

AGE AND SEX COMPOSITION OF EPIPALAEOLITHIC FALLOW DEER AND WILD GOAT FROM KSAR 'AKIL

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ABSTRACT: The age and sex composition of Epipalaeolithic fallow deer and wild goat from Ksar 'Akil was analysed to reconstruct the exploitation pattern as regards these economically most important species. Kebaran hunters from Ksar 'Akil evidently practised with respect to both fallow deer and wild goat some selective exploitation of fully grown specimens, and more or less random cropping of does and bucks.

KEYWORDS: Age-sex composition, exploitation pattern, fallow deer, wild goat, Epipalaeolithic, Ksar 'Akil, Lebanon.

1. INTRODUCTION

1.1. The site

The Palaeolithic rock shelter of Ksar 'Akil in the Lebanon is located 10 km north-east of the city of Beirut, about 3 km from the present coast, in the valley of Antelias. Ksar 'Akil was excavated in 1937/38 and in 1947/48 by an American team from Boston College (e.g. Ewing, 1947; Murphy, 1938). The excavators distinguished 37 stratigraphic levels, numbered I through XXXVII from top to bottom, in the 23 m thick accumulation of deposits against the base of the limestone cliff.

The lithic material represents a succession of Middle Palaeolithic, Upper Palaeolithic, and Epipalaeolithic occupations (Azoury, 1986; Bar-Yosef, 1970; Bergman, 1981; 1987; Marks & Volkman, 1986). Newcomer (1974) studied the bone tools, van Regteren Altena (1962) the molluscs and echinoderms, and Hooijer (1961) the vertebrate remains.

Although Hooijer's report renders a full and valuable taxonomic account of the vertebrate remains from Ksar 'Akil, an up-to-date re-analysis with emphasis on archaeozoological aspects became desirable.

1.2. The Epipalaeolithic

The Epipalaeolithic, which started to develop in the Levant about 19,000 years BP (Cauvin, 1981), comprises levels V through I. Level V contained a pre-Kebaran lithic industry, a transition from Upper Palaeolithic to Epipalaeolithic, whereas the industry of levels IV through I is early Kebaran (Waechter, unpublished, see Copeland, 1987; Bar-Yosef, 1970).

The excavated Epipalaeolithic faunal sample consists almost exclusively of ungulate remains (Hooijer, 1961; Kersten, in press). The change from a pre-Kebaran to an early Kebaran lithic industry was accompanied by an economic shift, involving an increase in the relative exploitation of the Mesopotamian fallow deer (*Dama (dama) mesopotamica*) over wild bezoar goat (*Capra aegagrus*) and roe deer (*Capreolus capreolus*) (Kersten, in press). Nevertheless, the order of relative abundances of the ungulate species remained similar during the Epipalaeolithic. Fallow deer constituted the major part of the game bag throughout the sequence from levels V through I, invariably followed by wild goat (Kersten, in press).

In the present study the age and sex composition of fallow deer and wild goat was analysed to reconstruct the exploitation pattern practised by Kebaran hunters from Ksar 'Akil as regards these major food animals.

1.3. Random versus selective exploitation

Theoretically, prehistoric hunters had two exploitation patterns at their disposal: random and selective exploitation. Random exploitation implies that sexes and age classes are killed according to their proportion in the population. Selective exploitation implies heavier cropping of certain age classes and/or one of both sexes.

Different opinions have been put forward concerning the question whether prehistoric hunters exploited their prey, usually ungulates, randomly or selectively. Several investigators (e.g. Ducos, 1968; Hecker, 1975) assumed that pre-Neolithic hunters exploited their prey more or less at random, whereas exploitation started to be selective with the

beginning of herding in Neolithic times. Others (Payne, 1972; Jarman & Wilkinson, 1972) have argued that prehistoric hunters often – if not invariably – exploited animals selectively with respect to age and sex, because random cropping from wild populations would have been, and is still, nearly a practical impossibility. Klein (1983) holds the opinion that both more or less random and highly selective exploitation of ungulates was practised by prehistoric man, depending on the hunting technique used, which was in turn dependent on such factors as the prey's ecology and behaviour. Klein proposed that a fossil mortality pattern which tends to reflect the age structure of the live ungulate population (a 'catastrophic' pattern), may imply that entire groups were killed by a hunting method such as communal driving over cliffs or into traps. A fossil ungulate sample in which prime-age (reproductively active) adults are very rare relative to old and especially to very young animals (an 'attritional' pattern), may indicate that individuals were killed by a hunting method such as stalking, whereby hunters obtained mainly the weakest prey – the very young and the old (Klein, 1983). Such an 'attritional' pattern may, according to Klein, eventually result from scavenging on carcasses by prehistoric man, because very young and old animals are also most vulnerable to natural death causes, such as disease, starvation and carnivore predation.

2. MATERIAL AND METHODS

The excavators used a two-metre grid system and sifted the earth with sieves of medium mesh (Ewing, 1947; Murphy, 1938). Levels were distinguished primarily on the basis of geological criteria, like texture and colour of the earth (Ewing, 1947).

The Epipalaeolithic vertebrate remains were packed in small boxes, labelled with level and square. This material was derived from 6-20 squares per level and, according to Hooijer (1961), collected in 1947/48.

Most of the bones were heavily encrusted with calcium carbonate concretions and were cleaned in a dilute solution of acetic acid (10%). This treatment slightly enhanced the degree of fragmentation of bones, though fresh fractures were glued as far as possible.

As a mammal matures after a period of growth, the cartilagenous zone between the shaft and the epiphysis (bony cap) at the ends of limb bones is progressively ossified. In adult animals the epiphyses and shaft are solidly fused. During dental development a set of permanent molars erupts behind the deciduous milk molars, while this latter set is replaced by permanent premolars. Once erupted, ungulate teeth are subject to wear, and

enamel of the occlusal surface gradually wears away, revealing the underlying dentine. The timing of these skeletal and dental changes can be used for age estimation in fossil material.

The age composition of fallow deer and wild goat was assessed on the basis of the proportion of unfused limb bones and the state of eruption and wear of mandibular teeth. Since ages of epiphyseal fusion and of dental eruption and wear in Mesopotamian fallow deer and bezoar goat are not available, data from related species were used. The age estimations for Mesopotamian fallow deer are based on ageing criteria for the smaller European fallow deer (Habermehl, 1985; Pohlmeier, 1985). The dental age estimations for bezoar goat are based on dental ageing criteria for the ibex (Habermehl, 1985), while the ages of epiphyseal fusion are based on data for domestic goats (Rajtova, 1974) and feral goats (Noddle, 1974), which are descended from the bezoar goat. The ages of epiphyseal fusion in domestic goats given by Rajtova (1974) approach those of feral goats (Noddle, 1974) and are more complete.

