Ahead of the Game: Middle and Upper Palaeolithic Hunting Behaviors in the Southern Caucasus

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by Daniel S. Adler, Guy Bar-Oz, Anna Belfer-Cohen, and Ofer Bar-Yosef

Over the past several decades a variety of models have been proposed to explain perceived behavioral and cognitive differences between Neanderthals and modern humans. A key element in many of these models and one often used as a proxy for behavioral "modernity" is the frequency and nature of hunting among Palaeolithic populations. Here new archaeological data from Ortvale Klde, a late Middle–early Upper Palaeolithic rockshelter in the Georgian Republic, are considered, and zooarchaeological methods are applied to the study of faunal acquisition patterns to test whether they changed significantly from the Middle to the Upper Palaeolithic. The analyses demonstrate that Neanderthals and modern humans practiced largely identical hunting tactics and that the two populations were equally and independently capable of acquiring and exploiting critical biogeographical information pertaining to resource availability and animal behavior. Like lithic techno-typological traditions, hunting behaviors are poor proxies for major behavioral differences between Neanderthals and modern humans, a conclusion that has important implications for debates surrounding the Middle–Upper Palaeolithic transition and what features constitute "modern" behavior. The proposition is advanced that developments in the social realm of Upper Palaeolithic societies allowed the replacement of Neanderthals in the Caucasus with little temporal or spatial overlap and that this process was widespread beyond traditional topographic and biogeographical barriers to Neanderthal mobility.

It is now acknowledged in palaeoanthropology that many of our traditional models of Neanderthal behavior and the Middle–Upper Palaeolithic "transition" are no longer valid. This perceptual shift has occurred as researchers have begun to study Middle Palaeolithic hominins in their own right, without direct reference to "modern" populations and their cultural, linguistic, and ideological achievements. After roughly two decades of such research we now recognize that Middle Palaeolithic hominins, specifically Neanderthals, were cognitively complex and capable of a wide range of sophisticated behaviors (e.g., Bar-Yosef and Kuhn 1999; Kolen 1999; Marean and Assefa 1999; Vaquero et al. 2001; d'Errico 2003; d'Errico et al. 2003; Hovers et al. 2003; Wynn and Coolidge 2004; Speth n.d.) that force us to reconsider our definition

of behavioral "modernity" and how or whether we can detect signs of it in the archaeological record (Klein 1999, 2000; McBrearty and Brooks 2000; Wadley 2001; Henshilwood and Marean 2003). In many respects this fundamental shift has as much to do with our ability to develop and test ever more sophisticated hypotheses regarding prehistoric lifeways as it does with the increased and integrated use of urbane analytical techniques in the context of interdisciplinary, field-based archaeological research. Another important new avenue of Palaeolithic research focuses on developing a social rather than a simply materialistic, economic, or techno-typological understanding of prehistory (e.g., Gamble 1999; Gamble and Porr 2005). As such research progresses it is becoming abundantly clear that, although Neanderthals and modern humans differed in salient ways, the vast behavioral and cognitive gulf that was once thought to exist between them has now narrowed considerably.

The long history of Palaeolithic research in Eurasia has allowed the development of a relatively detailed understanding of Middle and Upper Palaeolithic foraging strategies, social behavior, and landscape use. We know that Middle Palaeolithic lifeways varied considerably across time and space because of differing environments and changing environ-

Daniel S. Adler is an assistant professor in the Department of Anthropology at the University of Connecticut (U-2176, 354 Mansfield Rd., Storrs, CT 06269, U.S.A. [daniel.adler@uconn.edu]). **Guy Bar-Oz** is a senior lecturer in the Zinman Institute of Archaeology, University of Haifa. **Anna Belfer-Cohen** is a professor in the Institute of Archaeology of Hebrew University, Jerusalem. **Ofer Bar-Yosef** is a professor in the Department of Anthropology at Harvard University. This paper was submitted 12 XI 04 and accepted 11 II 05.

mental conditions (Pettitt 1999; Gamble 1999; Bar-Yosef 2004); thus as a whole Neanderthals must be considered well adapted and adaptable to numerous and diverse ecosystems. This realization is in opposition to notions that Neanderthals perished because they could not adapt quickly to change, be it climatic or cultural, or that modern humans were ultimately more successful because they possessed some clear technological advantage(s) (e.g., Finlayson and Giles Pacheco 2000; Mellars 1996, 1998; Finlayson et al. 2004). Another hypothesis posits that, unlike Neanderthals, modern humans were able to exploit resources more effectively, for example, through specialized hunting, increased diet breadth, and/or sophisticated food-processing behaviors that fostered better nutrition and higher population densities (e.g., Mellars 1996, 1998; see Marean and Assefa 1999 for discussion). During periods of competition between Middle and Upper Palaeolithic groups, these novel abilities are believed to have bestowed a critical advantage upon modern humans, allowing them to replace Neanderthals whenever and wherever they were encountered.

Unfortunately, categories of zooarchaeological data are often used to develop different interpretations of hunting economies depending on the hominin involved. For example, the hunting of many different taxa has been taken to reflect the *opportunistic* nature of Neanderthal hunting strategies, while the same data from modern human contexts are interpreted as indicating *increased diet breadth.* Likewise, the focus on a single mammal species by Neanderthals is taken to reflect an inability to exploit diverse resources (i.e., low diet breadth), while among modern humans this same practice is referred to as *specialization* (see d'Errico 2003). Clearly, zooarchaeological data derived from Neanderthal and modern human contexts must be measured and evaluated carefully, without a priori assumptions about their meaning with respect to behavior and cognition (i.e., modern versus archaic).

In this paper we test the hypothesis that there was a difference in hunting behaviors between Neanderthals and modern humans, a claim that has often been used to help explain the Middle–Upper Palaeolithic transition. Since the falsification of any given human behavioral hypothesis must be considered heavily dependent upon local, situational factors and thus not necessarily reflective of all populations in all places at all times, rather than attempt to build a broad-based, geographic model of Neanderthal and modern human behavioral variability we confine our observations and interpretations to the data currently available from the southern Caucasus. We hope that in so doing we may avoid many of the behavioral overgeneralizations that have plagued similar studies and in the process raise new questions that challenge traditional orthodoxies and stimulate research in novel directions in other regions.

Before we present our analyses it is important to discuss the hominin fossil record of the southern Caucasus. To date all the fossils recovered from Middle Palaeolithic contexts in the Georgian Republic have been attributed to Neanderthals (Liubin 1977, 1989; Gabunia, Nioradze, and Vekua 1978; D.

M. Tushabramishvili 1978; Vekua 1991; N. Tushabramishvili et al. 1999; Schwartz and Tattersall 2002). Compared with that in other regions (for example, the northern Caucasus), the frequency of hominin remains in the region is low and limited primarily to isolated teeth (e.g., Ortvale Klde, Djruchula Cave, Bronze Cave) (Adler and Tushabramishvili 2004). The most complete specimen, a fragmentary maxilla, was discovered at Sakhazia Cave in association with a Zagros-type Mousterian (Gabunia, Nioradze, and Vekua 1978; Nioradze 1992; Schwartz and Tattersall 2002, 327–29). Consequently, throughout this paper we use the term "Neanderthal" to refer to the hunter-gatherers occupying this region during the Middle Palaeolithic. To date no hominin fossils have been discovered in Upper Palaeolithic contexts in the Georgian Republic, and therefore we know nothing of the physical characteristics of local populations at this time. However, given the unprecedented and, we argue, intrusive nature of regional early Upper Palaeolithic stone and bone industries, their clear and rapid evolution through time, and the larger mobility and social network sizes that these assemblages suggest, we make the assumption throughout this paper that the Upper Palaeolithic in the southern Caucasus is the handiwork of modern humans. This unsatisfactory situation is akin to that recently recognized in Western Europe, where the direct radiocarbon dating of modern human fossils associated with Aurignacian deposits has shown these fossils to be much younger and therefore intrusive. In the case of Cro-Magnon the specimens have been dated to the Gravettian (27,769 years BP) (Henry-Gambier 2002), and at Vogelherd they have been dated to the Neolithic (5,000–3,000 years BP) (Conard, Grootes, and Smith 2004). Unless otherwise indicated, all dates presented here are uncalibrated. While the hypothesis that Neanderthals were responsible for some or all of the Upper Palaeolithic assemblages known from the southern Caucasus cannot be rejected on the grounds of the fossil data, the weight of the archaeological evidence to the contrary is, as we shall show, robust and persuasive.

The application of zooarchaeological and taphonomic methods of analysis to the study of Palaeolithic faunal acquisition and butchery patterns has contributed greatly to our overall understanding of hominin subsistence and mobility strategies throughout Eurasia and how these strategies may or may not have evolved from the Middle to the Upper Palaeolithic (e.g., Pike-Tay, Valdés, and de Quirós 1999; Speth and Tchernov 2001; Grayson and Delpech 2002, 2003; Burke 2004). Several recent studies have contributed to an ongoing debate regarding both the interpretation of zooarchaeological evidence and our understanding of Palaeolithic subsistence strategies (e.g., Farizy and David 1992; Marean and Kim 1998; Brugal 1999; Armand, Pubert, and Soressi 2001; Gaudzinski and Roebroeks 2000, 2003; Grayson et al. 2001; Stiner 2002; Adler, Prindiville, and Conard 2003; Munson and Marean 2003). With these debates in mind we conducted detailed taphonomic and zooarchaeological analyses of the late Middle Palaeolithic (LMP) and early Upper Palaeolithic (EUP) faunal

assemblages excavated recently at Ortvale Klde, a rockshelter located in the southern Caucasus in the Republic of Georgia. Our aim was to examine the regional hunting strategies of Neanderthals and modern humans in an effort to reconstruct how they extracted resources from the environment, how they acquired and dispensed landscape and resource knowledge, and whether these behaviors reflect larger cultural or cognitive differences between these two populations.

Ortvale Klde Rockshelter

Ortvale Klde ("Two Eyes Rock") rockshelter has been the focus of repeated excavation since the early 1970s and currently represents the primary source of information regarding the Middle and Upper Palaeolithic in the southern Caucasus. The site was first excavated by D. Tushabramishvili and later by N. Tushabramishvili as part of a long-term project of Palaeolithic research in the Imereti region (fig. 1). In 1997, under the direction of D. S. Adler and N. Tushabramishvili, excavations at Ortvale Klde were renewed, employing modern field and laboratory methods. Ortvale Klde was chosen for restudy because of its clear stratigraphy, its rich archaeological deposits, and its stratified Middle and Upper Palaeolithic horizons. The primary goals of the collaborative project were to collect new samples of carefully excavated lithic and faunal material with which to reconstruct mobility and land-use patterns, to retrieve appropriate samples for radiometric dating, and to use these data sets to investigate the regional shift from the Middle to the Upper Palaeolithic.

Ortvale Klde is located outside the town of Chiatura, approximately 35 m above the west bank of the Cherula River (ca. 530 m.a.s.l.), a tributary of the Kvirila River that flows into the Black Sea via the Rioni River. The site is a karstic rockshelter composed of Cretaceous limestone with two chambers opening to the east. The small southern chamber has received considerable attention, with over 40 m² excavated by D. Tushabramishvili and N. Tushabramishvili within the shelter and along the slope. All of the data presented here derive from the new excavations that were conducted in this portion of the rockshelter; the results of earlier excavations are summarized elsewhere (Tushabramishvili et al. 1999; Adler 2002; Adler and Tushabramishvili 2004).

Previous work in the southern chamber identified 11 lithostratigraphic layers of which 2 were assigned to the Upper Palaeolithic and 7 to the Middle Palaeolithic (table 1). The Middle and Upper Palaeolithic horizons were found to be rich in both lithic and faunal material, and a single lower left molar attributed to *Homo neanderthalensis* was discovered in Layer 9. N. Tushabramishvili described the Middle Palaeolithic assemblages as Typical Mousterian, non-Levallois, enriched with Charentian elements, while the assemblage from Layer 4 was classified as "transitional" from the Middle to the Upper Palaeolithic (Tushabramishvili 1994; Tushabramishvili et al. 1999). Unfortunately, the Upper Palaeolithic assemblage from these earlier excavations has never been described or published in detail, and most of the material has been lost.

Of the 19,372 faunal specimens recovered from 1973 to 1992, A. Vekua of the Georgian State Museum identified 12.4% of the specimens to 11 species, with Caucasian tur (*Capra caucasica*) dominating the assemblage (85%) (Tushabramishvili et al. 1999). The extinct steppe bison (*Bison priscus*, 6%) and red deer (*Cervus elaphus,* 3%) appear in all layers, while other ungulates such as the extinct aurochs (*Bos primigenius*), wild boar (*Sus scrofa*), and roe deer (*Capreolus capreolus*), and carnivores such as the extinct cave bear (*Ursus spelaeus*), brown bear (*Ursus arctos*), wolf (*Canis lupus*), and fox (*Vulpes vulpes*), are represented in small proportions (< 1% in all layers). Vekua associates the majority of these species with forest-mountainous environments; the Caucasian tur is associated with high-altitude, sub-Alpine habitats, while the roe and red deer indicate forest biotopes and the bison was well adapted to both forests and open habitats.

The new excavations at Ortvale Klde, conducted from 1997 to 2001, focused on 6 m² of Early Upper Palaeolithic and 5 m² of Late Middle Palaeolithic deposits and led to the recovery of approximately 12,000 Upper Palaeolithic and 22,000 Middle Palaeolithic stone artifacts from Layers 2–4 and Layers 5–7, respectively (Adler 2002; Adler and Tushabramishvili 2004). At the same time 3,209 Upper Palaeolithic and 12,541 Middle Palaeolithic faunal specimens were recovered. All artifacts and bones, including small fragments and splinters, were excavated, recorded, and collected in situ, and all sediments were dry-sieved through 2-mm mesh.

