
The Tortoise and the Hare

Small-Game Use, the Broad-Spectrum Revolution, and Paleolithic Demography¹

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This study illustrates the potential of small-game data for identifying and dating Paleolithic demographic pulses such as those associated with modern human origins and the later evolution of food-producing economies. Archaeofaunal series from Israel and Italy serve as our examples. Three important implications of this study are that (1) early Middle Paleolithic populations were exceptionally small and highly dispersed, (2) the first major population growth pulse in the eastern Mediterranean probably occurred before the end of the Middle Paleolithic, and (3) subsequent demographic pulses in the Upper and Epi-Paleolithic greatly reshaped the conditions of selection that operated on human subsistence ecology, technology, and society. The findings of this study are consistent with the main premise of Flannery's broad-spectrum-revolution hypothesis. However, ranking small prey in terms of work of capture (in the absence of special harvesting tools) proved far more effective in this investigation of human diet breadth than have the taxonomic-diversity analyses published previously.

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Hominids have subsisted from some combination of plants and animals for more than 2.5 million years. However, the nature of hominid diets, including the ways foods such as meat were obtained, the package sizes normally acquired, and the manner in which nutrients were extracted and processed, has changed dramatically over this time span. Several shifts in the human predatory niche are reflected by ungulate archaeofaunal remains in particular. These include a probable transition sometime in the Plio/Pleistocene from hunting smaller prey and scavenging larger ones to an increasing emphasis on hunting, from tool-assisted extraction of consolidated bone marrow to full-scale butchering, processing, and storage of animal tissue, and, recently, from large-game hunting to animal husbandry. It is therefore not surprising that most discussions of humans as predators focus on large game.

There exists, however, another dimension of the archaeofaunal record—small-game use—which provides unique information about the demographic conditions under which human predator-prey relations evolved. Although well short of dominant in most Paleolithic archaeofaunal collections, small animals were important to human diets in the Mediterranean Basin from at least the early Middle Paleolithic onward. The total contribution of small game to Paleolithic diets and the diversity of species consumed did not change very much over this last 200,000 years, but the types of small game emphasized certainly did. This is quite interesting if one considers the distinct biological properties of the small animals most commonly involved: littoral shellfish, tortoises, partridges, rabbits, and hares. These animals differ greatly in their reproductive potentials, maturation rates, and capacities for population recovery under conditions of heavy exploitation. They also differ in the ease with

which they can be caught by humans without the aid of special tools. Changes in humans' interest in these animals can testify to evolutionary shifts in the organization of forager adaptations (Stiner et al. 1999) and, as we argue below, rising human population densities during the later Pleistocene. Faunal signatures of this process will be most evident in environments where the range of species is naturally diverse, such as at lower latitudes in general and in the Mediterranean Basin in particular.

Here we consider the trends in small-game use from stratigraphic series dating to the early Middle Paleolithic through Epi-Paleolithic periods in northern Israel and western Italy. Our faunal series are up to the task at hand, as they were recovered completely by the site excavators, and taphonomic analyses indicate that they represent food eaten by humans (Stiner 1993, 1994, 2000, n.d.; Stiner and Tchernov 1998; Kuhn and Stiner 1998a). The Italian sequence spans approximately 110,000 to 9,000 years ago and the Israeli sequence 200,000 to 11,000 years ago (table 1). In Israel the Natufian was followed by the pre-pottery Neolithic around 10,500 years ago (Bar-Yosef 1981, Bar-Yosef and Belfer-Cohen 1989, Belfer-Cohen

1991). Neolithic lifeways appeared considerably later in Italy (≤ 8000 years ago [Dennell 1992]), apparently introduced from the southeast via cultural diffusion with local modification (Ammerman and Cavalli-Sforza 1984: 34–35; Bogucki 1996; Dennell 1992; Whittle 1996). Our data on Paleolithic subsistence suggest that the circumstances were already ripe for change in both Mediterranean regions, though earlier in the area now called Israel.

Flannery's broad-spectrum-revolution hypothesis (1969) and classic foraging theory (diet breadth [Stephens and Krebs 1986]) serve as points of departure for this investigation. Following a review of the issues, we examine the archaeofaunas from Italy and Israel for trends in prey species abundance and for indications of predator pressure in the form of prey body size diminution. Clear trends indeed exist in the data. Understanding them requires consideration of how prey escape behaviors, prey reproductive characteristics, and predator numbers relative to available prey interact to produce patterns at the scale of populations. We explore the human demographic implications of the faunal trends via predator-prey simulation modeling for three common small-prey taxa (tor-

TABLE 1
Age Ranges and Oxygen Isotope Stages for the Paleolithic Faunal Assemblages from Italy and Israel

Region, Site, Layer	Paleolithic Culture	Direct Dating	Associational Dating ^a	Oxygen Isotope Stage
Liguria, Italy				
RM Late Epigravettian (layer A)	EP	—	9,000–12,000	1
RM Early Epigravettian (layer C)	EP	—	17,000–19,000	2 ^b
RM Gravettian (layer D)	UP	—	24,000–28,000	2 ^b
RM Middle Aurignacian (layer F)	UP	—	27,000–32,000	2 ^b
RM Early Aurignacian (layer G)	UP	32,000–36,000	—	3
Latium, Italy				
GPo Late Epigravettian	EP	—	10,000–11,000	1
GPa Evolved Epigravettian	EP	15,000–16,000	—	2 ^b
GB Middle Paleolithic	MP	35,000–45,000	—	3
GS'A Middle Paleolithic	MP	40,000–55,000	—	3
GM Middle Paleolithic	MP	> 60,000–120,000	—	4 ^b
Galilee, Israel				
Hay Natufian (layer B)	EP	11,000–13,000	—	1
Hay Kebaran (layer C)	EP	14,000–17,000	—	2 ^b
Meg early Kebaran (<200 cm)	EP	18,000–19,000	—	2 ^b
Meg Pre-Kebaran (>199 cm)	UP	19,000–22,000	—	2 ^b
Hay Aurignacian (layer D)	UP	26,000–28,000	—	2 ^b
Hay 200–349 (layer E)	MP	70,000–100,000	—	5–6
Hay 350–419 (layer E)	MP	~150,000	—	6 ^b
Hay 420–469 (layer E)	MP	~170,000	—	6–7 ^b
Hay 470–539 (layer E)	MP	~200,000	—	7?

