Chapter 15
Paleoecology of Azokh 1

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Abstract The fauna and flora from Azokh 1 are analyzed to provide evidence on past and present environments. The large mammal fauna was accumulated by carnivore and human agents, and it is dominated by woodland species. The small mammals, amphibians and reptiles were accumulated mainly by avian predators, barn owls and eagle owls which hunt over open areas, and their prey may have been brought to the cave from some distance away. The amphibians and reptiles indicate warm dry conditions, with some taxa specific to mountainous regions and many indicating warm arid conditions. The small mammals similarly indicate mainly arid environments with minor elements from deciduous woodland. The difference between small vertebrates and large mammals is taphonomic, and all four groups indicate slight transition to more arid conditions up the section. Bats are present in all units, and it appears likely that they are derived from natural deaths within the cave. They indicate woodland conditions low in the section changing to a treeless, arid and cold environment towards the top. Plant data from charcoal indicate that the regional vegetation was broadleaved deciduous woodland with mainly small trees and shrubs. The location of the cave on the lower slopes of the mountains of the Lesser Caucasus is close to the forest/steppe boundary, with forest on the mountain slopes and steppe on the lowlands to the east, and relatively minor fluctuations in climate would shift the boundary or and down slope, towards or away from the cave, with changes in climate. It is concluded, therefore, that the large mammals and flora represent the local woodland environment, and the small mammals, reptiles and amphibians represent prey species brought from further away.

Резюме Материал по фауне и флоре из пещеры *Азох 1* проанализирован с целью получения предметных свидетельств о древней и современной экологии стоянки. В сегодняшней экофлоре окрестностей Азоха доминируют граб, дуб и ясень, которые встречаются на склонах горы, где расположена пещера; степной ландшафт находится ниже к востоку и не ближе 4–5 км к пещере. Локализация пещеры близко к краю гор Малого Кавказа указывает на то, что незначительные изменения климата могли повлиять на границу между лесом и степью по направлению к пещере или от нее.

Исследованы пять стратиграфических единиц – от подразделения *V* у основания седиментной последовательности, возрастом не более 200 тыс. лет, до недавних отложений голоцена в подразделении *I*, возрастом около 12 тыс. лет. Распределение мелких млекопитающих в отложениях *Азох 1* отличается от такового у крупных млекопитающих, указывая на различные тафономические траектории. Фауна крупных млекопитающих свидетельствует о присутствии хищников и человека; мелкие формы – земноводные и рептилии, имеющие сходное распределение в пяти стратиграфических слоях, – привнесены в пещеру главным образом хищными птицами. Фаунальные данные по земноводным и рептилиям указывают на преобладание теплых сухих условий с параллельным присутствием некоторых таксонов, специфичных для горных регионов и свидетельствующих о теплом аридном климате с небольшой тенденцией к более засушливой среде

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на поверхности отложений. Присутствие мелких млекопитающих также указывает на преимущественно степную экологию с редкой растительностью из лиственных деревьев. Максимальная плотность лесной растительности зарегистрирована в основании подразделения *V*, с постепенным повышением аридности по направлению к ее вершине. Останки крупных млекопитающих, напротив, свидетельствуют о смешении преимущественно лиственных лесов с незначительным компонентом из аридных и степных элементов; кроме того, обнаружены признаки большей аридности на вершине подразделения. Данные, полученные из фрагментов древесного угля, показывают, что растительность в окрестностях пещеры была представлена широколиственными формами – главным образом низкорослыми деревьями и кустарниками. Различия между экологическими сигналами от крупных млекопитающих и других источников информации объясняются тафономически; по общему мнению, пещера была расположена близко к границе лес/степь в течение всего рассмат-
риваемого периода, а сама граница поднималась вверх и опускалась вниз вместе с изменением климата.

Keywords Taphonomy • Armenia • Nagorno-Karabakh • Ordination • Fossil fauna • Fossil flora • Hominins

Introduction

The flora and fauna from Azokh 1 are investigated to reconstruct the paleoecology of the region during the middle to late Pleistocene. Sources of evidence for the reconstructions presented here draw on the following chapters in this volume: Chap. 6, large mammals by Van der Made et al.; Chap. 7, small mammals by Parfitt; Chap. 8, bats by Sevilla; Chap. 9, amphibians and reptiles by Blain; Chap. 13, phytoliths by Scott et al.; Chap. 14, charcoal by Allué. In addition, Chap. 10 on large mammal taphonomy (Marin-Monfort et al. 2016) is complemented in the present chapter with observations on small mammal taphonomy, both prerequisites for interpreting paleoecology.

Azokh Cave is situated in Nagorno-Karabakh, at 850 m asl, and about 200 m above the nearby village of Azokh. It is situated is on the edge of the mountains, opening into a broad river valley (Ishxanaget River) sheltered by the mountains of the Lesser Caucasus to the north and west. Drainage at the present time is to the south and east, and evidence of the cave formation indicates this was the case in the past (see Fig. 3 in Fernández-Jalvo et al. 2004, 2010). It is close to the transition from broadleaved forest on the mountain slopes (to the west) to arid steppe on the low-lying land to the east.

The biota is analyzed by stratigraphic unit (Murray et al. 2016; Domínguez-Alonso 2016), and the five sedimentary units are briefly summarized here. All units have produced mammal fossils and almost all also have evidence of human occupation. The most abundant mammals are *Ursus spelaeus* and up to 13 species of bats. Cervids and bovids are also relatively abundant, with several species of carnivore, including large felids and canids. There are at least 20 species of rodent and four lagomorph species, and the reptile and amphibian fauna includes three anurans, at least four lizards and seven snakes. Some species are present in all units, such as the cave bear, and many are present in several units, while others occur in only one, such as bison in Unit II; rhinoceros (*Stephanorhinus*) and badger in Unit Vu; and wolf, jackal, hyaena, *Megaloceros* and roe deer in Unit Vm. The taxonomy of the fauna and flora is described in other chapters of this volume, and the species lists from these chapters are summarized at the end of this chapter.

The stratigraphic sequence at Azokh 1 is as follows: (Murray et al. 2010, 2016):

- Unit Vm is the lowest part of the fossiliferous section excavated so far. It is a reddish-brown clay loam unit in which the partial mandible of Middle Pleistocene hominin was found (Kasimova 2001). *Ursus spelaeus* is common in this unit as is *Cervus elaphus*. Stone tools are present (Asryan et al. 2016).
- Unit Vu rests conformably on Unit Vm; it is a friable medium greyish-brown calcareous clay. Fossil remains include *Ursus spelaeus* and herbivore fossils (Van der Made et al. 2016) bearing cut marks related to human butchery (Marin-Monfort et al. 2016). The small mammal fauna is by far the largest in the Azokh 1 sequence.
- Unit IV has not yet been excavated, but it appears to contain lithics and mammal fossils, including cave bears.
- Unit III is a medium tan-brown clay. Fossil remains of mainly cave bears are abundant together with Mousterian stone tools.
- Unit II is a reddish-brown sandy loam, but it has been strongly diagenetically altered in the center of the passageway by accumulations of bat guano, and this has affected preservation of fossil bones. Next to the cave walls, neither the sediment nor the fossils have been altered and both have characteristic dark red-brown color. Fossils include mainly cave bears, some with cut marks. Stone tools of Levallois technology (Asryan et al. 2016) are present.
- The top of Unit II has an erosional disconformity obscuring the transition to Unit I, which is a 1.35–1.5 m thick, reddish-brown friable to loose clay.

Almost all units show evidence of human activity: hearths in the upper level, stone tools and cut marked bones in all levels. Faunal remains associated with human activity consist mainly of low meat- and marrow-bearing elements, including numerous fibulae, hand and foot bones, mostly complete. This pattern suggests that those bones that were not worth transporting due to low nutritional content were abandoned in the cave (Marin-Monfort et al. 2016). In Unit II this pattern slightly changes. This unit yields complete large limb bones of bears usually found close to the cave walls; these bones would have been highly rich in marrow, and they are found together with highly broken bones and stone tools. This pattern suggests that some of the bones may derive from hibernation deaths and were not eaten, perhaps because of advanced decay. In contrast, Unit Vm shows bear and herbivores bones, as well as stone tools, scattered and dispersed, suggesting no clear pattern of occupation.

