CLIMATIC CHANGE AND FAUNAL DIVERSITY IN EPIPALAEOLITHIC AND EARLY NEOLITHIC SITES FROM THE LOWER JORDAN VALLEY

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Abstract

A diachronic series of faunal assemblages dating from the Early Kebaran period (onset circa 17,000 BC) through to the end of the Pre-Pottery Neolithic B (PPNB) period (circa 6,000 BC), located in the Lower Jordan Valley were analyzed. For each period the Shannon-Wiener Diversity and Evenness Indices were calculated. Results show that the highest diversity and evenness are found in the Natnfian period and Khiamian phase of the PPNA periods. Examination of specific trends in species representation corroborates previous published findings that indicate a steady decrease in the proportion of artiodactyls and a marked increase in the quantity of smaller sized mammals such as birds, reptiles and rodents from the Kebaran onwards. In the PPNB there is an inverse trend with a marked increase in the quantity of artiodactyls, primarily caprines, a feature associated with the onset of domestication in this region. These findings are discussed in relation to both the palaeoclimatic and cultural sequence of the Lower Jordan Valley.

Résumé

Une série d'assemblages fauniques datant du début de la période kebarienne (commençant vers 17,000 BC) jusqu'à la fin de la période Néolithique pré-poterie B (PPNB) (ca. 6000 BC), située dans la basse vallée du Jourdain a été analysée. Pour chaque période, les indices de diversité et d'égalité de Shannon-Wiener ont été calculés. Les résultats montrent que les plus grandes diversité et égalité se trouvent dans les périodes natoufieune et khiamienne. L'analyse des tendances spécifiques dans la représentation des espèces concorde avec les résultats publiés précédemment, où une diminution progressive des proportions d'artiodactyles et une forte augmentation d'animaux de petite taille, tel que les oiseaux et les reptiles, est apparu. Du Kebarien au PPNB, on observe une tendance inverse marquée par une forte augmentation des artiodactyles, en premier lieu les caprinés, phénomène qui est associé aux prémices de la domestication dans la région. Ces résultats sont discutés en fonction du paléoclimat et de la séquence culturelle de la basse vallée du Jourdain.

Key Words: Kebaran, Natufian, Neolithic, Late Pleistocene – Early Holocene, Species Diversity, Lower Jordan Valley.

Mots Clés: Kebarien, Natoufien, Néolithique, Pléistocène final – Début Holocène, Diversité spécifique, Basse Vallée de Jourdain.

Introduction

In the southern Levant, the transformation from Late Pleistocene hunting and gathering societies to agro-pastoralism in the early Holocene was characterized by major changes in climate, population demography, settlement patterns and social organization as well as subsistence base and food procurement strategies (Bar-Yosef and Belfer-Cohen 1989, 1992; Bar-Yosef and Meadow 1995; Goring-Morris and Belfer-Cohen 1998; Tchernov 1998a). There is still no consensus on the precise interaction between these different factors - as causes or consequences (Bar-Yosef and Meadow 1995; Goring-Morris and Belfer-Cohen 1998; Henry 1998; Sanlaville 1998; Sherratt 1997; Tchernov 1998a,b). There is, however, general agreement that despite the small area covered by the southern Levant, there existed a high degree of regional variation in these features. This is most evident in the record of

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the two core areas; the Mediterranean phytogeographic zone versus that of the arid Saharo-Arabian zone (Fig. 1). Archaeological and palaeoclimatic data from these zones indicate differences between them in the timing, form and extent of socio-economic and climatic changes (Bar-Yosef and Belfer-Cohen 1989, 1992; Belfer-Cohen 1991; Kaufman 1992; Goring-Morris and Belfer-Cohen 1998).

Moreover, numerous localized traditions have been identified within these "core" areas (Goring-Morris 1980, 1989; Henry 1989, 1998; Kaufman 1992) providing further evidence for regional differentiation on an even more refined scale.

One way of assessing the impact of environmental change on human adaptations in the southern Levant is through the examination of diachronic data sets from a single, well defined geographic entity. For this reason we have chosen to study changes in the diversity and richness of fauna recovered from a diachronic series of archaeological sites from the Lower Jordan Valley. Previous studies of faunal diversity in early Holocene sites from the southern Levant as a whole (Horwitz 1996; Horwitz and Tchernov 1998) have shown that there is considerable diachronic change in species exploitation. A similar approach has been used here to study a longer time trajectory in relation to the climatic changes documented for the region.

Background to the Lower Jordan valley

(a) Physical environment

The Lower Jordan Valley lies within the Dead Sea Rift. The boundaries of this region are defined by the shores of the Dead Sea to its south and the Bet She'an Valley to its north (Fig. 1). It is bounded to the west by the hills of Samaria in Israel, and to its east by the high mountains of Moab in Jordan. Large portions of the valley bottom are covered by marls deposited by Lake Lisan, an extinct water body which filled most of the Jordan Valley up until the end of the Late Pleistocene when it began to recede (Begin *et al.* 1985).

Today, the study area has a varied vegetation cover as it is a transition zone between the arid Saharo-Arabian zone and Sudanian enclaves of the Dead Sea and environs which lies to its south, and the semi-arid Irano-Turanian steppe zone which lies to its north (Danin 1988). This north-south gradient is best expressed in annual rainfall with the northern part receiving circa 250mm per annum while the southern-most region receives 150mm per annum. Consequently, the Lower Jordan Valley is a mosaic of vegetation types which include desert Savannoid vegetation, enclaves of Sudanian vegetation, and areas of wet saline (halophytic) vegetation (Danin 1988). Mean annual temperature is 23 ^{0}C ranging from 12 ^{0}C to 39 ^{0}C.

(b) Paleoclimatic Changes

The extensive archaeological research that has taken place in the study area, has been accompanied by numerous palaeoenvironmental studies of the geology, hydrology, palynology and geomorphology of the area as well as of specific sites (Bar-Yosef *et al.* 1974; Begin *et al.* 1985; Darmon 1988; Horowitz 1979, 1992; Noy *et al.* 1980; Schuldenrein and Goldberg 1981). Although, in general these data support the palaeoclimatic record for the rest of the southern Levant, there are some indications that at certain points in time, local environmental conditions may have differed.

While the record of the southern Levant indicates that cold and dry conditions prevailed in the Early Kebaran, there is some evidence from the Fazael sites to suggest that a slightly more humid phase occurred in this region at this time. A definite increase in humidity and rainfall is attested to for both the southern Levant and the Lower Jordan Valley sequence during the Late Kebaran and Geometric Kebaran. This trend is confirmed by the increase in the frequency of arboreal pollen from the Lower Jordan Valley (Darmon 1988); it falls between 5-12% in the Kebaran, and then increases to over 10% in the Geometric Kebaran.

Table 1. Sites used in this study, their NISP counts, species richness and diversity indices.

