Chapter 7
Rodents, Lagomorphs and Insectivores from Azokh Cave

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Abstract Azokh Cave in the Karabakh range of the Lesser Caucasus has yielded one of the richest small mammal assemblages yet reported from the entire Caucasus region. Over 2770 dental and cranial remains from at least 24 taxa of insectivore, rodent and lagomorph have been studied from the Middle/Late Pleistocene (Units II–V) and Holocene (Unit 1) deposits at Azokh 1. Holocene samples were also studied from Azokh 5. The small mammal assemblages are dominated throughout by arvicoline rodents indicative of dry steppes and semi-deserts. Notable species include several regionally extinct arid-adapted or montane taxa, such as *Ochotona* (pika), *Marmota* sp. (marmot), *Spermophilus* sp. (ground squirrel), *Chionomys nivalis* (snow vole) and *Allactaga* spp. (jerboa). Hamsters (*Mesocricetus* sp., *Cricetulus migratorius*), jirds (*Meriones* spp.) and mole voles (*Ellobius* sp.) are also well represented throughout the sequence. Habitat preferences of extant representatives of the rodent and lagomorph fauna suggest that the landscape surrounding the cave was dominated by grassland/steppe interspersed with rocky ground. Small mammals that prefer more humid conditions and woodland or scrub vegetation are present as rare components of the Pleistocene fauna. Unit Vu has yielded the earliest Caucasian record of rat (*Rattus* sp.), a species previously thought to have been a relatively recent (late Holocene) introduction. Several species recovered from the Pleistocene and Holocene deposits are now scarce or no longer live in the region, adding to evidence for distributional changes of these taxa in the latter part of the Pleistocene and Holocene. The small mammal fauna shows broad similarities to those from semi-desert and steppe regions to the south, implying dispersals from the adjacent parts of Asia; there appear to be only tenuous links with the Pleistocene small mammals north of the Caucasus.

Резюме Азохская пещера, расположенная в горной цепи Карабаха (Малый Кавказ), является ключевой стоянкой для понимания развития кавказской малой фауны в эпохи плейстоцена и голоцена. Большая коллекция грызунов, зайцеобразных и насекомоядных (землеройка и крот), обнаруженная в период археологических раскопок 2002–2009 гг., включает в себя более 23 таксонов из различных горизонтов верхней части седиментной последовательности (подразделения *I–V*). Найденные образцы находятся в прямой ассоциации с останками по крайней мере двух видов гоминид (*Homo heidelbergensis* в *пласте V* и *Homo sapiens в пласте I*) наряду с мустерианскими артефактами в подразделениях *IV–II*, указывающими на возможное присутствие *H. neanderthalensis*. Проливая свет на четвертичную биогеографию различных видов мелких млекопитающих, обнаруженные образцы представляют собой прямые свидетельства экологических условий в период пребывания человека на данной стоянке.

Среди обнаруженных мелких млекопитающих доминируют грызуны подсемейства полевковых, особенно представители групп *Microtus arvalis* и *M. Socialis*, которые указывают, соответственно, на превалирование луговой и степной растительности. Наиболее распространенные виды, обнаруженные в пещере, относятся к различным, адаптированным к аридным или гористым условиям, таксонам, таким как *Ochotona* spp. (пищуха), *Marmota* sp. (сурок), *Spermophilus* sp. (бурундук), *Allocricetulus* sp. (хомяк), *Chionomys nivalis* (снеговая полевка) и *Allactaga* spp. (тушканчик). Хомяки (*Mesocricetus* sp., *Cricetulus migratorius*), песчанки (*Meriones* spp.) и слепушонки (*Ellobius* sp.) также хорошо представлены во всей последовательности отложений. Средовые предпочтения ныне живущих представителей грызунов и зайцеобразных

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Yolanda Fernández-Jalvo et al. (eds.), *Azokh Cave and the Transcaucasian Corridor*,
Vertebrate Paleobiology and Paleoanthropology, DOI 10.1007/978-3-319-24924-7_7

свидетельствуют о том, что в ландшафтном окружении пещеры доминировали луга и степи с вкраплением скалистых пород. У основания седиментной последовательности (подразделение *V*) находки включают мелких млекопитающих, что свидетельствует о более мезонных условиях с древесной или кустарниковой растительностью. Эти таксоны сохранились в качестве редких элементов в некоторых расположенных выше горизонтах. Пока еще невозможно определить, является ли комбинация таксонов, адаптированных к аридным или умеренным условиям, результатом гетерогенности среды или смесь отдельных групп находок появивилась по причине перемежения периодов с более теплыми/влажными и более холодными/сухими условиями.

Обнаружение останков крысы (*Rattus* sp.), представленной тремя особями из различных горизонтов подразделения *IV*, заслуживает особого внимания. Ранее считалось, что род *Rattus* появился здесь относительно недавно, но находки в Азохе доказывают его присутствие в регионе уже в эпоху среднего плейстоцена. Различные виды, найденные в плейстоценовых и голоценовых отложениях, уже не встречаются в данном регионе, что свидетельствует об изменении в структуре фауны в течение поздних фаз рассматриваемых геологических периодов. Фауна мелких млекопитающих имеет большое сходство с животным разнообразием полупустынь и степей, расположенных южнее, указывая тем самым на приход этих биологических форм из юго-западной Азии; вместе с тем отмечаются только слабые связи с плейстоценовыми мелкими млекопитающими Кавказа.

Keywords Biogeography • Lesser Caucasus • Pleistocene • Small mammals

Introduction

Small mammal research has provided significant insights into environmental and climatic history and biogeography. For example, in a number of recent studies, Quaternary small mammals have proven fundamental to achieving an understanding of the long-term history of mammalian communities (e.g., Blois et al. 2010; López-García et al. 2010; Schmitt and Lupo 2012), in reconstructing colonisation patterns and pacing (Barnes et al. 2006), to infer mode and rates of evolution (Martin 1993), and in the quantification of past changes in climate (e.g., Andrews 1990; Marean et al. 1994; Schmitt et al. 2002; Barnosky et al. 2004; Navarro et al. 2004). Small mammals are also routinely used in archaeological work to elucidate the environmental impact of early agriculture and urbanism (Tchernov 1991; O'Connor 1993; Audoin-Rouzeau and Vigne 1997; Cucci et al. 2005; Terry 2010) and to characterize the environments and landscapes in which past human activity took place (e.g., Agadjanian 2006; Cuenca-Bescós et al. 2009; Louchart et al. 2009; Rodríguez et al. 2011; Stoetzel et al. 2011). Ethnographic studies show that small mammals were commonly collected for food and pelts, and there is a growing body of archaeological evidence demonstrating that small mammals were also similarly exploited in the past (Stahl 1996; Fernández-Jalvo et al. 1999; Weissbrod et al. 2005; Jin et al. 2012).