Our research revealed several discrepancies within the original stratigraphic designations related to the association of specific lithostratigraphic layers with particular archaeological cultures. The corrections to the original stratigraphic scheme are outlined in table 1 and will be referred to throughout this paper (after Adler 2002, Adler and Tushabramishvili 2004). Contrary to previous reports, our reanalysis of Ortvale Klde found no evidence for an in situ cultural transition between the Middle and the Upper Palaeolithic. Instead we document a distinct archaeological, stratigraphic, and temporal break between Layer 5 (LMP) and Layer 4 (EUP), which highlights the culturally intrusive and technologically unprecedented nature of the latter and the abrupt disappearance of the former. The assemblage of Layer 4 contains unidirectional blade cores, end scrapers on blades, rounded flake scrapers, burins on truncation, numerous retouched bladelets (some 2–3 mm wide), and backed bladelets. Noteworthy are three bevel-based bone/antler points, two polished bone/antler abraders, and a single polished bone implement with a series of parallel linear incisions of unknown function or meaning. Similar lithic and bone materials were not encountered in the underlying LMP layers, which recent analyses have shown to be dominated by Levallois technology and a typical array of Middle Palaeolithic scraper types (Adler 2002).

The recently recovered material from Ortvale Klde and that from EUP contexts at the nearby site of Dzudzuana Cave
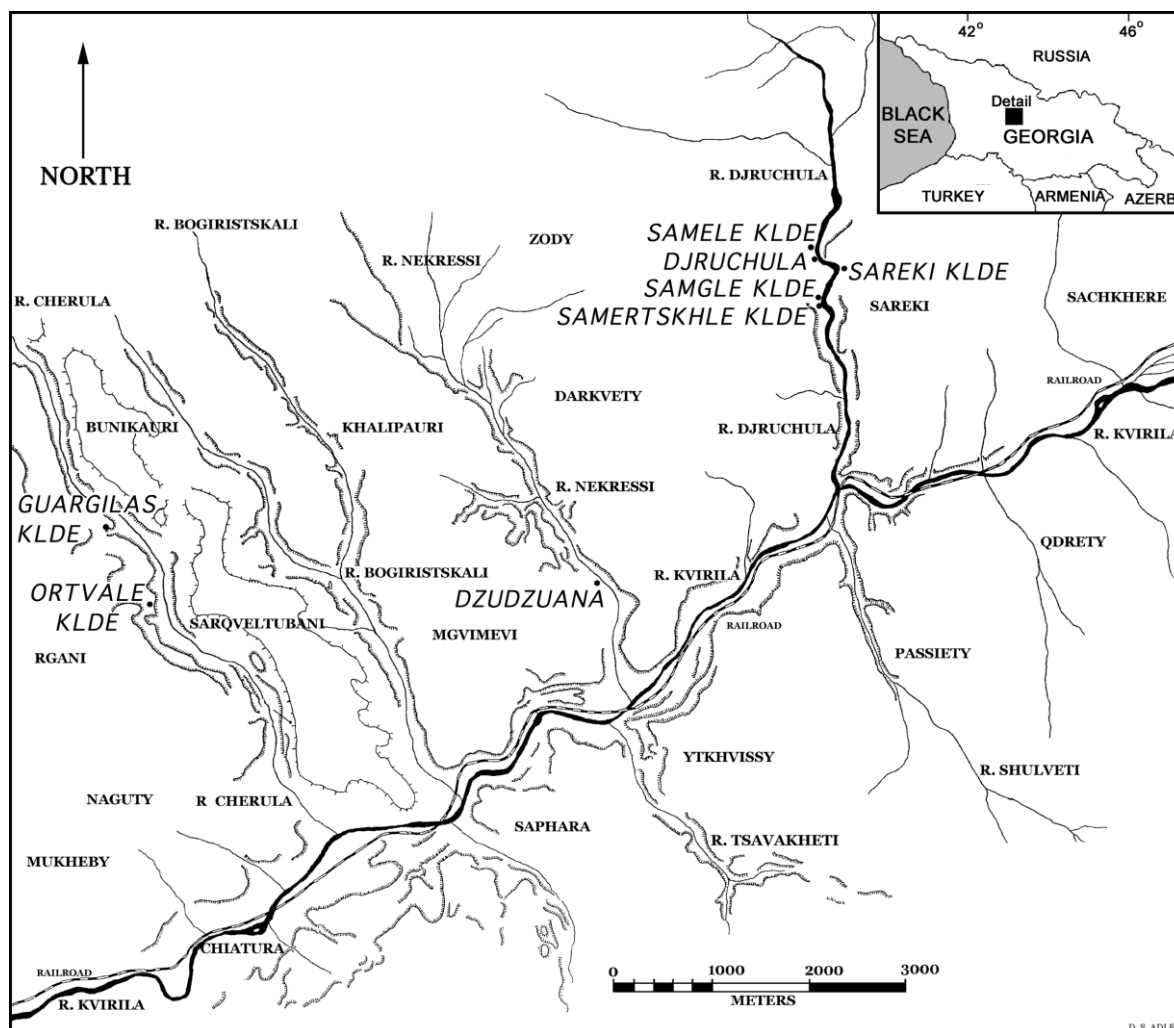
Figure 1.   The Imereti region in western Georgia. Archaeological sites spanning the early Middle Palaeolithic (Djruchula Cave), Middle Palaeolithic (Ortvale Klde and Samgle Klde), Upper Palaeolithic (Guargilas Klde, Ortvale Klde, Dzudzuana Cave, Sareki Klde, Samgle Klde, and Samertskhle Klde), and Neolithic (Samele Klde, Sareki Klde, and Dzudzuana Cave) are shown in italics (modified after Adler 2002).

(Meshveliani et al. 1999; Meshveliani, Bar-Yosef, and Belfer-Cohen 2004) represent the largest dated collections recovered during controlled excavations in the southern Caucasus. The closest similarly executed excavations are located approximately 400 km away on the northwestern slopes of the Caucasus (Hoffecker 2002; Golovanova and Doronichev 2003). Consequently, Ortvale Klde currently serves as the key LMP and EUP site in a vast region that stretches from the Caucasus to the Zagros and Taurus Mountains. While we recognize that no single archaeological site of any size or quality is sufficient to reconstruct complex prehistoric behavioral systems of settlement and subsistence within a territory of any significant size, we believe that Ortvale Klde serves as an excellent starting

point from which to test old hypotheses and generate new ones that can be tested directly through continued regional archaeological fieldwork and analysis.

Palaeoenvironment of the Southwestern Caucasus

The southern Caucasian environments within which Neanderthals and modern humans subsisted during oxygen-isotope stage 3 (fig. 2) can be characterized as mountainous, warm, humid, and well forested (Volodicheva 2002). As they do today, the numerous deep river valleys that drained the Caucasus in the Upper Pleistocene formed a patchwork of

Table 1. Comparison of the Original Stratigraphic and Archaeological Designations of Ortvale Klde with the New Scheme Based on Results from the 1997–2001 Excavations

1972–1992 Excavations		1997–2001 Excavations			
Layer	Archaeology	Layer	Archaeology	m² Excavated	m³ Excavated
I	Disturbed/mixed	1	Disturbed/mixed	Unrecorded	Unrecorded
II	1st Upper Palaeolithic	2	Upper Palaeolithic	6	1.38
III	2nd Upper Palaeolithic	3	Upper Palaeolithic	6	1.56
IV	1st Middle Palaeolithic	4a–d	Earliest Upper Palaeolithic	6	2.88
V	2nd Middle Palaeolithic	5	Latest Middle Palaeolithic	5	1.25
VI	3rd Middle Palaeolithic	6	Middle Palaeolithic	5	2.50
VII	4th Middle Palaeolithic	7	Middle Palaeolithic	5	2.50
VIII	Sterile	8	Sterile	Not excavated	Not excavated
IX	5th Middle Palaeolithic	9	Middle Palaeolithic	Not excavated	Not excavated
X	6th Middle Palaeolithic	10	Middle Palaeolithic	Not excavated	Not excavated
XI	7th Middle Palaeolithic	11	Sterile bedrock	Not excavated	Not excavated

Note: Layers 9–11 are not present in the southern portion of the site where the 1997–2001 excavations were conducted. Since none of the excavated layers maintain a uniform thickness across the site, cubic meters excavated can only be estimated.

ecological niches populated by a diverse flora and fauna. The discontinuous nature of environmental communities and the natural impediments to mobility presented by deep valleys, wide rivers, and high elevations likely influenced the settlement and subsistence behaviors of Neanderthals and modern humans, leading to limited exploitation of higher elevations during cold seasons. Since the landscape consisted of alternating forests and grasslands, animal biomass was probably considerably greater than in regions composed largely of dense, closed woodlands (Serebryanny 2002). High-quality lithic raw-materials were and are widely distributed throughout the study area, placing few limitations on occupation duration or lithic economy; any limitations placed on mobility or land use by raw-material availability were likely felt most acutely at higher elevations, where raw materials are more difficult to procure.

The onset of cooler and drier conditions during oxygen-isotope stage 3 led to the increase of coniferous species at the expense of broad-leaved elements, but large-mammal diversity and frequency do not appear to have been impacted greatly (Adler and Tushabramishvili 2004). These data suggest that the effects of environmental change on the floral, faunal, and hominin communities of the southern Caucasus during the Middle Pleniglacial, while palpable, were not dramatic. In this regard, the region appears to have served as a biogeographical refugium throughout the Middle Pleniglacial and even during the Late Pleniglacial (Tarasov et al. 2000). For example, the steppe-grass/steppe environments covering much of Europe during phases of this stage did not penetrate the region, and instead mosaic communities were maintained. During the Middle Pleniglacial, Neanderthals were able to exploit diverse ecosystems, and while the exact configuration of these was likely altered to some extent, changes appear to have been in scale rather than kind (Adler 2002; Tarasov et al. 2000). The climate-induced transgressions of the Black and Caspian seas during the Pleistocene influenced portions of

both the southern and the northern Caucasus, but the Chiatura region, in which Ortvale Klde is situated, was not directly impacted by these periodic events (Vereshchagin 1967; Dolukhanov 1982; Maruashvili 1991; Kozlowski 1998).

These favorable conditions were fostered by the ameliorating effects of the Black Sea, which continues to produce subtropical (warm and humid) conditions with ample rainfall (Tarasov et al. 2000; Volodicheva 2002), and the Caucasus Mountains, which buffer the region from cold winds originating in the north (Sankovski and Pridnia 1995, Volodicheva 2002). These features helped spare the southern Caucasus from the severe effects of the climatic oscillations of oxygen-isotope stage 3 and allowed Neanderthals and modern humans to prosper throughout much of the region for many millennia. The lack of significant and sustained local environmental alterations at the boundary between the Middle and the Upper Palaeolithic at Ortvale Klde (ca. 36,000–34,000 years BP) suggests that climate change played a minor role in this transition as it was played out locally (and perhaps elsewhere [see d'Errico and Sánchez Goñi 2003, 2004]).

The Chronology of Ortvale Klde

Prior to the implementation of an integrated dating program at Ortvale Klde, only a handful of radiometric, mostly conventional ¹⁴C readings were available for the entire Republic of Georgia (Tushabramishvili 1978; Liubin et al. 1985; Lioubine 2002). It has been impossible, therefore, to relate sites temporally or culturally without relying on coarse-grained lithic typologies and assuming climatic correlations (e.g., Doronichev 1993; Cohen and Stepanchuk 1999; Golovanova and Doronichev 2003; see Adler and Tushabramishvili 2004 for discussion). With the new dating of Ortvale Klde, a measure of clarity has been introduced to an otherwise murky picture of prehistoric development in the region. Three techniques, whose effective ranges overlap, were employed in the dating
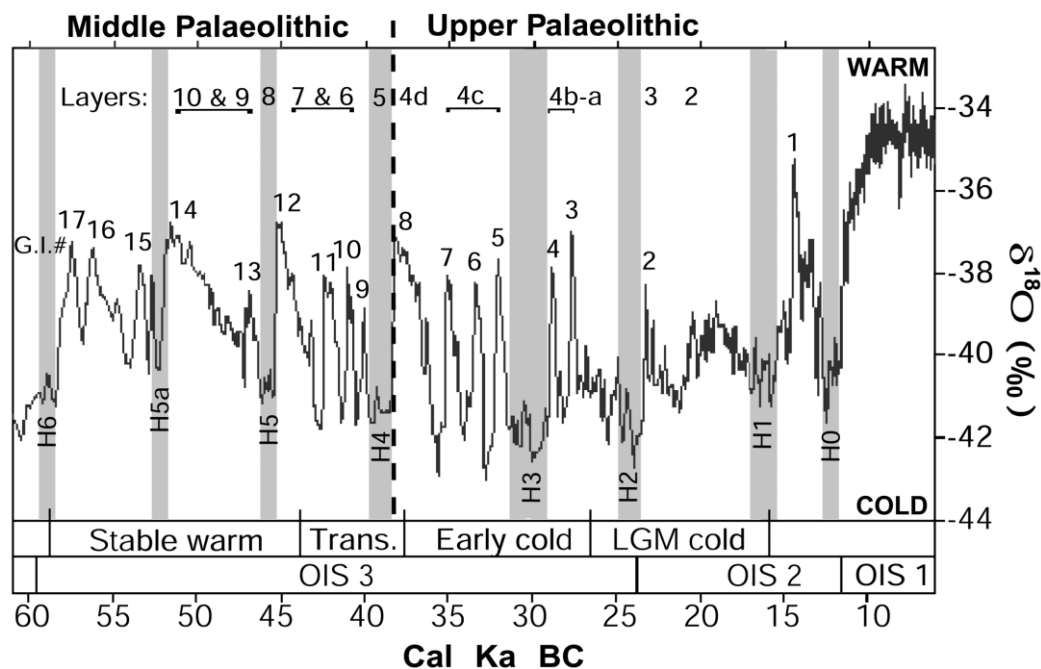
Figure 2.   The Middle and Upper Palaeolithic of Ortvale Klde (Layers 10–2) and proposed correlations with the Greenland Ice Sheet Project 2 (GISP2) ice-core chronology (after Meese et al. 1997; Johnsen et al. 2001; Stuiver and Grootes 2000), Greenland Interstadials (G.I. #17–1) (Dansgaard et al. 1993; Björck et al. 1998; Walker et al. 1999), and (vertical gray bars), Heinrich events (stadials H6–H0) (Heinrich 1988; Bond et al. 1993; Rashid, Hesse, and Piper 2003). Since the GISP2 δ¹⁸O record is linked to a calibrated BC time scale, correlations with Ortvale Klde are based on cal BC weighted means, not the BP dates referred to throughout the text.

program: accelerator mass spectrometry (AMS), thermoluminescence (TL), and electron spin resonance (ESR). The materials collected for dating include charcoal and bone collagen for AMS, burned flints for TL, and mammal teeth for ESR. To date 60 samples have been dated (table 2) by the Weizmann Institute of Science (Israel), the National Science Foundation Laboratory in Arizona (U.S.A), the Laboratoire des Sciences du Climat et de l'Environnement (France), and McMaster University (Canada).