PERIOD (Dates are uncalibrated BC)	Sites	NISP per Period	N Species per period	Reference	Shannon -Wiener Diversity Index	Shannon-Wiener Evenness Index
Early Kebaran (17,000-15,000)	1) Urkan er-Rubb IIa 2) Fazael IIIb	707	10	1) Hovers *et al.* 1988 2) Horwitz and Tchernov unpubl. data	0.2	0.1
Late Kebaran (15,000-12,500)	1) Fazael IIIa 2) Fazael VII	295	12	1) and 2) Horwitz and Tcher-nov unpubl. data	0.4	0.1
Geometric Kebaran (12,500-10,500)	Fazael VIII	18	6	Horwitz and Tchernov unpubl. data	0.4	0.2
Early Natufian (10,500-9,250)	Fazael VI	355	21	Horwitz and Tchernov unpubl. data	1.5	0.5
Late Natufian (9,250-8,300)	1) Salabiya I 2) Fazael IV	792	19	1) Crabtree *et al.* 1991; Horwitz and Tchernov unpubl. data 2) Horwitz and Tchernov unpubl. data	1.3	0.4
Khiamian (8,300-8,000)	Salabiya IX	824	22	Horwitz and Tchernov unpubl. data	1.5	0.5
Sultanian (8,000-7,300)	1) Jericho 2) Gilgal 3) Netiv Hagdud	727 (3994)*	36 (39.3)*	1) Clutton-Brock 1979; Cowles and Blandamer 1989 2) Noy *et al.* 1980 3) Tchernov 1994	1.1 (1.1)*	0.3 (0.3)*
PPNB (7,300-6,000)	Jericho	805	28	1) Clutton-Brock 1979; 2) Cowles and Blandamer 1989	0.4	0.1

Data in parentheses and marked with an * indicate calculations made including the extremely large assemblage of Netiv Hagdud. When this sample was wxcluded, neither the diversity or evenness indices changed.

Arboreal pollen frequencies then drop to 8-10% in the Early Natufian with a further reduction in the Late Natufian to 2-4%, reaching 0% in the Final Natufian. These data concur with the gradual desiccation that took place during the Early Natufian which was cold and dry. They are corroborated by the geomorphological evidence from the Fazael sites.

For the Lower Jordan Valley there is a contradiction between the arboreal pollen and geomorphological data for the Late Natufian sites in the Lower Jordan Valley do not tally (Bar-Yosef *et al.* 1974; Darmon 1988; Schuldenrein and Goldberg 1981). The arboreal pollen frequencies place this period as a dry phase while the geomorphology indicates that it was a wet phase.

This apparent contradiction may be due to problems of chronological resolution as for the southern Levant as a whole it is generally accepted that the Late Natufian was a wet phase, but that rainfall decreased by the terminal part of this period (Sanlaville 1998; but see Tchernov 1998a).

In the early Holocene (onset of the PPNA) there is evidence for substantial forest cover with arboreal pollen frequencies of 10-15%. These continue to increase in the PPNB up to 20% suggesting that the PPNB was even wetter than today as at present arboreal pollen frequencies for this region are between 1-2% (Horowitz 1979, 1992).

A major factor to be considered when discussing the prehistoric and palaeoclimatic record of the Lower Jordan Valley are the changes taking place in the water level of Lake Lisan (Begin *et al.* 1985). This water-body expanded following the glacial maximum, reaching a maximum by the Geometric Kebaran. The lake then underwent a period of fluctuation until the Late Natufian when it began to recede resulting in the creation of numerous small water bodies. It is unclear whether the early PPNA was a dry period or a wet one (most researchers favour a wet phase at least at its onset), however, during the onset of the PPNB wetter conditions prevailed. The increased rainfall does, however, not appear to have been sufficient to restore the lake to its previous level, and its desiccation continued.

(c) Archaeological record

The Lower Jordan Valley has long been the focus of prehistoric research with a marked increase in research activities during the 1970's and 1980's (Bar-Yosef 1987; Bar-Yosef and Gopher 1997; Bar Yosef *et al.* 1974; Goring-Morris 1980; Hovers 1989; Hovers and Bar-Yosef 1987; Noy *et al.* 1980; Tchernov 1994). Surveys carried out during the latter period located numerous sites spanning the Upper Paleolithic through to the Neolithic. Research by Bar-Yosef and colleagues concentrated on the exploration of Wadi systems such as that by Goring-Morris (1980) of Upper and Epipalaeolithic sites along Wadi Fazael, while at the same time focusing on the excavation of individual sites spanning the Late Pleistocene-Early Holocene, such as Gilgal (Noy *et al.*, 1980), Urkan er-Rub IIa (Hovers *et al.*, 1988), Salabiya I (Crabtree *et al.* 1991) and Netiv Hagdud (Bar-Yosef and Gopher 1998). The settlement pattern and site catchments of sites dating to the Epipalaeolithic through to the PPNA were examined by Hovers (1989).

Although situated a few kilometers to the west of the main concentration of sites, we have seen fit to include in this study the Tell of Jericho (Tell es-Sultan) which was extensively excavated by Kenyon (1957). This site yielded deposits dating to the Natufian period ("Kenyon's Mesolithic") through to the Middle Bronze Age, with the bulk of the finds dated to the Pre-Pottery Neolithic A and B periods.

The dramatic climatic changes experienced during the Late Pleistocene-Early Holocene are paralleled by equally far reaching socio-cultural and economic changes experienced by local human populations over this same period of time. As these events have been documented in great detail in the Levantine literature (e.g. Bar-Yosef 1998; Bar-Yosef and Belfer-Cohen 1989, 1992; Bar-Yosef and Meadow 1995; Belfer-Cohen 1991; Goring-Morris and Belfer-Cohen 1998; Henry 1989, 1998; Kaufman 1992) only a brief summary based on these references will be presented here, with emphasis placed on the Lower Jordan Valley sequence.

The Jordan Valley sites provided the first stratigraphic sequence for the Kebaran and Geometric Kebaran. On the basis of stylistic elements, Goring-Morris (1980) has suggested that the Lower Jordan Valley sites may represent a local tradition, confirming the local nature of this region. Site size is small in this period 100-150 sq meters, and in the Lower Jordan Valley there appears to be a close resemblance between the Kebaran and Geometric Kebaran sites in the size of their territories and site locations. This is not surprising as many Kebaran sites continued to be used in the later period. It has also been suggested that most Kebaran sites in this region represent seasonal occupations either between the Golan Heights/Damascus Basin (Bar-Yosef 1987) or the Mediterranean coast (Goring-Morris and Belfer-Cohen 1998) as attested to by the presence of exotic materials such as shells.

Architectural remains are scanty in sites of this period. The tool kit is primarily composed of microliths made on bladelets, with marked typological changes in their form from the Early Kebaran through to the Geometric Kebaran. Hunting of ungulates provided animal protein while there is some evidence for plant food processing attested to by the presence of ground stone artifacts such as mortars, pestles and cup-holes. Recently a rich and well preserved assemblage of organic remains was recovered from the site of Ohalo II, on the shores of the Sea of Galilee, dated to 19,000 B.C. But this site may be considered (see Nadel 1994) a transition from Upper Palaeolithic to early Epipalaeolithic.

