The Evolution of Hominin Diets

Integrating Approaches to the Study of Palaeolithic Subsistence

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Jean-Jacques Hublin
Max Planck Institute for Evolutionary Anthropology,
Leipzig, Germany

and

Michael P. Richards
Max Planck Institute for Evolutionary Anthropology,
Leipzig, Germany

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10. Epipaleolithic Subsistence Intensification in the Southern Levant: The Faunal Evidence

Natalie Munro
University of Connecticut
Department of Anthropology
Unit 2176, 354 Mansfield Road
Storrs, CT, USA
Natalie.Munro@uconn.edu

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Abstract Subsistence intensification – the extraction of increased amounts of energy from a given area at the expense of foraging efficiency – figures prominently in discussions of the Epipaleolithic period (ca. 21,000–11,500 cal BP). Despite their paramount status, intensification trends are not often subjected to rigorous testing using multiple archaeological data sets. This study aims to fill this gap by synthesizing relevant zooarchaeological data from Epipaleolithic sites in Southwest Asia. Intensification is examined not only at the level of the animal community, but also at the taxonomic, and individual carcass levels. Multiple lines of faunal evidence including prey age profiles, large and small game abundance, species diversity, and the fragmentation of animal bone support an intensification trend across the Epipaleolithic period that culminates in the “transition” to agriculture. The pathway toward intensification was not always gradual – variation in Southwest Asian hunting practices indicates that there were some stops and starts along the way. The intensification trend reported here corresponds with other long-term processes, including increased site use intensity and growing human populations, but crosscuts major climatic events.

Introduction

The intensification of hunter-gatherer subsistence strategies is commonly associated with the Epipaleolithic, the period immediately preceding the “transition” to agriculture in much of the Old World. It is generally assumed that intensification is caused by population packing – imbalances between human populations and resources lead to the extraction of more resources per unit area at a greater cost to the forager.

Epipaleolithic intensification is thus often linked to population pressure models, which have long figured prominently in explanations for agricultural origins (Boserup, 1965; Binford, 1968; Flannery, 1969; Cohen, 1977; Bar-Yosef and Belfer-Cohen, 1989, Henry, 1989; Bar-Yosef and Meadow, 1991; Bar-Yosef and Meadow, 1995; Bar-Oz, 2004; Munro, 2004b; Davis, 2005).

Epipaleolithic intensification has most often been investigated by searching for evidence of Flannery’s (1969) Broad Spectrum Revolution (BSR). The BSR is described as an expansion of human diets to include new small game species, and ultimately results in reduced foraging efficiency. Documentation of the BSR has focused primarily on recording prey diversity, which has not always been sufficiently sensitive to expose changes in foraging efficiency (Edwards, 1989; Neeley and Clark, 1993; Bar-Oz et al., 1999). This has led some researchers to conclude that the BSR and demographic sources of population imbalance were unimportant in the “transition” to agriculture. More recently, however, studies compiling multiple zooarchaeological measures of human foraging efficiency have pinpointed periods of human demographic expansion and clearly intensified resource use in the Epipaleolithic (Stiner et al., 1999, 2000; Stiner, 2001, Munro, 2003, 2004b; Bar-Oz, 2004; Stiner 2005; Munro and Bar-Oz, 2005). These studies differ from earlier attempts to characterize intensification by combining a number of complementary zooarchaeological measures, including the relative abundance of prey types exploited by humans, prey mortality profiles, and carcass butchering strategies. Below, a synthesis of multiple lines of zooarchaeological evidence for Epipaleolithic subsistence intensification in Southwest Asia, in particular the southern Levant, is presented at community, population, and individual animal scales.

Here, intensification is defined as an increase in the amount of energy extracted from a given environment per unit time. Intensification is thus synonymous with a reduction in foraging efficiency – more energy is invested for each unit of energy returned. Intensification is a common solution to imbalances between human population size and resource availability (carrying capacity). Resource imbalances can occur as the result of human demographic growth or as a change in the availability of high-ranked prey in response to
environmental change or localized predation (Lyman, 2003). Excellent ways to resolve imbalances include adding new, but less cost-effective resources to the diet, and intensifying the exploitation of already hunted species. The latter strategy can be executed by targeting previously unexploited age groups or intensifying the extraction of nutrients from individual animal carcasses. These solutions are effective, but because they return less energy for the amount invested in comparison to strategies focusing on higher-ranked taxa, age groups, or body-parts, they result in intensification.

The intensification of animal resources can take place on a number of ecological scales, including the community, the population, and the individual animal scale. Classically, detection of the broad spectrum revolution has occurred at the community scale by documenting the diversity (the number) of hunted prey species through time (Edwards, 1989; Neeley and Clark, 1993; Bar-Oz et al., 1999). In this case, an increase in species diversity is assumed to represent intensification as dietary breadth expands. Diversity measures can provide good gauges of intensification, but are less valuable if they do not also consider the relative abundances of each prey group and the differential costs and benefits of prey taxa in the diet. Relative abundance indices provide instructive alternatives to diversity analyses by comparing the frequency of high- to low-ranked game groups to detect evidence for declining foraging efficiency (Winterhalder, 1981; Szuter and Bayham, 1989; Broughton, 1994; Madsen and Schmitt, 1998; Stiner et al., 1999, 2000; Butler, 2000; Cannon, 2000; Stiner, 2001; Munro 2003, 2004b). Relative rankings are assigned according to the cost-benefits of each prey species, and are most often based on prey body size (Broughton, 1994) and cost of capture (Stiner et al., 1999, 2000). Prey relative abundance indices require that compared taxa have differential cost/benefits, and thus an increase in the relative representation of low- in relation to high-ranked prey indicates intensification – a decrease in foraging efficiency.