On the basis of preliminary correlations of Ortvale Klde with the δ¹⁸O record of Greenland Ice Sheet Project 2 (GISP2) Greenland Interstadials and Heinrich events (stadials) and following the conventions laid out in van Andel and Davies (2003), we suggest a series of regional occupations during global stadial (cool) and interstadial (warm) periods of the Middle Pleniglacial and the Last Glacial Maximum (fig. 2). Layers 2 and 3, made up of low-density, ephemeral Upper Palaeolithic occupations dated to ca. 21,000–19,000 years BP, are correlated with oxygen-isotope stage 2, during which much of Eurasia experienced severe climatic conditions (Tarasov et al. 2000). On the basis of its age we correlate Layer

3 with Greenland Interstadial 2. Layers 4a and 4b, containing low-density Upper Palaeolithic occupations, are dated to ca. 27,000 years BP and associated with a global period of increasing cold prior to the Last Glacial Maximum. Given their age, we believe that Layers 4a and 4b can be correlated with Greenland Interstadials 3 and 4, respectively, and are separated from Layer 4c by Heinrich 3. Layer 4c, dated to between 34,000 and 30,000 years BP and consisting of dense EUP occupations with a high frequency of burning, can be correlated, on the basis of its age, with Greenland Interstadials 7–5. Layer 4d represents the first EUP occupation at Ortvale Klde and contains a stone-lined hearth dated to 35,000–34,000 years BP, a period correlated with Greenland Interstadial 8 (see also d'Errico and Sánchez Goñi 2003).

The terminal LMP occupations represented in Layer 5 are dated to ca. 36,000 years BP, a period of global climatic flux (Heinrich 4) between the transitional phase represented by Layers 6 and 7 and the early cold phase represented by Layer 4 (fig. 2). The archaeological and stratigraphic data suggest that Layer 5 occupations were ephemeral, but, as with other periods, climatic conditions in the southern Caucasus do not

Table 2. Weighted Means for Completed AMS, TL, and ESR Samples and Preliminary Correlations with Greenland Interstadials

Layer	Method	Sample	BP Weighted Mean $\pm 1\sigma$	(CAL) BC of BP Weighted Mean $\pm 1\sigma$[a]	Greenland Interstadial
2	AMS	2 bone	19,325 ± 89	20,554 ± 266	2
3	AMS	2 charcoal	21,664 ± 159	23,086 ± 586	2
4a	AMS	0	< L. 4b, > L. 3	< 4b, > 3	3
4b	AMS	1 charcoal	27,000 ± 260	28,377 ± 181	4
4c upper	AMS	8 charcoal	30,600 ± 160	32,830 ± 265	5–6
4c lower	AMS	6 charcoal	33,433 ± 249	36,275 ± 717	6–7
4d	AMS	3 bone	34,314 ± 447	37,694 ± 735	8
5	AMS	3 bone	36,482 ± 517	39,131 ± 183	–
5	TL	4 flint	44,111 ± 2,137	42,161 ± 2,137	–
6	AMS	6 charcoal	42,763 ± 806	42,136 ± 907	9–12
6	TL	3 flint	46,050 ± 2,215	44,100 ± 2,215	
7	AMS	2 bone	41,992 ± 846	41,614 ± 831	
7	TL	8 flint	42,490 ± 1,479	40,540 ± 1,479	9–12
7	ESR (EU)[b]	5 tooth	42,468 ± 2,532	40,518 ± 2,532	
7	ESR (LU)[b]	5 tooth	45,802 ± 2,757	43,852 ± 2,752	
9	TL	2 flint	48,862 ± 3,814	46,912 ± 3,814	13
10	TL	5 flint	49,910 ± 2,587	47,960 ± 2,587	14

[a]Calibrated (CAL) BC dates were calculated using the Cologne Radiocarbon Calibration and Palaeoclimatic Research Package, February 2004 edition (Weninger and Jöris 2001). Calibrated BC dates for TL and ESR samples were calculated by subtracting 1,950 years. "(CAL) BC of BP Weighted Mean $\pm 1\sigma$" for AMS samples are simply calibrated "BP Weighted Mean $\pm 1\sigma$."
[b]Early-uptake (EU) and linear-uptake (LU) ages were measured at 30% ± 10% moisture.

appear to have deteriorated to the extent seen in neighboring regions. It is currently difficult, therefore, to claim a strict causal link between climatic degradation and the local shift from the Middle to the Upper Palaeolithic. Layers 6 and 7, dated to 43,000–42,000 years BP (Greenland Interstadials 12–9), consist of high-density LMP occupations, with thick accumulations of anthropogenic sediments and a high frequency of burning. Layer 8, a sterile deposit of *éboulis* (limestone roof-fall), is undated, but we make the tentative association with Heinrich 5 on the basis of its position between Layers 7 and 9. Layers 9 and 10 are dated to ca. 50,000 years BP and represent the stable warm phase of oxygen-isotope stage 3 (Greenland Interstadials 14–13).

These preliminary correlations are noteworthy when compared with the data from well-dated sites in other parts of Europe. For example, at Geissenklösterle (Richter et al. 2000), Abric Romani (Bischoff et al. 1994), l'Arbreda (Bischoff et al. 1989), El Castillo (Rink et al. 1996), Willendorf II (Damblon, Haesaerts, and van der Plicht 1996), and Bacho Kiro (Kozlowski 1988), the earliest Upper Palaeolithic layers have been dated to ca. 40,000–38,000 years BP, roughly 6,000–4,000 years older than the EUP in western Georgia (Adler 2002; Adler and Tushabramishvili 2004; Meshveliani, Bar-Yosef, and Belfer-Cohen 2004). Chronological data from the northern Caucasus (Golovanova et al. 1999) and Crimea (McKinney 1998; Rink et al. 1998; Pettitt 1998), and perhaps Iberia (d'Errico and Sánchez Goñi 2003; see also Jöris, Fernández, and Weninger 2003) suggest that these regions were bypassed by the earliest expanding Upper Palaeolithic populations and colonized several thousand years later. The reasons for the

delayed expansion into the Caucasus can only be speculated upon but may include geological, environmental, and climatic features that served to discourage initial modern human population expansion from the south, low population densities among modern humans, or the presence of entrenched Neanderthal populations that were not easily dispersed. These forces may have fostered an initial modern human expansion into familiar environments, perhaps along coastal Anatolia and then through the Danube corridor (Conard and Bolus 2003), followed by (and perhaps in lieu of population increases) later expansion into more northern latitudes and marginal areas.

This simplified model of Upper Palaeolithic expansion seems appropriate for the southern Caucasus because the region is effectively circumscribed and isolated by the Black and Caspian seas to the west and east and the mountains of the Lesser Caucasus, Zagros, and Taurus to the south. Interior regions such as the Anatolian plateau and the Lesser Caucasus did not benefit from the ameliorating effects of the Black Sea, and therefore climatic and environmental conditions were not particularly favorable during the earliest phase of Upper Palaeolithic expansion (ca. 48,000–46,000 years BP). This would have encouraged movement along the coast, where better conditions prevailed. The Initial Upper Palaeolithic dates recently reported for the Levantine coast of Turkey (Kuhn, Stiner, and Güleç 1999) and the late dates reported for the earliest Upper Palaeolithic in the southern Caucasus (Adler 2002; Adler and Tushabramishvili 2004; Meshveliani, Bar-Yosef, and Belfer-Cohen 2004), the northern Caucasus, and Crimea appear to support this model and point to a later

phase of Upper Palaeolithic population expansion ca. 36,000–35,000 years BP, during which the remaining pockets of Neanderthals in Eurasia began to disappear. While the reasons for the ultimate extinction of the Neanderthals are not known in detail and it is highly probable that this process of extinction varied considerably across time and space, the careful dating of Ortvale Klde provides the first opportunity for us to consider this issue in the context of the southern Caucasus.

The Faunal Assemblage of Ortvale Klde

Zooarchaeological analyses allow the investigation of behaviors related to the capture and processing of animal resources and how prehistoric hominins structured their movements and activities with regard to the location and availability of various prey species. Zooarchaeological research had not been conducted in the southern Caucasus prior to this study. Previous faunal investigations were carried out for palaeontological reasons only, resulting in the tabulation of species presence/absence lists based on teeth and epiphyses obtained through selective sampling of excavated assemblages. For example, previous NISP (number of identified specimens) values derived from unsieved sediments at Ortvale Klde between 1972 and 1992 were calculated on selected anatomical elements, without reference to shaft fragments or less identifiable body parts such as head fragments, vertebrae, and ribs. Also, bone surface modifications, the state of bone preservation, and the age and sex composition of the assemblages were not considered. Here we provide a summary of specific categories of faunal data from Ortvale Klde relevant to the main hypothesis being tested in this paper: that the hunting behaviors of Neanderthals differed from those of modern humans. The relevant categories are species representation, survivorship and mortality, sex ratio, and life history of the main hunted species identified in the assemblage.

A full taphonomic consideration of the Ortvale Klde faunal assemblage, which includes data on skeletal part representation, bone fragmentation, and bone surface modification, is presented elsewhere (Bar-Oz and Adler n.d.) and summarized in table 3. The taphonomic data attest to the excellent state of bone preservation and indicate that most bone destruction occurred during site occupations as a result of intensive bone processing by hominins. The presence of cut marks from all stages of butchery (i.e., skinning, dismembering, and filleting) and the absence of selective transport of elements suggest that carcass processing occurred at or within the immediate vicinity of the site. Other postdepositional processes, such as carnivore activity and bone weathering, were found to be only minor sources of bone loss. It is important to emphasize that the reconstructed taphonomic histories of the LMP and EUP bone assemblages are not significantly different, thus allowing for their direct comparison.

Species Representation

Our analysis of species representation supports the main conclusions of Vekua (Tushabramishvili et al. 1999), with 95% of the combined 1997–2001 ungulate assemblage represented by Caucasian tur (table 4), indicating that LMP and EUP inhabitants of Ortvale Klde subsisted mainly on Caucasian tur and that diet breadth was low. Steppe bison constitutes a small proportion of the assemblage (4%), and other large ungulates (red and roe deer) are nearly absent (< 1% in each layer); carnivores (*Ursus* sp. and fox) are represented in even smaller proportions (≤ 0.5% of total assemblage).

This economic focus on Caucasian tur differs from the pattern we documented at the neighboring and contemporaneous EUP site of Dzudzuana Cave, where steppe bison represented 57% of the assemblage and Caucasian tur 40% (Bar-Oz et al. 2004). The abundance of Caucasian tur at Ortvale Klde is remarkable and, as far as can be determined from published data, cannot be matched at other Palaeolithic sites in the Caucasus (see, e.g., Hoffecker, Baryshnikov, and Potapova 1991; Baryshnikov and Hoffecker 1994; Baryshnikov, Hoffecker, and Burgess 1996; Hoffecker 2002). Barakaevskaïa Cave, located roughly 350 km northwest of Ortvale Klde in the northern Caucasus, contains a faunal assemblage with one of the highest frequencies of Caucasian tur (28.2% [Liubin 1998]). Outside the Caucasus, high frequencies of mountain goat in Middle Palaeolithic contexts have been observed in Uzbekistan at Teshik-Tash (*Capra sibirica*: > 80% NISP [Gromova 1949]) and Obi-Rakhmat (*Capra sibirica*: 47.4–66.7% [Wrinn n.d.]), at the Spanish sites of Gabasa 1 (*Capra pyrenaica*: 33.7–52.2% NISP per layer [Blasco Sancho 1995]) and Axlor (*Capra ibex*: 25.6% combined ungulate sample [Altuna 1989, 1992]), and at Hortus in southern France (*Capra ibex*: 75.4% NISP combined sample [de Lumley 1972]).

Survivorship and Mortality

The targeting of a specific age-class of ungulate by prehistoric foragers marks an important shift that can first be detected at roughly 250,000 years BP (Gaudzinski 1995; Stiner 1990, 2002). The level of group planning and cooperation required for such hunting is considerable though difficult to assess in any concrete way and has direct implications for questions regarding hominin mobility and land use, as well as planning depth and anticipatory ability.

