Increasing the resolution of the Broad Spectrum Revolution in the Southern Levantine Epipaleolithic (19–12 ka)

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ABSTRACT

We analyze terminal Pleistocene archaeofaunal diversity trends in the Southern Levant by examining eight Epipaleolithic (ca. 19–12 ka) assemblages from the Western Galilee/Mt. Carmel, Israel subregion. We test predictions from a Broad Spectrum Revolution model of the population dynamics of human foragers and their prey. The study emphasizes control over geographic variability and archaeological recovery and recording methods, as we analyze a time series that samples the Epipaleolithic more fully than have previous studies. This provides a new opportunity to examine human population and economic change in the long-term transition to sedentism and agriculture.

We use the Mantel test to evaluate the significance of temporal trends in body-size-based big game diversity, as well as in diversity of small game prey types. Results demonstrate a highly significant decline through time in the relative abundance of medium and large big game, measured relative to small big game. This suggests that the apparent “gazelle specialization” by Late Epipaleolithic (Natufian) hunters reflects longer-term anthropogenic overexploitation of the largest prey types in the spectrum. While large and medium big game abundance declined, our results show small game increased in economic importance over time.

Considered with associated climate change data, the results provide substantial support for the hypothesis that local human populations expanded rapidly in size after the Last Glacial Maximum (LGM). We suggest that following the post-LGM population pulse, human foragers adopted a shifting series of intensification strategies mediated by changes in residential mobility.

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Introduction

In Southwest Asia the timeframe 19–12 ka encompassed key developments in what Flannery (1969) initially described as the “Broad Spectrum Revolution” (BSR). In his classic review of long-term foraging and food production development in the prehistoric Near East, he suggested that late Pleistocene hunter-gatherers underwent an important pre-agricultural shift away from ungulate big game, toward smaller, more expensive-to-acquire animal and plant food packages. Indeed, in Southwest Asian Upper Paleolithic and Epipaleolithic research—covering the period ca. 45–12 ka—archaeozoological and botanical analyses indicate that broad spectrum resources were diverse, including hare, game bird and waterfowl, fish and shellfish, and a wide diversity of wild grains, lentils, and other plant resources (Pichon, 1991; Kislev et al., 1992; Simmons and Nadel, 1998; Stiner et al., 1999, 2000; Hillman et al., 2001; Stiner, 2001, 2005; Stiner and Munro, 2002; Munro, 2003, 2004; Weiss et al., 2004; Savard et al., 2006).

As Stiner (2001) has since argued, the BSR concept may be fundamentally important in archaeological studies of long-term hunter-gatherer population and economic dynamics (see also Stiner and Munro, 2002). Starting with the general prey—or diet breadth—model in foraging theory (see Stephens and Krebs, 1986; Winterhalder, 1986), Stiner suggests that broad spectrum foraging was inextricably tied to a series of human population growth pulses, ranging from local to supra-regional in geographic scale (Stiner et al., 1999, 2000; Stiner, 2001, 2005). If human demographic growth reached a critical rate, then predation pressure on the energetically richest, largest prey types would have increased, thereby depressing those prey populations. Facing declining availability of preferred food resources, human foragers would have increased effort to obtain smaller, harder to capture/process prey types (see also Bettinger, 1993; Richerson et al., 2001). Thus, the BSR concept was initially presented as a synthetic archaeological observation—one that challenged the environmentally focused models of Childe and Braidwood (Flannery, 1969). Yet, the BSR may...
also be defined as a dual evolutionary ecological model—one that depicts the human behavioral response to changes in food resource availability, while also causally linking the population dynamics of human foragers to the demography of their prey (Stiner, 2001). In this article we further explore the BSR model, zooming in on a subregion of Southwest Asia, as we present new analyses of archaeofaunal time-series data from eight assemblages dated to the Epipaleolithic timeframe 19–12 ka in the Southern Levant (Tables 1 and 2; Fig. 1).

With improved sampling of Southern Levantine assemblages, this study builds on recent work (Munro, 2001, 2004; Stiner, 2001, 2005), as we present a more comprehensive test of the BSR model’s main hypothesis—that a human population growth pulse contributed significantly to the now well-documented broad spectrum pattern of intensified small game foraging. In investigating a region and time period for which archaeobotanical preservation is generally poor and patchy (but see Kislev et al., 1992), we use observations on multiple big and small game prey categories in testing the population-growth-pulse hypothesis.

The BSR model more specifically predicts that if human impact on preferred large prey types rose sufficiently, then the “biggest of the big” would have initially declined in availability. Archaeozoological assemblages are expected to reflect the impact of a population pulse and resulting overharvesting of preferred prey types. Over time, assemblages should incorporate smaller and smaller proportions of larger big game taxa. In the Upper Pleistocene of the Southern Levant, such taxa included aurochs (Bos primigenius), red deer (Cervus elaphus), and Persian fallow deer (Dama mesopotamica). We suggest that such a decline in medium and large ungulate availability would be especially apparent when measured relative to small ungulate abundance (e.g., mountain gazelle, Gazella gazella). The BSR model also predicts that if humans consequently added less nutritionally rewarding small prey to the diet, then cultural deposits of animal food remains would include not only a greater proportion of small game specimens; they would also incorporate a wider diversity of smaller, difficult-to-capture taxa, such as chukar partridge (Alectoris chukar) and hare (Lepus capensis; Stiner, 2001).

While the latter prediction has been supported by recent work on the Southern Levantine Epipaleolithic period, the former expectation—that of big game depression—has not been subject to detailed quantitative analysis. The Mantel test, as extended by Sokal and colleagues (see Smouse et al., 1986; Smouse and Long, 1992; Sokal and Rohlf, 1995), offers a robust, non-parametric statistical approach for analyzing change through time. We use the Mantel test, first, to evaluate in greater detail how small game foraging changed during the Epipaleolithic period. We then use Mantel test analyses to address whether our time series of faunal assemblages shows a significant relative decline in big game—especially larger big game—in association with the rise in small game.