SOURCES: Bar-Yosef (1981, 1995), Bar-Yosef and Belfer-Cohen (1988), Bar-Yosef et al. (1996), Bietti (1976–77, 1990), Gamble (1986), Hedges et al. (1994:347), Kuhn et al. (1998), Palma di Cesnola (1993), Stiner (1994), Shackleton and Opdyke (1973).

NOTE: Site codes are RM, Riparo Mochi; GPo, Grotta Polesini; GPa, Grotta Palidoro; GB, Grotta Breuil; GS'A, Grotta di Sant'Agostino; GM, Grotta dei Moscerini; Hay, Hayonim Cave; Meg, Meged Rockshelter. Culture codes are EP, Epi-Paleolithic; UP, Upper Paleolithic; MP, Middle Paleolithic. Upper Paleolithic chronology is based on uncalibrated radiocarbon dates; Middle Paleolithic chronology is based on a combination of electron spin resonance, uranium/thorium, and thermoluminescence techniques; estimated ages of Middle Paleolithic layers of Hayonim Cave are provisional (unpublished), based on work by Valladas and Mercier, Rink and Schwarcz.

^aBased on nearby sites that contain similar industries dated by absolute techniques.

^bGenerally colder and/or drier climatic conditions.

toises, partridges, and hares). In the Mediterranean Basin, a simple distinction in prey “catchability” corresponds closely to great differences in prey population resilience in the face of heavy, sustained predation. We show how rising human population density and associated predator pressure alter prey abundances and thereby select for changes in the small species emphasized by foragers. Our findings uphold the importance of population growth to subsistence and social change in the later Paleolithic. They expose, however, the limitations of species- or genus-based diversity analyses, meanwhile illustrating the explanatory power of ranking prey types according to predator-defense characteristics. The findings also underscore the importance of resource intensification early in the story of subsistence revolution in Eurasia (as with plant use [see Henry 1989; Redding 1988; Rindos 1984; Wills 1995]).

Because the faunal signatures of demographic “pressure” or “pulses” can be dated reliably and tied to specific regions of the world, trends in small-game use provide exceptional opportunities to test hypothesized relations between rising population densities and transitions in the structure of Paleolithic human societies. Our data do not address the question of why human population densities increased when they did. We propose nonetheless that small-game use and early food-processing and storage practices are related, as all may promote more consistent access to complete protein, fat, and other rare nutrients which improve child survivorship.

The Broad-Spectrum-Revolution Hypothesis

Ungulates are prevalent in Middle and Late Pleistocene archaeofaunas, suggesting that humans of these periods have evolved the means to catch them (Bar-Yosef et al. 1992; Chase 1986; David and Poulain 1990; Hoffecker, Baryshnikov, and Potapova 1991; Jaubert et al. 1990; Klein 1978, 1987; Rabinovich and Tchernov 1995; Speth and Tchernov 1998; Stiner 1992, 1994; Stiner and Tchernov 1998; Tozzi 1970). But if Middle and Upper Paleolithic humans were capable of felling relatively large species, why did small game figure in human diets at all? This question can be traced to issues raised three decades ago.

In two influential and conceptually linked articles, Binford (1968) and Flannery (1969) noted what appeared to be substantial expansions of the human food base during the terminal Paleolithic. The available evidence suggested that this occurred in more than one area of the Old World. Common to the two writers is the idea that economic change resulted from a complex interplay between demographic packing and territorial circumscription, possibly provoked by episodes of environmental disruption. Binford (1968) argued that the rapid technological radiations (especially in food processing and storage equipment) that accompanied the dietary shifts were symptoms of resource intensification. Flannery’s (1969) broad-spectrum-revolution hypothesis proposed that hu-

man population growth in western Asia, the cradle of village life, should be prefaced by increases in what is essentially dietary breadth. He argued that diversification, mainly through adding new species to the diet, raised the carrying capacity of an increasingly constrained environment. This process ultimately set the stage for qualitatively distinct solutions—specialized food production economies based on agriculture and animal husbandry.

The notion that human population growth was a leading evolutionary force has been questioned by many archaeologists. The role of demographic factors is largely dismissed by some (e.g., Bender 1985, Hayden 1995, Price and Gebauer 1995). Others argue that demographic factors were but one of several ingredients necessary to the process of change (Bar-Yosef and Meadow 1995, Keeley 1995, Redding 1988, Watson 1995). We agree that population pressure is unlikely to be an all-encompassing explanation for the cultural evolution of the later Pleistocene. Many evolutionary processes are nonetheless subject to density-dependent effects, and these effects can play decisive roles in shaping the evolutionary histories of species (Boutin 1992, Caughley 1977, Gasaway et al. 1992, Gavin 1991, Harpending and Bertram 1975, Layton, Foley, and Williams 1991, Pianka 1978, Sinclair 1991, Winterhalder and Goland 1993, Winterhalder et al. 1988). Changes in human population density must have influenced, for example, the rates of interspecific and intraspecific contact, the relative need (or lack of it) for controlling the outcomes of personal interactions, and the availability of critical foodstuffs. Any or all of these could have altered the kinds of selective factors that operated on foraging societies.

