PALEOLITHIC DIET BREADTH AT ÜÇAĞIZLI CAVE (HATAY, TURKEY) IN PAN-MEDITERRANEAN CONTEXT

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ABSTRACT

Recent excavations at Üçağızlı Cave in the Hatay region of Turkey have yielded abundant, well preserved faunal remains representing multiple phases of the Initial through Epi- Paleolithic culture periods. Some trends in prey exploitation at this site echo those documented elsewhere in the Mediterranean Basin, but other details of this faunal series appear to be unique to the Hatay region and adjoining provinces. The findings on small game use hold exceptional potential for identifying and dating increases in Paleolithic diet breadth and associated demographic pulses in time and space. Pan-Mediterranean comparisons of diet breadth expose a major shift in human predator-prey dynamics involving small game animals by 50-40 KYA in the Mediterranean Basin, with earliest indications occurring in the Levantine corridor based on new evidence from Üçağızlı Cave, along with Hayonim Cave and nearby sites in the Galilee of Israel.

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KEY WORDS: Zooarchaeology, diet breadth, demography, Mediterranean basin, hunter-gatherers, Paleolithic, Üçağızlı Cave, Turkey, Israel, Italy.

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AKDENİZ HAVZASI GENELİNDE ÜÇAĞIZLI MAĞARASI'NDA (HATAY, TÜRKİYE) PALEOLİTİK DİYET GENİŞLİĞİ

ÖZET

Türkiye, Hatay İli, Üçağızlı Mağarası'nda sürdürülen son kazılarda, Öncül Üst Paleolitikten başlayarak Epipaleolitiğe kadar uzanan birden fazla periyoda ait, çok iyi korunmuş bol miktarda hayvan kemiği elde edilmiştir. Bu mağarada, avlanmaya ilişkin bazı eğilimler, Akdeniz Havzası'nın herhangi bir bölgesinde kaydedilen bilgileri yansıtmaktadır. Ancak bu faunal serilere ait diğer detaylar Hatay bölgesine ve komşu bölgelerine özgüdür. Küçük av hayvanlarına ait bilgiler, Paleolitik diyet genişliğinin tanımlanması ve artışın tarihlenmesi ile zaman ve mekana bağlı olarak demografide gözlenen değişimlerin anlaşılmasında özel bir yere sahiptir. Diyet genişliğinin Akdeniz Çanağı'ndaki karşılaştırmaları Akdeniz Havzası'nda 50-40 bin yıl önce küçük av hayvanlarını kapsayan av-avcı dinamiklerinin insanı etkileyen ana değişimlerine ışık tutmaktadır. Bu göstergeler, Levant koridorunda, Üçağızlı Mağarası'ndan elde edilen yeni kanıtlar ile Hayonim Mağarası ve İsrail'in Galileo bölgesindeki paleolitik sitelerinden izlenebilmektedir.

Anahtar Kelimeler: Zooarkeoloji, diyet genişliği, demografi, Akdeniz havzası, avcı-toplayıcı, Paleolitik, Üçağızlı Mağarası, Türkiye, İsrail, İtalya.

INTRODUCTION

Two topics in cultural evolution—the Middle to Upper Paleolithic transition and Flannery's (1969) "Broad Spectrum Revolution" at the end of the Pleistocene—are united by themes of expanding dietary breadth, predator-prey dynamics, and paleodemography. Although some of the original arguments on this subject refer specifically to plant exploitation, expansion in forager diets can also be investigated through the archaeofaunal record. Here we begin with a detailed examination of one rich faunal series from the site of Üçağızlı Cave, in the Hatay region of Turkey (Figure 1), and then we consider how this local sequence fits with pan-Mediterranean patterns as documented previously by the first author (Stiner 2001). Constants in the pan-Mediterrean comparison are geographic setting, along with uniform data quality, range of prey types, and attribution of the faunas to human collectors via taphonomic analyses. Thus, patterns in the data are most likely to vary as the result of climate-induced shifts in faunal content or changes in human predatory behavior. We find that human diets did indeed expand in the Mediterranean region during the Late Pleistocene, a process that began earlier than supposed; and, the information provided by small game is among the most powerful on the subject of diet breadth and demography.

FAUNAL PATTERNS AT ÜÇAĞIZLI CAVE

At least 11 distinct cultural layers have been identified in Üçağızlı Cave as of August 2002 (Dinçer et al. 2001; Kuhn et al. 1999; 2001, 2003, 2004). The cultural sequence spans the Initial Upper Paleolithic (beginning before 41,000 uncalibrated radiocarbon years), followed by early Upper Paleolithic (ca. 34-36/37 uncal. radiocarbon years) and Ahmarian phases (ca. 29,000-34,000) (Figure 2); a significant hiatus in deposition seperates the Upper Paleolithic layers from an early Epipaleolithic component, the latter of which dates to ca. 17,000 uncal. radiocarbon years (Kuhn et al. 2001). The culture series in Üçağızlı Cave contains sterile or semi-sterile layers separating major cultural horizons, often sterile red clays.

The main opening of the shelter faces southwest and rests 18 m above modern sea level in a limestone promontory on an exceptionally steep coast. The site is adjacent to a high-walled, narrow valley that may have presented strategic advantages for hunting roe deer, fallow deer, and wild goat, remains of which dominate the cultural deposits. The diverse contents of the Upper and Epi-Paleolithic deposits in Üçağızlı Cave indicate that it was a residential camp for much or all of its occupation history (Stiner et al. 2002); cultural layers typically include a wide range of stone tools, bone and antler implements, cobble grinding stones and anvils, shell ornaments, and hearth features (Güleç et al. 2000; Kuhn et al. 1999, 2001). Üçağızlı Cave occurs in the NE biogeographic quadrant of the Mediterranean Basin, at the top if the levantine rift (see Figure 1). While data collection on the faunas of Üçağızlı Cave continues, preliminary results presented in Tables 1-3 provide reliable impressions about Paleolithic human diets at this site.

The cultural sequence of Üçağızlı Cave spans most of oxygen isotope stage (OIS) 3, along with a brief portion of OIS 2 (Figure 3). Significant variation in the representation of large herbivores is apparent in the faunal sequence, and a number of quasi-opposing patterns occur between wild pig (*Sus scrofa*), Mesopotamian fallow deer (*Dama mesopotamica*), wild goat (*Capra aegagrus*), and roe deer (*Capreolus capreolus*). Much of the variation in ungulate species abundance may relate to changes in local vegetation as world climate shifted, and specifically in accordance with changes in the site's distance from the shoreline. Shellfish were exploited as food only during certain phases, most notably the Ahmarian and Epipaleolithic, with modest occurrences in the much older Layer I. These phases seem to correspond to times when the shoreline would have been closest to the shelter (see Figure 3).