In the Southern Levant the timeframe 19–12 ka did not only encompass a well defined increase in broad spectrum small game foraging. We also see the regional environmental impact of global terminal Pleistocene climatic fluctuations (Bar-Matthews et al., 1999, 2003; Bar-Yosef, 2000; Bar-Yosef and Belfer-Cohen, 2002).

Table 1
Southern Levantine Epipaleolithic faunal assemblages analyzed in this study.

<table>
<thead>
<tr>
<th>Site</th>
<th>Code</th>
<th>Age (ka)</th>
<th>Archaeological culture</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nahal Hadera V</td>
<td>NHV</td>
<td>18.5</td>
<td>Kebaran</td>
</tr>
<tr>
<td>Neve David</td>
<td>NVD</td>
<td>17.0</td>
<td>Geometric Kebaran</td>
</tr>
<tr>
<td>Hefizibah</td>
<td>HFU</td>
<td>17.0</td>
<td>Geometric Kebaran</td>
</tr>
<tr>
<td>El Wad Cave</td>
<td>EWC</td>
<td>14.5</td>
<td>Early Natufian</td>
</tr>
<tr>
<td>Hayonim Cave</td>
<td>HCE</td>
<td>14.5</td>
<td>Early Natufian</td>
</tr>
<tr>
<td>Hayonim Cave</td>
<td>HCL</td>
<td>13.0</td>
<td>Late Natufian</td>
</tr>
<tr>
<td>Hayonim Terrace</td>
<td>HVT</td>
<td>13.0</td>
<td>Late Natufian</td>
</tr>
<tr>
<td>Hilazon Tachtit</td>
<td>HZT</td>
<td>13.0</td>
<td>Late Natufian</td>
</tr>
</tbody>
</table>

Just as striking, we see hallmark cultural changes—including key organizational and technological innovations—in the long-term transition to agriculture. Innovations include the proliferation of microlith technology, associated with the adoption of sickles, the bow and arrow, and probably a variety of other compound tools; increased production and use of groundstone bowls, mortars, slabs, and pestles for plant food processing; and settlement of the earliest long-term reoccupied seasonal and sedentary basecamps, specifically in the Early Natufian period (15–14 ka; Goring-Morris, 1987, 1995; Bar-Yosef and Belfer-Cohen, 1989; Wright, 1994; Bar-Yosef, 1998; Goring-Morris and Belfer-Cohen, 1998, 2003; Dubreuil, 2004). Moreover, in the 19–12 ka period in the Southern Levant, long-distance exchange became more common, and community mortuary ritual practices were elaborated and regularly associated with larger base camp sites, as well as with smaller cave sites.

Fig. 1. Epipaleolithic sites included in the analysis, viewed in regional geographic context.
(Goring-Morris, 1987, 1995; Weinstein-évron et al., 1999; Goring-Morris and Belfer-Cohen 2002; Grosman, 2003; Grosman and Munro, 2007). From the perspective of studying the long-term emergence of agriculture—where it remains a major scientific challenge to tease apart the exogenous impact of climate change and the endogenous systemic interactions among demographic, economic, sociopolitical, and even religious factors—the Broad Spectrum Revolution model provides just one relevant frame of reference. Yet, grounded theoretically in evolutionary ecology, the BSR model clearly defines archaeozoological predictions for our Southern Levantine Epipaleolithic case study. As a heuristic, the BSR model supports an explicit methodology for clarifying the role of human population dynamics in the emergence of sedentism and agriculture.

Materials

The Epipaleolithic faunal assemblages in this study are summarized in Tables 1 and 2 and Figure 1. Details of their archaeological contexts and taphonomic patterns are described elsewhere (Munro, 2001, 2004; Bar-Oz, 2004; Munro and Bar-Oz, 2005). As shown in Figure 2, the main prey types are ranked (from top to bottom) in order of increasing post-encounter caloric return rate (Stiner and Munro, 2002). The prey types are represented by a total of 56,968 identifiable bone specimens (see Table 2). The online supplemental information presents the methods used to calibrate radiocarbon dates and estimate the median archaeological period ages used in the time series analysis (Supplementary Online Material [SOM] for this article can be found in the online version at doi: 10.1016/j.jhevol.2008.10.004).

Archaeozoological assemblages

The assemblages were recovered from excavations with 50 × 50 cm square grid horizontal control and 5 cm arbitrary levels. Macromammals remained recovered through dry and wet screening with 2 mm mesh. Cleaning and identification of bone fragments, for all skeletal parts of all prey types, were carried out with closely identical methods, for both NDM and GBO’s study assemblages (see Munro and Bar-Oz, 2005: 227).