Materials and Methods

The fossil material is housed in the Stepanakert Museum. All identifications have been accepted without change from the other chapters in this volume, and the method of analysis adopted here is based on their taxonomic identifications. In some cases, the species present in the faunas and floras are extant, and direct comparison can be made with the environments where these taxa occur today. In the case of the mammals, some are extant and some extinct, and the faunal analysis of the fossil faunas uses the Taxonomic Habitat Index (THI) derived from weighted averages ordination of living species (Gauch 1989; Andrews 1990). The Taxonomic Habitat Index, as its name implies, is based on data that are primarily taxonomic, for the fossil material is not complete enough to employ methods such as ecomorphology (Kappelman 1988). Bats, amphibians and reptiles were not available for taphonomic analysis, and these also are not included in these analyses.

Habitat Weightings

Taxonomic lists of species are ordinated by weighted averages, a simple ordination technique (Whittaker 1948; Rowe 1956; Gauch 1989). It is designed to produce additive ordination scores based on previous knowledge of species from known habitats. The ordination scores for each habitat type investigated are based on the sums of the habitat weightings of the constituent species for each habitat (Gauch 1989) using an ecological scale based on the range of habitat preferences of each species. A seven habitat system is used here based in part on climate, in part on degree and type of vegetation cover and in part on altitude. There is some redundancy in this system, and for the purposes of the Azokh 1 paleoecological analysis some comparisons will be limited to three or four of the categories. The seven habitat types are as follows:

- Tundra – Characteristics of tundra include: extremely cold climate, low biotic diversity, simple vegetation structure, poor drainage, short season of growth, large population oscillations. Trees are absent or are low growing in protected areas.
- Boreal forest – Characteristics of boreal forest include very low temperatures, precipitation is primarily in the form of snow, cold dry winters and moist warm summers, the soil is thin, nutrient-poor, and acidic, trees mainly conifers, tree canopies may be dense so that ground cover is limited, and the flora consists mostly of cold-tolerant evergreen conifers with needle-like leaves, such as pine, fir, and spruce.
- Deciduous forest – Characteristics of temperate deciduous forest include moderate but variable temperature varying from –30 to 30 °C, precipitation is distributed evenly throughout the year, the soil is fertile, enriched with decaying litter, the tree canopy is moderately dense and allows light to penetrate, resulting in well-developed and richly diversified understory vegetation and stratification of animals, and the flora is characterized by 3–4 tree species per km^2. Trees are distinguished by broad leaves that are lost annually and include such species as oak, hornbeam, beech, hemlock, maple, basswood, cottonwood, elm, willow, and spring-flowering herbs.
- Mediterranean forest – Characteristics include hot dry summers and cool wet winters, the soil is less fertile as leaf litter is limited, and many of the tree and shrub species have sclerophyllous adaptations in which the leaves of the trees and shrubs are hard, thick, leathery, evergreen and usually small. These adaptations allow the plants to survive the pronounced hot, dry season.
- Steppe – Characteristics include dry areas of grassland with hot summers and cold winters, plants are usually greater than 30 cm tall, the soil is deep and dark, with fertile upper layers. It is nutrient-rich from the growth and decay of deep, many-branched grass roots. The rotted roots hold the soil together and provide a food source for living plants.
- Arid or semi-arid – Characteristics include low rainfall and extreme variations in temperature, soil ranges from sandy and fine-textured to loose rock fragments, gravel or sand, may develop caliche hardpans, vegetation with limited diversity of trees and shrubs, deciduous and often protected by thorns, ground vegetation sparse and dominated by annuals.

The full geographical range of each of the mammal species, taking into account seasonal variations, is assessed and is weighted according to the estimated importance of the above habitats to individual species across its species range and taking account of seasonal variation. For example, a species living mainly in boreal forest but ranging into tundra during the summer and into deciduous forest during winter, would be weighted as follows: boreal 0.6, tundra 0.3, deciduous forest 0.1. The weighting is both the most important aspect of this method, and it's most controversial, for there is limited information on habitat ranges for many mammal species. After each species is given its weighting, the habitat scores for all species present in a unit can then be added together, and when divided by the number of species it gives an average weighted score for each habitat for that faunal unit.

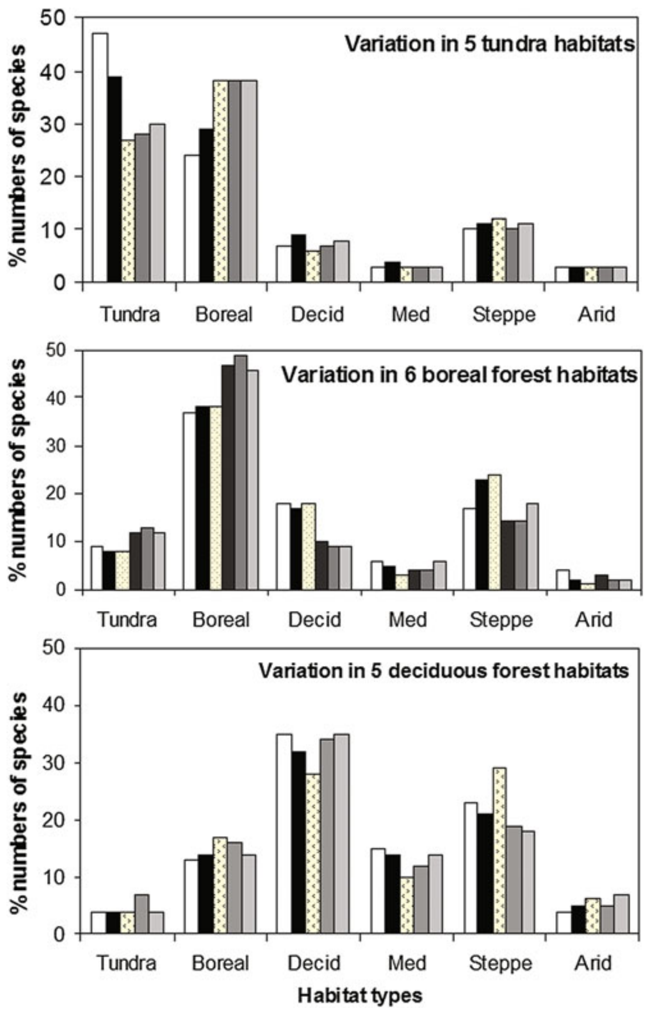


Fig. 15.1 Weighted average scores for modern temperate faunas (excluding bats). Top, average scores for five tundra faunas are shown as differently shaded bars for each locality. The five faunas are clustered as tundra and boreal forest, the two habitats which share many mammal species and between which there is considerable movement seasonally; middle, average scores for six boreal forest faunas, which show that large parts of the boreal faunas are restricted to this biome; and where there is movement across biomes it is into deciduous forest and steppe rather than tundra; bottom, average scores for five deciduous woodland faunas, which show highest numbers in deciduous woodland (Decid) and overlap in mammal distributions with Mediterranean woodlands (Med) and steppe and to a lesser extent with boreal forest. The locations of all 16 recent faunas are given in Andrews (2006)

To illustrate the degree of variation of the ordination scores for modern faunas of known habitat, Fig. 15.1 shows results from the analysis of 16 recent faunas from three ecological zones, the tundra biome, boreal forest biome and the temperate deciduous woodland biome (Andrews 2006). These 16 faunas show variations in habitat within each of the three biozones, and they were based on well documented habitats compiled from the literature (references in Andrews 2006). The tundra biome index (converted here into percentages) has high values for both tundra and boreal forest, for few mammals can subsist exclusively in tundra habitats. By contrast, the boreal forest faunas are dominated by boreal forest ordination values, with lower values for tundra, deciduous woodland and steppe environments. Similarly, the deciduous woodland faunas are dominated by deciduous woodland ordination values but with some boreal forest and steppe representation.

Calculation of Taxonomic Habitat Index (THI)

Extant species present in a fossil fauna can be assigned the habitat weighting of their living counterparts and their habitat ranges ordinated as described above. Where fossil species are extinct, however, their habitat preferences are unknown. If we can attribute the fossil species to an extant genus, the habitat weighting for all living species in that genus can be averaged to produce a genus score which can then be applied to any extinct species of that genus. This is the basis for calculation of THI scores (Evans et al. 1981), and this is what is done intuitively when habitats are assigned to extinct "indicator species", but in the present analysis the assignment is quantified by calculating average scores for all extant species in particular genera. It will obviously be less precise than the species scores, but since species in the same genus tend to occupy similar ranges of habitats, there is still useful information in the genus scores.