Table 1: Preliminary summary of game frequencies (Percentages of N)* for the Epipaleolithic (EPI), Ahmarian (B-B3), early Upper Paleolithic (C-D), and Initial Upper Paleolithic (E-I) layers of Üçağızlı Cave

Taxa	EPI %	B %	B1-3 %	C-D %	E-E2 %	F %	Fa-c %	G %	H %	H1-3 %	I %
a. By multiple, size-ordered game categories:											
SLOW SMALL GAME:											
shellfish	20	47	32	7	<	<	<	<	<	<	4
tortoise	3	<	<	<	-	<	<	<	1	<	4
QUICK SMALL GAME:											
hare & squirrel	20	<	1	1	1	1	2	1	1	1	<
birds	11	2	2	1	<	<	<	<	<	<	<
fish (rockfish)	1	<	<	<	<	-	-	-	-	-	-
LARGE GAME (UNGULATES):											
Aurochs	-	<	<	<	<	1	<	2	1	<	2
large ungulate	1	<	<	<	1	3	3	2	1	1	3
red deer	-	<	<	1	2	1	3	1	<	<	1
Cervidae	1	<	<	2	3	1	1	1	1	1	1
fallow deer	1	5	6	19	12	8	5	2	1	8	12
wild boar	1	<	<	2	2	4	5	5	3	3	4
bezoar goat	7	4	3	1	8	15	14	18	20	14	1
med. Ungulate	17	25	30	54	49	49	52	48	47	57	50
roe deer	7	6	10	4	10	6	4	10	9	5	11
small ungulate	4	8	12	7	11	8	6	8	12	7	5
CARNIVORES (HUNTED BY HUMANS):											
small spp.	3	<	<	<	<	1	3	1	2	1	1
large spp.**	1	<	-	1	-	<	<	-	<	<	<
brown bear	-	<	<	<	<	<	<	-	<	1	2
TOTAL	528	2110	3254	1972	1445	2082	1606	512	2081	3789	395
b. By general categories based on body size and predator defense behaviors:											
Slow small	25	47	33	7	<	<	<	1	1	<	5
Quick small	33	3	4	2	1	1	2	1	1	1	1
Large herbiv.	39	49	63	90	98	96	93	97	96	97	90
Carnivores	4	<	<	1	1	2	4	1	2	2	4
TOTAL	528	2110	3254	1972	1445	2082	1606	512	2081	3789	395

Notes: Samples composed on condensed species-specific and less diagnostic (e.g. small ungulate) material. (N) shellfish counts are MNI to correct for mean size differences relative to vertebrate remains; all other counts are NISP. (<) Value is much less than one but greater than zero. (**) Category includes all large carnivores except bear.

Tablo 2: Genus-specific summaries of game frequencies (Percentages of N) within the small game, ungulate, and carnivore fractions of the Epipaleolithic (EPI), Ahmarian (B-B3), early Upper Paleolithic (C-D), and Initial Upper Paleolithic (E-I) layers of Üçağızlı Cave.

vertebrate taxa	EPI %	B %	B1-3 %	C-D %	E-E2 %	F %	Fa-c %	G %	H %	H1-3 %	I %
a. taxa within small game fraction:											
shellfish	40	95	92	86	23	19	15	•	3	19	80
tortoise	6	1	1	2	-	44	15	•	69	50	15
hare	27	<	<	-	12	13	46	•	-	6	-
squirrel	-	-	-	-	-	-	-	•	6	-	-
birds	23	4	6	7	41	25	23	•	22	25	5
fish	3	<	<	5	23	-	-	•	-	-	-
TOTAL (N)	258	1046	1152	162	17	16	13	5	32	16	20
b. taxa within ungulate fraction:											
roe deer	42	41	51	14	29	16	12	27	27	15	36
fallow deer	10	31	30	72	34	21	16	4	3	26	37
red deer	-	<	<	2	6	4	9	2	<	1	4
aurochs	-	<	<	<	1	4	1	5	2	<	6
wild boar	6	3	2	6	6	12	15	14	10	10	13
bezoar goat	42	24	17	5	24	42	47	48	57	47	3
TOTAL NISP	83	336	652	528	486	738	496	190	726	1173	124
c. taxa within carnivore fraction:											
brown bear	-	89	73	31	25	26	7	-	8	40	67
leopard	-	-	-	12	-	9	3	-	3	4	-
hyena	-	-	-	19	-	-	-	-	-	-	-
wolf	-	-	-	-	-	-	-	-	-	4	-
wild cat/lynx	20	-	-	12	-	3	12	67	11	12	13
red fox	80	11	27	6	-	21	5	-	39	40	20
stone marten (+)	-	-	-	19	75	41	72	33	39	-	-
TOTAL NISP	15	9	15	16	8	34	58	6	37	68	15

Notes: Shellfish counts are MNI to correct for excan size differences relative to vertebrate remains; all other counts are genus-specific NISP (even NISP in the case of birds.

Tablo 3: Comparisons* of species and genus richness for all game animals in the Epipaleolithic (EPI), Ahmarian (B-B3), early Upper Paleolithic (C-D, and Initial Upper Paleolithic (E-I) layers of Üçağızlı Cave.

	EPI	B	B1-3	C-D	E-E2	F-Fc	G	H	H1-3	I
genus-specific NISP**	355	1384	1817	299	367	232	160	128	237	443
N-genera	16	17	18	16	16	14	12	9	14	15
N-genera/log(MNI)	6.27	5.41	5.52	6.45	6.25	5.93	5.45	4.26	5.51	5.66

* Estimates include 1997-2001 data; study is incomplete, and assumes that each bird body size group represents one genus; fish is one genus. Predatory animals are included as humans' prey based on modification evidence. NISP genus-specific counts for vertebrates, but MNI for shellfish to compensate for differences in fragment size.

