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## **Approaches to Prehistoric Diet Breadth, Demography, and Prey Ranking Systems in Time and Space**

**Mary C. Stiner<sup>1,3</sup> and Natalie D. Munro<sup>2</sup>**

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*Zooarchaeological data on small game use hold much potential for identifying and dating Paleolithic demographic pulses in time and space, such as those associated with modern human origins and the evolution of food-producing economies. Although small animals were important to human diets throughout the Middle, Upper, and Epi-Paleolithic periods in the Mediterranean Basin, the types of small prey emphasized by foragers shifted dramatically over the last 200,000 years. Slow-growing, slow-moving tortoises, and marine mollusks dominate the Middle Paleolithic record of small game exploitation. Later, agile, fast-maturing animals became increasingly important in human diets, first birds in the early Upper Paleolithic, and soon thereafter hares and rabbits. While the findings of this study are consistent with the main premise of Flannery's Broad Spectrum Revolution (BSR) hypothesis (Flannery, K. V. (1969). In Ucko, P. J., and Dimbleby, G. W. (eds.), *The Domestication and Exploitation of Plants and Animals*, Aldine Publishing Company, Chicago, pp. 73–100), it is now clear that human diet breadth began to expand much earlier than the Pleistocene/Holocene transition. Ranking small prey in terms of work of capture (in the absence of special harvesting tools) proves far more effective in this investigation of human diet breadth than taxonomy-based diversity analyses published previously. Our analyses expose a major shift in human predator–prey dynamics involving small game animals by 50–40 KYA in the Mediterranean Basin, with earliest population growth pulses occurring in the Levant. In a separate application to the Natufian period (13–10 KYA), just prior to the rise of Neolithic societies in the Levant, great intensification is apparent from small game use. This effect is most pronounced at the onset of this short culture period, and is followed by an episode of local depopulation during the Younger Dryas, without further changes in the nature of Natufian hunting adaptations. An*

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*essential feature of the diachronic and synchronic approaches outlined here is controlling the potentially conflating effects of spatial (biogeographic) and temporal variation in the faunal data sets.*

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**KEY WORDS:** zooarchaeology; diet breadth; demography; Mediterranean Basin; hunter-gatherers; Middle Paleolithic; Upper Paleolithic; Epi-Paleolithic; Natufian.

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## INTRODUCTION

Two topics in cultural evolution that seem widely separated in time—the Middle to Upper Paleolithic transition and Flannery's (1969) "Broad Spectrum Revolution" at the end of the Pleistocene—are united by similar themes of expanding dietary breadth, predator–prey dynamics, and paleodemography. Our evidence on this subject concerns game use, as the data are zooarchaeological, but it should be understood that the general phenomena we are dealing with must also have included changes in how humans made use of plants. Bones preserve better, however, and thus the possibilities for investigating diet breadth from a zooarchaeological perspective are relatively rich and geographically widespread. We make two major points in this study: (1) human diets did indeed expand in the Mediterranean region during the Late Pleistocene, a process that began earlier than supposed; and (2) the information provided by small game is among the most powerful on the subject of diet breadth and demography. The perspectives we present were inspired by apparent anomalies in the nature of Middle Paleolithic zooarchaeological records of the Mediterranean Basin relative to what had been reported previously, and some remarkable shifts in the balance of animal exploitation at the close of the Epi-Paleolithic (Natufian) in the Levant. Our approaches divide according to two dimensions that are the mainstay of archaeology—time and space—in order to isolate the causes of variation in the faunal records. The zooarchaeological expectations will vary accordingly.

The first approach undertakes a strictly diachronic comparison of human dietary breadth. The time depth is great (about 200,000 years), and the analysis benefits from extended accumulation times, such as would result from multiple visits to a site, but time-averaging was never so great as to destroy the overall chronological integrity of the faunal series. Constants in this approach 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.

The second approach also incorporates a temporal dimension, but it focuses on a single culture period of short duration, the Natufian, lasting roughly 2,500 years. The issue is the length of stay at sites and, with burgeoning sedentism, foragers' impacts on local food supplies. This approach assumes minimal time averaging of deposits and high temporal (chronostratigraphic) and spatial resolution. Not

surprisingly, the second approach is best suited to later periods, and, because the time frame is short, the scale of variation in the zooarchaeological patterns is more subtle. Constants in this approach differ from the first in that temporal variation is limited, and the spatial distribution and sizes of sites are allowed to vary within the confines of one relatively small biogeographic region.

## HISTORICAL BACKGROUND

Binford (1968) and Flannery (1969) first recognized links between culture change and expanding diets of Late Pleistocene foragers in Eurasia in the late 1960s. 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, 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, 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 in 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 increasingly constrained by climate instability at the end of the Pleistocene. Both 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 Paleolithic–Neolithic, or forager–farmer, transition from 10 KYA onward.

Binford’s and Flannery’s papers have stimulated much archaeological research and many debates over the last three decades, not least because they offer some explicit predictions for subsistence change. It is of historical interest that these anthropological arguments were influenced 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 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, which may also have altered the conditions of natural selection on human societies.

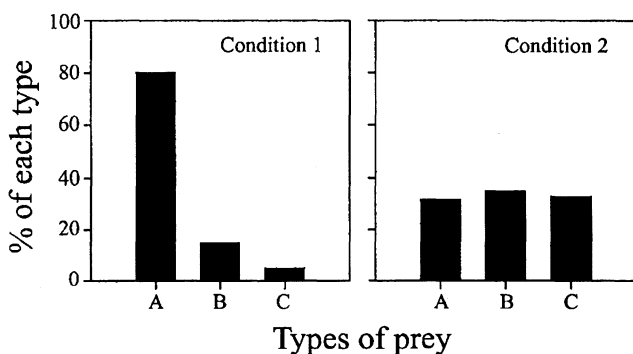
Some archaeologists are skeptical about the significance of “population pressure” in human social evolution (e.g., Hayden, 1995; Price and Gebauer, 1995), but most continue to think of demographic factors as one of several ingredients necessary to the forager–farmer transition (e.g., Bar-Yosef and Meadow, 1995; Binford, 1999; Davis *et al.*, 1994; Keeley, 1988; Redding, 1988; Watson, 1995).

Density-dependent effects can play decisive roles in shaping the evolutionary histories of predator-prey systems in general (Boutin, 1992; Gavin, 1991; 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 interspecific and intraspecific contact and the availability of critical foodstuffs. Under these conditions, people's solutions for getting enough to eat are bound to shift as well. Rapid technological change and increased densities of archaeological sites during the later Paleolithic lend some credence to this position.

### THEORETICAL EXPECTATIONS

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. These kinds of foraging conditions foster narrower diets that emphasize just a few favored types disproportionately to their availability in the environment (Fig. 1). 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 more diverse diets in the sense that the predator's emphasis is spread more evenly among the number of prey types that occur in the environment.

Broadening of Paleolithic diets in Eurasia certainly is apparent from greater exploitation of energy-rich nuts and large seeds with time. Because the nutritional



**Fig. 1.** 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; and (Condition 2) declining availability of the highest-ranked types such that the predator's choices must diversify to include more lower-ranked items.

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 (e.g., Hillman *et al.*, 1989; Miller, 1992). Under lean conditions people should also have become less selective about what animals to hunt rather than go hungry. Yet, the story from the faunal evidence was much less clear than that for plant use. Many analysts' measures of prey diversity are based on Linnean taxonomic categories (counting species or genera) and as such 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; Neeley and Clark, 1993). What variation could be found in the taxonomic diversity of archaeofaunas over the Middle, Upper, and Epi-Paleolithic 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, 1994). From this perspective, there seemed to be no zooarchaeological support for the BSR hypotheses of expanding diet breadth in the later Paleolithic.

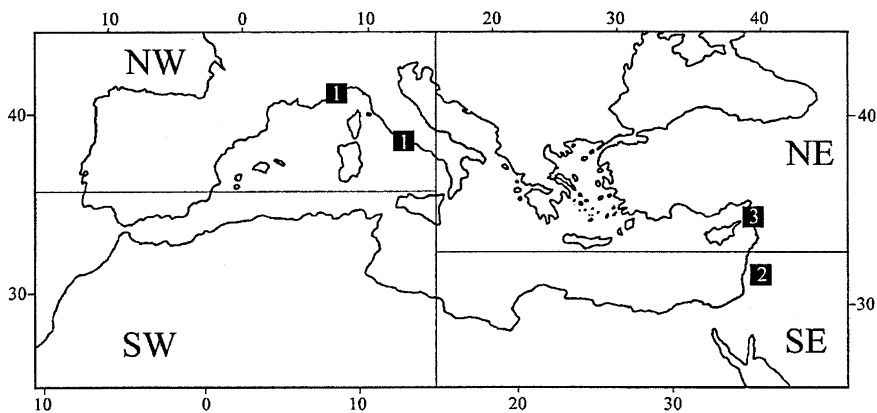
### TRENDS IN MEDITERRANEAN FAUNAL SERIES FROM ITALY, TURKEY, AND ISRAEL

The basic idea behind the BSR hypothesis remains a valuable one. The discrepancies between results on plant and animal exploitation actually stem from how zooarchaeologists have tended to categorize prey animals (Stiner *et al.*, 1999). 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 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 diet variation normally is examined strictly in terms of indexes of taxonomic richness (N-species or N-genera) and taxonomic evenness (proportionality in abundance) (Edwards, 1989; Grayson and Delpech, 1998; Neeley and Clark, 1993; Simek and Snyder, 1988). Such analyses employ either Kintigh's simulation-based technique (Kintigh, 1984) or a more long-standing regression approach (Grayson, 1984) that grew out of the work of Fisher, Corbet, and Williams (Fisher *et al.*, 1943) and others for problems of sampling in modern community ecology.