Table 2

<table>
<thead>
<tr>
<th>Body Size (kg)</th>
<th>Escape behavior</th>
</tr>
</thead>
<tbody>
<tr>
<td>Game Bird</td>
<td>0.5 fast</td>
</tr>
<tr>
<td>Hare</td>
<td>1 fast</td>
</tr>
<tr>
<td>Spur-Thighed Tortoise</td>
<td>1 slow</td>
</tr>
<tr>
<td>Small Big Game</td>
<td>20-50</td>
</tr>
<tr>
<td>Medium Big Game</td>
<td>80-200</td>
</tr>
<tr>
<td>Large Big Game</td>
<td>200-800</td>
</tr>
</tbody>
</table>

The assemblages span virtually the entire classic Southern Levantine Epipaleolithic sequence, from the Kebaran through Late
Natufian archaeological cultures as defined for the Mediterranean vegetation zone in the region (see Table 1; Bar-Yosef, 1970). Here, we emphasize some concerns relevant to the population growth-pulse hypothesis (for a broader recent review and discussion of the Levantine Epipaleolithic, including the Mediterranean and adjacent semi-arid zones, see Goring-Morris and Belfer-Cohen, 1998, 2002, 2003; Belfer-Cohen and Goring-Morris, 2002). Settlement pattern and site-use studies indicate that from the Kebaran through the Early Natufian residential mobility declined, while maximum base camp size and intensity of occupation increased (Hovers, 1988; Bar-Yosef and Belfer-Cohen, 1989; Kaufman, 1992). Several lines of evidence, including architectural and mortuary features, suggest a return to greater residential mobility in the Late Natufian (Goring-Morris and Belfer-Cohen, 1998, 2003; Bar-Yosef and Belfer-Cohen, 2002). Indeed, researchers have recently emphasized that the initial settlement of intensively reoccupied or year-round base camps at ca. 15–14 ka did not simply precipitate an unabated long-term rise in settlement aggregation (Belfer-Cohen and Bar-Yosef, 2000; Bar-Yosef, 2002; Munro, 2003, 2004).

We are especially interested in investigating big game resource depression and foraging intensification in the context of Early Natufian sedentism. Here, “sedentism” may be broadly but succinctly defined as reflecting recurrent habitation of seasonal or multi-seasonal base camps (Bar-Yosef and Belfer-Cohen, 1989; Valla, 1998; Hardy-Smith and Edwards, 2004). The physical size, social scale, and intensity of Early Natufian base camp occupation were substantially greater than that for the Kebaran and Geometric Kebaran periods (Bar-Yosef and Belfer-Cohen, 1989; Goring-Morris and Belfer-Cohen, 2003). Archaeological markers associated with sedentism exist in Kebaran and Geometric Kebaran deposits, but they occur sparsely. These indicators include groundstone mortars and pestles, shelters with simple stone foundations, and human burials, usually under house or structure floors (Wright, 1994; Goring-Morris and Belfer-Cohen, 2003; Dubreuil, 2004). All of these features are much more abundant and diverse in the Early Natufian, especially in the four very well-studied Early Natufian base camp sites of el-Wad, Hayonim Cave, Ain Mallaha, and Wadi Hammeh 27 (Goring-Morris and Belfer-Cohen, 2003). Late Natufian changes in settlement and mobility appear to have been complex. The EN-LN shift involved a spread of base-camp/logistical foraging strategies into new areas of the Levant, including the northern portion and the southern marginal zones (see Goring-Morris, 1987, 1991, 1995; Henry, 1989; Bar-Yosef, 1998; Goring-Morris and Belfer-Cohen, 1998, 2003; Moore et al., 2000). It is notable, though, that especially at el-Wad and Hayonim Cave, the long occupational sequences indicate a clear change in site use from Early Natufian base camp to Late Natufian mobile camp (Belfer-Cohen, 1988; Weinstein-Evron, 1998).

Paleoclimatic context

Our time series spans a period of dramatic climate change. This reflects global, hemispheric, and local developments (Rossignol-Strick, 1995; Bar-Matthews et al., 1999, 2003; Andersen et al., 2006; Rasmussen et al., 2006; Svensson et al., 2006). The Kebaran archaeological culture emerges roughly contemporaneously with the end of the Last Glacial Maximum (LGM). After 19 ka, climate in the Levant became warmer and somewhat wetter. The Geometric Kebaran period may have begun during this post-LGM warming trend, but it spans a break in this trend that began around 17.5 ka (Bar-Matthews et al., 1999; cf. Nadel et al., 2001). The reversal toward a cooler, drier climate was influenced by a series of major North Atlantic ice discharge episodes, known collectively as the Heinrich 1 event (17.5–16.0 ka; Bard et al., 2000; Alley and Agustsdottir, 2005). Correlated with the Older Dryas in northern Europe, Heinrich 1 is well dated in North Atlantic ice and deep sea cores (Vidal et al., 1997; Bard et al., 2000; Andersen et al., 2006). It is unclear whether the Geometric Kebaran archaeological culture persists into the subsequent period of rapid climatic amelioration after 16 ka.

The Early Natufian is clearly centered on the warm and wet phase that is contemporaneous with the Bölling-Allerød interstadial in Northwestern Europe (Bar-Matthews et al., 1999, 2003). This period was likely marked by further expansion of the oak-pistachio forest zone. Yet, atmospheric CO2 levels were rising, as a fully interglacial Mediterranean climate regime emerged. During the time period 15–14 ka, the Southern Levant may also have seen more microenvironments suitable for a diversity of large-seed C3 annual grasses, especially wild wheat and barley (Henry, 1989; Wright, 1994; Moore et al., 2000; Hillman et al., 2001; Richerson et al., 2001). In the western Galilee/Mt. Carmel region on which our study focuses, Mediterranean forest plant species would have benefited from higher environmental productivity during the Early Natufian period (Weinstein-Evron, 1998).