This principle can be extended to higher taxonomic levels, for example by averaging species scores in tribes or subfamilies, while still retaining some useful ecological information for some habitats. Calculation of the THI thus entails the taxonomic averaging of habitat scores based on the nearest identified taxonomic level for fossil species.

Faunal Bias

In addition to the fact that fossil faunas are largely composed of animals with unknown habitat preferences, most if not all fossil faunas have been subjected to processes which alter their taxonomic composition. These may reduce the numbers of species from those present in the source areas, usually as a result of taphonomic bias, or species numbers may be augmented if the faunas are derived from different or complex habitats or again as a result of taphonomic bias (Brain 1981; Andrews 1990; Lyman 1994, and references therein).

Results

Taxonomic Composition of the Azokh Faunas

The bat faunas from Azokh 1 are described by Sevilla (2016). Numbers of species for the five units in the cave range from 2 to 11 species, but the numbers of species are only weakly correlated with numbers of specimens. Unit Vu is the richest level, with the highest number of specimens (N = 2314) and the highest number of species (N = 11), but the Unit Vm fauna with 10 species has greater relative species richness for the sample size is only 133 specimens (Sevilla 2016). Similarly, species numbers in Units I and II do not relate closely with numbers of specimens. Unit III has only three bat specimens and is essentially sterile as far as bats are concerned. The two levels with the highest species richness relative to sample size are Units II and Vm, while Units I and Vu have relatively low species richness.

The Unit Vm bat fauna is dominated by *Miniopterus schreibersii*, a species common today in the Karabakh uplands (Sevilla 2016). *Myotus blythii* and *Rhinolophus* species are the other bat species common at this level. This situation is reversed in Unit Vu, with the latter species becoming much more common, and *M. schreibersii* declining in importance. Units II and I also have *Myotis blythii* as the most common species, together with varying numbers of *Rhinolophus* species, and the bat fauna in Unit I is said to represent a 'modern' sample of bats living today in the cave (Sevilla 2016).

The small mammal faunas from Azokh 1 range from 11 to 24 species in the five units studied here. The number of species per stratigraphic unit is directly related to sample size recovered from each unit (Fig. 15.2). Those units with least numbers of specimens have the lowest species numbers, and the unit with the biggest sample (Unit Vu) has by far the highest number of species. As a result, species richness does not of itself provide any indication of environment.

The list of small mammal species identified by Parfitt (2016) is placed here in Species List (S.L.) Table 15.2. The data provided by Parfitt show that small mammal assemblages are dominated by arvicolid rodents, especially members of the *Microtus arvalis* and *M. socialis* groups that are said to indicate woodland/meadows and steppic vegetation respectively. Hamsters (*Mesocricetus* sp., *Cricetulus migratorius*), jirds (*Meriones* spp.) and mole voles (*Ellobius* sp.) are also well represented throughout the sequence (Parfitt 2016). Many of the small mammals are related to or are extant dwellers of steppe and arid environments today.

Large mammal taxonomic data for the Azokh sequence have been provided by Van der Made et al. (2016) and included here as S.L. Table 15.3. In the whole sequence 29 species are represented. Some, such as *Cervus elaphus* (red deer) are present at all levels, and some are present in only one unit. Domestic horse and pig are present in Unit I, but they have been omitted from further analysis since they represent selection by the human population during historic times and do not reflect the local ecology. *Ursus spelaeus* is common in Units II to V (those that have been found in Unit I were almost certainly introduced by recent burrowing activities of animals living in the cave in recent times, see Marin-Monfort et al. 2016). The unit with greatest species richness is Unit Vm, with 21 species including 8 carnivores, two equids, two rhinoceros and nine artiodactyls. By contrast, Unit Vu has only seven large mammal species, and the other levels are intermediate (see S.L. Table 15.3). The fauna has a strong central Asian aspect.

There is no relationship between species numbers of large mammals compared with small mammals, for the largest species number for small mammals in Unit Vu is set alongside almost the lowest number for large mammals: see S.L. Tables 15.2 and 15.3. Similarly, the low number of small mammal species in Unit Vm contrasts with the highest number of large mammal species in the Azokh sequence. This suggests that the factors underlying the accumulation and preservation of large mammals are distinct from those for small mammals, and it might be expected, therefore, that the ecological signals of the two sets of data may also be different.

The herpetofauna of Azokh 1 is composed exclusively of extant genera and species. The list of amphibian and reptile species identified by Blain (2016) is taken from their chapter and placed here in S.L. Table 15.4. Sample sizes are not

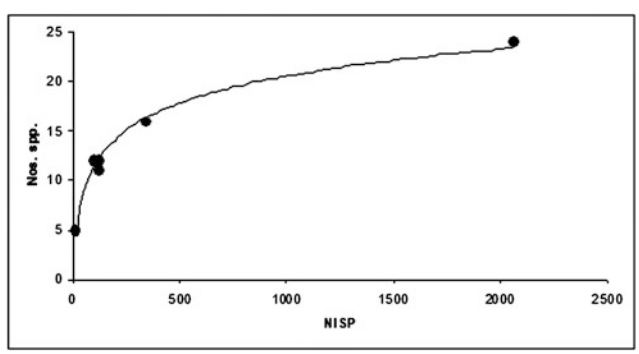


Fig. 15.2 Relationship between numbers of mammal species excluding bats in the six units of Azokh 1 (see Species List Tables) with numbers of specimens (NISP) recovered (least squares line)

available for the amphibians and reptiles, but species presence/absences are described by Blain (2016). The lowest unit, Unit Vm, has one lizard, *Lacerta* sp. and one snake, *Eryx jaculus*. Unit Vu has two each of amphibian and lizard species, and five snakes. They include the lizard *Pseudopus apodus* and the snakes *Elaphe sauromates* and *Malpolon insignatus*, while the exclusive presence of the snake *Pelophylax ridibundus*, which is associated with aquatic environments, suggests the nearby presence of water. Unit III has a single lizard species and three snakes, similar to those in Unit Vu, with the presence of *Vipera* (*Pelias*) sp. indicating high altitude environments. Unit II is similar to Unit Vu in having two amphibian species, two lizards and four snakes. Unit I has the highest species richness of lizards and snakes and includes one amphibian, four species of lizard and six snakes, higher even than Unit Vu.

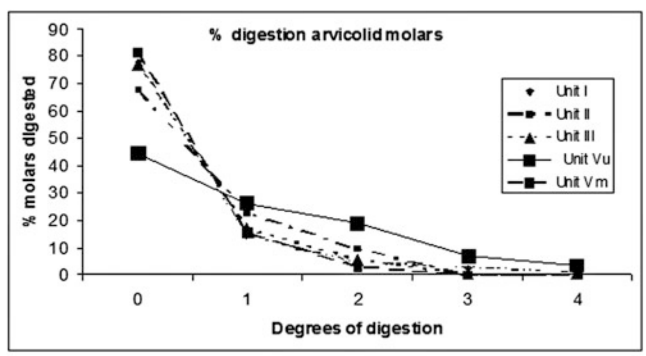
Taphonomy

In an investigation of the taphonomy of large mammals (Marin-Monfort 2016) state that some of the cave bear remains are relatively complete, with some associations between elements, and that the lack of any evidence of transport suggests that the bears were living in the cave, using it as a den. Remains of other mammals are rare in most units, and they are extremely fragmentary, consisting mainly of teeth, horn/antler cores, and foot bones. All are highly fragmentary, including most of the cave bears, and this was probably due to post-depositional breakage within the cave. Carnivore chewing marks are present on some fossil bones, both cave bear and other species, but most of the breakage so common at the site does not appear to be due to carnivore activity. Cut marks and percussion marks are present, again on all species, including cave bears, and a small number of burnt bones are also present. Signs of trampling are common, and it is considered likely that the trampling agent was the cave bears living in the cave. Many bone fragments are rounded, some heavily, but their taxonomic assignment is not known. Both trampling and carnivore activity are likely causes of the rounding, not transport.