The main weakness of diversity approaches that rely on fine-grained Linnean taxonomic units is their insensitivity to 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

much 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 and the long-term price of heavy exploitation 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 armfull of shellfish, are quick and maneuverable. Humans, because of their generalist dietary tendencies (e.g., Kelly, 1995), will exploit a wider range of prey as the resident species diversity in ecosystems increases (e.g., lower latitude), which further increases the possibilities for prey type interchangeability.

Differing prey type classification systems greatly affect archaeologists' perceptions of change in prehistoric diet breadth, and those bound most strictly 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  $1 / \sum (\rho_i)^2$ , where  $\rho$  represents the proportion of each prey type for array  $i$  in an assemblage (Levins, 1968; Simpson, 1949). The Mediterranean faunal series include a total of 32 assemblages from shelter sites in an inland valley of northern Israel (200–11 KYA) (Kuhn *et al.*, 1998; Munro, 2001; Stiner *et al.*, 2000), the western coast of Italy (110–9 KYA) (Stiner, 1994), and the south-central coast of Turkey (41–17 KYA) (Kuhn *et al.*, 1999) (Fig. 2). In the first analysis, diversity is examined on a single taxonomic plane—counts by genus (raw genus-specific counts are



**Fig. 2.** Geographic origins of the three Mediterranean faunal series, spanning three of four biogeographic quadrants of the Mediterranean Basin (following Blondel and Aronson, 1999): (1) western coast of Italy, with 16 assemblages; (2) Wadi Meged, inland Galilee of Israel, with 9 assemblages; (3) Hatay coast of south-central Turkey, with 7 assemblages.

provided in Appendices A–C). In subsequent treatments of the same data set, the prey categories will be manipulated, moving from one rooted strictly in biological systematics to categories progressively defined by independent energetic criteria, such as prey body size and, among small-bodied prey, predator avoidance strategies and speed.

### The Study Sample

Cultural affiliations and assemblage chronologies are summarized in Table I. 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 together span 200,000–10,000 years before present. Geographic context and site type are held generally constant in each series; the comparisons are confined to assemblages from limestone caves and rock shelters, places to which food would have been brought by foragers, and where the chances of skeletal preservation are high due to protection from the elements and favorable sediment chemistry. Other advantages of the samples are the uniformly high quality of recovery and site documentation. Systematic fine-screening was practiced in all cases, and damage to the faunal remains, such as burning, breakage patterns, and tool and percussion marks, along with near or total absence of damage from nonhuman predators, demonstrate that the small animals were consumed by Paleolithic humans, and not introduced into the shelters by other agencies (see Kuhn and Stiner, 1998; Stiner, 1994, 1999, in press; Stiner *et al.*, 2001; Stiner and Tchernov, 1998). Material of unclear origin, or representing mixed cultural entities, has been removed from consideration. Some of the data from Israel and Turkey are preliminary in the sense that they come from ongoing projects, but they are representative for our purposes.

Time-averaging effects are a concern for analyses of faunal series in a single site, since evidence of trends is being sought. The faunal series from Italy and Turkey benefit from the presence of sterile or semisterile layers separating major cultural horizons, such that sorting reliable components from those that may not be is relatively straightforward (for Italian series, see Kuhn and Stiner, 1992, 1998; Stiner, 1994, 1999). The data from Üçağızlı Cave, Turkey are part of a new project and as yet only partly published. However, there is clear stratigraphic separation of most of the cultural components by sterile red clays (Kuhn *et al.*, 2001). Hayonim Cave in Israel poses greater challenges on the question of time-averaging, because, while the major stratigraphic divisions in Hayonim Cave (Layers B, C, D, E, and F) and Meged Rockshelter are relatively clear, the very thick Layer E is subdivided on the basis of more subtle variation, not simply in terms of sediment characteristics, but also from variation in the vertical distributions of stone artifacts. One cannot claim that the Middle Paleolithic units represent discrete events, but we are certain that they represent a coherent



**Table 1.** Indexed Data for the Proportions of Animal Prey in Mediterranean Paleolithic Diets 10–200 KYA

Assemblage	Culture	KYA	Count	N-genera	Indexed genera	Indexed size and defense	Indexed small game defense	Percentage of ungulates <sup>a</sup>	Percentage of slow small game <sup>a</sup>
Italy									
R. Mochi A	EP	10	901	13	2.74	1.24	1.02	11	99
G. Polesini <sup>b</sup>	EP	10	—	—	—	—	1.95	97	0
G. Palidoro <sup>b</sup>	EP	15	—	—	—	—	1.39	99	0
R. Mochi C	EP	18	1860	24	6.45	2.36	2.49	43	14
R. Mochi D	UP	26	1549	23	5.58	1.94	2.74	67	19
R. Mochi F	UP	32	691	23	6.52	2.34	1.65	46	76
R. Mochi G	UP	35	860	22	5.27	2.16	1.85	32	71
G. Breuil 3/4	MP	36	351	10	3.01	1.00	—	100	—
G. Breuil br	MP	37	290	7	3.02	1.01	—	99	—
R. Mochi I	MP	38	335	9	4.49	1.02	—	99	—
G. St'Agostino 0	MP	40	771	10	5.34	1.07	—	96	—
G. St'Agostino 1	MP	44	771	10	5.06	1.05	—	97	—
G. St'Agostino 2	MP	50	355	10	3.72	1.03	—	98	—
G. St'Agostino 3	MP	55	164	9	4.09	1.05	—	98	—
G. Moscerini 1-2	MP	70	193	15	2.08	1.61	—	21	—
G. Moscerini 3	MP	80	471	16	3.23	1.65	—	73	—
G. Moscerini 4	MP	95	185	13	2.17	1.37	1.02	84	99
G. Moscerini 6	MP	110	276	14	3.33	1.66	—	73	—
Israel									
Hayonim B	EP	12	6010	19	4.22	2.91	2.75	27	44
Hayonim C	EP	15	2022	16	3.05	1.68	1.58	73	78
Meged Shelter	EP	18	1063	12	2.68	2.19	2.04	51	65
Meged Shelter	UP	21	334	10	2.69	2.01	1.60	60	77
Hayonim D	UP	27	9123	15	2.06	1.41	2.09	83	60
Hayonim E.1	MP	70	63	6	3.36	1.44	—	82	—
Hayonim E.2	MP	150	809	15	3.43	2.08	1.25	50	89
Hayonim E.3	MP	170	4214	14	2.81	1.98	1.06	38	97
Hayonim E.4	MP	200	3385	11	2.03	1.75	1.04	31	98
Turkey									
Üçagizli Epi	EP	17	321	9	5.79	2.91	2.55	25	52
Üçagizli B	UP	28	795	11	3.33	2.20	1.20	41	91
Üçagizli B1-4	UP	31	1247	11	3.33	2.22	1.20	42	91
Üçagizli C-D	UP	32–33	40	7	4.33	1.34	—	85	—
Üçagizli E-E2	UP	33–35	176	9	4.14	1.08	—	97	—
Üçagizli F-F2	UP	36–38	146	9	4.13	1.11	—	96	—
Üçagizli G-I	UP	>41	265	9	3.60	1.04	—	98	—

Note. (MP) Middle, (UP) Upper, and (EP) Epi-Paleolithic. Reciprocal of Simpson's index ranges are 1–20 for Linnean categories; 1–3 for size and defense criteria of second and third indexes. Order is substituted for genus for birds, an exceptionally diverse group.

<sup>a</sup>Calculations (for Fig. 6) differ from those used for genus-level diversity analyses by including specimens identified to avian and mammalian body size classes as well as genus-specific counts; the percentage of ungulates is calculated relative to the total faunal assemblage; the percentage of slow small game animals is calculated within the total small game subset only.