The subsequent Natufian appears to have acted as a bridge in the transition from mobile hunter-gatherers of the preceding Kebaran, and the sedentary village dwelling cultivators of the Sultanian (late PPNA), and has been defined as a complex hunting and gathering adaptation. The Natufian witnessed the development of specialized and intensive gathering and processing of wild cereals, indicating that incipient domestication of cereals was well underway by the latter part of this period. Sedentism appears then to be closely associated with this incipient phase of cereal cultivation; indeed the Natufian has been defined as a 'preagricultural sedentary society' by Henry (1989). The focus on cereals is reflected in the increased frequencies of ground stone tools and sickle blades from this period, as well as the increased degree of dental attrition observed in human skeletons.

Natufian sites are known from the Mediterranean, Irano-Turanian and Saharo-Arabian regions and include large base camps (mainly in the Mediterranean "core" region) with rounded structures that were probably roofed, as well as smaller, more ephemeral sites, primarily in the desert areas, often with little or no evidence for architecture. There is also some evidence for chronological changes in these features between the Early and Late Natufian. Both cave and open-air locations appear to have been used in both phases. Clearly distinct cemeteries may also be a Natufian innovation (Belfer-Cohen 1991). Although Natufian lithic assemblages resemble that of the preceding Kebaran in that they are still dominated by microliths, the material culture contains a wealth of new elements expressed in the rich and varied assemblages of bone artifacts and ornaments, ground stone tools as well as in the high frequencies of sickle blades and picks.

Natufian sites in the Jordan Valley lie in the periphery of the "core" Natufian area in the Mediterranean zone and as such it is not surprising that they differ in many features from the latter sites. The Lower Jordan Valley sites are generally small-sized, open-air sites, they lack architectural remains and there is some indication in their material culture of local stylistic traditions. According to Hovers (1989) the Natufian sites in this region differ markedly from those of the preceding Kebaran in their location and their tactical exploitation of the landscape, with larger areas being used.

In the PPNA sites in the southern Levant, there is evidence for an increase in settlement size relative to the Natufian with the largest sites known from the late PPNA (Sultanian). The geographic distribution of sites in this period is contracted, and they are primarily located within the Jordan Valley. Consequently, what is known about this period from the southern Levant is based primarily on data from the Lower Jordan Valley sites.

Architecture in this period is characterized by oval structures with stone foundations and mud-brick upper courses. There is evidence that in the PPNA both legumes and cereals were cultivated and there is evidence for constructed storage facilities (silos). The tower at Jericho and its associated storage facility may represent the earliest public structure in the southern Levant (Bar-Yosef and Meado 1995). The lithic assemblages from the Jordan Valley are characterized by high frequencies of sickle blades, tranchet ax-adzes, burins and perforators. In the Sultanian, the microlithic component decreases as do Khiam points, while ax-adzes are absent.

During the PPNB, there is evidence for further population growth both as sites increase in size (some reaching 10 hectares or more) and their density increases, especially in the mid-late PPNB. There is an expansion of settlements to incorporate a broader range of phytogeographic zones than in preceding periods. Imported objects such as shells, rare precious or semi-precious stones, obsidian all

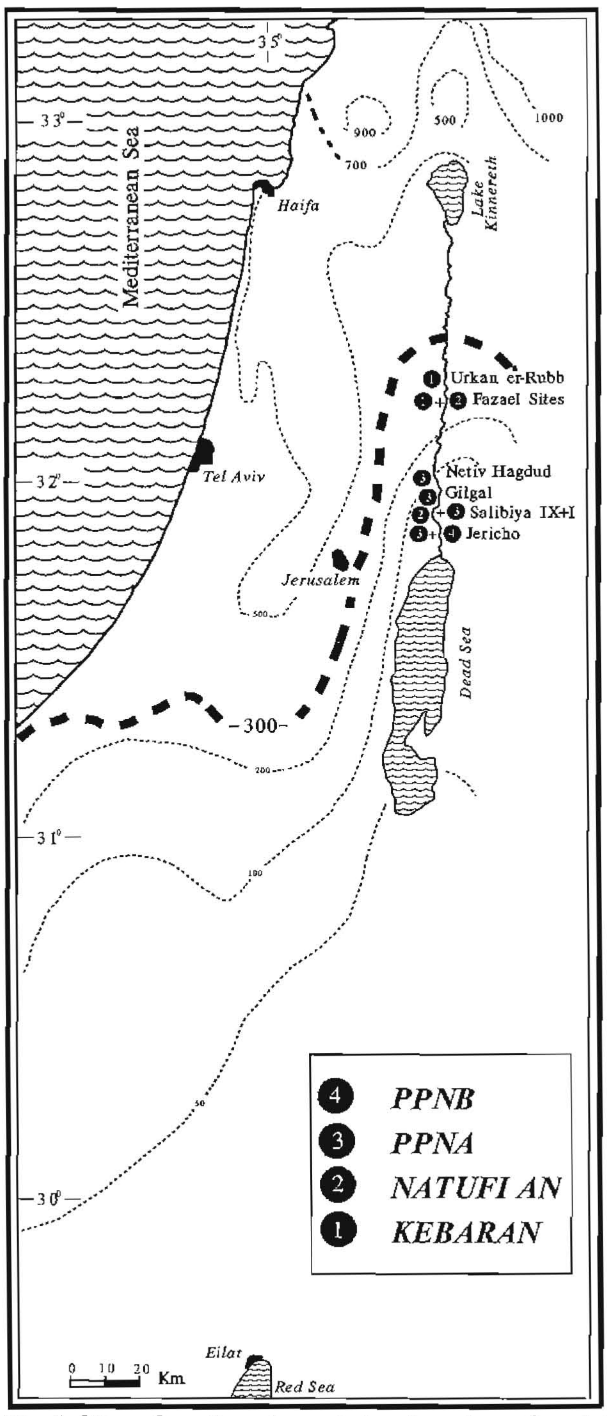

Fig. 1. Map of southern Levant showing sites referred to in this study. The 300 isohyte demarcates the Mediterranean zone.

point to extensive trade links. Architecture changes relative to the PPNA, with most structures rectangular in shape, larger and in many cases with evidence for two stories. Cultivation of cereals as well as legumes appears to be an integral part of the subsistence base by this time.

As outlined above, the Lower Jordan Valley sites document some of the major cultural and climatic changes that the region experienced. As such, they offer a unique cluster of well dated sites derived from a circumscribed geographic region.

Methods and materials

Thirteen archaeological sites dating to the Kebaran period through to the PPNB have yielded well preserved faunal assemblages (Table 1, Fig. 1). These have been examined, in part or whole, by the present authors and serve as the data base used in this study. These include some of the Fazael sites which were originally examined by Davis (1982). Consequently, inter-site variation stemming from differences in archaeozoological methodology, have been minimized.

In the case of the site of Jericho, the data published by Clutton-Brock (1979) as well as the unpublished data of Cowles and Blandamar (1989) for the avian fauna from the site, were used. However, the material has also been examined by one of us at the National Museum of Natural History, London. Similarly, the data used here for the site of Salabiya I include those published by Crabtree *et al.* (1991) as well as unpublished data by the present authors for birds and reptiles recovered from the original test pits excavated by O. Bar-Yosef and colleagues at this site.

