9. Seasonal Patterns of Prey Acquisition and Inter-group Competition During the Middle and Upper Palaeolithic of the Southern Caucasus

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Abstract Zooarchaeological and taphonomic analyses provide an essential backdrop to discussions of Late Middle Palaeolithic and Early Upper Palaeolithic patterns of mobility, land-use, and hunting, and the degree and manner(s) of Neanderthal and modern human competition within the southern Caucasus. Recent research at Ortvale Klde has documented the hunting of prime-age adult *Capra caucasica* and the organization of hunting activities according to this species' migratory behaviors, which made them locally abundant on a seasonal basis. Our analyses suggest that Neanderthals and modern humans occupied the same ecological niche and were equally capable of learning and exploiting key biogeographic information pertaining to the feeding, mating, migratory, and flight behaviors of this species. In these respects there appear to have been few alterations in medium/large game hunting practices between the Late Middle Palaeolithic and Early Upper Palaeolithic, with ungulate species abundance in the entire stratigraphic sequence of Ortvale Klde reflecting seasonal fluctuations in food supply rather than specialization, differences in diet breadth, hunting ability, or technology. Attention is paid to faunal data from neighboring sites to test whether patterns identified at Ortvale Klde are in any way representative of larger regional subsistence behaviors. We find that such patterns are only replicable at sites that have experienced similar zooarchaeological and taphonomic study. We conclude that Neanderthal and modern human populations occupied and exploited the same ecological niches, at least seasonally, and that the regional archaeological record documents a clear spatial and temporal disruption in Neanderthal settlement resulting from failed competition with expanding modern human groups. In terms of niche and resource preference, we suggest that Neanderthals and modern humans were sympatric to the point of exclusion.

Neanderthal-Modern Human Subsistence and Competition

The data presented in this paper are considered in light of ongoing questions concerning Neanderthal and modern human foraging behaviors and inter-group competition. At its core, the following discussion centers on the relative degree of niche overlap, prey choice, and population size between indigenous Neanderthals and expanding modern humans. Consideration of the primary literature relating to human behavioral ecology, the specific ethnographic data employed, and its application in archaeological contexts is beyond the scope of this paper, but detailed summaries are provided elsewhere (e.g., Winterhalder and Smith, 2000; Shennan, 2002; Bird and O'Connell, 2006). Particularly relevant to the main issues addressed here are several recent studies that consider the issue of forager competition from an ecological and evolutionary perspective. These focus on resource exploitation and

diet breadth, and the attendant influences these factors have on foraging efficiency and individual and group fitness (e.g., Finlayson, 2004; Kuhn and Stiner, 2006; O'Connell, 2006).

Finlayson (2004) proposes that competition between Middle and Upper Palaeolithic populations, if it occurred at all, was ephemeral and played little if any role in the extinction of the Neanderthals. This assessment is based on theoretical associations between population size and resource exploitation that suggest competition occurs only among populations at environmental carrying capacity who exploit similar resources at similar times (see Pianka, 1988). As Neanderthal populations are presumed to have been small (effective population size of 10,000–20,000), and thus below carrying capacity, the chance for competition was limited. In other words, there was ample territory to accommodate both populations within a given geographic zone, especially those containing heterogeneous environments.

Neanderthal-modern human coexistence is documented elsewhere (e.g., the Levant; Shea, 1998, 2003), which Finlayson attributes to the fact that both populations existed below carrying capacity and exploited different landscapes and geographic areas. Here he seems to suggest of a degree of allopatry, even though data highlighting niche overlap between the two populations are common during the Middle–Upper Palaeolithic "transition" (e.g., Grayson and Delpech, 2002, 2003, 2006). In those instances where Neanderthal territories were encroached upon by expanding modern humans, Finlayson argues, based on research by Wang et al. (2000), that native populations were competitively superior owing to their long-term, in-depth knowledge of local resource availability and distribution. While expansion into new territories entails risk (Kelly, 2003; Meltzer, 2003), Finlayson's conclusion implies that newcomers (modern humans) were unable to obtain and exploit such critical biogeographic information in a timely fashion. Ultimately, Finlayson attributes the cause of demographic change and Neanderthal extinction to climate change and the attendant natural contractions experienced by Neanderthal populations, especially those outside the Mediterranean zone. The potential impact of such climate change on contemporaneous modern human populations and the persistence of Neanderthal populations in refugia outside the Mediterranean zone (e.g., the Caucasus) require further consideration. That important medium–large size prey species remain viable and significant resources throughout the Upper Palaeolithic of the southern Caucasus argues against the general idea that Neanderthals may have been just another large-bodied mammal driven to extinction by Middle Pleniglacial climate fluctuations (see Stewart et al., 2003; Stewart, 2004).

Expanding forager populations who exploit a wider array of resources, and so operate a more expensive subsistence economy, typically occupy a wider array of habitats and may do so at higher densities (O'Connell, 2006). In the context of competition, such a foraging strategy can lead to the elimination of foraging opportunities among indigenous populations. Work by Stiner et al. (2000) provides evidence of increased

diet breadth among modern humans as compared to their Neanderthal contemporaries, with the former exploiting not only the same medium–large game upon which Neanderthals relied so heavily, but also smaller game that required increased effort to harvest relative to nutritional gain. Such resources are rarely encountered in Neanderthal assemblages; instead, Neanderthals appear to have focused much of their energies on the procurement of high-ranked terrestrial prey (see Stiner, 2002; Kuhn and Stiner, 2006; Speth and Clark, 2006). Under such conditions, and in combination with related factors such as specialized technologies, lower energy budgets, and larger populations, O'Connell (2006) argues that modern humans had a considerable competitive advantage over Neanderthals. Why Neanderthals did not simply adjust their economies to meet increasing subsistence pressures caused by competition can be linked to fitness-related opportunity costs that varied between males and females. Concerning subsistence, O'Connell (2006) argues that Neanderthal males had to balance efforts in the realms of alliance building and mating opportunities, perhaps via male–male competition in the arena of big-game hunting, with the need to maintain high return rates and provision their families. Shifting to a broader diet in the face of modern human competition would have required increased foraging effort, resulting in a reduction in time spent in the pursuit of other fitness-related activities, namely competition for mates.