Ratios of female and male specimens in the fallow deer and wild goat sample were estimated by plotting measurements of astragali and first phalanges as scatter diagrams. Measurements were taken according to von den Driesch (1976).

The age and sex composition of Epipalaeolithic fallow deer and wild goat populations in the Levant is unknown and, like ageing criteria, data on population structure have to be gleaned from recent related species, which can provide undoubtedly nothing more than a very rough approximation of their actual demographic structure.

If possible, differences between levels were tested on statistical significance with a chi-square (χ^2)-test. The level of significance was set at $p < 0.05$.

3. AGE AND SEX COMPOSITION

3.1. Recent living populations

Although wildlife populations are rarely static, but usually show a sequence of years of increase or decrease, they tend to shift towards stability and may often approach a stable age-sex structure (Eberhardt, 1971).

Stable natural populations usually display an age structure with progressively fewer animals in equally broad, successively older age classes. The steepness of this 'age pyramid' depends on the species' biological characteristics, such as reproductive potential, and on environmental conditions, such as carnivore predation and human hunting pressure.

The maximum potential lifespan of animals may be divided into 'physiological longevity', eventually

Table 1. Age-sex composition of European fallow deer and Cretan wild goat population. Data from: (1) Hypothetical stationary *Dama dama* population with normal age-sex structure (Ueckermann & Hansen, 1983: fig. 50). (2) Complete count of stationary *Capra aegagrus cretica* population, Theodorou, Crete, Greece (Papageorgiou, 1979: table 6).

Age(years)	European fallow deer (1)			Cretan wild goat (2)		
	Males	Females	%	Males	Females	%
Immatures:						
0-1	17	17	25.4	7	7	14.6
1-2	14	10	17.9	7	6	13.5
		1:0.87	43.3		1:0.93	28.1
Adults:						
2-3	10	7	12.7	2	5	7.3
3-4	6	7	9.7	6	4	10.4
4-5	6	7	9.7	4	5	9.4
5-6	4	6	7.5	3	3	6.3
6-7	4	5	6.7	1	4	5.2
7-8	3	4	5.2	1	2	3.1
8-9	2	3	3.7	4	6	10.4
9-10	1	1	1.5	11	2	13.5
10-11	-	-	-	3	1	4.2
11-12	-	-	-	1	1	2.1
		1:1.11	56.7		1:0.92	71.9

reached under optimal conditions in captivity, and an 'ecological longevity', several years shorter, reached under natural conditions (see Eberhardt, 1971).

The age-sex composition of a stable European fallow deer population and that of a stable Cretan wild goat (agrimi) population, is given in table 1. In modern management of fallow deer populations, carefully planned shooting programs are carried out to maintain healthy stationary populations with a normal structure (Ueckermann & Hansen, 1983). The 'physiological longevity' of fallow deer is 15-20 years, but individuals of 10 years and older are usually shot (Ueckermann & Hansen, 1983), resulting in a 'hunted longevity' of about 10 years (table 1). According to Ueckermann and Hansen (1983), European fallow deer populations generally exhibit an equal sex ratio, while Haltenorth (1959) also found indications of an equal sex ratio in Mesopotamian fallow deer populations, in those days inhabiting refuge areas along the Karcheh, Dez and Karun rivers in southwestern Iran. Data on European fallow deer (Ueckermann & Hansen, 1983) reveal that adult does tend to outnumber adult bucks, because of differences between sexes in age-specific mortality rates. However, differences are small and usually there is a tendency towards an equal proportion of adult does and bucks, as seen in table 1. The Cretan wild goat population (table 1) suffered from high density with impoverished food resources, and was characterized by a very low reproductive rate, reflected in the low kid and yearling percentages (Papageorgiou, 1979). In addition,

the population had an unusual abundance of old animals. Mortality in this non-hunted agrimi population, with an 'ecological longevity' of 12 years, resulted mainly from starvation (Papageorgiou, 1979). Although males tend to outnumber females, Papageorgiou (1979) showed this difference to be insignificant. Schaller and Laurie (1974) also observed an equal sex ratio in a population of bezoar goats in the Karchat Hills, in Pakistan, though the adult segment showed a similar tendency towards a predominance of bucks.

It is not unreasonable to suppose that the fallow deer and wild goat populations exploited by Ksar 'Akil hunters, during the time span covered by the Epipalaeolithic, had in general a more or less stable demographic structure, were exposed to carnivore predation and slight human hunting pressure, and exhibited a normal reproductive rate.

3.2. Epipalaeolithic remains from Ksar 'Akil

3.2.1. Age composition

The uncertainties involved in ageing methods, sample bias, and vertical grouping of data may introduce error into calculations of the relative proportions of different age classes, resulting in dissimilarity between the age composition of the collected sample and the actual kill-off pattern.

It is unlikely that the ageing criteria used are completely valid for Epipalaeolithic fallow deer and wild goat in the Levant. Epiphyseal fusion and dental eruption and wear sequences are variable

Table 2. Skeletal age composition of Epipalaeolithic fallow deer. Unfused and fused skeletal elements per level and from levels V through I. Epiphyseal fusion completed between 6 and 18 months (group A), between 22 and 24 months (group B), and between 27 and 72 months (group C) (after data from Pohlmeier, 1985). Key: p = proximal; d = distal; U = unfused, i.e. epiphysis and shaft separated or epiphyseal line still evident; F = fused, i.e. epiphyseal line disappeared.

