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# Zooarchaeological Measures of Hunting Pressure and Occupation Intensity in the Natufian

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## Implications for Agricultural Origins<sup>1</sup>

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by Natalie D. Munro

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Climatic change, population pressure, and environmental stress are frequently cited as major catalysts for the adoption of agriculture. The role of these factors immediately prior to the agricultural transition in the southern Levant is here explored by reconstructing human economic and demographic conditions in the Natufian period. Thorough processing of gazelle carcasses for edible products including meat, marrow, and bone grease and the capture of abundant juvenile animals reflect intensive yet stable ungulate-procurement strategies across the Natufian. Despite this stability, a dramatic shift in the ratio of high- to low-ranked game at the Early/Late Natufian boundary signals a reduction in site-occupation intensity and increased population mobility immediately prior to the agricultural transition. Contrary to current models, the faunal evidence suggests not that agriculture was adopted in immediate response to the cooling and drying of the Younger Dryas but that the Late Natufians embraced more cost-effective demographic solutions for coping with environmental stress.

NATALIE D. MUNRO is Assistant Professor of Anthropology at the University of Connecticut (Unit 2176, 354 Mansfield Rd., Storrs, CT 06269, U.S.A. [natalie.munro@uconn.edu]) and a research associate of the Smithsonian Institution. Born in 1970, she was educated at Southern Methodist University (B.Sc., 1991), Simon Fraser University (M.A., 1994), and the University of Arizona (Ph.D., 2001). She has published, with Mary C. Stiner and Todd A. Surovell, "The Tortoise and the Hare: Small-Game Use in the Broad-Spectrum Evolution and Paleolithic Demography" (CURRENT ANTHROPOLOGY 41:39–73) and, with those authors and Ofer Bar-Yosef, "Paleolithic Population Growth Pulses Evidenced by Small Animal Exploitation" (Science 283 [January 8, 1999]:190–94). The present paper was submitted 25 III 03 and accepted 22 I 04.

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Despite intensive research over a long period, there remains much to be learned about the conditions and timing of the transition to agriculture in southwestern Asia. Many classic models of agricultural origins emphasize a combination of ecological factors—namely, climatic change, environmental or resource stress, and population pressure—as significant precursors of and catalysts for agricultural economies (e.g., Bar-Yosef and Belfer-Cohen 1989, 1991; Bar-Yosef and Meadow 1995; Binford 1968; Braidwood 1960; Childe 1951; Cohen 1977; Flannery 1969; Henry 1989). Advances in paleoclimatic research have led to the identification of the Younger Dryas, a major drying and cooling event with worldwide significance (ca. 11,000–10,200 years ago), as a primary cause of the resource stress that pushed human groups to adopt agriculture (Bar-Yosef 1996, 1998, 2002; Belfer-Cohen and Bar-Yosef 2000; Bar-Yosef and Meadow 1995; McCorriston and Hole 1991; Moore and Hillman 1992). The effects of the Younger Dryas on preagricultural environments are well documented (Bar-Matthews et al. 1999; Baruch and Bottema 1991; Frumkin, Ford, and Schwarcz 1999; Heusser and Rabassa 1987; Kudrass et al. 1991; Yechieli et al. 1993), but its impact on human adaptations is not. This is partly because until recently it has been impossible to pinpoint archaeological deposits contemporaneous with that climatic event.

Agriculture first began in the Fertile Crescent, an arc of productive land that sweeps from the Mediterranean coast into the eastern Taurus Mountains of Anatolia and the western Zagros Mountains of Iran and Iraq. The most intensively studied region of the Fertile Crescent is the southern Levant (fig. 1), which is home to some of the earliest evidence for plant cultivation (Zohary and Hopf 2000). The period that directly precedes the transition to agriculture in the southern Levant is the Natufian, which lasted for ca. 2,600 years. The Natufian culture sprang up ca. 12,800 years ago in the Mediterranean hills of what are now Israel, Lebanon, and Jordan and is well known for its cultural sophistication relative to the Epipaleolithic and Paleolithic periods in the region. It has been distinguished from earlier cultures by its large sites, substantial architectural features, semipermanent occupations, diverse bone tool and ground stone traditions, cemeteries, and artistic elaboration (Bar-Yosef 1998, 2002; Bar-Yosef and Valla 1991; Belfer-Cohen 1991).

Past studies of the Natufian have focused more on

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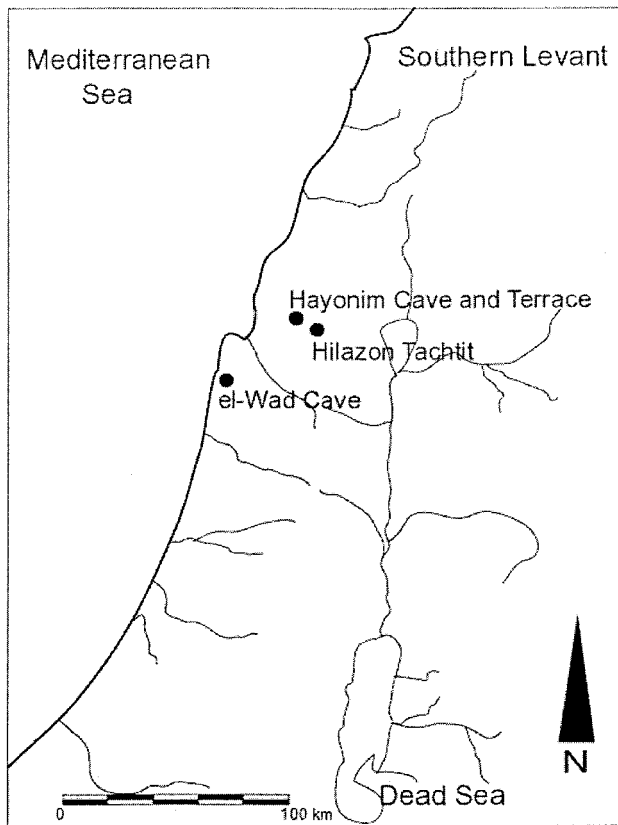


FIG. 1. The southern Levant, indicating the locations of Natufian sites in the study sample.

distinguishing it from preceding periods than on changes within the period itself (but see Belfer-Cohen 1988). The Natufian is proving to be an internally dynamic period and can be divided into two cultural phases based on lithic attributes—Early (ca. 12,800–11,000 years ago) and Late (ca. 11,000–10,200 years ago [Bar-Yosef and Valla 1979; but see Valla 1987]). This division corresponds to substantial cultural changes that appear to be linked to increased settlement mobility in the Late Natufian phase (Bar-Yosef 1996, 2002; Belfer-Cohen and Bar-Yosef 2000; Goring-Morris and Belfer-Cohen 1998; Valla 1998).

Three major climatic trends are relevant to the transition to agriculture in the Levant—the Bölling-Allerød interstadial, a postglacial warm and wet phase (ca. 13,000–11,000 years ago), the Younger Dryas, a brief harsh, cold, and dry event (ca. 11,000–10,200 years ago), and the Early Holocene, characterized by warm and wet conditions (ca. 10,200–6,000 years ago [Bar-Yosef 1996]). The Younger Dryas is of particular interest because it interrupted a major warming trend that began at the last glacial maximum and continued into the Holocene. The impact of this cold and dry period on the distribution of cereal grasses and other resources is important for understanding human adaptations. The transition to agriculture, previously considered smooth and unidirectional,

is proving to have been more of a “bumpy road” (Belfer-Cohen and Bar-Yosef 2000). It is undoubtedly significant that the division between the Early and the Late Natufian corresponds with the onset of the Younger Dryas and that the Late Natufian terminates at the end of this phase. Comparisons of Early and Late Natufian assemblages provide an ideal opportunity to monitor the effects of climatic change on Late Pleistocene human adaptations and to test current models for agricultural origins.

In this study I use zooarchaeological data to test for the presence of climatic, demographic, and resource stress across the Early-to-Late-Natufian transition in the Mediterranean hills and to assess the role of these stresses in agricultural origins. Economic and demographic pressures are measured at the local (site-occupation intensity) and regional (resource stress and human hunting pressure) levels. The Natufian data are set in a larger evolutionary context through long-term comparisons with Middle and Upper Paleolithic and Epipaleolithic cultures from the same region. Although questions of agricultural origins are best addressed by combining archaeobotanical and zooarchaeological data sets, no such ambitious project can be undertaken here. This paper details only the faunal remains and situates them within a broader framework incorporating published interpretations of archaeobotanical and other archaeological data sets.

### Optimization Models and the Ranking of Prey

According to optimization theory, foraging humans should maximize benefits as a means to maximize reproductive fitness (Charnov 1976, Stephens and Krebs 1986, Winterhalder 1986). For hunters this means the preferential selection of high-ranked game—those animals that provide the greatest returns for the energy invested in pursuit and processing. According to the classic prey-choice model, the prey types selected by humans are determined by encounter rates with high-ranked game and are not affected by the abundance of low-ranked taxa (Stephens and Krebs 1986). Declines in encounters with high-ranked prey—a source of resource stress—can thus be simply measured by calculating the ratio of high- to low-ranked game in faunal assemblages.

Archaeologists often interpret declines in prey encounter rates as evidence for human-driven resource depression (“exploitation depression,” according to Charnov, Orians, and Hyatt 1976). It is important, however, to distinguish decreased encounter rates caused by exploitation depression from those caused by shifts in prey behavior (i.e., behavioral depression resulting from changes in prey escape strategies or microhabitat depression caused by the movement of prey to areas with less threat of predation [Charnov, Orians, and Hyatt 1976, Lyman n.d.]). Changes in number of encounters with high-ranked prey may also stem from nonhuman factors such as climatic, environmental, or seasonal changes that affect distributions of high-ranked taxa (Broughton and Grayson 1993). Understanding the rela-

tive contributions of human hunting pressure, prey predator avoidance behaviors, and environmental factors are central for testing current models of agricultural origins, but the relative abundance of high- to low-ranked prey lacks the power to distinguish between them (Grayson and Cannon 1999). Prey relative abundance data are therefore combined with additional lines of faunal evidence (e.g., gazelle mortality profiles) and independent lines of climatic, archaeological, and environmental data to evaluate hunting pressure.

Understanding the conditions under which prehistoric animal assemblages were generated requires that prey species be ranked relative to one another. In archaeological studies prey are most often ranked by body size—the larger the animal, the higher its ranking (Broughton 1994, Butler 2000, Cannon 2000, Madsen and Schmitt 1998, Winterhalder 1981). In most cases body size is an effective measure of rank because the high caloric value of large animals more substantially outweighs the cost of capture than is the case for smaller taxa. Because of the sizable distinction between the return rates of individual large- and small-bodied prey, capture costs often play an insignificant role in the relative rankings of prey species. Capture costs, however, gain considerable importance in ranking prey of similar body size, particularly small-bodied prey with variable escape strategies (Stiner et al. 1999, Stiner, Munro, and Surovell 2000). Three dominant small prey types (excluding fish and migratory game birds, which have geographically restricted distributions) recur in Epipaleolithic assemblages in the Mediterranean Levant—the Mediterranean spur-thighed tortoise (*Testudo graeca*), the cape hare (*Lepus capensis*), and the chukar partridge (*Alectoris chukar*). Hares and partridges are fast-moving and therefore expensive to capture with or without special technology. Slow-moving species such as the tortoise, however, can be captured practically free when encountered. The cost of capture greatly affects the cost/benefit ratios obtained from these prey types and their rankings (Stiner et al. 1999, Stiner, Munro, and Surovell 2000). When accounting for body size and escape strategy, ungulates are the highest-ranked of the Mediterranean prey taxa. Of the small taxa, tortoises are the highest-ranked because of their low capture costs and are followed by fast-moving and therefore lower-ranked birds and hares. Hunting technology (e.g., nets, traps) may impact capture cost and energetic returns per hunting episode and thus affect prey ranking. Its role in Natufian prey selection is taken up below.

### Site-Occupation Intensity

Site-occupation intensity is synonymous with the degree of sedentism and is defined here as the number of human hours a site was occupied per unit time (e.g., per year). It is therefore a combined function of length of stay, frequency of visits, and resident population size. All else being equal, the influence of a site's inhabitants on local resources will increase as site occupation intensifies. Encounter rates with high-ranked game should be greatest when site-occupation intensity is low. As occupation in-

tensifies, declining encounter rates with high-ranked prey will eventually cross a threshold beyond which low-ranked species will enter the diet. The ratio of high- to low-ranked prey in archaeological assemblages thus provides a simple gauge for tracking the relative intensity of site occupation.

Site-occupation intensity should most significantly impact local animal resources living in the vicinity of a site (Hames 1980, Szuter and Bayham 1989, Tchernov 1993). For example, many small-game taxa (e.g., tortoises, hares, and ground birds) have small territories, thrive at high population densities even in disturbed areas, and are most often captured close to camp because they provide limited caloric returns and may be unworthy of search and transport over long distances. Changes in the natural composition of local small-game populations therefore provide particularly sensitive monitors of human hunting close to home (Stiner and Munro 2002). In the Mediterranean Levant the high-ranked tortoise should be preferred when site-occupation intensity is low. As site occupation intensifies and encounter rates with tortoises decrease, hunters will begin to hunt hares and partridges.

Unfortunately, research exploring the effects of climatic change on the distribution and relative abundance of Mediterranean small-game populations does not exist. We do know that the tortoises, partridges, and hares commonly hunted in the Mediterranean Levant have low sensitivities to climatic change—they are generalist feeders with broad geographic distributions covering multiple habitat types (Lambert 1982, Mendelssohn and Yom-Tov 1999). Unlike the cereal grasses, they are not expected to have been severely or differentially impacted by the degree of cooling and drying that characterized the Younger Dryas. They should therefore provide reasonably stable monitors of human hunting behavior.

### Human Hunting Pressure and Resource Stress

Human hunting pressure and resource stress are effectively studied at the regional level. A region is loosely defined as the home range of an interacting network of human groups. The region of interest here is the Mediterranean hill zone of the southern Levant, which is delimited by the presence of Mediterranean parkland forest (Zohary 1982). Restricting this study to the Mediterranean zone reduces the impact of environmental variation on the structure of the prey communities under consideration. As the home of the core Natufian population, the Mediterranean hills are the natural place to seek answers to questions of human hunting pressure and resource stress. Natufian foragers also occupied the Jordan Valley, the site of the earliest agricultural villages. In the Natufian, the Jordan Valley hosted permanent bodies of fresh water and a more diverse ecological community than the Mediterranean zone. Because ecological similarity is essential to test the models proposed herein and no comparable small-game data are available from Jordan

Valley sites (e.g., Ain Mallaha), they are not evaluated here.