The role of climate forcing in the cultural shift to the Late Natufian is a subject of some debate. At least some Late Natufian sites were clearly occupied during the globally documented Younger Dryas (YD) climatic event, quite precisely dated to 12.9–11.7/11.6 ka (Baal et al., 2002; Rasmussen et al., 2006). Hilaçan Tachtit Cave, included in this study, is among these sites (Grosman, 2003; Grosman and Munro, 2007). The YD resulted in more than a millennium of cooler, drier conditions throughout the Levant (Bar-Yosef, 2000). The clear YD signal in Southern Levantine paleoclimatic records (Bar-Matthews et al., 1999; Frumkin et al., 2000; Cohen-Seffer et al., 2005) raises an obvious but important, hypothesis that the Late Natufian archaeological culture reflects a stress response to a climate-driven decline in environmental productivity (Bar-Yosef, 2000; Munro, 2003, 2004; but see Lev-Yadun and Weinstein-Evron, 2005). However, many 14C dates from Late Natufian archaeological deposits unambiguously predate the YD (Fig. 3). The YD appears to have had some effect on Late Natufian societies, but it remains unresolved whether the YD triggered the initial Late Natufian return to greater residential mobility.

Methods

Measuring prey type abundance

We use NISP count indices, summarized in Table 4, to measure variation in relative abundance for the six prey types defined in Table 3. We predict that sustained big game resource depression will generate a signal of significant long-term decline in medium and large big game abundance (primarily fallow deer and wild cattle, respectively), and we measure abundance in these prey types relative to small big game (mainly mountain gazelle). This approach yields conservative recognition of overall big game resource depression, because it purposely does not measure resource depression in small ungulate prey. Thus, the “small ungulate standard” makes a false positive identification of long-term big game resource depression less likely.

### Table 3

<table>
<thead>
<tr>
<th>Southern Levantine faunal taxa included in the main prey types.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Prey type</strong></td>
</tr>
<tr>
<td>Terrestrial fast small prey</td>
</tr>
<tr>
<td>Avian fast small prey</td>
</tr>
<tr>
<td>Terrestrial slow small prey</td>
</tr>
<tr>
<td>Small big game</td>
</tr>
<tr>
<td>Medium big game</td>
</tr>
<tr>
<td>Large big game</td>
</tr>
</tbody>
</table>

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Our NISP-based relative abundance measures also have an advantage in dealing with an important potential source of equifinality—that of climate change. The measurement of medium big game relative abundance, *I*<sub>mbg</sub> (see Table 4), is analogous to Bate’s classic *Dama*–*Gazella* index. She recognized that fallow deer tend to browse in more forested environments, while mountain gazelle are mixed feeders with a preference for more open environments (Mendelssohn, 1974; Mendelssohn and Yom-Tov, 1999). Bate made a now-classic suggestion: the archaeozoological abundance of *Dama*, measured relative to *Gazella*, would have increased or decreased as climate forced expansion or contraction of Mediterranean forest (Garrod and Bate, 1937). Levantine prehistorians have long debated Bate’s proposal (Higgs, 1967; Ducos, 1968; Tchernov, 1968, 1979; Henry, 1975; Davis, 1982, 1987; Garrard, 1982; Bar-Oz et al., 1999; Speth and Tchernov, 2002; Bar-Oz, 2004; Stiner, 2005). In general, climate change—and its effects on prey abundance and distribution—may cause significant variations in archaeozoological relative abundance profiles (cf. Grayson et al., 2001; Grayson and Delpech, 2003). We emphasize that in the context of the post-LGM depression, we can obtain greater resolution of the same independently measured baseline used to measure larger big game levels, coupled with declines in large and medium big game levels, then we may conclude strong support for the population growth pulse model. By comparing fast and slow small game to the same independently measured baseline used to measure larger big game relative abundance, we can obtain greater resolution of a changing long-term response to ungulate population resource depression.

### Statistical methods

We use the Mantel matrix correlation test to evaluate changes in prey type abundance across the faunal assemblage time series. The Mantel test may be generally unfamiliar to archaeologists, but we...
adopt it for methodological reasons outlined here. We note that the test is widely used in biological anthropology, population genetics, and biostatistics (for a recent example, see Sokal and Thomson, 2006). It is based on a mathematically and conceptually straightforward non-parametric approach, which flexibly incorporates linear regression, correlation, and analysis of variance. Involving a simple random matrix-element permutation procedure, the Mantel test yields p-values that are valid in the context of the observed data, even when critical aspects of those observations violate the assumptions of standard parametric linear regression and correlation models (for a review, see Smouse and Long, 1992).

In the context of our case study, assemblages from similar time periods may display temporal autocorrelation patterns. In addition, assemblages from the same time period may not represent independent samples of human foraging behavior. For example, sites could have been occupied by different groups sharing a closely monitored and defended territorial boundary. Also, the analysis of standard NISP relative abundance indices (which vary between 0 and 1) may be straightforward and intuitive to archaeologists. Yet, random variation in such variables can easily deviate from a normal distribution when we compare values that are close to 0 or 1. Finally, we note that rank correlation statistics—including Spearman’s rho and Kendall’s tau—may often give similar results to the Mantel test, but they cannot take into account variation in absolute temporal distances between different assemblages. Moreover, unlike rank correlation measures, the Mantel method can measure partial correlations, providing associated p-values. In this study we use partial correlations to add additional interpretations of our main results.

Here, we present a brief technical description. Additional details may be found elsewhere (Smouse et al., 1986; Sokol and Rohlf, 1995). Each of our k = 8 assemblages can be described quantitatively by its approximate median calendar age, tk (see Table 1 and SOM), and the different prey-type relative abundance indices defined above (see Table 4). This yields prey abundance variables m = 1 . . . 6 and calendar age, t. For each variable, m, we define the above diagonal elements of a k x k matrix, Dm, as the distance of row assemblage i from column assemblage j, so that for all pairwise assemblage comparisons in which j > i, we define Dmi = xmin – xij. Here, x is the value of the mth variable in the ith or jth assemblage. We define an analogous above-diagonal temporal distance matrix, D, based on the difference in approximated calendar ages between assemblages i and j.