Group	Element	V		IV		III		II		I		V-I	
		U	F	U	F	U	F	U	F	U	F	U	F
A	Radius p	-	5	-	1	-	2	-	6	-	-	-	14
	Phalanx 1 p	1	24	-	3	-	-	-	18	-	10	1	55
	Phalanx 2 p	-	6	-	3	-	4	-	12	-	2	-	27
	Scapula	1	9	1	4	-	3	-	3	1	2	3	21
	Humerus d	-	11	1	7	-	1	-	5	-	2	1	26
	Tibia d	6	11	1	1	2	2	2	7	-	4	11	25
	Total	8	66	3	19	2	12	2	51	1	20	16	168
	Unfused	10.8%		13.6%		14.3%		3.8%		4.8%		8.7%	
B	Femur p	3	1	-	-	-	2	1	1	-	1	4	5
	Femur d	-	-	-	1	-	-	-	-	-	-	-	1
	Calcaneum	1	9	-	1	3	-	3	5	-	4	7	19
	Radius d	3	4	-	1	1	-	-	-	-	-	4	5
	Metapodial d	6	16	1	7	2	3	4	25	3	10	16	61
	Total	13	30	1	10	6	5	8	31	3	15	31	91
	Unfused	30.2%		(9.1%)		54.6%		20.5%		16.7%		25.4%	
C	Tibia p	-	1	-	-	-	-	-	-	-	-	-	1
	Humerus p	1	-	-	-	-	-	-	-	-	-	1	-
	Total	1	1	-	-	-	-	-	-	-	-	1	1

within species, both at an individual and population level. It may be affected by several factors, such as domestication, level of nutrition and habitat (Nodde, 1974; Riney, 1982). Therefore the ages suggested in the present study, in particular those based on dental wear, should be taken only as a rough guide.

Poor recovery and poor preservation are both likely to bias the sample towards older specimens, with more robust and dense bones than young individuals (Binford & Bertram, 1977; Payne, 1975). The Ksar 'Akil Epipalaeolithic bone assemblage showed no particular recovery bias at the expense of smaller elements, but bone fragments with a low resistance to destruction seem to have been at a disadvantage in preservation (Kersten, in press). This implies that at least some under-representation of fragile and soft immature limb bones and mandibles may be expected.

Grouping of data across levels may obscure changes in exploitation and represent a misleading picture (Payne, 1972). The age composition of fallow deer was analysed per level to trace significant changes in the course of the Epipalaeolithic sequence. However, the wild goat remains did not provide sufficient data for an analysis per level, and only pooled data were considered.

Fallow deer




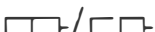


Data on the epiphyseal fusion of fallow deer limb bones are presented in table 2. In fallow deer epiphyseal closure of most limb bones is completed at an age of c. 24 month (Pohlmeier, 1985). Proximal tibiae and proximal humeri are nearly absent, probably because they are very vulnerable to destruction (Brain, 1981: fig. 148), which renders any calculation of the proportion of unfused specimens in age group C useless. The numbers of unfused limb bones are insufficient to test changes within age groups on statistical significance. However, the combined frequency of group A and group B unfused specimens shows no significant changes across levels ($\chi^2=8.40$, $df=4$, $0.05 < p < 0.10$), suggesting that the fallow deer samples from different levels are fairly homogeneous in skeletal age composition. Pooled data from levels V through I indicate that 9% of the fallow deer killed by Ksar 'Akil hunters were younger than c. 1½ years, and 25% were younger than c. 2 years at the time of death.

Data on the dental eruption and wear of fallow deer are given in tables 3 and 4. Fallow deer possess their permanent dentition at an age of 26 months (Habermehl, 1985), which was set at 2 years in the present analysis. All ageable mandible parts were

Table 3. Dental age composition of Epipalaeolithic fallow deer. Eruption and wear data of ageable mandible parts per level and from levels V through I. Ageing criteria after data from Habermehl (1985). Key: m = milk molar; P = premolar; M = molar; - = posterior cusps unworn; + = slightly worn; ++ = moderately worn; +++ = heavily worn.

Suggested age class (years)	Eruption and wear of teeth	V	IV	III	II	I	V-I
Infantile < c. 1/2 yr	m- to m+	-	-	-	-	-	-
	M1 not erupted/erupting	1	-	-	-	-	1
	Total	1	-	-	-	-	1
	%	1.4	-	-	-	-	0.4
Juvenile c. 1/2-1 yr	m+ to m++	1	4	3	4	5	17
	M1 erupted; M2 not erupted	3	1	3	-	1	8
	M1-/M1+	-	-	-	-	-	-
	M2 erupting	-	-	1	1	-	2
	Total	4	5	7	5	6	27
	%	5.6	11.4	14.3	6.7	14.0	9.6
Subadult c. 1-2 yr.	m++/m+++	3	1	1	2	1	8
	M2 erupted; M3 not erupted	-	-	-	-	-	-
	M2 erupted; m not replaced	3	2	2	2	2	11
	M1+	-	-	-	1	1	2
	M2-/M2+	-	-	-	-	-	-
	M3 erupting	1	-	-	1	-	2
	P erupting	-	-	-	-	-	-
	M3 erupted; m not replaced	1	-	-	4	-	5
	M3-	-	-	1	3	2	6
	P-	-	-	2	1	-	3
	Total	8	3	6	14	6	37
	%	11.3	6.8	12.2	18.7	14.0	13.1
Adult > c. 2 yr	M1++/M1+++	2	2	2	3	3	12
	M2+/M2++/M2+++	12	5	4	10	-	31
	M3+/M3++/M3+++	22	13	16	15	14	80
	P+/P++/P+++	22	16	14	28	14	94
	Total	58	36	36	56	31	217
	%	81.7	81.8	73.5	74.7	72.1	77.0
	Total	71	44	49	75	43	282

Table 4. Dental age composition of adult segment of Epipalaeolithic fallow deer. M3 wear stages of mandible parts with M3 in place and isolated M3's per level and from levels V through I. Ageing criteria after data from Habermehl (1985). *Wear stage symbols, based on the pattern of exposed dentine, after Payne (1973).

Suggested age class (years)	M3 wear stage*	V	IV	III	II	I	V-I
'Young adult' c. 2-6 yr	 to 	16	6	11	10	16	59
	%	48.5	35.3	55.0	47.6	80.0	53.2
'Mature' c. 6-9 yr	 to 	14	7	8	8	3	40
	%	42.4	41.2	40.0	38.1	15.0	36.0
'Aged' c. 9-10 yr		3	4	1	3	1	12
	%	9.1	23.5	5.0	14.3	5.0	10.8
'Senile' > c. 10 yr	post- 	-	-	-	-	-	-
	Total	33	17	20	21	20	111

assigned to an infantile, juvenile, subadult or adult age class on the basis of dental eruption and wear (table 3). Subdivision of adult specimens into age classes was based on M3 wear stages, comprising both mandible parts with the third molar in place and isolated third molars (table 4). Adult age classes were arbitrarily termed 'young adult', 'mature', 'aged' and 'senile'. To test changes in dental age composition across levels on statistical significance, age classes were combined. Neither the relative frequency of fallow deer under c. 2 years of age ($\chi^2=2.62$, $df=4$, $0.50 < p < 0.70$), nor the relative frequency of c. 2-6 year old fallow deer within the adult group ($\chi^2=8.56$, $df=4$, $0.05 < p < 0.10$) showed a significant change, and the samples from different levels were considered similar enough to allow vertical pooling. The age composition of the dental remains from levels V through I indicates that 10% of fallow deer were killed as juveniles, and 13% as subadults. Infants are represented by only one mandible part from level V. Within the adult segment of the dental sample 'young adults' and 'matures' are most abundant, while 'senile' fallow deer seem to be absent.