At the scale of a single animal population, the degree of intensification can be measured as the relative proportion of young to adult animals of a single prey species. Mortality profiles can be successful indicators of intensification for two primary reasons. First, because prey mortality increases with heightened hunting pressure, human hunting releases a prey population from the constraints of carrying capacity and thus encourages a prey population to grow (Elder, 1965; Caughley, 1977; Koike and Ohtaishi, 1985; Stiner, 1994). Growing populations have higher proportions of juvenile animals, which will in turn be hunted and deposited in the archaeological record. The ratio of juvenile to adult animals in a hunted population will thus be elevated in comparison to non-hunted populations. Second, like in the community scale analyses mentioned previously, intensification should result in an increased abundance of low- in relation to high-ranked animals or, in this case, in the abundance of smaller juvenile individuals that yield less meat and fat, in comparison to the significantly larger prime-aged adults (Stiner, 1994).

Intensified hunting of a given animal population should thus be expressed as an increase in the proportion of young individuals in the hunted assemblage. In animal populations that grow throughout their lives, such as tortoises, a decrease in the average age of the population will be depicted as a reduction in average body-size (Klein, 1999; Stiner et al., 1999, 2000).

Finally, intensification can be investigated at the level of the individual animal by examining how aggressively humans processed carcasses to extract edible products such as meat, marrow, and grease. Edible products are differentially distributed across animal carcasses and some cost more to extract than others (Binford, 1978; Lupo and Schmitt, 1997; Saint-Germaine, 1997; Munro and Bar-Oz, 2005). Thus, substantial variation in the costs and benefits of the extraction of different products and body parts exists. Carcass processing intensity can be measured first by determining what products (meat, marrow, grease) were regularly extracted from animal carcasses (Munro and Bar-Oz, 2005). Grease, for example requires more effort to extract than bone marrow, which itself requires more energy to process than most cuts of meat. Second, carcass processing intensity can be measured by the size and quality of the meat and fat packages that humans regularly butchered and consumed. Low intensity processing strategies should thus be represented by the focused removal of prime energy packages. This will be expressed zooarchaeologically by the presence of high-utility body-parts, associated cutmarks, and routine breakage of only the richest marrow-bearing bones. In contrast, intensive processing strategies will be indicated by the presence of both high- and low-utility body-parts, and the fragmentation of all marrow-bearing bones, including those with small marrow stores.

In combination, analyses from each of the three ecological scales have the power to provide a robust picture of dietary intensification. Here, I present faunal evidence from each scale to establish a broad picture of Epipaleolithic subsistence intensification in Southwest Asia. I focus primarily on the southern Levant because currently, it is home to the richest Epipaleolithic record in the region, and large comparative faunal databases exist. The Epipaleolithic of the southern Levant can be divided into three primary cultural periods (Table 10.1): the Kebaran (21,500–17,000 cal BP); the Geometric Kebaran (17,000–14,500 cal BP); and the Natufian which is commonly subdivided into Early (14,500–13,000 cal BP) and Late (13,000–11,500 cal BP) phases. Below, I combine my own data (Munro, 2001, 2004b) with comparable datasets published by Stiner (2005) and Bar-Oz (2004) from 11 discrete Epipaleolithic phases from nine archaeological sites (Fig. 10.1; Table 10.1). All sites are located in northern Israel and occupy either the Mediterranean zone or the ecotone between the Mediterranean hills and the coastal plain. The archaeological components are organized from oldest to youngest to depict changes in human subsistence use through time.
Table 10.1. Site names, cultural phases and time ranges of southern Levantine assemblages discussed herein.

<table>
<thead>
<tr>
<th>Site</th>
<th>Cultural period</th>
<th>Time range (cal BP)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>El-wad Terrace</td>
<td>Late Natufian</td>
<td>13,000–11,500</td>
<td>Bar-Oz, 2004; Bar-Oz et al., 2004</td>
</tr>
<tr>
<td>Hilazon Tachtit</td>
<td>Late Natufian</td>
<td>13,000–11,500</td>
<td>Munro, 2001, 2004b</td>
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<tr>
<td>Hayonim Terrace</td>
<td>Late Natufian</td>
<td>13,000–11,500</td>
<td>Munro, 2001, 2004b</td>
</tr>
<tr>
<td>Hayonim Cave</td>
<td>Late Natufian</td>
<td>13,000–11,500</td>
<td>Munro, 2001, 2004b</td>
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<tr>
<td>Hayonim Cave</td>
<td>Early Natufian</td>
<td>14,500–13,000</td>
<td>Munro, 2001, 2004b</td>
</tr>
<tr>
<td>El-wad Cave</td>
<td>Early Natufian</td>
<td>14,500–13,000</td>
<td>Rabinovich, 1998; Munro, 2001, 2004b</td>
</tr>
<tr>
<td>Hefzibah 7–18</td>
<td>Geometric Kebaran</td>
<td>17,000–14,500</td>
<td>Bar-Oz and Dayan, 2003; Bar-Oz, 2004</td>
</tr>
<tr>
<td>Neve David</td>
<td>Geometric Kebaran</td>
<td>17,000–14,500</td>
<td>Bar-Oz et al., 1999; Bar-Oz, 2004</td>
</tr>
<tr>
<td>Nahal Hadera V</td>
<td>Kebaran</td>
<td>21,000–17,000</td>
<td>Bar-Oz and Dayan, 2002; Bar-Oz, 2004</td>
</tr>
<tr>
<td>Hayonim Cave</td>
<td>Kebaran</td>
<td>21,500–17,000</td>
<td>Stiner, 2005</td>
</tr>
<tr>
<td>Meged Rockshelter</td>
<td>Kebaran</td>
<td>21,500–17,000</td>
<td>Stiner, 2005</td>
</tr>
</tbody>
</table>

