	3	0.0	4	0.0	1	0.0
Layer XI–XIV	28	0.0	12	8.3	9	33.3
Layer XV–XVII	34	2.9	13	0.0	12	58.3
Layer XVIII–XIX	45	0.0	15	13.3	25	64.0
Layer XXa–XXb	15	13.3	18	22.2	13	69.2
Lakonis Cave						
Unit I	8	0.0	6	17.0	6	0.0
Unit II	2	0.0	2	0.0	1	0.0
Unit IV	4	0.0	3	0.0	4	75.0

MNE: minimum number of elements.

for either a hunting strategy dominated by prime adults or a non-selective one. The likelihood interval for ungulate mortality in Lakonis Units I–II also overlaps with the old-dominant area, slightly complicating the interpretation of the results for this site. In Fig. 7, the mean values of fallow deer mortality for the six units suggest a prime-biased pattern. However, the sample size for Asprochaliko and Lakonis is too small for a statistically meaningful interpretation.

Discussion

The consistent predominance of large game in the assemblages we discuss in this paper demonstrates that no major shift in prey choice occurred during the MP at the three sites. However, we observe slight changes in the dietary spectrum, reflected by the inclusion of moderate amounts of small, slow-moving prey, in Lakonis Unit II, in addition to Layers XV–XVII at Klissoura. In contrast, we see no such changes at Asprochaliko, where the procurement of tortoise remained restricted in all layers. Analysts have further reported the exploitation of tortoises from another MP site in the

Peloponnese. At Kalamakia Cave in the Mani Peninsula, the fauna recovered from Units III and IV, dated between 100 ka and 40 ka BP, includes high proportions of tortoise, along with substantial numbers of medium ungulates, mainly fallow deer and ibex. Based on the relative taxonomic abundance presented by the authors, the fauna from Kalamakia differs from the assemblages discussed in this study, as tortoise appears to be the most abundant taxon in the assemblage (Darlas and Psathi, 2016). Despite their small size, tortoises are a highly nutritious prey with generous fat and protein reserves that require minimum effort to capture and transport. Hence, it comes as no surprise that they regularly supplemented hominin diets during the Pleistocene (Blasco *et al.*, 2016). Different mechanisms could have been responsible for the abundance of tortoise at Kalamakia and in specific layers at Lakonis and Klissoura; for example, seasonally mediated changes in encounter rates or the ability to use them for storage (Nabais and Zilhão, 2019).

Prey selection was most likely driven by the intentional targeting of high- and medium-ranked resources found in the vicinity of the sites. The differences in taxonomic evenness between Asprochaliko and the two sites in the southwest

Table 8. Ungulate age-at-death distribution by taxon and unit.

Site and layer	Taxon	Juvenile	Prime adult	Old adult	Total
Klissoura 1 (VIII–XIV)	<i>D. dama</i>	2	17	2	21
	<i>C. ibex</i>	1	0	0	1
	% All taxa	14%	77%	9%	100%
Klissoura 1 (XV–XXa-b)	<i>D. dama</i>	2	9	0	11
	% All taxa	18%	82%	0%	100%
Asprochaliko UM	<i>D. dama</i>	0	2	1	3
	<i>C. elaphus</i>	0	1	0	1
	<i>C. capreolus</i>	0	2	0	2
	<i>S. scrofa</i>	1	0	0	1
	% All taxa	14%	71%	14%	100%
Asprochaliko BM	<i>D. dama</i>	0	2	0	2
	<i>C. elaphus</i>	0	1	0	1
	<i>C. capreolus</i>	0	2	0	2
	% All taxa	0%	100%	0%	100%
Lakonis 1 Unit I–II	<i>D. dama</i>	0	5	2	7
	<i>S. scrofa</i>	0	1	0	1
	% All taxa	0%	75%	25%	100%
Lakonis 1 Unit IV	<i>D. dama</i>	0	2	0	2
	<i>B. primigenius</i>	0	1	0	1
	% All taxa	0%	100%	0%	100%