Little is known on the taphonomy of the bats. Evidence of digestion is seen on the teeth and bones of *Pipistrellus pipistrellus*, *Miniopterus schreibersii* and *Myotus blythii*, but no data are available on numbers of specimens affected. The latter two species are the most common at all levels (excluding Unit III which has almost no bats), so that there is some degree of predator action, but the absence of digestion on other species of bat does not by itself exclude the possibility of predator action since sample sizes are so small (Sevilla 2016). On the other hand, all of the bat species present at Azokh 1 are known to roost in caves or rock fissures, and it is likely that much of the bat fauna present in the cave came from natural deaths inside the cave. The collections of small mammals are strongly biased towards cranial and dental remains, with no postcrania available for study, and analysis of the small mammals has therefore been restricted exclusively to their teeth.

Many of the small mammal molars show evidence of digestion by predators. Digestion levels vary from around 20% of arvicolid molars in Units I and Vm up to 55% in Unit Vu. Degrees of digestion according to Andrews (1990) are light to moderate at all levels, and only Unit Vu has a small number of arvicolid molars that are heavily digested (Fig. 15.3). The high frequency of digested teeth is also shown in Fig. 15.4, which compares frequency of digestion of arvicolid teeth with that of murids and soricids. In nearly all cases, levels of digestion are lower for the two latter groups, and this appears to be the case because their teeth are lower crowned and thus less vulnerable to digestion. We are currently investigating this to try to measure the different degrees of digestion, and first indications are that small mammals with lower crowned teeth show evidence of digestion at least one category less than that seen in arvicolids when digested by the same predator (Fig. 15.4).

Rodent incisors have less morphological variation than do the molars, and in terms of the profile they present to digestive juices of predators, their main variation is that of size. Some rodent incisors are grooved, but this appears to have little effect on their susceptibility to digestion. It has been claimed, therefore, that rodent incisors are the single most useful body part for distinguishing digestion (Andrews



Percentage numbers of molars

Degrees of digestion	Unit I	Unit II	Unit III	Unit Vu	Unit Vm
0	78.0	67.9	77.4	44.5	81.6
1	14.3	22.6	17.0	26.3	15.5
2	4.5	9.5	5.7	19.2	2.9
3	2.2	0	0	6.7	0
4	0.9	0	0	3.4	0
N	223	84	106	1389	103

Fig. 15.3 Percentage digestion of arvicolid molars from five units of Azokh 1. Five digestion categories are shown on the horizontal axis (Andrews 1990), with the figure 0 signifying absence of digestion and 4 indicating heavy digestion, and the percentage number of teeth digested is shown on the vertical scale

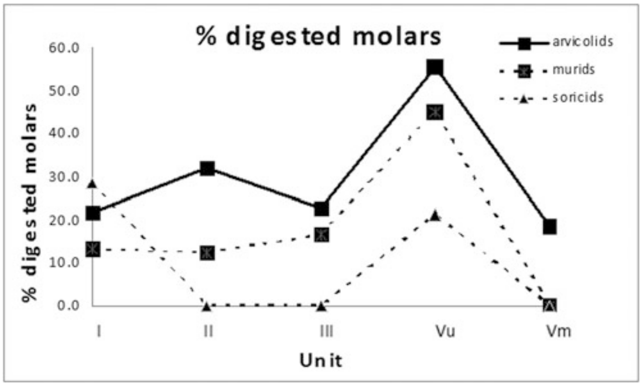
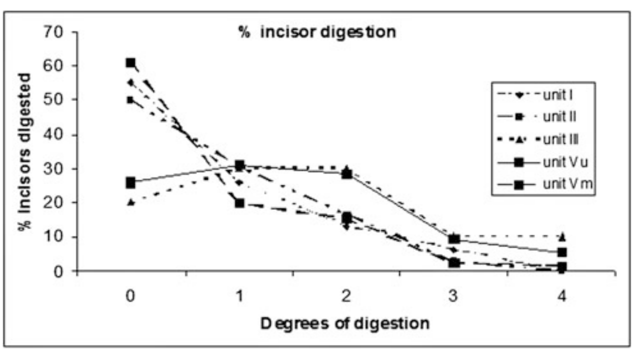


Fig. 15.4 Differences in percentage numbers of molars digested for arvicolids, murids and soricids, showing that within each of the Azokh 1 units there are consistent differences in degrees of digestion between the three mammal groups. The five Azokh units are shown on the horizontal scale and percentage numbers of teeth digested on the vertical scale

1990; Mathews and Parkington 2006). The pattern of digestion of all rodent incisors does not vary greatly, but numbers of digested teeth are greater than in arvicolid rodents, with three stratigraphic units having 40–50% of teeth showing evidence of digestion (Units I, II and Vm) and Unit Vu having 74% of teeth with digestion (Fig. 15.5). Unit III also appears to have a similar level of digestion to that of Unit Vu, but since the sample size is only ten it is likely that this result is anomalous, especially since the molars from Unit III also show no evidence of high digestion.



Percentage numbers of incisors

Degrees of digestion	Unit I	Unit II	Unit III	Unit Vu	Unit Vm
0	55.0	50.0	20.0	26.0	61.1
1	26.0	30.6	30.0	30.9	19.8
2	13.0	16.7	30.0	28.3	15.3
3	6.1	2.8	10.0	9.4	2.3
4	0.0	0.0	10.0	5.3	1.5
N	131	36	10	434	131

Fig. 15.5 Percentage digestion of rodent incisors from five units of Azokh 1. Five digestion categories are shown on the horizontal axis (Andrews 1990), with the figure 0 signifying absence of digestion and 4 indicating heavy digestion, and the percentage number of teeth digested is shown on the vertical scale

The conclusion from both molars and incisors is that Units I, II and Vm have similar distributions and degrees of digestion, and these show that the small mammal faunas were accumulated by a category 1 predator, following the Andrews (1990) classification. The Unit Vu small mammal sample has a different pattern of digestion, higher both in degree and in number, and this indicates that it was accumulated by a category 3 predator (Andrews 1990). The sample size of Unit III is too small for any conclusion to be drawn other than the fact that it was also evidently a predator accumulation. The most likely category 1 predator is the barn owl (*Tyto alba*), which is a vole specialist over much of its range across Europe and central Asia and which is also known to inhabit caves. It is by far the most common owl found in cave habitats, and it produces the least effect on its prey, with low degrees of digestion except at its nest site. The most likely category 3 predator is the European eagle owl (*Bubo bubo*), as the digestion levels of this species is less than that of the tawny owl, the only other category 3 predator known so far (Andrews 1990). This species does not inhabit caves, but it often nests on rocky cliffs or in small holes in cliffs, and the entrance to Azokh cave at the base of a cliff would be a suitable habitat for an eagle owl. It also feeds on a wider variety of prey than most other owls, and the high small mammal diversity in Unit Vu (S.L. Table 15.2) is probably a reflection of this.

Paleoecology

Weighted averages ordination has been described above for three temperate habitats (Fig. 15.1). In all three cases, the distribution of species ranges through six habitat types is shown, and it should be noted that these analyses exclude bats, since they are rarely preserved as fossils (Andrews 1990). These three analyses form the basis for comparison with the reconstructed ordination scores for the Azokh fossil faunas. The scores for fossil taxa have been estimated based on the Taxonomic Habitat Index, which assigns habitat distributions based on species scores, if the species is still extant, or on genus scores if the species is extinct. As explained above, this method seeks to reduce the bias inherent in assigning arbitrary habitats based only on closest living relatives. THI analyses have been performed separately on the large and small mammal as well as on the combined mammal fauna (Table 15.1, Fig. 15.6).

The large mammal fauna in Units II to V have the highest index values for deciduous woodland but also high values for Mediterranean evergreen woodland and, in the case of Unit Vm, high levels for steppe and arid environments. Unit I is the most distinct, with steppe and arid index values equal to or greater than deciduous woodland. From Unit Vm to Unit III there is a gradual increase in deciduous woodland indicated by the THI index, with slight reduction in arid environments and steppe, and while the small sample size in Unit Vu makes its value suspect, the trend is continued into Unit III with a slightly larger sample size. Overall, there is consistency in the proportions between different levels, suggesting the environment over most of the period represented by Units V to II consisted of areas of woodland mixed with steppe and arid environments, with slight increases in areas of woodland up to Unit III. Such a mixture could be the outcome of increasing woodland on mountain slopes and river valleys, with the low ground ranging from steppe to semi-desert and expanding in area in Units II and I (see below).