Humans often reduce resource stress by implementing a hierarchical sequence of responses that require progressively higher energetic investment and reduced foraging efficiency. These include increased population mobility, dietary diversification, dietary specialization, intensive processing (Colson 1979, Minnis 1985, Miracle 1995), and intensified food acquisition strategies. Hunting pressure and resource stress are evaluated here by reconstructing the cost/benefit of human hunting in three ways: (1) assessing dietary breadth in terms of the ratio of high- to low-ranked resources, (2) measuring the specialization of gazelle hunting on the basis of the ratio of juveniles to adults, and (3) examining the intensity of gazelle carcass processing.

#### THE RELATIVE ABUNDANCE OF PREY TAXA

Human pressure on animal resources at the regional scale should be expressed as exploitation depression of high-ranked taxa. In the Natufian, this applies most strongly to gazelle, the most commonly hunted high-ranked species. The proportion of large-bodied ungulates relative to smaller-bodied taxa reflects human encounter rates with high-ranked prey, assuming no differential preservation based on prey body size. The role of potentially confounding factors (e.g., hunting technology) is addressed below.

#### PREY MORTALITY PROFILES

The mortality profiles of ungulate populations provide additional evidence for human hunting pressure at the regional scale. Such evidence consists of a ranking of different age cohorts of a prey species. On average, individual prime-aged animals offer more body fat in relation to protein than juveniles (Stiner 1994:377) and provide greater overall returns because of their large body size. This is nearly exclusively the case for gazelle, since adult males are only slightly larger than adult females and therefore only the oldest juvenile males will exceed adult females in body size. If individually hunted, prime-aged animals should therefore be high-ranked and preferentially selected in most seasons. Prime-dominated mortality profiles are expected under conditions of low hunting pressure, and the proportion of juvenile animals should increase as hunting pressure increases.

Human hunting pressure may further augment the proportion of juveniles in ungulate mortality profiles by affecting prey demographic structures. Human hunting increases the mortality rate of a given prey population. If mortality rises to exceed annual recruitment, the prey population will become destabilized, fall below carrying capacity, and enter a prolonged period of growth until it returns to carrying capacity. Growing animal populations are characterized by heightened proportions of juvenile animals because of increased rates of population turnover (Caughley 1977). The growth rate of the prey population increases directly with hunting pressure, as

does the proportion of juvenile animals in the demographic structure (Elder 1965, Koike and Ohtaishi 1985, Stiner 1994). Increased encounter rates with young gazelle should be reflected in the mortality profile.

#### PREY-PROCESSING INTENSITY

Processing intensity refers to the amount of time and energy invested in relation to the total energetic returns extracted from prey carcasses and further reflects human-inflicted pressure on animal resources. Intensive processing increases the energetic yield per animal despite an overall decrease in foraging efficiency. Animal carcasses contain several edible products, including meat, marrow, and bone grease that require differential energetic investments for their acquisition. Meat has a low cost/benefit ratio. It can be removed from a carcass quickly and efficiently with minimal processing costs. Yellow marrow is a rich, fatty substance stored primarily in the hollow interiors of mammalian elements including long bones, mandibles, and phalanges (Currey 1984). Marrow from animals in good condition provides a concentrated energy supply that can be extracted by breaching the bone using cold processing techniques such as a hammerstone and anvil. Bone grease is dispersed in the spongy microstructure of mammalian cancellous bone (Brink 1997), and consequently its extraction calls for more time-consuming and energetically demanding techniques, such as crushing cancellous bone, immersing the pulp in boiling water to release the grease, and skimming the fat from the surface (see Binford 1978, Vehik 1977; but see Church and Lyman 2003). Because they are less accessible, marrow and especially bone grease require higher energy inputs to obtain returns comparable to those of meat processing (Saint-Germain 1997:155).

Although the intensity of fat rendering may be motivated by different nutritional or season demands from meat removal (Speth 1989, Speth and Spielmann 1983), identifying which food products were harvested from which portions of the carcass provides a simple measure of processing intensity. The intensity of carcass extraction can be measured in two ways. First, because processing is intensified as animal products with increasingly higher cost/benefit ratios (meat, marrow, then bone grease) are routinely harvested from animal skeletons, determining which of these products were regularly extracted by the Natufians provides a rough measure of extraction intensity. Second, marrow and bone grease are differentially distributed throughout an animal's skeleton (Binford 1978, Blumenshine and Madrigal 1993, Brink 1997, Metcalfe and Jones 1988), and as a result the cost/benefit of processing different body parts varies. By comparing the marrow and grease yields of bone portions with their survivorship, fragmentation rate, and frequency of impact damage, it is possible to assess how intensively humans extracted energy from their prey.

## The Natufian Sample from the Western Galilee

Archaeofaunal assemblages from four Natufian sites in the Mediterranean zone of northern Israel (fig. 1, table 1) are examined to address Natufian economic and demographic strategies. Sites were assigned to cultural period by their excavators largely on the basis of cultural attributes (i.e., the average length of lunate microliths and the frequency of Helwan [bifacial] retouch) and radiocarbon dates when available.

Hayonim Cave is a multicomponent cave site in the western Galilee. Cultural deposits from the Mousterian, Aurignacian, Kebaran, and Early and Late Natufian phases were excavated by Bar-Yosef and colleagues in the 1970s and '90s (Bar-Yosef 1991). The Natufian base camp preserves numerous architectural features, graves, and rich artifact assemblages with good spatial and temporal resolution. Faunal assemblages derive from both Early (number of identified specimens [NISP] = 8,096) and Late (NISP = 5,473) Natufian deposits. Hayonim Cave underwent a functional change at the Early/Late Natufian boundary, when it took on an increasingly ritual role as a cemetery.

Hayonim Terrace is an open-air site situated directly outside of the mouth of Hayonim Cave. The proximity of the terrace to the cave suggests contemporaneity, but a stratigraphic break at the mouth of the cave prevents linkage of the occupation areas. Both Early and Late Natufian phases are represented on the terrace, but the sample analyzed here (NISP = 9,700) originates solely from level II of Valla's (Valla et al. 1986, Valla, Le Mort, and Plisson 1991) excavations and dates exclusively to the Late Natufian phase. Evidence for both domestic and ritual activities was recovered and includes built walls, a slab-lined pit, and six shallow graves, some containing multiple individuals and one containing humans, canids, tortoise shells, and gazelle horn cores.

Hilazon Tachtit is a Late Natufian encampment situated in a small cave in a steep limestone ridge only 7 km southeast of Hayonim Cave and Terrace. The faunal sample (NISP = 1,777) derives from the first three excavation seasons at the sites (1995, 1997, 2000), directed

by L. Grosman. Numerous human burials in clear ritual contexts attest to the symbolic importance of the site (Grosman 2003).

El-Wad Cave is located in the Mount Carmel ridge at the juncture between the Mediterranean hills and the coastal plain. The sample originates from chamber III, which was excavated in the late 1980s as part of a salvage excavation directed by M. Weinstein-Evron. The assemblage is characterized by lower frequencies of defining Natufian tool types (lunates, sickle blades, and awls) than those from chambers I and II but contains typically Natufian ground stone, artwork, faunal remains, and lunate microliths. The latter led Weinstein-Evron (1998) to interpret the deposits as a garbage dump or specialized activity area associated with the Early Natufian phase. The ungulates and carnivores were analyzed by R. Rabinovich (1998) and the small-animal remains by me. The two data sets are combined here (NISP = 2,536).

Only taxa demonstrably collected by humans are considered. These consist of seven artiodactyl species: gazelle (*Gazella gazella*), fallow deer (*Dama mesopotamica*), wild boar (*Sus scrofa*), wild aurochs (*Bos primigenius*), wild goat (*Capra aegagrus*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and two species of equid (*Equus hemionus* and *E. caballus*). The origin of the carnivores and small game is more problematic, since these taxa are often invasive in archaeological sites. All specimens identified were carefully examined for evidence of human and carnivore activity including cut marks, burning, percussion fractures, breakage patterns, carnivore tooth and digestion marks, body-part distribution, and skeletal articulation (Munro 2001). Results indicate that nine carnivore species were captured by humans, although only five—fox (*Vulpes vulpes*), jungle cat (*Felis chaus*), badger (*Meles meles*), stone marten (*Martes foina*), and polecat (*Vormela peregusna*)—made more than incidental contributions to the assemblages. In the small-game category tortoises, hares, partridges, Falconiformes, and waterfowl bear ample evidence for human use in the form of cut marks, polish, grinding, piercing, percussion fractures, burning, and green breaks on a range of body parts and are therefore included here. Virtually no evidence for carnivore

TABLE 1  
*Natufian Sites Examined and Their Dates*

Site	Cultural Phase	Approx. Time Range (Uncal BP)	Radiocarbon Dates (Uncal BP)	Reference
el-Wad Cave (Chamber III)	Early Natufian	13,000–11,000	12,950 ± 200, 12,620 ± 120 10,740 ± 200, 10,680 ± 190	Weinstein-Evron (1998)
Hayonim Cave (Phases I–III)	Early Natufian	13,000–11,000	12,230 ± 160, 12,010 ± 180	Bar-Yosef (1991)
Hayonim Cave (Phases IV–V)	Late Natufian	11,000–10,200	n.a.	Bar-Yosef (1991)
Hayonim Terrace (Level II)	Late Natufian	11,000–10,200	n.a.	Valla, Le Mort, and Plisson (1991)
Hilazon Tachtit	Late Natufian	11,000–10,200	10,750 ± 50	Grosman (2003)

activity was detected in any of the assemblages. Rodents, amphibians, passerine birds, and lizards and snakes were excluded from the analysis because of the lack of evidence for human intervention.

Each assemblage was meticulously collected using dry-screening through 2-millimeter mesh, wet-screening, and picking through screened sediments for small bones. In general, the preservation of the assemblages is very good, particularly in the samples that originated from caves (Hayonim Cave, el-Wad Cave, and Hilazon Tachtit [Munro 2001]). The fauna from Hayonim Terrace was coated with a calcareous sheath. Once that was removed, the underlying fauna proved to be in remarkably good condition, but the strength of the concretions may have crushed small, fragile bones.

## The Faunal Results

To reconstruct Natufian site-occupation intensity and regional hunting pressure, prey relative abundance and gazelle mortality data are examined on three spatio-temporal scales. First, the evolutionary context for the Natufian data is provided using comparisons with published data from Paleolithic and Epipaleolithic sites in the Mediterranean zone. Published data sets are available from the Middle Paleolithic, Aurignacian, and Kebaran layers of Hayonim Cave and the Late Upper Paleolithic and early Kebaran components of Meged Rockshelter (Rabinovich 1997, Stiner n.d., Stiner et al. 1999, Stiner, Munro, and Surovell 2000). Second, an intrasite comparison is provided for five phases (three Early and two Late) of Natufian occupation at Hayonim Cave, the only site in the sample with the resolution to permit examination of fine-grained temporal change within the Natufian period. Third, intersite comparisons utilize the four Natufian sites described earlier. For the intersite analyses, the five Natufian phases at Hayonim Cave are collapsed into Early (phases I–III) and Late (phases IV and V). Gazelle butchery data are available only for Hayonim Cave.

### THE RELATIVE ABUNDANCE OF BROAD PREY GROUPS

Assemblages are lumped into three broad prey categories based loosely on taxonomic affiliation and body size (ungulates, carnivores, and small game) and compared with published data from the Middle Paleolithic, Aurignacian, and Kebaran layers (see appendix for Natufian data and Stiner, Munro, and Surovell 2000 for pre-Natufian data). The ungulate fraction is substantial throughout the sequence, but its composition changes. In the Natufian the ungulates are made up almost exclusively of gazelle (88%), whereas earlier assemblages contain notably higher proportions of large-bodied species such as fallow deer, red deer, wild boar, and wild cattle (gazelle make up less than half of the ungulates in the Middle Paleolithic, 82% in the Aurignacian, and 67% in the Kebaran [Stiner, Munro, and Surovell 2000]). The carnivore fraction is consistent throughout the Paleolithic and Epi-

paleolithic sequence and represents only a small proportion of identifiable specimens (1–5%). The ratio of small game to ungulates remains low from the Middle Paleolithic to the Kebaran (8–37%) but rises in the Natufian, when the proportion of small game reaches an unprecedented 63%. Although ungulates continued to provide a significant source of meat for the Natufians, they are surpassed in NISP by small game, which undoubtedly required increased efforts in pursuit and/or technology (Bailey and Aunger 1989, Lupo and Schmitt 2002).

Detailed examination of the Hayonim Cave Natufian fauna reveals great consistency in the frequency of small game across the five phases of Early and Late Natufian occupation (fig. 2). Ungulates, however, continue to meet the bulk of human demands for animal products. Of the ungulates at Hayonim Cave, gazelle (88%) were hunted almost exclusively, while other species such as wild boar (3%), fallow deer (3%), roe deer (<1%), red deer (1%), wild goat (<1%), and aurochs (<1%) played distinctly secondary roles. The composition of the Natufian large-game component is entirely consistent with published analyses of fauna from Hayonim Cave and other Natufian sites in the Mediterranean zone (Bar-Oz n.d., Bar-Yosef and Tchernov 1967, Bouchud 1987, Davis 1978, Davis, Lernau, and Pichon 1994, Rabinovich 1998, Valla et al. 1986).