Methods

Epipaleolithic intensification will be investigated using classic archaeozoological methods including: (a) relative taxonomic abundance indices; (b) mortality profiles; (c) average body-size data; and (d) bone fragmentation data.

The relative abundance analyses are comprised of three indices that compare the frequencies of taxa that are differentially ranked according to their body-size and escape strategy. A decline in the abundance of high-ranked game in relation to lower-ranked taxa indicates a decline in foraging efficiency and thus, intensification. First, an ungulate index compares the large and medium ungulates to the smaller-bodied (and thus lower-ranked) small ungulates. The large ungulates include wild cattle (*Bos primigenius*) and red deer-sized (*Cervus elaphus*) animals, while the medium ungulates are dominated by Persian fallow deer (*Dama mesopotamica*), but also include small frequencies of wild boar (*Sus scrofa*) and bezoar goat (*Capra aegagrus*). Finally the small ungulate category is nearly exclusively comprised of mountain gazelles (*Gazella gazella*), although roe deer (*Capreolus capreolus*) also make an occasional appearance. Second, a small game index compares the abundance of lower-ranked small game animals to the higher-ranked ungulates. The small game category is dominated by three species – Mediterranean spur-thighed tortoise (*Testudo*...
In combination, the three indices comparing different kinds of taxa provide a more comprehensive picture of local and regional intensification in the southern Levant than the use of a single index. The ungulate index compares large-bodied taxa that range over substantial territories, and thus provide good evidence for region-scale hunting pressure. In contrast, the comparisons of small game groups that have small home ranges and often live at high densities close to human habitation sites, provide a more local picture of intensification that most likely reflects the intensity of site occupation, rather than regional game depression (Hames, 1980; Szuter and Bayham, 1989; Tchernov, 1993; Stiner and Munro, 2002).

Intensification is investigated on a population scale by tracking the percentage of juvenile individuals in the populations of the two most common hunted species – the gazelle and the tortoise. In gazelle, the first phalanx fuses between 5–8 months of age (Davis, 1980), before the animal has reached reproductive maturity. Thus, the percentage of unfused first phalanges (based on MNE) represents the proportion of gazelle fawns in the assemblage. Unlike gazelles and other mammals, tortoises grow throughout their lives, and thus changes in the average age of individuals in a population are reflected in their average body size. The average body size of the tortoise population from each of the studied assemblages is estimated using the average breadth of the narrowest point on the humeral shaft. The humerus is one of the primary weight-bearing bones in the body and therefore provides a good proxy for overall body-size (G. Hartman, 2006, personal communication). The tortoise humerus is a small element, but its distinctive hourglass shape provides a natural constriction that can easily be measured. The narrow length of this constriction makes it easy to pinpoint, and thus the measurements are highly replicable.

Finally, carcass processing intensity is evaluated by considering the completeness indices of gazelle first and second phalanges. Gazelle first and second phalanges contain marrow, but in quantities that are substantially smaller than those provided by the six major limb bones (Phalanx 1 = 0.17 g; Phalanx 2 = 0.03 g average in seven sampled animals; Bar-Oz and Munro, 2007). It is likely that the large gap between these two groups of elements represents a point of diminishing returns, beyond which humans were unlikely to invest in the cracking of bones for marrow unless necessary (Bar-Oz and Munro, 2007).

The percentage of broken first and second phalanges should reflect how willing humans were to invest in even small packages of bone marrow. Breakage, however, may also occur in response to other pre- and post-depositional forces. Fortunately, because foot bones are small, compact, and relatively dense in relation to other body-parts, they are less likely to break in response to most other pre- and post-depositional processes (Marean, 1991). The percent completeness of compact foot bones that have no nutritional value (astragalus and third phalanx) in five of the Epipaleolithic sites of interest (Hezibah, Nahal Hadera V, Early and Late Natufian Hayonim Cave and el-Wad Terrace) emphasizes this point. In these assemblages, the astragalus and third phalanx contain no marrow and have relatively high completeness ratios (81.6% for the astragalus and 74.6% for the third phalanx on average; Munro and Bar-Oz, 2005). Because of their low nutritional content and high bone mineral density, the breakage of foot bones that do not contain bone marrow (astragalus and third phalanx) is most likely caused by post-depositional rather than pre-depositional processes (Marean, 1991). Indeed, of the five Epipaleolithic assemblages, the lowest completeness values originate in open air sites where they were subject to greater disturbance by post-depositional fluvial action, weathering, and other factors (Munro and Bar-Oz, 2005). In summary, the completeness values for the astragalus and the third phalanx indicate that some degree of toe bone breakage occurs post-depositionally and is unrelated to marrow extraction. Nevertheless, breakage of the marrow-bearing first and second phalanges above and beyond these figures undoubtedly reflects human agents.