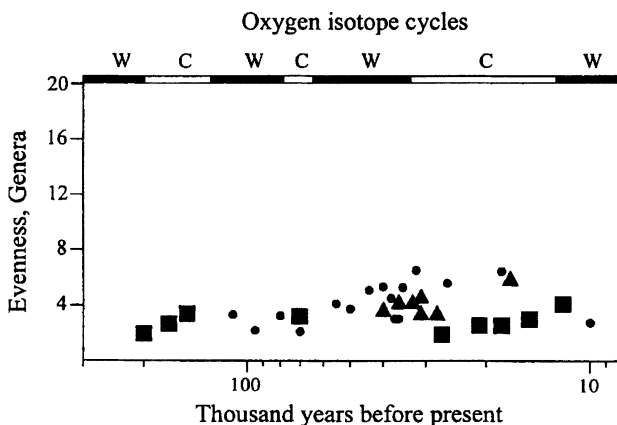
<sup>b</sup>Two inland EP sites added as qualification to anomalous case of Mochi A.

time series suitable for studies of long-term trends, based on minimal downward infiltration of time-diagnostic artifacts (Stiner *et al.*, 2001). Subdivisions of the Mousterian layer are essential for ensuring comparability to faunas from later Paleolithic periods.

The preferred counting unit is the number of identified specimens (NISP), in this case confined to specimens that could be identified to genus or finer taxonomic distinctions, because this counting unit is least subject to aggregation error. All of the sites considered are shelters. Small animals tend to be carried to these places in whole form, but ungulates are often sectioned prior to transport and some parts left behind (e.g., Stiner, 1994). Under these conditions, NISP is a closer (if still very crude) approximation of differential food volumes that arrive at a site than MNI, as long as fragment size variation is taken into account. In this data set, fragment size increases with prey body size but the gradation in fragmentation is similar among assemblages (e.g., Stiner, 1994; Stiner and Tchernov, 1998), and prehistoric humans' emphasis on large and small prey involved no apparent trends (see below), justifying the application of NISP here (see Grayson, 1984, for a full discussion of the advantages of NISP). MNI is a derived measure that embodies many more assumptions that can be wrong. On the other hand, MNI will be used in the case of 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).

### Evenness Based on Counts by Genus

Application of the Reciprocal of Simpson's Index to assemblages which potentially contain about 20 genera (Fig. 3) yields consistently low levels of evenness



**Fig. 3.** 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 (Shackleton and Opdyke, 1973) are expressed on a logged scale; (c) cold stage, (w) warm stage (from Stiner, 2001).

**Table II.** Summary of Life History, Predator Avoidance Characteristics, and Capture Requirements of the Common Prey in the Mediterranean Archaeofaunal Series

Prey name	Size class	Habitat	Predator defense mechanisms	Capture requirements	Population productivity <sup>a</sup>
Ungulates	Large	Terrestrial	Rapid running; freezing or charging	Hunt/trap	Low
Tortoises	Small	Terrestrial	Freezing, hiding, armor	Gather (S)	Low
Legless lizards	Small	Terrestrial	Hiding, armor	Gather (S)	Low
Ostrich eggs	Small	Terrestrial	Adult protection (periodic)	Gather (S)	Low
Shellfish	Small	Littoral	Safety in groups, armor, some cryptic	Gather (S)	Variable
Game birds	Small	Variable	Hiding, bolting, and rapid flight	Hunt/trap (Q)	High
Lagomorphs	Small	Terrestrial	Hiding, bolting, and rapid running	Hunt/trap (Q)	High

<sup>a</sup>Productivity classifications follow Stiner *et al.* (2001) and imply a prey population's relative resilience to heavy serial predation. Small game are (Q) quick or (S) slow.

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  $r = .386$ ,  $r^2 = .15$ ,  $p = .05$ ,  $n = 32$ ), and there is no correspondence to the 6–7 climatic oscillations indicated by oxygen isotope data from deep sea cores (e.g., Shackleton and Opdyke, 1973). While sample size varies among the assemblages (Table I), this fact does not explain the pattern in Fig. 3. No support for the BSR hypothesis is found 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 Based on Counts by Prey Size and Defense Characteristics

Regrouping the data into three categories based on a simplified combination of prey size and defense traits (Table II, big & small, and slow & quick among small types) reveals much temporal variation (Fig. 4) but no single overarching trend ( $r = .035$ ,  $r^2 = .001$ ,  $p = 1$ ,  $n = 32$ ). The Turkish series trends toward greater dietary evenness from beginning to end, but perhaps only by virtue of its brevity. One might expect cyclical rather than unidirectional change over the last 200 KY if climate were the principal cause of variation in faunal assemblage contents. Warm climate stages may increase evenness in human diets independent of adaptation changes by favoring the expansion of small animal species in communities (reviewed by Pianka, 1978). However, Fig. 4 indicates both insensitivity to climate cycles in the Mediterranean series and a tendency for minor increases in diet breadth after 50–40 KYA. A shortage of data from 80–50 KYA from Israel, which lies at the lowest latitude in the study sample, is not necessarily to blame, since the exploitation of slow, collectable small game appears to have continued through the late Middle Paleolithic in the Levant (Speth and Tchernov, 2002). Combining body size and defense traits in categorizing prey yields a provocative pattern, certainly more

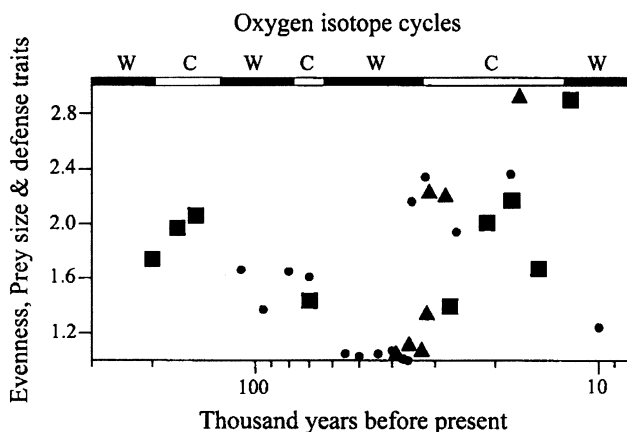


Fig. 4. Evenness in the representation of three prey categories based on body size and defense mechanisms (large game, small slow game, and small quick game), using the Reciprocal of Simpson's Index (3 = most even). Symbols as in Fig. 3.

exciting than Fig. 3, but it also appears to conflate more than one phenomenon and thus the data require further unpacking.

#### 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 (Table I, two columns are far right), however, with no trend except for a sharp increase at the close of certain Paleolithic sequences (Davis *et al.*, 1994; Munro, 1999). The spectrum of animal taxa eaten by Paleolithic peoples in the Mediterranean Basin did not vary much (Stiner, 1994; Tchernov, 1994), and included tortoises, marine shellfish, large legless lizards, ostrich eggs, game birds such as partridges, hares, and rabbits, in addition to ungulates such as deer, gazelles, and wild cattle. 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 series (Fig. 5) reveals a clear trend toward more even dependence on high-ranked and low-ranked small prey (see Table II), confirmation of expanding dietary breadth during the later part

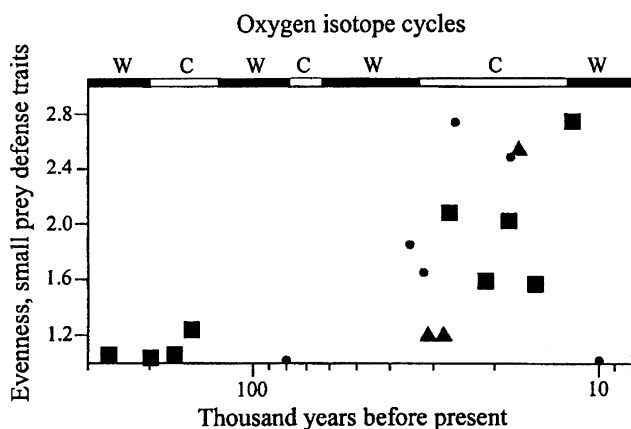
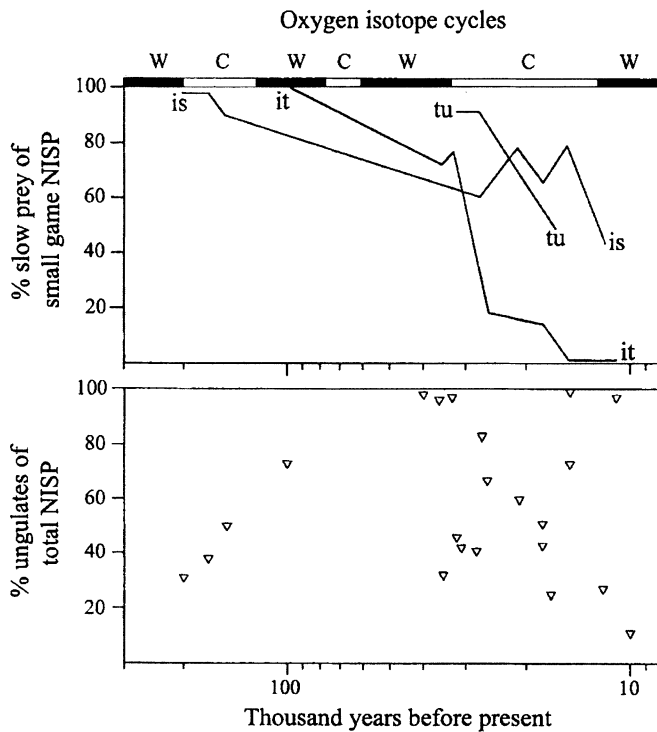