The age structure of the Caucasian tur recovered from Ortvale Klde was analyzed on the basis of tooth wear. Of the 652 tooth fragments recovered from Layers 6 and 7, 38 lower third molars were complete enough to provide crown height measurements (upper third molars and lower/upper first and second molars, which are sometimes difficult to differentiate, were too rare for detailed measurement). The most durable and common deciduous tooth in the LMP assemblage is the lower fourth premolar (*n* = 19); the small samples from Layers 4 and 5 did not permit similar analyses. Although the

Table 3. Summary of Multivariate Zooarchaeological Analysis

	Layer 4	Layer 5	Layer 6	Layer 7
Assemblage data				
Total number of fragments (> 10 mm)	2,821	1,594	6,999	3,702
Number of taxa	5	2	5	5
NISP	360	206	1,472	1,137
MNI	8	5	18	16
Bones per m³	143	165	589	455
% Caucasian tur based on NISP	90.0	92.7	95.6	96.6
% Other ungulate taxa based on NISP	6.4	7.3	4.3	3.3
% Carnivores based on NISP	3.6	0	0.1	0.1
% Caucasian tur young (< 20% life span)	–	–	23.6	20.0
% Caucasian tur prime age (20–70% life span)	–	–	76.5	76.0
Mode of preservation[a]				
% Caucasian tur complete astragalus	–	–	87.5	85.3
% Caucasian tur complete central and fourth tarsal	–	–	80.0	83.3
% Caucasian tur tooth/cranial based on MNI	–	75.0	70.0	63.6
Caucasian tur total NISP/MNE	2.5	2.7	3.1	2.9
Specific attritional processes				
% Weathered stage 2 or higher (out of 6)	12.8	11.0	6.8	24.2
% Carnivore-gnawed	5.5	4.9	3.3	2.7
% Rodent-gnawed	2.2	1.7	3.2	2.6
Human subsistence behavior[b]				
Number of butchery marks	4	2	32	13
% Cut marks of total NISP	1.4	1.0	2.2	1.1
% Dismemberment butchery marks	40.0	50.0	54.5	84.6
% Percussion marks adjacent to fracture edges	0.7	0.6	0.4	0.8
% Fresh fracture angle	88.0	80.0	74.0	74.0
% Fresh fracture outline	86.0	74.0	64.0	70.0
% Fresh fracture edge	92.0	87.0	72.0	70.0

Note: Data specific to Caucasian tur are indicated. FUI, food utility index; MAU, minimal animal units; MNE, minimum number of elements; MNI, minimum number of individuals; NISP, number of identified specimens.
[a]For Layers 6 and 7, Caucasian tur bone survivorship (% MNI) versus density is $y = 1.03x + 0.03$ and $y = 1.05x + 0.02$; Spearman's r bone survivorship versus density is 0.61 ($p < 0.001$) and 0.57 ($p < 0.01$).
[b]For Layers 6 and 7, Caucasian tur bone survivorship (% MAU) versus FUI is $y = -0.004x + 0.51$ and $0.001x + 0.52$; Spearman's r bone survivorship versus food value is 0.12 ($p = 0.66$) and 0.24 ($p = 0.37$).

eruption schedules of *Capra aegagrus* and *C. ibex* do not provide reliable estimates for the loss of the lower fourth premolar, we assume that the permanent fourth premolar comes to wear upon eruption. Most observations indicate that the lower fourth premolar and the lower third molar of wild goat erupt at the age of 36 months (Evins 1982; Habermehl 1985, as cited in Kersten 1987). The life span of Caucasian tur (both *C. caucasica* and *C. cylindricornis*) is not known precisely, but Heptner, Nasimovich, and Bannikov (1989) report that most individuals do not live beyond 12 years, which we take to define the average potential life span for this species. The "life" of the lower third molar is estimated at 9 years (from eruption at 3 years to no crown height at 12 years), and the "life" of the lower fourth premolar is estimated at 3 years. Mortality profiles expressed as 10% increments of potential life span of Caucasian tur for the combined LMP assemblage from Ortvale Klde, determined according to dental wear height of the lower fourth premolar and lower third molar, show that 32% of the specimens ($n = 18$) were hunted as juveniles (< 20% life span), while 66% of the specimens ($n = 38$) were hunted as prime-age adults (20–70% life span).

Old adults were taken in very low frequencies ($n = 1$), suggesting an emphasis on the hunting of prime-age individuals (fig. 3). While the tooth sample from the combined LMP layers is not as large as we would like for such analysis, the mortality profiles that we obtained resemble LMP and EUP ungulate profiles obtained at numerous sites in Eurasia on samples of similar size (e.g., see Stiner 1994, Steele 2004).

Following Stiner (1994), Steele and Weaver (2002), and Steele (2004), the ratios of juvenile, adult, and old Caucasian tur specimens in Layers 6 and 7 (LMP) are represented in a triangular plot (fig. 4). These data, like those from Spain, Italy, and Israel, indicate that Caucasian tur culling falls within the "ambush predator" portion of the triangular diagram. These results have several broad implications. The hunting of prime-age individuals may indicate the use of a sophisticated weapons technology, group coordination and anticipatory behavior, and/or an intimate knowledge of prey behavior. In fact it is likely that such knowledge, combined with the ability to identify and utilize key natural features that afforded cover and took advantage of the varied terrain, were important factors enabling LMP hunters at Ortvale Klde to cull eco-

Table 4. Relative Frequencies of Caucasian Tur and Steppe Bison from Layer 4 (EUP) and Layers 5–7 (LMP) at Ortvale Klde

| | Taxon and Measure | | | | | |
| | *Capra caucasia* | | | *Bison priscus* | | |
Layer	NISP	MNI	% Total NISP	NISP	MNI	% Total NISP
4	324	3	90.0	21	1	6.2
5	191	4	92.7	15	1	7.3
6	1,408	14	95.6	57	1	3.9
7	1,098	12	96.6	30	1	2.6
Total	3,021	33	95.0	123	4	4.0

Note: Other ungulate species not presented here include red deer and roe deer. Totals including other taxa not listed in table: NISP = 3,234; MNI = 53. Complete counts are provided in Bar-Oz and Adler (n.d.).

nomically important prime-age adults. As with the species-specific hunting practices outlined above, the selective procurement of prime-age adults has been recently documented elsewhere for the LMP and EUP of Eurasia (e.g., Levine 1983; Jaubert et al. 1990; Stiner 1990, 1994, 2002; Hoffecker, Baryshnikov, and Potapova 1991; Baryshnikov and Hoffecker 1994; Speth and Tchernov 1998; Pike-Tay, Valdés, and de Quirós 1999; Hoffecker 1999; Hoffecker and Cleghorn 2000) and for earlier periods (Gaudzinski and Roebroeks 2000, 2003; Steele 2004). Together these regional data document a significant shift in the faunal acquisition and organizational skills of Middle Palaeolithic hominins away from opportunistic scavenging and toward the systematic hunting of ungulate species, a shift that Stiner (2002) correlates roughly with the second half of the Upper Pleistocene. The procurement of economically important individuals of a specific species can no longer be considered the private domain of modern humans; rather, it is a hunting technique practiced by both archaic and modern populations throughout Eurasia armed with markedly different technological repertoires. Similar results have been attained at Grotte XVI, where Grayson and Delpech (2003) were unable to identify any significant changes in ungulate utilization between the Middle and the Upper Palaeolithic.

Sex Ratio

The ability to differentiate between males and females in zooarchaeological assemblages can provide information on sex-based strategies of animal exploitation (Klein and Cruz-Uribe 1984). The Caucasian tur is sexually dimorphic, with adult males being larger and heavier than adult females (the live weight of adult males is 65–100 kg and of females 50–60 kg [Heptner, Nasimovich, and Bannikov 1989]). The difference in weight is reflected in the breadth and width of portions of some elements; astragali and humeri show a particularly high degree of sexual dimorphism. Complete astragali and,

to a lesser extent, distal humeri were among the most abundant measurable skeletal elements in the assemblage. Only adult specimens (i.e., fused epiphyses and nonporous astragali) were included in the analysis. Table 5 shows that all Caucasian tur recovered from the LMP and EUP of Ortvale Klde are larger than the mean values obtained for recent specimens of both sexes of *C. caucasica* and *C. cylindricornis* collected in the Caucasus at the beginning of the twentieth century (5 females and 11 males from the St. Petersburg Zoological Institute and the Humboldt Zoologische Museum, Berlin). A similar pattern of decreased body size has been observed among numerous Late Pleistocene Levantine mammals (Davis 1981; Kurtén 1965) and is in accordance with Bergmann's rule. However, since we lack specific information on the geographic origin of the recent Caucasian tur specimens, the observed size difference may be affected by spatial rather than temporal differences. Although the archaeological sample from Ortvale Klde is limited, the broad range of bone measurements shows that both large and small specimens are present (table 5). Thus, it appears that both sexes are represented in the assemblage.

Modern adult male and female Caucasian tur live separately, in independent groups, with mixed herds forming only during the period of estrus (end of November to early January) and for one or two months thereafter (Heptner, Nasimovich, and Bannikov 1989). Caucasian tur herds encountered in the Caucasian preserves of alpine meadows exhibit a sex ratio among adult animals close to 1:1; however, females predominate in the forest, located at lower elevations, constituting 60–84% of the population (Nasimovich 1949, Zharkov 1940, cited in Heptner, Nasimovich, and Bannikov 1989). With the limited bone sample available we suggest that Caucasian tur does and bucks were hunted in the same frequencies as they occur in recent herds at different elevations and in different environmental settings. In other words, the LMP hunters occupying Ortvale Klde did not cull herds according to sex-based preferences. As one might expect of prepastoral groups, they ate what was immediately available, in this case Caucasian tur, probably in sex frequencies equal to their natural distribution in particular environments during particular seasons (see Bar-Yosef 2004). While intriguing, the careful testing of this observation can be accomplished only through the analysis of larger data sets, a goal toward which we are actively working.

Life-History Characteristics of the Caucasian Tur

Given the clear economic importance of Caucasian tur, it is important to discuss the life history characteristics of this species and how its behaviors may have influenced Neanderthal and modern human mobility and land use. The data provided by Vereshchagin (1967), Brown and Burton (1974), Heptner, Nasimovich, and Bannikov (1989), Parker (1990), and Nowak (1997), derived from observations of recent or extant Caucasian tur populations in small, isolated nature
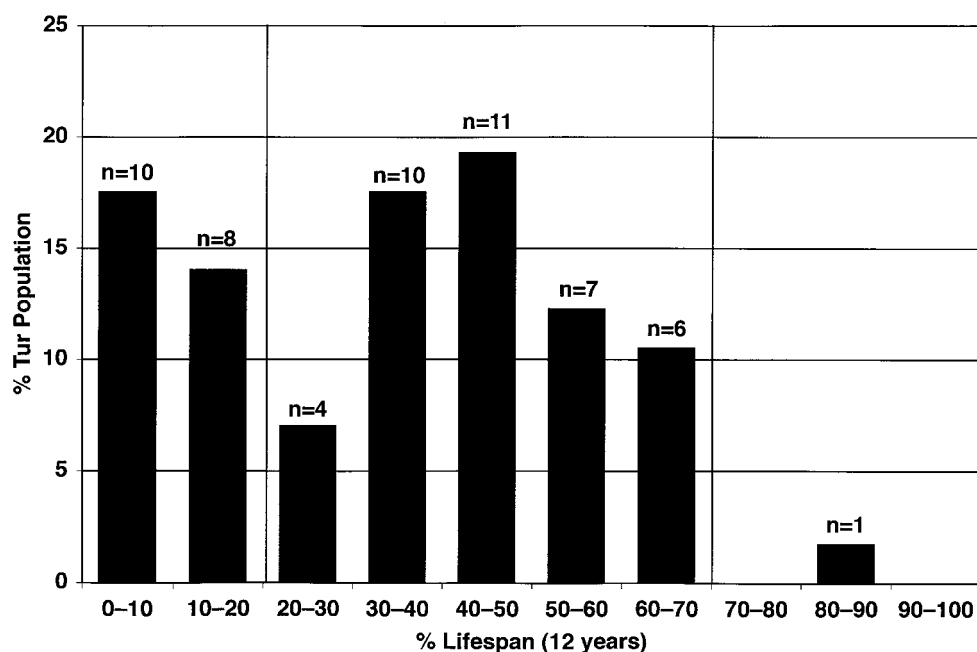
Figure 3.   Percentage mortality by percentage life-span categories for Caucasian tur recovered from Ortvale Klde Layers 6 and 7 (n = 57). Percentage life span < 20 = young; 20–70 = prime age; > 70 = old.

reserves in the Georgian Republic and on the northern side of the Caucasus, mainly in Daghastan, support the following general observations regarding species size and weight, reproduction, and life cycle:

Adult males are 150–165 cm long and 95–109 high at the shoulder and weight 65–100 kg; the corresponding figures for adult females are 120–140 cm, 78–90 cm, and 50–60 kg. Both sexes have horns. Females are sexually mature after 2 years of age and males after 4–5 years. Life expectancy is 12 years. Annual breeding between November and January produces one or two offspring per female in May and June (150–160 days). The proportion of young animals to the total population is 15%.

We assume throughout this paper that the behaviors of Pleistocene Caucasian tur were not significantly different from those of recent herds.

Caucasian tur have one of the smallest natural ranges of any ungulate today, covering approximately 4,500 km^2 in the western Caucasus that includes elevations of 800–4,200 m.a.s.l. They follow a seasonal migration cycle, moving upslope in May to take advantage of summer pastures and to avoid ticks, horseflies, deerflies, and other blood-sucking insects and downslope in October for mating and feeding (Heptner, Nasimovich, and Bannikov 1989). They thrive in alpine meadows, barren areas, and forests, and their diet is composed of a wide variety of plants, grasses, shrubs, and the leaves of trees. During the summer, Caucasian tur can cover

a daily vertical distance of up to 1,500–2,000 m, thereby taking advantage of numerous resources at different elevations. During the spring and summer they feed periodically throughout the late afternoon, night, and morning and spend the hottest portions of the day resting in shaded places. Adult males generally stay at higher altitudes than females, who are usually accompanied by young. Maternal herds of approximately 12 animals are joined by otherwise solitary adult males in the breeding season (late November–early January); adult males, in particular those in their reproductive prime (six–eight years old), compete violently for females during the rut. During winter, the home range size of Caucasian tur is much smaller. Within these home ranges Caucasian tur has a habit of utilizing the same trails, sometimes several kilometers long, for many generations; it has been noted that rocks in these trails have been polished by the repeated passage of herds. The average population density of Caucasian tur is estimated at 50–160 per 1,000 hectares, but because of recent over-hunting and continued habitat loss these numbers certainly underestimate historical and Pleistocene population densities. A recent estimate places the total population of Caucasian tur at only 300 individuals, making this species eligible for inclusion in the *IUCN Red Book* (Matcharashvili 2003).[1] Given

1. Caucasus Environmental NGO Network (CENN) and Noah's Ark Centre for the Recovery of Endangered Species (NACRES), both located in the Republic of Georgia, are actively involved in the establishment,
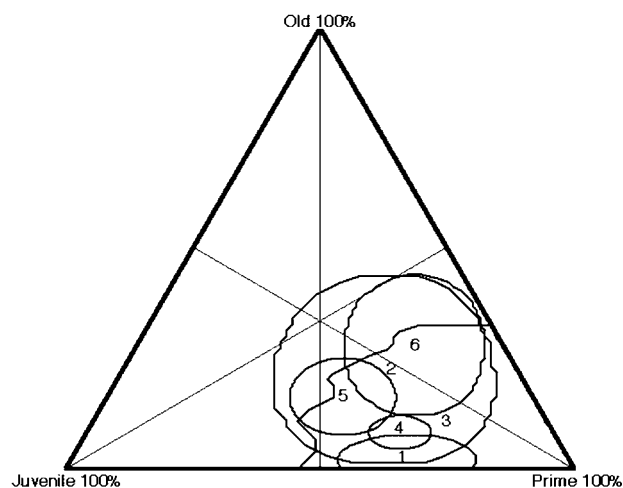
Figure 4.   Modified triangular plot (after Steele and Weaver 2002) of (1) Caucasian tur mortality patterns in the combined LMP sample from Layers 6 and 7 at Ortvale Klde ($n = 57$) compared with the median values for the (2) Middle ($n = 19$) and (3) Upper ($n = 10$) Palaeolithic of Italy (Stiner 1994, 2002), the mortality patterns of (4) gazelle ($n = 316$), (5) fallow deer ($n = 114$), and (6) red deer ($n = 40$) in the combined Middle Palaeolithic sample of Kebara Cave (Speth and Tchernov 1998), and (7) the combined Middle Palaeolithic sample from Gabasa 1, Spain ($n = 146$) (Blasco Sancho 1995). Bootstrapping of the raw data produces density contours that represent 95% confidence intervals around each data point (Steele and Weaver 2000), with assemblages 1, 4, 5, and 7 having tighter ranges than assemblages 2, 3, and 6.

these reduced numbers and the lack of historical documentation, it is difficult to ascertain potential herd size during seasonal periods of aggregation and breeding.