But this proposition, which is not currently possible to test archaeologically, hinges on whether Neanderthals divided labor between the sexes in a manner similar to that commonly documented among historic and current foragers (see Kelly, 1995; Winterhalder and Smith, 2000; Bird and O'Connell, 2006). The danger of projecting recent ethnographic observations into the distant past has long been recognized (e.g., Wobst, 1978) and the question of sexual divisions of labor in the Middle and Upper Palaeolithic has recently come under greater scrutiny. For example, Kuhn and Stiner (2006) claim that, because of their narrow diet breadth, sex-based divisions of labor were untenable among Neanderthals as there were too few subsistence roles to be filled.

Consequently, because Neanderthals pursued economies more narrowly focused than their modern human counterparts (i.e., medium–large game), Kuhn and Stiner argue that females participated closely in time and space with activities more commonly associated with men (i.e., hunting). Only during the Upper Palaeolithic did a sex-based division of labor emerge in response to an increased range of subsistence and social roles, as evidenced, for example, by an increase in diet breadth, the development of specialized technologies (e.g., cordage and basketry, non-utilitarian organic items), and the production of elaborate clothing, structures, and items of personal adornment. While Kuhn and Stiner do not speculate as to the sex or age of those who took on the new roles indicated by the technological and subsistence data, they do stress the point that, unlike in the Middle Palaeolithic, diverse roles were there to be filled.

Again, it is necessary to ask why the Neanderthals did not simply broaden their resource base in the face of increasing subsistence pressures. Kuhn and Stiner (2006) argue that the risks associated with a shift to more diversified subsistence, similar to that documented for the Upper Palaeolithic, may have been too great for the Neanderthals, who are argued to have maintained populations below carrying capacity through the exploitation of high-yield but risky resources. The inability to adapt to the new socioeconomic reality created by the appearance and perhaps growth of modern human populations put Neanderthals at a competitive disadvantage, tipping the reproductive and demographic balance in favor of modern humans.

In the following pages we consider these recent studies from the perspective of Ortvale Klde, a late Middle Palaeolithic (LMP) and early Upper Palaeolithic (EUP) rockshelter located in the southern Caucasus, where recent excavations and zooarchaeological and taphonomic studies document seasonal hunting behaviors prior to and following the Middle–Upper Palaeolithic "transition." Using data on species representation, age structure, life history, sex ratios, and processing behaviors we investigate (a) whether Neanderthals and modern humans were sympatric or allopatric; (b) whether diet breadth increased from the LMP to EUP; and (c) what, if any, competitive advantage either population may have enjoyed. We believe that Neanderthals and modern humans were sophisticated, flexible foragers capable of adapting to a wide variety of stable and changing environmental conditions in response to immediate and anticipated needs, a perspective based on the well recognized ability of foragers to shift easily between different modes of subsistence and mobility on a daily, seasonal, or yearly basis (see Butzer, 1982; Kelly, 1995; Kuhn, 1995). Therefore, the data presented here should be considered dependent upon local, situational factors, and thus not necessarily reflective of all populations, in all places, at all times. We do not attempt to build a broad-based geographic model of Neanderthal and modern human behavioral variability and competition, but confine our observations and interpretations to the data currently available from the southern Caucasus.

The Faunal Assemblage of Ortvale Klde

Ortvale Klde currently represents the only stratified LMP and EUP site within the southern Caucasus to have experienced careful excavation and detailed zooarchaeological and taphonomic analyses (Bar-Oz and Adler, 2005; Adler et al., 2006a; but see Cleghorn, 2006 for an example form the northern Caucasus). The site is situated in western Georgia (Imereti region) in the Cherula river valley, approximately 530 m above sea level (m.a.s.l.) and 35 m above the gorge (Fig. 9.1). It is a karstic rockshelter comprised of two chambers opening to the east (~300 m²). D. Tushabramishvili first investigated the rockshelter between 1973 and 1992, and

excavated roughly 40 m² at the front of the southern chamber (Tushabramishvili et al., 1999; Adler and Tushabramishvili, 2004). Faunal remains from this excavation were selectively collected and analyzed by the eminent palaeontologist, Prof. A. Vekua (Georgian Academy of Sciences), for the purpose of taxonomic identification based on teeth and selected long bone epiphyses.

Excavations resumed from 1997 to 2001 under the direction of Nicholas Tushabramishvili (Georgian State Museum) and Daniel S. Adler; a sample of 6 m² was excavated at the rear of the southern chamber where stratified LMP and EUP deposits were preserved. A total of 3,209 EUP and 12,541 LMP faunal specimens were recovered. All of the excavated sediments were carefully dry-screened through 2 mm mesh and sorted for small bones; all bone fragments were collected and processed according to their spatial and stratigraphic location. The faunal remains discussed here are associated with three EUP horizons (Layers 2–4; ~19.5–34.3 ka Uncal BP) and three LMP horizons (Layers 5–7; ~38/36.5–42 ka Uncal BP) and thus span the regional "transition" from the Middle to Upper Palaeolithic (Adler et al., 2006a; Adler et al., 2008).

In the following section we summarize several of the major features of the LMP and EUP faunal assemblages from Ortvale Klde (e.g., species representation; survivorship and mortality; bone modification) while also highlighting similarities with results obtained from previously excavated material analyzed by Vekua. These data allow us to consider the diachronic change in the relative importance of species-specific hunting practices at the site in relation to faunal processing behaviors, seasonality, and mobility.