The kill-off pattern of fallow deer is shown in figure 1. Although the dental remains contain a slightly greater proportion of specimens under c. 1½ years of age than the skeletal remains, the proportions of immatures (under c. 2 years) are almost identical. The kill-off pattern suggests that the majority of fallow deer exploited by Ksar 'Akil hunters was 'young adult' or 'mature', accounting

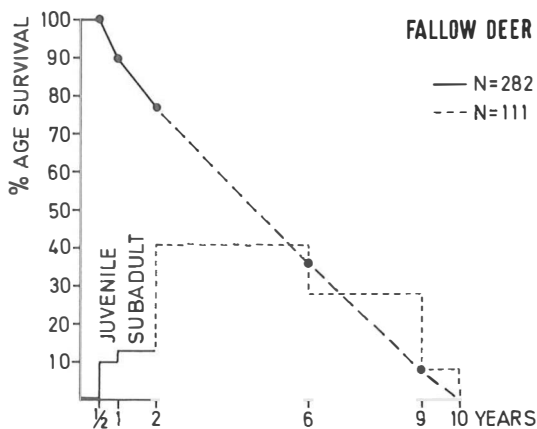


Fig. 1. Kill-off pattern of Epipalaeolithic fallow deer, based on dental remains. The 'curve' represents the percentage survival and the histogram the percentage mortality within each age class. The solid lines are based on eruption and wear data of ageable mandible parts (table 3), and the broken lines are based on M3 wear stages (table 4), with percentages for the adult segment converted to percentages for the sample of ageable mandible parts. For instance, 53.2% of the 217 adults, which is about 115 specimens, were killed between c. 2-6 years of age, constituting 40.8% of all ageable mandible parts.

for 69% of the total kill analysed. Juvenile, subadult and 'aged' fallow deer were apparently cropped in smaller proportions.

Compared to a European fallow deer population with a normal age structure (table 1), Epipalaeolithic fallow deer from Ksar 'Akil show an under-representation of immatures, especially fawns (c. 0-1 year), in favour of 'mature' and 'aged' specimens. The oldest individuals had reached an age of c. 9-10 years at the time of death, which is identical to the usual 'hunted longevity' in recent European fallow deer populations under management control.

Wild goat

Data on the epiphyseal fusion of wild goat limb bones from levels V through I are presented in table 5. In goats epiphyseal closure of several limb bones is only completed after an age of 24 months (Rajtova, 1974; Noddle, 1974). The epiphyseal fusion pattern suggests that of the wild goats killed only 3% was younger than c. 1 year, 7% was younger than c. 2 years, and 29% was younger than c. 5 years at most.

Data on the dental age composition of wild goat from levels V through I are given in tables 6 and 7. In ibex permanent premolar and molar dentition is complete at an age of 3 years (Habermehl, 1985).

Table 5. Skeletal age composition of Epipalaeolithic wild goats. Unfused and fused skeletal elements from levels V through I. Epiphyseal fusion completed between 6 and 12 months (group A), between 12 and 24 months (group B), and between 24 and 60 months (group C) (after data from Rajtova, 1974 and Noddle, 1974). Key: p = proximal; d = distal; U = unfused, i.e. epiphysis and shaft separated or epiphyseal line still evident; F = fused, i.e. epiphyseal line disappeared.

Group	Element	U	F
A	Radius p	-	12
	Humerus d	-	14
	Scapula	1	7
	Total	1	33
		2.9%	97.1%
B	Phalanx 2 p	3	35
	Phalanx 1 p	1	39
	Tibia d	2	8
	Total	6	82
		6.8%	93.2%
C	Metapodial d	17	41
	Calcaneum	2	3
	Femur d	-	1
	Radius d	-	2
Total	19	47	
		28.8%	71.2%

Like in the analysis of the fallow deer dental age composition, all ageable mandible parts were assigned to an infantile, juvenile, subadult or adult age class on the basis of dental eruption and wear (table 6). Adult specimens were subdivided into age classes on the basis of M3 wear stages (table 7). As well as in fallow deer, adult age classes in wild goat were arbitrarily termed 'young adult', 'mature', 'aged' and 'senile'. The dental age composition of wild goat indicates that 6% of the specimens were killed as juveniles, and 9% as subadults. Infants seem to be absent. The adult segment of the dental sample consists mainly of 'mature' and 'aged' specimens, while 'seniles' are not represented.

The kill-off pattern of wild goat is shown in figure 2. The 'survivorship curve' ends in an arrowhead

Table 6. Dental age composition of Epipalaeolithic wild goats. Eruption and wear data of ageable mandible parts from levels V through I. Ageing criteria after data from Habermehl (1985). Key: m = milk molar; P = premolar; M = molar; - = posterior cusps unworn; + = slightly worn; ++ = moderately worn; +++ = heavily worn.

Suggested age class (years)	Eruption and wear of teeth	I-V
Infantile < c. 1/2 yr	m- to m+	-
	M1 not erupted/erupting	-
	Total %	-
Juvenile c. 1/2-1 1/2 yr	m+ to m++	3
	M1 erupted; M2 not erupted	2
	M1-/M1+	-
	M2 erupting	-
	Total %	5 6.4
Subadult c. 1 1/2-3 yr	m+++ to m++++	1
	M2 erupted; M3 not erupted	1
	M2 erupted; m not replaced	3
	M1++	1
	M2-/M2+	-
	P erupting	1
	M3 erupting	-
	m replaced; M3 not erupted	-
	P-	-
	M3-	-
Total %	7 9.0	
Adults > c. 3 yr.	M1++/M1+++	4
	M2++/M2+++	4
	M3+/M3++/M3+++	27
	P+/P++/P+++	31
	Total %	66 84.6
	Total	78

because it may reach the horizontal axis anywhere between 9 and 15 years. The percentages of the different age groups based on the skeletal remains follow, up to an age of c. 5 years, exactly the 'survivorship curve' based on the dental remains. Apparently the major part of wild goats killed by Ksar 'Akil hunters consisted of 'mature' and 'aged' individuals, accounting for 73% of the total kill analysed. Juveniles, subadults and 'young adults' provided smaller proportions of the wild goat game bag.