The relative abundance of small game in the five Natufian assemblages varies but in all cases exceeds 40% of total NISP (fig. 3). Natufian small game consistently exceed the proportions in Paleolithic occupations in the region (Rabinovich 1997; Speth and Tchernov 1998, 2001; Stiner n.d.; Stiner, Munro, and Surovell 2000). Steady representation of the broad taxonomic groups also points to great stability in basic hunting strategies across

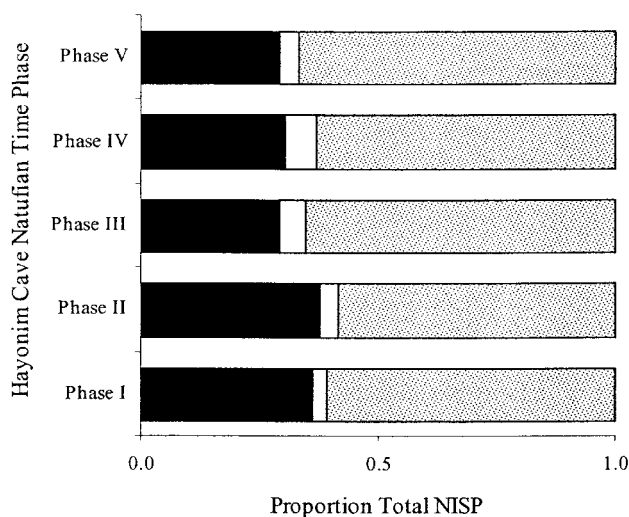


FIG. 2. Relative abundance of broad prey groups from five phases of Natufian occupation, ordered from oldest to most recent, at Hayonim Cave. Black, ungulates; white, carnivores; stippled, small game.

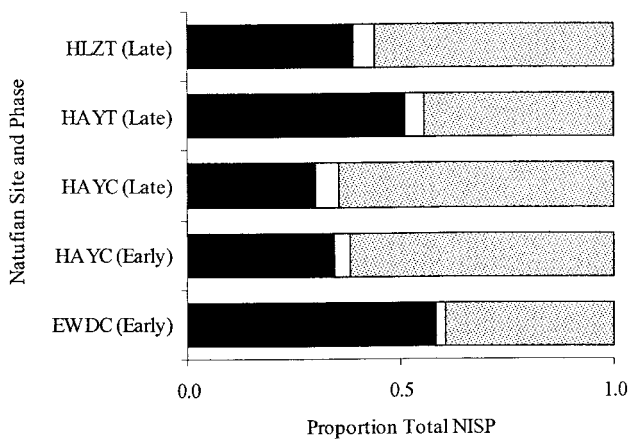


FIG. 3. *Relative abundance of broad prey groups from five Natufian occupations in the western Galilee.* EWDC, *el-Wad Cave*; HAYC, *Hayonim Cave*; HAYT, *Hayonim Terrace*; HLZT, *Hilazon Tachtit*. Early and Late refer to the Early and Late Natufian phases. Black, *ungulates*; white, *carnivores*; stippled, *small game*.

the Early-to-Late-Natufian transition in the Mediterranean zone. Increased proportions of small-game types indicate that the Natufians were meeting more of their meat requirements with species readily available near their habitations rather than large game, which tends to live farther away (Speth and Scott 1989, Szuter and Bayham 1989). This condition typifies all Natufian phases and indicates a reduced encounter rate with high-ranked ungulate prey. Reduced encounter rates with gazelle populations may have been caused by human exploitation depression, microhabitat or behavioral depression, and/or territorial constraints created by human social or ecological pressures (Speth and Scott 1989, Szuter and Bayham 1989). Regardless of the cause, high proportions of small game in Natufian sites resulted in increased human predation pressure and associated decreases in human foraging efficiency on a regional scale.

#### THE RELATIVE ABUNDANCE OF SMALL GAME

The small-game fraction is divided into categories of high-ranked tortoises and low-ranked small mammals (hares) and birds (partridges) to examine variation in site-occupation intensity over time at Hayonim Cave and among Natufian sites in the Mediterranean zone. Significant differences in the composition of the small-game fraction set the Early Natufian layer apart from all previous occupations at Hayonim Cave. The Early Natufian small-game fraction is represented by sizable samples of all three small-game groups, signifying increased investment in the capture of low-ranked prey types. Middle Paleolithic small-game assemblages are dominated by slow-moving tortoises (97% of small game). In fact, tortoises appear to have been a staple throughout the entire

Hayonim sequence (54% of small game in Aurignacian, 83% in Kebaran) but decline in frequency in the Early Natufian (36%) as fast-moving species were added to the diet. The frequency of tortoises returns to Kebaran-like proportions in the Late Natufian (73%).

A wide array of birds appears in abundance in the Aurignacian (43% of small game). The relative abundance of birds in the small-game fraction drops in the Early Natufian (33%), although they constitute a larger proportion of the total assemblage (20% of the Early Natufian assemblage) than the Aurignacian birds (8% of the Aurignacian assemblage). The leap in avian frequencies during the Aurignacian and the Natufian represents the culmination of two processes. The increase in the Aurignacian is partially the product of an increase in the frequency and variety of Falconiformes (Rabinovich 1997, Stiner n.d.). These birds are overwhelmingly represented by elements of the lower leg and wings and only sporadically by breast elements—coracoid, scapula, sternum, furculum, humerus. Clearly, Falconiformes were captured not for their meat but most likely for their feathers and lower leg bones. In contrast, the Natufian increase is nearly entirely the product of rising frequencies of meaty partridge elements. The partridge assemblage is dominated by the tibiotarsus, used in the manufacture of bone beads, and the breast bones, confirming their use for food (Munro 2001). Thus, we see a more pronounced subsistence-associated shift in avian use during the Natufian; much of the earlier increase is a product of ritual intensification. Regardless of the motive, the capture of raptors in the Upper Paleolithic signals a decrease in human hunting efficiency. Finally, hare, another fast-escape type, appears in large numbers (31% of small game) only during the Early Natufian phase.

The Natufian patterns at Hayonim Cave also hold up when scrutinized on a finer scale. Although the total contribution of small game to the Natufian diet remains consistent throughout the five phases of occupation, the relative proportion of fast- to slow-moving small prey in the assemblage changes dramatically (fig. 4, tables 2, 3 and 4). In phases I–III (Early Natufian) consistently higher proportions of hares and partridges were captured in comparison with tortoises. With the onset of the Late Natufian in phase IV, however, there is a complete reversal, and high-ranked tortoises increase markedly to the point that they surpass partridges and hares in sheer numbers. The trend continues into phase V, when tortoises constitute almost the entire small-game fraction (80%).

Analysis of small-game proportions at other Natufian sites suggests that the trend observed at Hayonim Cave is representative of Mediterranean Natufian sites in general (fig. 5). Foragers at the Early Natufian occupations of both el-Wad Cave and Hayonim Cave (phases I–III combined) hunted large quantities of low-ranked small game but continued to capture high-ranked tortoises when encountered. This trend is reversed in the Late Natufian assemblages (Hayonim Cave Phases IV–V, Hayonim Terrace, and Hilazon Tachtit), when higher-ranked

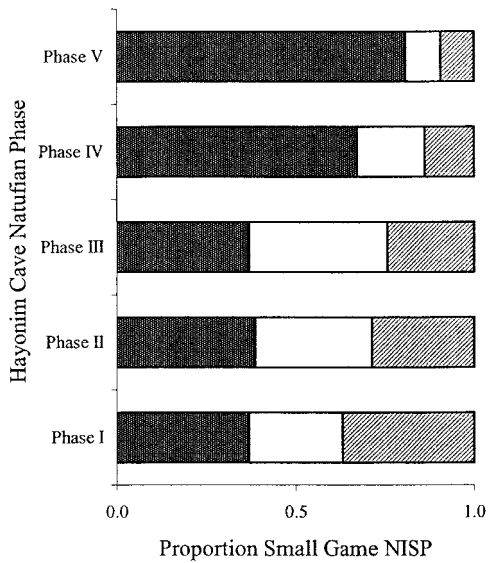


FIG. 4. Relative abundance of small-game types from five phases, ordered from oldest to most recent, of Natufian occupation at Hayonim Cave. Black, *Reptilia*; white, *Aves*; stippled, *Mammalia*. *Reptilia* includes tortoises, *Aves* includes *Phasianidae*, *Falconiformes*, and waterfowl, and *Mammalia* comprises hares.

species increase to frequencies comparable to those of the preceding Kebaran period. The shift in the composition of small-game faunas from predominantly high- to predominantly low-ranked animals culminates in the Early Natufian phase and mirrors shifts in site-occupation intensity across the Paleolithic and Epipaleolithic (Stiner et al. 1999, Stiner, Munro, and Surovell 2000). In the Middle Paleolithic, when site-occupation intensity was almost certainly lower, hunters could afford to focus exclusively on tortoises despite their profoundly lower rates of population turnover. Changing species composition indicates that this became more difficult through the Upper Paleolithic and even more so in the Early Natufian.

High proportions of fast small game in the Early Natufian assemblages indicate that encounter rates with high-ranked species were reduced. Hunters continued to capture tortoises when encountered, but the increased demand for animal products may have been sufficient to depress tortoise populations. After low-ranked species were added to the foraging regime, the system stabilized, and human demands for small game did not grow beyond the reproductive capacities of hares and partridges. The integration of fast-moving small animals into the Early Natufian hunting repertoire suggests more mouths to feed per unit foraging habitat and thus greater hunting pressure on the local ecosystem. Most important, higher demands for animal resources and increases in hunting pressure point to intensified site use, that is, greater

numbers of occupants at Early Natufian sites per unit time.

The return to diets emphasizing more high-ranked species is strongly correlated with the Early-to-Late-Natufian transition and the onset of the Younger Dryas. Although the continuing presence of hares and partridges attests to the Natufians' recognition of these animals as potential food sources, less was invested in their capture. This suggests that Late Natufian demands were greatly reduced in comparison with those of the Early Natufian, that higher-ranked small-game populations were sufficiently abundant to meet these needs, and that the Late Natufians occupied sites with much less intensity than their Early Natufian predecessors. Assuming that the protein contribution of small-animal resources was not increasingly being supplanted by less archaeologically visible resources such as insects or by legumes, cereals, and other protein-rich plants, this implies a substantial reduction in the number of people occupying Late Natufian sites per unit time and/or reduced numbers of visits per site in the Mediterranean hills.

Other factors (e.g., technology, site function) may independently influence the relative rankings or the abundance of prey collected by humans but provide less parsimonious explanations than those argued here. For example, technologies such as nets, which target prey en masse, can increase the returns of fast small prey per hunting episode and thus raise their ranking (Nagaoka 2000). These technologies are particularly well adapted to a sedentary lifestyle. New technologies such as bows and arrows, nets, and traps are likely to have played a role in Natufian hunting techniques. Although the use of these technologies may have facilitated the capture of fast small game in the Early Natufian, it cannot explain why such small game was neglected in the Late Natufian. Social changes associated with sedentary commu-

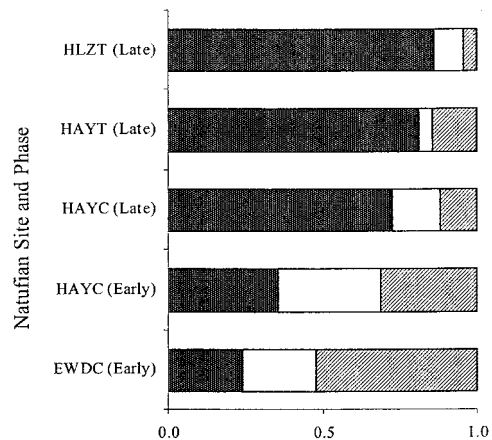


FIG. 5. Relative abundance of small-game taxa from five Natufian occupations in the western Galilee. EWDC, *el-Wad Cave*; HAYC, *Hayonim Cave*; HAYT, *Hayonim Terrace*; HLZT, *Hilazon Tachtit*. Black, *Reptilia*; white, *Aves*; stippled, *Mammalia*.



TABLE 2  
*Standard Deviations from Chi-square Analysis of Small-Game Frequency Data for the Paleolithic and Epi-paleolithic Sequence from Hayonim Cave*

	MP 470–539	MP 420–469	MP 200–419	Aurignacian	Kebaran	Early Natufian	Late Natufian
Reptilia	5.05015	21.2406	8.95480	-4.4585	5.81650	-23.2810	8.11814
Aves	-4.85524	-20.1592	-8.11466	18.1224	-3.80571	13.9598	-9.44181
Mammalia	-4.20561	-18.0143	-8.07310	-13.5166	-7.06824	29.8760	-4.72203

$$\chi^2 = 3896.1, df = 12, p < .0001$$

NOTE: MP, Middle Paleolithic.

TABLE 3  
*Standard Deviations from Chi-square Analysis of Small-Game Frequency Data for the Natufian Sequence from Hayonim Cave*

	Phase I (Early)	Phase II (Early)	Phase III (Early)	Phase IV (Late)	Phase V (Late)
Reptilia	-8.81650	-7.39792	-8.25045	8.54458	13.6376
Aves	1.41906	5.91713	10.24370	-5.09345	-10.8004
Mammalia	12.35568	5.34894	2.09525	-8.02648	-9.9746

$$\chi^2 = 1093.7, df = 8, p < .0001$$

nities, such as a reconfiguration of the division of labor, suffer from the same difficulty; these explanations cannot account for the return of small game to pre-Natufian proportions during the Younger Dryas.

Recent research suggests that Hayonim Cave and Hilazon Tachtit functioned largely as cemeteries that played significant social and ritual roles for local populations in the Late Natufian (Bar-Yosef and Belfer-Cohen n.d., Grosman 2003). Evidence for plant and animal exploitation indicates that domestic activities including the harvest of plant and animal resources were practiced at these sites and do not appear to have been motivated by ceremonial demands. Other than the shift in the relative abundance of small-game species, the mode of faunal exploitation is virtually identical in the Early and Late Natufian layers at Hayonim Cave despite the shift in the site's primary function (Munro 2001).

#### GAZELLE AGE PROFILES

Gazelle skeletons were aged using tooth eruption and wear sequences (following Davis 1980, 1983; Payne 1973;

Stutz n.d.) and bone fusion data (following Davis 1980, 1983). Tooth eruption and wear provide the most discrete and precise age stages for adult gazelles, although the robusticity of the technique is hampered by small sample sizes. This study relies on wear stages of the lower deciduous fourth premolar and the lower permanent third molar of gazelle recently derived by A. Stutz (n.d.). Stutz developed his wear stages using modern collections of mountain gazelle skulls of known ages housed in the mammalian collections at the Tel Aviv University Zoological Museum. The age stages are collapsed into two broad age categories—juvenile and adult—which roughly correspond to the fused (adult) and unfused (juvenile) categories used in the long bone analysis. In the tooth sample, juveniles are separated from adults by the presence of light wear on the lower third molar, which occurs when the animal is ca. 18 months of age (Stutz n.d.).