Bones and teeth of small mammals are often abundant in a range of depositional environments (Falk and Semken 1998) and are especially common in caves occupied by predatory birds (Andrews 1990). Accurate interpretation of fossil small mammal assemblages is reliant on correct taxonomic identification of unbiased samples (usually recovered by fine-mesh sieving), combined with information on its taphonomic history (Andrews 1990; Fernández-Jalvo and Andrews 1992; Fernández-Jalvo et al. 2011).

Quaternary small mammals in the Lesser Caucasus are scarce but important for reconstructing the paleoenvironment of early humans in the region (Pinhasi et al. 2008, 2011; Dennell 2009). Only a few cave sites in the Lesser Caucasus have been sampled for small vertebrates, and most of these contain relatively short sequences, dating to the Late Pleistocene or Holocene (Vereschagin 1967; Pinhasi et al. 2008, 2011). The presence of abundant small mammal remains from Azokh Cave offers the opportunity to scrutinize the small mammal assemblages from a longer sequence that extends into the Middle Pleistocene.

Azokh Cave is situated in the foothills of the Karabakh mountain range at the south-eastern end of the Lesser Caucasus, at an elevation of about 960 m above sea level.

The site was discovered in 1960 by M.M. Huseinov and subsequently excavated by his team. These excavations led to the discovery of a stratified succession of Middle Palaeolithic and Acheulean industries with a purported ‘Pebble Culture’ at the base of the sequence. In addition to stone tools, the 1968 excavation recovered a mandible fragment now attributed to *Homo heidelbergensis* (King et al. 2016). The importance of the paleoenvironmental evidence at the site was recognized by Velichko et al. (1980), who collected small mammal remains from nine levels (Markova 1982). Markova recorded 12 genera of lagomorphs and rodents, noting a prevalence of steppe species throughout the sequence. Since 2002, renewed excavations have recovered a much larger small mammal assemblage, together with herpetofauna (Blain 2016), fishes, birds and bats (Sevilla 2016). As well as many of the common taxa identified by Markova (1982) the new assemblage includes at least 13 small mammal taxa not previously known from the site.

In this chapter, preliminary results from the taxonomic identification of the small mammals collected between 2002 and 2009 are outlined. The primary aim is to shed light on the environmental conditions that characterized the region during its occupation by early humans. Subsidiary aims are to investigate the shifts in geographical distribution of small mammal taxa and biogeographical composition of the assemblages through the sequence.

Materials and Methods

Small mammals were recovered from all strata in the upper sequence (Units I–V), but the lower sequence was devoid of small mammal material. The specimens were concentrated by wet-screening excavated sediment, using sieves with a 0.5 mm mesh. Most of the samples were sieved in the field by the excavation team and the resulting residues were air-dried and sorted in the site laboratory. Five hundred and sixty-seven small bags of material sorted from these residues were examined for faunal remains. Two-thirds of the bags (n = 241) derive from Unit II and 28% (n = 161) from Unit I. A further 34 (6%) derive from Unit III, 35 (6%) from Unit Vu, and 131 (23%) from Unit Vm.

In 2002, a separate series of 32 samples from Unit Vu was processed in London and the residues were meticulously sorted with the aid of a variable-magnification binocular microscope. These samples yielded particularly rich and diverse small vertebrate assemblages comprising mostly isolated teeth. Nine of these samples were selected for detailed study in order to obtain a small mammal succession covering the complete stratigraphic sequence of Unit Vu.

Every bone fragment from the sieved samples has been retained and the cranial remains cleaned and numbered sequentially. The preservation of the small mammal remains was generally good throughout, with some physical breakage, but little sign of weathering, rounding or soil corrosion (Andrews et al. 2016). However, many of the bones were partially encrusted by manganese and carbonate concretions. Where these obscured diagnostic surfaces and diagnostic features of the teeth, the specimen was cleaned using a combination of chemical (buffered dilute acetic acid) and careful mechanical preparation.

Isolated cheek teeth, mandibles and maxillae were used for taxonomic identification. Small mammal identifications were confirmed using descriptions in the literature (e.g., Kryštufek and Vohralík 2001, 2005) and direct comparison with the osteological reference collections. Ecological affinities and distributions of individual taxa were obtained from Aulagnier et al. (2009), Vereschagin (1967) and Vinogradov and Argiropulo (1968). Nomenclature and taxonomic order follows IUCN Red List of Threatened Species (IUCN 2010).

Results

In all, some 2770 small mammal cheek teeth, mandibles and maxillae from Azokh were analysed. These were picked from many thousands of unidentified rodent and insectivore post-cranial bones. The results are presented in Tables 7.1 and 7.2, and plotted graphically in Fig. 7.1, where each species is shown as a percentage of the total. In the five lithologically defined horizons, Unit Vu accounts for 75% of the identifiable elements, with 12% from Unit I, while Unit II, III and Vm had around 4% of the total assemblage each.

Table 7.1 Stratigraphical occurrence of insectivores, lagomorphs, rodents and small carnivores from Azokh 1

Unit	Vm	Vu	III	II/III	II	I
Lipotyphla						
Soricidae						
Sorex minutus group		+				
Sorex araneus group	+	+				+
Crocidura spp.	+	+	+	+		+
Talpidae						
Talpa sp.	+					
Carnivora						
Mustelidae						
Mustela nivalis		+				
Lagomorpha						
Ochotonidae						
Ochotona spp.		+	+		+	+
Leporidae						
Lepus sp.		+				+
Rodentia						
Sciuridae						
Marmota sp.					+	
Spermophilus sp.					+	
Muridae						
Cricetulus migratorius	+	+			+	+
Mesocricetus sp.		+	+		+	+
Allocricetus sp.	+	+			+	
Clethrionomys glareolus	+	+	+			
Microtus arvalis/socialis	+	+	+	+	+	+
Microtus (*Terricola*) spp.	+	+	+		+	+
Chionomys nivalis	+	+			+	+
Chionomys gud	+	+				+
Ellobius sp.	+	+	+	+	+	+
Meriones spp.		+	+	+	+	+
Apodemus spp.	+	+	+		+	+
Rattus sp.		+				
Mus cf. *macedonicus*		+	+			+
Gliridae						
Dryomys nitedula		+				
Dipodidae						
Allactaga spp.		+				+
NISP[a]	120	2065	121	17	101	346

Notes
Ochotona spp. – two or more species (including one similar to *O. rufescens* and one much larger species) are present in Unit Vu
Microtus arvalis/socialis group – Based on M_1 and M^2 morphology, members of both groups are present throughout sequence
Pine voles – Probably more than one species, but difficult to separate on basis of M_1 morphology
Meriones spp. – possibly as many as three species in Unit Vu (small, medium and large forms). Small *Meriones* also present in Units I and III, with medium-large forms in Units I, II and III
Allactaga spp. – Unit Vu, large and small forms; Unit I, large form only
[a]– Number of identified specimens based on cranio-dental elements