Fig. 5. Evenness among three prey categories within the small game fraction only, based on prey defense mechanisms (slow game, quick running terrestrial mammals, and quick flying birds), using the Reciprocal of Simpson's Index (3 = most even). Symbols as in Fig. 2 (from Stiner, 2001).

of the Mediterranean Paleolithic. This regrouping of the data distinguishes only between slow-moving, easily collected types (tortoises & 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 (Table I), 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 ( $r = .606$ ,  $r^2 = .37$ ,  $p = .01$ ,  $n = 18$ ). It also shows that most of the expansion took place during a cold climate stage (OIS 2). This 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 indicates a categorical or step-wise change in how humans interacted with small animal populations after about 40–50 KY, but surprisingly little change in how humans interacted with populations of large mammals.

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 pretty 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 nontaxonomic criterion for ranking the potential returns of prey, but it too has its limits because of the additional complications of capture costs (e.g., Jochim, 1976) and, in some cases, also 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 Fig. 6 (Table I), is largely trendless ( $r = .276$ ,  $p = 1$ ,  $n = 18$ ). By contrast, the proportion of slow animals within the small game fraction of each assemblage clearly declines with time ( $r = .572$ ,  $.02 > p > .01$ ,  $n = 18$ ), 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).



**Fig. 6.** (a) Trends by region (lines) in the percentage of slow small prey within the small game fraction of each assemblage in (is) Israel, (it) Italy, and (tu) Turkey; (b) the percentage of ungulate remains (inverted triangle) in the total count of each assemblage (from Stiner, 2001).

## THE HEURISTIC VALUE OF SMALL GAME DATA

It seems unlikely that all faunal series to be examined in the future will adhere to the patterns found in the three Mediterranean series. Animal communities vary in their composition, as do the choices of prey species available to foragers. On the other hand, the Mediterranean Basin constitutes a major part of the total geographic range of Paleolithic humans. Forming the intersection of three continents, it is a textbook case of exceptional diversity in animals and plants, a quality that has changed little over the course of the Pleistocene if compared to the rest of Europe and much of Asia (e.g., Blondel and Aronson, 1999). The Mediterranean Basin thus should be an ideal laboratory for testing ideas about dietary expansion in human evolution, with more small species to choose from and high inherent potential to express shifting predator–prey dynamics from small game data.

Experimenting with prey type categories, albeit with attention to independently documented characteristics of the subject species, allows the evidence for increased diet breadth during the later Paleolithic of the Mediterranean region to spring into focus. 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; for related applications, see Broughton, 1994; Clark and Straus, 1983; Klein and Cruz-Urbe, 1983). 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—like fume-sensitive canaries carried into coal shafts by nineteenth century miners.

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 overharvesting 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 they certainly would have been aware of declining availability of prey and thus declining returns for the same level of foraging effort.

Because tortoises and shellfish grow throughout much of their life span, overharvesting also causes *diminution* or a reduction in the mean size of individuals subsequently available to foragers. Humans’ strong preference for the largest individuals exerts exceptionally harsh impacts on the size and sex structures of tortoise

and certain shellfish populations (Blasco *et al.*, 1986–87; Dye *et al.*, 1994). Interestingly, slow-growing, slow-moving tortoises, and marine mollusks dominate the small game fractions of the Mediterranean Middle Paleolithic record, constituting up to half of all identified specimens in several of the assemblages (Stiner *et al.*, 2000). What is more, the individuals taken by Middle Paleolithic foragers were larger on average than those collected by later Paleolithic foragers. Body size diminution occurred quite early for tortoises in Israel ( $\geq 44$  KYA), by the late Middle Paleolithic or earliest Upper Paleolithic, and was sustained over multiple climate cycles thereafter. Limpet diminution began by 23 KYA in Italy (Stiner *et al.*, 1999), but considerably later to the west in Spain (Clark and Straus, 1983). The timing and duration of the diminution effects are largely independent of global climate trends—the other potential cause of diminution—and thus point to a human cause (Stiner *et al.*, 1999). Klein and Cruz-Urbe (1983) note a similar phenomenon for angulate tortoises in South Africa around the time of the Middle–Late Stone Age boundary.

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 & rabbits). These quick small animals mature in  $\leq 1$  year, and their populations rebound easily from heavy hunting by humans. Predator–prey simulation modeling indicates 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. Thus greater dependence on slow-growing animals during the Middle Paleolithic, and on larger individuals on average, implies that these early human 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.

Contrary to the results of interim studies, the data on small game use in southern Europe and western Asia during the late Pleistocene supports Flannery’s “Broad Spectrum Revolution” hypothesis of expanding dietary breadth in response to demographic packing. However, clear indications of more even dependence on high- and low-ranked prey were obtained only when small animals are classified according to development rates and predator escape strategies, rather than by counting species or genera, or simply organizing prey taxa along a body size gradient.

The findings for the three Mediterranean faunal series present an interesting twist to Flannery’s original predictions with respect to the timing of the Broad Spectrum Revolution. While it does seem that the BSR began in the eastern end of this vast region, earliest evidence of dietary expansion and demographic pulses associate with the spread of Upper Paleolithic cultures from Asia into Europe, the same general path as the spread of Neolithic adaptations after 10 KYA (Ammerman



and Cavalli-Sforza, 1984; Reich and Goldstein, 1998). The dietary shifts identified by Binford and Flannery between 12 and 8 KYA were merely the last in a longer series of economic changes. That these changes began earlier in the eastern Mediterranean Basin than at its northern and western ends reinforces the likelihood that prehistoric human populations were largest in the semiarid subtropical to tropical latitudes of Asia and Africa (Harpending and Bertram, 1975; Keeley, 1988). Demographic pulses emanated from southwestern Asia into Europe several times. The surge in bird exploitation and tortoise diminution are the earliest symptoms of Upper Paleolithic demographic expansion. Lagomorph exploitation seems to be more diagnostic of the later stages of this process and involves a wide range of environments including Iberia, northern and eastern Europe, and even North Africa (reviewed in Kuhn and Stiner, 2001; see also Hockett and Bicho, 2000; Jochim, 1998, among others). Middle Paleolithic people rarely hunted lagomorphs in the ecosystems where other predators, such as denning wolves, frequently did (Stiner, 1994); Upper Paleolithic people exploited lagomorphs in modest quantities, but Epipaleolithic and Mesolithic people hunted them most of all (but see Hockett and Bicho, 2000, on Portugal).

#### **INFERRING SITE OCCUPATION INTENSITY FROM PREDATOR-PREY INTERACTIONS: THE CASE OF THE NATUFIAN**

The relative abundance of small game is shown to be an effective indicator of human demography on a grand temporal scale. This concept can also be used to monitor spatial variation in human demography over much shorter time periods. In particular, the relative abundance of small prey types provides a way to gauge site occupation intensity, a phenomenon of great significance for later archaeological periods that has been difficult to measure, even in relative terms.

Sedentism refers to the settling down of human populations into permanent or semipermanent residential camps (Hitchcock, 1987; Kelly, 1995). The term "site occupation intensity" here refers to the number of human hours an archaeological site was occupied per unit time. The intensity of site occupation is a combined function of the length of stay, the frequency of visits, and the size of the resident population at a site per unit time. As any or all of these factors increase, the intensity of human hunting and the associated impact of a site's inhabitants on local animal (and plant) resources must also increase. Much archaeological research has focused on the permanence of human settlements and whether occupation was year-round or only seasonal. However, most scholars have used presence/absence indicators to suggest long-term investment in habitation sites. While data derived from biological sources, including commensal animals and seasonal indicators, are generally preferred (Bar-Yosef and Belfer-Cohen, 1989, 1991; Belfer-Cohen and Bar-Yosef, 2000), architecture, artwork, the thickness of site deposits, and the relative density of artifacts also figure prominently in archaeologists' inferences

of site occupation intensity. Though suggestive, the results of these studies remain inconclusive, since none of these indicators proves year-round occupation or distinguishes effectively between degrees of site occupation intensity. But the intensity of site occupation must have a direct impact on the availability of local resources, and in turn, on the foraging decisions of the site's inhabitants (Broughton, 1997; Kelly, 1995; Szuter and Bayham, 1989). Methods based on relative prey abundance therefore provide an alternative way to study site occupation intensity.