A combined sample of long bone epiphyses (distal tibia, tuber calcis of the calcaneum, distal femur, distal radius, and distal metapodial) that fuse between 8 and 18 months of age were selected for bone fusion analysis (Davis 1980, 1983). Although combining elements that

TABLE 4  
*Standard Deviations from Chi-square Analysis of Small-Game Frequency Data for the Early and Late Natufian Assemblages from the Mediterranean Zone*

	EWDC (Early)	HAYC (Early)	HAYC (Late)	HAYT (Late)	HLZT (Late)
Reptilia	-14.9928	-22.1443	9.4357	17.6408	10.3930
Aves	4.3454	23.9446	-3.7615	-21.4517	-6.2898
Mammalia	21.0532	14.9583	-12.3046	-9.7276	-11.5763

$$\chi^2 = 3376.5, df = 8, p < .0001$$

NOTE: EWDC, el-Wad Cave; HAYC, Hayonim Cave; HAYT, Hayonim Terrace; HLZT, Hilazon Tachtit.

TABLE 5  
*Proportion of Unfused Gazelle Elements from Paleolithic and Epipaleolithic Sites from the Mediterranean Zone of the Southern Levant*

Site and Cultural Period	% Unfused	Reference
Middle Paleolithic		
Kebara	16.9	Davis (1983)
Hayonim Cave	17.6	Davis (1983)
Average	17.3 ± 0.5	
Upper Paleolithic		
Hayonim Cave	26.3	Davis (1983)
Kebara	26.4	Davis (1983)
Sephunim	15.9	Davis (1983)
Average	22.8 ± 6.0	
Kebaran		
Hayonim Cave	26.7	Davis (1983)
Ein Gev I	26.4	Davis (1983)
Nahal Hadera V	28.0	Bar-Oz (n.d.)
Average	27.0 ± 0.9	
Geometric Kebaran		
Hefzibah (7–18)	27.0	Bar-Oz (n.d.)
Neve David	29.0	Bar-Oz (n.d.)
Average	28.0 ± 1.4	
Natufian		
Hayonim Cave (Early)	34.3	Munro (2001)
Hayonim Cave (Late)	35.5	Munro (2001)
Hilazon Tachtit	37.0	Munro (2001)
Hatoula	30.1	Davis, Lerna, and Pichon (1994)
Hayonim Terrace (Early)	33.3	Henry, Leroi-Gourhan, and Davis (1981)
el-Wad Cave (Early)	37.0	Rabinovich (1998)
el-Wad Terrace	34.5	Bar-Oz (n.d.)
Average	34.5 ± 2.4	

NOTE: The % unfused category includes the distal tibia, tuber calcis of the calcaneum, distal femur, distal metapodial, and distal radius.

fuse at different ages can be problematic, it allows for the compilation of small, otherwise unusable data sets into informative samples, thus enabling larger-scale comparisons. The proportion of unfused elements was calculated using minimum number of elements (MNE) rather than NISP to minimize double counting. Assem-

blages were used in the following comparisons only if they had large sample sizes and compatible age data.

Long-term trends in gazelle age profiles are identified using published data on bone fusion from Levantine Paleolithic sites (Davis 1983) in the Mediterranean hill zone (table 5). An increase in the proportion of juvenile gazelles upholds the trend originally observed by Davis (1989, 1991) in the expanded sample of gazelle fusion data from Levantine Middle and Upper Paleolithic, Kebaran, Geometric Kebaran, and Natufian sites. These new data also reveal a unidirectional trend characterized by the incremental addition of increasingly younger age-groups with successive Paleolithic periods. The average proportion of unfused elements in the combined sample climbs from 17% in the Middle Paleolithic to 23% in the Upper Paleolithic, 27% in the Kebaran, and 28% in the Geometric Kebaran and culminates in an average of 35% in the Natufian period. All ten of the pre-Natufian assemblages contain less than 30% unfused elements, while the seven Natufian assemblages are represented by more than 30% unfused specimens. The difference between the Natufian and the pre-Natufian assemblages is statistically significant (Mann-Whitney,  $z = 2.84, p < .004$ ).

Figure 6 depicts the proportion of juvenile gazelles from Paleolithic and Epipaleolithic sites in the Wadi Meged, Israel, according to tooth eruption and wear data. The sample includes Mousterian, Kebaran, and Natufian

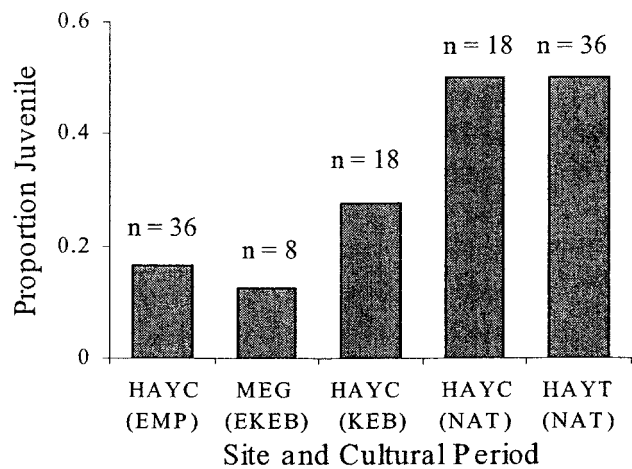


FIG. 6. Relative proportion of juvenile and adult gazelles based on tooth wear and eruption data for the deciduous lower third premolar and permanent lower third molar. Assemblages are from Epipaleolithic and Paleolithic sites in the western Galilee and include Hayonim Cave (HAYC), Meged Rockshelter (MEG), and Hayonim Terrace (HAYT). Data from Middle Paleolithic and Kebaran components are from Stiner (n.d.). EMP, Early Middle Paleolithic; EKEB, Early Kebaran; KEB, Kebaran; NAT, Natufian. The Early and Late Natufian assemblages from Hayonim Cave are combined in the Natufian sample.

assemblages from Hayonim Cave, a Late Natufian sample from Hayonim Terrace, and Early Kebaran and Geometric Kebaran layers from Meged Rockshelter. The Early and Late Natufian assemblages from Hayonim Cave are similar and were therefore combined to increase sample size. Comparative data on gazelle tooth wear and eruption stages from the pre-Natufian samples derive from Stiner (n.d.). The same clear trend emerges from this comparison; there is a stark contrast between the proportions of juveniles represented in pre-Natufian versus Natufian sites. According to the tooth wear data, over half of the gazelles hunted by the Natufian occupants at both Hayonim Cave and Terrace were juveniles, compared with a maximum of 26% in pre-Natufian assemblages. Of the Natufian juveniles nearly half (44%; juvenile MNI = 9) are fawns less than three months of age. Prime-aged animals are conspicuously underrepresented in the Natufian assemblages, which is the exact opposite of earlier culling practices. Although similar, the tooth wear data show higher overall proportions of juveniles than the fusion data. This may be a product of the differential preservation of bones and teeth but is more likely caused by the difference in the age boundaries separating juveniles from adults in the two methods (ca. 18 months for tooth wear and 8–18 months for bone fusion).

Hayonim Cave is the only site with the temporal resolution and the sample size to assess diachronic change in Natufian gazelle age structures using fusion data. The proportion of unfused gazelle epiphyses from the proximal first phalanx, distal tibia, tuber calcis of the calcaneum, distal metapodial, distal femur, and distal radius are plotted according to the age at which they fuse (in months [fig. 7]). Interestingly, the proportion of unfused proximal first (P1) and second (P2) phalanges is extremely high in both the Early (P1 = 38%, P2 = 28%) and Late (P1 = 43%, P2 = 35%) Natufian assemblages. The proportion of unfused gazelle epiphyses recovered from the Late Natufian is slightly and also consistently inflated relative to the Early Natufian.

The high proportion of unfused gazelle first phalanges in the Hayonim Cave Natufian assemblages suggests that nearly half of the gazelles were captured as fawns younger than eight months of age. This pattern contrasts sharply with the proportions of unfused gazelle first phalanges in other Paleolithic and Epipaleolithic sites in the region, which range between 3 and 9% (Bar-Oz n.d.; J. Speth, personal communication, 2002; Stiner n.d.). These results confirm the gradual but widespread shift in the nature of human-gazelle relationships from the Middle Paleolithic to the Natufian period in the southern Levant (Stiner n.d.). At Hayonim Cave, this trend is typified by increased representation of progressively younger age-cohorts in human-collected gazelle assemblages through time.

Several factors may have a significant and predictable influence on the age composition of prey demographic structures (e.g., Stiner 1991 and papers therein). Potential explanations for the patterning in the gazelle age profiles include innovations in human hunting strategies, vari-

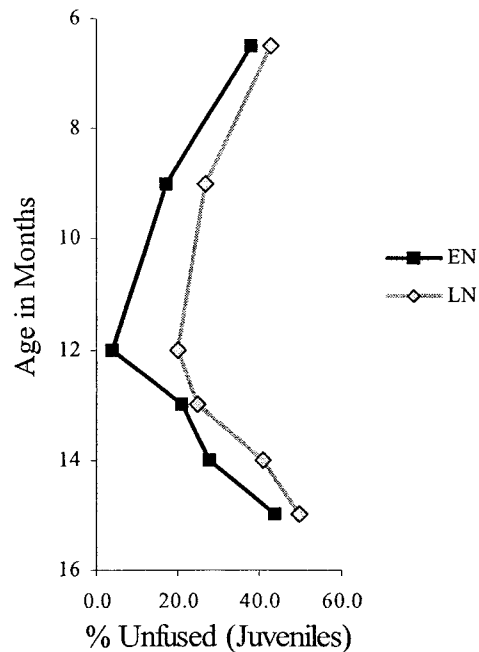


FIG. 7. Percentage of unfused gazelle proximal elements, including phalanx 1, distal tibia, tuber calcis of calcaneum, proximal femur, distal metapodial, and distal radius, from the Early (EN) and Late (LN) Natufian assemblages from Hayonim Cave (age at fusion following Davis 1980).

ation in the seasonality of site occupation, and an intensified gazelle hunting regime which may or may not have been associated with small-scale depression of gazelle populations.

Although the season of capture can affect the composition of prey age profiles, a purely seasonal explanation is difficult to accept given the long-term directional nature of the shift in gazelle exploitation in the Mediterranean Levant. Multiple lines of archaeological data indicate that this region was occupied by residential human groups, at least in the Natufian period (Belfer-Cohen and Bar-Yosef 2000, Byrd 1989), and therefore the regional settlement pattern should incorporate occupations from the full spectrum of seasons. The widespread distribution of juvenile-biased gazelle assemblages across Natufian sites of varying size, function, and occupation intensity precludes this narrow interpretation.

Strategies such as communal hunting could also procure a random sample of age-groups in proportion to their abundance in a living herd. The resemblance of Natufian gazelle mortality profiles to demographic structures has prompted interpretations that gazelles were subject to age-indiscriminate communal hunting, possibly using new technologies such as nets or drives (Campana and Crabtree 1990, Legge and Rowley-Conwy 1987, Moore, Hillman, and Legge 2000). Communal gazelle hunting may be a reasonable interpretation for the goitered ga-

TABLE 6

*Frequency of Impact Fractures, Marrow Utility Index, and Fragmentation Index (NISP:MNE) for Gazelle Marrow-bearing Elements from the Hayonim Cave Natufian Assemblage*

Element and Portion	% Impacts (n Impacts)	Marrow Index	MNE	NISP	NISP:MNE
Scapula, blade	0.0 (0)	6.23	10	33	3.3
Humerus, shaft	4.5 (7)	34.8	14	32	2.3
Radius, shaft	3.8 (5)	52.2	19	41	2.2
Ulna, shaft	2.6 (2)	5.0	15	23	1.5
Femur, shaft	2.5 (3)	47.34	15	43	2.8
Tibia, shaft	4.9 (9)	78.52	17	81	4.8
Metapodial, shaft	3.0 (19)	68.2	42	189	4.5
Calcaneum	< 0.1 (0)	23.11	66	87	1.2
First phalanx	0.0 (0)	33.77	242	429	1.8
Second phalanx	0.0 (0)	25.11	299	299	1.3

NOTE: In the “% Impacts” column, numbers outside parentheses represent the percentage of specimens with impact fractures, while those inside parentheses represent the number of specimens with impact fractures. MNE values are for the portion (e.g., tibia shaft) not for the element (e.g., tibia). Marrow values are derived from Binford’s (1981) index for domestic sheep.

zelle (*G. subgutturosa*), a seasonally migratory species that occupied the dry steppe habitats of Syria and traveled in large herds, but does not fit the permanent gazelle populations of the more productive Mediterranean habitat. Although they may be affected by historical disturbances, today’s mountain gazelles occupy smaller home ranges and form smaller, often sexually segregated social groupings throughout much of the year (up to 40 individuals [Mendelssohn and Yom-Tov 1999]). Communal hunting of segregated herds should not produce assemblages that mimic the herd’s demographic structure, especially since the assemblages represent palimpsests accumulated from multiple, discrete hunting events over hundreds of years. If communal hunting was practiced in the Mediterranean Natufian, it occurred on a small scale at best and did not constitute the dominant hunting strategy.

It is precisely the length, ubiquity, and directionality of the trend in the gazelle age data that leads to a more inclusive interpretation—that there was a widespread and gradual increase in the degree of human hunting pressure on gazelle populations throughout the Paleolithic and Epipaleolithic, culminating in the Natufian period (Davis 1989, 1991). By the Late Natufian there were no untapped gazelle age-groups left to be exploited. The subsequent maintenance of hunting at this level must have incurred increased search costs and decreased returns per hunting episode. Although the procurement of all age categories maximized the amount of meat that could be extracted from a gazelle herd, the Natufians experienced an overall decrease in hunting efficiency. Regardless of the cause of the imbalance between human demands and gazelle populations, there is no question that the Natufians were hunting gazelle populations more intensively than in any preceding cultural period.