Temporal change in the intensification indices described above are depicted below in a series of graphs that present the results from relevant sites in chronological order from bottom to top. The time scale is not continuous because the occupation of some sites overlap in time, and the duration of site occupation, the rate of accumulation of material, and the amount of time between site occupations varies within and between sites. Nevertheless, these graphs provide good general indicators of the nature of subsistence change throughout the southern Levantine Epipaleolithic.

Results

Indices of Relative Taxonomic Abundance

Ungulate Index

The ungulate index indicates a clear, gradual increase in the abundance of small ungulates at the expense of medium and large ungulates across the Epipaleolithic periods (Figs. 10.2 and 10.3). A Spearman’s rank-order correlation coefficient indicates a statistically significant increase in the abundance of small ungulates from the Kebaran through the Late Natufian periods (Figs. 10.2 and 10.3; Spearman’s rho = 0.887, p < .0001, n = 11). Throughout the sequence, large ungulates make
only incidental appearances, and thus the bulk of this shift is in the relative abundance of medium and small ungulates. Patterened variation in the relative abundance of gazelle and fallow deer during the Paleolithic and Epipaleolithic was first observed by Dorothy Bate in the 1930s. Bate (Garrod and Bate, 1937) argued that the fluctuations in *Gazella:Dama* abundance reflected climatic changes and associated shifts in the distribution of forested and open habitats. Fallow deer favor forested, closed environments; therefore their numbers are expected to blossom during wet and warm periods, and contract during cool and dry periods. In contrast, gazelle favor open grassland habitats which expand during cool and dry climatic episodes. The majority of the Epipaleolithic coincides with a warming trend that begins after the Late Glacial Maximum (ca. 18,000 BP), and continues until the onset of the Younger Dryas, a major drying and cooling event contemporaneous with the Late Natufian phase (Baruch and Bottema, 1991; Bar-Matthews et al., 1999; Frumkin et al., 1999). In Fig. 10.2, fallow deer (medium ungulates) decline in abundance in relation to gazelles (small ungulates) throughout the Epipaleolithic sequence. Thus the pattern shown in the Epipaleolithic faunas is the opposite of what is expected if climate is driving ungulate abundances. While fluctuations in *Gazella Dama* abundance may be linked to climatic change in the preceding Paleolithic periods, this explanation does not hold up for the Epipaleolithic. Instead, the Epipaleolithic trend is unidirectional in nature and shows

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**Fig. 10.2.** Ungulate Index – Relative abundance of small, medium and large ungulates in Epipaleolithic assemblages from the southern Levant. Sites are arranged in chronological order from bottom to top. Cultural period abbreviations are as follows: KEB – Kebaran; GKEB – Geometric Kebaran; ENAT – Early Natufian; and LNAT – Late Natufian. Site abbreviations are as follows: MEGD – Meged Rockshelter; HAYC – Hayonim Cave; NHV – Nahal Hadera V; NVD – Neve David; HEFZ – Hefzibah; ELWC – el-Wad Cave; ELWD – el-Wad Terrace; HAYT – Hayonim Terrace; and HLZT – Hilazon Tacthit.

**Fig. 10.3.** The average abundance of small ungulates in the Kebaran, Geometric Kebaran, and Early and Late Natufian periods. The bars indicate one standard deviation. The trend toward increasing small ungulate abundance is statistically significant (Spearman’s rho = 0.887, p < .0001, n = 11).
no major interruptions, despite the pronounced climatic changes of the Younger Dryas.

The gradual decline in large and medium ungulate abundance despite favorable environmental conditions supports an interpretation of large game depression in the Epipaleolithic, especially during the Natufian period. The dramatic increase in gazelle abundance during the Natufian has classically been described as the beginning of a specialized gazelle economy (Davis, 1982, 1983; Cope, 1991; Tchernov, 1991, 1993). The results presented here demonstrate that the focus on gazelle is not the result of human selectivity, but a response to changing resource availability. Human-derived resource depression is argued to have depleted large and medium game assemblages, producing a landscape dominated by gazelle and other small game species. Fallow deer and larger animals were still collected when encountered, but clearly encounter rates declined substantially throughout the duration of this period. The shift in investment from the capture of higher-ranked large ungulates to lower-ranked gazelle reflects gradual intensification across the Epipaleolithic period.

