

Carnivore Diversity in the Late Quaternary of Israel

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During the past 70,000 years, Israeli carnivore faunas have varied only slightly in richness (number of species), but widely in diversity (including the relative abundances of the different species). Human population growth, sedentism, and the beginning of agriculture are often considered to have caused habitat destruction toward the end of the Pleistocene that may have affected animal populations. However, patterns of changing carnivore diversities from three sites in the Mediterranean region of Israel correlate well with changes in precipitation: species diversity is higher during more humid phases and lower during drier phases. The environmental effect of sedentism may have accelerated the later drop in carnivore diversity but cannot account for fluctuations in diversity preceding it. ©1994 University of Washington.

INTRODUCTION

Geological studies, pollen analyses, and studies of human settlement depict fluctuating climatic conditions during 70,000 years in Israel and allow a tentative sequence of climatic events to be constructed. This period also saw the appearance of modern humans and changes in human technology, settlement, and subsistence patterns, culminating in the advent of sedentism (ca. 12,500 yr B.P.), soon followed by the beginning of plant and animal domestication. These developments in human use of the environment are sometimes inferred to have greatly affected the fauna of Israel through habitat destruction and/or increasingly intense hunting (e.g., Garrard, 1982; Davis, 1989). If environmental changes brought about by increasing human population size and sedentism (e.g., habitat destruction, overhunting, attraction of specific species to permanent human habitations) had an appreciable effect on the Israeli fauna, one might expect a directional trend in diversity related to developing human technologies, or a change following sedentism and farming. An alternative hypothesis is that faunal diversity would relate to Late Quaternary paleoclimatic fluctuations; a relationship between climate and faunal diversity has often been established both in space (e.g., Brown, 1973; Abramsky and Rosenzweig, 1984) and in time (e.g., Avery, 1982; Cruz-Urbe, 1988). In this study I examined changes in carnivore diversity in Israel during the past 70,000 years and test these alternative hypotheses.

THE FAUNAL ASSEMBLAGES

I analyzed carnivore remains from sites within the northern mountainous region of the Mediterranean zone of Israel (Fig. 1). The region currently holds the same carnivores throughout (Yom-Tov, 1988). I used faunal assemblages only from prehistoric sites where all the carnivore remains unearthed were available for analysis.

Excavations of Hayonim Cave and Terrace in the Western Galilee unearthed Natufian, Kebaran, Aurignacian, and Mousterian layers, each separated from the others by a gap (e.g., Henry *et al.*, 1981; Hopf and Bar-Yosef, 1987). The Terrace was attributed to the Early Natufian culture (ca. 12,500–11,000 yr B.P.) (Henry *et al.*, 1981; Belfer-Cohen, 1988). Hayonim Cave layer B contains Early to Late Natufian remains (Bar-Yosef and Goren, 1973; Bar-Yosef, 1991). The earliest ^{14}C date is $12,360 \pm 160$ yr B.P., and occupation lasted until ca. 11,000–10,700 yr B.P. (Bar-Yosef, 1991). Lithic assemblages underlying this layer are early Kebaran, ca. 24,000 to 14,000 yr B.P. Layer D contained tools of the Late Levantine–Aurignacian industry, ca. 29,000–27,000 yr B.P. (Belfer-Cohen, 1988). Middle Paleolithic layer E contains Mousterian assemblages of Levallois facies that originated earlier than the Mousterian layers of Kebara Cave.

Kebara Cave is located at the western foot of the Carmel ridge and contains Upper and Middle Paleolithic layers (Schick and Stekelis, 1977). Thermoluminescence dates for the Middle Paleolithic (Mousterian) occupation range between 60,000 and 48,000 yr B.P. (Valladas *et al.*, 1987). The Upper Paleolithic assemblage belongs to the Aurignacian (ca. 35,000 yr B.P.); it is earlier than layer D of Hayonim Cave (Schick and Stekelis, 1977), but no absolute dates are available.

Yiftahel is an open-air Pre-Pottery Neolithic B (seventh millennium B.C.) site in the lower Galilee, a small village that contained about 250 people (Garfinkel, 1987) (see Fig. 2 for cultural and site chronologies and paleoclimatic reconstructions).

ESTIMATING DIVERSITY

The two most widely employed methods for quantifying zooarcheological assemblages are the Number of

Identified Specimens (NISP) and the Minimum Number of Individuals (MNI) (e.g., Klein and Cruz-Urbe, 1984). The chief drawback to using MNI for small samples is the overrepresentation of rare species, which results in artifactual species evenness in these samples. I follow Grayson (1984) in using NISP as a basic measure of taxonomic abundance in archaeological faunas.