#### PREY-PROCESSING INTENSITY AT HAYONIM CAVE

The sample sizes and quality of data required to evaluate prey-processing intensity were available only from Hayonim Cave. To enlarge sample sizes the Early and Late Natufian assemblages were combined. A cursory examination of the data shows no significant variation in butchery patterns between the Early and the Late Natufian (Munro 2001). Much of the following is devoted to gazelle, since they contributed the most meat and fat to Natufian diets. Some skeletal elements store larger quantities of fat than others, and therefore if bones were processed for marrow the frequency of impact fractures and the rate of fragmentation should be directly correlated with marrow content (Marshall and Pilgram 1991). To test for medullary marrow extraction at Hayonim Cave, the frequency of cone fractures and the fragmentation indices (NISP:MNE) of gazelle long bone shafts are compared with their bone marrow content (Lyman 1994:281–82). All gazelle long bone shafts are included in this test, as are the marrow-bearing first and second phalanges and the calcaneum (table 6). The marrow content of gazelle skeletal elements is adopted from the closest available analogue, Binford’s (1981:27) values for domestic sheep. Both cone fractures and fragmentation indices are strongly and positively correlated with bone marrow content ( $r_s = .636, p < .05, n = 10$  for cone fractures;  $r_s = .648, p < .05, n = 10$  for fragmentation). The long bone shafts encasing the largest marrow stores have the highest fragmentation indices and the greatest frequency of cone fractures. These results provide good evidence that humans routinely breached gazelle long bone cavities to harvest marrow.

Because cancellous bone has low structural density (Lyman 1994), the density values of gazelle postcranial elements are used as tentative measures of grease content. The Hayonim Cave Natufian gazelles were exam-

ined for the destruction of grease-rich areas by comparing the structural density of skeletal portions based on Lyman's (1994:246–47) values for pronghorn antelope with their percentage survivorship (table 7; survivorship calculated following Lyman 1994:239). Clearly, there is a density-mediated bias in the Hayonim Cave gazelle assemblage—low-density cancellous bone either has been preferentially destroyed or has not been transported to the site ( $r_s = .546, p < .05, n = 17$ ; fig. 8). Because density-mediated attrition is common in archaeological assemblages in response to a variety of postdepositional processes, many unrelated to bone butchery [e.g., trampling and mechanical weathering], a similar test was performed for hare, a much smaller prey species. Although hare and gazelle skeletal postcranial elements encompass a similar range of structural densities (Lyman 1994, Pavao and Stahl 1999; table 7), the relationship between bone survivorship and density is *not* significant for hare ( $r_s = .393, p > .05, n = 19$ ; fig. 8). Instead, low survivorship and heavy fragmentation of low-density cancellous bone are restricted to gazelle, which is the only well-represented large mammal in the Hayonim Cave assemblage.

Because grease rendering requires some crushing of cancellous bone tissue to release the fat stored within its matrix, it should produce skeletal assemblages in which cancellous bone is both underrepresented and fragmented (Binford 1978, Vehik 1977; but see Church and Lyman 2003). The relationship between the poor sur-

ivorship and the fragmentation of cancellous gazelle bone in the Hayonim Cave Natufian assemblage is highly significant ( $r_s = -.511, p < .001, n = 13$ ; tables 6 and 7). Clearly, cancellous long bone ends are not only visually underrepresented but highly fragmented.

The preceding results meet expectations for a combination of marrow and grease processing. Other mechanical processes, such as trampling, may mimic some of these results but should affect different taxa equally, which is not the case here. Klein (1989) notes that the bones of large ungulate taxa are more susceptible to postdepositional breakage than those of small ones, but why and whether this observation is transferable to those of even smaller-bodied taxa such as hares and birds remains unclear. Here, the poor survivorship and high fragmentation of cancellous bone is limited to gazelle elements and was most likely caused by the intentional bone processing activities of human hunters.

Gazelle, hare, and partridge skeletons contain substantially different quantities of bone marrow. The gazelle skeleton holds the richest marrow stores, followed by the hare and finally the partridge, which contains no marrow at all. The data presented in table 8 indicate a positive correlation between the extent of fragmentation—the proportion of complete elements or bone portions (following Lyman 1994:333–34)—and the marrow concentration of Natufian gazelle, hare, and partridge long bone shafts from Hayonim Cave. Partridge long bone shafts are the most fragile of the three taxa but

TABLE 7  
*Bone Density and Percentage Survivorship Values of Gazelle and Hare Limb Bones from the Hayonim Cave Natufian Assemblage*

Element and Portion	Gazelle			Hare		
	Bone Density	MNE	% Surv	Bone Density	MNE	% Surv
Scapula, proximal	0.3	16	20.0	0.24	30	45.5
Scapula, blade	0.21	10	12.5	0.07	13	19.7
Humerus, proximal	0.12	8	10.0	0.45	11	16.7
Humerus, shaft	0.25	14	17.5	0.22	4	6.1
Humerus, distal	0.44	80	100.0	0.32	66	1.0
Radius, proximal	0.26	41	51.3	0.18	59	89.4
Radius, shaft	0.57	19	23.8	0.21	5	7.6
Radius, distal	0.34	24	30.0	0.28	32	48.5
Ulna, proximal	0.28	36	45.0	0.16	39	59.1
Ulna, shaft	n.a.	23	28.8	0.001	2	3.0
Ulna, distal	n.a.	6	7.5	0.001	3	4.5
Femur, proximal	0.21	17	21.3	0.33	44	66.7
Femur, shaft	0.33	15	18.9	0.33	4	6.0
Femur, distal	0.27	20	25.0	0.54	41	62.1
Tibia, proximal	0.18	25	31.3	0.56	25	37.9
Tibia, shaft	0.48	17	21.3	0.32	24	36.4
Tibia, distal	0.4	45	56.3	0.43	41	62.1
Calcaneus	0.55	66	82.5	0.43	34	51.5
Astragalus	0.57	65	81.3	0.19	31	47.0
Maximum MNE		80			66	

NOTE: Bone density for gazelle is based on Lyman's (1994) values for pronghorn antelope (*Antilocapra americana*). Bone density values for hares are from Pavao and Stahl's (1999) density values for California jackrabbit (*Lepus californicus*). Maximum density values for each portion are used here. Percentage survivorship (% Surv) is calculated by dividing the MNE of a bone portion by the maximum MNE and multiplying by 100%.

were the most often recovered intact—more than half of the time in all cases. The cortical bone of hare is thicker but more fragmented. Hare long bone shafts were recovered complete 4–53% of the time. Finally, the long bone shafts of gazelle were the least likely to be recovered complete (2–25% of long bone shafts), despite the fact that gazelle cortical bone is the thickest of the three taxa and the least likely to be snapped or crushed by trampling or other postdepositional factors. Later scavenging by carnivores can be ruled out as a possible cause of this pattern because the assemblage is nearly devoid of evidence for carnivore activity (e.g., gnaw mark, digestion [Munro 2001]). These results confirm earlier observations that the breakage of long bone shafts is most strongly linked to marrow extraction.

The evidence for bone-processing activities at Hayonim Cave provides strong evidence for intensive, routine processing of gazelle carcasses. Gazelle were stripped of meat, processed for marrow and possibly grease, and used as raw materials for the manufacture of bone tools and ornaments (Munro 2001). The gazelle assemblage is highly fragmented, with an average specimen size of  $2.6 \pm 2.0$  cm (NISP = 2,976), attesting to the tendency of Natufian foragers toward intensive processing of their prey. Low fragmentation indices for hare in relation to partridge suggest that the Natufians also consumed the small stores of hare bone marrow. Because of the difficulty in distinguishing boiled from unboiled bone (Speth 2000), it cannot be determined whether hare bones were processed for grease.

Good evidence for intensive marrow extraction in the Natufian is not surprising in Paleolithic contexts and is well known among contemporary desert and other foragers worldwide (e.g., Binford 1978, 1981; Enloe 1993; O’Connell and Hawkes 1988; Yellen 1977). What is unusual is the likelihood that the Natufians invested in the extraction of a much more labor-intensive product such as bone grease, which may be linked to the diversification and spread of ground-stone milling tools at the be-

TABLE 8  
*Percentage of Complete Gazelle, Hare, and Partridge Long Bone Shafts (MNE) from the Natufian Layer at Hayonim Cave*

Long Bone Shaft	Gazelle	Hare	Partridge
Humerus	2 (60)	4 (49)	100 (74)
Radius	11 (19)	25 (51)	71 (7)
Ulna	0 (35)	14 (36)	100 (24)
Femur	25 (12)	7 (27)	96 (26)
Tibia	16 (31)	53 (32)	55 (190)
Metapodial	18 (95)	53 (218)	87 (117)
Total	12 (252)	37 (413)	76 (438)

NOTE: Numbers in parentheses represent MNE of shafts, while numbers outside parentheses represent percentage of complete shafts (MNE). Partridge metapodials include the carpometacarpus and tarsometatarsus.

ginning of the Epipaleolithic (ca. 20,000 years ago [Bar-Oz n.d., Wright 1994]). Finally, while it can be concluded that gazelle carcasses were thoroughly and intensively processed in the Natufian period, it is more difficult to assess processing intensity relative to earlier periods because of the scarcity of the data required for these comparisons.

### Summary of Faunal Trends

Evidence from relative prey abundances, gazelle age profiles, and butchery data indicate that the Natufians exerted sufficient pressure to depress but not entirely deplete ungulate resources in the Mediterranean zone. On a regional scale, Natufian hunting pressure was more intense than in any earlier period but remained stable across both the Early and Late phases. Intensive extraction of animal resources is confirmed by the routine consumption of low-ranked products including bone grease,

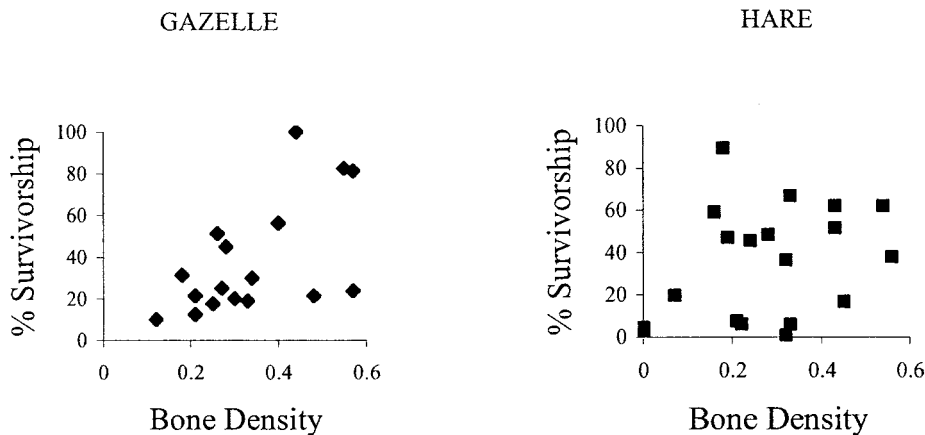


FIG. 8. Bone density and percentage survivorship for gazelle and hare elements from the Natufian assemblage from Hayonim Cave.

juvenile gazelles including fawns, and fast-moving small game. Each of these has a low rate of energy acquisition in comparison with its high-ranked counterpart. In contrast to the stability that characterized Natufian large-game hunting, dramatic shifts in the relative frequencies of small game mirror significant transitions in the intensity of site occupation between the Early and the Late Natufian phase.

### Supporting Archaeological Data

The faunal interpretations are strongly supported by other archaeological indicators of occupational intensity at each of the sampled sites. In general, the Natufian sites with the highest proportions of low-ranked game are the earliest and largest and demonstrate the greatest investment in the construction of site features. The excavators of Hayonim Cave and el-Wad Cave interpret the Early Natufian phase as the most intensive occupation at these sites (Bar-Yosef and Belfer-Cohen n.d., Garrod and Bate 1937). At Hayonim Cave nine circular structures, many of them with formalized floors and hearths and rich domestic and ritual debris, were constructed and utilized during the Early Natufian phase (Bar-Yosef 1991, Bar-Yosef and Belfer-Cohen n.d., Belfer-Cohen 1988). Architectural features from el-Wad Terrace including undressed stone walls, a built hearth, a stone slab pavement, and several cup marks were also constructed and used exclusively during the Early Natufian phase (Garrod and Bate 1937). In combination this evidence points to great settlement stability and longevity in the Early Natufian and associated intensifications in hunting, the harvesting of wild cereals, material culture, and social and ritual life.

The Late Natufian occupations at Hayonim Cave, Hayonim Terrace, and Hilazon Tachtit signify substantially lighter use than the Early Natufian sites in the sample. At the three sites architectural features are rare, material culture is less diverse, and human burials are more common than their Early Natufian counterparts (Bar-Yosef and Belfer-Cohen n.d., Belfer-Cohen 1988, Grosman 2003, Valla, Le Mort, and Plisson 1991). Hayonim Cave structures were abandoned by the Late Natufian, and in most instances graves were dug in the fill. Three caches containing gazelle horn cores, ground stones, and bovid ribs were recovered from recesses in the cave walls, implying abandonment with the intention to return. Bar-Yosef and Belfer-Cohen (n.d.) interpret this occupation as sporadic and ephemeral in comparison with the Early Natufian layer. Hayonim Terrace has comparatively few architectural features and a more restricted material culture (Valla, Le Mort, and Plisson 1991), as does Hilazon Tachtit, which yielded few examples of ornaments and art and less diverse ground-stone and bone tool assemblages than the Early Natufian occupations at Hayonim Cave and el-Wad Cave (Grosman 2003). The Late Natufian occupations examined here required low energetic investments and contained a narrow repertoire of material objects. These results

point to decreased site-occupation intensity and increased settlement mobility more on a par with the Kebaran than with the Early Natufian phase.

Despite major shifts in site-occupation intensity during the Late Natufian, humans utilized similar hunting strategies and exerted similar pressures on ungulate resources in the two Natufian phases. Although little direct evidence for plant exploitation exists, increases in the proportion and diversity of ground stone, the introduction of sickle blades, and a marked increase in the attrition of human teeth indicate that in comparison with Paleolithic peoples, the Natufians were more dependent on small, labor-intensive plant resources such as cereals and nuts (Smith 1991, Unger-Hamilton 1989, Wright 1994). Consistencies in the abundance of ground stone and sickle blades in Early and Late Natufian assemblages (Belfer-Cohen 1988) suggest that the intensity of plant exploitation was similar in the two phases despite changes in population mobility. Both plant and faunal evidence suggest that although resource availability and human population size fluctuated across the Natufian, the two were in balance during both the Early and Late Natufian phases.

### The Early-to-Late-Natufian Transition and the Origins of Agriculture

The faunal evidence illuminates three major trends in Natufian demography. First, Early Natufian settlements in the Mediterranean region were occupied on a scale never before witnessed in the Paleolithic Levant. Second, site-occupation intensity at Mediterranean base camps was greatly reduced in the Late Natufian, when populations reverted to more mobile strategies (Goring-Morris and Belfer-Cohen 1998) reminiscent of pre-Natufian populations in the region. Finally, despite major shifts in settlement strategies, Natufian populations exerted intense but surprisingly uniform pressure on animal resources at a regional scale throughout the Natufian period. The following discussion integrates these faunal trends with the greater body of knowledge on the transition to agriculture in southwestern Asia. The details that make up this picture rely on the scholarship of multiple researchers who have contributed data on a vast range of cultural and environmental variables.