That plants, especially nuts and large seeds, were integral to the subsistence revolution in western Asia is clear from the proliferation of milling tools in the later Paleolithic (Wright 1994) and, to a lesser extent, from the presence of storage facilities and preserved plant parts (Bar-Yosef and Belfer-Cohen 1989; Bar-Yosef and Meadow 1995; Byrd 1994; Cowan and Watson 1992; Henry 1985, 1989; Hillman, Colledge, and Harris 1989; Kislev 1989; Kislev, Nadel, and Carmi 1992; Miller 1992; also experiments by Unger-Hamilton 1989) and the rise of commensal rodents (Tchernov 1984). Keeley’s (1995) stimulating essay, based on ethnographic and environmental comparisons, shows how and why plants were pivotal to subsistence evolution in dry subtropical environments. Most important were large-seeded plant species, whose nutritional benefits require considerable work to extract.

The story from the faunal evidence is less clear. Most efforts to test the prediction of increasing diet breadth in the later Paleolithic employ some measure of taxonomic diversity, and all of these studies have yielded ambiguous results. Incomplete recovery practices and/or lack of taphonomic data linking small-animal remains to human activities are recognized obstacles (cf. Edwards

1989, Neeley and Clark 1993).² Unequal time increments, time-averaging, and biogeographic variation also play havoc with the kinds of large-scale comparisons needed to test the broad-spectrum-revolution hypothesis (Bar-Oz, Dayan, and Kaufman 1999, Stiner 1992). Yet another difficulty has been weak contact among the initial propositions, classic foraging theory, and zooarchaeological research designs. The foundations of foraging theory (Odum and Odum 1959; see also Emlen 1966, MacArthur and Pianka 1966, among others) were published only a few years before Binford's and Flannery's articles and were inspirations to both. Numerous refinements to foraging theory, including the diet-breadth concept, have been made since then (e.g., Maynard Smith 1974, 1982; Stephens and Krebs 1986). Only some of these refinements have been assimilated by archaeological investigations of the broad-spectrum-revolution hypothesis and related phenomena elsewhere in the world (e.g., Christenson 1980, Cohen 1977, Earle 1980, Redding 1988, Winterhalder 1981; for reviews see Durham 1981; Kelly 1995:78–90).

At issue here are the ways of detecting subsistence change. If general increases in dietary breadth are expected, what is meant by breadth, and what measures of change (*sensu* Stephens and Krebs 1986:7) would be most sensitive for long but coarse-grained prehistoric records? Formal diet-breadth models predict that lower-ranked species will be sought as the encounter rates for highly ranked types decline. "Breadth" concerns only the magnitude of difference between the net returns of the highest- and lowest-ranked resources in the diet. It is, moreover, quite sensitive to the diversity of living organisms in the environment(s) considered. Diet-breadth models do not specify all of the appropriate criteria for ranking resources, because one kind of organism may interact with its environment differently from the next (Stephens and Krebs 1986).

Species-diversity comparisons have nonetheless dominated the search for faunal signatures of the broad-spectrum revolution (e.g., Edwards 1989, Neeley and Clark 1993). Diversity approaches normally examine archaeofaunal variation in terms of taxonomic richness (N species or N genera) and/or taxonomic evenness (proportionality in species abundance). Most studies employ Kintigh's simulation-based technique (1984, 1989) or the regression approach developed by Fisher, Corbet, and Williams (1943) for problems in modern community ecology and adapted for zooarchaeology by Grayson (e.g., 1984). The expectation is that, if human population packing was occurring, foragers should have scoured available foraging territories more thoroughly, resulting in more species in the diet and/or more even emphasis on those species (see Christenson 1980, Earle 1980, and Redding 1988; for a review see Neeley and Clark 1993).

We have no quarrel with the premises of formal diet-

breadth models or with the mathematical conventions for calculating diversity. Rather, we see problems with the taxonomy-bound units of analysis in broad-spectrum studies and related assumptions about resource rank. Technological and human skeletal evidence, as well as site structures and numbers, testify to remarkable changes in human existence from the Middle through the Epi-Paleolithic period. Yet even the most rigorous applications of taxonomic-diversity measures register only one economic transition, that from foragers to farmers in the early Neolithic (Henry 1989, Horwitz 1996, Neeley and Clark 1993; for related faunal changes, see Bar-Yosef 1981; Bar-Yosef and Meadow 1995; Clark 1987; Clutton-Brock 1981; Garrard 1980; Davis 1978, 1982; Ducos 1968; Meadow 1984; Saxon 1976; Tchernov 1994a). Correcting for sample-size effects, diachronic variation in species diversity in pre-Neolithic diets is best explained by climate-driven adjustments in local animal and plant community structure, not human dietary preferences (e.g., Stiner 1994; Stiner and Tchernov 1998; Tchernov 1992, 1994b; see also Simek and Snyder 1988). Taxonomic-diversity analyses reveal little if any behavioral change over the entire Middle, Upper, and Epi-Paleolithic, when all humans were foragers of some kind.

The experiences described above suggest two possible conclusions. Either no economic change occurred during the Paleolithic or the prevailing tools for investigating change in foraging societies are rather ineffective (for related essays see Bar-Oz, Dayan, and Kaufman 1999; Neeley and Clark 1993:236; Dunnell 1989; Stiner 1992, 1994). The main limitation of taxonomic-diversity approaches is their lack of sensitivity to biological differences among prey beyond straight phylogeny; the only qualification normally added to taxonomic units is prey body size. The habits and physical properties of prey animals must affect humans' access to them. Small animals are broadly equivalent with respect to protein content and package size, but they differ tremendously with respect to handling costs, the number of individuals that can feasibly be harvested at once, and the long-term price of heavy exploitation (see also Belovsky 1988, Botkin 1980, Harpending and Bertram 1975, Winterhalder et al. 1988).