The Cretan subspecies of wild goats (*agrimi*) is considered adult at an age of 2 years (Papageorgiou, 1979). Therefore, a comparison between the age composition of this subspecies and the wild goats from Ksar 'Akil should be based on similar but not identical age classes. Assuming a normal age structure for the *agrimi* population (table 1), with more kids and yearlings, the Epipalaeolithic wild goats from Ksar 'Akil show relative to a live population an under-representation of immatures (c. 0-3 years) and 'young adults', in favour of 'mature' and 'aged' animals. The oldest wild goats had reached an age somewhere between c. 9 and 15 years at the time of death, possibly more or less similar to the 'ecological longevity' of the *agrimi*.

3.2.2. Sex composition

Both fallow deer and wild goats display sexual dimorphism, with adult males being in general larger and heavier than adult females. This sexual dimorphism may be revealed by plotting measurements of skeletal elements as scatter diagrams. Ideally, such an analysis comprises only skeletal

Table 7. Dental age composition of the adult segment of Epipalaeolithic wild goats. M3 wear stages of mandible parts with M3 in place and isolated M3's from levels V through I. Ageing criteria after data from Habermehl (1985).

*Wear stage symbols, based on the pattern of exposed dentine, after Payne (1973).

Suggested age class (years)	M3 wear stage*	V-I
'Young adult' c. 3-5 yr	to -	6 14.0 %
'Mature' c. 5-9 yr	to / -	24 55.8 %
'Aged' c. 9-15 yr	-	13. 30.2 %
'Senile' > c. 15 yr	post- -	-
Total		43

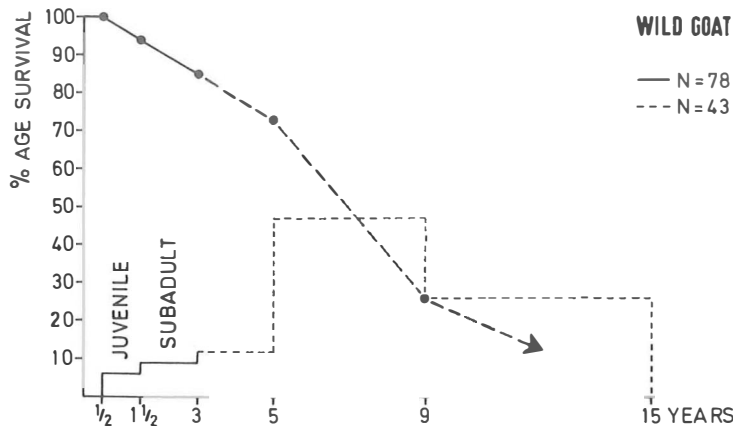


Fig. 2. Kill-off pattern of Epipalaeolithic wild goats, based on dental remains. The 'curve' represents the percentage survival and the histogram the percentage mortality within each age class. The solid lines are based on eruption and wear data of ageable mandible parts (table 6), and the broken lines are based on M3 wear stages (table 7), with percentages for the adult segment converted to percentages for the sample of ageable mandible parts. For example, 14.0% of 66 adults, which is about 9 specimens, were killed between c. 3-5 years of age, constituting 11.5% of all ageable mandible parts.

elements which provide the possibility to make a clear-cut distinction between immature and adult specimens, like distal metapodials. However, no limb bone that fuses relatively late in the growth period was well-preserved. Astragali and first phalanges were among the most abundant measurable skeletal elements. Astragali of infants and juveniles can be distinguished from those of subadults and adults on the basis of their greater porosity. In fallow deer and wild goat the distal epiphysis of the first phalanx fuses before birth, while the proximal epiphysis fuses to the shaft when the animal is subadult. Although only 'adult' phalanges (i.e. phalanges with fused epiphyses) were involved in the analysis, part of them may still have belonged to subadult individuals. Samples were too small for a breakdown into sexes per level, and only pooled data from levels V through I were considered.

Several astragali and first phalanges showed traces of burning, varying from partial charring to complete calcination, which may have caused size reduction of these bones. It has been demonstrated that there is polynomial relationship between the percentage shrinkage and the maximum temperature reached by bones, with a mean shrinkage between 0% and 5% below a temperature of about 700°C and a rapid increase in shrinkage to a mean percentage of about 15% in bones heated to 940°C (Shipman et al., 1984).

Fallow deer

The scatter diagrams of fallow deer astragali (fig. 3) and first phalanges (fig. 4) both reveal clustering of values around an imaginary regression line. The individual values of the Mesopotamian fallow deer from Ksar 'Akil are in general considerably larger than the mean values of recent European fallow deer of both sexes. In European fallow deer there is no overlap between minimal adult male and maximal female dimensions of astragali, but there is

overlap between those of adult females and subadult males (Pohlmeyer, 1985). Measurements from Bosold (1966) on skeletal elements of European fallow deer indicate that dimensions of female first phalanges may slightly overlap with those of adult and subadult males. The astragali and first phalanges of the fallow deer from Ksar 'Akil display no pronounced separation in two size-groups. Nevertheless, the larger astragali and first phalanges (on the upper right side) presumably represent bucks and the smaller specimens (on the lower left side) presumably represent mainly does.

The charred specimens are not concentrated in the smaller size-range, suggesting that charring of astragali and phalanges did not affect the dimensions to such an extent that the charred specimens of the female size-group originally belonged to the male size-group.

There seems to be a slight tendency towards a preponderance of specimens on the female side, especially in the scatter diagram of phalanges. The female size-range may, however, accommodate some subadult males, and neither the astragali nor the first phalanges reveal a conspicuous bias towards either sex. This suggests that the sex ratio of fallow deer killed is approximately equal, which reflects the usual sex ratio of recent fallow deer populations (see section 3.1).