According to dietary breadth models from optimal foraging theory, humans, like other animals, are expected to maximize the rate of energy acquisition while foraging (e.g., Kelly, 1995; Stephens and Krebs, 1986; Winterhalder, 1986), and should thus select resources that provide the largest quantity of energy per hunting episode (i.e., large prey such as ungulates; or those with low capture costs such as tortoises). Short-term, ephemeral human occupations have smaller requirements for animal resources and are less likely to deplete high-ranked animal populations. The occupants should be able to meet their demands with high-ranked prey, which will then be deposited in the archaeological record. As human demands increase per unit time, hunting will intensify, and humans will eventually cross a threshold beyond which the most attractive resources are no longer encountered at adequate rates to meet energy requirements. Sustained pressure on resources may also lead to the depression of local plant and animal communities (e.g., Blondel and Aronson, 1999; Broughton, 1994, 1997; Speth and Scott, 1989; Tchernov, 1993). Humans must therefore respond to human-induced disturbances in resource distribution and abundance. An effective solution is to expand dietary breadth to include less cost-effective (low-ranked) resources (Colson, 1979; Kelly, 1995; Minnis, 1985; Stephens and Krebs, 1986). In the Mediterranean Basin, and prior to the development of energy-saving equipment, such animals included fast-moving birds and hares, notorious for their high productivity and their ability to withstand intensive harvesting (Stiner *et al.*, 2000).

The archaeological expectation is that substantial increases in site occupation intensity will ultimately alter the ratio of high- and low-ranked small species captured by humans and deposited in the archaeological record of that locality. The small game taxa of interest here have small territories, thrive at high densities in the absence of predator pressure, and are likely to be captured close to camp because they provide limited caloric returns and may be unworthy of search and transport over long distances. The relative abundance of small game taxa thus provide good indicators of local hunting intensity. Low-intensity occupations should create assemblages with higher proportions of high-ranked small prey taxa. Thus the relative abundance of small prey species that both reproduce and move slowly (tortoises & other reptiles in the Levant) versus those that reproduce and move quickly (hares & partridges)—a small game index—provides a simple yet elegant gauge of change in site use intensity. Specifically, this index pits the absolute abundance (NISP) of slow-moving tortoises against that of fast-moving partridges and hares (slow small prey/[fast + slow small species]) on a scale of 0 to 1. Under conditions

of low site occupation intensity, the index value should be closer to one. The value will decrease as the intensity of site occupation increases—whether because of prolonged stays, increased population size, or a combination of the two—as hunters incorporate more low-ranked, fast-moving species into their foraging repertoire.

The small game index cannot be used to compute the number of consecutive days or the number of people that occupied an archaeological site. However, it does have the power to trace the relative intensity of land use across space and time in a more general way, in this case from site to site and among phases of a short culture period. This approach lends a more quantitative dimension to current conceptions of sedentism and population pressure, allowing us to move beyond ambiguous interpretations of presence/absence data and view human demographics on local and regional scales.

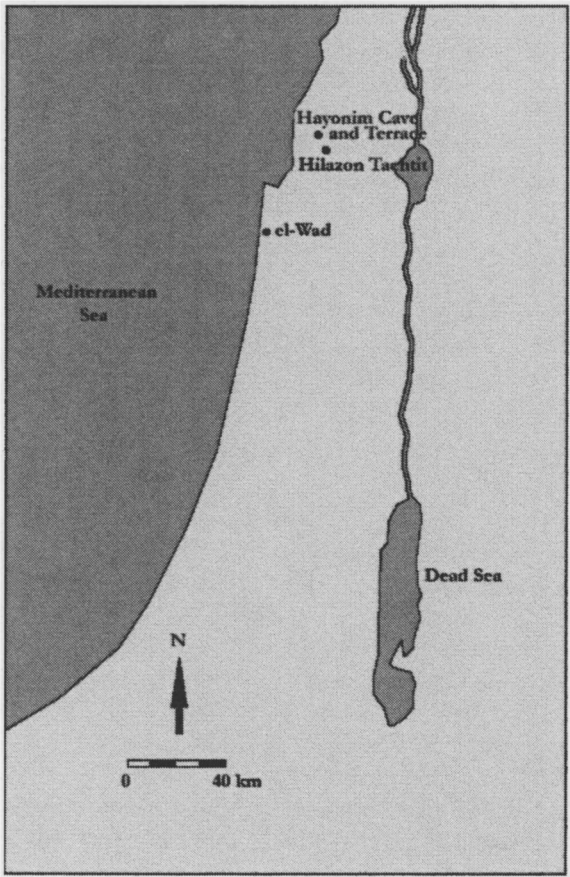
### **The Natufian Culture in the Levant**

In the southern Levant, the Natufian period (ca. 12,800–10,200 B.P.) immediately preceded the appearance of agriculture. Many claims for the earliest sedentism have been attributed to large Natufian sites located in the Mediterranean hill zone (Bar-Yosef and Belfer-Cohen, 1989, 1991; Belfer-Cohen and Bar-Yosef, 2000; Davis, 1983; Edwards, 1989; Kaufman, 1992; Lieberman, 1991, 1993; Rosenberg, 1998; Tchernov, 1984, 1991, 1993). Thus it is the Mediterranean zone, with its abundant archaeofaunas, that provides the best opportunity to apply new approaches to the question of early changes in site occupation intensity (Munro, 1999, 2001). The presence of large habitation sites with thick cultural deposits and rich material remains, including architecture, ornaments, art, commensal animals, and conspicuous human cemeteries, sets the Natufian culture of the Mediterranean zone apart from all preceding Paleolithic cultures and, to a large extent, from all other hunter-gatherers in the surrounding regions (Bar-Yosef and Belfer-Cohen, 1991; Henry, 1989; Tchernov, 1991). Because the large Natufian “base camps” of the western Mediterranean hills (Bar-Yosef, 1970) form the basis for arguments of early sedentism and population pressure in the Natufian period, they naturally are the focus here.

This case study begins with the Natufian layer from Hayonim Cave, a multi-component site excavated under the direction of Bar-Yosef and colleagues in the western Galilee, Israel (Bar-Yosef, 1991; Belfer-Cohen, 1988). Hayonim Cave is especially appropriate for small-scale diachronic comparisons, because the thick Natufian Layer B preserves good spatial and temporal resolution. Sublayers dating to both the Early (ca. 12,800–11,000 B.P.) and Late (ca. 11,000–10,200 B.P.) phases are present (Table III), and the total number of faunal specimens is large (NISP ca. 15,000). Archaeofaunal assemblages from three additional Natufian sites—el-Wad Cave, Hayonim Terrace, and Hilazon Tachtit (Fig. 7, Table III)—are examined next

**Table III.** Natufian Sites and the Cultural Phase and Approximate Time Range Analyzed From Each Site

Site	Cultural phase	Approx. time range uncal. B.P.
el-Wad Cave: Chamber III	Early Natufian	12,800–11,000
Hayonim Cave: Phases I–III	Early Natufian	12,800–11,000
Hayonim Cave: Phases IV–V	Late Natufian	11,000–10,200
Hayonim Terrace: Niveau II	Late Natufian	11,000–10,200
Hilazon Tachtit	Late Natufian	11,000–10,200



**Fig. 7.** The southern Levant and locations of sites in the Natufian study sample.

to provide a regional cross-section of Natufian subsistence and settlement strategies in the Mediterranean hills. Hayonim Terrace is a Natufian base camp located just outside the mouth of Hayonim Cave. Although the precise stratigraphic relationship between the two sites was never fully established, it is likely that occupation of the two areas at least partially overlapped in time, but only the assemblage from Hayonim Cave contains Early and Late phases (Bar-Yosef, 1991; Belfer-Cohen, 1988; Valla *et al.*, 1989, 1991), whereas the Hayonim Terrace sample studied here dates mainly to the Late phase (Valla *et al.*, 1989, 1991). The sample from Hayonim Terrace is quite large (NISP ca. 10,000) and was recovered entirely from Niveau (Level) II of the main trench by Valla. El-Wad is a large cave on Mount Carmel and was occupied throughout the Natufian, although the study sample examined here derives solely from an Early Natufian deposit in Chamber III, excavated as part of a salvage effort by Weinstein-Evron in the late 1980s (Weinstein-Evron, 1998). The majority of the el-Wad sample was analyzed by Rabinovich (1998); the results presented include the NISP counts for ungulates and carnivores from her report, as well as counts made by Munro of the birds, fish, and tortoises (total NISP ca. 2600). Finally, Hilazon Tachtit is a small Natufian cave site located approximately 7 km southeast of Hayonim Cave that was occupied only at the end of the Late Natufian (Grosman, in preparation). This faunal sample (NISP ca. 2000) derives from the first three seasons of excavation (1995, 1997 & 2000) directed by Grosman. While evidence from four sites is insufficient to build a complete picture of Natufian settlement and subsistence, the data reveal pronounced trends in site occupation intensity and shifts in regional human population density within the Natufian period.