Calculation of the THI scores for the small mammal faunas for the five units from Azokh 1 (middle bar chart in Fig. 15.6) show that all five stratigraphic units are dominated by animals living today in steppe and semi-desert. Index values for deciduous woodland are lower than those for steppe and semi-desert in all samples except Unit Vm, which is the only unit to have a relatively high value for deciduous woodland, although even here the highest THI value is for steppe. The proportion of steppe/arid species increases from Unit V to Unit II, while at the same time the THI index values for deciduous woodland decreases. There is a minor reversal of this trend in Unit I at the top of the sequence. Again there is a high degree of consistency in the results from the small mammals, showing a mixture of woodland and steppe/semi-desert environments, with the arid environments greater in extent and increasing up the section and woodland decreasing.

One explanation for the differences in paleoecological reconstruction between large and small mammal accumulations at Azokh Cave is that they had different taphonomic trajectories. The two predators identified for the small mammal assemblages, barn owls and eagle owls, are both generalists and open country hunters, whether quartering the ground (barn owl) or perch and pounce (eagle owl), they habitually seek open spaces to hunt. This could well explain the greater prominence of small mammals with steppe and arid country affinities. By contrast, many of the large mammals, such as the cervids, suids and felids, are woodland dwellers and may have been living closer to the fossil site, which is half way up a mountain and like today's habitats probably had woodland vegetation. It is evident from this that some knowledge of the taphonomy of an assemblage is necessary in order to clarify an otherwise confusing contrast in data.

When the large and small mammals are combined into a single THI analysis, the results become less clear. This could be predicted from the separate analyses, for the two samples provide evidence of different proportions of habitat resulting from different taphonomic histories. The bottom bar chart in Fig. 15.6 reflects this contrast and does not indicate any clear trend or pattern in Units V to II other than the fact that woodland and steppe were more or less equally represented. Only in Unit I does the value for deciduous woodland

Table 15.1 Taxonomic Habitat scores for the faunas from the five stratigraphic units at Azokh 1. THI scores are shown for six modern habitat types for each fossil fauna, and the analyses have been shown for small and large mammals separately and for the two combined. N = numbers of species

		Unit Vm	Unit Vu	Unit III	Unit II	Unit I
Small mammal fauna	Tundra	0.021	0.019	0.006	0.008	0.021
	Boreal forest	0.065	0.048	0.046	0.038	0.057
	Deciduous forest	0.182	0.132	0.155	0.089	0.116
	Mediterranean	0.149	0.126	0.118	0.071	0.100
	Steppe	0.279	0.318	0.312	0.381	0.313
	Arid	0.177	0.254	0.275	0.336	0.270
	N	12	24	14	14	16
Large mammal fauna	Tundra	0.007	0.000	0.000	0.014	0.000
	Boreal forest	0.076	0.100	0.055	0.111	0.083
	Deciduous forest	0.247	0.314	0.336	0.300	0.217
	Mediterranean	0.190	0.257	0.236	0.209	0.167
	Steppe	0.209	0.157	0.173	0.136	0.217
	Arid	0.212	0.129	0.164	0.118	0.250
	N	21	7	6	11	6
All mammals	Tundra	0.012	0.015	0.004	0.010	0.015
	Boreal forest	0.072	0.059	0.056	0.070	0.064
	Deciduous forest	0.223	0.172	0.270	0.182	0.145
	Mediterranean	0.175	0.155	0.195	0.132	0.119
	Steppe	0.234	0.283	0.267	0.273	0.285
	Arid	0.199	0.227	0.241	0.240	0.264
	N	33	31	20	25	22

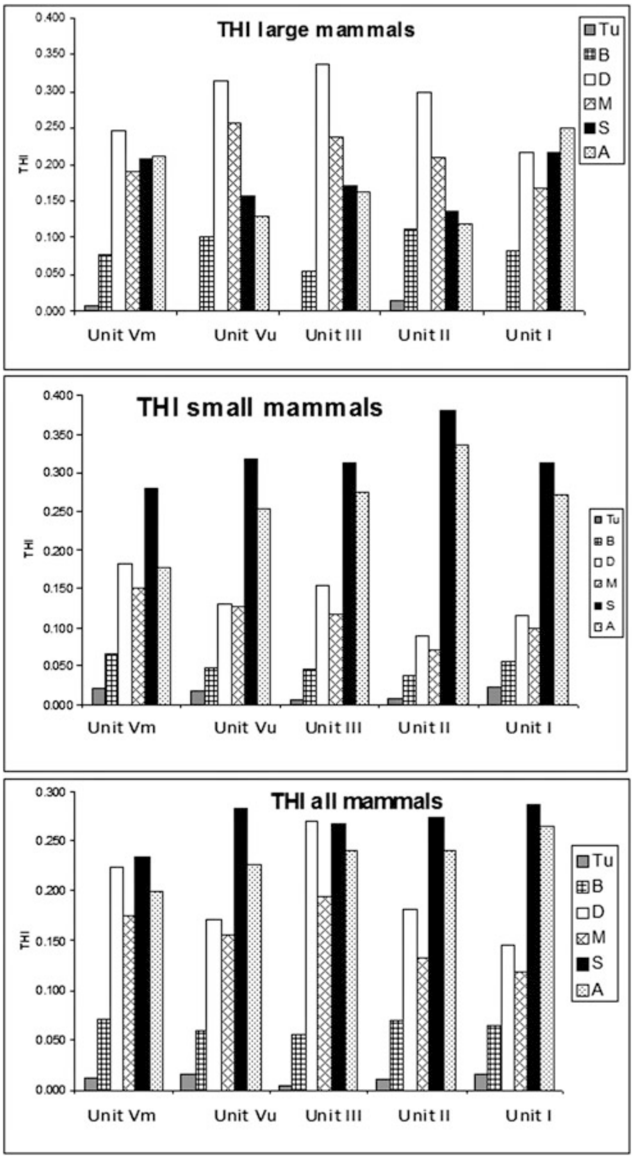


Fig. 15.6 THI analyses for large mammals (top), small mammals (middle) and the two combined (bottom). The five stratigraphic units are shown on the horizontal axis and THI values on the vertical axis

decrease significantly and the values for steppe and semi-desert increase.

The bat fauna from Azokh 1 is made up of extant genera and species, and their species richness is strongly linked with distribution of vegetation (Sevilla 2016). "The richest habitats in bat species are the mountain steppes, closely followed by mountain forest habitats. The lowest values are observed in mountain grasslands" (Sevilla 2016). These of course are the habitats the insectivorous bats are adapted to hunt over, and it shows the presence of these habitats within the hunting ranges of the bats and not necessarily what the habitat was like in the immediate vicinity of the cave. The level with the greatest relative species richness, Unit V, is dominated by species with Mediterranean or humid affinities, so the evidence from the bats indicates woodland conditions at this level. Unit Vu has 11 bat species compared with the 10 species in Unit Vm, but bats are 20 times more abundant based mainly on the large number of specimens of *Myotis blythii* and *Rhinolophus* species. These indicate a change to open steppe environments, with a warmer and more arid climate (but see below). Unit III has almost no bats, but the Unit II bat fauna suggests a change to cooler conditions. The Unit I bats are similar to those from Unit II, but with a minor change suggesting a slight increase in aridity (Sevilla 2016).

The majority of snakes and amphibians belong to thermophilous and xeric-adapted forms (e.g., *Pelobates syriacus*, Agamidae, *Pseudopus apodus*, *Eryx jaculus*, *Elaphe sauromates*, *Malpolon insignatus* etc.). Sample sizes are not available for the amphibians and reptiles, but species presence/absences are described by Blain (2016). The lowest unit, Unit Vm, has *Lacerta* sp. and *Eryx jaculus*, both associated today with warm xeric conditions (Blain 2016). Unit Vu has *Pseudopus apodus* and the snakes *Elaphe sauromates* and *Malpolon insignatus* that are also associated today with warm xeric conditions (Blain 2016), while the exclusive presence of the snake *Pelophylax ridibundus*, which is associated with aquatic environments, suggests the nearby presence of water. All these species in Unit Vu, with one exception, frequent woody environments. Unit III is similar to Unit Vu, with the presence of *Vipera* (*Pelias*) sp. indicating high altitude environments (Blain 2016). Unit II is also similar to Unit Vu in having eight species indicating warm xeric conditions with an element of high altitude environments. Unit I has the highest species richness of lizards and snakes and with 11 taxa, and the presence of an agamid lizard suggests more arid conditions than present at lower levels (Blain 2016). In general, however, most of the taxa present in the Azokh sequence frequent wooded or bushy areas, and while there is some indication of a trend towards more arid conditions from Units V to I, the evidence is based to some extent on the presence of agamids in the uppermost unit. On the other hand, the slight increase in species richness from Unit V to Unit I suggests that if conditions were more arid, there was also greater habitat variability in the upper units.