The archaeofaunal examples from Italy and Israel (fig. 1) indicate considerable restructuring of the human subsistence base prior to the end of the Paleolithic. The data presented below suggest that differences in prey population *resilience* and *work of capture* constrained Paleolithic people's use of small game in predictable ways. "Resilience" here refers to a prey population's ability to withstand heavy, cyclical predation and is linked to individual maturation rate. Prey population resilience is especially important in situations where predator densities are high. "Work of capture" concerns how a prey animal's defense and escape mechanisms affect a predator's ability to obtain it. Work of capture may be the cost of searching for prey, investment in technological aids, and/or the energetics of a true chase. It may also include processing costs, although in our study areas peo-

2. Edwards's (1989) results are controversial because of the lack of taphonomic discrimination, but his results are nearly indistinguishable from those obtained by Neeley and Clark (1993) in their analysis of corrected data.

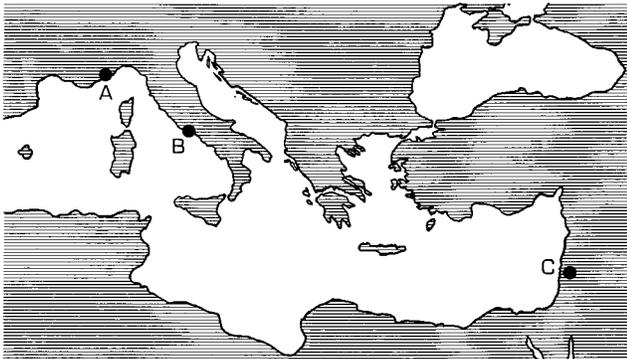


FIG. 1. Study areas and sites in the Mediterranean Basin. A, Riparo Mochi, in coastal Liguria, northwestern Italy; B, Grotta dei Moscerini, Grotta Breuil, and Grotta di Sant'Agostino on the coast and Grotta Palidoro and Grotta Polesini inland in Latium, west-central Italy; C, Hayonim Cave and Meged Rockshelter in an inland valley of the western Galilee, Israel.

ple used fire to do much of the work for them (roasting [Stiner and Tchernov 1998], light heating to open live mussels [Stiner n.d.]).

Archaeological Evidence from Italy and Israel

The trends in small-game use are much the same in Italy and Israel, although the timing of change varies, as do some of the small taxa involved. Because the series from Italy and Israel represent distinct ecogeographic zones, the trends cannot be dismissed as local phenomena. Another advantage of the samples is the uniformly high quality of recovery and documentation. Systematic fine-screening was practiced during excavation in all cases. Small-animal remains can be deposited in shelters in a number of ways: predatory birds may regurgitate prey parts in shelters, wild and domestic canids may defecate there, marine shells may be washed into shoreline sites by waves, and small rodents and land snails may preferentially live and die in the vicinity of human habitations. In our samples, damage to the faunal remains such as burning, breakage patterns, and tool and percussion marks, along with near or total absence of damage from nonhuman predators, demonstrates that the small animals were consumed by Paleolithic humans and not introduced into the shelters by other agencies. For reasons of economy, taphonomic research on these faunas that has been presented elsewhere (Stiner 1993, 1994; Stiner and Tchernov 1998; Stiner 2000, n.d.; Kuhn and Stiner 1998a) will not be reported here. Material of unclear origin or representing mixed cultural entities has been removed from consideration. The data are preliminary in the sense that they come from ongoing projects, but they are representative for the purposes at hand. The archaeofaunal assemblages together span 200,000 to 9,000 years

before present. Geographic context and site type are held generally constant in each series; the comparisons are confined to assemblages from limestone caves and rock shelters, places to which food would have been brought by foragers and in which the chances of skeletal preservation are high because of protection from the elements and favorable sediment chemistry.

THE FAUNAL SERIES FROM COASTAL ITALY

The composite Italian sequence spans the Middle-to-Upper-Paleolithic technological transition and terminates not long before the end of Paleolithic lifeways in this region. The faunal samples are from shelters along the western coast of Italy. Riparo Mochi is one of the Balzi Rossi or Grimaldi caves of Liguria (fig. 1, region A) (Blanc 1953; Cardini and Biddittu 1967; Kuhn and Stiner 1992, 1998a; Laplace 1977; Lumley-Woodyear 1969). Late Epigravettian, Early Epigravettian, Gravettian, Middle Aurignacian, Early Aurignacian, and Mousterian components are represented at Riparo Mochi (36,000–9,000 years ago). The associated industrial sequence conforms to those documented previously in southern France and northern Italy; the ages of the cultural horizons not directly dated by the radiocarbon technique are assumed to be equivalent to other dated sites with similar lithic industries (see table 1). Faunal remains from the Middle Paleolithic layers in Riparo Mochi unfortunately are few. This fact, along with peculiarities of the youngest Upper Paleolithic sample from Riparo Mochi, calls for examination of coeval cases elsewhere in Italy. Assemblages from the inland Epi-Paleolithic shelters in Latium (fig. 1, region B), Grotta Polesini (Radmilli 1974) and Grotta Palidoro (Bietti 1976–77, Cassoli 1976–77), and, for the Middle Paleolithic, the coastal caves of Grotta dei Moscerini (Kuhn 1995, Stiner 1994) and Grotta Breuil (Bietti et al. 1990–91, Kuhn 1995, Stiner 1994), also in Latium, are used to create a composite coastal sequence that begins around 110,000 years ago and ends around 9,000 years ago.