Species Representation

Our analyses support the main conclusions of Vekua (Tushabramishvili et al., 1999), with 95% of the combined 1997–2001 ungulate assemblage, based on the number of identified specimens (NISP), dominated by Caucasian tur (*Capra caucasica*; Table 9.1), suggesting that diet breadth at the site was relatively low during both the LMP and EUP. Steppe bison (*Bison priscus*) constitutes a small proportion of the assemblage (4%), and other large ungulates, such as red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) are nearly absent (<1% in each layer). Noteworthy are the even smaller proportions (≤0.5% of total assemblage) of carnivores (e.g., *Ursus* sp. and fox [*Vulpes vulpes*]). It is not currently possible to find such species-specific hunting behaviors mirrored at other Palaeolithic sites in the region or in the northern Caucasus. Within the EUP faunal assemblage of Dzudzuana Cave, located in an adjacent river valley approximately 4.6 km to the east (see Fig. 9.1; Meshveliani et al., 1999, 2004), the proportions of steppe bison and aurochs (*Bos primigenius*) increase considerably (over 40% in all levels) at the expense of Caucasian tur (Bar-Oz et al., 2007). Similarly, Barakaevskaïa Cave, located roughly 350 km northwest of Ortvale Klde in the northern Caucasus, contains a faunal
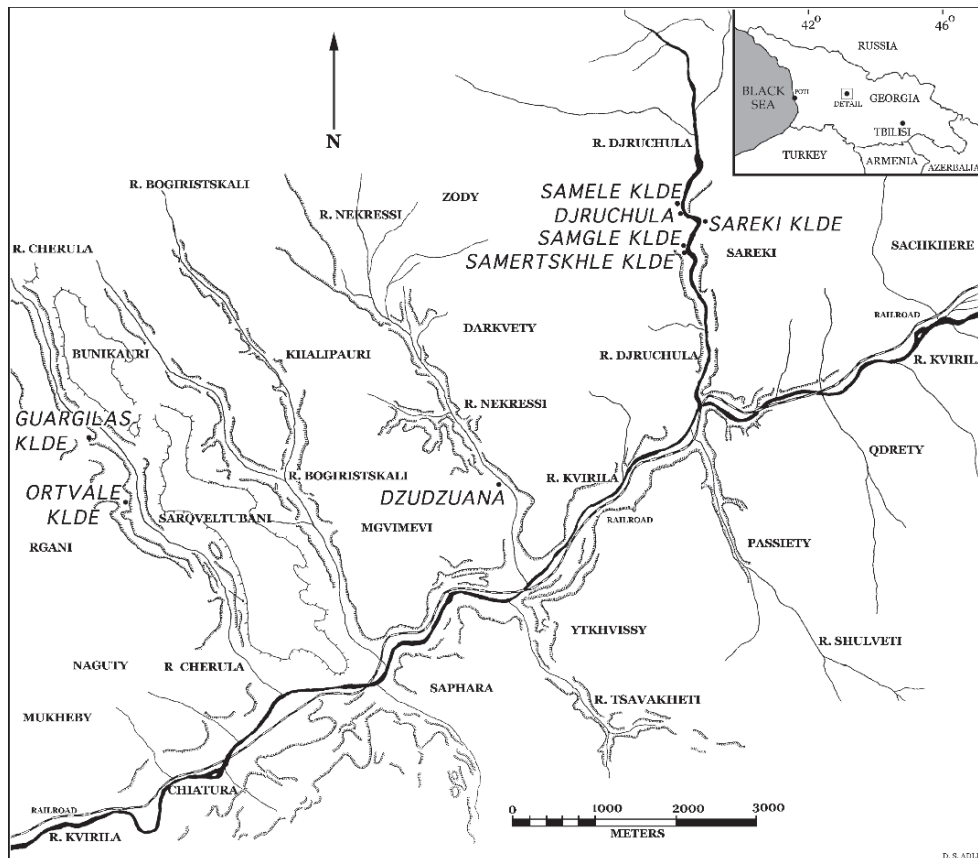
FIG. 9.1. Kvirila River Valley, Imereti region, Republic of Georgia. Archaeological sites are uppercase and italicized. Bronze Cave is located approximately 35 km due southwest (Modified after Adler, 2002).

assemblage with one of the highest frequencies of Caucasian tur (28.2%; Liubin, 1998). The recently analyzed fauna from Mezmaiskaya Cave (Cleghorn, 2006) indicates that while the frequency by NISP of *Capra/Ovis* is not as large as that for Bos/Bison, the very large number of size 2 bovid/cervids and ungulates likely represent sheep and goat. Thus, with only a few exceptions, Caucasian tur is generally poorly represented at most LMP and EUP sites in the Caucasus (e.g., Hoffecker et al., 1991; Baryshnikov and Hoffecker, 1994; Baryshnikov et al., 1996; Hoffecker and Cleghorn, 2000; Hoffecker, 2002).

Survivorship and Mortality

The age structure of the Caucasian tur recovered from Ortvale Klde was analyzed on the basis of tooth wear (see Bar-Oz and Adler, 2005; Adler et al., 2006a). Mortality profiles, expressed as 10% increments of potential lifespan (see Klein, 1976; Klein et al., 1981; Munson and Marean, 2003), of Caucasian tur for the combined LMP assemblage, determined according to dental wear height of the dP4 and M3, show that 32% of the specimens (n = 18) were hunted as juveniles (<20% lifespan), while 66% of the specimens (n = 38) were hunted as prime-age adults (between 20–70% lifespan); old adults were taken in

very low frequencies (n = 1). These data highlight a bias toward prime-age individuals (Table 9.1) and resemble LMP and EUP ungulate profiles obtained at numerous sites in Eurasia on samples of similar size (e.g., Stiner, 1994; Speth and Tchernov, 1998; Steele, 2004; Speth and Clark, 2006).

The hunting of prime-age individuals may indicate the use of 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 economically important prime-age adults. As with the species-specific hunting practices outlined above, the procurement of prime-age adults is documented elsewhere in Eurasia during the LMP and EUP (e.g., Levine, 1983; Jaubert et al., 1990; Stiner, 1990, Hoffecker et al., 1991; Stainer, 1994; Baryshnikov and Hoffecker, 1994; Speth and Tchernov, 1998; Baryshnikov and Hoffecker, 1999; Pike-Tay et al., 1999; Hoffecker and Cleghorn, 2000; Stainer, 2002; Miracle, 2005), as well as earlier periods (Gaudzinski and Roebroeks, 2000, 2003; Steele, 2004; Stiner, 2005; Speth and Clark, 2006). This situation is in line with Stiner's (2002)

proposal that carnivory, or more specifically prime-adult-biased hunting, among hominins dates to at least 250 ka and was a common adaptive feature among archaic populations. If true, then it is not surprising to find well-developed hunting skills among both Neanderthals and modern humans, especially if one considers the projected daily caloric requirements of Neanderthals (Aiello and Wheeler, 2003) or recent stable isotope studies (Bocherens et al., 1999; Richards et al., 2000, 2001; Bocherens et al., 2005; Bocherens and Drucker, 2006). In terms of hunting and niche preference it appears that Neanderthals and modern humans in the southern Caucasus were sympatric and thus in direct competition for the same limited resources.