Wood is present in two units at Azokh, in both cases preserved as charcoal. The wood may have been carried into the cave by the hominin populations and so may reflect their choice as the most suitable firewood, but it may also have been carried in by animals or even fallen in through avens in the cave roof after natural surface fires. The list of plant species identified by Allué (2016) is taken from their chapter and placed here in S.L. Table 15.5. Just over 80% of the wood identified in Unit II is attributed to *Prunus* species (N = 709 out of a total of 886 specimens). This is a genus of small trees and shrubs with a broad distribution in temperate and tropical (montane) regions of the world. Also present are remains of maples (*Acer*), deciduous oak species (*Quercus*), and species of the apple family (Maloideae), a combination of large woodland trees and small trees and shrubs. Allué (2016) makes the point that this plant association has no equivalent in the area today, but it shows the presence of broadleaved forests with understorey trees and shrubs in the vicinity of the cave. Pollen evidence cited by Allué (2016) from areas near the site also shows the presence of broad leaved woodland although without the curious dominance of *Prunus* species. The Unit Vu flora, although much smaller than that from Unit II, has the same species represented and in similar proportions (N = 21), and it is also dominated by *Prunus* and Maloideae species, both of which include many species with edible fruits.

Searches for pollen were for the most part unsuccessful, both in the cave sediment and in fossil coprolites (Scott et al. 2016), and the few pollen grains found were not diagnostic. Greater success came with the discovery of abundant phytolith assemblages, and nine different types of grass silica short cell phytoliths were identified, indicating a temperate C_3-grass steppe mosaic (Scott et al. 2016). There is clearly greater potential for further phytolith studies at Azokh, and a key issue here will be identifying how the phytoliths entered the cave system.

Present Day Vegetation in the Azokh Region

Indications from the fossil faunas and floras from Azokh 1 of the past environmental trends call into question what is the nature of the present vegetation in the vicinity of the cave. Both woodland and steppe conditions have been indicated, but the area today is heavily wooded with the nearest steppe environments 4–6 km east of the cave.

A number of vegetation transects and sample plots have been measured, but the one in the immediate vicinity of the cave is suspect because the area has been largely cleared of trees by fire and grazing by livestock. The few remnants of woodland indicate an association of (*Zelkova*-*Quercus*), with an understory of field maple (*Acer campestre*), *Prunus* species, dogwood (*Cornus sanguinea*), hazel (*Corylus*) and hawthorn (*Cretaegus*). The mountain slopes below Azokh 1 are covered by a dense association of Jerusalem thorn (*Paliurus spina-christi*), which would have been present as an under-story bush but which has spread over the whole hillside after clearing. Hackberry trees (*Celtis*), *Zelkova* and figs occur in patches (see Table 15.6) for botanical names of plants. This is similar to the tree associations that are widespread on the mountains surrounding the site, where *Zelkova*, hornbeam and ash (*Fraxinus*) are the dominant species on north sloping faces and oak (*Quercus macranthera*) and *Zelkova* on the south facing faces, with less *Prunus* and dogwood and the addition of elm, beech and second species each of ash and oak. It is also the association found in the river valley below the site, with greater frequencies of ash and hackberry and the addition of plane trees, more lime, and willow actually by the water's edge. However, it should be noted that all woodlands seen were secondary, with evidence of extensive felling and secondary regrowth. The majority of hornbeam and ash had evidently regrown from cut stumps, for the rotting stumps could still be seen, and based on two 900 m^2 sample plots the secondary growth of hornbeam and ash is estimated to be about 60–70 years old. Information from local people is that the forests were extensively cut during Soviet times, but they are still being cut for firewood and used for grazing stock by local communities.

The river valleys are highly altered by human activity, but two 100 m transects along the valley adjacent to the site demonstrated the importance of variations in soil and geology. One association where the valley cut through limestone differed little from the upper slopes of the valley except in the dominance of *Zelkova*. There were few oaks and there was a lower canopy of hazel in places. This association may have been altered by human activity, with some species like oak being selectively removed, but the other association, however, was dominated by oak and ash, with hornbeam and field maple and with willows by the water's edge. This association was growing on volcanic tuffs, which outcropped on one side of the valley (the trend of the valley was 340°), almost north-south, and the tuffs outcropped on the south facing side of the valley, and this may also have affected the change in vegetation. The lower canopy in all cases is dominated by hazel, dogwood and some field maple. The vegetation of the permanent Ishkhanaget River, which drains the Azokh region, has been greatly altered by human action, and the trees observed along one short section of the river were mainly willows and one large plane tree.

For comparison with Azokh Cave, three vegetation sample plots were examined in the region of Karintak. Two 30 m diameter sample plots had 90–94% hornbeam, with oak and field maple the only other tree species. One sample plot had an understory of hazel, but the other had almost no hazel. This area again had clearly been felled, an estimated 100 years ago, and the hornbeam had regrown alongside the rotting stumps. For comparison with this relatively undisturbed forest, A 30 m square sample plot was placed immediately outside the entrance of a large cave in the Karintak forest, on the steep slope down from the cave. The woodland was nearly half ash and field maple, and hornbeam and *Prunus* species were also common, the latter mainly by the cave entrance, with Maloideae, *Zelkova*, elder and dogwood also present. Here too there was evidence that the area had been cleared, and the trees were approximately 40–

60 years in age, but there were also some much larger trees of lime and maple which apparently survived the felling.

The concentration close to cave entrances of *Prunus*, Maloideae and *Sambucus*, and their rarity in woodlands removed from caves, is strongly suggestive. All of them are fruit-bearing small trees with fruits both accessible and edible for humans and bears, and we may speculate that their presence close to cave entrances may be the result of self-seeding from seeds discarded by humans or bears living in the cave. It is probable that the self-seeding was unintentional, but it is interesting to compare this with the high proportions of *Prunus* species identified by charcoal remains in Units II and V. It is possible that there was a self-seeded concentration of *Prunus* species (and pomes) in the vicinity of Azokh 1 during the Pleistocene, unintentionally brought there by the human population, and this then provided an easily accessible firewood source.

A second cave was also investigated towards one end of the Shushi Gorge. This is a precipitous gorge over 350 m deep with near vertical cliffs. The cave had a narrow shelf running approximately north-south along the side of the gorge with a thin strip of woodland extending along it. Because of limitations of space, a 300 m transect was run along this strip, and plants recorded both by abundance and by their proximity to the cave. Elder was abundant at the cave entrance but rare elsewhere; *Prunus* species and figs were common immediately outside the cave entrance (see above), but less common elsewhere; *Zelkova* was the most common species away from the cave, with ash, dogwood and hawthorn next most common along the cliff shelf; hazel, *hackberry* and field maple were also present. The ground vegetation was brambles, grasses, nettles in open areas and dogs mercury and celandines under woodland canopy.

Two of the higher mountains in Nagorno-Karabakh (Mets Kir and Dizapayt) are visible from the upper slopes above Azokh Cave, but we were not able to visit them. Above the tree line they probably had mountain steppe vegetation or alpine meadow, and one at least would have been within the range of larger birds of prey and large mammals (18 km by line of sight). The more extensive areas of upland alpine meadow in Nagorno-Karabakh, however, are far to the north of the country at the present time, and we were not able to visit them.

The vegetation map of Nagorno-Karabakh shows the presence of a broad belt of semi-xerophyll woodland on the lowlands 4–6 km to the east of Azokh (Manuk 2010). The areas we saw are either under cultivation or are remnant patches of juniper and evergreen oaks, together with Jerusalem Thorn, *Pistacia* and almond, that seem to have taken over areas cleared of broadleaved forest. Further to the east are belts of sagebrush steppe and sagebrush desert, and both would have been within the ranges of larger mammals and birds of prey. Unfortunately we were not able to visit any of these areas, and some at least are now greatly degraded. Given the location of Azokh on the eastern edge of the mountainous region of the country, it can be concluded that climatic variations would have brought about movements of vegetation zones between steppe and forest associations towards and away from the mountainous regions. Drier conditions would have led to the spread of the xerophyl/sagebrush steppe closer to Azokh, and retreat of broadleaved forest up the mountain slopes; and wetter conditions would have led to the reverse trend. This is entirely consistent with the palaeontological and palaeobotanical evidence from Azokh 1, and it suggests that the range of palaeoenvironments present for the past 200 kyr was little different from that existing today.