Table 2 compares the proportions of small and large game in the coastal Italian archaeofaunas from Liguria and Latium combined. Counts by taxonomic category are based on the number of identified specimens (NISP) for vertebrates and the number of individuals (MNI) for mollusks, the latter to ensure specimen size comparability to vertebrate remains in the frequency comparisons. These data indicate that small game were important food sources throughout the Middle, Upper, and Epi-Paleolithic periods. There is no directional trend in the relative contribution of small game to total animal intake based on the small-game/ungulate index. Large-game species are mostly red deer (*Cervus elaphus*), aurochs (*Bos primigenius*), roe deer (*Capreolus capreolus*), and, in some instances, ibex (*Capra ibex*), wild ass (*Equus hydruntinus*), and/or wild boar (*Sus scrofa*) (see Stiner 1990–91, 1992, 1994). Carnivore remains occur in very small quantities in all of the layers considered here, and they appear to have been collected by humans.

Figure 2, left, illustrates a strong trend in the propor-

TABLE 2
Relative Abundances of Carnivores, Ungulates, and Small Game Animals in the Paleolithic Series from Italy

Culture Period, Site, and Phase	Total	% Carnivores	% Ungulates	% Small Game	Small-Game/Ungulate Index	Inferred Oxygen-Isotope Stage	Geographic Setting
EP RM Late Epigravettian	980	1	17	81	.83	1	Coastal
EP GPo Late Epigravettian	44,403	3	94	3	.02	1	Inland
EP GPa Evolved Epigravettian	2,079	2	97	1	.01	2 ^a	Inland
EP RM Early Epigravettian	2,971	1	59	40	.40	2 ^a	Coastal
UP RM Gravettian	3,653	2	77	21	.21	2 ^a	Coastal
UP RM Middle Aurignacian	930	2	53	45	.46	2 ^a	Coastal
UP RM Early Aurignacian	1,592	2	53	44	.46	3	Coastal
MP GB Middle Paleolithic	1,571	4	96	≪1	.01	3	Near coastal
MP GM Middle Paleolithic	1,422	≪1	53	46	.47	4 ^a	Coastal

NOTE: Total counts are NISP for vertebrates but MNI for mollusks to correct for significant differences in fragment sizes. Small-game/ungulate index calculated as the number of small-game remains divided by the sum of small-game and ungulate remains. EP, Epi-Paleolithic; UP, Upper Paleolithic; MP, Middle Paleolithic. Site codes are RM, Riparo Mochi; GPo, Grotta Polesini; GPa, Grotta Palidoro; GB, Grotta Breuil; and GM, Grotta dei Moscerini. Data for Polesini are from Radmilli (1974); for Palidoro, from Cassoli (1976-77).

^aColder and/or drier climatic conditions.

tions of three categories of small animals within the small-game fraction (table 3). Relatively sessile (= slow or immobile) animals—edible shellfish (*Patella* spp., *Mytilus galloprovincialis*, *Monodonta turbinata*, *Ostrea edulis*, *Callista chione*, *Glycymeris* spp.), and tortoises (*Testudo graeca* and *Emys orbicularis*)—appear early in the sequence, and shellfish persist in human diets thereafter. These animals are easily gathered, although some are easier to find than others. Birds, which are quick, became important only with the beginning of the Upper Paleolithic (Early Aurignacian, ca. 35,000 years ago). These were mostly gray partridges (*Perdix perdix*) and quail (*Coturnix coturnix*), along with lower frequencies of doves (*Columba livia*) and aquatic (Anseriform) birds, among others.³ Though present in faunas throughout the sequence, small mammals, mainly hares (*Lepus capensis*) and rabbits (*Oryctolagus cuniculus*), became numerically important in human diets only in the Epi-Paleolithic. Thus, the diachronic changes in the contents of the small-game fractions at these sites are directional, while variation in the contribution of small animals to total game intake is not.

The preponderance of shellfish in the Late Epigravettian (layer A) of Riparo Mochi is enigmatic relative to the Upper Paleolithic phases before it (fig. 2) and more closely resembles the situation in the Middle Paleolithic assemblage from Grotta dei Moscerini. However, inland Late Epigravettian samples from Grotta Palidoro and Grotta Polesini indicate that birds and lagomorphs figured prominently in small-game fractions elsewhere at this time (see also Cassoli 1976-77, Radmilli 1974). The final Paleolithic occupation at Riparo Mochi probably

represents a special-use camp, when sea level transgressed nearly to the foot of the shelter.

The Middle Paleolithic sample from Grotta dei Moscerini is peculiar in its own right, as many sites of this period in Italy (e.g., Grotta Breuil) lack substantial small-game components. Where small-game remains are present in sites and clearly attributable to Middle Paleolithic humans, the focus nonetheless is on sessile types (see also Blanc 1958-61; Palma di Cesnola 1969; Stiner 1993; 1994:176-92; and, on North Africa, Klein and Scott 1986). At Moscerini, shellfish and tortoise collection (46% of total game) combines with an odd pattern of terrestrial foraging—occasional collecting (scavenging) of ungulate head parts (Stiner 1991, 1994). Small-mammal remains have been reported in the Middle Paleolithic layers of Grotta di Sant'Agostino (Tozzi 1970), but taphonomic evidence associates these materials principally with denning wolves, not humans (Stiner 1994: 166-71). The wolf dens of Sant'Agostino nonetheless are important to establishing the abundant presence of lagomorphs in coastal Italy during Middle Paleolithic times despite their rare occurrence in early Paleolithic archaeofaunas.