Wild goat

The scatter diagrams of wild goat astragali (fig. 5) and first phalanges (fig. 6) both show, like in fallow deer, clustering of values around an imaginary regression line. Measurements of wild goat or ibex astragali of known sex were not available. The mean values of first phalanges in recent ibex of both sexes lie around the same imaginary regression line as the individual values of the wild goats from Ksar 'Akil, though the ibex phalanges are in the smaller size-range. Measurements from Bosold (1966) on recent

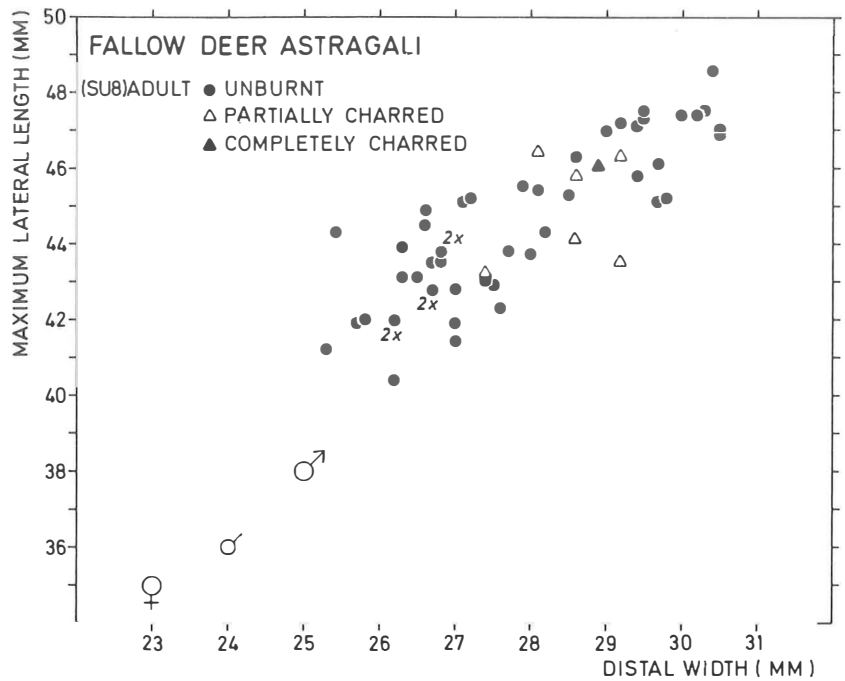


Fig. 3. Scatter diagram of distal width against maximum length of astragali in Epipalaeolithic fallow deer (2x = 2 specimens).

♀ ♂ ♂ The means of recent European adult female, adult male and subadult male fallow deer specimens (Pohlmeyer, 1985).

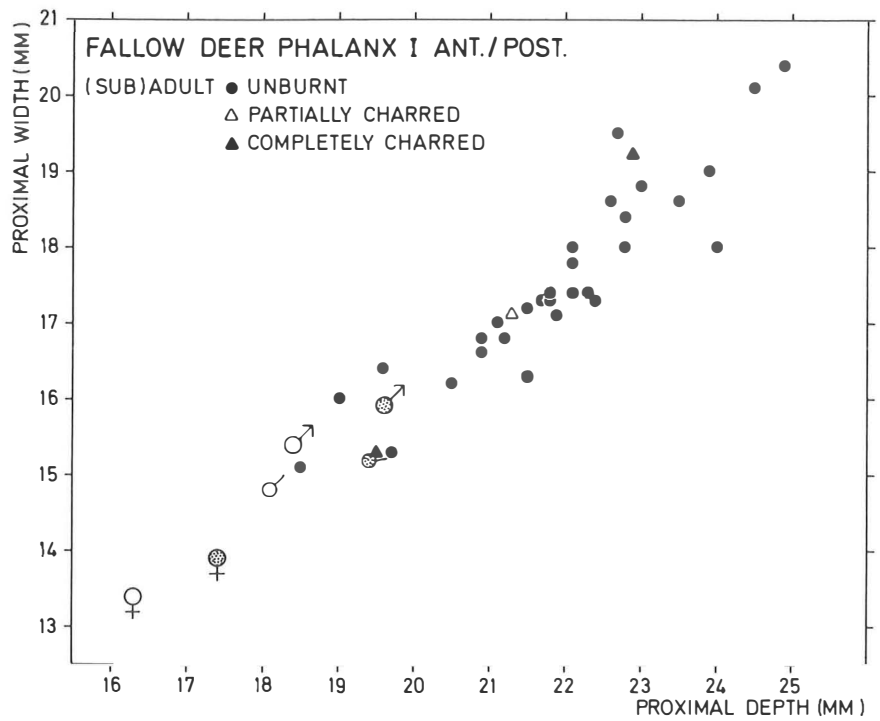


Fig. 4. Scatter diagram of proximal depth against proximal width of fore and hind first phalanges in Epipalaeolithic fallow deer.

♀ ♂ ♂ - Anterior
 ♀ ♂ ♂ - Posterior
 The means of recent European adult female, adult male and subadult male fallow deer specimens. Subadult males with phalanges fused, but metapodials still unfused (Bosold, 1966).

ibex indicate that there is some overlap between the dimensions of first phalanges of females and those of adult and subadult males. Nonetheless, the wild goat specimens from Ksar 'Akil display in both scatter diagrams a distinct separation in two size-groups, which seems to reflect the very pronounced sexual dimorphism in wild goats (Nievergelt, 1986).

Most probably the larger astragali and first phalanges (on the upper right side) represent bucks, and the smaller specimens (on the lower left side) does.

Calcined astragali, in contrast to charred astragali and phalanges, are concentrated in the smaller size-range. A completely calcined astragalus approaches the dimensions of an unburnt juvenile