Discussion

A number of sites in the Caucasus have provided evidence of the palaeoenvironment during the second half of the Pleistocene. The site of Akhalkalaki at 1600 m altitude had a fauna for which it is said that 23 species are inhabitants of open habitats and seven are forest dwellers (Vekua 1962). The paleobotanical data supports the development of xerophitic landscapes (Vekua 1962, 1987). On the other hand, the palynological data and faunal remains from Kudaro suggest that the Lower Paleolithic layers accumulated under warm and humid conditions (Zelikson and Gubonina 1985; Mamatsashvili 1987). During the late Pleistocene, several cave sites found near Kutaisi (Bronze cave, Double Cave, Bizon, Bears Cave and the Upper Cave) yielded rich Mousterian assemblages that were dominated by cave bears, with bison and *Capra* also well represented (Vekua 1987). The palynological data shows that forests were widespread near the cave during the accumulation of the Mousterian levels (Mamatsashvili 1978). Later on during the last glaciation (Ollivier et al. 2010), the site of Dzudzuana showed a transition from a mixed coniferous-deciduous forest to more open pine-spruce forests combined with open steppe occupied by Chenopodiaceae, Poaceae and Asteraceae. Floral remains from the upper portion of the section then show the expansion of deciduous forests. The structure of the recovered faunal remains is in agreement with the evidence from floral data (Vekua and Lordkipanidze 1998). The evidence from these sites indicates the alternation of forests and steppe conditions through the Pleistocene, which is what is seen in the Azokh sequence.

A feature of the Azokh sequence is that there is an apparent conflict of evidence between the botanical and large mammal evidence on the one hand and the small mammal and herpetofaunal evidence on the other. The first indicates woodland in the vicinity of Azokh Cave during the time of accumulation of the sediment and faunas, and the second indicates steppe/arid environments. How do we interpret this?

Evidence for Woodland

It has been shown that the evidence from charcoal is available from two levels only, Units II and Vu, both of which share a similar profile (Allué 2016). Both are also said to be the result of human action, collecting fire wood and carrying it to the cave, although there is no direct evidence for this, and for both units the charcoal is derived from the wood of *Prunus* species, and it is interesting to speculate that the preponderance of small trees with edible fruits may have entered the cave through human or animal action, the fruits having been collected for consumption in the cave, and the nuts/seeds discarded in the vicinity of the cave so that they then grow naturally around the cave. Be that as it may, the combination of these trees with other broad leaved tree species identified from the charcoal indicates deciduous woodland in the vicinity of the cave.

A similar conclusion is reached from the analysis of large mammals (Van der Made et al. 2016). The largest sample is available from Unit Vm (N = 21 species), which has an estimated age of 2–300 ka (see Appendix, ESR and racemization). The fauna has elements indicating deciduous woodland, evergreen (Mediterranean) woodland, steppe and semi-desert in almost equal proportions (Fig. 15.6), so that while deciduous woodland was present in the area, there was clearly considerable habitat heterogeneity. Figure 15.1 showed the variability in five deciduous woodland habitats, but the Unit Vm ecological spectrum does not match any of these (compare Fig. 15.6 with Fig. 15.1). We therefore investigated the effects of mixing faunas from different habitats, following the procedure in Andrews (2006). Equal mixtures of woodland with steppe faunas was weighted towards the steppe faunal elements, but when the faunas were mixed in a 2:1 ratio, i.e. with an entire woodland fauna mixed with half a steppe fauna, there was a close match with the Azokh faunas. The results for four such mixtures are shown in Fig. 15.7, which is shown here compared with the large mammal analysis of the Azokh faunas from Units Vu and I. These two fossil faunas were selected as representing the extremes of the stratigraphic section, but in fact they vary little from each other and little also from most of the modern mixes of deciduous forest with a minor steppe element. It should also be noted that Unit III has an even higher representation of woodland elements than Units I and Vm (Fig. 15.6), and they are closest to the index values for pure woodland, with only a minor steppe element. The large mammals therefore indicate a preponderance of woodland habitats throughout the section, increasing from Unit Vm through Unit III, and then dropping again to Unit I, with increase in steppe elements at the top of the section.

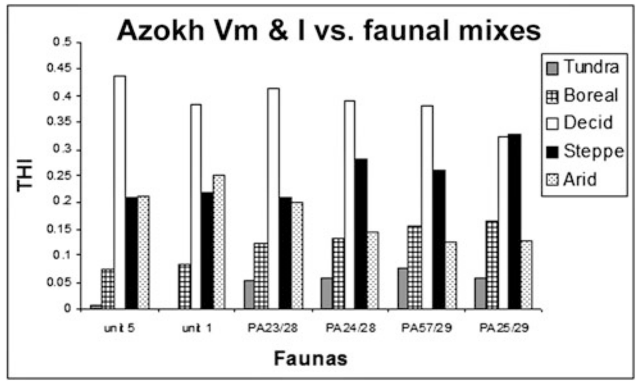


Fig. 15.7 The large mammal faunas from Unit Vm at the bottom of the Azokh 1 stratigraphic sequence and Unit I at the top are compared with four modern faunas derived from mixtures of deciduous woodland faunas and steppe faunas. The mixtures are in the ratio 2:1 woodland: steppe. The four recent faunas details as follows: PA23 woodland, 50° N 10° E, N = 43; PA24 woodland, 50° N 20° E, N = 46; PA25 woodland, 50° N 30° E, N = 51; PA28 steppe, 50° N 60° E, N = 39; PA29 steppe, 50° N 70° E; PA57 woodland, N = 22. The habitats that the modern faunas represent are Tu, tundra, B, boreal forest, D, deciduous forest, Mediterranean forest, S, steppe, A, arid environments

Evidence for Steppe

The richest level for small mammals is Unit Vu (Parfitt 2016) (S.L. Table 15.2). Despite differences in sample size the THI patterns for the small mammals from all units are similar, with steppe and arid environments predominant (Fig. 15.6). There is, however, a trend of increasing steppe elements from Unit V to Unit II and decreasing proportions of deciduous woodland elements, suggesting this pattern is changing through time (Fig. 15.6). These trends are reversed in Unit I, but given small sample sizes this may not be significant.

None of the small mammal faunas have an exact match with any of the modern faunas we have investigated. Steppe faunas tend to be dominated by steppe and arid elements, almost to the exclusion of all else, whereas the Azokh faunas also have significant elements of woodland. We therefore compared them with a mixture of habitats (Andrews 2006), mixing steppe with woodland. In this case, however, the steppe and woodland faunas were mixed in the ratio of 2:1; that is complete steppe faunas combined with half woodland faunas. As would be expected, this has had the effect of increasing the woodland component similar to that seen in the Azokh faunas, indicating that these faunas were derived from an area of steppe with minor amounts of woodland.

The amphibians and reptiles in the Azokh faunas are mostly small, equivalent in body size to the small mammals, and they also indicate the presence of steppe and arid conditions throughout the sequence and increasing up the section (Blain 2016). It is most likely that the differences between them may be accounted for by the fact that they were derived from different parts of the environment. This is all the more likely to be true if some part of the Azokh fauna and flora has been transported to the site, and it has been shown that the small mammals were brought to the site by predators, interpreted as barn owls and eagle owls, which are predators that habitually hunt over open steppe and semi-desert. Predators hunt by size and availability rather than by taxonomic group (Andrews 1990), and it is common to find reptiles and mammal together in the prey remains of some predators. The taphonomy of the former group has not yet been investigated, but it can be predicted that the reptiles and amphibians will also be shown to have been predated, probably by the same predators as the small mammals.

Combining all lines of evidence, the evidence at Azokh from the middle to late Pleistocene deposits is that the cave was situated close to both woodland and steppe environments. The most likely explanation for this is to be seen in its location part way up a mountain slope, with woodland immediately adjacent to the cave, covering the mountain slopes as it does today, and steppe environments on the lower lands to the south and east of the mountains but within a few kilometres of the cave. The steppe would have been within the hunting range of the predators accumulating the small mammal faunas, and there may also have been alpine steppe on the tops of nearby mountains also within the predators' hunting ranges.