**Small Game Index**

Despite some variability, there is a substantial increase in the proportion of low-ranked small game in relation to higher-ranked ungulates between the early Epipaleolithic and Natufian periods (Fig. 10.4). This florescence in small game abundance is undoubtedly the phenomenon that Flannery (1969) observed when he identified the broad spectrum revolution, although he did not quantify it at the time. Because the small game species that increase in abundance in the Natufian were also being captured in smaller numbers in earlier Epipaleolithic periods, this dietary expansion can not be detected using classic taxonomic diversity indices (Edwards, 1989; Neeley and Clark, 1993; Bar-Oz et al., 1999). Nevertheless, evidence for the BSR is abundant using other indicators of expanding dietary breadth including relative abundance indices, age profiles, and carcass processing strategies (Munro, 2003, 2004b). Like the ungulate index, the small game index depicts a decline in foraging efficiency and thus an intensification in human foraging strategies. In this case, however, the shift begins in the Natufian period rather than in the early Epipaleolithic and is likely partially linked to contemporaneous increases in site use intensity (see below).

**Fast Small Game Index**

Further evidence for intensification is apparent within the small game fraction itself (Fig. 10.5). The small game component is comprised of animals of similar body size. In this
case, relative cost effectiveness is differentiated by cost of capture, which varies according to escape strategy. Slow small game, namely tortoises, are highly ranked because they can be hunted more efficiently than fast small game species like hares and partridges. Although, fast small game were undoubtedly captured using special technologies (i.e., bow and arrow, traps, and nets), these technologies incur high production, maintenance, and acquisition costs. Although they may ultimately defray the cost of capture, operational costs are still substantially higher than the collection of tortoises using bare hands (Bailey and Aunger, 1989; Churchill, 1993; Lupo and Schmitt, 2002). Although hunting innovations enabled small shifts in small game acquisition early in the Epipaleolithic, they cannot account for the dramatic reversion in fast small game abundance in the Late Natufian when these technologies were clearly in use. Nor can they explain why technologies that existed in the early Epipaleolithic were not used in earnest until at least 7,000 years later in the Early Natufian period.

Figure 10.5 depicts an initial increase in the abundance of fast small game starting in the Late Kebaran period. Unlike the preceding two indices, the path of this index is not unidirectional. Although initially there is a clear trend toward intensification, the direction reverses and prey abundances return to Kebaran-like proportions in the Late Natufian phase. The ratio of slow to fast small game likely indicates something quite different than the preceding two indices. Because small game tends to be captured in local environments surrounding archaeological sites, it provides a more sensitive monitor of site use intensity (i.e., the degree of sedentism) than of region-wide resource depression. Changes in the fast small game index are thus argued to reflect an increase in sedentization during the Geometric Kebaran and Early Natufian periods, followed by a return to less permanent settlements and increased mobility in the Late Natufian, immediately preceding the origins of agriculture (Munro, 2004b). This interpretation is supported by numerous other archaeological indicators, in particular architectural investment, site size, diversity of material culture, and human burial patterns (Garrod and Bate, 1937; Belfer-Cohen, 1991; Valla et al., 1991; Bar-Yosef, 1996; Goring-Morris and Belfer-Cohen, 1998; Valla, 1998; Belfer-Cohen and Bar-Yosef, 2000; Grosman, 2003; Munro, 2003, 2004b).

Together, the relative abundance indices provide a nuanced picture of subsistence intensification throughout the Epipaleolithic period. All three indices indicate considerable
resource intensification both at the local and regional scale, especially between the Geometric Kebaran and Early Natufian periods. Although intensive region-wide subsistence strategies continue into the Late Natufian, they are accompanied by a drop in site occupation intensity.

Mortality Profiles

Gazelle Mortality Profiles

The proportion of gazelle fawns in hunted Epipaleolithic assemblages increases considerably – from less than 10% in the Geometric Kebaran and Kebaran periods to between 20% and 40% in the Early Natufian (Fig. 10.6). The hunting of high proportions of fawns is sustained (up to 45%) throughout the Late Natufian (up to 45%). The increased hunting of gazelle fawns, which are substantially smaller than adults, again indicates an intensified gazelle hunting regime. This trend corresponds exactly with the increase in the abundance of small game, confirming that humans expanded dietary breadth at this critical juncture by adding smaller, lower-ranked resources to the diet. By the Late Natufian, humans were actively hunting all available gazelle age classes. It is therefore not surprising that intensive gazelle exploitation was quickly followed by the adoption of domestic goat and sheep in the mid Pre-Pottery Neolithic B (Helmer, 1989; Legge, 1996; Bar-Yosef, 2000; Munro, 2004a). Because gazelles are not well-suited for domestication (Clutton-Brock, 1999; Diamond, 1999), the adoption of other small ungulate species more amenable to increased production through human selection was the only direction left to go for further extraction of ungulate products from Mediterranean environments.

Tortoise Body-Size Data

Although a clear decline in tortoise body-size exists from the Middle to the Upper Paleolithic to the Epipaleolithic period in the southern Levant (Stiner et al., 1999, 2000; Stiner, 2005), the diminution trend does not continue across the Epipaleolithic sequence (Fig. 10.7). All Epipaleolithic tortoise populations are smaller on average than Paleolithic populations, but seemingly random fluctuations in average body size occur within the Epipaleolithic sequence itself. The only obvious pattern that springs from the body-size...
data is an inverse relationship between average body-size and the proportion of tortoises in each assemblage. In other words, when the body size of the tortoises increases, there is a decrease in the abundance of tortoises in the assemblage and vice versa. This trend is not directly proportional, and likely reflects localized hunting pressure on tortoise populations. As hunting pressure, and hence the mortality, of a tortoise population in a given area grew, average body size became correspondingly smaller. This is the combined result of intentional human selection for the largest individuals in the population and the fact that smaller individuals did not have the opportunity to reach full body size before they were predated.