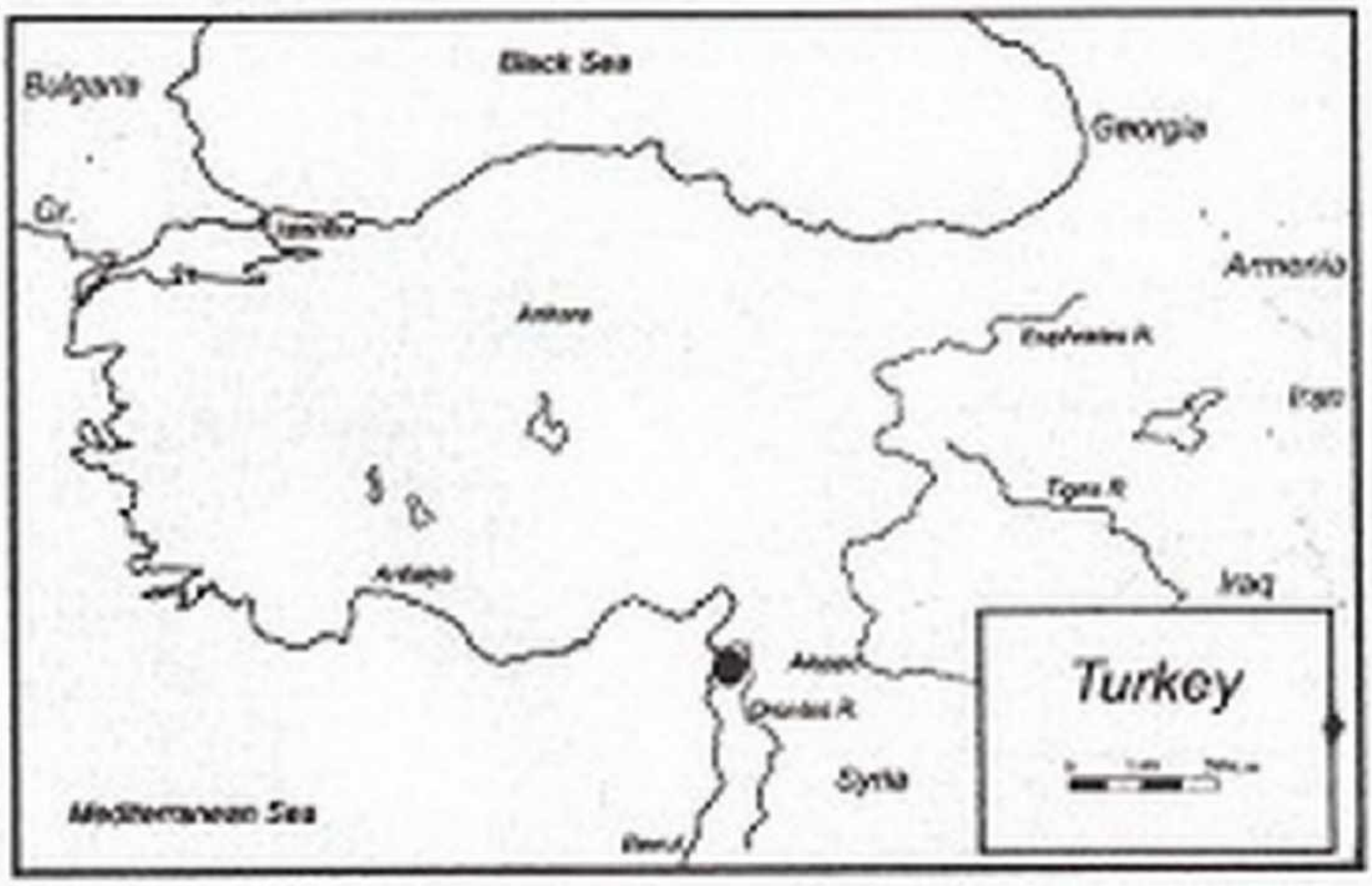

Figure 1: Location of Üçağızlı Cave (filled circle) in the Hatay region of southern Turkey

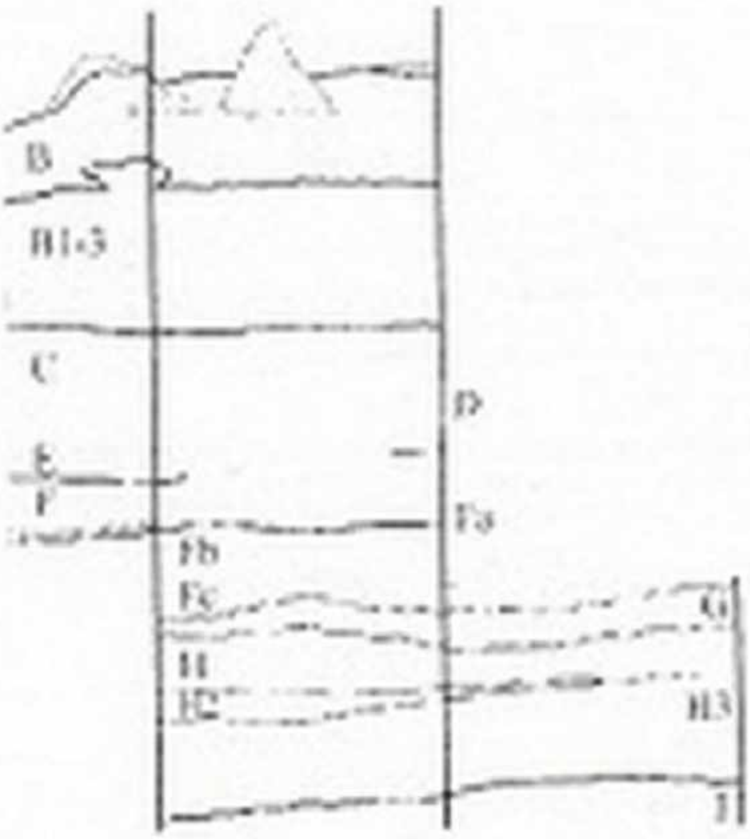

Figure 2: Schematic stratigraphic section of the Ahmarian, early Upper Paleolithic, and Initial Upper Paleolithic layers of Üçağızlı Cave (Hatay), Turkey

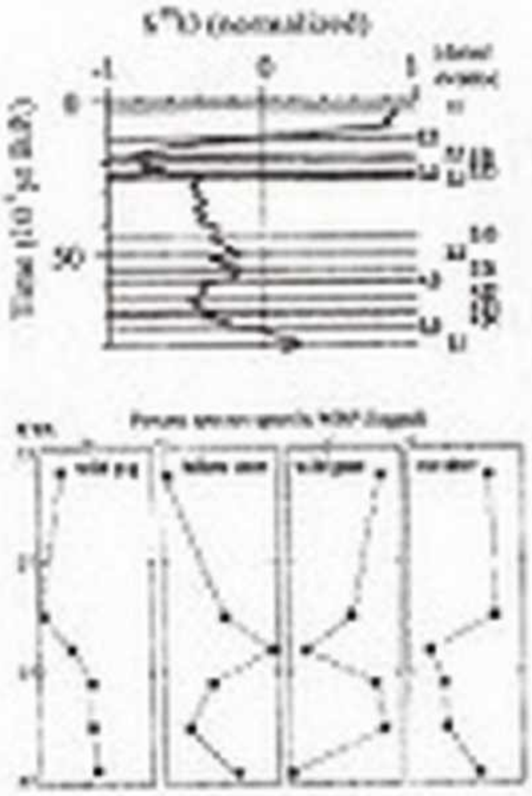

Figure 3: Trends in the relative abundance of four important ungulate taxa in the Initial Upper Paleolithic through early Epipaleolithic layers of Üçağızlı Cave (Hatay, Turkey) in relation to a general oxygen isotope chronology (OIS) spanning the last 300,000 years (adapted from Martinson et al. 1987: Fig 18).

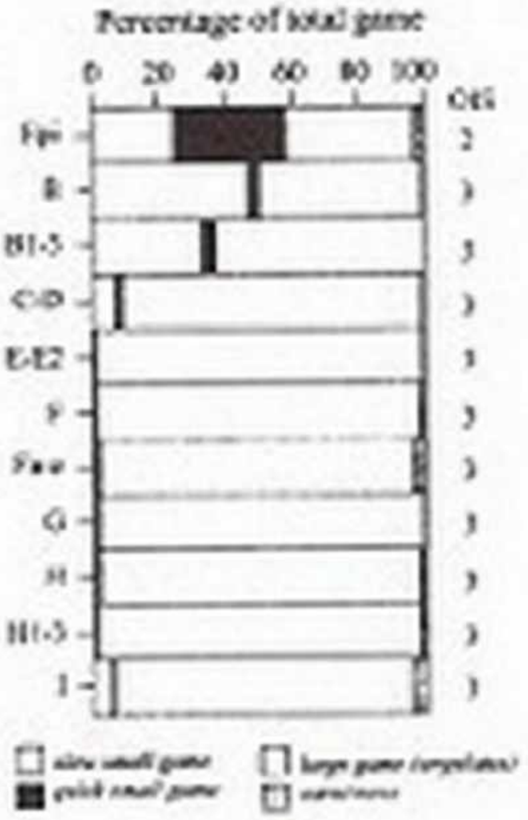

Figure 4: Increasing use of slow and quick small game animals relative to large game (ungulates) in the Initial Upper Paleolithic through early Epipaleolithic of Üçağızlı Cave (Hatay, Turkey). Oxygen isotope stages (OIS) follow Martinson et al. (1987).