Human Modifications

Faunal Transport, Butchery, Bone Fragmentation, and Burning

Examination of element abundance in relation to associated food utility index (FUI; Metcalfe and Jones, 1988) reveals that Caucasian tur skeletal profiles are not altered by selective transport decisions (Table 9.1). Detailed analysis of LMP skeletal part abundance shows some bias against axial elements (vertebrae and ribs) and higher representations of toes (Bar-Oz and Adler, 2005: Fig. 7). The lack of evidence for selective transport, coupled with the low occurrence of axial elements suggests that prey was subject to extensive butchery, either in the field prior to import to the site or within the site itself, and that hunters at Ortvale Klde returned large portions of carcasses to the site.

Butchery marks on Caucasian tur document all stages of carcass processing (n = 53, combined EUP and LMP assemblage): dismemberment, filleting, and skinning (Table 9.1). The overall proportion of butchery marks on Caucasian tur is low for all archaeological layers (<3%). However, the presence of cut marks from all stages of the butchering process suggests that the full range of butchering activities is represented within each layer. The most obvious similarity in butchery patterns from each layer is the location of cut marks on and around the major limb joints. We also identify higher frequencies of cut marks on head and limb bones, and fewer on axial elements and foot bones. These data indicate that Caucasian tur carcasses underwent thorough dismemberment and preparation following arrival on site, and that carcass processing included both low and high utility elements.

The intensity of bone fragmentation and the analysis of bone breakage patterns (fracture angle, fracture outline, and fracture edge) of long bone shaft fragments (Villa and Mahieu, 1991) point to the prevalence of oblique, V-shaped, and jagged bone fractures, indicating that the majority of bones from each layer were broken while fresh (Table 9.1). These data demonstrate that the faunal assemblage results from intensive bone processing, possibly related to the extraction of bone marrow. Such bone processing behaviors produce high frequencies of fresh/green fractures and likely account for the high number of small, unidentified shaft fragments within each layer. The presence of percussion fractures (Blumenschine and Selvaggio, 1988) close to the fracture edge of long bone shaft fragments (Table 9.1) and average fragment length further support this interpretation. In addition, the high rate of fresh breakage among the first phalanges (>60% in each layer) (Bar-Oz and Adler, 2005) and the low relative frequency of complete bones (22.0% of MNE; following Munro and Bar-Oz, 2005) suggest that these elements were also systematically split open for marrow extraction.

Burned specimens are observed in all of the archaeological horizons and appear randomly distributed. Layers 2 and 3 (EUP) are characterized by low rates of burning (2–3%) while within Layer 4 (EUP) and Layers 5–7 (LMP) the rate of burning increases (Table 9.1). The frequencies of burned bones among the identified Caucasian tur and bison remains are too small to analyze by anatomical unit. Burning was most common on small, unidentified fragments (n = 1,030, mean = 25 mm, SD = 11 mm) from the combined LMP sample. As Speth argues (in Bar-Yosef et al., 1992) the relationship between burning and specimen size support the view that burning is related to food preparation; if bones were accidentally burned by later activities, larger bones with bigger surface areas should display high rates of burning (Stiner et al., 1995).

Non-human Modifications

Carnivore activity (e.g., chewing, gnawing, and scratch marks) is infrequent (<10%, excluding teeth) among the identifiable elements of Caucasian tur and declines in frequency from Layers 4–7 (Table 9.1). Likewise, no signs of digestion are found on any bones in the assemblage. The non-identifiable elements (fragments >40 mm), mainly mid-shafts fragments, bear even lower rates of carnivore tooth marks (<2% in all levels), demonstrating that carnivores had only secondary access to bones (see discussion in Dominguez-Rodrigo, 2002) and that the assemblage was not accumulated or significantly altered by carnivores. Examples of carnivore marks on the inner surface of Caucasian tur bones (n = 4) further indicate that carnivores had access to discarded bones only following site abandonment by hominins.

The low frequency of carnivore damage at Ortvale Klde likely results from long-term human habitation, perhaps on the order of weeks–months, during which carnivores could not gain access to discarded remains (i.e., Bunn, 1993) or, the intensive and thorough processing of faunal resources occurred, after which little remained for carnivores to ravage (Lupo, 1995). Our results are in accordance with natural experiments and actualistic studies with captive spotted hyena (*Hyaena hyaena*) that show few carnivore tooth marks on assemblages processed by humans (Marean and Spencer, 1991; Marean et al., 1992). Decreasing rates of carnivore damage on identifiable bone fragments within the LMP layers may reflect intensive use of the site by Neanderthals.

The Seasonal Exploitation of Caucasian Tur at Ortvale Klde

Life History Characteristics

Given the economic importance of Caucasian tur to the inhabitants of Ortvale Klde, we summarize the life history characteristics of this species and discuss how such behaviors may have structured mobility and land-use patterns during LMP and EUP. Based on the data provided by Brown and Burton (1974), Heptner et al. (1988, 1989), Parker (1990), and Nowak (1991) several general observations may be made regarding species size and weight, reproduction and life cycle, diet, habitat, seasonality, and group structure (Table 9.2). These data are derived from recent observations of extant Caucasian tur populations located within small, isolated nature reserves in the Georgian Republic and on the northern side of the Caucasus, mainly in Daghastan. Although these populations have undergone some interbreeding with other closely related species, mainly East Caucasian tur (*Capra cylindricornis*), they remain important sources of information regarding Caucasian tur (Vereshchagin, 1967) and we assume that the behaviors of Pleistocene Caucasian tur were not significantly different from those of recent herds.

Body Size, Sexual Dimorphism, and Breeding

Caucasian tur, also known as the west Caucasian tur, is closely related to the east Caucasian tur in morphology and behavior. On average, adult males exhibit a body length of 150–165 cm, a shoulder height of 95–109 cm, and weigh between 65 and 100 kg. Females are on average smaller: 120–140 cm long, 78–90 cm tall, and weigh 50–60 kg. Both males and females have horns that in cross-section approximate rounded triangles. Male horns are scimitar-shaped and exhibit heavy ridges; these average 75 cm in length. The horns of females are considerably shorter and narrower, and exhibit fewer and smaller ridges. Therefore, sexual dimorphism is expressed in horn morphology and overall body size.