Interestingly, the fluctuations in tortoise body size do not correspond to the u-shaped pattern indicated by the fast small game index as might be expected. A decline in tortoise body size indicates increased hunting pressure, but in the case of Late Natufian populations, it was not sufficiently severe to have pushed humans to further broaden their diets by adding new resources. Thus, in the Epipaleolithic case, tortoise body size seems to be a better measure of local variation in hunting pressures than of overall foraging efficiency.

Gazelle Carcass Processing

Completeness values for gazelle first and second phalanges are available only for a subsample of the Epipaleolithic assemblages (Fig. 10.8a, b). The results inspire three noteworthy observations. First, the results vary tremendously among sites and do not follow a temporal trend. Second, in all cases the first and second phalanges from open air sites (Nahal Hadera V, Hefzibah, el-Wad Terrace, Hayonim Terrace) have lower completeness indices than those from cave sites (Hayonim Cave and Hilazon Tacttit). Third, in all cases the first phalanx, which contains considerably more marrow than the second phalanx, is breached more often. These observations lead to two conclusions regarding the cause of breakage of the gazelle phalanges. First, as previously mentioned, the degree of breakage of astragali and third phalanges which do not contain marrow and the high rates of breakage of first and second phalanges at open air versus cave sites indicate that postdepositional processes are responsible for some damage. Second, lower completeness values for first than second phalanges despite similar structural densities indicate that humans preferentially broke gazelle toes with higher marrow content. Nevertheless, the fact that on average 40.2% of first phalanges and 62.3% of second phalanges are complete, while gazelle marrow-bearing long bone shafts are complete less than 5% of the time (Munro, 2004b; Munro and Bar-Oz, 2005) indicates that there is indeed a point of diminishing returns in the extraction of gazelle bone marrow. The fact that humans still bothered to invest in the extraction of very small marrow stores even half of the time indicates an intensive marrow-extraction strategy that stopped just short of exhausting gazelle marrow supplies (Bar-Oz and Munro, 2007).

That long bone breakage was largely determined by marrow extraction is supported by additional data from select Epipaleolithic assemblages. At Nahal Hadera V, Hefzibah, Hayonim Cave, and el-Wad Terrace bone breakage (measured using NISP/MNE ratios) is significantly correlated with marrow content in gazelle long bones (Munro and Bar-Oz 2005; Bar-Oz and Munro, 2007). Furthermore, the relationship between bone fragmentation and marrow content is maintained across taxa and age groups in both the Early and Late Natufian layers at Hayonim Cave. In both Natufian layers, gazelle bones are substantially more fragmented than hare and partridge bones, which contain little or no marrow. The fragmentation of adult gazelle long bones from the same site is significantly greater than of juvenile gazelles, which use their long bone cavities more for red blood cell production than fat.
storage. More intensive fragmentation of hare (little marrow) than partridge bones (no marrow), despite similar body-size, indicates that humans still bothered to access small marrow stores at least half of the time, again attesting to an intensive marrow exploitation strategy (Bar-Oz and Munro, 2004; Munro, 2004b).

Other Parts of Southwest Asia

Although comparative data from other regions of Southwest Asia is rapidly increasing, the details required to replicate the analyses presented here are not currently available. One study (Munro, 2004a) on the small game faunas from sites dating to the agricultural “transition” in the Zagros region provides some comparative data, at least for the small game index. Unfortunately, this data provides only a small taste of how Epipaleolithic intensification trends are expressed in neighboring regions of Southwest Asia (Fig. 10.9).

The small game index presented in Fig. 10.9 represents a different time scale than that of the southern Levantine series. While, the oldest two sites (Palegawra, Asiab) are Late Epipaleolithic in age, the remaining sites (Ganj Dareh, Ali Gosh, Tepe Gurun, and Tepe Sarab) date to Aceramic and Ceramic phases of the Early Neolithic (Fig. 10.1; Table 10.2). Nevertheless, the data show a similar pattern to that depicted in the southern Levant, though on a more restricted scale. Epipaleolithic assemblages in the Zagros region are represented by rich collections of small game fauna which, like in the southern Levant, are comprised of partridge, hare, tortoises, and an additional species, the freshwater turtle, *Maurmys caspica*. Although the Epipaleolithic is represented by only two data points in Fig. 10.9, the comparison with Neolithic assemblages highlights the magnitude of the florescence in small game abundance. By the onset of the Aceramic Neolithic, small game animals begin to drop rapidly from human-collected assemblages. They are replaced by small ungulates, in this case sheep and goat, in the early stages of animal management and domestication. The innovation of herd management relaxed the need for the plethora of subsistence intensification strategies innovated in the Epipaleolithic. Herd animals quickly filled the top slot in the prey rankings, and because of their great productivity, and hence increased availability, eventually eliminated the need for broad diets. Thus, soon after the appearance of managed sheep and goat, small game take a sudden drop from their elevated position during the Epipaleolithic to become a periodic and likely opportunistic dietary supplement.