THE FAUNAL SERIES FROM INLAND ISRAEL

The faunal sequence from Israel begins about 200,000 and ends 11,000 years ago. It spans the early Middle Paleolithic, much of the Upper Paleolithic (Aurignacian and pre-Kebaran), and the Epi-Paleolithic (Kebaran and Natufian). The series is based on two inland sites, Hayonim Cave (Bar-Yosef 1991, Belfer-Cohen and Bar-Yosef 1981) and Meged Rockshelter (Kuhn et al. 1998) in the western Galilee, near the modern city of Karmiel (fig. 1, region C). Both shelters face south, though Hayonim

3. Species-specific identifications of the Riparo Mochi avifauna were made by A. Recchi, Università di Roma.

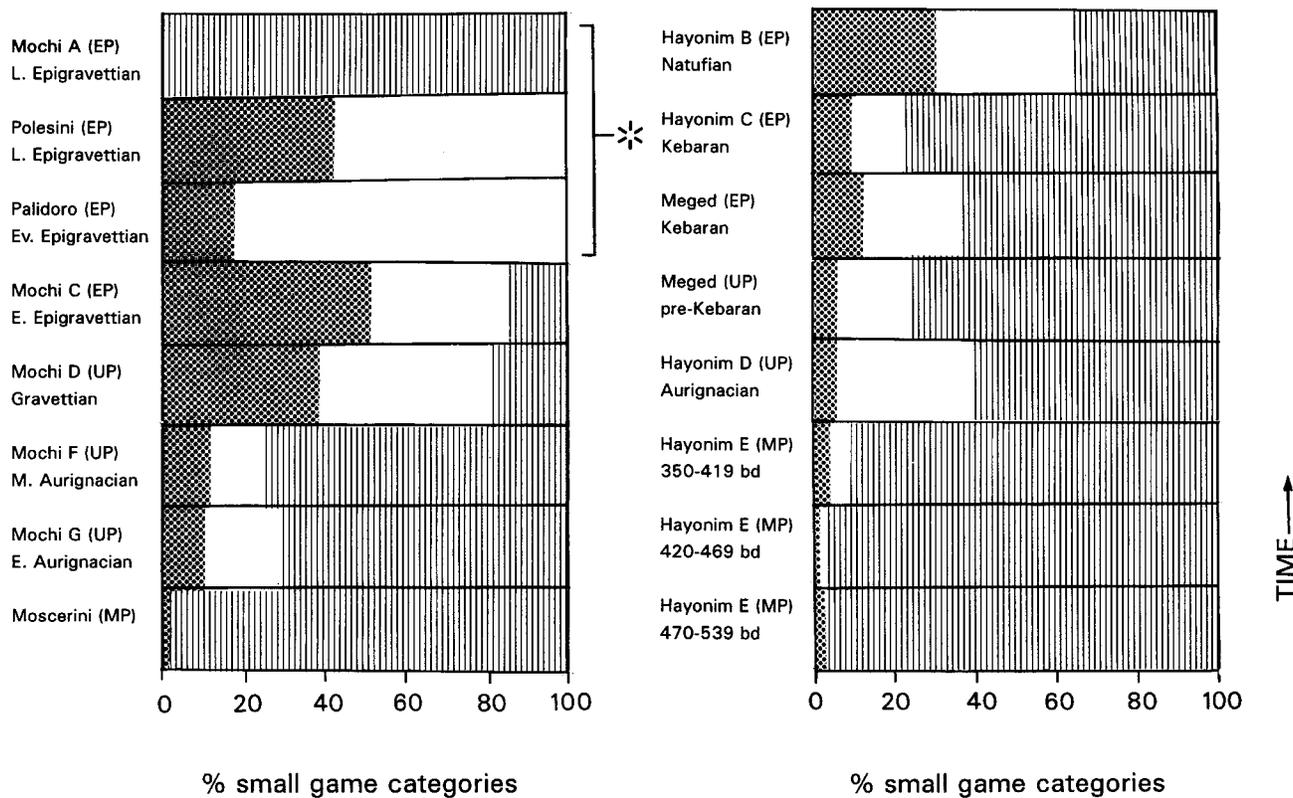


FIG. 2. Variation in the relative frequencies of slow or sessile prey, marine mollusks and/or tortoises (vertical stripes), versus birds (white) and lagomorphs (stippled) in the small-game fractions of Paleolithic assemblages from (left) Italy, 110,000–9,000 years ago, and (right) Israel, 200,000–11,000 years ago. Assemblages are time-ordered from oldest (bottom) to youngest (top). All Italian samples except Epi-Paleolithic Palidoro and Polesini are from coastal contexts; uppermost three assemblages are roughly coeval. The samples from Israel come from one small inland valley known as the Nahal Meged. EP, Epi-Paleolithic; UP, Upper Paleolithic; MP, Middle Paleolithic; bd, below site datum.

Cave is large and preserves multiple Paleolithic phases and Meged Rockshelter quite small and preserves two relatively late phases. These sites lie within 1 km of one another in the upper Nahal Meged, a wadi that empties to the Mediterranean coast 15 km to the west. Most of the sequence is represented in Hayonim Cave, supplemented by early Kebaran and late Upper Paleolithic assemblages from Meged Rockshelter. A substantial time gap separates the Middle and Upper Paleolithic in this sequence; missing are the late Middle Paleolithic and Ahmarian (early Upper Paleolithic) phases. For this reason osteometric data on tortoises from Kebara Cave on Mount Carmel (Bar-Yosef et al. 1992) are also considered.