Unit Vm

The fine-grained silts, clays and loams (c. 4.5 m thick), immediately above the limestone floor in the interior of the cave, yielded the oldest small mammal assemblages studied here. A peculiar feature of the small mammal bones from this horizon is that a proportion of the teeth have characteristics that suggest that they have a different taphonomic history from the rest of the bones in the assemblage, possibly resulting from differences in burial environment or digestion (Andrews et al. 2016). Mostly this takes the form of the teeth being lighter in colour than other teeth from the same sample. On the whole the material was well preserved with most of the cheek teeth *in situ*. However, this may reflect selective picking of more complete and easily recognisable specimens. Reworking or incorporation into the deposit of more recent small mammal remains can probably be excluded as the deposit has not been disturbed by burrowing. The differences in preservation may simply reflect lumping of material from different subunits within the Unit. Evidence of digestion is seen on many of the arvicolid molars with a pattern and degree of digestion suggesting that a category 1 predator (probably barn owl *Tyto alba*) was the primary agent responsible for accumulating the small mammal bones in Unit Vm (Andrews et al. 2016).

Archaeological material recovered during the recent excavations includes possible Acheulian artefacts. Unit Vm also yielded the partial human mandible found in 1968. Further indications for human activity may include evidence of burning, with some small mammals affected.

The small mammal fauna from Unit Vm is moderately diverse with at least 12 taxa, dominated by arvicoline (microtine) rodents (Table 7.1). Other rodents include hamsters, mole voles and mice; insectivores are rare, but include both red-toothed (*Sorex araneus* group) and white-toothed shrews (*Crocidura*), as well as mole (*Talpa* sp.). The arvicoline assemblage includes first lower molars of pine voles (*Microtus* (*Terricola*) spp.) and *M. arvalis* group/social voles (*Microtus arvalis/socialis*). The first lower molars (M_1) of the *arvalis* group and social voles are difficult to distinguish morphologically, but the second upper molars (M^2) can be distinguished by the presence of an extra loop, which is common in the social voles but absent in the *arvalis* group (Kryštufek and Vohralík 2005; Kryštufek and Kefelioğlu 2008). Ecologically, the distinction between these two groups is important as social voles inhabitant dry steppes and semi-deserts, whereas voles of the *arvalis* group prefer humid grassland. This is reflected in their current distributions in the southern Caucasus, where the social vole is found in steppic and semi-desert regions (e.g., Azerbaijan shrub desert and steppe, and Eastern Anatolian montane steppe), while the *arvalis* voles (*Microtus arvalis* and *M. levis*) are found throughout the 'Caucasian mixed forest' zone; Azokh Cave is located close to the boundary between these two regions (Vereschagin 1967). In the Unit Vm assemblage, a relatively high percentage of the M^2s lack an additional loop (Fig. 7.1), suggesting that the *arvalis* group was present and relatively abundant in the region when this unit was deposited. Relatively humid conditions supporting scrub and woodland may be indicated by the presence of *Apodemus*, which is also well represented in the assemblage, as well as the bank vole *Clethrionomys glareolus*.

From a zoogeographical perspective, the most significant taxon is undoubtedly *Clethrionomys glareolus*. This species is today found no closer than the 'Euxine-Colchic deciduous forest' bordering the Black Sea in Georgia and Turkey. Its preferred habitat in this region includes coniferous, mixed and deciduous woodland. Two other vole species no longer found in the Azokh region are the snow voles *Chionomys nivalis* and *Chionomys gud*, which are represented in the Unit Vm assemblage by single specimens. The European snow vole (*Chionomys nivalis*) has a patchy distribution restricted to rocky and mountainous habitats across southern Europe and Asia (Castiglia et al. 2009). It is found in the Lesser Caucasus, but its distribution does not extend as far east as Azokh (Vereschagin 1967). The Caucasian snow vole (*Chionomys gud*) is also closely associated with open rocky habitats, but it inhabits a wider range of montane habitats, including sparse fir and spruce forests, alpine meadows and in valleys with streams or small rivers. Although endemic to the Caucasus and the easternmost part of the Pontic Mountains of Turkey, it is scarce in the Lesser Caucasus and occurs no closer to Azokh than south-west Georgia.

Relatively common in the assemblage are rooted cheek teeth of mole voles *Ellobius* sp. Mole voles are highly specialized fossorial voles that feed on underground storage organs of plants and especially starchy tubers and bulbs. They are particularly common in mountain grassland and steppes, but also inhabit thin soils of rocky mountainsides and sandy semi-deserts. The only species found today in the southern Caucasus is the Transcaucasian mole vole *Ellobius lutescens*, with a distribution in arid regions bordering the Lesser Caucasus, approximately 100 km from Azokh. Another indicator of dry grassland, steppes and semi-deserts is the grey hamster *Cricetulus migratorius*, which has a strong preference for arid areas with relatively sparse vegetation; it avoids forests and damp areas.

Overall, the assemblage contains a mixture of species indicative of woodland or scrub and temperate/humid conditions, together with obligate inhabitants of arid open habitats, as well as montane species that require rocky habitats.

Unit Vu

The small mammal assemblage from this unit is by far the richest in number of remains as well as the number of taxa (Tables 7.1 and 7.2). Samples processed in London yielded nearly all the material ($n = 2022$), with only 43 identifiable cranial elements from samples processed on-site. The greater concentration of small vertebrates in the laboratory-processed samples may be due to better preservation, differences in recovery techniques or a higher concentration of small mammal bones possibly relating to proximity of the roost sites. Small mammal samples were

Table 7.2 Stratigraphical occurrence of small mammal taxa and number of specimens from Azokh 1 and 5. The Azokh 5 assemblage was obtained during preliminary sampling of the Holocene deposits (Unit A)

	Azokh 1						Azokh 5
Unit	Vm	Vu	III	II/III	II	I	Holocene
Lipotyphla							
Sorex minutus group		4					
Sorex araneus group	1	2				1	
Crocidura spp.	1	48	1	1		1	1
Soricidae gen. et sp. indet.		7				2	
Talpa sp.	1						
Carnivora							
Mustela nivalis		1					
Lagomorpha							
Ochotona spp.		37	1		3	3	
Lepus sp.		1				1	
Indeterminate lagomorph		23				3	
Rodentia							
Marmota sp.					1		
Spermophilus sp.					1		
Cricetulus migratorius	4	23			1	3	6
Mesocricetus sp.		25	1		4	25	1
Allocricetus sp.	1	2			1		
Indeterminate hamster		2				9	
Clethrionomys glareolus	1	6	1				
Microtus arvalis/socialis	41	227	25	4	17	33	11
Microtus (*Terricola*) spp.	4	15	2		2	1	
Chionomys nivalis	1	3			1	1	1
Chionomys gud	1	2				1	
Indeterminate vole	50	1152	76	9	57	211	3
Ellobius sp.	5	95	6	1	3	18	1
Meriones spp.		235	5	1	2	20	
Apodemus spp.	9	84	1		8	8	
Rattus sp.		3					
Mus cf. *macedonicus*		61	2			2	
Dryomys nitedula		1					
Allactaga spp.		2				3	
Total	120	2065[a]	121	17[b]	101	346	24

Totals include: [a]two indeterminate murid molars, fragment of insectivore tooth and an incisor fragment from a large rodent, [b]one indeterminate rodent maxilla with extremely worn M^{2-3}

analysed from nine different levels within the succession (Fig. 7.1), each with between 94 and 261 identified specimens per sample.