Conclusions

1. Present day vegetation in the mountainous region around Azokh is exclusively deciduous woodland, with variations of hornbeam, *Zelkova*, oak, ash, field maple, lime and many smaller species, including *Prunus* and Maloideae species. The area around the cave entrances has been degraded by fire and grazing and is not typical of the area, having pomegranates (*Punica granatum*) mulberry and figs. The nearest steppe vegetation at present is 4–6 km to the east of the cave.
2. The large mammal fauna indicates woodland close to Azokh Cave with some evidence of steppe conditions in an approximate ratio of 2:1 (woodland:steppe). This ratio increased from Unit Vm to Unit III, with greater proportions of woodland, and then it decreased from Unit II to Unit I, with increasing steppe.
3. The small mammal fauna indicates steppe conditions and less woodland in the approximate ratio of 1:2 (woodland: steppe). Taphonomic evidence showed that the faunas were brought to the cave by barn owls and eagle owls that habitually hunt over open areas, and it is inferred that steppe conditions may have been some distance from the cave. Steppe conditions expanded slightly in the upper levels. There is slight evidence of increasing aridity in the upper units of the Azokh 1 sequence.
4. The bat fauna indicates Mediterranean woodland conditions at the bottom of the cave sequence changing first to warmer, more arid steppe environments and then to cooler steppe environments at the top of the sequence.
5. The amphibian and reptile fauna indicates steppe conditions in the vicinity of the cave and less woodland, similar to the evidence from the small mammals, but taphonomic analyses have not yet been done to see if it was accumulated in the same way as the small mammals.
6. The botanical evidence indicates woodland, with some of the wood possibly entering the cave through human or animal action and some possibly blown in from natural fires. In either event, it suggests woodland in the vicinity of the cave, dominated by fruit-bearing *Prunus* species that may have been self-seeded near the cave as a result of human or animal (cave bear) activity.
7. Phytoliths collected from the sediments and from coprolites show the presence of numerous types of grasses, indicating temperate steppe grasslands.

Acknowledgments We are grateful to Ethel Allué, Marion Bamford, Levon Yepiskoposyan and three anonymous referees for discussion and help with this chapter.

Species List Tables

Table 15.2 Presence/absence of small mammals at Azokh 1. Data from Parfitt (2016)

Unit number	Vm	Vu	III	II	I
Insectivora					
Soricidae					
Sorex minutus group		+			
Sorex araneus group	+	+			+
Crocidura spp.	+	+	+		+
Talpidae					
Talpa sp.	+				
Carnivora					
Mustelidae					
Mustela nivalis		+			
Lagomorpha					
Ochotonidae					
Ochotona sp.		+	+	+	+
Ochotona cf. rufescens					
Ochotona sp. large					
Leporidae					
Lepus sp.		+			+
Rodentia					
Sciuridae					
Marmota sp.				+	
Spermophilus sp.				+	

(continued)

Table 15.2 (continued)

Unit number	Vm	Vu	III	II	I
Muridae					
Cricetulus migratorius	+	+		+	+
Mesocricetus sp.		+	+	+	+
Allocricetulus sp.	+	+		+	
Myodes glareolus	+	+	+		
Microtus arvalis/socialis	+	+	+	+	+
Microtus (*Terricola*) spp.	+	+	+	+	+
Chionomys nivalis	+	+		+	+
Chionomys gud	+	+			+
Ellobius sp.	+	+	+	+	+
Meriones small		+	+		+
Meriones medium		+		+	
Meriones large sp		+	+		+
Apodemus spp.	+	+	+	+	+
Rattus sp.		+			
Mus cf. *macedonicus*		+	+		+
Gliridae					
Dryomys nitedula		+			
Dipodidae					
Allactaga large		+			+
Allactaga small		+			
NISP	120	2065	121	101	346
Number of species	12	24	11	12	16

Table 15.3 Presence/absence of large mammals at Azokh 1. Data from Van der Made et al. (2016)

	Units				
	Vm	Vu	III	II	I
Canis lupus	cf	x		x	
Canis aureus	x				
Vulpes vulpes				x	
Meles meles	x	x			
Martes cf. *foina*	x				
Crocuta crocuta	x	x			
Felis chaus	x				
Panthera pardus	x		x	x	
Ursus spelaeus	x	x	x	x	
Ursus sp (aff. *arctos/thibetanus*)				x	
Equus hydruntinus	x		x		
Equus asinus					cf
Equus ferus	x				
Equus caballus					cf
Stephanorhinus hemitoechus	x	?	x		
Stephanorhinus kirchbergensis	x	?	x		
Sus scrofa	x		x	x	
Sus scrofa – domestic					x
Capreolus pygargus	x		x	x	
Dama aff. *peloponesiaca*	x	?			
Dama sp.			x	x	x
Megaloceros solilhacus	x				

(continued)

Table 15.3 (continued)

	Units				
	Vm	Vu	III	II	I
Cervus elaphus	x	x	x	x	x
Bison schoetensacki/Bison-Bos	x		cf	x	
Ovis ammon	x		x		x
Capra aegagrus	x	x	x	x	
Capra hircus					cf
Saiga tatarica	x			x	
Bovidae indet.	x				

Table 15.4 Presence/absence of amphibians and reptiles at Azokh 1. Data from Hugues-Alexandre Blain (2016)

Unit number	Vm	Vu	III	II	I
Pelobates cf. *syriacus*				+	
Bufo viridis		+		+	+
cf. *Pelophylax ridibundus*		+			
Agamidae indet.					+
Pseudopus apodus		+		+	+
Lacerta sp.	+	+	+	+	+
Lacertidae indet.					+
Eryx jaculus	+	+	+	+	+
cf. *Coronella austriaca*		+		+	+
cf. *Elaphe* sp. 1 (*sauromates*)		+		+	+
cf. *Elaphe* sp. 2		+	+	+	+
cf. *Malpolon* sp. (*insignitus*)		+			
Vipera (*Pelias*) sp. ('*ursinii*' complex)			+		+
Viperidae indet. ('Oriental' vipers)					+

Table 15.5 Charcoal analysis from Units II and Vu from Azokh 1 cave. Data from Allué (2016)

Taxa	Unit II		Unit Vu
	Num. frags	%	Num. frags
Acer	34	3.84	
Carpinus	1	0.11	
Celtis/Zelkova	4	0.45	
Euonymus	2	0.23	
Lonicera	9	1.02	
Maloideae	23	2.60	3
Prunus	709	80.02	15
Quercus sp. decidous	28	3.16	2
Quercus/Castanea	2	0.23	
Paliurus/Ziziphus	3	0.34	
Ulmaceae	4	0.45	
cf. *Acer*	3	0.34	
cf. Maloideae	1	0.11	
cf. *Prunus*	13	1.47	
cf. *Quercus*			1
cf. Ulmaceae	1	0.11	
Undetermined angiosperm	48	5.42	
Undetermined	1	0.11	
Total number of fragments	886		21

Table 15.6 List of recent tree species in the Azokh region

Hornbeam	*Carpinus caucasica*
Zelkova	*Zelkova carpinifolia*
Oak, deciduous	*Quercus iberica*
Mountain oak	*Quercus macranthera*
Oak, evergreen	*Quercus* sp.
Ash	*Fraxinus excelsior*
Field maple	*Acer campestre*
Hazel	*Corylus avellana*
Prunus*	*Prunus* spp. (*Amygdalus* sp.)
Fig*	*Ficus* sp.
Beech	*Fagus orientalis*
Celtis	*Celtis caucasica*
Maple	*Acer platanoides*
Apple*	Maloidea, cf. *Malus orientalis*
Willow	*Salix* sp.
Plane	*Platanus orientalis*
Pine	*Pinus kochiana*
Lime (small leaf)	*Tilia cordata*
Lime (large leaf)	*Tilia platyphylous*
Jerusalem thorn	*Paliurus spina-christi*
Rose	*Rosa* sp.
Dogwood	*Cornus sanguinea*
Service tree	*Sorbus torminalis*
Hawthorn	*Crataegus monogyna*
Privet	*Ligustrum vulgare*
Elder	*Sambucus nigra*
Juniper	*Juniperus* sp.
Spindle	*Euonomys europaeus*
Buckthorn	*Hippophae rhamnoides*
Nettles	*Urtica* sp.
Brambles	*Rubus* sp.

*Usually found associated with human habitation, past or present

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