Implications of the Zooarchaeological Analyses

The zooarchaeological results from Ortvale Klde reflect a strong emphasis on Caucasian tur procurement during both the LMP and the EUP, suggesting that this species remained a valuable and predictable resource throughout the Middle and Late Pleniglacial. Analysis of Caucasian tur age-classes demonstrates that Neanderthals and modern humans were equally capable hunters, exploiting all age-groups but preferentially targeting prime-age adults. It remains unclear whether hunting tactics were random or selective, focusing on isolated adults or small groups of adults, but we find no evidence for the preferential culling of males or females. The technology or degree of group coordination required for hunting Caucasian tur remains difficult to estimate, but the

dominance of prime-age adults is indicative of ambush or intercept hunting rather than some form of encounter hunting (Shea 1998). In any case, Caucasian tur can be particularly elusive and difficult to hunt given their predilection for rocky heights and steep crags, terrain to which they often retreat after being disturbed (Lay 1967; Roberts 1977; Marean and Kim 1998). The hunting of Caucasian tur was therefore no simple matter for Neanderthals or modern humans, although the seasonal migration and hence local abundance of this species likely established it as a high-rank food item (i.e., low search cost and high encounter rate).

Several independent lines of evidence suggest the seasonal exploitation of Caucasian tur. Ortvale Klde would have been a key site for the ambush of herds during their seasonal movements through the Cherula Valley. As figure 5 indicates, however, it is located below the current lower range of the documented distribution of the species. During the occupation of the site the sub-alpine zone was periodically as much as 1,000 m lower than the current level. It is assumed that Caucasian tur populations responded to warmer Holocene temperatures by reorganizing their migratory behaviors to take advantage of resources available at higher elevations. Thus during the Pleistocene Ortvale Klde would have been situated within the lower, late fall–early spring range of observed Caucasian tur seasonal movements as dictated by the location of the sub-alpine zone.

During much of the late spring and summer, populations of Caucasian tur would have been dispersed throughout the higher elevations, thereby lowering prey densities in the immediate vicinity of Ortvale Klde and resulting in increased search costs and lower encounter rates. Consequently, Ortvale Klde was likely excluded from intensive use during the summer. The dominance of prime-age adults in the assemblage suggests that prey densities were high enough to allow Neanderthal and modern human hunters to cull herds by age. The presence of young animals in the assemblage fits well with the breeding data and indicates the local presence of calves born the previous season (May–June). The efficiency of ambush hunting would have been elevated at this time (late fall–early spring) because of the increased density and vulnerability of prey in the Cherula Valley and the animals' habit of utilizing the same trails from season to season and from generation to generation (Heptner, Nasimovich, and Bannikov 1989).

The combined zooarchaeological data suggest that Ortvale Klde served as a key target location in the landscape from late fall through early spring. Since Caucasian tur is "fixed" as a resource only seasonally, it stands to reason that Neanderthals and modern humans, given the appropriate weapons technology and organizational skills (which both populations appear to have possessed), would have maximized their food-gathering efforts by exploiting the seasonal behaviors of this species. Pursuing solitary males or small, dispersed, fast-moving maternal herds through dense forests and along steep slopes probably did not qualify as an efficient expenditure of

Table 5. Range of Variability, Means, and Standard Deviations of Caucasian Tur Bone Measurements from the LMP and EUP of Ortvale Klde and Modern Caucasian Tur from the Caucasus

Element and Assemblage	Range of Variability	Mean	S.D.	*N*
Breadth of distal condyle of the humerus				
LMP	43.12–48.60	45.02	2.50	4
EUP	–	–	–	–
Modern male	41.06–46.32	43.11	1.80	11
Modern female	34.01–37.90	36.42	1.66	5
Height of the distal condyle of the humerus				
LMP	19.28–21.59	20.50	1.07	4
EUP	–	–	–	–
Modern male	17.27–20.94	18.99	1.10	11
Modern female	15.23–17.88	16.93	1.04	5
Breadth of the astragalus				
LMP	24.90–31.09	27.41	2.26	13
EUP	24.90–33.01	29.29	4.10	3
Modern male	24.57–27.62	25.95	1.07	11
Modern female	20.81–23.26	22.28	1.04	4
Length of the astragalus				
LMP	37.05–46.33	41.38	2.55	13
EUP	39.78–47.54	43.92	3.91	3
Modern male	36.37–40.26	38.53	1.21	11
Modern female	34.15–36.33	35.26	1.11	4

Note: Measurements in millimeters were taken according to von den Driesch (1976).

time or energy. Instead, large numbers of animals of specific size and age could have been exploited by small groups of hunters during periods of Caucasian tur migration and breeding. One would have needed only to sit and wait to ambush them as they moved along traditional and predictable routes or utilized known salt licks—a hunting practice that was in effect in recent historical periods (Heptner, Nasimovich, and Bannikov 1989; Z. Kikodze, personal communication, 2003). These data point to the consumption, at least seasonally, of large amounts of meat, a Middle and Upper Palaeolithic behavior suggested by recent analyses of carbon- and nitrogen-isotope ratios (Bocherens 1997; Bocherens et al. 1999; Richards et al. 2000; Drucker and Bocherens 2004). Such behaviors likely also resulted in the aggregation of Neanderthal and modern human populations in the area surrounding Ortvale Klde, a pattern observed among recent hunter-gatherer groups when resources are abundant and predictable (see Winterhalder and Smith 1981; Butzer 1982; Johnson and Earle 1987; Kelly 1995). The density of anthropogenic sediments and archaeological materials in particular layers at Ortvale Klde (Layers 7–4) may speak to this point. Such aggregations served multiple economic and social purposes the exact forms of which can only be speculated upon but which likely included the exchange of resources, knowledge, and mates. We believe that these should be considered important social occasions at least as much as periods of optimal resource acquisition. We also believe that, while Neanderthals and modern human groups were equally capable of practicing the same hunting techniques using distinct technological repertoires, it was dif-

ferences in the form, function, and perhaps magnitude and frequency of these social occasions that highlighted important distinctions between them.

Mobility and Land Use in the Southern Caucasus

The zooarchaeological data presented here provide essential background information for the discussion of LMP and EUP mobility, land-use patterns, and hunting practices in the southern Caucasus. It has been argued that LMP and EUP hunters targeted prime-age adult Caucasian tur and that hunting activities in and around Ortvale Klde were structured according to the migratory behaviors of this species, which made them locally abundant on a seasonal basis. Unfortunately, data concerning the floral component of the LMP diet, a particular measure of the relative breadth of a foraging economy, is currently lacking at the site and in the region (Flannery 1969; Madella et al. 2002).

Diverse faunal assemblages from neighboring Middle Palaeolithic sites such as Djruchula Cave and Bronze Cave indicate the exploitation of a wider array of species and increased diet breadth (Adler and Tushabramishvili 2004). Although not unprecedented elsewhere in Eurasia (e.g., Chase 1986; Jaubert et al. 1990; Hoffecker, Baryshnikov, and Potapova 1991; Baryshnikov and Hoffecker 1994; Stiner 1994; Gaudzinski 1995; Rabinovich and Tchernoy 1995; Marean and Kim 1998; Speth and Tchernov 1998; Hoffecker and Cleghorn 2000; Hoffecker 2002) Ortvale Klde and, to a lesser
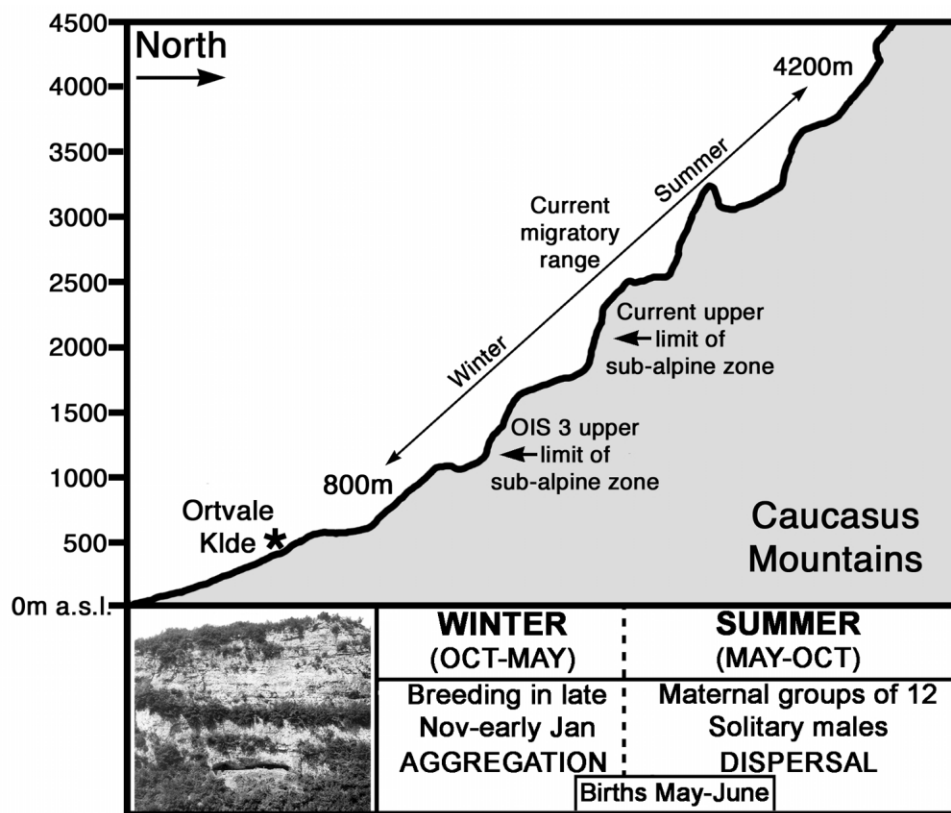
Figure 5. Key migratory, reproductive, and social behaviors of the Caucasian tur in the southern Caucasus (vertical scale exaggerated), showing the position of the upper limit of the sub-alpine zone today and in oxygen-isotope stage 3 (modified after Adler 2002). Inset shows Ortvale Klde Rockshelter.

extent, Dzudzuana Cave currently represent the only well-documented instances of intensive species-specific exploitation in the southern Caucasus. It is difficult to assess all of the potential reasons for these intraregional differences in faunal economy, but we suggest that species-specific hunting at Ortvale Klde was predicated largely on the site's location within the lower migratory range of the Caucasian tur. By the same token, we agree with Stiner (1992) that specialization can often be related to temporary foraging adjustments instigated by fluctuations in food supply rather than real changes in human adaptation. If site location were the main determinant of hunting practices and faunal assemblage composition, however, we would expect to see similar patterns at sites in neighboring river valleys where topographic and environmental conditions appear largely identical. This pattern of Caucasian tur exploitation cannot currently be replicated at any known site in the region except the Upper Palaeolithic occupations at Guargilas Klde, a small rockshelter less than 1 km north of Ortvale Klde in the Cherula Valley (A. Vekua, personal communication, 2004). At Dzudzuana Cave, ca. 4.6

km to the east, EUP assemblages dated to ca. 32,000–21,000 years BP and contemporary with Layers 4–2 at Ortvale Klde (Meshveliani et al. 1999, 2004; Adler and Tushabramishvili 2004) are dominated by bison and Caucasian tur (Bar-Oz et al. 2004), perhaps reflecting differences in seasonal site use or site-specific taphonomic histories. The critical fact is that Neanderthals and modern humans were equally quick to recognize and capitalize on the feeding and mating habits of Caucasian tur in and around the Cherula drainage.