#### THE EARLY NATUFIAN PHASE

Pollen and other oxygen isotope data indicate that the extent of the Mediterranean forest and its potential productivity (i.e., in consumable calories per unit area) reached unprecedented levels for the Late Paleolithic during the Early Natufian phase in the southern Levant (Bar-Matthews et al. 1999, Baruch and Bottema 1991, Colledge 1991, Henry and Turnbull 1985). Moreover, Early Natufian groups invested more in resource extraction than ever before with the aid of intensive plant-processing equipment (e.g., ground stone and sickles) and

hunting techniques. Together the evidence indicates a remarkable increase in the procurement of consumable energy both per unit area in the Mediterranean zone and in absolute quantities for the southern Levant in general. This must reflect increase energetic demands from what could only be dense human populations that could not meet their needs simply by moving to new areas. In fact, in the Early Natufian phase the southern Levant likely supported the densest and, because of greatly expanded Mediterranean habitats, the highest net population sizes the region had seen to this point.

Why did human population density increase during the Late Epipaleolithic? First, the expansion of the Mediterranean belt beginning ca. 14,500 years ago in response to a warm, wet climatic regime greatly increased the region's productivity (Baruch and Bottema 1991, Bar-Yosef 1996). This, however, was not the first time the Mediterranean forest had expanded, and pulses of population growth do not coincide with each favorable period (Stiner et al. 1999, Stiner, Munro, and Surovell 2000). Instead, it was the combined influence of broadening habitats and the availability of technologies facilitating the extraction of spatially concentrated but previously untapped resources that greatly increased the carrying capacity of the region and allowed for population growth.

Why human populations chose to settle in more permanent villages and adopt intensive foraging regimes during the Early Natufian is a more complex problem. Certainly, site permanence, high population density, and intensive foraging modes are causally linked, but which came first and how they influenced one another in the Natufian case are more difficult to resolve. Settling down and investing in the labor-intensive harvest of small food packages requires substantial energetic investment. Foragers are not expected to choose such options unless mobility is already compromised (Kelly 1995). Resource demands often exceed the availability of high-ranked resources, but population decline is the most common result in animal (and human) populations. According to all the lines of evidence presented here, human population packing and territorial circumscription undoubtedly characterized the cultural context of the Early Natufian Levant. Clearly, this was a period in which environmental carrying capacity was effectively raised to a new level (Tchernov 1993).

#### THE LATE NATUFIAN PHASE

Relative changes in prey abundance in Late Natufian contexts indicate that human groups met their demands for meat mainly with high-ranked game. The already intensive use of all gazelle age-groups in the Late Natufian means that this strategy could have been effective only if accompanied by dramatic reductions in site-occupation intensity. Forager mobility is closely linked to the productivity of local resources (Kelly 1995). The productivity and geographic extent of the Mediterranean forest contracted with the onset of the Younger Dryas ca. 11,000 years ago, so Natufian foragers were forced to move more frequently and/or travel in smaller groups

than in the Early Natufian. We have seen that these people were already engaged in other viable solutions to food stress brought on by deteriorating conditions in several resource dimensions (e.g., intensive processing, dietary diversification, and specialization). Heavy plant-processing equipment is common at Late Natufian sites, and it is clear that human groups did not abandon the exploitation of seeds and nuts that had sustained their populations in the Early Natufian. By this time, wild resource extraction had already been pushed to its limits and probably could not have been intensified much further without agriculture. The late Natufians, however, did not, as far as we know, turn to agriculture at this point but instead relied on adjustments in settlement strategy to combat growing pressure added by the climate deterioration of the Younger Dryas. Increased mobility and reduced site-occupation intensity could not have been successful under Late Natufian conditions without an associated drop in human population density, which caused partial depopulation of the region ca. 11,000 years ago.

Late Natufian depopulation of the Mediterranean zone must have occurred via reduced population growth rates, population emigration, or both. Imperceptible changes in population growth rates most likely occurred from year to year as human populations naturally adjusted to climate-induced declines in environmental carrying capacity. Some population movement, possibly to surrounding regions, may also have occurred as conditions worsened, but arid zones could not have absorbed all of the population stress. An expansion in the number of small to medium-sized Natufian sites in the deserts of Jordan and the Negev—habitats which may not have been hit as hard by the Younger Dryas as the Mediterranean zone—does occur in the Late Natufian (e.g., Betts 1998, Goring-Morris 1987, Goring-Morris and Belfer-Cohen 1998). Some of this expansion may have been fed by populations from the Mediterranean zone.

#### IMPLICATIONS FOR AGRICULTURAL ORIGINS

Intensive resource use by Natufian foragers suggests that they experienced continuous resource pressure throughout the period even in the face of major environmental change and population reduction. The consistency of human pressure on several resource classes has major implications for models of agricultural origins. For example, contrary to the expectations of many current models, there is no good evidence that the Natufians responded to potential food stress brought on by the Younger Dryas by further intensifying resource use or adopting agriculture. Indeed, the results of this study suggest that human population shrank in the Late Natufian, then restabilized at a lower carrying capacity and remained there until the end of the period. It is important to distinguish here between changes in carrying capacity associated with technological change (as in the Early Natufian) and those provoked directly by climate change (as in the Late Natufian).

The importance of the Natufian period for agricultural



origins thus lies in the presence of constant resource pressure which undoubtedly encouraged preadaptation to cereal “management” in the region. In the southern Levant, the manipulation of cereals was one of the most remarkable developments of the Natufian and no doubt contributed to the evolution of the agricultural adaptation. The Natufians may have played a direct role in cereal domestication by initiating the first experiments. When conditions did improve ca. 10,000 years ago, cereal agriculture was adopted immediately. Other facets of the Neolithic may, however, have originated elsewhere, perhaps to the north. For example, sites in such less explored regions as the Euphrates Valley (e.g., Abu Hureyra and Mureybet), southeastern Anatolia (e.g., Hallan Çemi), and the Zagros foothills (e.g., Palegawra Cave and Asiab) provide evidence for intensive resource use throughout the Epipaleolithic period (Cauvin and Watkins 2000, Moore, Hillman, and Legge 2000, Munro 2002, Rosenberg et al. 1998). Both genetic and phytogeographic evidence point to a southeastern Anatolian origin for domestic wheat and legumes, although barley may have been locally domesticated in the southern Levant (Levy-Yadun, Gopher, and Abbo 2000, Özkan et al. 2002).

The uniformity of the Neolithic complex and the speed of its adoption over a large geographic area suggest that a preadaptation for agriculture was widespread across the Fertile Crescent in the Epipaleolithic. The general tendency to manipulate the growth conditions of staple animal and plant resources is central to the success of the Neolithic adaptation. The unique prop-

erties and biogeography of the species involved in this process were important in determining which taxa were the most successful domesticates (e.g., wheat, barley, sheep, and goat [Garrard 1984]) and influenced the geographic origins of the Neolithic economy. During the Late Epipaleolithic groups from across the Fertile Crescent intensively manipulated wild resources, in effect performing the earliest experiments with domestication. These experiments, however, could lead to domestication only where there were species with the appropriate behavioral and reproductive characteristics. For example, although the gazelle was intensively exploited by the Natufians, these animals make poor domesticates (Diamond 1999, Garrard 1984) and consequently were never domesticated. Instead, animals such as sheep and goat, textbook examples of domestic animals, not surprisingly became the first domesticates in regions where they were intensively used by Epipaleolithic populations (Zeder and Hesse 2000). Regions of southwestern Asia that hosted species suitable for domestication thus became the geographic hearths of agriculture. Those that lacked such species did not, but this does not mean that their economic strategies were less intensive. In sum, the different components of the Neolithic adaptation likely originated in different localities within the Fertile Crescent in response to similar selective pressures. These components eventually locked together to form the more uniform Neolithic adaptation which quickly spread across southwestern Asia and beyond.

## Appendix: NISP Counts for Sampled Natufian Assemblages

Taxon	EWDC EN	HAYC EN	HAYC LN	HAYT LN	HLZT LN
Small Game					
Indeterminate	n.a.	23	8	10	8
Reptilia					
<i>Testudo graeca</i>	247	1,777	2,542	3,483	848
Aves					
<i>Alectoris chukar</i>	n.a.	818	231	53	41
Other Galliformes	n.a.	9	9	0	1
Falconiformes	n.a.	279	96	81	23
Waterfowl	n.a.	27	12	n.a.	1
Medium Aves	162	408	158	43	27
Large Aves	70	72	30	7	3
Huge Aves	16	15	9	0	0
Aves subtotal	248	1,628	545	184	96
Small Mammals					
<i>Lepus capensis</i>	536	1,559	417	630	44
Total	1,031	4,987	3,512	4,307	996
Carnivores					
Indeterminate	0	79	59	191	21
<i>Panthera pardus</i>	0	3	2	0	0
<i>Felis cf. chaus</i>	0	54	51	39	12
<i>Ursus arctos</i>	1	0	0	0	0
<i>Canis sp.</i>	15	3	3	9	6

Continued

<i>Vulpes vulpes</i>	32	116	153	153	30
<i>Meles meles</i>	2	13	20	16	1
<i>Martes foina</i>	7	17	15	11	10
<i>Vormela peregusna</i>	0	12	5	3	2
Mustelidae	0	8	8	8	4
Total	57	305	316	430	86
Ungulates					
<i>Capreolus capreolus</i>	2	5	1	1	0
<i>Dama mesopotamica</i>	124	47	30	55	2
<i>Cervus elaphus</i>	12	23	13	9	0
Cervidae	7	41	27	0	7
<i>Gazella gazella</i>	654	1,483	883	4,249	362
<i>Capra aegagrus</i>	7	17	8	19	7
<i>Bos primigenius</i>	0	11	4	78	2
<i>Sus scrofa</i>	18	50	43	51	12
<i>Equus</i> sp.	0	0	1	0	1
Small ungulate	519	1,018	574	357	289
Medium ungulate	90	87	51	132	9
Large ungulate	15	22	10	11	4
Total	1,448	2,804	1,645	4,962	695
Total	2,536	8,096	5,473	9,699	1,777

NOTE: HAYC, Hayonim Cave; HAYT, Hayonim Terrace; HLZT, Hilazon Tachtit; EWDC, el-Wad Cave; EN, Early Natufian; LN, Late Natufian. Only general avian categories are presented; species-specific lists may be found in Munro (2001). Only taxa demonstrably modified by humans are included. Mammals assigned to general taxonomic categories based on size (e.g., small, medium, large mammal) are not included in analyses presented here.

## Comments

GUY BAR-OZ AND TAMAR DAYAN  
*Zinman Institute of Archaeology, University of Haifa,  
 Haifa 31905, Israel (guybar@research.haifa.ac.il)/  
 Department of Zoology, Tel-Aviv University, Tel-Aviv  
 69978, Israel (dayant@post.tau.ac.il). 19 v 04*

Munro writes about one of the most exciting issues in the evolution of human culture and economy—animal exploitation patterns during the Natufian of the southern Levant, when semisedentary settlements occur and incipient animal and plant domestication have been identified (e.g., Davis and Valla 1978, Dayan 1994, Tchernov 1992, Tchernov and Valla 1997). Since the process of animal and plant domestication has had a profound effect on the economy, culture, and eventually demography of humans, as well as on natural environments, it is not surprising that much research in the past few decades has focused on gaining insight into the origins of this development and specifically on Natufian sites, often considered key to this issue. Munro builds upon this long tradition of scientific research and adds some new data to an intriguing picture. Her data accord with interesting previously published patterns: an increase in lower-ranked species (Davis 1989, 1991; Stiner et al. 1999, Stiner, Munro, and Surovell 2000, Stiner and Munro 2002) and an increase in the exploitation of gazelle young (Davis 1983, 1991) during the Natufian as a whole. Munro's specific contribution here is in fine-tuning the analysis of these two patterns within the Natufian. By comparing

Early Natufian with Late Natufian assemblages, she reveals an increase in high-ranked small species within the Late Natufian but no change in the percentage of gazelle young. These results are taken to support the pattern emerging from the study of human settlement patterns during this period.

Munro also analyzes bone marrow and grease exploitation by analyzing fragmentation and survivorship of gazelle bones of the Hayonim Cave assemblage. The difference between them and the hare bones probably reflects the fact that gazelle bones were used for marrow and grease extraction while the bones of hares were not. This pattern is taken by Munro to show that gazelle carcasses were thoroughly and intensively processed in the Natufian period, but she concedes that the published data are insufficient to assess processing intensity relative to other periods. Thus, unfortunately, this interesting analytical approach cannot contribute to our understanding of diachronic patterns during this period but can rather be taken as a first step which requires future data sets and analyses to provide a real picture of bone marrow and grease processing in the Levantine Epi-Paleolithic.

Munro summarizes the anthropological literature dealing with settlement patterns during the Natufian and finds congruence between this literature and her data. She also reviews some of the literature on the origins of cereal crop and animal domestication, suggesting that the above-mentioned patterns of exploitation support a hypothesis of continuous resource pressure across the duration of the period, which ultimately led to domestication. Gazelles, although heavily exploited by Natufians, make poor domesticates (Simmons and Ilany

1977); Munro, however, does not go into the debate over the possible status of “proto-domestication” of Natufian gazelles (Cope 1991, Dayan and Simberloff 1995, Bar-Oz, Dayan, and Kaufman 1999, Bar-Oz et al. 2004). Although we are skeptical of some of the evidence and of its interpretation (Dayan and Simberloff 1995, Bar-Oz, Dayan, and Kaufman 1999, Bar-Oz et al. 2004), we feel that much remains to be understood of gazelle exploitation patterns during the later Epi-Paleolithic. For example, sexing is required for a more insightful look into this issue (e.g., Horwitz, Cape, and Tchernov 1990, Bar-Oz et al. 2004), as is a more detailed age-structure reconstruction. An analysis of economic trends within the full Epi-Paleolithic sequence of the southern Levant including the predecessors of the Natufian culture, taking into account possible taphonomic biases related to site formation processes (e.g., Bar-Oz and Dayan 2002, 2003), remains to be carried out.