To measure carnivore diversities, I used the Shannon-Weaver index (Shannon and Weaver, 1949), $H' = -\sum p_i \log p_i$, where p_i is the percentage of individuals in the i th species. Diversity indices confound the actual number of species (richness) and their relative abundance (evenness), both of which should be defined precisely and examined separately before communities are compared (James and Rathbun, 1981). Since identical diversity values of the index can result from various combinations of values of these variables (Pielou, 1975), I have also used a method suggested by James and Rathbun (1981). In this method the logarithms of the relative abundances of the species are arranged in decreasing order. In a community having equal numbers of all species the resultant plot of logarithm vs rank is horizontal; the extent of the deviation from a horizontal line is a function of the difference between this hypothetical case and the community in question. This method directly depicts diversity, and is not affected by sample size (James and Rathbun, 1981).

I have also measured species richness using rarefaction, a technique developed by Sanders (1968) to compare species richness between collections of very different size. This method enables us to ask how many species

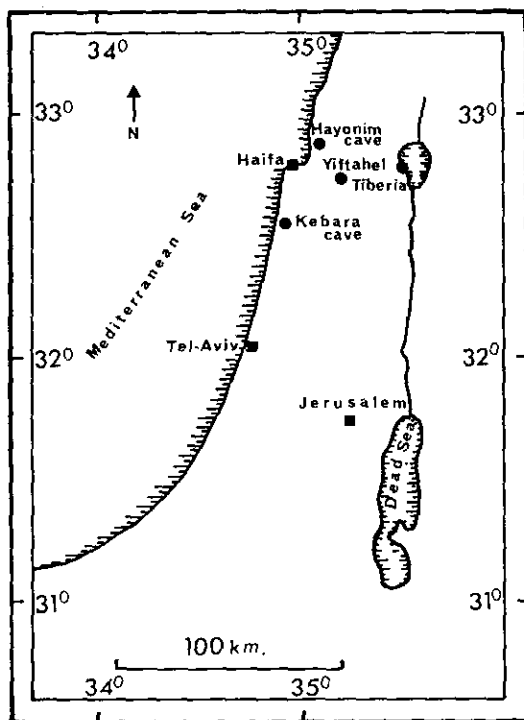
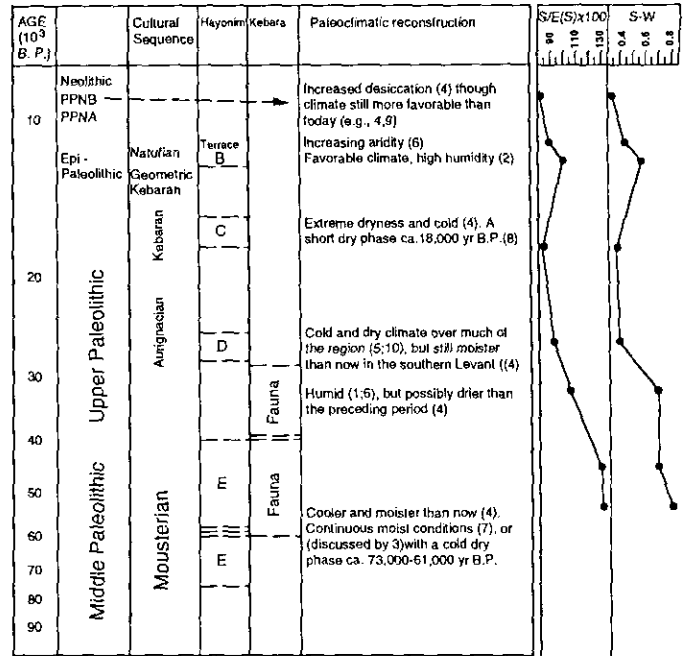


FIG. 1. Map showing locations of the study sites.