Due to the small size of assemblages from individual sites, the data from contemporaneous sites were combined. The smallest sample with an NISP of 18 bones (from the Geometric Kebaran period), was included in order to complete the sequence (Table 1). However, due to its small size this sample is obviously problematic and all results based on it should be treated with extreme caution. In order to increase chronological resolution, where possible the internal phasing within periods was maintained. Consequently, data for the early and late phases of the Kebaran and Natufian were kept distinct, as were the Khiamian and Sultanian phases of the PPNA.

In order to assess changes in species diversity and richness over time, the Shannon-Wiener Diversity and Evenness indices were calculated for each period using standard formulae (Magurran 1988).

The Diversity Index increases as species diversity increases, while the closer the Evenness value is to 1.0, the more equally abundant the species are represented (Fig. 2).

The significance of inter-period differences was assessed using paired t-tests derived from the data-set. The formula used is that given in Magurran (1988) where:

$$t = \frac{\mathbf{H'1 - H'2}}{(Var\mathbf{H''1} + VarH''2)} 0.5$$

where H'1 is the diversity of period 1 and Var H"1 is its variance; H'2 is the diversity of period 2 and Var H"2 is its variance (Magurran, 1988).

As 28 different pairs were tested, the level of significance ("P") was adjusted using the Bonferroni additive inequality test (SAS, 1988: 595). Accordingly, the new significance level was set at $P < 0.003$.

Examination of the effect of sample size on the data was made by running two sets of calculations for the Sultanian sample which is the largest used in this study. One test included the largest single assemblage - from the site of Netiv Hagdud with an NISP of 3267 bones, and another test excluded this sample. By excluding Netiv Hagdud, the total NISP for this period was reduced to 727 bones which falls well within the sample size range for the other periods (Table 1). In addition, NISP counts for each period were plotted against species numbers in order to see whether any clear association existed between the two (Fig. 3).

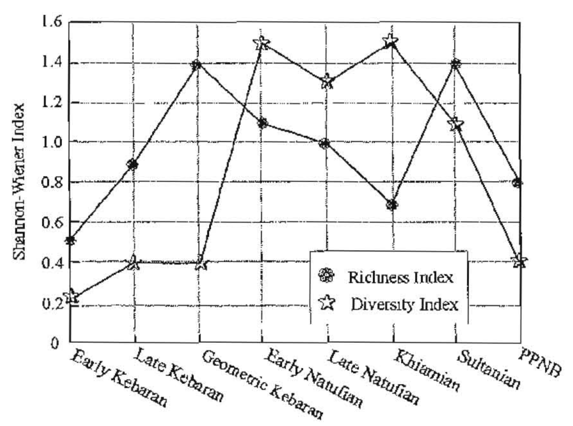

Fig. 2. Graph showing Shannon-Wiener Diversity and Evenness Indices for all periods studied here.

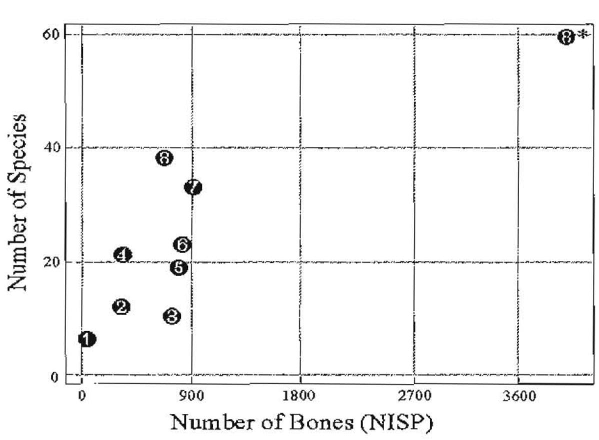

Fig. 3. Scattergram of total bone counts (NISP) versns total number of species for the periods studied here. (1 = Geom. Kebaran, 2 = Late Kebaran, 3 = Early Natufian, 4 = Early Kebaran, 5 = Late Natufian, 6 = PPNB, 7 = Khiamian, 8 = Sultanian without Netiv Hagdud. 8* = Sultanian with Netiv Hagdud).

Although diversity indices enable us to track and quantify changes occurring over time in species representation, they do not provide information regarding diachronic trends for individual species, data which are crucial for an understanding of the archaeozoological and palaeoclimatic sequence. Such data can only be obtained by examining the record of each species/animal order over time. As a means of investigating this feature, cumulative frequencies (Simpson *et al.*, 1960) were calculated for the different species/animal orders represented in each period (Fig. 4). The three most important artiodactyl species were each counted separately, while other ungulates were placed in a combined group that included pigs, cattle, equids and antelopes. Other fauna were pooled by order and included: carnivores, lagomorphs, rodents, insectivores, birds, reptiles, and a pooled "aquatic" category of amphibia, fish and crustacea.

Finally, the same data sets were divided up based on their associations with specific habitats in order to examine changes in the extent and availability of these different niches over time and/or changes in human food procurement strategies (Fig. 5). Four habitat types were recognized:

1. grassland species - e.g. gazelle, aurochs, hare, spur-thighed tortoise, Palestine molerat and East European hedgehog
2. forest species - e.g. wild boar, fallow deer, red deer, roe deer, squirrel, chamelion
3. wetland species - e.g. freshwater crab, fish, amphibia
4. cliff or rock dwelling species - e.g. wild goat, sunlizard, Wagner's gerbil

In order to create Figure 5, for each period all species or animal orders were categorized according to their associated habitat. The relative frequency of all species belonging to a particular habitat type was calculated per period using their NISP counts. Only bird species were excluded from this study as many of them inhabit a wide range of habitats or are seasonal migrants to the region.

Results

Table 1 and Figure 2 illustrate the Shannon-Wiener Diversity and Evenness indices for the different periods. Results for the three Kebaran samples are similar with relatively low species diversity (0.2-0.4) and low species evenness (0.1-0.2) showing that few species are present and that they are not represented in the samples in equal proportions.

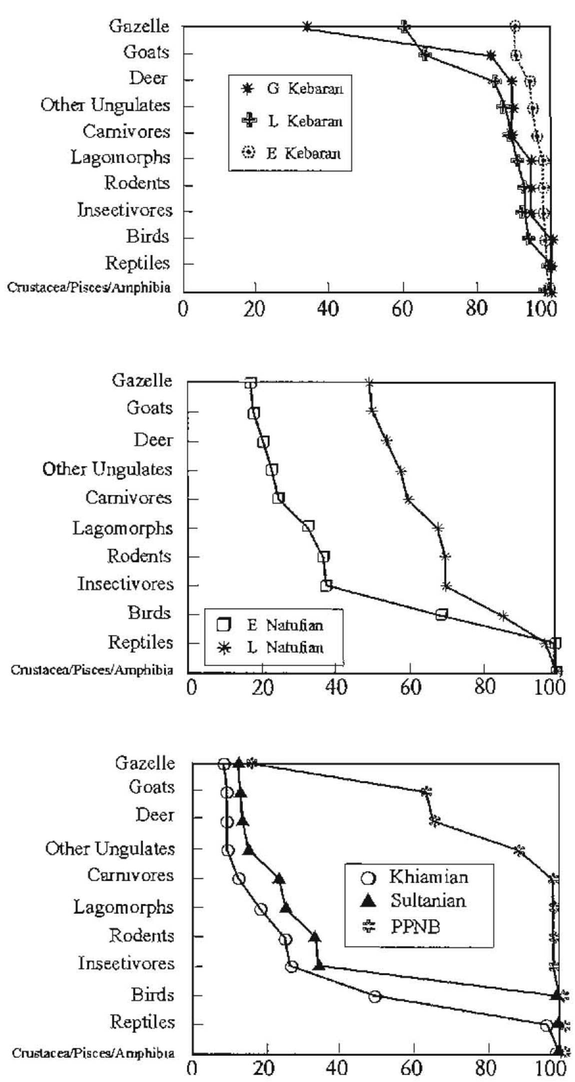

Fig. 4. Graphs showing cumulative frequencies for main ungulate species and animal orders for the different periods.