We follow the method introduced in Smouse et al. (1986) to define and measure the correlation coefficient, r, and slope, b, between any two matrices Dk and Dl. We also define and measure temporal correlation coefficients, rkl and regression coefficients (that is, slopes), bkl, between each Dm and Dl. We use Monte Carlo simulation, with 10,000 repeated random permutations of both matrices being compared. In this procedure we estimate the probability, p, that the observed r2 or b value is the result of essentially random, independent association between the two variables of interest. We use both the b1 and r2 values as test statistics for evaluating the significance of temporal trends, in comparison of each Dm with Dl. We use r2 as the test statistic for evaluating the significance of observed positive or negative correlations between two relative abundance indices.

Following inspection of the temporal correlation results, we use additional Mantel test applications to investigate two informative, potentially significant patterns. First, we examine partial correlation coefficients (Smouse et al., 1986: 630), which can provide independent arguments concerning the hypothesized causal link between ungulate prey depression and intensification. Second, for cases where a particular index appears to fluctuate significantly in multiple directions through time, we use the modified ANOVA approach to matrix correlation suggested by Sokal and Rohlf (1995: 818). This approach allows us to examine how chronological period contributes to variation in the given relative abundance index, independent of that period’s temporal distance from other periods. It provides a valid analysis of between-period change, even when no single significant linear time-trend is observed.

**Results**

The Epipaleolithic time series studied here provides evidence that in the Southern Levant, the human foraging spectrum widened substantially around 15 ka with the transition to the Early Natufian archaeological culture (Stiner, 2001, 2005; Munro, 2004). In the sampled archaeozoological assemblages, total small game increased significantly through time in relative abundance. At the same time, larger big game exhibits a significant long-term decline (Fig. 4, Table 5). This pattern is consistent with the basic behavioral predictions of the BSR/population growth-pulse hypothesis. The foraging spectrum appears to have widened as preferred big game resources declined in availability (Munro, 2004).1

The more detailed, size-based big game prey type indices (lhg and Ilbg) also follow temporal trends that fit the predictions of the population growth-pulse hypothesis. The decline in larger big game levels is almost entirely accounted for by a drop in medium big game relative abundance (Fig. 5; see Table 5). Large ungulates (measured by lqg) appear to have been rarely encountered throughout the Epipaleolithic period. This pattern is fully consistent with big game population depression. At the same time, these results fit poorly with the hypothesis that climate-induced shifts in habitat distribution drove the changes in medium big game (mainly fallow deer) relative abundance. As discussed above, the climate forcing hypothesis—when updated according to recent paleoclimatic data—predicts constant or increasing medium large game abundance, at least from the Kebaran to the Early Natufian. We observe the opposite trend in our time series.

Visual inspection of Figure 5 indicates that the decline in medium big game relative abundance continued at roughly a linear rate throughout the study period. This observation is supported by the high negative temporal correlation coefficient for the fallow deer-dominated Ilbg (Table 5). Yet, the long-term rise in overall small game abundance is defined by a substantial leap from the Kebaran/Geometric Kebaran periods to the Early/Late Natufian periods (that is, roughly between 16–15 ka; Fig. 4). Moreover, the increase in small game masks a somewhat more complicated pattern, in which fast versus slow small prey contribute differentially through time to human foraging patterns. As shown in Figure 6, hare and partridge initially drive the broad spectrum shift in the Early Natufian period. Yet, they decline markedly in relative abundance in the transition to the Late Natufian, after ca. 13.5 ka (Munro, 2001, 2004). When we group the assemblages into three time periods, combining Kebaran and Geometric Kebaran (so that we have pre-Natufian [n = 3], Early Natufian [n = 2], and Late Natufian [n = 3]), a Mantel test of...

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1 Even within the Mt. Carmel/Western Galilee subregion, our assemblages exhibit two geographic clusters, which coincidentally also tend to represent two time periods. With the exception of the el-Wad Cave Early Natufian assemblage, the Mt. Carmel sites fall into the Kebaran and Geometric Kebaran periods. The Western Galilee sites all fall into the Early and Late Natufian periods. Is it possible that the variation we have documented is actually shaped by geographical factors? In other words, was the Mt. Carmel area simply richer in fallow deer and poorer in smaller game during the Epipaleolithic? We suggest that this is unlikely. Work by Stiner (2005) and Speth and Tchernov (2002) demonstrates that in earlier periods—from the early Middle Paleolithic through the Early Kebaran periods (ca. 200–20 ka)—humans occupying the Mt. Carmel area collected relatively more tortoise than did the Kebaran and Geometric Kebaran occupants of Hadera V, Neve David, and Hefesibah. At the same time, Middle and Upper Paleolithic hunter-gatherers in the Western Galilee captured relatively more fallow deer than did the inhabitants of the Early and Late Natufian sites at Hayonim and Hilaazon.
between-time-period variation suggests that fast small prey relative abundance fluctuated significantly through time \((p = 0.04)\). Alongside this up-and-down change in fast small prey, spur-thighed tortoise shows persistent long-term increasing abundance (see Fig. 6 and Table 5). In fact, we identify a highly significant monotonic rise in slow small prey abundance. A Mantel test of between-time-period variation for \(I_{mg}\) shows highly significant results. Nearly 97% of the variability occurs between time periods \((p < 0.005)\). In the Late Natufian period, the relative abundance of overall small game stabilizes or increases slightly over the Early Natufian levels. Within the small prey category, fast small game falls in abundance from the Early to Late Natufian periods, although it does not dip to the very low pre-15 ka levels. However, slow small game reaches its highest relative abundance in the Late Natufian.