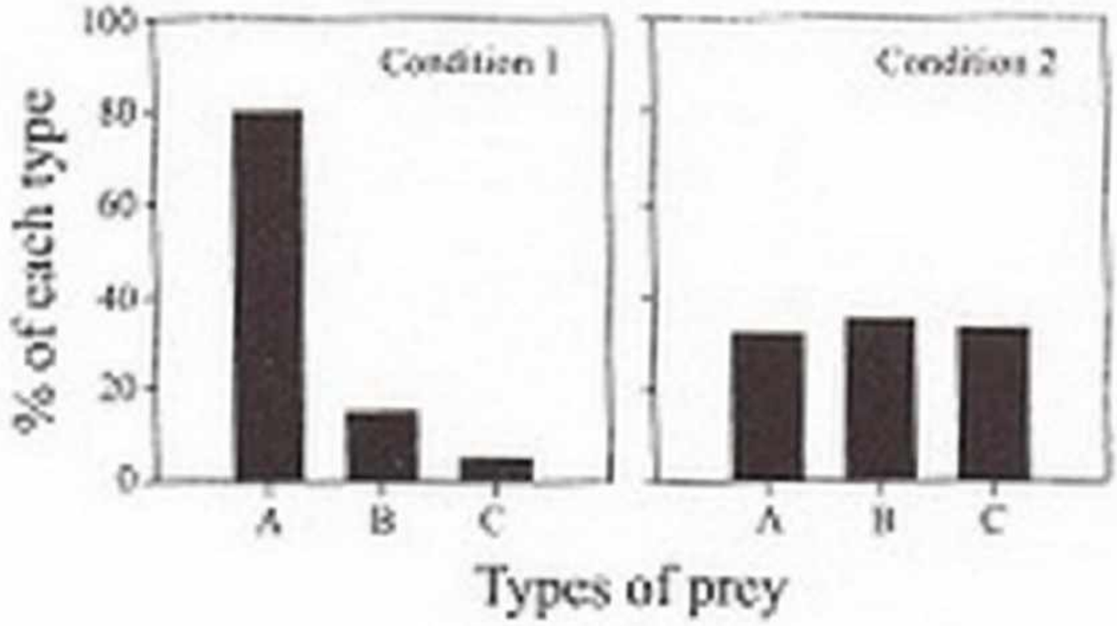

Figure 5: Predicted differences in the degree of evenness among prey types (A-C) taken by predators under distinct foraging conditions: (Condition 1) high availability of the highest-ranked prey types; (Condition 2) declining availability of the highest-ranked types such that the predator's choices must diversify to include more lower-ranked items.

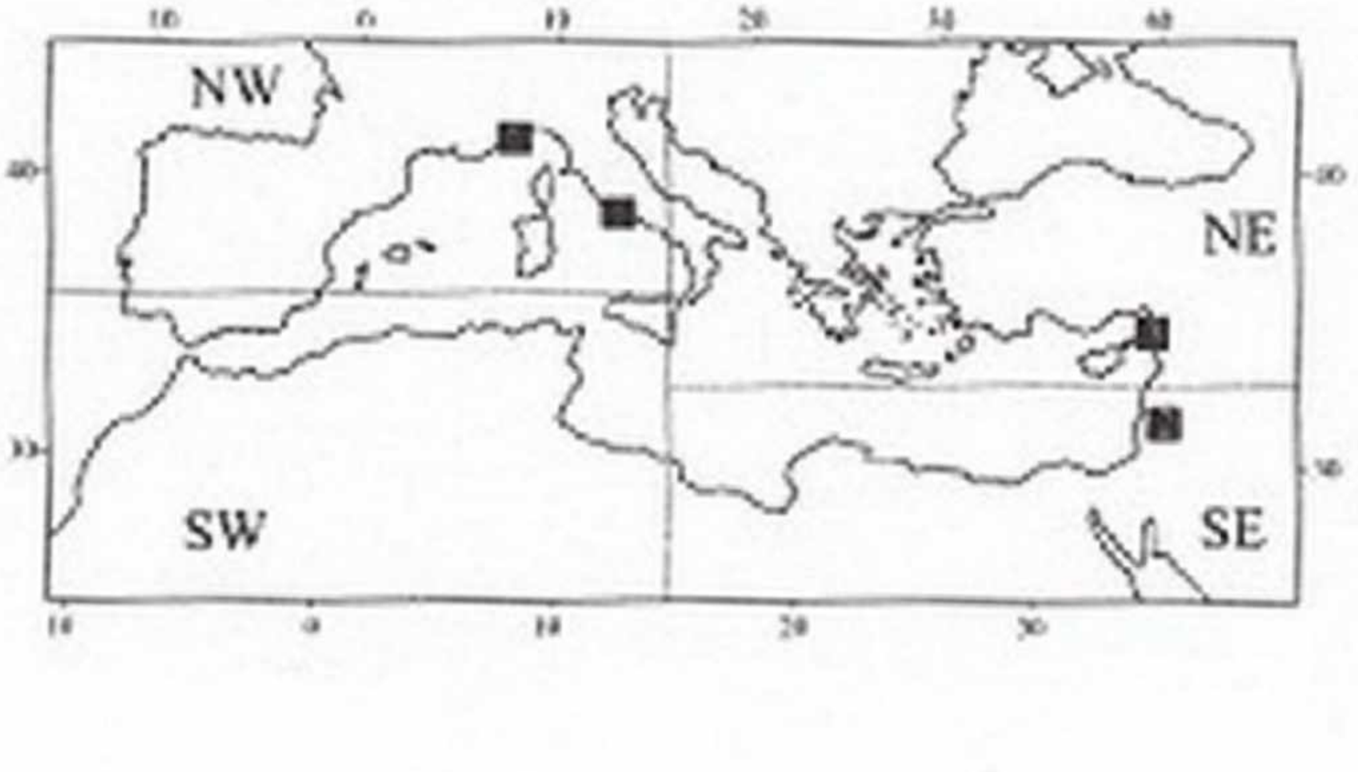

Figure 6: Geographic origins of the three Mediterranean faunal series, spanning three of four of the biogeographic quadrants of the Mediterranean Basin (followin Blondel and Aronson 1999); (1) western coast of Italy, with 16 assemblages; (2) Wadi Meged, inland Galilee of Israel, with 9 assemblages; (3) Üçağızlı Cave, Hatay coast of south-central Turkey, with 11 assemblages.