Although it provides only a single line of evidence, the small game index from the Zagros region suggests that at least some of the intensification strategies employed in the
southern Levant were practiced in other parts of the Fertile Crescent. Active research programs and zooarchaeological research investigating the “transition” to agriculture, especially in southeastern Anatolia, will hopefully soon fill out the picture of Epipaleolithic intensification in the broader Southwest Asian region in general.

Discussion

Together, several lines of evidence provide a robust picture for subsistence intensification during the Epipaleolithic of the southern Levant. Some aspects of the intensification process occurred steadily over the course of the Epipaleolithic, while others make a pronounced jump between the Geometric Kebaran and the Natufian periods. Gradual intensification across the Epipaleolithic is supported by both the ungulate and small game indices. A steady reduction in the abundance of high-ranked game and a simultaneous increase in the numbers of small ungulates and small game animals mark a classic expansion in dietary breadth and decreased foraging efficiency, beginning in the Geometric Kebaran and continuing into the Natufian periods.

Together, the small game index and gazelle age profiles evidence a prominent shift in the nature of resource extraction between the Geometric Kebaran and the Natufian periods.

**Table 10.2.** Site names, cultural phases and time ranges of the Zagros assemblages discussed herein.

<table>
<thead>
<tr>
<th>Site</th>
<th>Cultural period</th>
<th>Time range (cal BP)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sarab</td>
<td>Ceramic Neolithic</td>
<td>9,000–8,000</td>
<td>Bölönyi, 1977; Munro, 2004a</td>
</tr>
<tr>
<td>Guran</td>
<td>Ceramic Neolithic</td>
<td>9,000–8,000</td>
<td>Flannery, n.d.; Munro, 2004a</td>
</tr>
<tr>
<td>Ali kosh</td>
<td>Ceramic Neolithic</td>
<td>9,000</td>
<td>Hole et al., 1969; Munro, 2004a</td>
</tr>
<tr>
<td>Guran</td>
<td>Aceramic Neolithic</td>
<td>9,200–9,000</td>
<td>Flannery, n.d.; Munro, 2004a</td>
</tr>
<tr>
<td>Ali kosh</td>
<td>Aceramic Neolithic</td>
<td>9,400–9,000</td>
<td>Hole et al., 1969; Munro, 2004a</td>
</tr>
<tr>
<td>Ganj Dareh</td>
<td>Aceramic Neolithic</td>
<td>9,900–9,700</td>
<td>Hesse, 1978; Munro, 2004a</td>
</tr>
<tr>
<td>Asiab</td>
<td>Epipaleolithic</td>
<td>10,700</td>
<td>Bölönyi, 1977; Munro, 2004a</td>
</tr>
<tr>
<td>Palegawra</td>
<td>Epipaleolithic</td>
<td>15,000–11,500</td>
<td>Turnbull and Reed, 1974; Munro, 2004a</td>
</tr>
</tbody>
</table>

**Fig. 10.9.** Relative abundance of ungulates and small game in Epipaleolithic and Early Neolithic assemblages from the Zagros region. Sites are arranged in chronological order from bottom to top. Cultural period abbreviations are as follows: EPIP – Epipaleolithic; ACRM – Aceramic Neolithic; CERM – Ceramic Neolithic. Site abbreviations are as follows: PLGW – Palegawra; ASIB – Asiab; GANJ – Ganj Dareh; ALIK – Ali Kosh; GURN – Tepe Guran; SARB – Tepe Sarab.
Because early Epipaleolithic foragers had already depressed populations of the most highly ranked animals such as fallow deer and red deer, the Natufians first intensified game extraction by boosting their exploitation of gazelle – the most abundant ungulate on the landscape by this time. Gazelle intensification is marked first by an expansion in the demographic spectrum (i.e., the range of age groups) included in the hunted population. In particular, this includes the unprecedented hunting of fawns that are substantially smaller than adults. Fawns not only make their first appearance in the Natufian period – very few fawns were consumed in the preceding Paleolithic and Epipaleolithic (Bar-Oz, 2004; J. Speth, 2004, personal communication; Stiner, 2005) – they also appear in considerable numbers. In addition, the Natufians consumed greater percentages of older juvenile gazelles (6–18 months of age) than preceding foragers (Munro, 2004b). The exploitation of older juvenile gazelles increases gradually throughout the Epipaleolithic, again peaking in the Natufian period. Finally, gazelle utilization was also intensified by maximizing the use of individual animal carcasses. Virtually all marrow-bearing gazelle long bones were breached to remove bone fat, and even small marrow supplies from gazelle first phalanges were extracted at least half of the time.

In addition to intensifying gazelle exploitation, the Natufians increased their extraction of animal biomass from their environments in relation to preceding Epipaleolithic and Paleolithic periods. This move is indicated by the addition of progressively more costly species to the hunting repertoire – most importantly hares, partridges, and waterfowl, which require the use of special technologies for their capture. Together, the adoption of these new hunting and processing strategies contributed to an overall increase in the total amount of energy that the Natufians extracted from their environments per unit area, albeit at a greater total expense.