probably reflect climatic and environmental variation. A closer look at the species composition demonstrates a stronger representation of forest-dwelling taxa in addition to those living in rocky areas at Asprochaliko, indicating a mix of different ecotones in the surroundings. Along with fallow deer, ibex, red deer and roe deer were important prey species for the Asprochaliko occupants, whereas fallow deer was by far the most abundant resource at Klissoura and Lakonis. A small assemblage recovered from recent test excavations at Mavri Spilia in the Mani Peninsula provided a few taxonomic identifications that, along with the remains from Kalamakia, further testify to the prevalence of small to medium-sized ungulates and the commonness of fallow deer and caprines in the region (Tourloukis *et al.*, 2016). The low ungulate evenness at Lakonis and Klissoura, as well as the species composition, suggests ecological homogeneity and higher aridity in the Peloponnese, with open vegetation dominating the landscape. In Epirus, the faunal spectrum reflects a landscape with open valleys alternating with forested patches, which provided habitats for a wider range of large and small herbivores. Moreover, ungulate mortality in MP Greece was largely consistent with the patterns observed around the Mediterranean basin (Stiner, 1994, 2005, 2009). Whether a non-selective strategy was followed, or hominins focused on the procurement of prime-aged individuals, the composite profiles presented in this study do not indicate hunting pressure on ungulate populations.

Regarding carcass exploitation, taphonomic data from ungulate phalanges suggest a diachronic increase in phalanx-processing intensity in the Peloponnese. Of great interest is the fact that the decline in complete phalanges

began in the same layer (XV–XVII) in which a small increase in tortoise exploitation is observed at Klissoura. Furthermore, the lowest percentage of complete third phalanges in Layers XI–XIV coincides with a slight increase in small, fast-moving prey. Based on wood charcoal analysis, Ntinou (2020) reports that the abundance of thermophilic olive (*Olea* sp.) woodland, which dominated the earlier levels at Klissoura, drops in Layer XVII and is completely absent from Layers XVI–XIV. Progressively cooler and drier conditions favoured the expansion of open *Amygdalus* woodland instead. Terminal phalanges are seemingly processed more intensively in the two upper units of Lakonis as well, whereas at Asprochaliko, hominins rarely fractured phalanges. One could argue that some of these observations are a consequence of sample size restrictions. While such a scenario cannot be rejected, it is noteworthy that the numbers between Asprochaliko, Lakonis and even Layer X from Klissoura do not differ much, yet the intersite comparison demonstrates disparate processing practices between the sites. Nevertheless, considering the brecciated nature of the deposit and the excavation techniques employed at Lakonis, the degree to which taphonomic observations from this site actually reflect hominin carcass-processing should be evaluated further. Despite some subtle shifts in MP subsistence practices, especially in the Peloponnese, the phenomenon is no match for the situation in the early Upper Palaeolithic (EUP) and Aurignacian of the region. The Uluzzian phase from Klissoura Cave incorporated 30% of small prey, of which 43% was fast-moving. In the subsequent stratigraphically lower Aurignacian (Layer IV), the percentage of small game drops again to 13% and ranges between 10% and 24% for the rest of the Aurignacian. From this phase on, small prey includes almost exclusively fast-moving taxa (Starkovich, 2012; Starkovich *et al.*, 2018b; Starkovich and Ntinou, 2017). Other sites in the Peloponnese that yielded EUP and Aurignacian deposits present similar trends. More than half of the Aurignacian assemblage (Layer R) from Franchthi Cave comprised small game, of which 84% was fast prey (Starkovich *et al.*, 2018b; Stiner *et al.*, 2012). The preliminary estimations of taxonomic abundance in the Uluzzian and Aurignacian layers from Kephalaria Cave indicated 71% and 56% of small game, respectively, with both layers lacking slow-moving prey (Starkovich *et al.*, 2018b; Starkovich and Ntinou, 2017). Mortality profiles and information on carcass processing for the Aurignacian exist only for the faunal collection of Klissoura Cave. During the lower Aurignacian, the processing of ungulate phalanges is intense, while the percentage of complete terminal phalanges reached its lowest value (21%). In the same layer, juvenile ungulate mortality increases, with the trend persisting for the rest of the phase (Starkovich, 2011, 2017). Analysts have interpreted these trends with population pulses of modern humans in the region at the onset of the Upper Palaeolithic, as well as with the severity of the climatic fluctuations during MIS 3 and towards the last glacial maximum (Starkovich *et al.*, 2018b; Starkovich and Ntinou, 2017). Consequently, the possibility that the minor subsistence changes in the younger MP of the Peloponnese reflect the beginning of these conditions, amplified by the area's inherent aridity, is highly probable. However, the intensity of the phenomenon was evidently smaller than during the EUP, possibly due to lower population densities before the expansion of *Homo sapiens*.