The wildlife literature indicates that Caucasian tur spend most of the late spring and summer at much higher elevations, but to date no LMP or EUP sites have been identified at these altitudes. It is possible that Neanderthals and modern human groups followed migrating herds of Caucasian tur into the mountains during the summer, but it is unclear whether the gains would have outweighed the increased risks and costs associated with procurement and transport, as Caucasian tur generally disperse at this time and therefore are more difficult to hunt. If Neanderthals and modern humans did exploit Caucasian tur during the summer, we would expect to find

Table 6. Frequencies of Local and Nonlocal Raw Materials

| Period and Layer | m³ | Local | | Nonlocal | | Total | Local/ m³ | Nonlocal/ m³ | Local/m³: Nonlocal/m³ |
		#	%	#	%				
EUP									
2	1.38	1,635	99.8	4	0.2	1,639	1,184.8	2.9	408.6:1
3	1.56	1,208	99.8	2	0.2	1,210	774.4	1.3	595.7:1
4a	0.60	88	96.7	3	3.3	91	146.7	5.0	29.3:1
4b	0.84	164	96.5	6	3.5	170	195.2	7.1	27.5:1
4c	0.84	4,329	93.3	308	6.6	4,637	5,153.6	366.7	14.0:1
4d	0.60	4,034	96.9	124	3.0	4,158	6,723.3	206.7	32.5:1
LMP									
5	1.25	2,353	99.1	21	0.9	2,374	1,882.4	16.8	112.0:1
6	2.50	12,247	99.6	46	0.4	12,293	4,898.8	18.4	266.2:1
7	2.50	7,358	99.6	26	0.4	7,384	2,942.2	10.4	283.0:1
EUP 4a–d	2.88	8,615	95.1	441	4.9	9,056	2,991.3	153.1	19.5:1
LMP 5–7	6.25	21,958	99.6	93	0.4	22,051	3,513.3	14.9	235.8:1

Note: Local raw materials (available within 20 km of Ortvale Klde) include flint/chert, andesite, limestone, quartzite, argillite, indeterminate volcanics, and silicified shale. All seven were used in the LMP while only flint/chert and andesite were used in the EUP. Nonlocal raw materials (available more than 20 km from Ortvale Klde) include obsidian only.

faunal assemblages dominated by females and young, as males are solitary at this time. We consider it more likely that hominins shifted to the exploitation of larger areas by smaller, perhaps family units during the late spring and summer. Although many resources would still have remained readily available throughout the region during this part of the year, some, such as large ungulates, would have been more dispersed and more difficult to hunt in the overgrown forests and summer vegetation. Under such conditions, human group dispersion, the reorganization of foraging behaviors around the intensive exploitation of seasonally abundant floral resources, and an increase in residential mobility may have been the best way to minimize dietary risk (Johnson and Earle 1987; Kelly 1995). This hypothesis can be tested by conducting archaeological surveys and excavations at higher elevations and by investigating the open-air component of Palaeolithic settlement.

The importance of caves and rockshelters as key loci of archaeological data cannot be denied, but such features were not occupied to the exclusion of other parts of the landscape. Well-excavated LMP and EUP open-air sites (e.g., logistical loci such as hunting camps) are currently absent from the regional archaeological record, but this absence cannot be attributed to specific settlement or land-use patterns; rather, it stems from the narrow focus of past excavation and research. Several open-air sites are known from past surveys (Liubin 1977), but these have never been investigated systematically, and few are stratified. Without this critical component of Palaeolithic settlement and subsistence, it will be impossible to develop a reasonable understanding of the distribution and importance of logistical loci and how such sites might be linked to larger foraging systems. A current project in the Mashavera Gorge in the Dmanisi region under the direction of D. S. Adler and C. Reid Ferring is focusing on the exca-

vation and analysis of stratified Palaeolithic localities in low-energy alluvial contexts and is beginning to offset the shortcomings of regional cave- and rockshelter-based research.

Another important element strongly influencing mobility and land use at Ortvale Klde and in the region as a whole was the distribution of raw materials suitable for the production of lithic artifacts. High-quality Cenomanian-Turonian flint deposits were scattered throughout the region during the Palaeolithic and, in combination with other local raw materials, were exploited heavily during the LMP (99.6% of the total assemblage at Ortvale Klde) and EUP (95.1% of the total assemblage at Ortvale Klde) (see table 6). These materials could be procured easily from deposits on the plateaus above Ortvale Klde or in alluvial deposits in river valleys such as the Cherula. The local abundance of high-quality materials afforded Neanderthals and modern humans a degree of technological flexibility and relaxed constraints on occupation duration and the need for curated technologies or frequent residential moves. In this respect, the data from Ortvale Klde suggest that during particular seasons (e.g., winter), places and individuals were routinely provisioned with local raw materials (see Kuhn 1995).

Nonlocal raw materials, specifically high-quality obsidian, the nearest possible source of which is in the Javakheti region approximately 100 km to the southeast (Blackman et al. 1998), are also present at Ortvale Klde (see table 6). In the LMP occupations, obsidian artifacts appear as small debitage (< 10 mm) and heavily reduced tools whose use lives have been greatly extended through extensive resharpening, recycling, and curation, a common Middle Palaeolithic phenomenon documented throughout Eurasia (Geneste 1988*a*, *b*; Roebroeks, Kolen, and Rensink 1988; Kuhn 1992, 1995; Floss 1994; Gamble 1999; Conard and Adler 1997; Adler, Prindiville, and Conard 2003). Obsidian makes up 0.4% of the combined LMP assem-

blage. This pattern of nonlocal-raw-material use differs from that observed in Layers 4a–d, where obsidian is represented by full reduction sequences, including cores and debitage, and constitutes roughly 5% of the total assemblage; in Layer 4c the frequency reaches almost 7% (table 6). These data may reflect differences in Neanderthal and modern human mobility, land use, home range, and social network size, combined features referred to by Gamble as the "landscape of habit"—"the wider region, traversed by the individual and all those with whom he or she interacts, [that] forms a spatial network of intersecting paths" (1999:87).

The data presented here suggest that the Neanderthal landscape of habit stretched as far south as 100 km, where the nearest obsidian sources are located. Yet the consistently low frequency of obsidian artifacts (Layers 5–7: $n = 93$, 14.9 pieces/m³ [table 6]) and their heavily reduced state suggest that movements between the two regions were infrequent and that when they did occur Neanderthals may have progressed through the landscape slowly, consuming raw material as they went. In fact, from these observations it seems plausible that many individual Neanderthals occupying the Chiatura region never came into direct contact with this material. We conclude that the true Neanderthal landscape of habit was likely much smaller. It appears that local Neanderthal activities and social relations were structured within small territories, perhaps on the order of tens or hundreds of square kilometers, and that residential mobility was relatively low for at least part of the year (Adler 2002). Given the rugged terrain of western Georgia and the richness and diversity of its resources, it may not have been necessary for these territories to be larger. Data from across Eurasia suggest that this reliance on local commodities, whether flint outcrops, key ambush or habitation sites, animal and plant resources, or mating and exchange networks, characterizes much of the Middle Palaeolithic (Gamble 1986, 1999). In contrast, the raw material data suggest that modern human movements between Ortvale Klde and obsidian sources to the south were initially more frequent (Layers 4a–d: $n = 441$, 153.1 pieces/m³ [table 6]). During the EUP, modern humans exploited distant resources throughout the southern Caucasus, and we believe that this ability to maneuver within and exploit larger territories, perhaps on the order of hundreds or thousands of square kilometers, was predicated on the establishment and maintenance of larger social networks that encompassed numerous groups with whom individuals had some common bond, be it language, ideology, or identity.

Methods of lithic reduction and tool manufacture also bear directly on the issue of mobility and land use. The primary method of core reduction at Ortvale Klde during the LMP was highly standardized, following the *récurrent* unidirectional Levallois technique, and led to the production of numerous elongated blanks with parallel or converging edges (Adler 2002). Dorsal convexities were maintained through the detachment of *débordants*, and obstructions to core reduction, such as step or hinge fractures, were removed via the detachment of *outrepassé* flakes. These methods of core reduc-

tion and management enabled LMP knappers to maximize the number of elongated blanks produced per core. A secondary method, linked to later stages of core reduction, when core volume was greatly reduced and dorsal convexities more difficult to maintain, entailed the lateral and distal trimming of cores. These data suggest that numerous cores were reduced extensively on site following formal methods and that blank yield and size were maximized.

The manufacture of retouched tools during the LMP was based on the preferential selection of elongated blanks for the production of various scraper forms (Adler 2002). The most common retouched implements, simple, double, and convergent/*déjeté* scrapers, resulted from continuous resharpening and use rather than from single manufacturing episodes during which an implement of predesigned form or function was produced (Dibble 1987*a*, *b*, 1988, 1995; Adler 2002). The large size of many of these tools, indicating their potential for extended use, even among the convergent/*déjeté* scrapers, suggests that tool consumption was not maximized (Adler 2002). Therefore a large proportion of the blanks produced on site were intended for immediate use and/or transformation into retouched tools. The various scrapers experienced considerable and extended use and resharpening, being discarded only after the completion of numerous activities but not necessarily because of exhaustion. In this regard, the manufacture and use of both blanks and tools occurred close together in time and space as part of complete on-site reduction sequences, and consequently we conclude that these assemblages reflect periods of prolonged site use (Adler 2002).

The patterns of raw material transport and exploitation documented at Ortvale Klde point to the almost exclusive reliance on local raw materials during the LMP and the increased use of nonlocal raw materials during the EUP (table 6). We suggest that this shift in lithic resource procurement and transport occurred during a more profound shift that included the establishment of larger social networks and the exploitation of larger territories by modern humans. We also suggest that this shift was accompanied by increased group mobility and perhaps the establishment of exchange networks, patterns that have been documented throughout much of Europe for the Upper Palaeolithic (Gamble 1986, 1999).

Conclusions

The available data from Ortvale Klde and the southern Caucasus suggest that Neanderthal and modern human hunting behaviors in the region were not significantly different. Because observations made in one region do not necessarily reflect accurately the complexity or diversity of prehistoric hominin behavior across time and space, we limit the following conclusions to the data available from the southern Caucasus while proposing new avenues of inquiry that can be pursued in other regions.

We conclude that Neanderthal populations in the southern Caucasus and the modern human populations that followed

them were equally adept at exploiting a wide range of ecological niches as and when they chose to on the basis of a deep understanding of the local environment and the permanent and seasonal distribution of key resources. LMP and EUP occupations at Ortvale Klde were both predicated on the seasonal abundance of Caucasian tur in the Cherula Valley, with ungulate species abundance in the entire stratigraphic sequence reflecting seasonal fluctuations in food supply rather than specialization or differences in hunting ability or technology. The possession and perpetuation of such knowledge from parent to offspring over many generations is an ancient adaptation, and the degree of planning depth and group coordination necessary to exploit this knowledge appears to have been largely equivalent between Neanderthals and modern humans. Therefore there appear to have been few tangible diachronic differences in methods of prey exploitation or biogeographical information acquisition and exploitation in the southern Caucasus at the Middle–Upper Palaeolithic boundary. Consequently, we argue that prey acquisition patterns and hunting techniques cannot be considered useful measures of "archaic" versus "modern" behavior during this period. If such behaviors did vary considerably between different groups of hominins, we suggest that these differences first arose among Early Stone Age populations in Africa, not among Upper Pleistocene populations in Eurasia.

While the data presented here demonstrate that the ways in which different individuals or groups chose to exploit this knowledge were largely identical, it can also be demonstrated that the technological aids (toolkits) with which Neanderthals and modern humans effected this exploitation varied considerably. Neanderthals relied heavily on various scrapers and most likely wooden projectiles, perhaps tipped with stone. For modern humans composite tools, microliths, and bone/antler points made up the bulk of the toolkit. In the absence of any clear method for distinguishing how such technological differences may have affected the rates at which animals were successfully hunted (i.e., energetic returns [see Grayson and Delpech 2003]), we propose that this difference may result from stylistic traditions of stone and bone tool making shared among immediate and extended group members rather than any perceived or demonstrable functional advantage. This observation is true of the various Middle Palaeolithic populations and later Upper Palaeolithic groups that occupied the southern and northern Caucasus (see Golovanova and Doronichev 2003; Adler and Tushabramishvili 2004). In other words, different hominin populations, whether biologically related or not, were able to effect the same results in terms of hunting and resource procurement with markedly different technological repertoires. This suggests that while no major changes in hunting behavior are evident at the Middle–Upper Palaeolithic boundary, there were considerable and unprecedented alterations in material culture that contradict the notion of cultural continuity between the two periods or the formation of so-called transitional industries. We believe that the perceived "advances" in EUP hunting technologies (e.g., composite tools, microliths, and bone/antler points), often touted as signs of modern human behavioral superiority, were in this context largely the material expressions of culturally mediated developments and preferences that did not necessarily bestow any distinct technological advantage on their makers and thus did not necessarily play a critical role in the "competitive" or "economic" demise of the Neanderthals in the southern Caucasus.

The procurement of other critical resources, namely, lithic raw materials, indicates that there were rifts in mobility and land use between the LMP and the EUP in the southern Caucasus. We interpret the available data as evidence that modern humans exploited larger territories, probably logistically, covering these territories rapidly and frequently (see Kelly 2003; Meltzer 2003) and establishing far-reaching extended social networks which allowed them to construct rich social landscapes unlike those experienced by the Neanderthals (Gamble 1999). Evidence for the scale and rapidity of this shift in mobility and social network is suggested at Mezmaiskaya Cave on the northern slopes of the Caucasus, where EUP deposits (Level 2: 32,230 ± 740 years BP [Golovanova and Doronichev 2003]) roughly contemporaneous with Layer 4 at Ortvale Klde contain largely identical and similarly unprecedented assemblages of lithic and bone tools deposited atop terminal LMP layers (Adler 2002). These data suggest that modern humans were able to penetrate the Caucasus Mountains, the biogeographical barrier that Neanderthals were apparently loath to cross with any degree of regularity (see Adler 2002; Golovanova and Doronichev 2003). Therefore we hypothesize that it is the development and maintenance of larger social networks, rather than technological innovations or increased hunting prowess, that distinguish modern humans from Neanderthals in the southern Caucasus. This dramatic shift, referred to by Gamble (1999) as the "release from proximity," opened up a much larger world to modern humans than that enjoyed by their Neanderthal contemporaries, and we suggest that this development in the social realm of hominin behavior, perhaps instigated by more complex oral and non-oral forms of symbolic communication (see Wynn and Coolidge 2004), was a key adaptation that allowed modern human populations to expand and prosper at the ultimate expense of the Neanderthals. While this is by no means a simple hypothesis to test and it is one whose underlying assumptions will evolve over time, palaeoanthropologists should not shy away from considering old questions from new angles. Thus we encourage scholars to join us in conducting more field- and laboratory-based research that considers regionally contextualized archaeological data through an interpretive lens as sensitive to issues concerning the social relationships of extinct hominins as it is to materialist or economic ones.