Breeding occurs from late November to early January, with the birth of one to two offspring in May and June, representing a 150–160 day gestation period. Weaning occurs gradually, and sexual maturity among females is reached following the second year after which they may breed annually. Among males sexual maturity is not reached until the fourth or fifth year and it is at this time that adult males compete vigorously for females. Life expectancy of both males and females is 12–13 years.

Home Range, Seasonality, Diet, and Group Size

The Caucasian tur has one of the smallest natural ranges of any ungulate today, spanning an approximately 4,500 km² region 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 avoid insects (e.g., ticks, horseflies, deerflies, and other blood-sucking pests), and downslope in October for mating and feeding (Heptner et al., 1989). They thrive in alpine meadows, barren areas, or forests, and their diet is composed of a wide variety of plants and grasses in summer and the leaves of trees and shrubs in winter. 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 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. During winter months, herds often remain in open pastures, alternately grazing and resting. Adult males (>4–5 years old) generally stay at higher altitudes than females, who are usually accompanied by young. Maternal herds of approximately 12 animals are joined by otherwise solitary males (in particular those in their reproductive prime [6–8 years old]) in the breeding season (late November–early January), during which competition for females is often violent (Heptner et al., 1989). Unfortunately, it is not clear from the literature to what extent the behaviors of sexually immature males vary from those of adult males.

During winter, the home range is much reduced (Heptner et al., 1989) and within the range Caucasian tur have the habit of utilizing the same trails, sometimes several kilometers long, for many generations. Heptner et al. (1989) note that rocks in these trails have been literally polished by the repeated passage of herds. The average population density of Caucasian tur is currently estimated at 50–160 per 1,000 ha, but due to overhunting and habitat lose related to farming and herding, these numbers likely underestimate Pleistocene population densities.

Sex Ratio

Since males are generally solitary and therefore more difficult to hunt throughout much of the year, especially the summer months, their representation within an archaeological assemblage is a sensitive indicator of season of procurement. Alternatively, an over-representation of females within the assemblage might indicate hunting prior to and/or following the breeding season when males disperse and are therefore more difficult to locate and hunt.

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). As discussed above the Caucasian tur is sexually dimorphic, with adult males being larger and heavier than adult females. The difference in weight is reflected in the breadth and width of portions of some elements. Complete astragali and, to a lesser extent, distal humeri are among the most abundant measurable skeletal elements in the assemblage. Only adult specimens (i.e., fused epiphyses and non-porous astragali) are included in the analysis. Table 9.3 presents data showing that the 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 *Capra caucasica* collected in the Caucasus at the beginning of the twentieth century (three females and four males from 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 (Kurten, 1965; Davis, 1981; Bar-Oz et al., 2004a) and is in accordance with Bergmann's rule (1847). However, since we lack specific information on the geographic origin of recent Caucasian tur specimens, the observed size difference may also be affected by spatial rather than temporal differences. The broad range of bone measurements shows that both large and small specimens are present (Table 9.3), thus it appears that both males and females are represented at Ortvale Klde.

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 1 or 2 months thereafter (Heptner et al., 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 predominant in the forest, located at lower elevations, constituting between 60–84% of the entire population (Heptner et al., 1989). Based on the limited available bone sample we suggest that Caucasian tur does and bucks were hunted in the same frequencies as they occur in recent herds at different elevations and thus within different environmental settings. Pleistocene hunters did not cull herds according to sex-based preferences. As one might expect of pre-pastoral groups, the occupants of Ortvale Klde ate what was immediately available, in this case Caucasian tur, probably in sex frequencies equal to their natural distribution within particular environments during particular seasons (see also Marks and Chabai, 2001; Bar-Yosef, 2004; Marks and Chabai, 2006).

Discussion

The zooarchaeological and taphonomic results from Ortvale Klde indicate that LMP and EUP hunters focused their foraging efforts on Caucasian tur, a high-ranked species that remained a predictable seasonal resource throughout the Middle and Late Pleniglacial. We find no evidence for the preferential culling of herds by sex and propose that the observed sex ratios reflect seasonally determined frequencies of males and females. Caucasian tur age classes demonstrate that Neanderthals exploited all age groups, with a bias toward prime-age adults, suggesting ambush or intercept hunting rather than some form of encounter hunting. As 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 no simple matter. However, the migratory and mating behaviors discussed here likely lowered search

cost and enhanced encounter rates, establishing this taxon as a high-rank food item on a seasonal basis.

The seasonal exploitation of Caucasian tur is strongly suggested by several independent lines of evidence. As mentioned above, Caucasian tur migrate upslope in May and downslope in October. While Ortvale Klde lies below the historic lower range (800 m.a.s.l.) of Caucasian tur distribution, the topography surrounding the site is quite steep and the plateau immediately above Ortvale Klde quickly reaches an elevation of 800 m. During Oxygen Isotope Stage 3 (OIS 3) the sub-alpine zone was periodically as much as 1,000 m lower than the current level due to climatic oscillations, although compared to surrounding regions, such oscillations were muted by the ameliorating affects of the Black Sea (Adler et al., 2006a, b). It is assumed that Caucasian tur populations responded to this environmental shift by reorganizing their migratory behaviors to take advantage of resources available at lower elevations. This would have placed Ortvale Klde well within the lower, late fall–early spring range of their seasonal movements and established the site as a strategic position within the landscape, serving as a central place adjacent to rich resources from which foragers radiate and to which they return (Fig. 9.2).

The bias at Ortvale Klde towards prime-age adults suggests that prey densities were high enough to allow LMP hunters to target the largest, most nutritious members of the herd. Still, bone fusion and dental wear data indicate that some juveniles (<2 years) are present in the assemblage. This pattern again suggests late fall–early spring occupation of the site when otherwise solitary males and small maternal herds with young aggregated for mating at lower elevations. Hunting efficiency would be maximized at this time due to the increased density and vulnerability of prey in and around the site. At least seasonally then, both LMP and EUP diet breadth appears to have been equivalently low.