- 1 Bar-Yosef, 1989
- 2 Bar-Yosef and Beller-Cohen, 1982
- 3 Bar-Yosef and Beller-Cohen, 1988
- 4 Binah, 1982
- 5 Farrand, 1979
- 6 Goodfriend and Magaritz, 1988
- 7 Horowitz, 1988
- 8 Horowitz, 1989
- 9 Tchamov and Bar-Yosef, 1982
- 10 Van-Zeist and Bottema, 1982

FIG. 2. Cultural and site chronologies, paleoclimatic reconstructions, and results of the Shannon-Weaver diversity index, S-W, and the expected number of species as a percentage of the actual number. $S/E(S) \times 100$ (based on rarefaction). Analyses are performed excluding spotted hyenas from assemblages where juveniles were found. Yiftahel is denoted by PPNB, the period of the site's occupation.

a given sample would encompass, were that sample restricted (rarefied). Because species diversity for modern carnivores in Israel is not known, I compared all the smaller fossil collections to the largest one (Hayonim B) (Tipper, 1979). I calculated the actual species number (S) as a percentage of number of species expected on the basis of rarefaction analysis ($E[S]$). We can thus compare carnivore diversity in different periods to the Natufian baseline. For the rarefaction analysis I assume interdependence is minimal (for an opposite view see Grayson, 1984), an assumption that also underlies the use of NISP as an abundance measure. I incorporated Simberloff's modification to Sanders' method (Simberloff, 1972).

In addition I calculated the proportion of individuals of the most dominant carnivore at all periods (the red fox, *Vulpes vulpes*) and for the combined proportion of red fox and wild cat (*Felis silvestris*), the second most abundant species in all periods. The resultant values provide a measure of dominance (May, 1975).

POSSIBLE TAPHONOMIC BIAS

Carnivore remains in cave sites may result either from hunting by humans or by other carnivores, or from the

use of caves as dens or rest sites. If cave-dwelling carnivores and humans differ in their hunting or collecting of carnivores, the difference could bias an analysis based on mixed accumulations. Also, individuals of species that den in caves may die *in situ*, leading to greater skeletal representation as well as to their general overrepresentation. Different collector behavior is often found also among human populations. All this should be taken into account in an analysis of diversity based on cave deposits.

The carnivore bones in this study derive from strata that showed clear signs of human occupation. Nevertheless, one cannot yet rule out carnivore occupation for a short period of time. Among Israeli carnivores, the spotted hyena (*Crocuta crocuta*), leopard (*Panthera pardus*), and brown bear (*Ursus arctos*) use caves as dens or lairs. Evidence for carnivore residence (coprolites) was found only for spotted hyenas in the Mousterian and Upper Paleolithic levels of Kebara Cave, but whether they antedate the human occupation is difficult to assess, as is the time interval between human and hyena occupations (Horwitz and Goldberg, 1989). The presence of juveniles also usually indicates that a site served as a den. In order to remove the possible bias of individuals that died *in situ*, I also analyzed the carnivore remains excluding those of young spotted hyenas and remains of adults found in the same strata. I also analyzed carnivore remains excluding all spotted hyenas, leopards, and bears. This very conservative method has a major drawback: it excludes valuable information in spite of lack of direct evidence of these species' residence in the caves.

Differentiation between human deposits and carnivore collections is complex (e.g., Brain, 1981; Scott and Klein, 1981). A high carnivore-to-ungulate ratio characterizes heavy carnivore involvement in the deposition of the faunal remains (Klein, 1977). These ratios for the Israeli assemblages are low (Table 1) and comparable to those at Upper Paleolithic sites in Cantabrian Spain (Straus, 1982) and Middle and Late Paleolithic sites in South Africa (Brain, 1981). There, relatively low ratios were considered to indicate human activity.

However, differences in collector behavior may also reflect human cultural differences. In Jericho, Clutton-Brock (1979) noted the relative dominance of foxes (18.8% for the Proto-Neolithic and 24.1% for the Pre-Pottery Neolithic A) and suggested they were selectively hunted. She found a relatively high percentage of charred and broken fox bones. Soffer (1985) suggests a pattern of specialized, active hunting of arctic foxes for their pelt in several Upper Paleolithic sites of the Russian plain, where NISP percentages reach 62.9%, 53.5%, 29.1%, and 22.4%. She notes an increase in arctic fox exploitation through time. There is no progressive or directional trend for foxes at the sites studied here; remains of carnivores from different strata and sites were similar in

TABLE 1
Percentage of Carnivore and Fox Bones, and Carnivore-to-Ungulate Ratios in the Faunal Remains of the Different Sites and Strata Ordered Chronologically