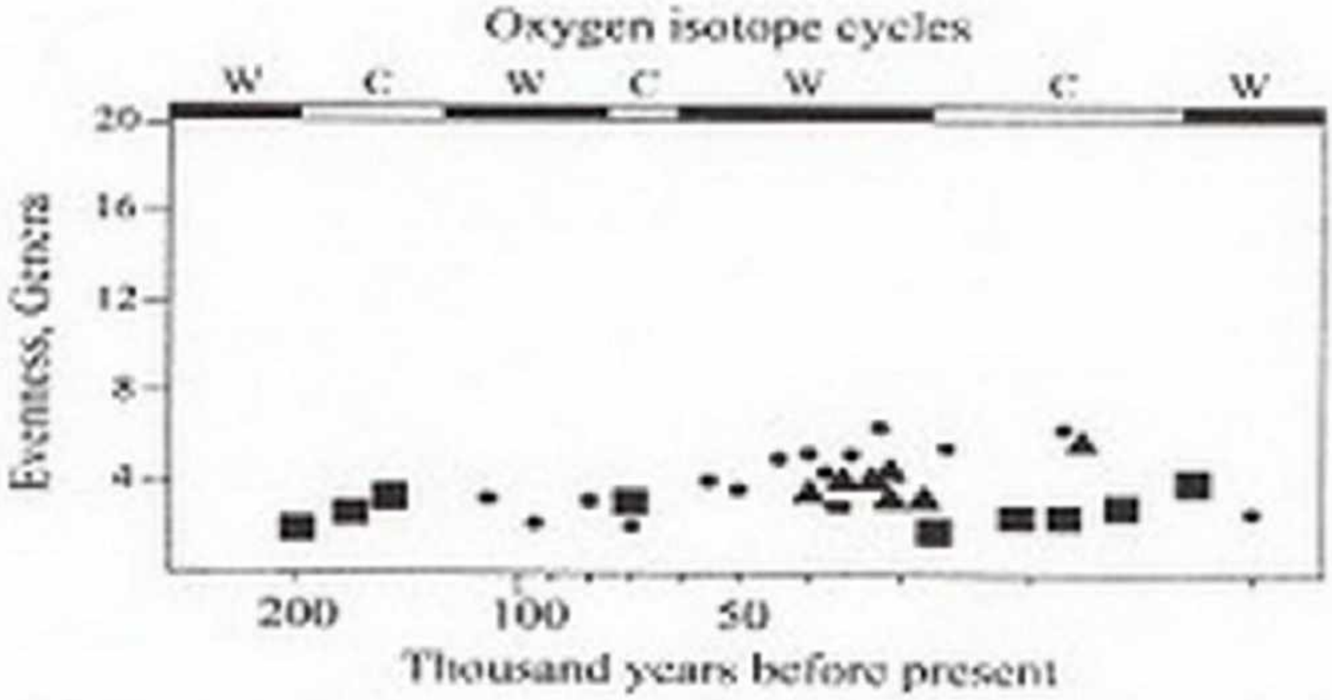

Figure 7: Evenness in the representation of Linnean genera for the faunal series from Italy (circle), Israel (square), and Turkey (triangle), using the Reciprocal of Simpson's Index (20=most even). Time and oxygen isotope climate cycles are expressed on a logged scale; (c) cold stage, (w) warm stage (from Stiner 2001).

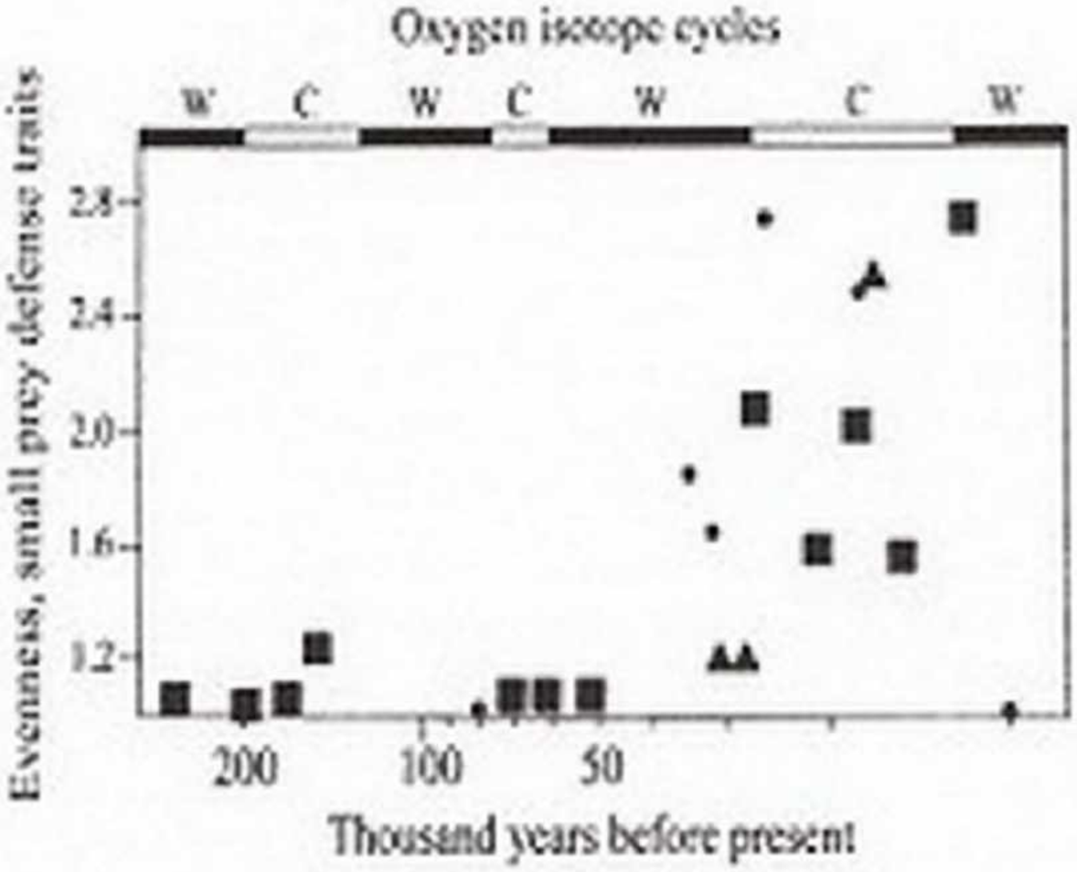

Figure 8: Evenness among three prey categories within the small game fraction only, based on prey defense mechanisms (slow game, quick running terrestrial mammals, and quick flying birds) using on the Reciprocal of Simpson's Index (3=most even). Symbols as in Figure 7 (from Stiner 2001).

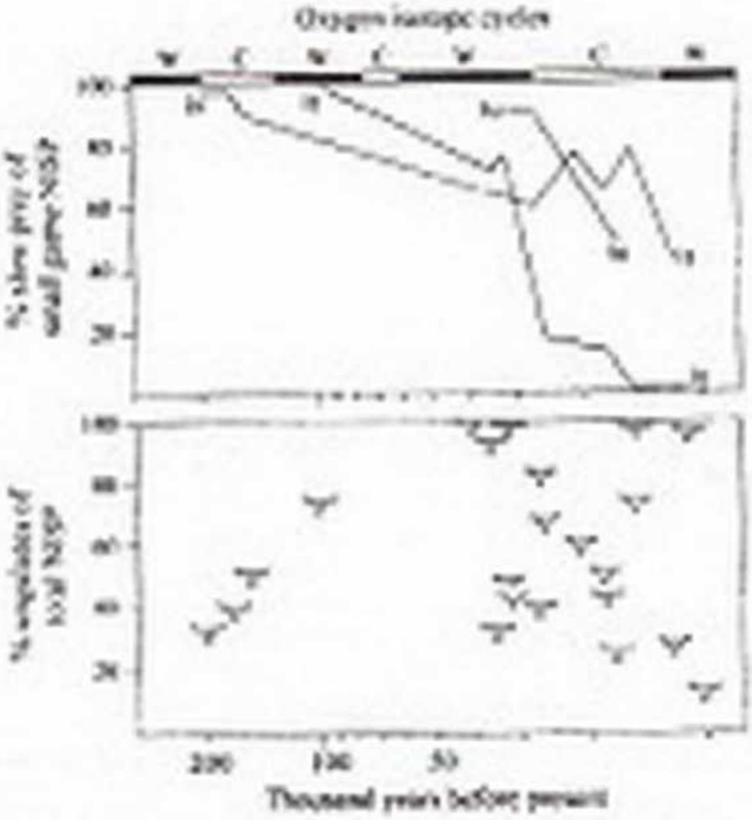

Figure 9: (a) Trends by region (lines) in the percentage of slow small prey within the small game fraction of each assemblages in (is) Israel, (it) Italy, and at (tu) Üçağızlı Cave in Turkey; (b) the percentage of ungulate remains (inverted triangle) in the total count of each assemblage (from Stiner 2001).

yet some of the temporal variation in the ungulate faunas cannot be explained by changing climate alone. Most notably, there this a progressive decline in the body sizes of the ungulate species most commonly hunted in the later periods (Stiner in press). This aspect of the data, along with trends in small game use, are consistent with observations elsewhere in the Mediterranean Basin.