The processing of Caucasian tur long bones indicates, not unexpectedly, that hominins extracted and consumed large amounts of fat-rich marrow. The presence of Caucasian tur heads at Ortvale Klde may further support habitation during late fall–early spring when animals were leaner and long bones contained less marrow. Brains may have been exploited at this time in order to maximize fat intake during such periods when Caucasian tur were experiencing some degree of dietary stress. If so, the most effective way of maximizing the nutritional value of brains would be through roasting (Stiner, 1994), a practice for which little direct evidence (e.g., burned cranial fragments) exists at Ortvale Klde. While the process of fat mobilization among ungulates has been outlined (Speth, 1983; Bar-Oz and Munro, 2007), the timing, actual extent, and effects of dietary stress on the fat levels of Caucasian tur remain unknown.

Speth and Spielmann (1983), and Speth (1987, 1989, 1990) demonstrate that, with respect to available ethnographic data, hunter-gatherer groups who rely on high levels of lean-meat consumption, usually in the spring, require very high kill
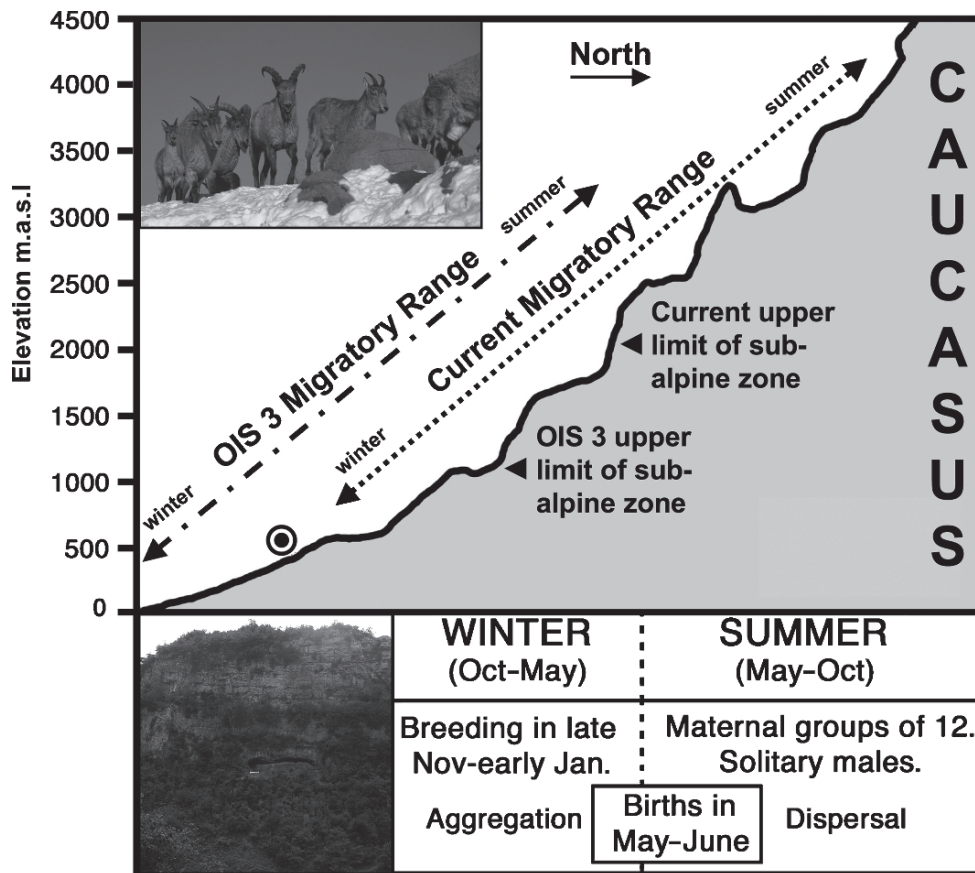
FIG. 9.2. Schematic cross-section of the Southern Caucasus (not to scale), illustrating current migratory range, and reproductive and social behaviors of Caucasian tur (*Capra caucasica*). OIS 3 migratory range is proposed. The nested circle indicates the relative elevation of Ortvale Klde. Upper left inset is a photograph of a mixed herd of west Caucasian tur (© Brent Huffman, Ultimate/Ungulate); lower left inset is a view of Ortvale Klde from the east (Photograph by D.S. Adler; Figure modified after Adler, 2002).

rates that are difficult to maintain over extended periods of time. Speth suggests that such examples likely reflect serious shortfalls in other non-protein foods, and that this subsistence approach reflects a stop-gap measure rather than a long-term solution to seasonal caloric shortages (1987: 16). Therefore, the targeting of prime-age adults, the thorough processing of marrow-rich elements, and the consumption of heads may actually indicate a strategy whereby LMP hominins at Ortvale Klde sought to maintain body fat as a hedge against predicted dietary shortfalls later in the season. According to Speth:

When under stress (i.e., losing weight and subsisting on marginal calorific intakes), hunter-gatherers would avoid high intakes of lean meat and other high-protein food sources that are low in fat or carbohydrate. Thus male ungulates of prime age or females of similar age that are neither pregnant nor lactating become principal targets of spring hunts. (Speth, 1987: 20)

The use of brains as an agent in hide tanning should also be considered. The late fall–early spring exploitation of Caucasian tur for meat and fat may have also been accompanied by the removal and preparation of skins in anticipation of colder weather and/or in association with the general need

to service or replace clothing. In this respect the seasonal availability of Caucasian tur in the Cherula valley may have marked one of the most anticipated events in the yearly subsistence cycle of hominins, during which meat, fat, and hides could be readily procured, consumed, and prepared prior to the onset of winter conditions and the anticipated declines in food availability and quality.

Species-specific hunting from late fall–early spring is a hominin behavior attested to in many parts of Eurasia (Stiner, 1994, 2002), but one that must have been predicated on an intimate knowledge of the specified prey's life history characteristics. For example, since Caucasian tur is "fixed" as a resource seasonally, it stands to reason that hominins, given appropriate weapons technology and/or organizational skills, would maximize their food gathering efforts by learning and exploiting this prey species' seasonal behaviors. If carnivores can map onto and exploit seasonally mobile terrestrial prey, why couldn't Neanderthals or modern humans (see Henshilwood and Marean, 2003)? Chasing solitary animals or small, dispersed, fast moving herds through the forests and along the steep slopes of the southern Caucasus probably did not qualify as an efficient expenditure of time

or energy. Instead, large numbers of animals or specific size/age/sex could be exploited by small groups of hunters during periods of Caucasian tur population aggregation. Such behaviors may have also resulted in the aggregation of hominins, which served multiple social and economic purposes, the exact form and function of which can only be speculated for the LMP and EUP, but which likely included the exchange of resources, knowledge, and mates.