Munro’s analysis of stages within the Natufian is an excellent step forward; her analysis of grease and marrow extraction is the first step on what may prove to be a highly profitable scientific path. In sum, her work is another solid building block in our understanding of the Epi-Paleolithic economies of the southern Levant.

JACK M. BROUGHTON AND ANDREW UGAN  
*Department of Anthropology, University of Utah, 270  
 S. 1400 E., Rm. 102, Salt Lake City, UT 84112, U.S.A.  
 (jack.broughton@anthro.utah.edu). 20 v 04*

Munro uses the Levantine faunal record to examine the role of climate change, population pressure, and environmental stress in structuring Natufian subsistence and the subsequent shift to agriculture. The articulation of models from evolutionary ecology with faunal data to examine prehistoric subsistence and settlement is an effort with which we are very sympathetic, and the questions of domestication and agricultural origins are certainly crucial ones. Thus, we applaud Munro’s attempt to address these topics and see interesting questions arising out of her analysis. Our perspectives do differ in some ways, however, and we appreciate the opportunity to address some of the general issues she raises.

While Munro explicitly draws on evolutionary ecology in the context of measuring foraging efficiency and resource stress, that approach does not extend to her discussions regarding the catalysts for domestication. Without a theoretical anchor, the paper is vague as regards the relationship between domestication and the key causal variables involved. Within an evolutionary ecological framework, domestication can be viewed as one response to broadening diets as foragers faced with low overall returns and high handling costs manipulate resources in ways which improve their handling efficiency (e.g., selecting for larger seeds, stiffer rachises, etc.). The key requirements are a low-ranked resource with characteristics suitable for domestication, the economic motivation to exploit it intensively, and a lifestyle sufficiently sedentary to permit repeated interaction (e.g.,

Hawkes and O’Connell 1992). All of these requirements can be affected by climatic change, human population densities, and mobility in ways that are potentially testable. This is relevant in the current context because many of the archaeological data presented speak directly to the key issues of economic motivation and residential mobility.

With few exceptions, we find Munro’s middle-range measures of foraging efficiency appropriate and informative, and at least four of them suggest that overall return rates had declined substantially by Natufian times. These include an increase in the proportion of small-bodied prey relative to ungulates, a gazelle sample increasingly dominated by younger individuals, the intensive processing of gazelle carcasses for marrow and grease, and an abundance of ground stone and sickle blades suggesting the intensive use of low-ranked plants. Contrary to Munro’s assertion, however, these characteristics of broader diets do not “relieve resource stress” but are symptoms of it. Together, they indicate lower overall foraging returns, one of the prerequisites for domestication given the evolutionary ecological model mentioned above. Insofar as domestication occurred in this context, Munro has marshaled considerable empirical support for that model.

But what of the suggestion that increases in the relative frequencies of slow-moving tortoises relative to faster-moving partridges and hares reflect Late Natufian reductions in site occupation intensity *and increased overall returns*? We find ourselves intrigued by the former proposition but skeptical of the latter. Tortoises are the most abundant small prey in any Levantine assemblage except the early Natufian and Aurignacian, and Munro suggests that the latter may result from the introduction of raptor specimens unrelated to subsistence activities. This raises the possibility that the Aurignacian small-game sample would also be dominated by tortoises, making their presence a marker of shorter-term occupations consistent with other aspects of the archaeological record.

The relationship between tortoise abundances and return rates is less clear, however, since the intensity of plant exploitation and especially the gazelle age-structure data suggest that Late Natufian returns were as low as *or lower than* the Early Natufian. The suggestion that population size also declined during the Younger Dryas/Late Natufian period serves to underscore this point, since we expect populations to drop as a result of climate-based declines in resource abundances. A thinning population by itself need not entail improvements in foraging returns.

Because we suspect that tortoise trends are telling us more about mobility than anything else and because mobility represents a potentially key variable in the process of domestication, it becomes worth considering what structures it. Recent modeling work suggests that the distributions and productivities of low-return gathered resources have a strong influence on residential site distributions (Zeanah 2004), and the low-return cereal grasses used throughout the Natufian were, according to

Munro, environmentally sensitive. Insofar as the onset of the Younger Dryas altered the return rates and distribution of wild grasses, we can anticipate changes in site occupation intensity. This, in turn, would affect the harvest rates of prey types with different mobility and life-history characteristics (tortoises, hares, gazelles) for the reasons Munro points out. To the extent that domestication relies on repeated, longer-term interaction and interference with cereals, the process may well have been delayed as a result.

In sum, Munro makes important strides in demonstrating the utility of an evolutionary-ecology-informed zooarchaeological approach to the context of agricultural origins, and we hope that future research can build on this start.

SIMON DAVIS

*Instituto Português de Arqueologia, Avenida da Índia 136, P-1300-300 Lisboa, Portugal (sdavis@ipa.min-cultura.pt). 17 v 04*

Besides identifying faunal remains from archaeological sites, the zooarchaeologist generally makes quantitative observations. These include the frequencies of different species and their age-at-death profiles. In this contribution Munro does this, clearly inspired by two early interpretations of such quantitative data, the studies of Kent Flannery (1969) and William Elder (1965).

In the Near East a diachronic widening of the spectrum of exploited resources was recognized by Flannery, who termed it “the broad-spectrum revolution.” Elsewhere similar changes have been observed. At the caves of Franchthi, Greece, and Nerja, Andalusia, Payne (1975) and Morales, Roselló, and Hernández (1998) found that fishing began in the Mesolithic and Magdalenian periods respectively, and Morales et al. call this the “Tardiglacial paradigm.”

In North America Elder (1965) interpreted a shift in the age-at-death profiles of a prey species in terms of hunting pressure. He noticed a marked increase of juvenile deer hunted by Missouri Indians in the eighteenth century AD and linked it to increased hunting intensity and efficiency—a consequence of the introduction by Europeans of firearms and horses and the remunerative trade in venison. In South Africa Klein (1979) noticed that limpets found in Late Stone Age sites were smaller (i.e., younger) than those from the Middle Stone Age and suggested that this reflected increased foraging pressure.

Here Munro considers a succession of Mousterian-to-Natufian faunal assemblages in the western Galilee (Israel). She describes a diachronic shift towards smaller prey and an increase in the proportion of juvenile gazelles hunted (gazelle was the most important ungulate). By sensibly restricting her study to the western Galilee, she avoids complications due to geographic variation, which are especially severe in the Levant, where topographic,

climatic, and vegetation variations are among the highest in the world.

Munro’s study highlights two methodological aspects of zooarchaeology. The first is the need to screen. Failure to screen (and preferably wet-screen) results in the loss of smaller bones (Payne 1972), which tends to bias quantitative considerations. Here Munro restricts her study to fauna recovered from the meticulous excavations undertaken by Israeli and French teams during the past 35 or so years, when wet-screening on site was normal practice. The second is the importance of studying the “whole” faunal assemblage. In the early days scholars with a palaeontological or zoological background sometimes restricted themselves to particular groups such as ungulates, carnivores, or rodents. Given zooarchaeology’s aim of understanding man-animal relations, it is vital to consider *all* parts of an archaeological faunal assemblage. Munro’s approach clearly conforms to this need.

At a more personal level, it is encouraging to see that her results corroborate my tentative interpretations made in the 1980s following studies of two other faunal successions from this region—Biq’at Quneitra–Ein Gev (Mousterian to Natufian) in the Golan Heights/eastern Galilee and Hatoula (Natufian to PPNA) in central Israel. At Biq’at Quneitra–Ein Gev the Mousterian mammals included “giants” like rhinoceros, aurochs, equids, and red deer as well as the smaller fallow deer and gazelle. Subsequently the larger species became scarce or disappeared, and by Natufian times gazelle and an abundance of small mammals, especially hares, dominate the faunal assemblage. A continuation of this reduction in size of prey also occurred at Hatoula. While gazelle is the dominant species in the earlier (Natufian) period there, the PPNA fauna contains abundant small mammals, fish, and birds. Pooled gazelle age-at-death profiles from a large number of sites in the Levant revealed an increase of juveniles in the Natufian and an even greater increase in the PPNA (see Davis 1989, 1991; Davis, Rabinovich, and Goren-Inbar 1988). The reduction in size of prey and increased juvenile-gazelle cull in the course of the Mousterian-to-PPNA period were also viewed in terms of increased predator pressure. This represented a revision of an earlier seasonal-change interpretation (Davis 1983). With the adoption of sedentism in the Natufian (Perrot 1966), population increase must have been more rapid. We know from modern examples of newly settled nomads that sedentism is soon followed by substantial population increase (Sussman 1972). A rise in pressure on the environment just before the appearance of domesticated food animals in the Levant explains why it became necessary for people to take control of their meat sources and begin domesticating—people were *forced* by demographic pressure. Otherwise, as Lee (1968) pointed out, hunting and gathering peoples living at low population density have little need to go to the effort of managing livestock. Husbanding animals is more arduous than simply going out and hunting them.

BRIAN HAYDEN

*Archaeology Department, Simon Fraser University,  
Burnaby, B.C., Canada V5A 1S6 (bhayden@sfu.ca).  
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This is a welcome, provocative, and insightful addition to the corpus of analyses concerning the Natufian and domestication. I would, however, place a slightly different spin on several interpretations.

Munro equates hunting pressure with food or resource pressure, but this is unwarranted given that an abundance of other resources is consistent with the overexploitation of large game because of the high value usually placed on meat. In the North American Northwest very dense populations placed intense pressure on ungulate populations but arguably procured more than enough food from other sources (especially fish and geophytes) to avoid resource stress—and, indeed, to support major surplus-consuming activities such as potlatching. Ungulate assemblages from the Northwest Plateau are remarkably similar to the Natufian assemblages in terms of intensity of bone fracturing for marrow and grease, yet one cannot argue for resource pressure at these sites. Thus, food stress may well not have been a significant feature at any time in the Natufian core area, even if hunting stress did exist.

There is also little basis for maintaining that human populations in the core area declined in the Late Natufian. There is a continuing emphasis on small local game, site numbers increase in Jordan and the Negev, and populations exerted “uniform pressure on animal resources at a regional scale.” It simply does not follow that “increased mobility and reduced site occupation intensity could not have been successful . . . without an associated drop in human population density.” As Henry (1989: 47–54, 218–19) has argued, Late Natufian populations simply needed to move more frequently to exploit cereal and nut resources that became increasingly distant because of climatic changes. There is no need for populations or cultural complexity to decline, and the reduced length of residence may well explain why higher-ranked small game became more available around Late Natufian base camps. A high Late Natufian human population density is the only way to explain the consistently intense hunting pressure on gazelles that Munro documents.

Moreover, as ungulates became more difficult to procure, their food status must also have changed. In the Southwest during Pueblo times and on the Northwest Plateau, as ungulates became scarcer deer meat became a prized food and was used predominantly for feasting (Romanoff 1992; Muir and Driver 2002, 2004; Speth and Scott 1989), and in the Northwest more labor-intensive hunting techniques such as communal hunts and deer fences were used. Munro argues that communal hunting was insignificant during the Natufian because “segregated herds should not produce assemblages that mimic the herd’s demographic structure,” but how can base camp assemblages be expected to provide information on the number, age, or sex of the animals from any *spe-*

*cific* kill episode? In the Northwest Plateau deer were generally hunted communally, but the number of animals taken was usually small, and, aside from *general* age/sex profiles like those of the Natufian, no such strategy has ever been evident in the general base camp assemblages. Moreover, this kind of communal hunting is not at all inconsistent with widespread and pronounced hunting pressure. In fact, this is precisely the condition under which one expects it to emerge. Thus, the age structure of Natufian ungulate assemblages most plausibly does result from communal hunting.

The above factors and others indicate that the Natufians were complex hunter-gatherers who engaged in substantial feasting and ritual (see Hayden n.d.). Munro is correct in observing that any food stress associated with the Younger Dryas did not lead to domestication and that technology is critical to understanding the increases in Natufian population densities (cf. Hayden 1981, n.d.). Contrary to claims that the Late Natufians reverted to egalitarian nomadic bands or became simplified, Munro’s evidence indicates that they were just as complex as the Early Natufians. She is probably also correct that Natufians began experimenting with “wild food production” prior to the development of domestication in the Neolithic, when climatic conditions did improve.

What Munro fails to develop is the idea that the new technologies, new extractable resource potentials, sedentism, art, and population densities were part of a new transegalitarian type of society that generated powerful sociopolitical pressure to intensify resource extraction and create ever larger surpluses. This is the key factor in understanding the transition to economies with domesticated plants and animals. From this perspective, climate change is indeed of secondary importance in explaining domestication, and Munro’s conclusions support this model. Her playing down of energy investments and her assumptions of constant resource pressure at Late Natufian sites seems to be weak attempts to shore up an old resource-stress model that would be better discarded. In fact, there are substantial structures at Mallaha in the Late Natufian excavated by Valla, cemeteries are maintained, and the effort required to transport 100+-kg basalt mortars the 80 km from their sources certainly indicates heavy investments in at least some Late Natufian sites.

Finally, perhaps we need to rethink our assumptions of what ritual food may have been in these early sites and/or our assumptions about the staple versus feasting use of ungulates in “domestic” structures of complex hunter-gatherers, where, I suspect, these remains may largely represent feasting events.

EMILY LENA JONES

*Department of Anthropology, University of  
Washington, Box 353100, Seattle, WA 98195, U.S.A.  
(emljones@u.washington.edu). 19 v 04*

Munro has provided a clear and intriguing analysis of hunting pressure and site occupation intensity in the

Natufian and the potential contribution of these two factors to the development of agricultural economies in the southern Levant. She makes use of numerous lines of evidence, particularly relying on ratios of higher- to lower-ranked game (both large and small) and on analyses of gazelle processing and procurement strategies. Her analysis provides a picture more complex than that often seen in archaeological studies of the Pleistocene-Holocene transition period while remaining both straightforward and parsimonious.

One part of Munro's analysis does concern me. She uses ratios of small- to large-bodied prey and ratios of quick to slower small prey to argue for a steady increase in the human population of the southern Levant through time. This conclusion may be accurate; however, the interpretation of these relative-abundance indices as data supporting this conclusion seems to me premature. Given the coincidence of a sharp increase in the proportion of small to large game and in the proportion of quick to slow small game at the Natufian and the general amelioration of climate at this time, it seems to me that the changes in relative abundances cited by Munro could possibly reflect not the impacts of human hunting but climate-driven ones (as discussed in Grayson and Cannon 1999). Likewise, the decrease in slower, lower-ranked smaller prey items that she identifies in the Late Natufian roughly correlates with the onset of the Younger Dryas (as, indeed, she points out). It is possible that climate differentially impacted the different prey types represented in the assemblages discussed by Munro and that climate is driving the changes in relative abundance presented here.