	Carnivores (%)	Fox (%)	Carnivore to ungulate (%)
Yiftabel	7.59	5.75	8.21
Hayonim Terrace	2.77	2.00	2.85
Hayonim B	4.85	2.80	5.10
Hayonim C	12.54	9.33	14.33
Hayonim D	2.99	1.86	3.08
Kebara Upper Paleolithic	13.30	5.98	15.33
Kebara Middle Paleolithic	2.90	1.36	2.98
Hayonim E	12.20	2.85	13.89

Note. Data on ungulates are from Davis (1977, 1982), Garfinkel and Horwitz, (1988), Cope (1990), and R. Rabinovich (personal communication, 1990).

their preservation. Foxes do not exceed 9.33%, and are usually much lower. In general, the percentage of carnivores is low (<15%, Table 1) and thus they may have been utilized infrequently, at a level similar to that of other, less abundant carnivores in Soffer's (1985) study. She suggests that those species might have been taken opportunistically but were not objects of specific exploitation. Thus, the diversity of carnivore remains in the present study probably reflects their richness and abundance.

Whether these carnivore remains were collected by humans and/or other carnivores, they constitute a small percentage of the fauna in all sites. Other macromammals were preferred sources of protein and were probably regularly sought and hunted; therefore, their hunters may have exercised selective practices in their procurement. Carnivores are of low significance in their contribution to economy, so less-rigorous (if any) selection would be expected. Nevertheless, one must recall that small sample sizes are more susceptible to collecting or preservation bias. The gradual accumulation of excavated fossil carnivore material and further study of taphonomic processes will enable us to differentiate between humans and carnivores as accumulating agents, and allow finer understanding of the economy of these sites, which may further elucidate changes in diversity.

RESULTS

A total of 1233 identifiable carnivore remains representing 13–15 species were analyzed and are presented in Table 2. Most species are represented in all collections. Large carnivores are less abundant than small ones, as is true also in extant faunas. Nearly all specimens are adult, recognized by fused epiphyses and permanent dentitions.

TABLE 2
Carnivore Remains Analyzed in This Study (Sites and Strata Ordered Chronologically)

	Hayonim E	Kebara Middle Paleolithic	Kebara Upper Paleolithic	Hayonim D	Hayonim C	Hayonim B	Hayonim Terrace	Yiftahel
<i>Vulpes vulpes</i>	7	47	94	115 (1)	32	166 (11)	177 (6)	100
<i>Canis aureus</i>	2	3	5	1		4		
<i>Canis lupus</i>		5		1				
<i>Canis</i> spp.					2			
<i>Ursus arctos</i>	3	2					8	
<i>Meles meles</i>		1	12			15	10	
<i>Martes foina</i>	4	2	19	5	1	28	13	8
<i>Vormela peregusna</i>	1		4	1	1	16	6	1
<i>Mustela nivalis</i>						1		1
<i>Herpestes ichneumon/</i> <i>viverrid</i>	5 (1)			1				1
<i>Felis silvestris</i>	7	21	26	61	7	47	27	21
<i>Felis chaus</i>		4						
<i>Panthera pardus</i>			11			4		
<i>Felis</i> spp.			13				1	
<i>Crocota crocuta</i>	1 (1)	15	25 (8)					
TOTAL	30	100	209	185	43	288	246	132

Note. Numbers of juveniles are in parentheses.

Juvenile spotted hyenas are present at Hayonim E and the Upper Paleolithic strata of Kebara, raising the possibility that these caves at one time served as dens.

With two exceptions, all the carnivore species listed in Table 2 were represented in the Mediterranean region of Israel until the past few centuries (Dayan, 1989). The exceptions are the spotted hyena (*Crocota crocuta*), whose latest remains date to ca. 10,000 yr B.C. (Kurten, 1965), and the common weasel (*Mustela nivalis*), whose latest remains date to the Iron Age (ca. 1000 yr B.C.) (Dayan and Tchernov, 1988). The fact that spotted hyenas may have become extinct in Israel after the Natufian period might have affected carnivore diversity in the later Pre-Pottery Neolithic B (Yiftahel). As I will discuss, however, analysis of carnivore diversity excluding fossil hyenas of all periods results in a pattern similar to those which include them (Table 3).

Table 3 presents the Shannon-Weaver indices, results of rarefaction, and the percentage of the dominant species including and excluding possible sources of bias. Carnivore richness in Israel remains virtually unchanged throughout the period covered here (Dayan, 1989). Therefore, the results of the rarefaction analysis represent not changes in richness but changes in diversity; a higher-than-expected number of species reflects increasing diversity, and a lower one decreasing diversity.