During late spring and summer, populations of Caucasian tur disperse throughout higher elevations, thus prey densities within the immediate vicinity of Ortvale Klde were lowered, and the increased costs associated with the search for and transport of kills far from their place of procurement likely excluded the site from intensive use. To date no LMP or EUP sites have been identified at higher elevations, but it is possible that Neanderthals and modern humans followed migrating herds of into the mountains, in which case we would expect to find faunal assemblages dominated by females and young, as males are solitary at this time. It is equally plausible that hominins shifted to the exploitation of larger areas by smaller, perhaps family units during the late spring and summer. Many resources would still have remained readily available during this part of the year while others, such as large ungulates, would be dispersed and more difficult to hunt in the overgrown forests and summer vegetation. Under such conditions 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 (Kelly, 1995). If either population continued the committed pursuit of Caucasian tur during the late spring and summer, they were likely faced with higher search costs and relatively lower returns.

Regional Perspective on Seasonality in the Southern Caucasus

Based on detailed zooarchaeological and taphonomic analyses we have established a working understanding of seasonal exploitation patterns and mobility at Ortvale Klde. But how representative are these data of LMP and EUP hunting patterns at the larger regional scale? Is Ortvale Klde a special locality or is it part of a wider system of seasonally based mobility? In the following section we summarize the main zooarchaeological characteristics of three neighboring Paleolithic sites in an attempt to answer these questions. Unfortunately, in most instances the lack of secure chronometric estimates and methodological variability make such comparison difficult (see Adler and Tushabramishvili, 2004).

Faunal assemblages from most neighboring Paleolithic sites have been studied from a palaeontological perspective only and are of limited comparative value. For example, Djruchula Cave, an early Middle Paleolithic (late Middle Pleistocene–early Upper Pleistocene) site located approximately 7.5 km northeast of Ortvale Klde (Fig. 9.1), experienced palaeontological study in the 1970s and 1980s. The results indicate

the dominance of cave bear (*Ursus spelaeus*) at the base of the sequence (Layer 2) and Bos/Bison and red deer at the top of the sequence (Layer 1) (Lioubin and Barychnikov, 1984; Adler and Tushabramishvili, 2004: Table 7) (Table 9.4). These data are interpreted as evidence that cave bears and humans utilized the site intermittently, with the remains of the former resulting from deaths during hibernation (Layer 2) or perhaps human predation. In either event, competing use such as this may help explain the relatively ephemeral archaeological signature in Layer 2. The faunal assemblage from Layer 1 is most likely the result of active hunting and is accompanied by a lithic assemblage of large retouched points (see Adler and Tushabramishvili, 2004). This pattern of fluctuating site use is thought to reflect changes in faunal exploitation patterns between the two layers, although to date, systematic zooarchaeological analyses have not been conducted and the faunal assemblage is no longer available for reanalysis. Lithic and faunal data point to the intermittent (Layer 2) and task-specific (Layer 1) use of this cave, an interpretation largely consistent with that offered by previous researchers (e.g., Liubin, 1977; Tushabramishvili, 1984; Liubin, 1989; Tushabramishvili, 1994). In this respect Djruchula Cave does not represent a central habitation site, but rather a specialized hunting camp. Regrettably, the available faunal data are not of suitable quality to allow detailed consideration of seasonal foraging behaviors or diet breadth.

The faunal assemblage from Bronze Cave, one among a series of stratified LMP sites located near the village of Tsutskhvati, approximately 35 km southwest of Ortvale Klde (Fig. 9.1), contains diverse taxa, but is dominated by steppe bison (80.0% by NISP for all layers), followed by lower frequencies of Caucasian tur (10.4% by NISP for all layers) (Tushabramishvili, 1978; Adler and Tushabramishvili, 2004) (Table 9.4). This assemblage is notable because it contains a relatively high frequency of carnivore remains in each layer (3–20%), specifically cave bear (Table 9.4), however this species does not dominate the assemblage as it does in Layer 2 at Djruchula Cave (Tushabramishvili, 1978; A. Vekua, 2001, personal commmunication; Adler and Tushabramishvili, 2004: Table 9). The available lithic and faunal data suggest that Bronze Cave served periodically as a campsite but that occupations were intermittent and often ephemeral in comparison to those documented at Ortvale Klde (Adler and Tushabramishvili, 2004: Table 10). Again, the available faunal data from Bronze Cave do not allow us to consider the issue of seasonality in any meaningful way, and increased diet breadth is only weakly suggested (Table 9.4).

Dzudzuana Cave, a neighboring site contemporaneous with and archaeologically identical to the EUP of Ortvale Klde, represents a valuable comparative case. Studies by Bar-Oz et al. (2004b, 2007), employing identical research methods and protocols to those used at Ortvale Klde, show a greater reliance on steppe bison and aurochs in all layers relative to that witnessed at Ortvale Klde (Table 9.4). Direct comparisons are hampered slightly since the taphonomic histories

of the two sites are not identical, with the assemblage from Ortvale Klde spanning the full range of bone densities while that from Dzudzuana Cave is dominated by dense bones – mainly shaft fragments and teeth (Bar-Oz et al., 2007). We find that the density-mediated bias identified in Dzudzuana Cave is partially caused by in situ attrition resulting from a combination of post-depositional forces (weathering, trampling, and physical erosion). However, this observation is not likely to account for the apparent increase in steppe bison, as durable skeletal elements such as teeth are abundant among the remains of both steppe bison and Caucasian tur. While the demographic data for Caucasian tur suggests that Ortvale Klde was occupied during late fall–early spring, the demographic pattern of bison and aurochs at Dzudzuana Cave, and in particular the presence of newborn Bos/Bison, suggest that most individuals were procured during the summer and possibly early fall (Bar-Oz et al., 2007). While still relatively narrow in terms of taxonomic diversity, the data in Table 9.4 suggest a possible increase in diet breadth compared to Ortvale Klde or seasonal fluctuations in prey availability.