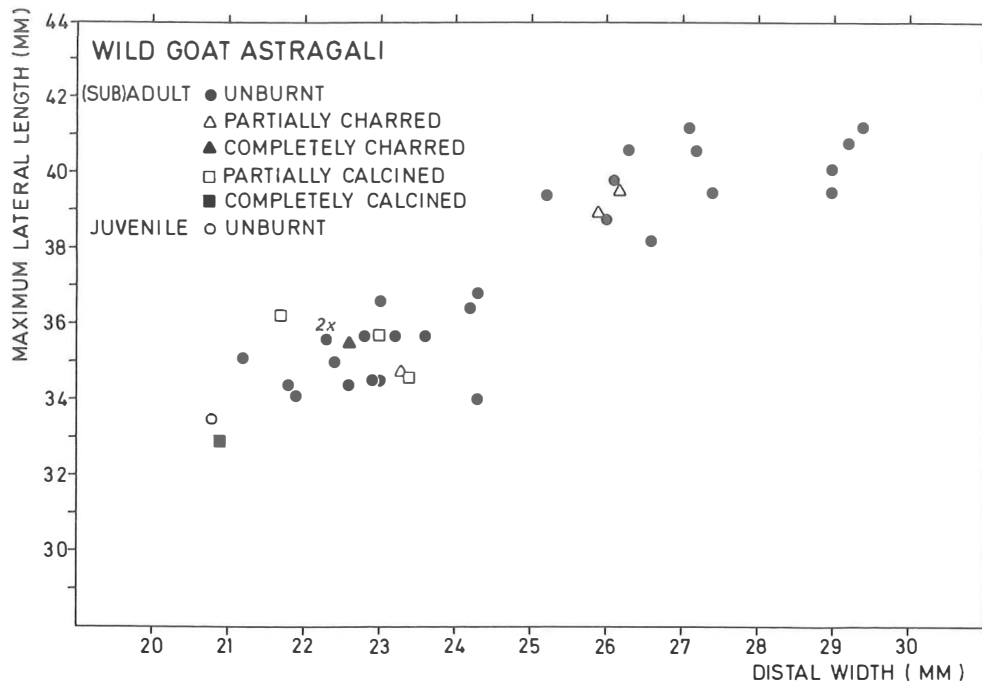


Fig. 5. Scatter diagram of distal width against maximum length of astragali in Epipalaeolithic wild goat (2x = 2 specimens).

specimen. Assuming a maximum mean shrinkage of about 15% (Shipman et al., 1984), whether or not the bones ever reached a temperature over 900°C, the calcined specimens may originally have belonged to the male size-group.

If the calcined astragali are excluded from the

analysis, the scatter diagram indicates a (sub)adult sex ratio of 14 males versus 18 females. The scatter diagram of first phalanges, on the other hand, indicates a (sub)adult sex ratio of 20 males versus 13 females. In sum, this yields 34 bucks and 31 does, which is not significantly different from unity ($p <$

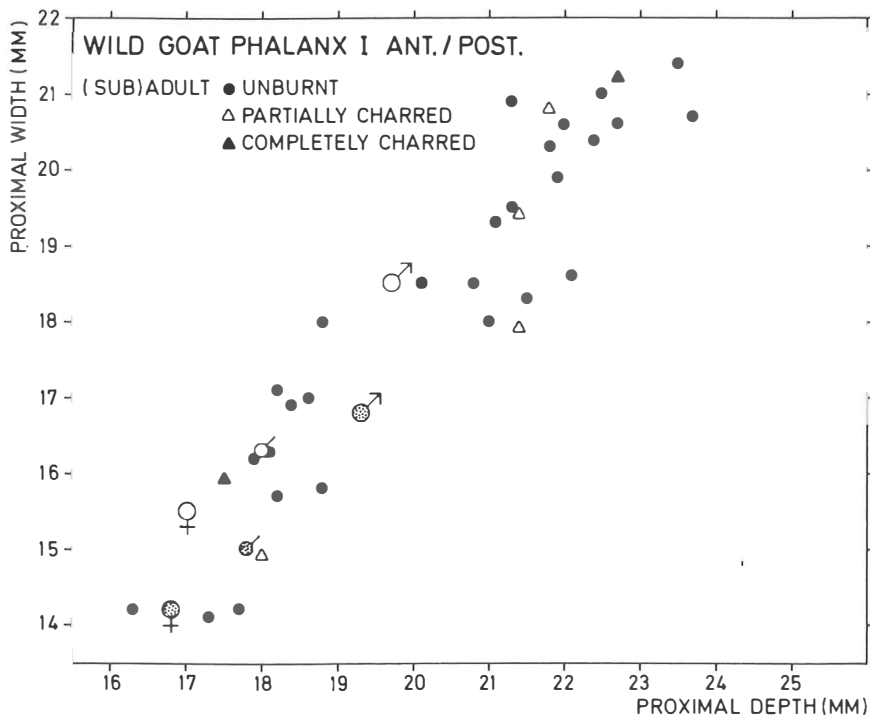


Fig. 6. Scatter diagram of proximal depth against proximal width of fore and hind first phalanges in Epipalaeolithic wild goat.

♀ ♂ ♂ - Anterior

♀ ♂ ♂ - Posterior

The means of recent adult female, adult male and subadult male ibex specimens. Subadult males with phalanges fused, but metapodials still unfused (Bosold, 1966).

0.90). These results suggest that wild goat does and bucks were killed in equal proportions, which reflects the sex ratio of recent wild goat populations (see section 3.1).

4. DISCUSSION

The age composition of fallow deer did not change significantly across levels, indicating that the exploitation pattern as regards the age of this species remained fairly similar during the Epipalaeolithic sequence. It was assumed that the pattern with respect to the sex of fallow deer killed and the age and sex of wild goat killed did not undergo essential changes either during this sequence.

A conspicuous characteristic of both the fallow deer and wild goat remains is the paucity of infants (under c. $\frac{1}{2}$ year of age). The limb bone samples contained no infants, as suggested by the lack of radii with an unfused proximal epiphysis. In addition, the mandible remains, apart from one infantile fallow deer specimen from level V, included no infants either. Inspection of isolated milk molars, not included in the age analyses, yielded only one additional infantile specimen. This isolated milk molar originated from the same level and square as the infantile mandible part, and both specimens may have belonged to one infant. Although preservation bias operates at the expense of immature specimens (Binford & Bertram, 1977), the Epipalaeolithic bone assemblage comprised 5 foetal limb bones, most probably representing fallow deer and/or wild goats, indicating that even extremely fragile and soft foetal bones did not disappear completely as a result of pre- and postdepositional destructive factors. In all probability the behaviour of Ksar 'Akil people played an essential role in causing a paucity of infants. Newborn fallow deer fawns and wild goat kids are well-hidden in isolated places, and very difficult to locate (Harrington, 1977; Ueckermann & Hansen, 1983). Although fawns and kids may follow their mother within a few days, they are extremely agile and can quickly hide (Harrington, 1977; Ueckermann & Hansen, 1983). The assumption that very young animals are more readily killed with hand-held weapons than prime adults (Klein, 1983) possibly does not apply to fallow deer and wild goat infants. The lack of infants may signify that Ksar 'Akil hunters cropped fallow deer and wild goats individually, with infants being rejected as prey because of their low meat yield relative to the effort required to locate or stalk them. On the other hand, the paucity of infants is also explicable in terms of seasonal abandonment of the rock shelter. Assuming that the fallow deer fawns and wild goat kids were usually born in spring, as reported for the Mesopotamian fallow

deer and wild goats of Iran (Harrington, 1977), this would imply abandonment of the rock shelter in summer. Davis (1983) analysed the age composition of several Late Pleistocene gazelle assemblages from different sites in Israel, and found indications of seasonal occupation in winter. In view of the topographic situation of the rock shelter of Ksar 'Akil, in a valley just outside the edge of the coastal plain at the foot of the Lebanon mountains, it could have served as a suitable winter residence. However, this hypothesis of winter occupation during the Epipalaeolithic requires evaluation on the basis of further analyses.