Species diversity changes reflected by the diversity index and rarefaction are similar. Only some of the rarefaction results differ significantly from the observed values, possibly in part as a result of small sample sizes. Omitting possible sources of bias does not change the overall pattern. Figure 3 presents relative abundance curves plotted

using all data except for spotted hyenas where juveniles were found. Using all three methods we see higher diversity during the more humid phases (e.g., Kebara Middle Paleolithic, Hayonim B) and lower diversity in drier phases (e.g., Kebara C, Yiftahel), whether cooler or warmer (Fig. 2). In periods of low diversity, there is a rising dominance of the red fox coupled with an increase in the dominance of the wild cat (Table 3).

There is no relationship between sample size and the diversity index (cf. Grayson, 1981). For example, for the data excluding spotted hyenas where juveniles were found, the Spearman's correlation coefficient between sample size and the diversity index is -0.071 ($p = 0.447$).

There is no relationship between percentage of carnivores in an assemblage (data in Table 1) and carnivore species diversity. With all data included, except for spotted hyenas where juveniles were found, the Spearman's correlation coefficient between this percentage and the diversity index is 0.143 ($p = 0.394$). The ranked correlation coefficient between these ratios and the diversity index is 0.143 ($p = 0.394$).

DISCUSSION

A clear relationship between climatic conditions and carnivore diversity can be seen: species diversity is higher during the more humid phases, and lower in drier phases, whether cooler or warmer. Species diversity is often correlated with primary plant productivity (e.g., Owen, 1990). In relatively dry regions primary productivity is more strongly affected by changes in humidity

TABLE 3
Diversity and Dominance in Israeli Late Quaternary Carnivores (Sites and Strata Ordered Chronologically)

	<i>N</i>	<i>S</i>	<i>E(S)</i>	s.d.	(<i>S/E(S)</i>) × 100	<i>S</i> - <i>W</i>	Fox (%)	Fox + wildcat (%)
(A) All specimens included								
Yiftahel	132	6	8.28*	0.64	72.50	0.3403	75.76	91.67
Hayonim Terrace	246	8	8.85*	0.35	90.36	0.4587	71.95	82.93
Hayonim B	288	9	—	—	(100%)	0.6008	57.64	73.96
Hayonim C	43	5	6.63	0.97	75.46	0.3618	74.72	90.70
Hayonim D	185	7	8.61*	0.51	81.30	0.3786	62.16	95.14
Kebara Upper Paleolithic	209	9	8.71	0.46	103.33	0.7589	44.98	57.42
Kebara Middle Paleolithic	100	9	7.94	0.75	113.39	0.6746	47	68
Hayonim E	30	8	5.97*	1.02	134	0.8182	23.33	46.67
(B) Excluding spotted hyenas from strata where juveniles were found								
Yiftahel	132	6	7.31*	0.62	82.03	0.3403	75.76	91.67
Hayonim Terrace	242	7	7.86*	0.35	89.05	0.4296	73.14	84.30
Hayonim B	281	8	—	—	(100%)	0.5648	59.08	75.80
Hayonim C	43	5	5.98	0.86	83.64	0.3618	74.42	90.70
Hayonim D	185	7	7.63	0.56	91.72	0.3786	62.16	95.14
Kebara Upper Paleolithic	184	8	7.63	0.50	104.88	0.6814	51.09	65.22
Kebara Middle Paleolithic	100	9	7.01*	0.71	128.32	0.6746	47	68
Hayonim E	29	7	5.42	0.91	129.24	0.7807	24.14	48.28
(C) Excluding potential cave dwellers or users								
Yiftahel	132	6	6.40*	0.56	93.71	0.3403	75.76	91.67
Hayonim Terrace	234	6	6.84*	0.36	87.66	0.3791	75.64	87.18
Hayonim B	277	7	—	—	(100%)	0.5401	59.93	76.90
Hayonim C	43	5	5.51	0.71	90.82	0.3618	74.42	90.70
Hayonim D	185	7	6.66	0.48	105.17	0.3786	62.16	95.14
Kebara Upper Paleolithic	173	7	6.61	0.50	105.97	0.6202	54.34	69.36
Kebara Middle Paleolithic	83	7	6.05	0.63	115.62	0.5421	56.63	81.93
Hayonim E	26	6	4.94	0.81	121.34	0.7097	26.92	53.85

Note. *N*, number of specimens; *S*, actual number of species; *E(S)*, expected number of species (on the basis of rarefaction); s.d., standard deviation; *S*-*W*, Shannon-Weaver index; *, difference between *S* and *E(S)* significant.

than by temperature changes, and it has been previously estimated that in Israel fluctuations of precipitation averages and distribution, more than temperature changes, affect changes in vegetational belts (Bottema and Van Zeist, 1981; Van Zeist and Bottema, 1982). Therefore, the relationship between Quaternary carnivore diversity and humidity is the expected faunal response to paleoclimatic change.