The dual nature of the Epipaleolithic intensification trend (i.e., gradual intensification throughout much of the Epipaleolithic and a punctuated leap in the Early Natufian) indicated by the faunal data is supported by the archaeological record. The Epipaleolithic record is characterized by a series of major developments, including the expansion of human populations, increased site permanence, and documented resource intensification evidenced by an increased abundance of groundstone tools, sickle blades, small grain grass seeds, and small animals (Henry, 1989; Bar-Yosef and Belfer-Cohen, 1989, 1991; Tchernov, 1993; Bar-Yosef and Meadow, 1995; Stiner et al., 1999, 2000; Belfer-Cohen and Bar-Yosef, 2000; Munro, 2004a, b; Weiss et al., 2004). These processes intensify over the course of the Epipaleolithic, but the most dramatic changes coincide with the onset of the Early Natufian. The Early Natufian is characterized by the establishment of a number of large settlement sites in the Mediterranean zone, which are typically classified as “basecamps” due to their more permanent nature, size, and diverse material culture (Bar-Yosef and Belfer-Cohen, 1989, 1991). These sites are on a scale of magnitude larger than those occupied in previous periods, and reflect both a shift in the organization of human populations into more aggregated, permanent settlements, and an increase in human population size in the Mediterranean region in general.

For the most part, the data presented here depict unidirectional changes, indicating a one-way intensification trend through time. Despite major climatic changes during the Epipaleolithic, this trend in resource intensification crosscuts major climatic and environmental events. There is, however, one anomaly in the otherwise unidirectional trend. In the Late Natufian, there is a reversion in the ratios of fast to slow small game to more Kebaran-like proportions. This reversion suggests that despite continued intensive hunting at the regional scale, as attested by the ungulate and small game indices and the gazelle age data, there was a change in site use intensity. The fast small game index suggests that people settled down into increasingly permanent villages and had greater impacts on local environments starting in the Geometric Kebaran and continuing through the Early Natufian, but that they reverted to a more mobile settlement pattern in the Late Natufian phase. This shift is supported by numerous lines of archaeological evidence (see above) and corresponds to the onset of the Younger Dryas. The Younger Dryas had a drying and cooling effect on the southern Levant and likely altered the distribution of resources, in particular wild grasses whose distribution was undoubtedly a major determinant in the location and duration of occupation of local villages (Bar-Yosef, 1996). Increased mobility will alleviate human pressure on the environments surrounding habitation sites as fewer local resources are harvested and longer recovery periods occur between exploitation episodes. Pressure on large game resources, however, would not have been alleviated as human populations continued to range over wide territories more on par with those of the largest game themselves. This shift in occupation intensity explains why the dramatic Late Natufian shift in the fast small game index is the only major change in the otherwise unidirectional trend toward intensification.

In the Late Natufian phase, humans continued to intensively exploit animals on a regional scale, but there was a brief respite when pressures on local resources lessened. This respite, however, occurred only in localized patches and on small animal resources within the Natufian landscape. Although the leap in intensification at the regional level that occurs with the onset of the Early Natufian continues into the Late Natufian phase, it does not strengthen, but instead levels off. Thus, the intensification trend that ultimately culminates in the origins of agriculture does not actually increase in the period immediately prior to the “transition.” The Late Natufians chose mobility, rather than animal management and agriculture, as an immediate solution to the environmental restrictions imposed by the Younger Dryas. Agriculture did not become a viable option until conditions became warmer, wetter, and more stable in the early Holocene (Richerson et al., 2001). Thus, although resource stress or population pressure and corresponding intensification trends were crucial
ingredients in the “transition” to agriculture, they proved to be only one of several necessary conditions. The faunal data indicate that the favorable environment provided by a more stable Holocene climate was a second essential factor.

By the Natufian period, the faunal record indicates that there was little place to go to further intensify hunting strategies. Humans were already hunting small, costly species, and the full spectrum of gazelle age groups, and were squeezing the nutrients out of gazelle carcasses. The natural next step along this intensification trajectory was the management of herd animals. Unlike gazelles, sheep and goat are well disposed for this task (Clutton-Brock, 1999; Diamond, 1999), and by ca. 10,000 cal bp managed sheep and goat populations had entered the southern Levant from the north (Helmer, 1989; Legge, 1996; Bar-Yosef, 2000). The role of intensive hunting in the process of animal domestication and the “transition” to agriculture remains poorly understood, and is thus the subject of more detailed investigation under the auspices of the recently launched gazelle project. The gazelle project investigates the impacts of intensive human hunting on Epipaleolithic and Early Neolithic gazelle population structure, body-size and allometry, and how these impacts may have contributed to the domestication process.

Conclusion

Multiple lines of evidence provide a robust picture of faunal resource intensification during the Epipaleolithic periods in the southern Levant and likely also in other parts of Southwest Asia. Despite the growing clarity of the Epipaleolithic intensification process in the southern Levant, the fine details required for comparative analyses are only beginning to surface in neighboring regions. Nevertheless, emerging evidence suggests that similar intensification processes occurred elsewhere in Southwest Asia and served as important precursors to animal domestication (Rosenberg et al., 1998; Ervynck et al., 2002; Munro, 2004a). The origin of agriculture represents the natural next step in the intensification trend that pushed natural resources, in particular gazelle, to their limits by the Natufian period. Agriculture, however, was not adopted until a few thousand years after this point, indicating that several ingredients — including resource pressure and stable climatic conditions — had to coalesce to enable the “transition” to agriculture.

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References