In contrast, both the Early and Late Natufian samples and the Khiamian assemblage have very high species diversities (1.3-1.5) and also relatively high evenness indices (0.4-0.5), indicating the exploitation of many species in more or less similar quantities. There is a drop in species diversity (1.1) and evenness (0.3) at the end of the PPNA (in the Sultanian), which decreases even further in the PPNB (Table 1, Fig. 2). This indicates a return to a Kebaran-type exploitation pattern with fewer species being exploited, and these in unequal quantities. However, in the case of the PPNB this is due to the exploitation of goats undergoing domestication, while in the Kebaran, this trend is due to the hunting of gazelle.

The results of the t-tests (Magurran, 1988) indicate that with the exception of two pairs, differences between all periods are highly significant ($P < 0.003$). The two exceptions are the Early Kebaran - Late Kebaran and Early Kebaran - Khiamian for which no significant differences were found. In addition, tests of the Late Kebaran - Geometric Kebaran and Geometric Kebaran - PPNB were non-significant. However, due to the extremely small size of the Geometric Kebaran sample, the results of tests using this period cannot be considered as reliable.

It is common knowledge that there is a direct correlation between sample size and species diversity (Grayson, 1984). This primarily affects the proportion of rare species, which tend to be underrepresented if not altogether absent, in small samples. This is an obvious issue that needs to be addressed in this study - whether the diachronic changes in species diversity and evenness observed here are artifacts of sample size or whether they truly reflect diachronic trends.

Aside from the Sultanian sample from Netiv Hagdud, all samples studied comprise less than 1000 bones. There is however quite a large size range with the smallest assemblage (excluding the excessively small Geometric Kebaran sample) composed of only 295 bones and the largest sample, excluding Netiv Hagdud, composed of 928 bones (Table 1). However, samples studied here that have similar NISP counts e.g Early Kebaran and Late Natufian (both with an NISP count of around 700) or Late Kebaran and Early Natufian (circa 300 bones), have markedly different numbers of species suggesting that the observed inter-period differences do not stem from variation in sample size (Fig. 3). Similarly, when the excessively large sample from Netiv Hagdud was excluded from the Sultanian sample in order to reduce sample size to a proportion similar to that of the other assemblages (i.e. NISP of 727), neither the diversity not the evenness indices changed (Table 1). Thus, despite the known correlation between sample size and species number, the diachronic pattern of change in species diversity and evenness illustrated in Figure 2 appears to be due to other factors.

Figure 4 illustrates the cumulative frequency plots for species/animal orders from the different periods. It is evident that in the three Kebaran periods the same range of animals were exploited. These three periods also resemble each other in the relative proportions of the different species. Primarily artiodactyls were exploited, notably gazelle, with few carnivores and small-sized mammals, and even fewer birds, reptiles and aquatic elements.

In the Early and Late Natufian there is a change in the faunal composition, with fewer artiodactyls exploited although gazelle still predominates in this group (Fig. 4). Most marked in the Natufian periods is the increase in lagomorphs, small mammals and aquatic elements and the even greater increase in the quantity of birds being exploited. The Late Natufian differs from the Early Natufian in that it has a higher ungulate component and relatively fewer small mammals. However, these differences were not statistically significant. In both these periods there is a marked increase in the quantity of lagomorphs and birds exploited.

In the PPNA small mammals, birds and reptiles contribute an even larger proportion of the overall faunal spectrum than in the Natufian, while the quantity of ungulates decreases even more (Fig. 4). Although overall, the Khiamian and Sultanian follow a similar trend, they differ slightly with a marked decrease in the representation of birds and reptiles and slightly higher frequency of ungulates in the Sultanian period relative to the Khiamian (Fig. 4). Thus, from the Natufian onwards there is a progressive reduction in the quantity and hence the importance of large and medium-sized ungulates and a concomitant increase in the importance of smaller-sized fauna such as reptiles, birds and small mammals.

In contrast, in the PPNB there is a marked increase in the quantity of ungulates exploited, especially goats. Gazelle maintain a similar low frequency to that found in the preceding PPNA periods. However, carnivores, small mammals, reptiles and birds all decrease markedly in importance, returning to frequencies that are reminiscent of the Kebaran periods. As the PPNB sites examined here are dated to the mid-PPNB, it seems feasible that the observed increase in the quantity of goats is related to the incipient domestication of this species. Despite the sudden abundance of this species in the mid-PPNB, their skeletal morphology and size are still those of wild animals (Ducos 1993; Tchernov 1998a).

Figure 5 illustrates changes in the faunal spectrum based on habitat associations of the different species. It is evident that grassland species predominate in all periods followed by forest species. Furthermore, these two biotopes exhibit an inverse association, with the one increasing as the other decreases. The early Natufian has the highest frequency of grassland species and a relatively low frequency of forest elements. Another period with a high proportion of grassland species is the late PPNA (Khiamian) which also has a very low number of forest species. The highest proportion of forest species is in the Early Kebaran which also has the lowest frequency of grassland elements. The Late Kebaran exhibits a marked increase in grassland fauna and a slight drop in forest elements. The period with the third highest proportion of forest elements is the Late Natufian which also has the second lowest frequency of grassland species. The PPNA sees a gradual decrease in forest species and increase in grassland element while in the PPNB grassland elements decrease and forest elements increase so that they are about equally represented.

The Kebaran periods have the lowest frequency of wetland species but these increase gradually throughout the Natufian peaking in the Khiamian period. They then decrease in frequency during the late PPNA (Sultanian) and continue to reduce in importance in the PPNB. Cliff or rock dwelling species show minor fluctuations throughout the Kebaran and Natufian periods, followed by a marked decrease in the Khiamian. This is followed by a steady increase in frequencies throughout the Sultanian and PPNB.