No directional temporal trend is evident. The decrease in carnivore diversity starting with the Middle and Late Natufian assemblages could be related to environmental effects of human population growth and increasing sedentism. This process, however, cannot explain the drop in diversity in the earlier Hayonim C and D fossil assemblages that predate these cultural and population changes. Although sedentism and population growth possibly accelerated the effect of the decrease in precipitation, the strong relationship between climatic factors and carnivore diversity throughout all periods studied suggests a common causal explanation.

In periods of low diversity, there is a rising dominance of the red fox and a marked, but lower, dominance of the

wild cat. Both species are widely distributed and occupy a wide range of habitats (e.g., Corbet, 1978). Perhaps these traits, coupled with small body size and short generation length, enabled these species to predominate under less favorable conditions.

There is no reason to assume that carnivore diversity is directly related to primary plant productivity; this relationship must be mediated by their prey species (e.g., Owen, 1988). However, there has not been a comprehensive quantitative study of changes in diversity of ungulates (or other mammalian species) in Israel. Study of changes in herbivore diversity in this region may give us further insight into the impact of the last glacial age on the fauna of the Middle East.

Bate (1937), Bokonyi (1982), Garrard (1982, 1984), Davis *et al.* (1988), Bar-Yosef and Belfer-Cohen (1989), and Davis (1989) have interpreted changes in species numbers and percentage occurrence at certain sites as possibly related to paleoclimatic change, human preference, and increasingly intense hunting. Ungulates have been preferred sources of protein in this region; their remains may be strongly biased by hunting selection. An

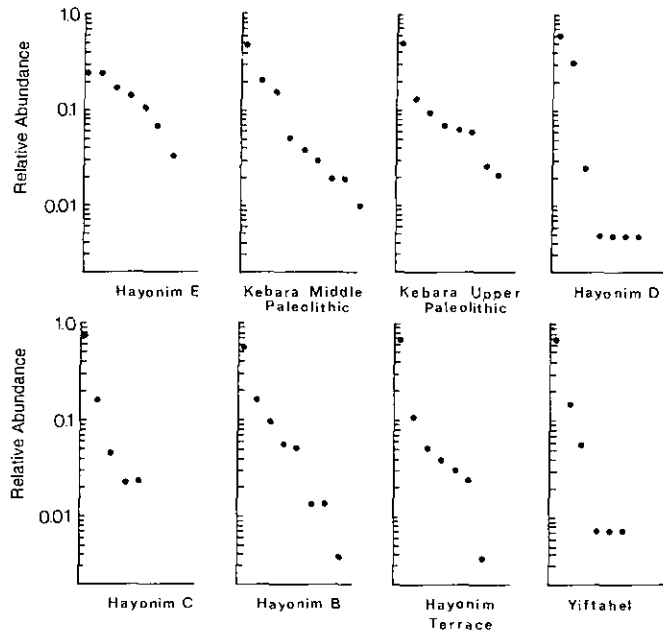


FIG. 3. Abundance curves for Israeli late Quaternary carnivores, excluding spotted hyenas from levels in which juveniles were present. The y axis depicts the logarithms of the relative abundances of the species arranged in decreasing order.

understanding of diversity patterns of carnivores, which are probably not under similar strong human selection, may help tease apart the effects of paleoclimatic change and possibly unrelated changes in the human subsistence base.

CONCLUSIONS

Although changes in carnivore richness in the Late Quaternary of Israel were slight, changes in diversity through time were substantial. These changes are correlated with changes in precipitation: greater diversity and lower dominance during the more humid periods and lower diversity and greater dominance during the drier phases of the Late Quaternary, whether warmer or cooler. Changes in species diversity of carnivores must be mediated through changes in their prey species. Because ungulates, preferred sources of protein, are probably strongly selected for by people, their abundances at archaeological sites may not accurately reflect changes in natural diversity. A comparison with changes of diversity in carnivores may enable us to separate changes in the fauna of Israel from possibly unrelated changes in human subsistence.

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