The main results suggest an intriguing pattern. While medium big game, fast small game, and slow small game all show highly significant change in relative abundance through time, each prey type exhibits a somewhat different dynamic. Indeed, partial correlation analysis reveals that when larger big game relative abundance \((I_{bg})\) is held constant, small game \((I_{sg})\) exhibits only a moderate and not quite statistically significant temporal increase \((r = 0.592; p = 0.06)\). Similarly, when we hold medium big game relative abundance constant, slow small game exhibits neither a strong nor a significant temporal increase \((r = 0.578; p = 0.08)\). We cannot confidently conclude that variation in big game relative abundance directly drove temporal change in small game abundance. This may simply be an effect of our limited assemblage sample, but it may also reflect how the relative caloric returns of small game foraging activities were mediated by residential mobility and plant food processing and storage technologies.

**Table 5** Mantel test results of linear temporal trends in detailed prey-type abundance indices*.

<table>
<thead>
<tr>
<th>Prey Type</th>
<th>Temporal slope, (b_t)</th>
<th>(p)-value</th>
<th>Temporal correlation coefficient, (r_t)</th>
<th>(p)-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(I_{bg}) Overall big game</td>
<td>(-0.040)</td>
<td>0.05</td>
<td>(-0.905)</td>
<td>0.01</td>
</tr>
<tr>
<td>(I_{bg}) Overall small game</td>
<td>(-0.130)</td>
<td>0.05</td>
<td>(-0.830)</td>
<td>0.01</td>
</tr>
<tr>
<td>(I_{bg}) Large big game</td>
<td>(-0.001)</td>
<td>0.25</td>
<td>(-0.202)</td>
<td>0.54</td>
</tr>
<tr>
<td>(I_{bg}) Medium big game</td>
<td>(-0.040)</td>
<td>0.05</td>
<td>(-0.779)</td>
<td>0.005</td>
</tr>
<tr>
<td>(I_{bg}) Slow small game</td>
<td>(-0.057)</td>
<td>0.03</td>
<td>(-0.788)</td>
<td>0.04</td>
</tr>
<tr>
<td>(I_{bg}) Fast small game</td>
<td>(-0.088)</td>
<td>0.02</td>
<td>(-0.585)</td>
<td>0.04</td>
</tr>
</tbody>
</table>

*The main results summarized here are from Mantel test comparisons of pairwise assemblage differences in prey-type relative abundance and absolute temporal distance. Statistically significant results at the 0.05 level are shown in bold italic, with associated \(p\)-values underlined. The highly significant \(p\)-value for the \(I_{mg}\) (medium big game) correlation coefficient is emphasized in bold.

**Fig. 4.** Long-term trends in number of indentified specimens (NISP) relative abundance of big and small game.

**Discussion**

The results presented here provide new support for Stiner’s (2001) population pulse hypothesis. In this discussion we specifically address the dynamic link between big game depression, population growth, and sedentism, as we seek to trace the origins,
development, and eventual dampening of the inferred Epipaleolithic population pulse.

**Evolutionary ecological theory**

Our discussion draws on recent population models, in which human demographic growth is seen as responding to carrying-capacity-raising innovations or environmental changes; in turn, demographic pressure may lead to intensification, population regulation, further carrying-capacity-raising innovation, or dein- tensification (Lee, 1986; Cohen, 1995; Wood, 1998; Richerson et al., 2001). These models are general enough that they can be used to represent hunter-gatherer foraging behavior, incorporating the general prey model that underlies Stiner’s BSR framework (Richerson et al., 2001). However, they consist of very simple descriptive equations, which do not specify the culturally embedded decision-making processes—occurring at the individual, family, and community levels—that underlie changes in population-scale demographic rates. Nor do the equations define cultural processes involved in the adoption of organizational and technological innovations. Human foraging behavior is fundamentally social, with cooperation involving complex intergenerational and horizontal patterns of information, technological raw material, product, and food sharing. At least in the face of short term environmental fluctuations, human social solutions can successfully minimize risk. Yet, over years or generations, cooperative social solutions—culturally reproduced (with modifications) over generations—can maximize average foraging returns. This pattern may be suggested by basic formal analysis of sharing in risky foraging environments (Winterhalder, 1986). On the other hand, successful cultural systems of cooperation involve group mobilization, encouragement of generosity, and effective monitoring and enforcement of sharing values and practices. Social adaptations cannot emerge spontaneously. The basic formal population models considered here—including so-called reconciled Malthus-Boserup models (Lee, 1986; Wood, 1998)—allow not only for innovation and growth, but also for population and economic stagnation and cultural maladaptation (Richerson et al., 2001).

**Big game depression and the Epipaleolithic population pulse**

In a foraging-based subsistence economy, resource consumption is driven by the number of mouths to feed. Supply of calories and nutrients is limited by net foraging return rates. At a given population size, supply is shaped by a dynamic balance—that between the availability of animal and plant food resources and the organization and technology deployed to search for, capture, transport, and process hunted and collected resources. Millennium-scale heavy anthropogenic predation pressure on all three size categories of big game implies, quite simply, that over time Epipaleolithic human foraging activity involved feeding a growing number of people. There were more hunter-gatherers occupying the Western Galilee/Mt. Carmel area at the onset of the Early Natufian period (ca. 15 ka) than in the preceding Kebaran and Geometric Kebaran periods (ca. 19–16 ka).

How would mobile Southern Levantine hunter-gatherers have achieved population growth over century or millennium time scales, eventually overexploiting the most calorie-rich prey types in their foraging spectrum? We suggest that three key factors—climatic, technological, and socio-demographic in nature—would have been most important.

First, post-LGM climatic amelioration, associated with higher rainfall, higher annual temperatures, and higher atmospheric CO2 levels, would have had a positive impact on the highest ranked animal and plant food resources. As noted above, the trend toward warmer and wetter climate was associated with expansion of preferred fallow deer habitat. At the same time, rising primary productivity and water availability would have supported greater fertility and juvenile survival—other factors being equal—for fallow deer and gazelle alike, suggesting that Kebaran and Geometric Kebaran hunters would have experienced relatively high big game encounter rates.