Discussion

Bar-Yosef and Meadow (1995), and more recently Sherratt (1997) and Goring-Morris and Belfer-Cohen (1998) have argued that the origins of agriculture in the Levant need to be pictured against the fluctuating climatic conditions of the Late Pleistocene-Early Holocene which altered the availability of the different resources. These resources either fluctuated in availability, became unevenly distributed, diminished or even disappeared. Hesse (1982) used similar arguments in his discussion on the origins of animal domestication in Southwest Asia and South America. He suggested that resource stress caused by climatic oscillations could be resolved through three possible paths - emigration, shifting to alternative resources unaffected by the climatic change or changing modes of production to more efficient ones. Based on these scenarios, we outline below four possibilities that could have been applied in the southern Levant and then briefly discuss them against the faunal sequence of the Lower Jordan Valley:

1. *Dispersal* - the movement of organisms away from the point of origin: this may result in extending the range of the margin of an existing population by the colonization of a new habitat within the range of the population, or by the colonization of a distant location across a major physical barrier or unfavourable habitat (Tchernov, 1992a).
2. Increased *mobility* within the region including movement between resource patches. Increased residential and/or logistical mobility (Binford, 1980).
3. *Diversification* - increase in the number of resources used as food items.
4. *Intensification/Specialization* by remaining in the same location but intensifying exploitation of known resources through technological innovations or more efficient methods of food exploitation.

Examination of the data on population size and settlement pattern (Bar-Yosef, 1987, 1998; Bar-Yosef and Belfer-Cohen, 1989, 1992; Bar-Yosef and Meadow, 1995; Goring-Morris and Belfer-Cohen, 1998) indicates that in the Early Natufian there was a marked shift to more permanent settlements as well as an increase in site size and density in contrast to the smaller more mobile social groupings which characterized the Kebaran and Geometric Kebaran. However, the Late Natufian sees a shift in strategy, with evidence for increased mobility associated with expansion into new regions (Goring-Morris and Belfer-Cohen, 1998), which accords with a strategy of "dispersal" as outlined above. This geographic expansion appears to be short-lived and is followed in the PPNA by a population contraction and a return to a more sedentary lifestyle, probably as a result of the warmer, more arid climatic regime which set in.

According to Garrard *et al.* (1996: 20) "there is no evidence from Jordan and elsewhere in the Levant to support models that propose that plant and animal domestication first developed in the Marginal Zone". They argued that there was a time lapse between the earliest appearance of crop cultivars and domestic livestock in the "Levantine Corridor" (Bar-Yosef, 1989) and in the arid zone. Thus, the shift in the faunal spectrum is reflected in the PPNB sites which are exclusively located within the "corridor:" from the Damascus basin through the Jordan Valley. It is only somewhat later that both the western hilly slopes of Cis- and Trans-Jordan and their desert fringes acquired the farming tradition. The inhabitants of the desert regions of the southern Levant did not appear to have either practiced or adapted animal domestication until a much later (Pottery Neolithic or even Chalcolithic periods).

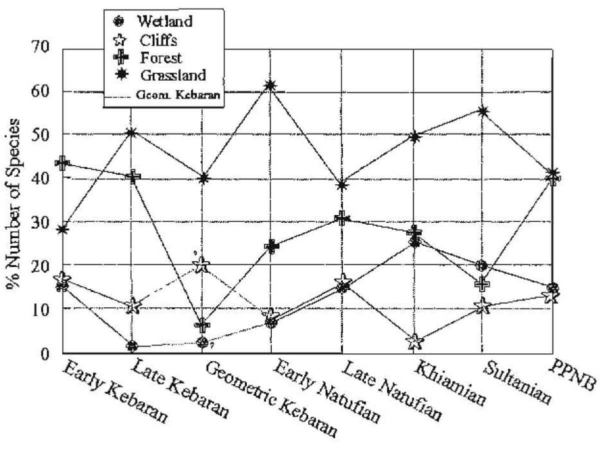

Fig. 5. Plots of species representation for each period based on four habitat associations. For each period the sum of the four habitat types is 100 %.
Forest species = wild boar, deer, squirrel, chamelion.
Grassland species = gazelle, aurochs, har, tortoise, molerat, hedgehog.
Cliffs species = goat, sun lizard, gerbil.
Wetland species = freshwater crab, fish, amphibia.

From this point onwards, population growth continues as attested to by the large, sedentary Sultanian settlements in the Jordan Valley. The steadily increasing population size would have automatically restricted the range of options open to past human communities, making migration into other regions difficult if not impossible following the PPNA. Similarly, increasing human mobility aimed at exploiting different resource patches may have become less viable due to increased population size and inter-community competition for them, while the intensity of animal and plant exploitation would have increased within this circumscribed region. This may have served as an important factor in the decimation of local fauna and flora. Tchernov (1991) has written at length about the negative impact of sedentism on the environment, and discussed the resulting impoverishment of environmental resources.

An additional factor to consider is the impact of the oscillating climates on the abundance and distribution of fauna. As suggested by Hesse (1982), such unstable climatic conditions would have changed the spatial distributions of vegetation communities as well as their biomass, a factor that would have had a direct impact on faunal abundance and distributions. It is possible that faunal diversity and abundance was reduced to levels that made hunting increasingly difficult and a higher economic risk forcing human communities to turn to alternative modes of production. Concomitantly, other regions would have become less attractive as the natural resources there also diminished.

We may conclude that within a relatively short period of time, increased mobility and migration - as possible solutions to the Late Pleistocene-Early Holocene climatic fluctuations - would have become less viable options, and communities would have had to turn to other solutions to counter resource stress.

Examination of the faunal record for the Lower Jordan Valley indicates that with regard to animals, resource procurement strategies changed over time. Diversification characterizes the Natufian and early PPNA, while specialization characterizes the PPNB. Thus, it is possible to view the Epipalaeolithic-early Holocene record for the Lower Jordan Valley (and probably for the entire southern Levant), as a diachronic series of shifts in resource procurement strategies carried out by human communities who outgrew the available resources, and were either unable to disperse out of the area or chose not to do so. The climatic and faunal record are summarized in Figure 6.

The Lower Jordan Valley sequence indicates that the cold and dry Early Kebaran was characterized by a low diversity of animal species and a low evenness index. This indicates that the hunters concentrated on a small range of species, and that they were not hunted in equal concentrations. The data indicate that hunting was concentrated on gazelle followed by goat and to a lesser extent deer. Hovers (1989) notes that the stable water supply in the Lower Jordan Valley during this period may have facilitated a higher carrying capacity for gazelles than at present, with a density for this species that may have exceeded 23 animals per square km. In this period, forest species are well represented (Fig. 5). In contrast few aquatic elements are represented. This is not surprising considering that the Lisan Lake level was low during the glacial maximum.

The Late Kebaran and Geometric Kebaran periods experienced increased rainfall and humidity facilitating the expansion of the lake. The faunal record for this time exhibits a marked increase in grassland fauna and a slight drop in forest elements. Even fewer aquatic resources are exploited. Despite the fact that the lake appears to have expanded during the Late/Geometric Kebaran its high level of salinity would probably have prevented it being used as a significant resource base for the prehistoric inhabitants at this time (Hovers, 1989). Thus, throughout the Kebaran human communities continued to rely upon a hunting and gathering mode of production with some degree of specialization on the exploitation of medium sized artiodactyls. Results of t-tests of species diversity carried out between the different phases of this period were all non-significant.