This criticism, however, does not negate Munro's multifaceted argument concerning the relationship of climate, human subsistence, and the eventual onset of agriculture. She suggests that Late Natufians adjusted to the pressure of the Younger Dryas by increasing mobility and reducing site occupation intensity; both of these strategies were, she argues, facilitated by an associated drop in human population density (caused by reduced human population growth rates and/or emigration). Understanding the details of this process might be an interesting avenue for future research. If human population packing and territorial circumscription were as intense in the Early Natufian as Munro suggests, then the onset of the Younger Dryas, which occurred with remarkable rapidity (Alley et al. 1993, Tschudi et al. 2003), would have been a momentous event. The transition from a densely packed population to a more mobile one should be visible in other archaeological assemblages; likewise, evidence for emigration should be available.

Finally, Munro makes the point that, while the faunal evidence she presents does not support the hypothesis that agriculture was adopted in immediate response to the Younger Dryas event, this climate event may have contributed to the preadaptation for agriculture in the region. When climate conditions improved around 10,000 years ago the peoples of the southern Levant immediately adopted cereal agriculture. She thus depicts a situation in which climate and human behavior together influenced

the onset of agriculture, an elegant and realistic alternative to environmentally deterministic models.

R. LEE LYMAN

*Department of Anthropology, University of Missouri, Columbia, MO 65211-1440, U.S.A (lymanr@missouri.edu). 19 IV 04*

Munro's analysis adds yet another case to the growing number of zooarchaeological studies employing foraging-theory-based models to generate predictions regarding the effects of human predation on prey encounter rates and human responses to changes in those rates. It goes beyond many previous studies, however, in its innovative use of changes in prey demography that result from predation and in its examination of the covariation of destruction of faunal remains and ontogenetic age of the animals represented. Other variables Munro examines, such as butchering and fragmentation intensity, are now rather commonplace in such studies. All of this is good, solid, noteworthy work. Two items require comment.

First, I worry a bit about the fact that both cultural change and climatic change coincide temporally with faunal change from Early to Late Natufian times. I do not worry a lot, though, because the Hayonim Cave materials provide finer temporal resolution than the coarse-grained Early-Late temporal distinctions. Those temporally fine-grained materials display the same faunal trends within the Early and the Late cultural phase and within the early warm-wet climatic phase and the subsequent cold-dry (Younger Dryas) climatic phase as the simple Early and Late materials. This suggests that the faunal trends are driven not by technological or climatic change but by the effects of human predation. Some of the faunal trends represent human adaptive responses to anthropogenic change in the faunal resource base. Such anthropogenic change is becoming more widely documented in time and space as these sorts of analyses are applied in ever more diverse settings (Grayson 2001). Caution with respect to generalization is warranted, however, because, though clearly widespread, this sort of anthropogenic change cannot be assumed to have been ubiquitous in human prehistory (Lyman 2003). These observations mean that our job as zooarchaeologists has become more difficult, tedious, and time-consuming but also much more exciting and potentially significant with respect to modern conservation biology and historical anthropogenic change (Lyman and Cannon 2004).

There is a fundamental weakness in Munro's analysis. The Natufian is said to be a "period" and also a "culture," but it is also said to consist of "two cultural phases," an Early and a Late. I was a bit confused as to what a culture is, what a cultural phase is, and how they differ. When I learned that at Hayonim Cave the early "phase" is divisible into "three early phases" and the late "phase" is divisible into "two late phases," I became quite confused. Perhaps the term "phase" is being used commonsensically to denote a time period, but that is not made clear, and this is not the way the term is used

by most Americanist archaeologists. My point is simple. A series of archaeological units is mentioned, but what kind of unit each constitutes is obscure. Are they spatial, temporal, formal, or some combination of these? The answer is critically important because these units serve as the antecedent aggregates for defining the faunal assemblages Munro studies. The problem is, however, not Munro's alone. It is one that plagues archaeology generally (e.g., Lyman and O'Brien 2002, O'Brien and Lyman 2002), and until such time as we all learn to define our analytical units explicitly, it will continue to weaken our otherwise thoughtful and innovative contributions such as this one.

F. VALLA

*Maison René Ginouvhs, 21, allée de l'Université, F-92023 Nanterre Cedex, France (shimsh5@netvision.net.il). 19 v 04*

Not being a paleontologist or a biologist, I may just say, as a specialist in Natufian studies, that this work includes a number of observations capable of illuminating some of the questions raised by Natufian faunas. Not many works offer so many details about gazelle remains in one place, and few studies take full consideration of small game such as hares and tortoises and try to incorporate them into an integrated understanding of the behavior of Natufian hunters. The analysis is all the more interesting in that hares and tortoises are not simply food; separately and together they play a well-known role in the human imagination, as is exemplified by religious precepts, mythologies, and fables in many parts of the world. Moreover, it is possible to show in the case of tortoises that the animal had a symbolic meaning for Natufian people. In this context, I wonder if the deterministic approach adopted by Munro is relevant. It has obvious heuristic value, but it may be misleading. Is the relation between hunters and their prey (and carcasses) controlled exclusively by rational laws? Many scientists working in the hard sciences today insist on the complexity of physical phenomena beyond pure determinism. It seems that archeology could benefit from adopting this more realistic point of view.

The way in which sites were used by their Natufian inhabitants is probably one of the key questions we have to answer to order to arrive at better interpretations of their culture. It is no longer sufficient to speak of "sedentism" versus "mobility" or of "more or less sedentary groups" as we currently do. Munro's analysis is very welcome in that it raises these questions and provides fuel for discussion. Only taking into consideration all of the archaeological data will allow a proper approach to the problem. Certainly no one is in a better situation to discuss the matter in the case of Hayonim Cave than the excavators, Ofer Bar-Yosef and Anna Belfer-Cohen. I wonder if it might be a possibility that the cave was occupied repeatedly for relatively short periods of time (at most a few hundred years) during the 2,500 years or so of the Natufian culture. Perhaps this could contribute

to explaining the relative scarcity of cultural remains in the excavated area? Needless to say, other explanations are, of course, possible.

Finally, I congratulate Munro without any reservation for her effort to tackle the difficult problems raised by Natufian faunas, many of which are still awaiting study on laboratory shelves. We urgently need more such analyses. Each Natufian site (and each layer at these sites) has its own particularities. It is only from in-depth multidisciplinary analyses of each of these sites that pictures may emerge that, taken together, will improve our understanding of the Natufian and its meaning in Near Eastern cultural development.

## Reply

NATALIE D. MUNRO

*Storrs, Conn., U.S.A. 8 vi 04*

First, I thank the commentators for their thoughtful remarks. I am pleased about the overall support for the methods employed and the major trends identified. Most criticisms concern the conclusions or implications of these results for the transition to agriculture. This is unsurprising given the widespread interest in the question of agricultural origins and the vast range of approaches that have been used to investigate it.

This point is epitomized in the contrasting responses to my theoretical approach. For example, Valla charges that my interpretations are overly deterministic, whereas Jones suggests that I be commended for my "realistic alternative to environmentally deterministic models." The opposition of these perspectives appropriately reflects the broad range of often conflicting theoretical approaches followed by prehistorians today—a larger topic that affects all archaeological studies and therefore is not elaborated here. Undoubtedly the animals consumed by Natufian foragers had symbolic, social, and economic meaning. Most of the sites evaluated in this study also contain human graves, which commonly occur at Natufian sites in the Mediterranean zone. This does not mean that the core choices made by humans were not strongly linked to energy maximization. I encourage analysts who believe that human choices were not only influenced but driven by social and ideological factors to test those ideas using faunal data. As Valla mentions, numerous assemblages await analysis.

I am largely in agreement with Broughton and Ugan's comment, although they are more explicit about the evolutionary ecological underpinnings of the transition to agriculture. As they say, I do argue for reduced site-use intensity in the Late Natufian; however, I do *not* argue for increased overall returns. I contend only that because of reduced site-occupation intensity in the Late Natufian, changes in the proportions of small game reflect alleviation of resource pressure on the local scale. The

final interpretations that Broughton and Ugan provide therefore accord with those presented here.

Hayden argues that hunting pressure cannot be equated with resource pressure in general. Certainly we cannot reconstruct the degree of resource pressure from the faunal signal alone. Up until recently, arguments for plant intensification have been made primarily on the basis of secondary data (i.e., ground stones). The lack of primary data for intensification in the Epipaleolithic botanical record has stemmed from the absence of evidence. This is due in part to the poor preservation of plant seeds in the often clay-rich Levantine sediments and in part to a research bias favoring the detection of the earliest domesticates. New data presented by Weiss et al. (n.d.) not only tackle this issue but identify corresponding signals of resource depression in the Epipaleolithic botanical record. Weiss et al. note a fluorescence in the exploitation of labor-intensive small-grained grasses starting in the early Epipalaeolithic and continuing up to the early Neolithic, when these grasses all but disappear. Given the small size of these grains, their absence in the Paleolithic periods, and the effort required to prepare them for consumption, this result corroborates the faunal trends for increased human investment in resource extraction in the periods leading up to agricultural origins. The correspondence between independent faunal and floral data in the Epipaleolithic indicates a shared response to the same instigator—increased resource pressure.

Hayden argues that gazelle were communally hunted in the Natufian, whereas I suggest that communal hunting occurred on a small scale at best. The basis of this disagreement is largely one of definition. The commonly accepted model for Natufian communal hunting was first proposed by Legge and Rowley-Conwy (1987) for the site of Abu Hureyra in the northern Levant. It views communal hunting as a large-scale community effort involving the use of natural features and/or constructed game drives to mass-kill animals from migratory herds. This is quite different from the cooperative hunting involving small groups of hunters and small numbers of animals that Hayden proposes. I agree that some Natufian hunting undoubtedly occurred via small-scale cooperative efforts, but we find no evidence for large-scale mass kills in the southern Levant.

Hayden also argues for human population stability throughout the Natufian. He contends that the increased number of settlements in the surrounding desert regions (i.e., Jordan and the Negev desert) supports the idea of population stability. These areas, however, are outside the study region, and a population increase likely reflects some emigration from the core area. The climatic changes effected by the Younger Dryas would have not only reorganized the distribution of resource patches but reduced the carrying capacity of the region. This would have reduced the number of people that could have been supported in the Mediterranean zone. Cross-cultural data indicate that more mobile human groups use larger territories than sedentary ones (Kelly 1995) and fewer people are supported per unit area. Hayden is, however,

correct in saying that increased mobility and decreased population size in the Late Natufian should not be equated with decreased cultural complexity. The results of this study and the archaeological record show that the level of complexity is constant throughout the Natufian period. Hayden views sociopolitical pressure as the driving force behind the agricultural transition. I agree that Natufian society is significantly more complex than preceding periods and that this played a role in restructuring many facets of the Natufian adaptation. In addition, I agree that climate and population pressure were not the sole factors pushing the transition. Nonetheless, there is undeniable evidence for intensification and increased resource pressure in all facets of Natufian foraging. Intensive foraging undoubtedly provided the Natufians with agricultural know-how, and I firmly believe that these factors were indispensable in getting the agricultural ball rolling.

Both Jones and Lyman are concerned about the correlation between the relative proportions of small game and the climatic changes wrought by the Younger Dryas. I argue that the Younger Dryas caused environmental changes that led the Natufians to become more mobile to offset resource stress and that this in turn influenced the relative abundance of small game. The shift in the use of small game is thus unavoidably linked to climatic change, though not directly. Certainly climate change is capable of altering the natural proportions of small game. Unfortunately, without a naturally deposited assemblage (i.e., one that has not been through the cultural filter), it is impossible to know the proportions of small game prior to their hunting by the Natufians with certainty. Multiple lines of evidence, however, point to human hunting pressure rather than climatic change as the best explanation for shifts in small-game abundance. For example, as Lyman reasons, the changes in small game are consistently expressed in both high- and low-resolution Natufian faunas. In addition, multiple lines of evidence, including Natufian settlement patterns, architecture, and human burial patterns, support the site-intensity trends, as do the interpretations of the excavators of the sites (Bar-Yosef and Belfer-Cohen n.d.).

Lyman is also concerned with the terminology used to define temporal and spatial divisions not only in the Natufian period but in general. To clarify, my choice of archaeological terminology follows that used by the archaeologists who designated the temporal and geographic dimensions of the Natufian (Bar-Yosef 1981). The Natufian has long been considered both a temporal unit (a period) and a culture (i.e., the people who occupied the Levant between 13,000 and 10,200 years ago). The temporal breakdown within this period is more complex, particularly the use of the term “phase.” “Phase” was chosen as a term to divide the Natufian into two discrete temporal units (Early and Late) that differ in several aspects of material culture but not sufficiently to warrant the designation of distinct cultures. The stratigraphic layers of Hayonim Cave were also divided into five “phases” during excavation. These, however, were relative designations, and the correlation between them and



the absolute Early and Late Natufian distinctions was not determined until after the excavations (Bar-Yosef and Belfer-Cohen n.d.). The fact that the Early and Late Natufian division at Hayonim Cave correlates exactly with changes in the faunal record and major climatic change is a testament to the remarkable precision with which Bar-Yosef and Belfer-Cohen determined the occupational sequence at the site. This was achieved despite the fact that they had to assign deposits from widely separated contexts to the five phases. In sum, the term "phase" is used herein to subdivide the Natufian period either into the absolutely dated Early or Late Natufian phases or into the relative phases of occupation initially defined by Bar-Yosef and Belfer-Cohen at Hayonim Cave (Bar-Yosef 1991, Belfer-Cohen 1988). Certainly, as Lyman suggests, clarification of these terms is warranted.

Bar-Oz and Dayan recommend launching comparative projects to investigate the temporal and spatial extent of trends identified by this research. In particular, we need to determine when less well-documented trends such as grease processing first began. This is an undertaking that Bar-Oz and I have already begun. We have also initiated a more elaborate gazelle project that will take a high-resolution look at multiple dimensions of the human-gazelle relationship in the Levant over the past 300,000 years. This research will build on many previous studies, including those succinctly reviewed by Davis.

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