Climatic amelioration would also have increased the distribution and abundance of seed, legume, and nut resources (Henry, 1989; McCorriston and Hole, 1991; Hillman, 2000; cf. Weiss et al., 2004). When seasonally available, at least some plant food types would have yielded higher post-encounter return rates than for slow small game. Many seed and nut resources would have had higher post-encounter return rates than for fast small game. For example, Wright (1994) reports that in preparing acorns, an individual adult forager can achieve net return rates of over 3000 kcal/hour. For wild wheat, barley, and other large-grain grasses, the figure is lower but still substantial: over 1000 kcal/hour. These estimates are based on ethnographic and experimental data. They do not take into account collecting and transport costs. Yet, we emphasize that plant food exploitation often entails lower search costs. Individual plant food resources would only have been ripe during brief seasonal windows, but in contrast to big and small game, higher ranked plant foods—especially nuts and large-grained grasses, such as wild wheat and barley—would have been encountered in predictable locations. Even as preferred habitat was becoming more productive for small and medium large game, key seed and nut resources would have provided an increasingly important seasonal complement to the diet. The Late Upper Paleolithic site of Ohalo II has preserved the waterlogged traces of
returns on par with big game. resources would not have yielded post-encounter nutritional benefits of scale. With higher fertility and lower mortality, larger social networks would also support more complex division of labor between multiple labor-task groups, achieved in large part through parallel logistical mobility trips. They may have achieved more efficient practices for sharing environmental and social information, resolving conflicts, and monitoring and punishing free riders—within the context of a small group of economically interdependent adults working on production, food search, and food processing tasks that were increasingly routinized and predictable. Although direct archaeological evidence is scant, Early Natufian societies may also have adopted technological innovations involving some storage, effectively achieving higher and more predictable return rates for key seasonally ripe plant foods (Belfer-Cohen and Bar-Yosef, 2000; Boyd, 2006).

We suggest, though, that Early Natufian sedentism would have generated some key long-term demographic stresses. Sedentary foraging entails an economic focus on food resources that are predictably located and sustainably harvested. Cape hare and chukar partridge exploitation reached a peak in the Early Natufian, before it declined in the Late Natufian. In general, intensification of fast small game foraging would have involved increasing time allocation to technological production and food processing tasks. If economies of scale were sufficient, caloric returns from plant and fast small game exploitation could have outpaced the costs of working more. Yet, if women spent more time working, at the expense of breastfeeding, then population-wide fecundity would have increased, potentially translating into higher fertility (Kelly, 1992, 1995). Moreover, if starchy plant foods comprised an increasing component of the diet, then young child survival might have been sustained or increased, even in the face of earlier weaning. As Pennington (2001) has suggested, the shift to sedentism may regional human population densities and falling big game encounter rates would likely have escalated scalar stress in the social negotiation and competition over access to territory and its highest ranked resources (cf. Johnson, 1982). The big game population depression trend fits with an already well-established view that Early Natufian sedentism was initially an intensification strategy (Bar-Yosef, 1998; Rosenberg, 1998; Belfer-Cohen and Bar-Yosef, 2000; Munro, 2003, 2004).

With increasing sedentism, small animal prey and seasonally available highly ranked plant foods are expected to have increased in dietary and economic importance in the Early Natufian period. Indeed, our main results confirm and extend previous observations of increasing small game relative abundance in both the Early and Late Natufian periods. Also, as described above, there is a well-documented increase, from the early Epipaleolithic to the Natufian periods, in the frequency and diversity of ground stone food processing artifacts (Wright, 1994; Dubreuil, 2004). The Natufian periods are also marked by a striking increase in bone tools, many of which were likely used for basketry production (Campana, 1989, 1991). Thus, although macrobotanical remains have preserved poorly in Southern Levantine Epipaleolithic archaeological deposits (cf. Colledge, 1991; Lieberman and Bar-Yosef, 1994), Natufian material culture indicates an increase in plant food exploitation after ca. 15 ka.

Human demographic expansion, then, likely occurred during the Kebaran and Geometric Kebaran periods (ca. 19–16 ka), strongly influenced a reduction in residential mobility during the Early Natufian period (ca. 15–14 ka). Yet, we suggest that the cultural transition to Early Natufian sedentism also involved a demographic shift into a period of dampened population growth. While big game prey—which provided the highest post-encounter caloric return rates in the Epipaleolithic foraging spectrum—was already being overexploited, Early Natufian populations may have been able to maintain per capita net caloric return rates at or near earlier Geometric Kebaran levels. In shifting foraging and processing tasks toward a broader range of small animal and plant foods, Early Natufian hunter-gatherers may have been able to achieve further economies of scale. Semi-sedentary groups could have added more parallel logistical mobility trips. They may have achieved more efficient practices for sharing environmental and social information, resolving conflicts, and monitoring and punishing free riders—within the context of a small group of economically interdependent adults working on production, food search, and food processing tasks that were increasingly routinized and predictable.
have involved a transitional demographic pattern, in which adults faced a task of feeding more dependents who received enough calories to survive early childhood, but who experienced more frequent stress episodes during the entire juvenile period. The result would have been greater frailty among those surviving beyond the age of 20 or so. Early Natufian societies may have initially experienced population growth due to higher fertility, even as adult mortality also increased (Pennington, 2001). Over many centuries, though, the higher dependent ratios and, possibly, adult mortality would have strained the limits of the Early Natufian BSR economy. When we consider the major shifts in mobility, technology, and time allocation to technological production and food processing, we would expect a long-term shift in fertility and mortality. By the end of the Early Natufian period, 14–13 ka, it is most likely that human population growth likely slowed or reached a plateau.