A major change is observed in the faunal record from the onset of the Early Natufian, characterized by a marked decrease in the relative frequency of medium-sized ungulates exploited and an increase in the numbers of all other species - carnivores, hares, rodents, reptiles and birds. Accordingly, the species diversity and evenness indices for this period increase and are the highest for the entire chronological sequence discussed here. The differences in diversity indices between the Kebaran and Early Natufian, as well as between the Early Natufian and all other periods proved to be highly significant. This reflects a broadening of the resource base in the early Natufian - diversification and a shift away from the specialized Kebaran-type resource procurement strategy which concentrated on a single species.

According to the palynological record for the Natufian, there was a decline in the frequency of arboreal pollen suggesting the onset of drier conditions. The latter data best support the faunal record which reflects a drop in the frequency of forest and cliff dwelling species and a marked increase in grassland elements, especially gazelle, and to a lesser extent also of aquatic fauna. Hovers (1989) has suggested that the shrinking of Lake Lisan during this period would have resulted in the expansion of territories exploited by Natufian and Neolithic communities. These previously submerged areas would have been covered with alluvial soils and supported herbaceous and semi-steppe vegetation. They could have supported wild cereals as well as offered new grazing areas for ungulates.

By the Late Natufian there is a slight increase in forest species and decrease in grassland elements. This is accompanied by the increased exploitation of medium-sized ungulates relative to the preceding early Natufian. Diversity and evenness indices decrease slightly as a result and were found to differ significantly from the preceding phase, as well as from the subsequent PPNA. However, aquatic elements continue to increase in importance, probably reflecting increasing exploitation of Lake Lisan. Although the arboreal pollen data indicate that the Late Natufian was relatively dry, the geomorphology from the same sites suggests that this period may have experienced a wet phase, which to some extent is corroborated by the faunal data which indicate a slight increase in forest species and concomitant decrease in grassland fauna. That the climatic shift that occurred between the Early and Late Natufian was of some magnitude is evidenced by the fact that gazelle and aurochs underwent a marked size increase over this time period (Ducos and Horwitz, 1998), a trend that is usually associated with dry and cold conditions.

Evidence for the palaeoenvironmental conditions that prevailed during the PPNA in this region comes from the salty Lake Lisan which covered the entire Jordan Valley during the last Glacial. It has been shown by Begin *et al.* (1985) and Magaritz and Goodfriend (1988) that during the arid spell of the eleventh millennium BP, the Lake Lisan greatly receded, leaving behind the track of a flat muddy-marly lake bottom and a trail of small residual water bodies (Tchernov, 1994, 1998a). Around 10,300 BP a return to a wetter phase, although not as wet as in former Upper Pleistocene phases, took place (Magaritz and Goodfriend, 1988; Bar-Yosef, 1989). It was during this period that the trail of water bodies appeared in the area, considerably enriching the local biota. The trail of freshwater to semi-freshwater bodies could have been further enlarged during the wetter conditions that prevailed in the PPNA period and dispersed from the marshes of Fazael southward towards Jericho, as argued by Bar-Yosef (1989). This phenomenon would explain the abundance of aquatic plants and animals in all the PPNA sites. The wetter phase could have lasted during the PPNA and the PPNB periods, greatly affecting the southern Levantine ecosystems. This wetter phase would also explain the existence of Palaearctic and Mediterranean elements at much lower latitudes within the present Sinai desert (Tchernov, 1981, 1988a,b, 1991; Tchernov and Bar-Yosef, 1982; Dayan *et al.*, 1986).

The PPNA experienced a gradual decrease in forest species and increase in grassland element while diversity and evenness indices are as high as those of the Early Natufian. This indicates the continuation of a broad spectrum exploitation strategy that had begun in the Natufian. The extent of the exploitation of medium-sized ungulates resembles that of the preceding Early Natufian. The onset

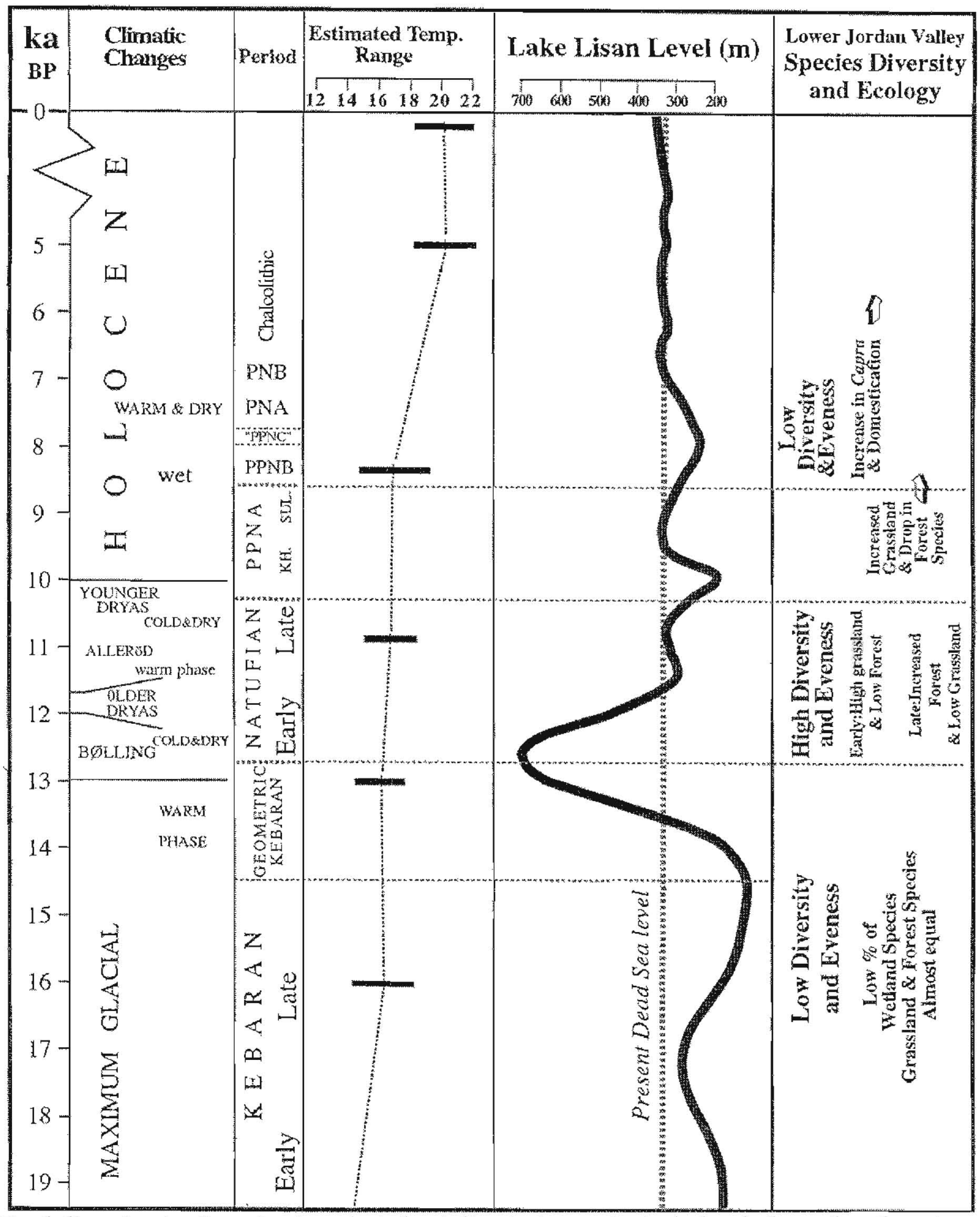

Fig. 6. Chart showing the major chronological and climatic changes that took place in the southern Levant against trends in faunal diversity, evenness and habitat associations in the Lower Jordan Valley sequence

of the PPNA (Khiamian) appears to have experienced a cold and dry regime - which would best fit the faunal record.