### **Intrasite Comparison of Five Natufian Phases in Hayonim Cave**

Hayonim Cave is the only site in the sample that preserves the level of resolution required to investigate diachronic change within the Natufian period at a single location (see Bar-Yosef, 1991 and Belfer-Cohen, 1988, for phase divisions). Fig. 8 shows the relative proportions (percentages) of ungulates, carnivores, and small game for the Early (Phases I–III) and Late (Phases IV and V) Natufian occupations at Hayonim Cave (also see Table IV). The consistency in the relative proportions of the three major animal groups—ungulates, carnivores, and small game animals—through time is remarkable, indicating stability in this aspect of resource use for about 2500 years. It is significant that the small game fraction consistently outnumbers the large game component, a categorical increase in small game use for the Natufian period relative to most earlier cultural periods (see also Bar-El and Tchernov, 2001; Davis *et al.*, 1994; Tchernov, 1993).

At first glance the faunal samples from Hayonim Cave appear “typically Natufian,” with the usual array of species. However, temporal patterns in the Hayonim Cave fauna are anything but static. Figure 9 indicates substantial change

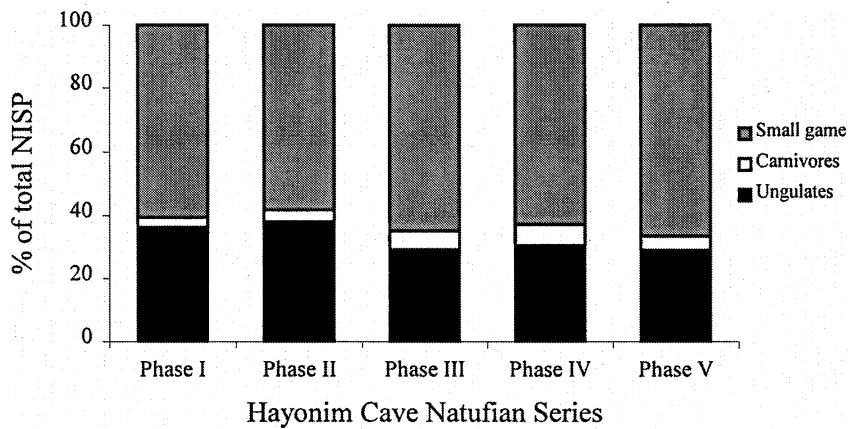


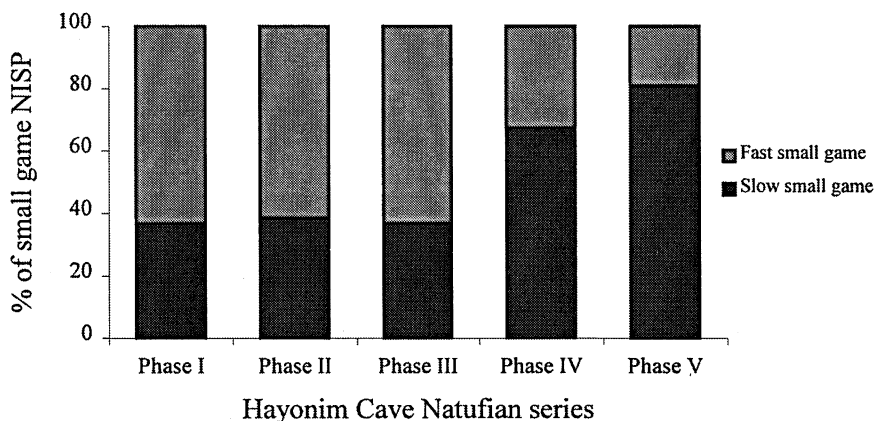
Fig. 8. Relative abundance of major prey groups during five phases of Natufian occupation at Hayonim Cave, ordered from oldest to most recent. The Early Natufian is represented by Phases I–III, Late Natufian by Phases IV and V.

in the small game index—the relative balance between the three types of small game animals defined in the sections above—across the five phases of occupation (also see Table IV). Thus, while the total contribution of small game to the Natufian diet remains consistent across the five phases (Fig. 8), the relative proportion of fast to slow-moving small prey animals in the assemblage shifts dramatically: Phases I–III (Early Natufian) consistently show higher proportions of fast to slow small prey. During Phase IV, at the beginning of the Late Natufian, a reversal occurs, with the slow-moving types increasing markedly such that they exceed the proportions of fast game. The trend continues through Phase V, and slow prey (e.g., tortoises) constitute much of the total small game fraction (81%).

Table IV. NISP of Broad Taxonomic Groups and Small Game Types From the Hayonim Cave Natufian

NISP	Phase I	Phase II	Phase III	Phase IV	Phase V	Total
Ungulates	884	839	588	1047	598	3956
Carnivores	74	80	117	227	89	587
Small game	1472	1283	1300	2151	1361	7567
Total	2430	2202	2005	3425	2048	12110
Small game NISP						
Slow small game	540	493	477	1443	1099	4052
Fast small game	925	785	815	702	260	3487
Total	1465	1278	1292	2145	1359	7539

Note. Phases I–III are Early Natufian; Phases IV–V Late Natufian. Slow small game animals are tortoises only; fast small game are birds and small mammals, including Phasinidae, Falconiformes, waterfowl, and hares.



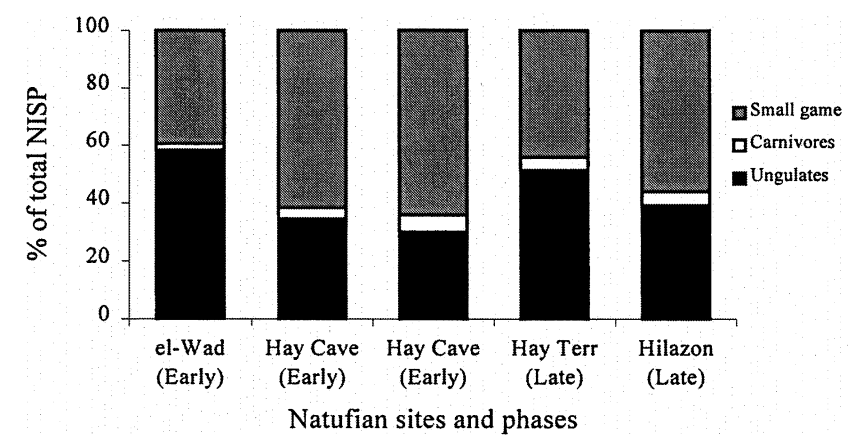
**Fig. 9.** Relative abundance of small game types during five phases of Natufian occupation at Hayonim Cave, ordered from oldest to most recent. The Early Natufian is represented by Phases I–III, Late Natufian by Phases IV and V. Slow small game include tortoises only; fast small game are birds and small mammals including Phasinidae, Falconiformes, waterfowl, and hares.

This pattern is upheld across the many time-ordered Natufian features in Hayonim Cave, confirming that the trends described for the small game fraction at this large site are robust. Quick-moving small game animals were especially abundant in human diets during the Early and most intensive phase of occupation of the cave, but these resources were largely ignored in favor of slow small game during the Late Natufian (Phases IV–V) to an extent not unlike what has been observed for the preceding Kebaran period (ca. 20,000–16,000 B.P.; Stiner *et al.*, 2000).

### Intersite Comparison of Four Natufian Sites in the Mediterranean Zone

Collapsing the samples from Hayonim Cave into two groups corresponding to the Early (Phase I–III) and Late (Phase IV–V) Natufian phases, these data can now be compared to the time-ordered assemblages from el-Wad Cave, Hayonim Terrace, and Hilazon Tachtit. Figure 10 compares the relative proportions of the major animal prey groups at each site (also see Table V). The results indicate some variation, more than was seen among phases at Hayonim Cave, but there is no trend in the relative abundance of ungulates and small game among the sites. All of the sites display very high proportions of small game, which comprise 40–60% of the assemblages. This is a distinctly Natufian phenomenon, usually exceeding the proportions of small game from earlier Paleolithic cultures in the Levant (but see Middle Paleolithic data in Table I).

Much of the taxonomic diversity in Natufian faunas is found at the small-bodied end of the prey spectrum. This is also where the greatest differences occur in the types of animals exploited (Fig. 11, Table V). The Early Natufian assemblages



**Fig. 10.** Relative abundance of three major prey groups from five early and late Natufian occupations in the western Galilee of northern Israel: el-Wad, Hayonim Cave, Hayonim Terrace, and Hilazon Tachtit.