**Whither the population pulse in the Late Natufian period?**

The phase of restricted population growth would have continued into the Late Natufian period (ca. 13–12 ka). At this time, growth may have even become slightly negative as the Younger Dryas climate imposed lower environmental productivity levels on the region (Munro, 2003, 2004). The Late Natufian period is marked by settlement patterns, architectural features, and mortuary practices that indicate a return to greater residential mobility (Goring-Morris and Belfer-Cohen, 2003). As an archaeological culture, the Late Natufian likely represents a nexus of foraging societies that adopted more flexible residential and logistical mobility strategies in response to long-term sustained human population pressure on resources. However, we emphasize that the evidence for big game resource depression extends into the Late Natufian period. If regional population size shrank after 13 ka, it likely did not contract much. In fact, it is possible that the relatively high frequencies of spur-thighed tortoise bones observed in our Late Natufian assemblage are an artifact of anthropogenic predation pressure on the standard prey type, small big game. In other words, from the Early to Late Natufian periods, small game foraging may have actually fallen in economic importance, even as big game populations remained under persistently heavy predation. If this were indeed the case, then we would expect plant foods to have assumed greater economic importance during the Late Natufian period. In fact, some archaeological evidence (use-wear data for sickle blades and grinding stones, along with detailed analysis of the exceptionally well-preserved archaeobotanical assemblage from the Late Natufian site of Abu Hureyra) suggests that the initial experiments with grain and lentil horticulture occurred between 13 and 12 ka (Anderson, 1991; Bar-Yosef, 1998; Belfer-Cohen and Bar-Yosef, 2000; Hillman et al., 2001; Dubreuil, 2004).

From this perspective, the Late Natufian return to greater residential mobility would have involved substantially more investment in social practices for maintaining cooperative alliances and negotiating access to foraging territories, in which fixed patches of seasonally available plant resources took on increasing economic importance (cf. Grosman, 2003). We may turn this proposition around, suggesting that intensified mutual management and exploitation of social resources would have required greater geographic mobility. Indeed, such social intensification may have facilitated the precise labor task scheduling needed to invest successfully in horticulture.

The Late Natufian period is clearly an important time of dynamic cultural, demographic, and economic change. In comparison with preceding Epipaleolithic and later Prepottery Neolithic periods though, the Late Natufian conspicuously diverges from key long-term trends (Goring-Morris and Belfer-Cohen, 1998). Much, if not all, of the Late Natufian falls within Younger Dryas climatic reversal, the cooler and dryer regional conditions of which punctuated a roughly 10,000 year trend of post-LGM amelioration. The Late Natufian also represents a temporary departure from a long-term decline in residential mobility, which was associated with a rise in sedentism and settlement size that may be traced from the Kebaran through the Prepottery Neolithic B periods (Bar-Yosef and Belfer-Cohen, 1989, 1991). Our results indicate that anthropogenic predation pressure on preferred big game resources, including mountain gazelle, persisted unabated from the Early to the Late Natufian periods. These data suggest that the Late Natufian residential mobility differed qualitatively from that of Kebaran and Geometric Kebaran societies (Goring-Morris, 1987, 1995; Goring-Morris and Belfer-Cohen, 1998, 2003). We infer that in our study area—that is the Western Galilee/Mt. Carmel area, with a Mediterranean climate and vegetation—the pre-Natufian residential mobility and foraging strategies were organized much more substantially around the hunting of fallow deer and gazelle. We argue that the Late Natufian return to greater residential mobility was likely focused on exploiting more highly ranked seasonal seed, nut, and pulse resources. Late Natufian settlement, land-use, and resource exploitation strategies appear to have differed from those of the Early Natufian period. Yet, the Late Natufian increase in mobility may have sustained support regional human population densities at or near Early Natufian levels, especially if more frequent residential moves focused in substantial part on exploiting a wider range of marginal zones and resources.

**Conclusion**

With improved chronological sampling of archaeofaunal assemblages throughout the Epipaleolithic period in the Southern Levant, we have presented the most comprehensive archaeological test to date of the big game depression/population pulse hypothesis. In addition to providing continued support for Flannery’s (1969) Broad Spectrum Revolution, our results demonstrate sustained big game depression starting in the early Epipaleolithic and peaking in the Natufian period. Long-term big game depression crosscuts major climatic events, confirming that shifting big and small game abundance is related to long-term anthropogenic predation pressure rather than environmental change. In addition, sustained depression of all big game categories throughout the Early and Late Natufian periods sheds light on other important trends—in particular, reduced mobility and increasing use of fast small game in the Early Natufian and increased mobility and an inferred increased reliance on plant foods in the Late Natufian. In the Early Natufian period, big game depression may have encouraged decreased mobility as it became economical to capture local small game types, as encounter rates with big game fell. In the Late Natufian period, mobility has often been attributed to climate-forced environmental degradation related to the Younger Dryas event. Here, we emphasize that anthropogenic depression of big game persisted or rose in intensity during the Late Natufian, and we propose that Late Natufian mobility may also have been part of alternative intensification strategy, which focused more on exploiting a broad spectrum of small game and plant foods across a wider range of ecological zones. In the spirit of encouraging further discussion and research on this topic, we note that the shift to a new, more plant-focused economy could potentially have sustained regional human population levels at or near those prevailing in the Early Natufian. Such a change in hunter-gatherer intensification strategies may help to explain why the transition to cultivation and domestication was a long-term process that transgressed the Pleistocene-Holocene boundary.

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Supplementary data

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