The preservation of the small mammals was good, although many of the bones and teeth have a coating of mineral deposits. Small mammal teeth from Unit Vu exhibit a different pattern of digestion to the other levels and include a small number of heavily digested molars and an overall pattern of alterations consistent with a category 3 predator most likely the European eagle owl *Bubo bubo* (Andrews et al. 2016). Eagle owls feed on a wider variety of prey than do barn owls and this may account for the high diversity of microvertebrate remains in this level (Table 7.2).

Rodents are by far the most numerous group (number of identified specimens (NISP) = 1931), with soricids (NISP = 73) and lagomorphs (NISP = 61) making up just 3.5 and 3% of the assemblage, respectively. A single weasel (*Mustela nivalis*) tooth represents the only identifiable small carnivore from this unit.

Shrews are represented by the *Sorex minutus* group, the *Sorex araneus* group and *Crocidura* (white-toothed shrews). *Crocidura* is by far the most common shrew and at least two species are represented. There are several unresolved taxonomic issues with this group of shrews (Kryštufek and Vohralík 2001), particularly in the Caucasus, where as many as five species have been recorded. There is very little information available regarding the distribution, habitat and ecology of several of these species, for example *Crocidura armenica*, Armenian white-toothed shrew, *Crocidura caspica*, Caspian white-toothed shrew and *Crocidura serezkyensis*, Serezkaya shrew. Diagnostic dental characters that can be used to identify fossil dental material from the

Caucasus have not yet to be described, which has made it difficult to identify the Azokh soricids. Nevertheless, it is possible to make some observations on palaeoecology. Eurasian white-toothed shrews avoid dense forest, but have wide habitat preferences that include subtropical humid lowlands, dense tall grass and rocky areas in mountains, dry Mediterranean shrubland and densely vegetated damp areas near water. In arid areas, white-toothed shrews tend to be mainly associated with humid conditions near springs and water courses. Red-toothed shrews include rare specimens of a small shrew of the *Sorex minutus* group and specimens of the larger *Sorex araneus* group (Zaitsev 1998; Zaitsev and Ospipova 2004). Caucasian red-toothed shrews, for example *Sorex volnuchini*, Caucasian pygmy shrew, *Sorex raddei*, Radde's shrew and *Sorex satunini*, Caucasian shrew, prefer humid environments with dense vegetation often in forest; they also inhabit alpine meadows.

Microtus voles are overwhelmingly the dominant small mammals in the assemblage. Voles of the *arvalis/socialis* group are particularly numerous, with a predominance of social voles indicated by M^2 morphology. Voles of the *Microtus* (*Terricola*) group are less common, and it has not been possible to identify these beyond genus level. Caucasian Pine voles are found in a range of habitats: *Microtus daghestanicus* (Daghestan pine vole) and *Microtus nasarovi* (Nasarov's pine vole) prefer pastures, alpine meadows (both mesic and dry) and steppe; *Microtus majori* (sibling vole) favours clearings in forests and shrubland, as well as alpine pastures; *Microtus schidlovskii* (Schidlovsky pine vole) is more closely associated with xerophytic steppes and meadow-steppes.

The pika, was originally identified as an element of the Azokh fauna by Markova (1982), who recorded several cheek-teeth, which she attributed to *Proochotona*. More recent work has revised the taxonomy of this material, and suggests that two species are present, including one with morphological affinities to *Ochotona rufescens* (Čermák et al. 2006). Isolated and fragmentary pika teeth are relatively common in the current sample. At the present stage of analysis it is difficult to determine the number and identity of the species represented. Today, *Ochotona rufescens* (Afghan pika) is the only pika species found in the Lesser Caucasus. The Afghan pika is a widespread species that occurs in the mountains of Pakistan, Afghanistan, parts of Turkmenistan, Iran, eastern Turkey and Armenia. Holocene subfossil finds suggest that the pika was formerly more widespread with finds from several sites in the Caucasus from southern Armenia and Georgia (Čermák et al. 2006). Pikas prefer habitats with relatively sparse vegetation cover and favour steppe, rocky deserts and mountains.

Two species of hamster, *Cricetulus migratorius* (grey hamster) and *Mesocricetus* are equally common and occur together, with much rarer material of a small hamster provisionally assigned to *Allocricetus* (see Hír 1993; Kowalski 2001 and Cuenca-Bescós 2003 for contrasting views on the validity of this genus). *Cricetulus migratorius* and *Mesocricetus* are good indicators of dry grassland, steppes and semi-deserts.

Similar habitats are indicated by *Ellobius* (mole vole) and *Meriones* (jird). The jird sample may include more than three species, however, and taxonomic identification of isolated jird teeth is notoriously difficult, so that at the current stage of analysis it is not possible to take the identifications beyond the genus level. Today, five jird species are found in the Lesser Caucasus: *Meriones Dahlia* (Dahl's jird), *Meriones lybicus* (Libyan jird), *Meriones persicus* (Persian jird), *Meriones tristrami* (Tristram's jird) and *Meriones vinogradovi* (Vinogradov's jird). Jirds are strong indicators of arid conditions and desert, semi-deserts and steppic habitats.

Mus cf. *macedonicus* (Macedonian mouse) is the dominant murid in Unit Vu. This mouse is found in a wide range of habitats, including sand dunes, Mediterranean shrubland and densely vegetated riverbanks. It is absent from dense forests, and in Mediterranean regions it is restricted to areas that receive more than 400 mm of rain per year. It is common and widespread in the southern Caucasus at the present day.

Mice of the *Apodemus* group are also present in relatively large numbers in Unit Vu. The Caucasus region is notable for its high diversity of *Apodemus* species (Filippucci et al. 1996, 2002; Frynta et al. 2001; Çolak et al. 2007), some of which are difficult to distinguish from isolated cheek teeth alone. In terms of ecology, most of the species are dependent on woodland or shrubland, but most can also be found in more open situations, including reed beds and pastures (*Apodemus agrarius*) and open grasslands (*Apodemus uralensis*), provided suitable cover is nearby.