Acknowledgments

Comments

Clive Gamble
Department of Geography, Royal Holloway University of London, Egham TW20 0EX, England (clive.gamble@rhul. ac.uk). 14 VII 05

In this impressive paper the authors have provided further evidence that the past 100,000 years of human evolution need to be rethought. For 40 years it has been assumed that one of the major differences between hominin populations was the extractive efficiency of their subsistence. Although rarely stated, the driver for such efficiency is assumed to have been reproductive success. Bettinger (1991, 213) has pointed out that most archaeological examples of relative efficiency between, say, Neanderthals and *sapiens* are not evolutionary in a Darwinian sense because they express only a theory of consequences that stem from adaptation, but a series of models has nevertheless emerged to account for variation in the Palaeolithic archaeology of diet, technology, and settlement systems. These models are now normal science for palaeoanthropologists, expressed in a series of behavioural spectra that include archaic to modern, hunting to scavenging, collectors to foragers, and expedient to curated (Gamble 1999, table 1.3). The task of the archaeologist has been to position evidence along these spectra in order to observe the transition towards an end point, the appearance of the unfortunately named fully modern humans.

Adler and his colleagues provide evidence that at least two of these spectra, technology and diet, do not measure differences. The faunal evidence for hunting of prime-aged Caucasian tur chimes well with what we know about Middle Palaeolithic hunting of aurochs (Jaubert et al. 1990), bison (Farizy, David, and Jaubert 1994; Gaudzinski 1992) reindeer (Gaudzinski and Roebroeks 2000), mammoth (Boismier 2003), and several other species including mountain caprids (Gaudzinski and Turner 1999; Roebroeks and Gamble 1999). But what the Ortvale Klde evidence underlines is that similar hunting success was achieved with markedly different technologies. This has long been known in comparisons of the Pleistocene archaeology of Australia and Europe (Jones 1990; Pike-Tay and Cosgrove 2002), where technologies are very different, and the Georgian data extend the pattern back in time and to other hominins. I therefore welcome Adler et al.'s call for a social framework to account for change and variation, but I am left wondering what this might be. The raw-material evidence from Georgia supports the view that for Neanderthals social life was local while for *sapiens* it was extended. I would go farther, as follows:

The initial step is to rethink the primary economic metaphor (Gudeman 1986) that underpins present studies of the past 100,000 years. As Earle (1980, 14) has suggested, hunters and gatherers can be understood as a small diversified firm in which economic success is governed by balancing supply and demand and cost-benefit analysis informs strategic planning to maximize profit margins. According to the corner-store analogy and the idea that hunters are engaged in a game *against* their environment (e.g., Jochim 1976), *sapiens* were simply better managers than Neanderthals, while change is understood as any reduction in environmental resistance. It is this economic analogy that the Ortvale Klde data challenge. Instead of the corner store, Bird-David (1992) has suggested the analogy of the environment as a local bank that depends on trust and confidence rather than competition and profit margins and the primary metaphor is that of the giving environment. The difference is fundamental for Palaeolithic societies. Where the primary metaphor that structures investigation is resistance, analyses are framed in rational terms, as shown by the behavioural spectra mentioned earlier. However, when the primary metaphor shifts to giving, the prospect is opened for an alternative, relational view of the evidence.

Elsewhere I have presented, with Sabine Gaudzinski (Gamble and Gaudzinski 2005), an example of a relational approach to the faunal remains from Salzgitter-Lebenstedt, a Middle Palaeolithic locale in northern Germany where prime-aged reindeer were hunted. The locale has evidence from both fauna and lithics for the social actions of fragmentation and consumption that contributed to the construction of an individual's identity through the accumulation and enchainment of material culture (Gamble 2004). It therefore seems to me that

in terms of the social approach advocated by Adler et al. the significant differences between Middle and Upper Palaeolithic technologies were the result not of extractive efficiency but of people's metaphorical understanding of their worlds through their material culture. Social technologies will therefore vary by locale rather than by hominin fossil. In this case the material metaphors (Chapman 2000; Tilley 1999) of flakes and blades will have to be understood in the context of establishing relatedness not only with people but with objects (Knappett 2005). The difference between flakes and blades lies not in extractive advantage but in the role of fragmentation in negotiating identity through hybrid networks of people and objects. This is perhaps a rather different social framework from the one Adler et al. intended.

John F. Hoffecker
Institute of Arctic and Alpine Research, University of Colorado, Boulder, CO 80309-0450, U.S.A. (jfhoffeck@aol.com). 12 IX 05

I have followed with interest the ongoing research undertaken by Adler and his colleagues in the southern Caucasus, and I am pleased to see this paper, which—along with other recent publications—is an indication that they have used their precious funding dollars well. The southern Caucasus is a particularly suitable region for the comparative study of Neanderthals and modern humans. In this paper, Adler et al. have chosen to address this study specifically in terms of the inferred hunting behaviors of the two hominin taxa. Their conclusion that there were no significant differences in large-mammal hunting tactics between Neanderthals and modern humans extends to advanced planning abilities and the role of technology in hunting and buttresses similar conclusions reached during the past two decades in other parts of Eurasia. More generally, they conclude that hunting tactics and technology related to hunting provide a poor basis for identifying major behavioral differences between Neanderthals and modern humans and probably were not critical variables in the replacement of the former by the latter. Along with other recent research that has contributed to a more sophisticated portrait of the Neanderthals, this "force(s) us to reconsider our definition of behavioral 'modernity,' " and Adler et al. observe that "the vast behavioral and cognitive gulf that was once thought to exist . . . has now narrowed considerably."

While I have reached similar conclusions about Neanderthal hunting (at least with respect to large mammals), I think that some of their broader observations could be qualified. Although it is to some extent merely a question of perspective and emphasis, I believe that the behavioral and cognitive gulf between Neanderthals and moderns was a vast one despite the lack of differences in hunting behavior. Moreover, I think that this gulf is apparent in the archaeological record (although I do not deny that it is less obvious in the Early Upper Palaeolithic

[EUP]). Much of the problem lies in an excessive focus among archaeologists on the economic aspects of that record.

I think that modern humans are virtually unique among animals in their ability to communicate and project mental constructs not only through language, art, music, dance, and so forth, but also through technology and organization. Although EUP settlements tend to be small, they exhibit collectively the archaeological imprint of such constructs—or their means of articulation—in the form of sculptures, musical instruments, and traces of burial ritual. Similar structural complexity is evident in the artificial shelters, sewn clothing (inferred from eyed needles), and other technological means by which EUP people remade themselves and the world around them. And some of their technology did have an impact on their foraging tactics—EUP folk designed technologies for harvesting small mammals that apparently eluded the Neanderthals and thereby broadened their niche.

Some archaeologists have complained that comparisons between Neanderthals and modern humans have exaggerated the contrast by incorporating later segments of the Upper Palaeolithic record, including the Magdalenian. I would argue the reverse—that in the absence of any evidence for major behavioral or cognitive differences between EUP people and their successors, the Middle and Late Upper Palaeolithic (and everything since) are implicit in the EUP. The difference simply reflects accumulated technological knowledge and its effect on the size of the groups and their settlements. It is the same sort of contrast that may be seen in Western Europe between AD 1200 and 1700, and the tendency to accumulate such knowledge through the engagement of mental constructs with the material world—clearly evident throughout the Upper Palaeolithic—is a crucial part of modernity.

Finally, I would suggest that the Neanderthals are the least suitable nonmodern hominins on which to base a comparative definition of modernity. Of all the Eurasian nonmodern hominins, they are the most closely related to modern humans, and their archaeological record may yield some evidence for the expression of mental constructs in the form of, for example, burial of the dead. The Neanderthals seem to have evolved their own version of modernity. Comparisons with the East Asian contemporaries of the Neanderthals or earlier Afro-Eurasian forms of *Homo* provide a clearer picture of what modernity is not.

Jean-Jacques Hublin and Teresa E. Steele
Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany (hublin@eva.mpg.de and steele@eva.mpg.de). 8 IX 05

Differences in ecogeographical adaptation, technology, cognitive abilities, and social organization have previously been considered as possible explanations for the replacement of Neandertals by humans displaying anatomically modern fea-

tures who entered western Eurasia ca. 40,000 years ago. While in the recent literature several writers have minimized the distance between late Neandertals and early modern Europeans, the fact remains that not just Neandertals but all local non-modern populations were essentially, if not totally, replaced by modern humans. Further, these modern populations colonized many geographical areas that had previously remained inaccessible to earlier hominins. In addressing the question of what made modern humans different from others 50,000–40,000 years ago, Adler and collaborators have focused on the site of Ortvale Klde, and this is both the strength and the weakness of their paper.

Adler et al. consider two aspects of Paleolithic economy before and after 38,000 years ago at Ortvale Klde: big-game hunting strategy and lithic raw-material procurement. Although the human paleontological evidence at this site is very limited, they assume that this comparison applies to Neandertal versus modern populations, which seems reasonable given the regional context. The site has been carefully excavated and well dated, and by focusing on a single site the authors are able to provide a detailed picture of hominin behavior in the Middle and Early Upper Paleolithic. They argue that the exploitation of large mammals is similar throughout the sequence, although the existence of extended social networks revealed by raw-material circulation is demonstrable only during the Early Upper Paleolithic.

The Ortvale Klde rockshelter is in a rather unusual location in which hominins exploited, almost exclusively and perhaps seasonally, a single species, the Causasian tur. Neandertals and modern humans were both able to harvest this locally abundant resource. This paper follows several others in reporting that Neandertals practiced big-game hunting strategies similar to those of modern humans, including concentration on a single species (summarized in Gamble 1999, 235). These results also include data showing that Neandertals, like modern humans, were capable of hunting prime-age animals, but the seasonal targeting of prime-age game has not been clearly demonstrated for Neandertals from Ortvale Klde. In the triangular graph presented by Adler et al., the confidence intervals for the assemblages fall within the zone identified by Stiner (1990) as indicating that prey were being taken in proportion to their natural abundance in the landscape. Prime-age-dominated hunting can be shown only when samples fall within the lower-righthand corner of the graph and when pre- and post-depositional factors (especially those that remove juveniles) have not influenced the mortality profile. The analysis of mortality profiles using both the histogram and triangular plot methods is most productive when comparisons are made between assemblages of the same species with similar pre- and post-depositional histories. Unfortunately, this is not possible at Ortvale Klde, because the sample size of tur from the Upper Paleolithic is too small to allow the construction of a mortality profile.

When a larger number of sites is considered, the general picture shows some differences between Neandertals and modern humans in their relationship with animals. Isotopic and zooarchaeological studies suggest that one of the major differences in exploitation of fauna between Neandertals and modern humans was not so much in the hunting of large game as in the enlargement of the game spectrum to include small carnivores, hares, birds, and aquatic prey (Richards et al. 2001; Stiner, Munro, and Surovell 2000). Ortvale Klde is a specialized site that does not permit the exploration of this key difference. Finally, Adler and collaborators propose that differences in the weight and range of projectiles between Middle and Upper Paleolithic weapon kits should be considered stylistic differences with no economic impact. However, we would argue that it may be differences in technology rather than the age or sex of the individual animals obtained that influence the rate of success in hunting and the energy it requires. Changes in efficiency of resource procurement may have notable demographic effects (increases in modern human population size and density) and probably depend significantly on social organization, as Adler et al. suggest. We look forward to the further exploration of this issue.

The Ortvale Klde rockshelter tells us two stories. The zooarchaeological evidence primarily reveals local conditions and the ability of two different groups of hominins to acquire a given species of mammal. On a larger scale, the raw materials used to produce the lithics reveal quite different "landscapes of habit." We agree with Adler and colleagues that the best explanation for the expansion of modern populations may rest with sociological differences, but these differences must have had subsistence consequences if they led to the demographic expansion of modern humans at the expense of the Neandertals.

Richard G. Klein
Program in Human Biology, Bldg. 80, Stanford University, Stanford, CA 94305, U.S.A. (rklein@stanford.edu). 3 IX 05

Adler et al. argue that the animal bones from Ortvale Klde, Georgia, indicate that Mousterians hunted as effectively as their Upper Paleolithic successors, and they conclude from differences in stone raw-material usage that the Upper Paleolithic advantage lay solely in the development and maintenance of larger social networks. I don't think the animal bones support their conclusion.

They particularly stress mortality in the Caucasian tur, which dominates the Ortvale Klde sequence. Mortality analyses of fossil large ungulates often begin by reference to the age structure of a live population in which the structure is stationary and to its complement, the age profile of those individuals whose deaths occur within stationary age-classes (Deevey 1947; Kurtén 1953; Voorhies 1969). The precise characteristics of each age profile will vary from population to population within and between species, but my figure 1 illustrates profiles that are probably typical. They come from a census of females in a stationary, free-ranging population
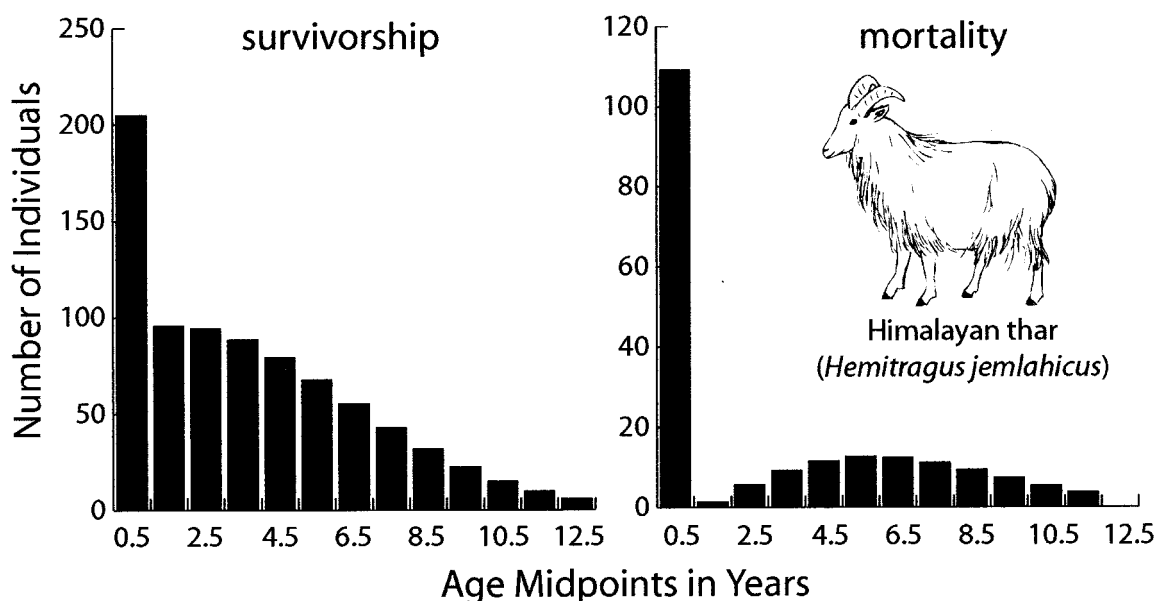
Figure 1. Survivorship and mortality in a stationary population of free-ranging female Himalayan thar (data from Caughley 1966).

of Himalayan thar (Caughley 1966), and they are especially relevant here in that the thar closely resembles the Caucasian tur in its ecology and life history. The profile on the left, labeled "survivorship," represents the age structure of the live females. The one on the right, labeled "mortality," represents the age profile of the females that died in each stationary age-class. Broadly speaking, the two profiles reflect the tendency for the rate of mortality to be highest among individuals in the first 10% of potential life span, much lower and relatively constant among those between about 10% and 50% of life span, and higher again among those who are beyond 50%. Individuals between 10% and 50% are sometimes referred to as prime-age (reproductively active) adults, and they are the least vulnerable to predation, endemic disease, and other everyday mortality factors. Individuals beyond 50% are then called postprime-age, and physical senescence increases their susceptibility to predation, disease, etc.