The dental samples comprised no heavily worn third molars, suggesting that senile animals did not contribute to the game bag any more than infants. Although teeth with little enamel left may have been at disadvantage in preservation, the presence of heavily worn first and second molars indicates that the absence of heavily worn third molars resulted not merely from preservation bias. Very old animals usually suffer from high natural mortality. Wild goats, for example, inhabit steep, rocky terrain, but very old goats seem unable to climb properly and are forced to stay at the base of rocky slopes, where they mostly fall prey to large carnivores (Harrington, 1977). The absence of seniles in the excavated assemblage most probably reflects their paucity in the exploited populations.

Compared to recent living populations with a normal age structure, both fallow deer and wild goats showed biasing towards 'mature' and 'aged' specimens at the expense of immatures. 'Young adult' fallow deer appeared to be well-represented, in contrast to 'young adult' wild goats. However, the relative abundances of separate M3 wear stages, not presented in this paper, revealed that in the fallow deer kill as well as in the wild goat kill, animals under about 4 years of age were under-represented in favour of animals over about 5 years of age. Fallow deer females start to participate in reproduction at an age of 2 years, and males are sexually adult at an age of 4-5 years, though they seem to mate little until 6 years of age, when they become master bucks and are able to defend a rutting territory (Espmark & Brunner, 1974; Ueckermann & Hansen, 1983). In general wild goat females are reproductively active from an age of 3 years on, whereas males mate little before an age of 5-6 years and are fully adult at an age of 6-7 years, at least (Schaller & Laurie, 1974). The 'mature' and 'aged' fallow deer and wild goat specimens in the fossil assemblage thus seem to represent physically and behaviourally fully adult does and nearly to fully adult bucks, with wild goats being roughly one year behind on fallow deer in maturation. The disproportionate abundance of these adults presumably did not result merely from preservation bias. A

more plausible explanation for this phenomenon is that Ksar 'Akil hunters practised some selective cropping of heavier animals.

Fallow deer and wild goat populations consist of mixed social groups during the rutting season in autumn, but split up into groups of bucks and groups of does and young animals after the rut or some months later (Espmark & Brunner, 1974; Nievergelt, 1986; Schaller & Laurie, 1974; Ueckermann & Hansen, 1983). Despite this sexual segregation for part of the year, Kebaran hunters from Ksar 'Akil apparently cropped virtually equal proportions of both male and female fallow deer and wild goats, suggesting random exploitation of sexes.

Mousterian and Upper Palaeolithic fallow deer from Kebara Cave, Israel, also showed biasing towards adults and an equal sex ratio, but the wild goats exhibited a preponderance of young specimens (Davis, 1977). Davis suggested that this might reflect man's inability to pursue adult wild goats in difficult rocky mountains, but the extremely small sample size may have produced a spurious picture.

Driving of fallow deer and wild goats may have been practically impossible. Fallow deer inhabit open woodland areas, where the strategy of driving is considered effective (Riney, 1982). However, in response to driving fallow deer show a strong reluctance to move forward; instead they repeatedly stop at a safe distance from the drivers and unexpectedly break out sideward, which makes this species not or hardly amenable to driving (Ueckermann & Hansen, 1983). Wild goats, on the other hand, inhabit areas of dissected topography, where drives seem least effective. A species living in such areas appears to have more clearly specified and more consistent home range boundaries than the same species inhabiting open, level, plains-type areas, raising the difficulty that animals refuse to leave their home range and tend to double back through or around the drivers (Riney, 1982). In addition, communal driving into traps would have resulted in a relatively greater abundance of immature animals. It is thus unlikely that Ksar 'Akil hunters killed entire fallow deer groups or – usually larger – wild goat herds, by driving them into traps. These prey species have rather been killed individually by hunting methods, such as stalking and ambushing, which apparently need not invariably cause a predominance of the weakest specimens in the kill (an 'attritional' pattern), as has been suggested by Klein (1983). Bergman (1981) analysed stone points from Ksar 'Akil and reported that there might have been a change from hunting with a spear to hunting with bow and arrow in Upper Palaeolithic times. This implies that Kebaran hunters from Ksar 'Akil presumably had bows and arrows, which enabled them to shoot a relatively high proportion of fully grown prime adults. Any-

how, Ksar 'Akil hunters seem to have practised with regard to both fallow deer and wild goat more or less random exploitation of sexes and some selective exploitation of age classes. As noted by Payne (1972) and Jarman and Wilkinson (1972) completely random hunting of wild populations by prehistoric man was probably practically impossible. Virtually all modern methods for sampling wild populations are susceptible to biases as well (Eberhardt, 1971; Riney, 1982). Nevertheless, both random and selective cropping is practised in modern wildlife management for practical purposes (Riney, 1982). Thus even if not random in the statistical sense, the concept of random exploitation may be useful in appraising the basic trend.

5. SUMMARY

In the present study the age and sex composition of Epipalaeolithic fallow deer and wild goat from Ksar 'Akil was analysed to reconstruct the exploitation pattern practised as regards these major food animals.

The age composition of the kills was assessed on the basis of the state of epiphyseal fusion of limb bones and eruption and wear of mandibular teeth. The sex composition was estimated by means of scatter diagrams of astragali and first phalanges.

A conspicuous characteristic of the fallow deer as well as the wild goat sample was the paucity of infants (c. 0-1/2 year), which may indicate that hunters from Ksar 'Akil rejected infants as prey. On the other hand, it may reflect abandonment of the rock shelter in summer, but this hypothesis requires further analyses, including other hunted species.

Compared to recent living populations of related species, both fallow deer and wild goat showed biasing towards fully grown specimens but no biasing towards one of both sexes. It is suggested that Kebaran hunters from Ksar 'Akil practised with respect to both fallow deer and wild goat some selective exploitation of age classes and more or less random exploitation of bucks and does. Most probably both game species have been cropped by hunting methods focused on individuals, such as stalking and ambushing.

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