(el-Wad & Phases I–III of Hayonim Cave) are richest in quick-moving, low-ranked small prey. This relation reverses in the Late Natufian assemblages (Phases IV–V of Hayonim Cave, Hayonim Terrace & Hilazon Tachtit), when high-ranked types resurge to a level seen for the Kebaran period.

**Changes in Site Occupation Intensity During the Natufian**

The relative proportions of prey types from Natufian sites, and specifically within the Natufian sequence of Hayonim Cave, show an unambiguous trend in small game use. The high proportions of fast-moving small game animals in the Early Natufian deposits from Hayonim Cave and el-Wad indicate that foragers’

**Table V.** NISP of Broad Taxonomic Groups and Small Game Types From Natufian Sites

NISP	El-Wad (early)	Hay Cave (early)	Hay Cave (late)	Hay Terrace (late)	Hilazon (late)
Ungulates	1538	2311	1645	4983	695
Carnivores	57	271	316	430	86
Small game	1043	4055	3512	4307	996
Total	2638	6637	5473	9720	1777
NISP small Game					
Slow small game	247	1510	2542	3483	848
Fast small game	784	2525	962	814	140
Total	1031	4035	3504	4297	988

*Note.* Slow small game includes tortoises only; fast small game animals are birds and small mammals, including Phasinidae, Falconiformes, waterfowl, and hares.



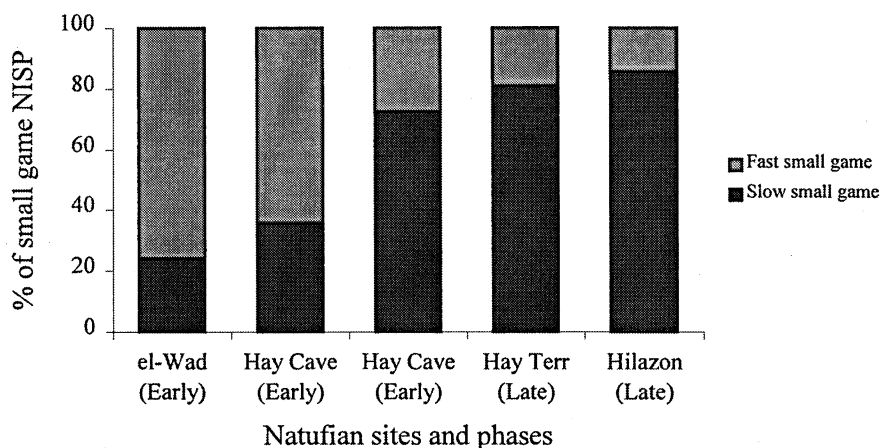


Fig. 11. Relative abundance of small game types from five early and late Natufian occupations in the western Galilee of northern Israel: el-Wad, Hayonim Cave, Hayonim Terrace, and Hilazon Tachtit. Slow small game include tortoises only; fast small game are birds and small mammals including Phasinidae, Falconiformes, waterfowl, and hares.

encounter rates with high-ranked prey types were locally insufficient to meet human demands. More low-ranked hares and partridges were incorporated into human diets as a consequence. Hunters continued to capture tortoises at fairly high rates, as suggested by tortoise body size diminution throughout the Natufian, but increased demands for small game put yet more emphasis on alternative types, as well as on large-seeded plants. In effect, a negative feedback loop may have been provoked by the reduced availability of high-ranked prey, escalating the need for low-ranked ones. Because the latter types also reproduce more efficiently, human demands apparently did not exceed the enormous reproductive capacity of hares and partridges. After many more low-ranked species were added to Early Natufian diets, the foraging system restabilized.

By the Late Natufian, another shift in human foraging occurred. A return to heavy dependence on tortoises in the Late Natufian indicates that high-ranked resources that may have been depleted previously were able to recover. Pressure on tortoises did not change, based on diminution data, but it does appear that, in the Late Natufian, people could once again rely on relatively more high-ranked prey, not unlike the mobile Upper Paleolithic populations before them. Though the presence of hares and partridges attests to the Natufian's continued recognition of these animals as potential food sources, they did not invest as much in their capture in the later phases. This suggests that human demands for meat were reduced relative to its availability, and thus high-ranked game populations were sufficiently abundant to meet the requirements of the human population.

According to the expectations laid out above, trends in the relative abundance of small game in the Natufian sample, and on a smaller scale at Hayonim Cave, are argued to reflect a dramatic change in the intensity of site use from the Early to the Late Natufian. The largest encampments in the Mediterranean hills, or for that matter, at any time or place in the Natufian, are confined to the Early phases. The increased integration of low-ranked animals into the Early Natufian hunting repertoire shows that human groups required higher total energetic returns and thus exerted greater hunting pressure on the surrounding ecosystem than any previous occupants of the region.

Increased demands for animal resources and inferred increases in hunting pressure appear to be linked to greater numbers of occupants (in human hours) at the Early Natufian sites, basically an intensification in site use. Conditions changed dramatically in the Late Natufian, when sites became smaller again and humans exerted less hunting pressure on the local animal community. Game use in the Late Natufian implies a sharp reduction in the number of people occupying Hayonim Cave and other Late Natufian base camps per unit time, and probably the number of people in the Mediterranean Hills in general. Late Natufian sites were occupied more sporadically, most likely by smaller groups.

The beginning of the Late Natufian at 11 KYA corresponds to the onset of the Younger Dryas, a severe cooling and drying event (Bar-Matthews *et al.*, 1999; Baruch and Bottema, 1991; Frumkin *et al.*, 1999; Kudrass *et al.*, 1991; Overpeck *et al.*, 1989) that undoubtedly lowered the carrying capacity of the region and contributed to its depopulation. The Late Natufian population of the Mediterranean region adjusted successfully to reduced environmental productivity and near glacial conditions for the next 500–1000 years. Interestingly, experimentation with the reproductive cycle of cereal grains began in the Early Natufian period, presumably in response to continuous levels of resource pressure. Tough times in the Late Natufian merely scattered people, reducing population density and seems to represent a simple demographic response, rather than further changes in the nature of Natufian adaptations. The Natufians did not abandon their unique habits of manipulating cereals and other large-seeded plants, but there is no evidence for cultivation either. It was not until climate grew warmer and wetter ca. 10,000 years ago that cereal cultivation became feasible again in the Mediterranean Levant and the Neolithic adaptation emerged.

## CONCLUSION

Formal diet breadth models hold that resource ranking systems will vary with the type of consumer. Because game animals are composed of similar tissues, simple body size gradients are widely used for ranking taxa in zooarchaeological research on subsistence evolution, in conjunction with numbers of Linnean taxa. Oddly, neither approach exposes significant changes in diet breadth in the

Paleolithic sequence of Mediterranean Eurasia, despite radical transformations in other aspects of the archaeological record. The interplay of archaeological anomalies and wildlife data for disparate Mediterranean faunal series reveals that absolute differences in prey size were recalibrated from the foragers' point of view by the costs of capturing distinct sorts of small prey. It is striking that most of the shifts in predator-prey dynamics noted here concern small animals, not big ones. These insights into prehistoric diet breadth could not be had without careful control of other potential sources of variation in archaeofaunas, so that attributions to cause could be excluded systematically. One or the other of two key archaeological variables, space or time, serves as a loose constant in the analyses above.

Our 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) lifestyles, 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.

More than one ecologist has suggested that any factor that reduces seasonality from the environmental challenges that a foraging species must face can lead to substantial population increases (e.g., Blondel and Aronson, 1999). Perhaps one early shift in this regard occurred via use of a wider range of meat sources, some of which are a good deal more resilient in the face of heavy exploitation. Of course, by the later Upper Paleolithic and Epi-Paleolithic, food storage (plants in lower latitudes, also dried or smoked meat and rendered fat in other areas) was also part of the subsistence equation. The latter developments are quite familiar to archaeologists who work on these prehistoric cultures. But, returning to the first point, an interesting quality of warm-blooded small prey populations that rebound quickly is their greater reliability as a cross-season food source, if capture costs are reduced artificially with technology. Any forager population that can grow faster on lower value but more resilient foods will have a demographic advantage over competing populations. In the late Pleistocene this involved a subtle but significant drop in humans' position in the food chain of some arid, low latitude ecosystems, largely because greater plant use was also part of the BSR. Large-seeded plants

permit more direct access to primary production, despite higher collection and processing costs, and thus may support humans at higher population densities when and where mobility is no longer an option (Keeley, 1988; Harpending and Bertram, 1975). Small quick animals also present this possibility to a lesser extent, but to the same end and often complementary to the intensified use of plant seeds in the absence of domesticated ungulates worldwide.