Rare remains of a large murid indistinguishable from *Rattus* sp. (rat) are of considerable significance. The material consists of three molars (M_1, M^1 and M_3), each from different samples. The Azokh material of this rat is in the same state of preservation as the associated small mammal teeth and there is no question of modern intrusion. Although humans have unwittingly transported rats around the world, *Rattus* has been shown to be a genuine member of Pleistocene faunas in the Near East, having been recorded from Palaeolithic sites in Israel and Turkey (Santel and von Koenigswald 1998; Ervynck 2002). These finds suggest that *Rattus* colonized these regions surprisingly early, spreading naturally from its assumed area of origin in southeastern Asia during the Pleistocene.

A single tooth of *Dryomys nitedula* is the sole record of forest dormouse from Azokh Cave. Although its common name suggests a woodland animal, the species inhabits a broad variety of habitats, including broad-leaved, mixed and coniferous woodland, as well as evergreen shrubland and dense herbaceous vegetation. In mountainous areas it also lives in boulder-fields and alpine pastures. *Dryomys nitedula* inhabits the Azokh region today. Its distribution extends into the nearby steppe, where it is closely associated with densely vegetated banks of streams and rivers.

A small number of highly distinctive cheek teeth of jerboas have been found. Three species are currently found in the Caucasus, the small five-toed jerboa (*Allactaga elator*) and Williams's jerboa (*Allactaga williamsi*) are both found in the southern Caucasus, whereas the larger great jerboa (*A. major*) has a range that extends into northern foothills of the Caucasus. Jerboas are highly specialized for a saltorial way of life and are good indicators of local steppe and semi-desert with hard ground; marshy areas, dense grass and thicket vegetation are avoided.

Although there is no suggestion of any clear taphonomic change during the period when the Unit Vu sediments were accumulating, changes in faunal composition through sequence are apparent. These hint at fluctuations in local ecological conditions during the deposition of this unit, with humid conditions at the base, becoming increasingly arid, followed by a return to more humid conditions in the upper samples (Fig. 7.1).

One notable feature of the assemblage is the presence of charred and calcined bones and teeth in the upper part of the sequence (Fig. 7.1). Charcoal has also been recovered from this unit (Allué 2016). Peak values for burnt bone abundance were encountered in the middle of the sequence, with up to 6.5% of the teeth either charred or calcined. Burnt material also occurs in the upper part of the sequence, but at much lower frequencies (0.4–2.1%). The presence of butchered large mammal in this horizon suggests that the burnt small mammal material is probably linked to human activity in the cave, possibly through the lighting of fires on surfaces where bones had already accumulated.

Unit III

This unit yielded a total of 121 identifiable cranial elements (Table 7.2). Overwhelmingly the most important small mammals are voles of the *Microtus arvalis/socialis* group. All of the *Microtus* M^2s ($n = 17$) have an extra loop indicative of the social voles group. This dominance suggests steppe or semi-desert habitats were prevalent, a conclusion supported by the relatively high numbers of mole voles and jirds. The remaining taxa, represented by at most two specimens each, include white-toothed shrew (*Crocidura* sp.), pika (*Ochotona* sp.), murids (*Apodemus* sp., *Mus* cf. *macedonicus*), hamster (*Mesocricetus* sp.) and voles (*Clethrionomys glareolus*, *Microtus* (*Terricola*) spp.). The presence in this small assemblage of *Clethrionomys glareolus* is noteworthy. None of the teeth are burnt (possibly due to the small size of the sample). Digested rodent teeth are present in Unit III, but the sample is too small to identify the type of predator responsible for accumulating the small mammal bones (Andrews et al. 2016).

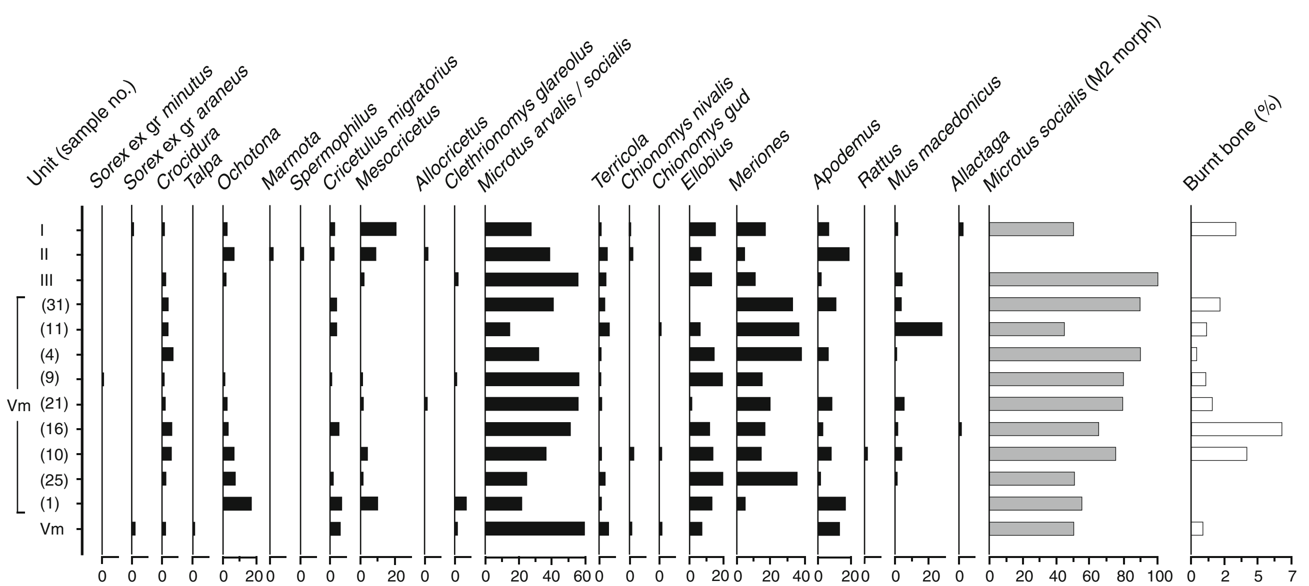

Fig. 7.1 Stratigraphical distribution and relative abundances of rodent taxa at Azokh 1. The taxa are arranged in an approximate ecological order with 'humid' taxa on the left and 'arid' taxa on the right. Values of taxonomic abundance are expressed as percentages of the total number of identified small mammal specimens, excluding all arvicoline molars other than M_1s. Alteration by burning was noted as either charred (blackened) or calcined (ash grey with flaking or mosaic cracking) as described by Preece et al. (2007). Fluctuations in the numbers of burnt bones may indicate differences in the intensity of fire use or changes in the nature of the human occupation. Fire intensity appears to vary with environmental conditions, as indicated by changes in the relative proportions of steppic voles (*M. socialis* group) and mesic grassland voles (*M. arvalis* group and *Terricola* sp.) through the sequence

Unit II

This unit is relatively poor in small mammals and only 101 identified cranial remains were recovered. The sample is noteworthy as it includes the only record of ground squirrel (*Spermophilus* sp.) from the site and the sole specimen of marmot (*Marmota* sp.) from the recent excavations (Tables 7.1 and 7.2).