The faunal series from Israel reveals some dramatic shifts in small-game use by Paleolithic humans paralleling those in Italy. The small-game/ungulate index in table 4 shows that small animals were important food sources for humans throughout the time range considered. Large game, mostly mountain gazelle (*Gazella gazella*) and fallow deer (*Dama mesopotamica*), usually constitute more than half the identifiable material in

each assemblage, but seldom are ungulates an overwhelming majority. The small-game/ungulate index is highest in the Natufian but is nearly matched by values for the early Middle Paleolithic. As was the case in Paleolithic Italy, however, the relative contributions of tortoises, birds, and lagomorphs to the small-game fractions shifted greatly with time (table 5). Middle Paleolithic foragers in Israel focused almost exclusively on gatherable, slow-moving types (fig. 2, right), mostly tortoises (*Testudo graeca*), supplemented on occasion by legless lizards (*Ophisaurus apodus*), ostrich eggs (assuming that the shell contents were eaten), and probably also large snakes (Calubridae); $\geq 89\%$ of small-game NISP was tortoises. By the Upper Paleolithic (Aurignacian, 26,000–28,000 years ago), birds, especially chukar partridges (*Alectoris chukar*), were being consumed in substantial quantities (see also Pichon 1983, 1984, 1987). The contribution of hares (*Lepus capensis*) and, rarely, other small mammals such as the Persian squirrel (*Sciurus anomalous*) to human diets increased most in the

TABLE 3
Main Taxa in Small-Game Fraction in the Paleolithic Series from Italy

Culture Period, Site, and Phase	Total	% Tortoises	% Lagomorphs	% Other Small Mammals	% Birds	% Shellfish
EP RM Late Epigravettian	797	0	<1	0	0	100
EP GPo Late Epigravettian	889	0	41	1	58	0
EP GPa Evolved Epigravettian	30	0	17	0	83	0
EP RM Early Epigravettian	1,191	0	45	6	34	14
UP RM Gravettian	769	0	23	15	43	19
UP RM Middle Aurignacian	420	0	2	9	12	76
UP RM Early Aurignacian	710	0	4	6	18	71
MP GB early Middle Paleolithic	660	6	1	0	0	93

NOTE: Total counts are NISP for vertebrates but MNI for mollusks to correct for significant differences in fragment sizes. EP, Epi-Paleolithic; UP, Upper Paleolithic; MP, Middle Paleolithic. Site codes are RM, Riparo Mochi; GPo, Grotta Polesini; GPa, Grotta Palidoro; GB, Grotta Breuil; and GM, Grotta dei Moscerini. Data for Polesini are from Radmilli (1974) but materials also examined by Stiner; for Palidoro, from Cassoli (1976–77). Lagomorphs are primarily hares, but rabbits and, rarely, marmots and hedgehogs are also present. Birds are mostly partridges, with fewer doves, waterfowl, and large passerines. Edible shellfish include mussels, limpets, and turbanes (Stiner 1994, 2000; Kuhn and Stiner 1998a).

Natufian period (Davis, Lernau, and Pichon 1994, Munro 1999).

SUMMARY OF THE ARCHAEOFAUNAL PATTERNS

Whereas no clear trends exist for the ratio of small to large (ungulate) game in Italy or Israel, there are well-defined trends in the types of small game emphasized by foragers in both study areas. Each small-game series begins in the early Middle Paleolithic with nearly exclusive use of sessile prey. This is followed in the early Upper Paleolithic by major proportional increases in common game birds and, by the Epi-Paleolithic, also lagomorphs. The trends involve only mild expansions in the core of staple species, however. Highly ranked prey, as defined by Middle Paleolithic exploitation, were slow-moving tortoises and/or shellfish. Use of these animals continued through the Upper and Epi-Paleolithic, but agile types (birds, rabbits, and hares) supplemented the diet in ever-greater proportions. A heavy reliance on lagomorphs has also been noted for late Pleistocene/early Holocene faunas in Spain (Villaverde et al. 1996), Portugal (B. Hockett, personal communication, 1998), Germany (e.g., Albrecht and Berke 1982–83, Berke 1984), and North Africa (Smith 1998).

The changes in small-game use occur in the context of relatively stable biotic communities, where small animals were consistently diverse and abundant. Variation in animal community content, based on the numbers of species recruited and lost, was minor during the Late Pleistocene in Italy (Stiner 1994:68–77) and Israel (Tchernov 1981, 1992). Greater variation in living species availability may have occurred during the Middle Pleistocene (Tchernov 1992, 1994b), but the most pronounced shifts in humans' use of small game took place in the Late Pleistocene.

More significant than any expansion of the taxonomic spectrum in human diets was a rising emphasis on a few

taxa which are less easily caught by hand. The generally high productivity of galliform birds and lagomorphs is well known; here they are termed "high-turnover" populations. Humans continued to collect slow-moving, slow-growing prey in the later periods, but this exploitation may have provoked declines in prey abundance. A separate line of evidence concerning early favorites on the small-game menu lends credence to the idea that their availability was conditioned by the interplay between predator densities and prey population resilience or turnover rates.

Size Diminution in Slow-growing Prey

Differences in population turnover rates are important to modeling the long-term outcomes of population interactions, a concept articulated by MacArthur and Wilson (1967), Odum (1971), and Pianka (1978), among others. Intensive harvesting over intervals shorter than a population's regeneration time is known to reduce mean individual age in a wide variety of modern vertebrate and invertebrate species (Caughley 1977; Dye et al. 1994; Keck et al. 1973; Koslow 1997; Lambert 1982; Levinton 1995:94–95; McCullough et al. 1990; Russell 1942). Species with slow rates of development and prolonged reproductive careers are particularly sensitive to losses of mature, reproducing adults (on shellfish, see Botkin 1980; on tortoises, Blasco, Crespillo, and Sanchez 1986–87, Hailey, Wright, and Steer 1988, Lambert 1982; on fish, Koslow 1997, Russell 1942). For convenience's sake, we will call these "low-turnover" species. Of interest is the pace of prey population recovery in relation to foragers' needs and available options (see also Bayham 1979, 1982; Stiner 1994; Winterhalder et al. 1988). If a prey species is slow-growing, recruitment from neighboring areas cannot easily compensate for local losses in less than a few years.