APPENDIX A

Genus-Specific Counts<sup>a</sup> for Pleistocene Faunal Assemblages From the Inland Sites of Hayonim Cave and Meged Rockshelter (Wadi Meged, Galilee, Israel), Spanning 200,000–10,000 years B.P.

Taxonomy	Hay B	Hay C	Meged Keb	Meged pre-Keb	Hay D	Hay E.1	Hay E.2	Hay E.3	Hay E.4
Large game									
<i>Gazella</i>	1483	1039	451	160	6253	30	185	721	674
<i>Capreolus</i>	5	16	1	—	77	—	6	1	—
<i>Sus</i>	50	63	7	4	52	—	17	66	61
<i>Capra</i>	17	36	21	7	103	—	4	1	—
<i>Equus</i>	—	3	1	1	3	—	5	10	6
<i>Dama</i>	47	198	58	16	798	12	140	587	199
<i>Cervus</i>	23	72	7	6	236	2	19	98	21
<i>Alcelaphus</i>	—	—	—	—	12	—	—	—	—
<i>Bos</i>	11	53	1	5	77	8	27	139	81
<i>Dicerorhinus</i>	—	2	—	—	1	—	1	1	—
Slow small game									
<i>Testudo</i>	1777	453	462	124	1118	8	367	2326	2268
<i>Ophisaurus</i>	9	34	4	—	18	—	21	170	29
<i>Agama</i>	113	—	—	—	87	—	—	—	—
<i>Struthio</i> , egg only	—	11	0	0	?	—	1	48	32
Quick small game									
Fliers									
Anseriformes	2	—	—	—	—	—	—	—	—
Galliformes or medium bird	823	≈25	—	—	≈306	3	12	39	12
Gruiformes	25	—	—	—	—	—	—	—	—
Columbiformes	5	—	—	—	—	—	—	—	—
Passeriformes	—	—	—	—	—	—	—	—	—
Falconiformes (human coll.)	—	—	≈25	≈10	—	—	—	—	—
Runners									
<i>Lepus</i>	1559	12	25	—	72	—	3	—	—
<i>Sciurus</i>	27	4	—	1	—	—	1	7	—
<i>Erinaceus</i>	11	1	—	—	—	—	—	—	2
Swimmers									
Fish (one genus)	23	—	—	—	—	—	—	—	—
Total	6010	2022	1063	334	9213	63	809	4214	3385

<sup>a</sup>Counts are number of specimens identified to genus in the case of all vertebrates (NISP); specimens that could be identified to anatomical element but not to genus or finer level taxonomic affiliations are omitted. Taphonomic evidence indicates that all of these animals were consumed by Paleolithic humans. Data are subsets of total samples from the two sites, as studies are ongoing, but the samples are representative. ‘?’ indicates that the taxon may be present, but it is uncertain.

APPENDIX B

Genus-Specific Counts<sup>a</sup> for Pleistocene Faunal Assemblages From Coastal Sites in Italy (Lazio and Liguria), Spanning 110,000–10,000 years B.P.

Taxonomy	Mochi A	Mochi C	Mochi D	Mochi F	Mochi G	Breuil B3/4	Breuil Br	Mochi I
Large game								
<i>Rupicapra</i>	—	7	—	1	—	1	—	—
<i>Capreolus</i>	25	117	189	26	35	14	35	14
<i>Sus</i>	—	29	16	36	44	—	1	89
<i>Capra</i>	32	360	229	74	29	184	22	22
<i>Equus</i>	1	18	1	3	5	9	14	42
<i>Dama</i>	—	3	12	1	—	9	2	4
<i>Cervus</i>	45	238	542	150	124	112	168	111
<i>Megaceros</i>	—	21	1	—	8	—	—	3
<i>Bos</i>	1	4	42	30	35	22	40	48
<i>Dicerorhinus</i>	—	—	—	—	—	—	6	—
<i>Elaphas</i>	—	—	—	—	—	—	1	—
Slow small game								
<i>Patella</i>	498	43	43	164	98	—	—	—
<i>Monodonta</i>	87	18	3	9	12	—	—	—
<i>Glycymeris</i>	3	5	12	5	23	—	—	—
<i>Mytilus</i>	191	88	57	122	327	—	—	—
<i>Pecten</i>	9	15	21	9	35	—	—	—
<i>Acanthocardia/Cerastoderma</i>	3	3	3	8	8	—	—	—
<i>Callista</i>	4	5	6	2	4	—	—	—
Quick small game								
Fliers								
Anseriformes	—	8	11	2	8	—	—	—
Galliformes	—	41	74	5	9	—	—	—
Gruiformes	—	5	11	4	5	—	—	—
Columbiformes	—	110	22	1	3	—	—	—
Passeriformes	—	180	51	18	13	—	—	—
Runners								
<i>Lepus</i>	—	7	2	5	3	—	1	—
<i>Oryctolagus</i>	2	529	173	6	28	—	—	2
<i>Marmota</i>	—	6	28	10	4	—	—	—
Total	901	1860	1549	691	860	351	290	335
	S0	S1	S2	S3	M1-2	M3	M6	M4
Large game								
<i>Capreolus</i>	146	106	52	28	8	65	16	18
<i>Sus</i>	71	68	30	13	—	4	—	—
<i>Capra</i>	74	73	33	17	—	15	5	—
<i>Equus</i>	9	22	7	3	—	1	—	—
<i>Dama</i>	138	118	47	23	4	13	8	28
<i>Cervus</i>	246	283	162	69	25	240	123	120
<i>Bos</i>	51	72	16	7	2	4	—	8
<i>Hippopotamus</i>	—	—	—	—	—	—	2	—
<i>Dicerorhinus</i>	9	10	2	—	2	2	1	—
Slow small game								
<i>Testudo</i>	—	—	—	—	—	—	—	10
<i>Emys</i>	—	—	—	—	—	—	—	29

# Appendix B (Continued)

Taxonomy	S0	S1	S2	S3	M1-2	M3	M6	M4
<i>Patella</i>	—	—	—	—	5	6	6	—
<i>Monodonta</i>	—	—	—	—	2	3	1	1
<i>Glycymeris</i>	—	—	—	—	2	10	5	13
<i>Mytilus</i>	—	—	—	—	131	30	11	—
<i>Pecten</i>	—	—	—	—	1	—	—	1
<i>Acanthocardia/Cerastoderma</i>	—	—	—	—	1	2	1	1
<i>Callista</i>	—	—	—	—	1	69	4	5
<i>Ostrea</i>	—	—	—	—	1	4	—	1
<i>Conch (one genus)</i>	—	—	—	—	2	3	2	1
Runners								
<i>Lepus</i>	17	13	4	3	6	—	—	1
<i>Oryctolagus</i>	10	6	2	1	—	—	—	—
Total	771	771	355	164	193	471	185	237

<sup>a</sup>Counts are number of specimens identified to genus in the case of all vertebrates (NISP), but MNI is used for mollusks to control for much higher degrees of fragmentation in the latter group. Vertebrate specimens that could be identified to anatomical element but not to genus or finer level taxonomic affiliations are omitted. Taphonomic evidence indicates that all of these animals were consumed by Paleolithic humans.

# APPENDIX C

Genus-Specific Counts<sup>a</sup> for Pleistocene Faunal Assemblages From Üçağızlı Cave (Hatay, Turkey, 1999 excavation season only), spanning >41,000–17,000 years B.P.

Taxonomy	Epi	B	B1-4	C-D	E-E2	F-F2	G-I
Large game							
<i>Capreolus</i>	35	131	276	14	55	37	55
<i>Sus</i>	3	11	9	2	8	24	31
<i>Capra</i>	35	74	64	12	66	59	133
<i>Dama</i>	8	106	178	5	20	1	13
<i>Cervus</i>	—	1	1	—	18	7	1
<i>Bos</i>	—	1	2	1	3	12	26
Slow small game							
<i>Testudo</i>	16	8	15	1	—	4	1
<i>Patella</i>	33	80	165	1	—	—	1
<i>Monodonta</i>	72	342	471	4	1	—	1
Quick small game							
Fliers							
Galliformes or medium bird	41	39	58	—	3	1	3
Other							
Runners							
<i>Lepus</i>	71	1	2	—	1	1	—
Mustelids (human-predated)	15	1	3	—	—	—	6
Swimmers							
Rockfish (one genus)	7	1	6	—	—	—	—
Total	336	796	1250	40	176	146	175

<sup>a</sup>Counts are number of specimens identified to genus in the case of all vertebrates (NISP), but MNI is used for mollusks to control for much higher degrees of fragmentation in the latter group. Vertebrate specimens that could be identified to anatomical element but not to genus or finer level taxonomic affiliation are omitted. Taphonomic evidence indicates that all of these animals were consumed by Paleolithic humans. Data are subsets (1999 excavation year only) of the current total sample from this site, as studies are ongoing, but the samples are representative.

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