Table 2 presents genus-specific summaries of game frequencies within the small game, ungulate, and carnivore fractions. An expedient measure of diversity (N-genera/log[MNI]) in Table 3 indicates great stability in taxonomic richness for the full spectrum of game animals in the cultural layers of Üçağızlı Cave. Figure 4 nonetheless reveals a marked trend in the small vs. large game fractions (based on Table 1b). The relative emphasis of small prey increases late in OIS 3, first with respect to slow moving (collectible) small game animals such as shellfish and tortoises. By the Epi-paleolithic, quick small game (mainly lagomorphs and birds) also became very important. Carnivore representation differs little with time. These are mainly small fur-bearing species and brown bears, tool marks and burning damage on which indicate that they were prey of human hunters.

CONCEPTS ABOUT DIET BREADTH AND DEMOGRAPHY IN ARCHAEOLOGY

All Paleolithic hominids lived by hunting and collecting wild foods, an aspect of existence that began to disappear only with the emergence of farming and herding societies of the Neolithic ≤10 KYA. The roots of this remarkable economic transformation lie in equally revolutionary changes that took place within certain Stone Age cultures several millennia beforehand. Binford (1968) and Flannery (1969) first recognized links between the expanding diets of Late Pleistocene foragers in Eurasia and culture change. Binford described substantial diversification of human diets in middle and high latitude Europe at the end of the Paleolithic, or Mesolithic, roughly 12-8 KYA. Rapid diversification in hunting practices, food processing, and food storage equipment generally accompanied the dietary shifts, which he took to be symptoms of intensified use of habitats and fuller exploitation of the potential foodstuffs they contained. Some of this behavior was directed to grinding, drying, and storing nuts, but it also involved small animals (see also Clark and Straus 1983; Coles [Ed.] 1992; Jochim 1998; Keeley 1988; Price and Gebauer 1995).

Flannery pushed these observations further in 1969 with his "Broad Spectrum Revolution" (BSR) hypothesis, proposing that the emergence of the Neolithic in western Asia was prefaced by local increases in dietary breadth among foraging societies of the late Epipaleolithic. He argued that subsistence diversification, mainly through adding new species to the diet, raised the carrying capacity of an environment that was increasingly constrained by climate instability at the end of the Pleistocene. These authors suggested that local imbalances in human population density relative to available food were somehow integral to the remarkable changes that took place in human societies just prior to the forager-farmer transition. Binford's and Flannery's papers have stimulated much archaeological research and many debates over the last three decades, not least because they offered some explicit predictions about subsistence change. One of the most widely used of these predictions in zooarchaeology is Flannery's suggestion that the actual number of species in human diets increased with the BSR.

The arguments forwarded by Binford and Flannery about human subsistence evolution were influenced directly by early works in the science of population ecology, including what later came to be known as foraging theory and diet breadth models. Inspired particularly by the works of Odum and Odum (1959), Emlen (1966), and MacArthur and Pianka (1966), Binford and Flannery argued that economic change could have resulted from demographic crowding in certain regions of the world and somehow altered some of the conditions of selection on human societies. Most archaeologists continue to think of demographic factors as one of several ingredients necessary to the forager-farmer transition (e.g., Keeley 1988; Bar-Yosef and Meadow 1995; Binford 1999; Davis et al. 1994; Redding 1988; Rosenberg 1998; Watson 1995). We know that density-dependent effects can play decisive roles in shaping the evolutionary histories of predator-prey systems in general (Boutin 1992; Pianka 1978; Sinclair 1991), and humans should not be altogether immune to these effects in principle (Harpending and Bertram 1975; Winterhalder and Goland 1993). Changes in human population density certainly influence the rates of inter-specific and intraspecific contact and the availability of critical foodstuffs. With increases in population density, people's solutions for getting enough to eat are bound to shift as well. Rapid technological change and the greater densities of archaeological sites during the later Paleolithic lend some credence to this position.

THEORETICAL EXPECTATIONS FOR DIETARY BREADTH

Evidence of increasing dietary breadth is expected to take the form of more species in the diet and/or greater proportional evenness among high-ranked and low-ranked prey items in response to declining availability of preferred types. A predator can afford to ignore lower quality prey at little cost if the chance of finding a superior type in the near future is high, fostering a narrower diet that emphasizes a favored type disproportionately to its availability in the environment (Condition 1 in Figure 5). As the supply of preferred prey dwindles, however, broadening the diet to include common but lower yield prey types maximizes a predator's returns per unit expenditure by reducing search time (Pianka 1978). This second set of conditions therefore encourages a more diverse diet in the sense that the predator's emphasis is spread more evenly among two or more prey types that occur in the environment (Condition 2).

Broadening of Paleolithic diets in Eurasia certainly is apparent from greater exploitation of energy-rich nuts and large seeds from the Epi-Paleolithic onward. Because the nutritional benefits of these resources require considerable work and equipment to extract (Keeley 1988), the trend is most readily apparent from the proliferation of milling tools after the Last Glacial Maximum (Wright 1994), and, to a lesser extent, from increasing evidence of storage facilities and preserved plant parts (Hillman et al. 1989; Miller 1992) and the rise of commensal rodents (Tchernov 1984). Under lean conditions people should also have become less selective about what animals to hunt rather than go hungry. Yet, the measures of diversity in game use based on Linnean taxonomic categories (counts of species or genera) register only one clear economic transition—that from foragers to farmers in the early Neolithic, when there was gradual *decline* in dietary breadth (Davis 1982; Edwards 1989; Horwitz 1996; Munro n.d.; Neeley and Clark 1993). What variation could be found in the taxonomic diversity of archaeofaunas across the Middle, Upper, and Epi-Paleolithic periods was more easily explained by climate-driven environmental changes or geographic variation in animal and plant community composition (Bar-Oz et al. 1999; Simek and Snyder 1988; Stiner 1992). Until recently, there seemed to be no zooarchaeological support for the BSR hypotheses of expanding diet breadth in the later Paleolithic.