Conclusions

From a faunal perspective, we see neither resource depletion as a result of extreme climatic oscillations, nor resource

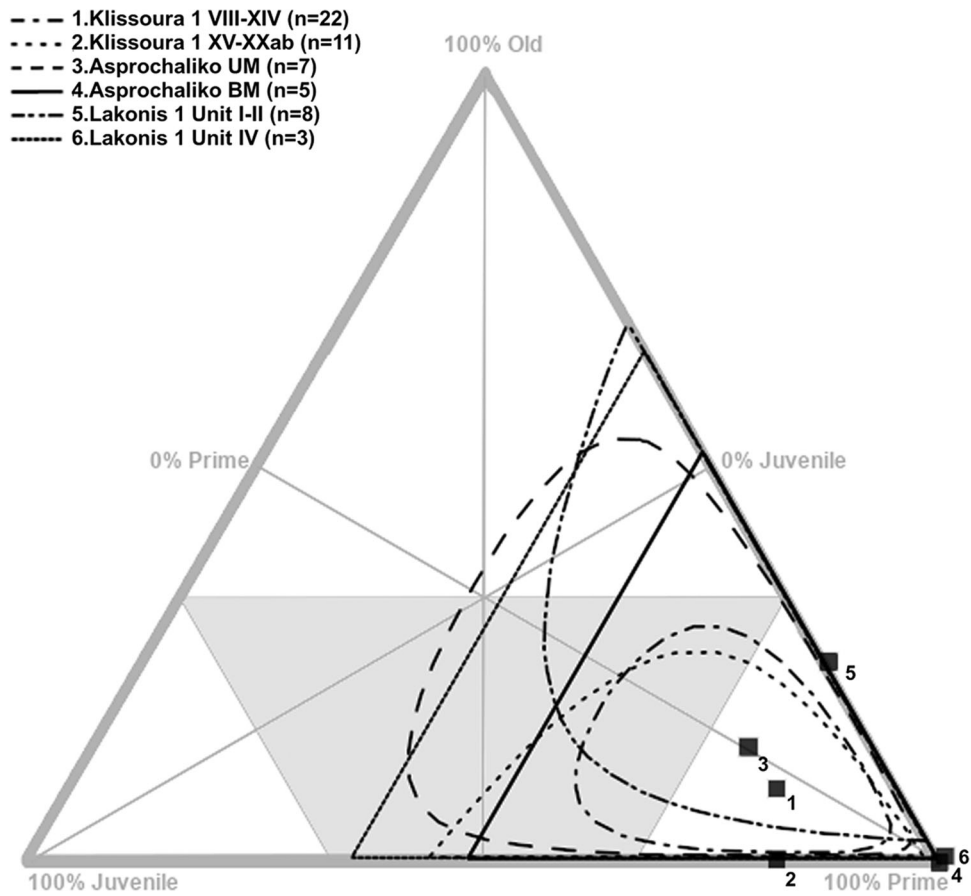


Figure 6. Composite ungulate mortality profiles with 95% confidence interval contour. Definition of zoning system following Stiner (1990, 1994).