Unfortunately, it is difficult to construct a regional understanding of seasonal site use and species exploitation patterns based on the aforementioned data (Adler and Tushabramishvili, 2004: Table 11). Only two sites, Ortvale Klde and Dzudzuana Cave, have been studied with these specific questions in mind, while the others, Djruchula and Bronze caves, experienced excavation and analysis long before the advent of zooarchaeological and taphonomic techniques. So the question remains whether the differences observed between these sites reflect differences in seasonal hunting patterns, site use, environment, relative availability of taxa on the landscape and thus encounter rate, diet breadth, butchery and processing behaviors, taphonomy, or methods of analysis. Without the re-excavation of key sites and the discovery of new ones, this issue cannot be resolved. While it is not possible at present to assess how representative Ortvale Klde might be of regional Neanderthal or modern human hunting behaviors, the site does serve as a sensitive behavioral gauge of temporal trends in resource acquisition at a particular point on the landscape. These data demonstrate continuity between the LMP and EUP in resource knowledge and acquisition, specifically with respect to seasonal prey choice, culling practices, and niche preference.

Conclusions

Relying primarily on zooarchaeological and taphonomic analyses we document the hunting, butchering, and processing behaviors of the LMP and EUP inhabitants of Ortvale Klde and show that LMP groups targeted prime-age adult Caucasian tur and transported entire, or near entire carcasses back to the site for processing and consumption, behaviors attested also to for modern humans elsewhere across Eurasia. Consideration of Caucasian tur life history characteristics suggests that hunting activities in and around Ortvale Klde

were structured according to this species' specific migratory behaviors, which made males, females, and young locally abundant from late fall to early spring. These data allow us to build a case for the intensive, seasonal use of the site, whereby Ortvale Klde operated as a locus from which hunting forays could be launched and to which hunted prey could be returned for processing and consumption.

Where direct comparisons were possible we found no significant economic differences between the LMP and EUP. This is not surprising if we accept that Neanderthals and modern humans were top predators in their chosen environments and that, given this position in the predator-prey hierarchy, each population exploited the same niches in a similar manner, especially in the arena of medium–large game procurement. Within the southern Caucasus, where populations are largely circumscribed by their surrounding landscape (greater and lesser Caucasus mountains to the north and south, respectively; Black and Caspian seas to the west and east, respectively), it is difficult for two top predators armed with equally effective methods of acquiring ecological knowledge and the same medium–large prey to occupy the same ecological niche for long. Following the principle of competitive exclusion (see Pianka, 1988; Begon et al., 1996), we contend that if these two populations encountered one another there was little chance for long-term coexistence; two populations in direct competition for identical limited resources cannot remain sympatric, especially if one population possesses or develops a major technological, biological, demographic, or social advantage.

In this paper we document the exploitation of the same limited resources by both groups. We have also explored the differential existence of technological, biological, demographic, or social advantages in a series of recent publications (Bar-Oz and Adler, 2005; Adler et al., 2006a, b; Bar-Yosef et al., 2006), but lacking human fossil material and reliable data on demography – a perennial shortcoming of the Palaeolithic record – we have only been able to conduct tests based on technology and mobility. Regarding the former we find clear rifts in material culture across the Middle–Upper Palaeolithic "transition" represented by the abrupt and unanticipated appearance of sophisticated projectile technology (backed microliths and bone points) in the EUP, and the synchronous (within the precision of radiocarbon) disappearance of typical LMP assemblages of scrapers and Levallois technology on the southern side of the mountains (e.g., Ortvale Klde, Adler et al., 2006a, b) and para-Micoquian, non-Levallois assemblages on the northern side of the mountains (e.g., Adler et al., 2006b; Cleghorn, 2006; Mezmaiskaya Cave, Golovanova and Doronichev, 2003). In the present context it is unclear what advantage(s) this new technology offered but it may have served to increase foraging efficiency (e.g., increased kill vs. encounter rate) as well as the distance between predators and prey (Shea, 2006). Technological and tactical modifications such as these should correlate with profound alterations in hunting efficiency and thus individual and group fitness, but the faunal data from Ortvale Klde do not document any significant

difference in patterns of prey exploitation or diet breadth between those with and those without such technology. Instead cultural (stylistic) needs that serve to build and maintain social relationships between immediate and extended group members may be linked closely to the development of elaborate projectile technology. The foraging data from Ortvale Klde indicate that, at least seasonally, both Neanderthal and modern human technological repertoires were equally well suited to the task of medium–large game acquisition.

Regarding mobility, the EUP occupants of Ortvale Klde routinely exploited obsidian sources located in excess of 100 km to the south, a behavior for which there is no parallel among local Neanderthals (Adler et al., 2006a). These patterns of raw material exploitation are generally representative of both populations, with modern humans routinely exploiting relatively large territories and establishing extended social networks, while Neanderthals foraged in relatively small territories and likely interacted with far fewer individuals (Adler et al., 2006a). Given the available data, we argue that Neanderthal-modern human coexistence in the southern Caucasus, if it occurred, was probably very short, and the major behavioral edge that would have allowed modern human populations to grow at the expense of the Neanderthals was a cultural one, namely their ability to establish larger extended social networks (see Gamble, 1999; Whallon, 2006) and exploit larger territories, behaviors that in and of themselves likely elevated individual and group fitness, affording a considerable competitive advantage (see Adler et al., 2006a).

Archaeological, taphonomic and chronometric data from Ortvale Klde suggest that the arrival of modern humans likely signaled the rapid – and by all accounts permanent – cessation of local Neanderthal traditions within the southern Caucasus. Modern humans may have gained further advantage by exploiting a wider array of resources (Stiner et al., 2000; Hockett and Haws, 2005), although such data are currently lacking at Ortvale Klde and only weakly suggested at Dzudzuana Cave. This may be due to the early state of zooarchaeological and taphonomic research in the region as much as the seasonally structured economic record currently available for study. We find no evidence that Neanderthal populations attempted to broaden their resource base prior to extinction or that local densities of Caucasian tur were in decline. From a purely ecological perspective we argue that the "transition" from the LMP to the EUP in the southern Caucasus represents the replacement of one top predator (Neanderthals) by another (modern humans), with little discernable shift in the predator-prey hierarchy, the medium–large game hunted, or their seasons of exploitation. In terms of resource and niche preference, we suggest that local Neanderthal and modern human populations, if they coexisted, were sympatric to the point of exclusion.

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