Fossil age profiles rarely correspond closely to either the survivorship or the mortality profile of a live population and tend to be particularly deficient for the very young (Klein 1982). This must mean either that young bones often failed to enter the fossil record or that they were selectively removed afterwards, even from seemingly well-preserved samples. The interpretation of fossil samples must therefore depend primarily on the ratio of prime-age to postprime-age adults. In addition, to accommodate the biases that may affect fossil samples, fossil age profiles should be compared not directly with live ones but with fossil profiles for other samples that accumulated under similar conditions. Prime-age adults will tend to outnumber postprime-age individuals in all fossil

samples because they are so much more numerous in life, but if one sample contains significantly more prime-age adults than another, we might conclude that its human accumulators were better equipped to hunt the least vulnerable prey.

Adler et al. argue that prime-age adults predominate among the Middle Paleolithic tur from Ortvale Klde, but this depends on placing the prime-postprime boundary at 70% of potential life span. If it were placed closer to 50%, as observations like those in figure 1 suggest it should be, the number of prime-age individuals would be much smaller, and the interpretation might be that Middle Paleolithic people were unable to obtain prime-age tur in proportion to their live abundance. Much more important, however, the Upper Paleolithic layers at Ortvale Klde have provided too few tur to calculate an age profile, and it is therefore impossible to detect a Middle/Upper Paleolithic difference. The bottom line is that Ortvale Klde does not bear on whether Upper Paleolithic technology boosted hunting.

Still, save for hints that Upper Paleolithic people were the first to systematically exploit hares, game birds, and fish (Richards et al. 2001; Stiner, Munro, and Surovell 2000), archaeologists have reported little to indicate a significant difference between Middle and Upper Paleolithic foraging. Much enlarged samples from carefully excavated sites like Ortvale Klde may yet show that Upper Paleolithic success was partly grounded in an enhanced ability to hunt large mammals. Upper Paleolithic people could simultaneously have benefited from the development and maintenance of larger social networks like those that Adler et al. infer from stone raw materials.

Adie Whitaker
Department of Anthropology, University of California, Davis,
CA 95616, U.S.A. (arwhitaker@ucdavis.edu). 16 VI 05

Adler and colleagues add intriguing behavioral data to the
debate on the definition of "modern" behavior in hominids.
More important, however, they suggest an approach to the
study of early hominid behavior which would encompass
broader regional studies of target populations and, in doing
so, draw on a well-established body of hunter-gatherer lit-
erature. The zooarchaeological data strongly support their
claim that the Caucasian tur was hunted in the same manner
throughout the transition from the Late Middle Paleolithic
(LMP) to the Early Upper Paleolithic (EUP). These data sup-
port the theory that LMP and EUP populations were equally
skilled at logistically planning and carrying out the hunting
of this seasonally abundant resource. This evidence of the
organizational abilities of LMP populations adds to the grow-
ing body of evidence that the behavioral and cognitive gulf
between Neanderthals and modern humans may not be so
vast, after all.

From the faunal evidence presented I am not convinced,
however, that "Neanderthal populations in the southern Cau-
casus and the modern human populations that followed were
equally adept at exploiting a wide range of ecological niches."
As Adler et al. point out, Caucasian tur was a seasonally
abundant resource, and Ortvale Klde was likely occupied only
at times during which tur aggregated. To refute the contention
that the LMP/EUP transition is the result of replacement of
archaic populations by better-equipped modern humans,
more than just this one seasonal resource must be examined.
As Adler et al. suggest, regional study is crucial to answering
this question. The comparison of the uses of local versus
nonlocal raw material indicate that EUP populations occupied
a larger area and perhaps maintained large social networks
through symbolic behavior and trade. If EUP populations
were indeed moving over larger areas, it is possible that they
were better able to adjust their seasonal movements in the
event of local niche shortfalls. Since the late-fall/early-spring
hunting of Caucasian tur accounts for only a small portion
of the yearly diet of these prehistoric populations, the im-
portant selective advantages of EUP populations may have
been their ability to exploit a broader range of species in the
leaner times of the year. Stiner, Munro, and Surovell (2000)
address this kind of change in Middle Paleolithic assemblages
from Italy and Israel. Because large ungulate remains are pre-
sent in equal abundances throughout the Middle Paleolithic,
they conclude that the increased exploitation of smaller and
faster species such as hare are the key to behavioral transitions
in emerging *Homo*. Is it possible that a similar scenario applies
to the southern Caucasus during the LMP/EUP transition?

The situation in the southern Caucasus is reminiscent of
archaeology in the American Great Basin in the early 1960s.
In both cases the majority of evidence was gathered from
well-preserved, stratified caves and rockshelters. In the Great
Basin the location of many of these caves near lake margins
and other lower-elevation ecological niches biased the sample
toward resources which were locally available without regard
for higher-elevation and nonlocal resources. The work of
Thomas (1973) and Bettinger and Baumhoff (1982) dem-
onstrated the importance of looking at the full range of avail-
able environmental zones and the uses of the resources in
these zones over time. In this connection, Adler et al.'s sug-
gestion that regional survey and excavation are necessary to
answer these questions is perhaps the most important con-
tribution of this paper. Reconstructing the hunting behaviors
of LMP and EUP populations in broader regional contexts
might begin to address the questions of modernity that they
raise.

Reply

We are grateful to our six colleagues for their constructive
critiques of our research in the Caucasus, and we are pleased
that certain among our interpretations did not generate as
considerable a debate as they might have done in the not too
distant past. This suggests that a consensus is growing among
palaeoanthropologists regarding the capabilities of Neander-
thals and the limited importance of certain behavioral dif-
ferences that have been traditionally drawn between Nean-
derthals and modern humans. But it is also clear from the
comments that the development of new theoretical ap-
proaches to the study of Palaeolithic populations is progress-
ing at a pace that will soon require palaeoanthropologists to
rethink the specific methods and goals of their research. Un-
derstanding this, we address the reviewers' comments ac-
cording to (*a*) those that question specific aspects of our
zooarchaeological analyses and general issues related to faunal
acquisition and (*b*) those that consider larger issues relating
to Palaeolithic technology and identity.

Regarding zooarchaeological analyses, Klein questions our
interpretation of the age profile and mortality patterns for
Caucasian tur, suggesting that our research would have ben-
efited from comparison with mortality data established for
living populations of Himalayan thar (Caughley 1966). While
such data can provide useful insights into the life-history
cycles of extant populations in particular regions, we expect
that such patterns, for example, age profiles, will vary within
and between species depending on whether the living pop-
ulation is in a stable, growing, or declining state (Caughley
1977, 121). Unfortunately, data similar to those for Himalayan
thar do not currently exist for Caucasian tur, and it is unlikely
that such data will ever become available given the endangered
state of this species. Thus in the present context the issue for
Pleistocene zooarchaeological assemblages becomes one of
where to place the prime-postprime boundary. On the basis

of the Himalayan thar data Klein suggests that this boundary should be placed at 50% potential life span rather than 70% as we have done. In our analysis we separated the sample into three broad age-groups: juveniles (birth to the age that the deciduous lower fourth premolar is normally shed), prime-age adult, and old adult (more than half of the lower third molar crown is worn). These three age cohorts represent major life-history transitions typical of many ungulates (see Stiner 1994, 290). We acknowledge that the prime-postprime boundary is more ambiguous and prone to error than the boundary separating juveniles and prime-age adults, but the use of only three mortality age-groups minimizes such potential errors. If we shift the boundary of prime-postprime from 70% to 50% potential life span, as suggested by Klein, the percentage of prime-age adult individuals in our data set decreases from 66% to 44% but still represents the majority of kills. Consequently, because of the left-skewed LMP mortality pattern and the strong mode at 30–50% potential life span, the data from Ortvale Klde are not altered significantly by the shifting of this prime-postprime boundary.

Klein and Hublin and Steele are correct to point out that the mortality data from Ortvale Klde do not allow direct comparison between the LMP and the EUP; the EUP sample is simply too small to allow detailed analysis. We acknowledged this limitation and chose instead to highlight the remarkable degree to which our LMP mortality data resemble those from numerous UP sites elsewhere (e.g., Munson and Marean 2003). For example, the confidence intervals for the LMP assemblage of Ortvale Klde (fig. 4) fall within the range of the median values of UP assemblages from Italy, overlapping the prime-dominated–living-structure zones (Stiner 1994, fig. 11.3). There is little doubt that, given appropriate sample sizes, direct comparison between our LMP and EUP data would have been productive. As we stated, larger samples from carefully excavated sites in the southern Caucasus, particularly those dating to the EUP, are required before this issue can be resolved at a regional level. Our ongoing field-based research in the region has as one of its specific aims the amelioration of this situation.

We are in full accord with Klein, Hoffecker, Hublin and Steele, and Whitaker, who mention evidence for the expansion of the resource base during the EUP (Stiner, Munro, and Surovell 2000) and the potential importance of this for EUP populations vis-à-vis their LMP contemporaries. This is clearly an important avenue of research, but since the remains of small game represent a negligible portion of the LMP and EUP assemblages at Ortvale Klde we focused our study on the issue of large-game hunting. The lack of taxonomic diversity in the faunal assemblage, together with other lines of evidence outlined in the text, suggests that LMP and EUP populations used Ortvale Klde as a seasonal hunting station. Hublin and Steele are correct, therefore, to conclude that Ortvale Klde is not an appropriate locality at which to examine changes in the faunal spectrum through time, a conclusion we drew early on in our research. It is important to note that,

as stated in the text, there are neighboring MP localities with diverse faunal assemblages at which this issue can be investigated, and we expect that EUP localities suitable for such analysis await discovery and excavation in the region and are actively working to this end.

Ortvale Klde also allows consideration of differences in LMP and EUP technology and identity, issues raised by Gamble, Hoffecker, and Hublin and Steele. While we were fully aware of the importance of organic technologies, the relative rarity of such perishable materials in Palaeolithic contexts (an issue largely of taphonomy) and their complete absence at Ortvale Klde forced us to limit our discussion to lithic technology. We know, for example, that LMP and EUP populations throughout much of Eurasia designed and manufactured distinct toolkits, but this distinctiveness is not limited to LMP and EUP populations; considerable variability also existed between various LMP populations, including those in the Caucasus (Adler and Tushabramishvili 2004). The meaning of this variability must be considered from at least two perspectives: the cultural and the economic (or extractive). Comparisons of Ortvale Klde with neighboring LMP sites on the southern and northern sides of the Caucasus suggest that populations subsisting in largely identical environments manufactured distinctive toolkits with which to hunt largely identical game. Was this distinctiveness the result of a perceived extractive advantage in one toolkit over another or cultural preference? The data suggest the latter, with different LMP populations exploiting largely identical faunal resources in largely the same way employing different technological repertoires. In the context of the Caucasus we interpret this as evidence of a pronounced cultural rather than simply extractive influence on tool design and manufacture. For similar reasons we believe this interpretation is appropriate for the LMP and EUP at Ortvale Klde, where the two populations obtained the same hunting results employing dramatically different toolkits. This is not to say, however, that the influences of culture and economy in tool design and manufacture are mutually exclusive. Clearly the extractive potential of a specific toolkit must be realized before it can undergo design modification according to prevailing aesthetics or the experiences shared among individual group members. What we cannot investigate at Ortvake Klde or at any other Palaeolithic locality is the degree to which differences in technology (lithic or organic) between different LMP populations or between LMP and EUP populations may have fostered differences in kill rate and energy expenditure. While we agree with Hublin and Steele that such differences, if they existed, may have had important demographic effects on EUP populations, we much reiterate that the analytical tools with which to test such a hypothesis simply do not exist.

This discussion of technological change is closely linked to another important issue raised by Gamble and echoed by Hoffecker, namely, which theoretical approach is best designed to consider the true nature of hominin behavioral variation. Gamble questions the predominantly extractive

metaphors traditionally employed by palaeoanthropologists and instead proposes a relational approach that considers "the social actions . . . that contributed to the construction of an individual's identity through the accumulation and enchainment of material culture." We are sympathetic to this perspective, and our data from Ortvale Klde, particularly those on hunting and technological variability, appear largely in line with his overall approach. We do not, however, subscribe to the notion that extractive efficiency, be it in terms of faunal procurement or lithic technology, played a minor or secondary role in hominin societies regardless of "the metaphorical understanding that people had of their worlds through their material culture." As mentioned above, the extractive potential of each element within a toolkit must be realized before it can enter the realm of material culture and undergo stylistic transformation according to the needs or preferences of group members. In this respect Gamble is correct to conclude that the social framework we espouse differs from his own, but we view this difference as a matter of degree. Ultimately, it is from this linkage between Palaeolithic material culture and social identity that critical new insights into hominin lifeways will emerge. In the context of palaeoanthropology, the greatest challenge in forging this link is the construction of testable hypotheses sensitive to such an inherently humanistic endeavor.

—Daniel S. Adler, Guy Bar-Oz, Anna Belfer-Cohen, and Ofer Bar-Yosef

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