The basic idea behind the BSR hypothesis remains a good one. Discrepancies between the results on plant and animal exploitation seem to stem from how zooarchaeologists tend to categorize prey animals (Stiner et al. 2000). Because the cultures of interest are extinct, prey-ranking systems cannot be inferred from watching people make decisions. The relative values (pay-offs) of prey must instead be evaluated from knowledge of modern variants of the animals whose bones occur in archaeological deposits. Species and genera present the most obvious (and accessible) analytical categories, and the most literal expectation of Flannery's BSR hypothesis is indeed more species in the diet and/or more even emphasis on those species. Thus zooarchaeologists normally examine diet variation in terms of indexes of taxonomic richness (N-species or N-genera) and taxonomic evenness (proportionality in abundance) (Edwards 1989; Neeley and Clark 1993; Simek and Snyder 1988; Grayson and Delpech 1998). Such analyses employ either Kintigh's simulation-based technique (Kintigh 1984) or a more long-standing regression approach (Grayson 1984) that apparently grew out of the work of Fisher, Corbet, and Williams (Fisher et al. 1943) for problems of sampling in modern community ecology.

The main weakness of diversity approaches that rely on Linnean taxonomic units is their insensitivity to the physical and behavioral differences among prey animals. The only qualification normally added to such analyses is prey body size, since all game animals are composed of similar tissues and large animals yield more food than small ones, even if they are more difficult to catch. The logic of this practice is fine as far as it goes, but it potentially overlooks great differences in prey handling costs among animals that are broadly equivalent in food content and package size. In fact, some distantly related taxa are nearly equivalent from the viewpoint of handling costs because of their locomotor habits or ways of avoiding predators. Tortoises and rock-dwelling marine shellfish, for example, are sluggish or immobile. Hares and partridges, though similar in body weight to tortoises or an arm-full of shellfish, are quick and maneuverable. Humans, because of their generalist dietary tendencies, will exploit a wider range of prey as the resident species diversity in ecosystems increases. During the Pleistocene, resident species diversity was subject to change with climate-driven shifts in effective latitude, which in some cases further increased the potential for prey type interchangeability. Climate-driven effects on animal community structure therefore must be taken into account in research on human dietary breadth. In this study we appeal mainly to global OIS chronology to separate anthropogenic (behavioral) from independent environmental changes.

DIET TRENDS IN MEDITERRANEAN ITALY, TURKEY AND ISRAEL

Differing prey type classification systems greatly affect archaeologists' perceptions of change in prehistoric diet breadth, and those approaches most strictly bound by taxonomy have obscured critical information. This can be demonstrated by applying a simple measure of diversity to three faunal assemblage series from the Mediterranean Basin, the Reciprocal of Simpson's Index, or $1/?(?_i)^2$, where ? represents the proportion of each prey type for array ,in an assemblage (Simpson 1949; Levins 1968). In two treatments of the same data, the prey categories are manipulated and progressively simplified, from categories rooted strictly in biological systematics to those defined by independent energetic criteria, such as prey body size and predator avoidance strategies.

The Mediterranean faunal series include a total of 32 assemblages from shelter sites in the Wadi Meged, Israel (200-11 KYA) (Stiner in press; Stiner et al. 2000; Munro 2001), the western coast of Italy (110-9 KYA) (Stiner 1994, 1999), and Üçağızlı Cave in south-central coastal Turkey (42-17 KYA). Three distinct quadrants of the Mediterranean Basin are represented (Figure 6), each with its own set of endemic species. Each faunal series coincides geographically with Mediterranean vegetation refugia during peak glaciations (see Blondel and Aronson 1999: 28). Thus the chances for stability in community composition in the study areas are as high as they can be for any Mediterranean ecosystem. The spectrum of animal taxa eaten by Paleolithic peoples in the Mediterranean Basin did not vary much: tortoises, marine shellfish, ostrich eggs, game birds such as partridges, hares, and rabbits, in addition to a wide range of ungulate species.

Because the series from Italy, Israel, and Turkey represent distinct ecogeographic zones, the trends to be discussed below cannot be dismissed as local phenomena. The archaeofaunal assemblages collectively span 200,000 to 9,000 years before present. Geographic context and site type are held generally constant in each series, and the comparisons are confined to assemblages from limestone caves and rock shelters, places to which food would have been brought by foragers. The samples are uniformly high in quality, with thorough recovery and site documentation. Systematic fine-screening was practiced in all cases, and prehistoric damage to the faunal remains, such as burning, breakage patterns, and tool and percussion marks, along with near or total absence of damage from non-human predators, demonstrate that the small animals were consumed by Paleolithic humans (see Stiner 1994, 1999, in press; Stiner and Tchernov 1998; Stiner et al. 2001; Kuhn and Stiner 1998). Material of unclear origin, or representing mixed cultural entities, has been removed from consideration. The data from Üçağızlı Cave in Turkey used in this comparison are an early subset from the project (Stiner and Munro 2002).

The preferred counting unit for the diversity analysis is the number of identified specimens (NISP), here confined to specimens that could be identified to genus or finer taxonomic distinctions. NISP is least subject to aggregation error (see Grayson 1984 for a full discussion of the advantages of NISP). Fragment size increases with prey body size in all of these faunas, but the gradation in fragmentation is similar among assemblages (e.g., Stiner 1994, in press; Stiner and Tchernov 1998). Although MNI is a derived measure that embodies many more assumptions, it is used for shellfish remains to control for much higher levels of fragmentation, substantially smaller body sizes, and the fact that marine mollusks shells have exceptionally high identifiability quotients owing to their distinctive morphologies and surface textures (Stiner 1999).

DIETARY EVENNESS BASED ON COUNTS BY GENERA

Application of the Reciprocal of Simpson's Index to assemblages which potentially contain about 20 genera (Figure 7) yields consistently low levels of evenness in dietary breadth in the three faunal series over a 200 KY time span. There is only a very weak correlation with time (Pearson's r 0.386, r^2=.15, p=.05, n=32), and there is no correspondence to the 6-7 climatic oscillations indicated by oxygen isotope data from deep sea cores (e.g., Martinson et al. 1987; Shackleton and Opdyke 1973). While sample size varies among the assemblages, this fact does not explain the pattern in Figure 7. This treatment of the data provides no support for the BSR hypothesis within the Paleolithic, just as Edwards (1989), Neeley and Clark (1993), and Horwitz (1996) observed from their studies of other Old World faunas. Most investigations of diet breadth changes have stopped here.

EVENNESS AMONG SMALL PREY TYPES BASED ON DEFENSE CHARACTERISTICS

What about small animal exploitation? This is where Binford and Flannery expected to see the greatest changes in game use. We know that small animals were important to human diets in the Mediterranean Basin from at least the early Middle Paleolithic onward (Klein and Scott 1986; Stiner 1994; Stiner and Tchernov 1998). The proportional contribution of small game to total meat intake varied from staple to supplement, however, with no pan-Mediterranean trend except for a sharp increase at the close of the Paleolithic sequences (Davis et al. 1994; Munro 1999; Stiner in press); for reasons not yet determine, the faunal series from Üçağızlı Cave poses an interesting exception to this generalization. We also see that the spectrum of animal taxa eaten by Paleolithic peoples in the Mediterranean Basin did not vary much (Stiner 1994; Tchernov 1994). However, the relative emphasis that humans placed on three general types of small animals changed dramatically with time. Middle Paleolithic foragers seldom bothered with small prey unless they were easily obtained (collectable small prey such as tortoises, shellfish, large lizards, ostrich eggs). This was not the case in many areas from the early Upper Paleolithic onward.