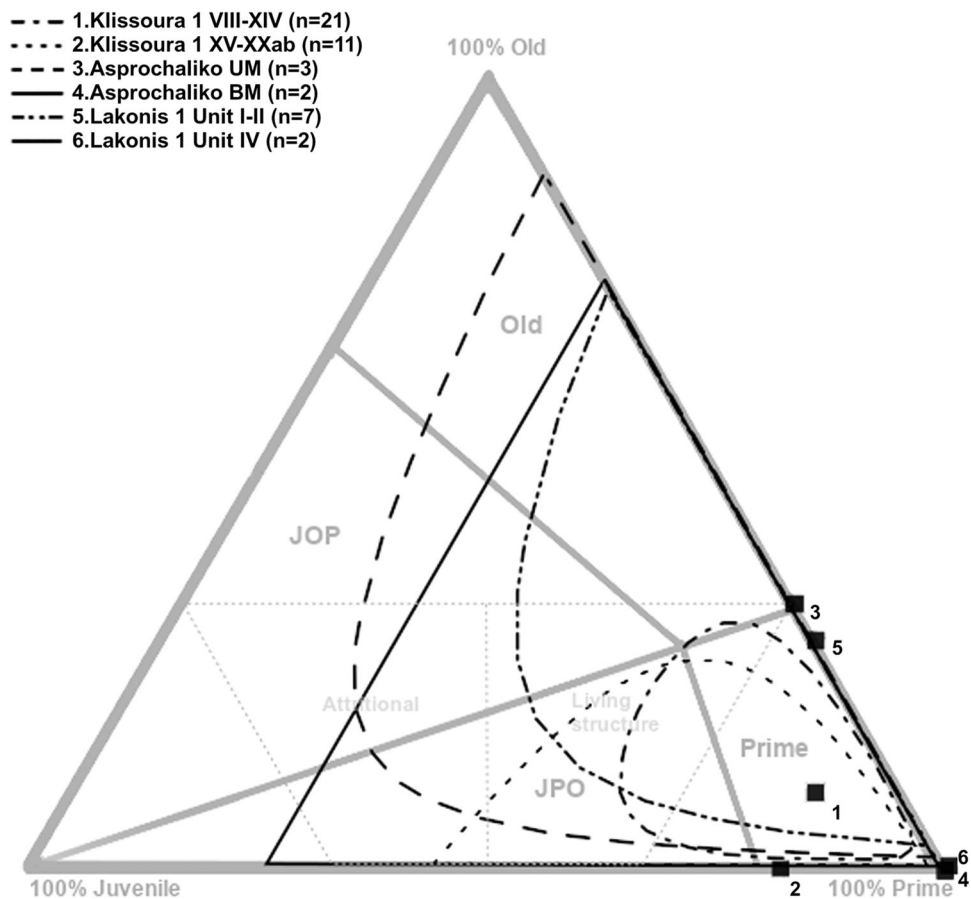


Figure 7. Fallow deer mortality profiles with 95% confidence interval. Definition of zoning system (Discamps and Costamagno, 2015) with modified lifespan for fallow deer.

intensification as a consequence of demographic crowding in MP Greece. Therefore, a scenario in which the areas under study experienced only mild environmental ramifications and served as passive refugia for small populations seems more plausible. Nevertheless, we should note that this a hypothesis based on the limited archaeological record of the region. The fauna alone does not represent the entire spectrum of available food sources. The role of plant resources, which certainly supplemented the diet of MP hominins, remains largely unexplored, due to biases in the preservation and recovery of organic remains. In addition to this, a major limitation is the lack of dating control that characterises the Greek record, evident from the large dating ranges presented for at least two of the sites discussed (Tourloukis and Harvati, 2018). Together with the palimpsest nature of the deposits, which introduces time-averaging effects, and the loose associations of occupational phases with climatic data, it is difficult to establish possible gaps in site use during glacial phases or infer short-scale events of subsistence change. The potential of the region's role as a refugium is undoubted but the investigation of its precise nature should not be drawn to a close just yet. Future directions should focus on establishing a better chronological framework, combined with comprehensive environmental studies of the conditions that prevailed during different occupational phases at individual sites. Additionally, intersite comparisons of faunal remains should be ideally accompanied by more data sources, such as changes in lithic technology and variation in material input rates. Despite this, the growing record of MP sites will hopefully allow us in the coming years to better understand the role of Greece in the survival and maintenance of hominin populations under scenarios with significant climate change.

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