Resource diversification which characterizes the Natufian, continues through to the early part of the Pre-Pottery Neolithic (Khiamian), during which species until now not exploited or exploited rarely become a common resource item. As suggested by Bar-Yosef and Meadow (1995), this may have been initiated as a result of the depletion of local resources beginning in the Late Natufian. This perspective is supported by the fact that the transition from specialized hunting of a few species of medium-sized mammals in the Kebaran to increasing reliance on smaller sized animals in the Natufian and early PPNA, involved greater energy expenditure for smaller returns. This would have resulted in a negative balance between these two features which runs contrary to the goals of subsistence strategies. This suggests that the observed changes in strategies of food procurement were born out of necessity rather than choice.

However, Tchernov (1998a) has argued that the abrupt replacement of many small Geometric Kebaran seasonal sites with a few relatively large long-term Natufian habitations emerged without any trace of intermediate stages. He argued that the main socio-economic transformations in human evolution were basically detached from the impact of the environment, at least since the Upper Palaeolithic. No causal or temporal matching between the local cultural changes and the global climatic events can be inferred, in particular during the abrupt shift to sedentism in the early Natufian and the transformation to incipient domestication during the PPNB. The cohesiveness of the southern Levantine palaeocommunities lasted uninterruptedly from early Natufian to late PPNB, during which time the Southwest Asian arid belt supported a rich diversity of Palaearctic species, relicts of which still occupy the mountainous region of this area (Tchernov, 1981, 1994). Moreover, economic systems obey rules set by the cost and benefit of competition and cooperation among component entities throughout the world of the organisms. Human evolution is no exception to these rules, and is not necessarily driven by external environmental fluctuations. Tchernov's (1998a,b) basic argument is that we do not need to rely on climatological factors to explain basic changes in complex systems. As for human societies it enables individuals to use, for instance, the society's inclusive fitness, and consequently advance technology and expand exploitation of resources. Thus the components gain new qualities by being parts of the system. The increase in the complexities of human systems, and consequently the proximate needs for ever more elaborated technologies and devices for the more efficient exploitation of resources (=energy consumption), were basically driven by intrinsic human traits and not by climatic changes. Hence we can ask from which moment do we have to stop explaining historic events as reflections of the physical world? During the history of humans we witness unidirectional changes in the bio-social structure and a widening of their niche that eventually became severed from environmental or biological causes.

A counter-argument to this view is expressed by Goring-Morris and Belfer-Cohen (1998). They propose that during the PPNA, the Jordan Valley represented a refugium within a regime undergoing aridification. During this period, communities concentrated their settlements around the residual water resources that remained as Lake Lisan receded. We would argue that despite the fact that these communities were involved in agricultural production, this was probably quite limited in terms of the surplus they could create. Moreover, cultivation production was probably limited by the fluctuating climatic conditions of the early Holocene (especially if the trend was that of warming and aridification). Consequently, as the small lakes or pools dried up or their fauna were decimated through overhunting, these communities were forced yet again to find a way to ameliorate their subsistence economy. In so doing they initiated the first steps towards animal domestication. However, domestication is not "a day to day process". Cauvin (1989) already pointed out that it is the lengthy sociological and cultural maturation which emerged within the Natufian domain of sedentism and led humans to food production. Neolithization for Cauvin (1989) appears as a progressive and overall transformation, in which the food production is more the consequence of a cultural and mental change than the true cause of other changes. Indeed, the long 'incubation" period was mentally, socially and economically obligatory in order to reach the point of intentional management of a wild population of just the right species; a process that had already begun in the early Natufian by selective culling by age and sex of gazelles (unfortunately just the wrong kind of animal to start domestication). Even during the period when domestication was already on its way, the earliest agriculturists had no preconceived ideas of the end product through intentional selection. Rather, morphogenetic changes associated with domestication essentially resulted from unconscious or indirect selection by humans as a natural by-product of induced environmental conditions created under domestication (Tchernov, 1993, 1995; Tchernov and Horwitz, 1991; Zohary *et al.*, 1998). Morphogenetic changes observed in primeval domesticates were initially due to the spontaneous responses of the animals to special anthropogenic quasi-isolated habitats.

By the PPNB pluvial conditions had set in. During this period in the Lower Jordan Valley sites, species associated with grasslands decrease in frequency and forest elements increase so that these two habitat types are almost equally represented in the faunal record. From the Khiamian onwards, aquatic resources diminish in importance which correlates well with the desiccation of Lake Lisan. The most salient feature of the PPNB assemblages is a drop in the frequency of gazelles being hunted and a marked increase in the frequency of goats. This trend appears to be associated with the process of incipient domestication of the goat (Horwitz, 1996; Ducos, 1993). The increased numbers of this species in the faunal record probably result from the close contact imposed by human communities who initiated this process through the creation of founder herds which were kept under different environmental conditions and in genetic isolation from their wild relatives (Zohary *et al.*, 1998). Following the PPNB there was a further decline in species diversity in this region probably due to both ongoing desiccation and anthropogenic causes.

Based on the data presented in this study and summarized in Figure 6, we would suggest that at least a partial correlation exists between the faunal sequence of the Lower Jordan Valley and the climatic sequence of this local region. These data support the contention that changes in the subsistence base of prehistoric communities took place within a landscape characterized by fluctuating availability of floral and faunal resources which might have led to conditions of resource amelioration. The large difference in the exploitation of caprovids may have been due to the critical attrition of gazelle populations along the Jordan valley, which compelled people to rely on the more difficult hunting of Capra, due to the growing scarcity of gazelles. A complete reliance on the hunting of wild (small and large) game during the PPNB is well known from the desert areas of southern Sinai such as Wadi Tbeik and 'Ujrat-el-Mehed (Dayan *et al.*, 1986; Tchernov and Bar-Yosef, 1982). These regions during this period were still much more mesic and allowed intense hunting. Faced with only a limited number of options, Natufian communities applied two different strategies to the problem of food procurement: specialization through the incipient cultivation of plants, and diversification with regard to animal resources. When even these solutions proved inadequate in the face of changes in climatic conditions and/or due to depletion of their nearby hunting grounds, and increasing population size in the PPNA, they were forced to shift strategies of animal resource acquisition. This led to specialization and the incipient domestication of the goat.

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