Variation within the *small game fraction* of each Mediterranean faunal series (Figure 8) reveals a clear trend toward more even dependence on high-ranked and low-ranked small prey, confirmation of expanding dietary breadth during the later part of the Mediterranean Paleolithic. This regrouping of the data distinguishes only between slow-moving, easily collected types (tortoises and shellfish), fast-running mammals (mostly lagomorphs), and quick flying game birds. Only 18 assemblages in the Mediterranean series contain small game components large enough to be compared, with four from the early Middle Paleolithic of Italy collapsed into one to increase sample size. Removing large game from the comparison allows clear expression of expanding diet breadth in small game exploitation (r 0.606, r^2=.37, p=.01, n=18). (Three Mousterian components of Kebara Cave [Speth and Tchernov 2002] have been added to Fig. 8 but are not included in the statistical calculations.)

These data indicate that much of the expansion took place during a cold climate stage (OIS 2), although the trend began in OIS 3. That the trend continued unabated into OIS 2 is the opposite of what is expected to result from climate-driven changes in animal community composition, since the number of small animal species tends to be greater in warmer environments (Blondel and Aronson 1999; Pianka 1978). The evidence therefore indicates a categorical or step-wise change in how humans interacted with small animal populations after about 40-50 KYA.

INFLUENCE OF BODY SIZE AND CAPTURE COSTS ON PREY RANK

If different ways of categorizing prey in studies of Paleolithic diet breadth produce contradictory results, which approach is more appropriate? The answer depends on how we think foragers should have ranked prey according to expected energy returns. Linnean taxonomy is a powerful tool in biology and zooarchaeology, not least because there is considerable agreement about what animals should be called and how they are related to one another genetically. However, foragers' perceptions of prey do not necessarily follow the rules of biological systematics—in fact it is clear that they do not—and variation in the relative abundances of species or genera does not seem to be sensitive to behavioral changes in prehistoric human predators, at least in the geographic areas considered here.

Prey body size should be a valuable non-taxonomic criterion for ranking the potential returns of prey, and indeed it was of direct significance in the Üçağızlı faunal series. However, prey body size more often fails to dominate foragers' prey ranking systems, because of the additional complications of capture costs (e.g., Jochim 1976) and, in some cases, processing costs (Madsen and Schmitt 1998; Stiner et al. 2000). The large to small body size contrast in the three Mediterranean series, expressed as the percentage of ungulates in the total count for each assemblage in Figure 9, is largely trendless (*r* 0.276, p=1, n=18). By contrast, the proportion of slow animals within the small game fraction of each assemblage clearly declines with time in all three Mediterranean series (*r* 0.572, .02>p>.01, n=18), the converse of which is increasing reliance on small quick animals.

Prey body size must have had some economic significance, but it seems that the absolute differences in prey size often were recalibrated from the foragers' point of view by the differing capture costs among small prey animals. This expectation is compatible with optimal foraging theory, which ranks prey in terms of costs of pursuit and handling vs. energetic returns (Pianka 1978; Stephens and Krebs 1986).

DISCUSSION

The Mediterranean Basin constitutes a major part of the total geographic range of Paleolithic humans, and it is a textbook example of high diversity in animals and plants, a quality that has changed little over the course of the Late Pleistocene, in contrast to the rest of Europe and much of Asia (reviewed in Blondel and Aronson 1999). The Mediterranean Basin therefore is an ideal laboratory for testing ideas about dietary expansion in human evolution: there were many small species for Paleolithic foragers to choose from and thus high inherent potential to express shifting predator-prey dynamics from small game data.

Independent standards for prey classification were isolated from wildlife data and linked to demographic increase by predator-prey simulation modeling and examination of diminution effects in certain slow-growing species (Stiner et al. 2000). The fact that small prey animals differ tremendously in their development rates permits an unusually clear view of how increases in Paleolithic diet breadth shifted with local demographic growth. This is not a matter of how much small game animals contributed to total game intake so much as how certain very sensitive species serve as symptoms of threshold effects in predator-prey systems.

In the Mediterranean Basin, a simple distinction in the "catchability" of small animals happens to correspond to great differences in prey population resilience, the latter governed mainly by individual maturation rate (Stiner et al. 2000). Slow-moving Mediterranean tortoises (*Testudo graeca*, maturing at 8-12 years) and some shellfish such as limpets (*Patella*) and large predatory gastropods such as *Thais* (1-5 years) are especially susceptible to over-harvesting because of slow maturation rates (Blasco et al. 1986-87; Dye et al. 1994; Hailey et al. 1988; Hockey 1994; Siegfried et al. 1994). It is unlikely that Paleolithic foragers viewed prey in terms of their potentials for population recovery, but foragers certainly would have been aware of declining availability of prey and thus declining returns for the same level of foraging effort.

With evidence of harvesting pressure on "low turnover" prey populations during the later Paleolithic in the Mediterranean region, there was a corresponding increase in the exploitation of agile, warm-blooded small animals, mainly birds such as partridges and lagomorphs (hares and rabbits). These quick small animals mature in I1 year, and their populations rebound easily from heavy hunting by humans. Predator-prey simulation modeling results have demonstrated that hare and partridge populations can support seven to ten times the annual off-take that tortoise populations can support (Stiner et al. 2000). Limpets and large predatory mollusks (e.g., *Thais*) are only somewhat more resilient than tortoises. Humans' greater dependence on slow-growing animals during the Middle Paleolithic, and on larger individuals on average, implies that these early populations were very small and dispersed. Paleolithic foragers' emphasis on slow (highly ranked) and quick (lower ranked) small prey grew more "even" with time, the predicted outcome of hunting pressure and demographic increase in the absence of a correlation to climate warming. We should expect to encounter local variation in the story of diet breadth, and the Paleolithic culture series from Üçağızlı Cave is a fine example of this. Disparate faunal series nonetheless conform to the larger phenomenon of expanding forager diets, signalling fundamental changes in the place of human beings in Late Pleistocene ecosystems throughout the Mediterranean Basin and elsewhere. These changes began earlier in the eastern Mediterranean Basin than at its northern and western ends, underscoring the likelihood that prehistoric human populations were largest in the semi-arid subtropical to tropical latitudes of Asia and Africa (Keeley 1988; Harpending and Bertram 1975). Demographic pulses emanated from southwestern Asia into Europe several times after the Middle-Upper Paleolithic transition.

The zooarchaeological results place demographic forces squarely in the evolutionary arena in which changes in human dietary breadth and society occurred during the Late Pleistocene. This observation need not represent back-pedaling to the days of simplistic or linear explanations of population pressure as the engine of culture change. It simply shows us that demographic processes were somehow part of the substrate upon which selective factors may have operated, whether the question is about the emergence of Upper Paleolithic (so-called behaviorally modern) lifeways, social complexity in hunter-gatherers, or the origins of plant cultivation and animal husbandry. In most periods, human populations adjusted to environmental stresses in a straightforward demographic way, without substantive changes in behavioral adaptations. In rarer instances, there is evidence of behavioral evolution. While the zooarchaeological data on diet breadth do not by themselves explain unprecedented human responses to declining resource availability, they play an important role in refining the questions we can ask of archaeological records in general.

Üçağızlı Cave provides one of the key reference data sets for the NW Mediterranean biogeographic quadrant, owing to excavations that employ current taphonomic, chemical, and dating techniques. The Üçağızlı series displays numerous similarities to the Upper Paleolithic layers of Ksar 'Akil on the coast of Lebanon (reviewed in Kuhn et al. 2001), an important site but whose faunal contents were incompletely recovered.

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