Geochemical evidence suggests that the poor preservation of vertebrate fossils in this unit may be due to highly alkaline burial conditions and leaching of the organic content of the bones associated with localized accumulations of bat guano (Murray et al. 2016). On the whole, however, the small mammal material is rather well preserved with no obvious signs of post-depositional corrosion of the teeth. The pattern and degree of digestion on the small mammal teeth suggests that they were accumulated by a category 1 predator (Andrews et al. 2016).

Ecologically, the assemblage is consistent with steppe with areas of rocky ground and arid conditions. The ecological significance of *Apodemus* is unclear as the sample may include species adapted to open conditions. Rare elements, such as marmot are also closely associated a variety of open and steppic habitats. Today, marmot (*Marmota bobak*) lives no nearer than the Ukraine and southern Russia in the valley of the Don River, although isolated populations of marmot were present in the Caucasus Mountains as recently as the early 1900s (Vereschagin 1967). A more extensive distribution occurred during the Late Pleistocene, when marmots inhabited large parts of the periglacial zone in Eurasia (Zimina and Gerasimov 1973). Markova (1982) recorded a single specimen of marmot from Azokh Cave (level 10). In the northern Caucasus, marmot bones have been identified from Kudaro I (associated with Lower and Middle Palaeolithic artefacts), Akhalkalaki (Early Pleistocene), both in Georgia, and Matuzka Cave and Mezmajskaya Cave in the Krasnodar region, Russia (Nadachowski and Baryshnikov 1991). Ground squirrels also inhabit steppe, semi-deserts and rocky mountain slopes, avoiding areas with dense high grasses. Today, ground squirrels are no longer found in the Caucasus Mountains, but in the southern Caucasus region, the Asia Minor ground squirrel (*S. xanthoprymnus*) extends into northern part of the 'Eastern Anatolian Montane Steppe' to the east of Yerevan (Gür and Gür 2009).

Unit I

The Holocene sediments in Azokh 1 rest unconformably on Unit II. This unit contains much material from the burning of animal excrement and food waste when the cave was used to house livestock (Fernández-Jalvo et al. 2016). The small mammal remains are notable for the relatively high percentage (over 3%) of charred and calcined teeth. Human activity in Azokh 1 has also resulted in disturbance of the Pleistocene deposits and reworking of Late Palaeolithic stone tools, which were found together with pottery and other recent artefacts.

The Holocene levels in Azokh 1 yielded 346 identified cranial remains, and a smaller assemblage ($n = 25$) has also been recovered from Holocene deposits in Azokh 5 (Table 7.2). Overall, the small mammals are consistent with open conditions. In terms of taxonomic composition, the assemblage includes several taxa such as *Ochotona* sp., *Ellobius* sp., *Allactaga* sp., *Chionomys nivalis* and *Chionomys gud*, that appear to be absent from the environs of Azokh at the present day. Whether any of these represent reworked Pleistocene material cannot be resolved without direct dating of individual specimens. It may be significant that both *Ellobius* sp. and *Chionomys nivalis* are also present in the Holocene sediments in Azokh 5. Another small mammal that has shifted its range during the Holocene is *Ochotona*. According to Vereschagin (1967), pika is present at a number of Holocene localities in the Lesser Caucasus, where it no longer lives.

Discussion

The sequence of small mammal assemblages from Azokh Cave adds significantly to our knowledge of the Transcaucasian small mammals. There appears to be no significant turnover of rodent and insectivore taxa at any particular level, and all samples examined contained similar rodent and insectivore assemblages. At its broadest level this could signify that comparable environments existed throughout the deposition of the Middle (Unit V) to Late Pleistocene (Units III and II) sediments at Azokh, with subtle differences in faunal composition indicating changes in aridity and temperature, combined with fluctuations in woodland cover and the proximity of trees to the site. Interpretation of the Holocene small mammal assemblage from Azokh 1 is problematic as there is evidence of mixing; however, the less disturbed Holocene sediments in Azokh 5 offer the possibility of recovering a better-resolved sequence for this time period.

The Pleistocene small mammal faunas consist predominantly of species that today are associated either with open dry environments or with rocky biotopes; woodland species are rare throughout the sequence. In terms of biogeography, the fauna has a strong Asiatic aspect, with many species typical of steppe and semi-desert environments. This picture is broadly comparable to the results of earlier small mammal analyses undertaken by Markova (1982).

Taphonomic analysis of the small mammal assemblages has identified similar taphonomic trajectories for all five major stratigraphic units (Andrews et al. 2016). The results

Table 7.3 Small mammal species present in the southern Caucasus (Georgia, Armenia and Azerbaijan) and within a 50 km radius of Azokh Cave, (Y) compiled from the *IUCN Red List of Threatened Species* (IUCN 2010). Introduced species are not included

	Azokh region
Lipotyphla	
Erinaceidae	
Erinaceus concolor, eastern European hedgehog	Y
Erinaceus roumanicus, northern white-breasted hedgehog	
Hemiechinus auritus, long-eared hedgehog	Y
Soricidae	
Sorex volnuchini, Caucasian pygmy shrew	Y
Sorex raddei, Radde's shrew	
Sorex satunini, Caucasian shrew	
Neomys teres, Transcaucasian water shrew	Y
Crocidura armenica, Armenian white-toothed shrew	
Crocidura caspica, Caspian white-toothed shrew	
Crocidura leucodon, bicoloured white-toothed shrew	Y
Crocidura serezkyensis, Serezkaya white-toothed shrew	Y
Crocidura suaveolens, lesser white-toothed shrew	Y
Suncus etruscus, Etruscan shrew	Y
Talpidae	
Talpa caucasica, Caucasian mole	
Talpa levantis, Levant mole	Y
Lagomorpha	
Ochotonidae	
Ochotona rufescens, Afghan pika[a]	
Leporidae	
Lepus europaeus, brown hare	Y
Rodentia	
Sciuridae	
Sciurus anomalus, Caucasian squirrel	
Spermophilus xanthoprymnus, Asia Minor ground squirrel	
Muridae	
Cricetus Cricetus, common hamster	
Cricetulus migratorius, grey hamster	Y
Mesocricetus brandti, Brandt's hamster	Y
Mesocricetus raddei, Ciscaucasian hamster	
Clethrionomys glareolus, bank vole	
Arvicola terrestris, water vole	Y
Chionomys gud, Caucasian snow vole	
Chionomys nivalis, snow vole	
Microtus arvalis, common vole	Y
Microtus daghestanicus, Daghestan pine vole	Y
Microtus levis, sibling vole	
Microtus majori, sibling vole	Y
Microtus nasarovi, Nasarov's vole	
Microtus schelkovnikovi, Schelkovnikov's pine vole	
Microtus schidlovskii, Schidlovsky pine vole	
Microtus socialis, social vole	Y
Ellobius lutescens, Transcaucasian mole vole	
Meriones dahli, Dahl's jird	

(continued)

Table 7.3 (continued)

	Azokh region
Meriones lybicus, Libyan jird	Y
Meriones persicus, Persian jird	Y
Meriones tristrami, Tristram's jird	Y
Meriones vinogradovi, Vinogradov's jird	Y
Micromys minutus, harvest mouse	
Apodemus agrarius, striped field mouse	
Apodemus flavicollis, yellow-necked mouse	
Apodemus hyracinus, Caucasian mouse	
Apodemus mystacinus, broad-toothed mouse	
Apodemus ponticus, Black Sea mouse	Y
Apodemus uralensis, pygmy field mouse	Y
Apodemus whitherbyi, steppe field mouse	Y
Mus macedonicus, Macedonian mouse	Y
Nannospalax nehringi, Nehring's blind mole	
Gliridae	
Glis glis, fat dormouse	Y
Dryomys nitedula, forest dormouse	Y
Dipodidae	
Allactaga elater, small five-toed jerboa	?
Allactaga williamsi, Williams's jerboa	
Sicista caucasica, Caucasian birch mouse	
Hystricidae	
Hystrix indica, Indian crested porcupine	

[a]Although several authors have reported pika bones in Eagle owl pellets from the southern Caucasus region (Čermák et al. 2006), pikas have not been observed in the wild in Transcaucasia or the Armenian highlands of Turkey and Iran

suggest that most of the small mammals were brought to the site by barn owls (Units Vm, II, I and possibly III) and European eagle owls (Unit Vu), where the remains of their food were habitually deposited in regurgitated pellets around their roosts and nests. The dominant role of these two open-country hunters in accumulating the small mammal remains provides additional support for the persistence of extensive areas of open vegetation within their hunting range.

The small mammal assemblages from Azokh consist of mixtures of taxa with no modern analogue, including species which either no longer live in the region or which are extinct (i.e. *Allocricetus*). Although most of the small mammals identified from Azokh Cave inhabit the region today, the assemblage includes at least eight rodent and lagomorphs that are no longer found in the vicinity of the site (Table 7.3). These can be divided into arid-adapted species that favour steppic and semi-desert conditions, and a second group that includes mesic rodents, which inhabit high altitudes in the Caucasus region at the present day. The arid-adapted rodents include jerboas (*Allactaga*) present only in Units Vu and I. Today, jerboas are found no closer than the arid regions along the eastern and southern borders of Nagorno-Karabakh. In this region, two jerboa species are commonly found: the small five-toed jerboa *Allactaga elater*, which prefers areas with a mixture of vegetation in deserts and semi-deserts, and Williams's jerboa *Allactaga williamsi*, which favours steppe regions with sparse vegetation. It is possible that jerboas occurred closer to the site in the recent past, before irrigation and agricultural degradation of their habitats (IUCN 2010). Mole voles, present in Units Vu, Vm, III, II and I, also favour xeric habitats, such as dry grassy habitats, meadows and semi-deserts. The nearest population of *Ellobius*, represented by the Transcaucasian mole vole *Ellobius lutescens*, is located some 70 km to the east of Azokh, but its main area of distribution is further to the south and extends as far as the Zagros Mountains in central Iran. Similar environments are also inhabited today by the ground squirrel (*Spermophilus*), which was present in Unit II. Today, the nearest population of ground squirrels to Azokh is the Asia Minor ground squirrel (*S. xanthoprymnus*), which is found no closer than the Armenian border with Turkey (Gür and Gür 2009). Another open-ground extralimital small mammal is the pika (*Ochotona*) represented in the Azokh assemblage by fossils from Units Vu, III, II and I. The identity of the *Ochotona* from Azokh is currently uncertain. Ecologically, pikas are closely associated with open landscapes, typically rocky habitats and steppe. Similar habitats are occupied by marmots (*Marmota*), which today mainly inhabit alpine meadows and steppes, from lowland plains to hills and rocky outcrops in mountains. At Azokh the single record of marmot comes from Unit II. Vereschagin (1967) noted that marmots were present in the Caucasus during historical times and suggested that the contraction in range and eventual extirpation of the Caucasian marmot may have resulted from persecution and over-hunting.

The second group of extralimital species includes the bank vole (*Clethrionomys glareolus*), which occurs only in low frequencies at Azokh. This vole, present in Units Vu, Vm and III, is a typical woodland species that is closely associated with mesic habitats and relatively low temperatures. It has a western (mainly European) Palaearctic distribution and, with the exception of the humid coastal belt to the south of the Black Sea, the northern slopes of the Taurus mountains and spruce forests of the Adzhar-Imeretian range, is absent from the southeastern Mediterranean. Vereschagin (1967, p. 323) speculated that the bank vole 'penetrated the Black Sea coast very late, during the period of maximum cooling in the Upper Pleistocene', from the southern Balkans and Asia Minor. The new records from Azokh, however, document a much earlier incursion, with a history extending at least into the Middle Pleistocene.

Finally, the two species of snow vole, *Chionomys gud* (Units Vu, Vm and I) and *Chionomys nivalis* (Units Vu, Vm, II and I), are inhabitants of humid mountains and rocky habitats. The snow vole *Chionomys nivalis* inhabits mountain forests, alpine habitats with overgrown rocky taluses and steppe meadows; it is also found amongst rocks on mountain slopes. Its current distribution includes most of the higher mountains in the Lesser Caucasus, but it does not appear to reach as far as Azokh at the present day. The distribution of the Caucasian snow vole *Chionomys gud* includes the Greater Caucasus, with isolated populations occurring in southern Georgia and northern Turkey. It prefers more humid conditions than the snow vole and is most common in the alpine or subalpine zone. Alpine meadows and rock taluses overgrown with pine, birch and willow are favoured habitats.

The occurrence of a mixture of small mammals, today found at high altitude, together those that live in mesic woodland and steppic or semi-desert environments poses interesting questions in terms of the paleoenvironmental interpretation. Several scenarios may account for such 'mixed' assemblages. For example, the assemblage may include an amalgamation of formerly stratified faunas from different habitats and climatic conditions that became mixed at death or during burial. Such assemblages can also result from time averaging where bones accumulate together over a long period of time and incorporate elements from different, temporally discrete environments. The latter factor is a particular problem during periods of rapid climatic change and in burial contexts with a low sedimentation rate (Roy et al. 1996). This situation may have pertained at Azokh Cave, where the fossiliferous deposits span at least 300,000 years, during which global temperatures alternated between relatively short interglacials and longer glacial periods, both incorporating numerous shorter (millennial, centennial or even decadal) high-amplitude climatic oscillations (Dansgaard et al. 1993; McManus et al. 1999; EPICA 2004; Jouzel et al. 2007). In Asia Minor and the Caucasus, these temperature oscillations were associated with marked changes in precipitation; as a consequence the region experienced alternating periods of aridity and increased humidity. Palaeobotoanical studies of pollen and plant macrofossils from southern Georgia (Connor 2006) and Armenia (Ollivier et al. 2010) show that the vegetation was largely controlled by aridity during the entire Pleistocene, with wetter periods supporting woodland and more arid (generally colder) conditions associated with an expansion of the steppic vegetation (Dodonov et al. 2000; Connor 2006; Markova and Puzachenko 2007; Kehl 2009; Litt et al. 2009; Ollivier et al. 2010, but see El-Moslimany 1987). Today, Azokh is located close to the boundary between a semi-arid subtropical climate characterized by semi-deserts or dry shrubland-steppe, and a region with a thermo-moderate humid climate that supports forests of hornbeam, oak and pine. Even relatively minor perturbations in rainfall and climatic fluctuations are therefore likely to have resulted in significant changes in the distribution of small mammals and other biota during the Pleistocene. At Azokh Cave, comparisons between different environmental proxies would appear to indicate a heterogeneous landscape with a mix of open-ground and woodland/mesic elements during the deposition of the fossiliferous units. The wood charcoal from Unit Vu, in particular, provides conclusive evidence that broadleaved deciduous woodland grew near the site, whereas the associated small mammals indicate an essentially open environment (Andrews et al. 2016). If these represent contemporaneous samples of the local biota, a much steeper environmental gradient is indicated, possibly combining a relatively high biotic diversity with contrasting local ecological niches, which could have supported the non-analogue Pleistocene fauna (cf. Stafford et al. 1999).

The occurrence of other sites with a relatively good record of small mammals in the Caucasus may help to clarify aspects of the ecological background, dating and biogeographical context of early human occupations in this region. For example, the cave deposits at Hovk (Pinhasi et al. 2008, 2011), has yielded small mammals from the same horizons that contain archaeological evidence for sporadic and low-intensity human occupation during the Late Pleistocene and Holocene. Hovk-1 is located approximately 200 km to the northwest of Azokh, but at a higher altitude (2040 m above sea level). Although the climatic context of the human occupation at Hovk-1 is less clear, the nature of the archaeological record contrasts markedly with that from Azokh Cave, where the higher density of butchered bones and stone tools indicate greater continuity of human occupation, as well as more intensive use of the cave. The contrasting archaeological signature at these two cave sites suggests that in the Lesser Caucasus range conditions at higher altitudes were less favourable for human occupation than at sites located at lower elevation, bordering the Transcaucasian plain (Pinhasi et al. 2011). The Hovk-1 fauna shares many small mammal species with that of Azokh, with the notable inclusion of common hamster *Cricetus cricetus*. Today, the common hamster occupies an extensive range, stretching from Western Europe to the Altai Mountains in Asian Russia, wherever there is suitable fertile steppe or grassland. The presence of common hamster at Hovk-1 is biogeographically significant, as its current range does not cross the Greater Caucasus range. In contrast, the Azokh small mammal faunas have a stronger affinity with the region to the south of the Caucasus Mountains, with the notable presence of the bank vole suggesting earlier links with the Balkans and Asia Minor.

Although Transcaucasia is geographically at the crossroads between the Mediterranean, Europe and Asia, the Pleistocene small mammal fauna suggests that the region cannot simply be considered as a passive corridor linking these areas. Throughout much of the Pleistocene (Gabunia et al. 2000), the Greater Caucasus Mountains formed a major climatic and topographical barrier separating the east European plain to the north from the Transcaucasian highlands to the south; this separation is clearly reflected in the small mammal faunas on either side of the mountains. There is stronger evidence for refugia during Pleistocene glacial periods when the region was surrounded by 'hostile' arid, hyper-arid and periglacial landscapes, with extensive glaciation in the mountains (Hoffecker 2002; Dennell 2009). During these intensely cold periods, the region sheltered a large number of temperate plant species, including so-called 'Tertiary relics', which require warm and humid conditions to grow (Connor 2006). Pockets of relatively stable, climatically favourable conditions are also indicated by the presence of many endemic animals, including several small mammal species. Identifying the location(s) of these refugia, and their potential for sustaining early human occupation, will require the excavation and study of fossil remains from further well-dated, stratified archaeological sites in the region.

Conclusions

1. There is no significant turnover of rodent and insectivore taxa through the stratigraphic sequence of Azokh 1, and all samples examined contained broadly similar rodent and insectivore assemblages.
2. This could signify that comparable environments existed throughout the deposition of the Middle (Unit V) to Late Pleistocene (Units III and II) sediments at Azokh, with small differences in faunal composition.
3. The small mammal assemblages from Azokh consist of mixtures of taxa with no modern analogue, including species, which either no longer live in the region or which are extinct (i.e. *Allocricetus*).
4. In terms of biogeography, the fauna has a strong Asiatic aspect, with many species typical of steppe and semi-desert environments.
5. Transcaucasia is geographically at the crossroads between the Mediterranean, Europe and Asia, but the Pleistocene small mammal fauna suggests that the region acted more as a barrier to small mammal dispersal rather than as a passive corridor linking these areas.
6. The area formed refugia during Pleistocene glacial periods when the region was surrounded by arid, hyper-arid and periglacial landscapes, with extensive glaciation in the mountains.
7. Taphonomic analysis of the small mammal assemblages has identified taphonomic trajectories for all five major stratigraphic units: prey assemblages of barn owls (Units Vm, II, I and possibly III) and European eagle owls (Unit Vu).
8. There is a mixture of small mammals from different habitats: some found only at high altitude mixed with those that live in mesic woodland and steppic or semi-desert environments.
9. The small mammal faunas consist predominantly of species that today are associated either with open dry environments or with rocky biotopes; woodland species are rare throughout the sequence.
10. These differences could indicate minor changes in aridity and temperature, combined with fluctuations in woodland cover and the proximity of trees to the site.

Acknowledgments We are indebted to Glenys Salter and Lena Asryan for their meticulous sorting of the sieved residues. David Harrison is thanked for help with the identification of problematic specimens.

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