TABLE 4

Relative Abundances of Carnivores, Ungulates, and Small Game Animals in the Inland Paleolithic Series from Israel

Culture Period, Site, and Phase	Total	% Carnivores	% Ungulates	% Small Game	Small-Game/Ungulate Index	Inferred Oxygen-Isotope Stage
EP Hay Natufian	2,089	3	41	56	.57	1
EP Hay Kebaran	3,183	<1	79	20	.17	2 ^a
EP Meg early Kebaran	1,958	<1	62	37	.37	2 ^a
UP Meg Pre-Kebaran	595	<1	72	27	.27	2 ^a
UP Hay Aurignacian	10,834	2	71	29	.28	2 ^a
MP Hay 200-349 bd	172 ^b	1	89	9	.09	5-6
MP Hay 350-419 bd	1,582	<1	67	32	.29	6 ^a
MP Hay 420-469 bd	7,190	<1	58	41	.39	6-7? ^a
MP Hay 470-539 bd	4,719	<1	47	52	.52	7?

NOTE: Total counts are NISP. Small-game/ungulate index calculated as the number of small-game remains divided by the sum of small-game and ungulate remains. EP, Epi-Paleolithic; UP, Upper Paleolithic; MP, Middle Paleolithic. Carnivore and ungulate counts for the Aurignacian of Hayonim (Layer D) are from Rabinovich (1999). A time gap separates the Middle and Upper Paleolithic series in Hayonim Cave, and the data are separated accordingly. Snake remains, although common, have been excluded because their taphonomic origin is not yet clear.

^aGenerally colder and/or drier climate conditions.

^bVery small sample.

When humans collect sessile small-bodied animals, they should and apparently do prefer adults, because adults represent the largest packages of their type (e.g., Yesner 1981). There is an appreciable difference, for example, between mature tortoises or mussels and youthful ones in terms of food units gained for the effort. Heavy exploitation easily alters the age and size structure of such populations, and a predator's preference for larger individuals accelerates the effect. Because age corresponds to body size in species that require several years to reach adulthood and continue to grow thereafter, a reduction in mean age therefore also brings about a reduction in average size. This kind of pressure will not necessarily destroy the prey population as long as its intrinsic potential for growth (r) is not exceeded. Most populations have some tolerance for this kind of pressure, as younger/smaller adults can reproduce, but they tend to produce fewer young (Hailey and Loumbourdis 1988; Levinton 1995:90, 94-95).

LIMPET DIMINUTION IN COASTAL ITALY

Commercially important shellfish populations (mussels, oysters, and various clams) are known to experience rapid declines in average age and size if exploited too intensively (e.g., Dye et al. 1994, Levinton 1995). These facts about modern shellfish ecology have been used to advantage in research on human predation intensities in prehistory (e.g., Botkin 1980, Clark and Straus 1983, Jerardino 1997, Klein 1979; on fish, see Broughton 1997). Only limited consideration of the subject is possible here, because whole limpet shells in the Italian series are comparatively few (fig. 3), many having been fragmented by trampling and/or heat from fire (Stiner 1994, 2000; Kuhn and Stiner 1998a).

Figure 3 presents mean sizes and ranges (cm) for whole limpet shells from five consecutive Upper and Epi-Paleolithic phases in Riparo Mochi. Size reduction occurred abruptly between the Gravettian and the Early Epigravettian. The samples appear to form only two size-groups, and an analysis of variance shows that the size differences among assemblages deviate significantly from random (F -ratio = 75.92, $p < .001$, d.f. = [4, 403]). Because suppression of mean limpet size is constant through both the Last Glacial Maximum (Mochi C) and the warm conditions of the terminal Pleistocene (Mochi A), the diminution trend is not explained by climate change. Nor is it a result of variation in the relative frequencies of the constituent species (predominantly *Patella caerulea* throughout). Changes in habitat quality associated with the rise and fall of sea level could in principle account for size diminution in shellfish populations independently of Paleolithic forager effects (e.g., Bailey 1983a, Jerardino 1997). However, this is unlikely in the case of Riparo Mochi. The steep coastal topography of the Balzi Rossi and its widespread rocky surfaces lent unusual stability to habitat configurations there (Stiner 2000). Whatever the importance of shellfish to Middle Paleolithic diet at sites such as Grotta dei Moscerini, humans' net impact on the age/size structures of shellfish colonies was minimal. Most mussel, clam, and oyster shells in the Middle Paleolithic samples are not measurable—at least in terms of complete dimensions—but it is clear that the individual animals were quite large on average.

Shellfish diminution during the later Paleolithic has been documented at other localities as well. In South Africa Klein (1979) reports depression in mean limpet sizes for the Late Stone Age as a whole but not in the Middle Stone Age or among modern populations of the same species. Clark and Straus (1983) report limpet dim-

TABLE 5
Main Taxa in Small-Game Fraction in the Inland Paleolithic Series from Israel

Culture Period, Site, and Phase	Total	% Tortoises/Lizards	% Hares and Other Mammals	% Ostrich Eggshell	% Birds
EP Hay Natufian	1,154	35	30	0	35
EP Hay Kebaran	532	77	9	2	13
EP Meg early Kebaran	730	64	12	0	23
UP Meg Pre-Kebaran	160	77	6	0	16
UP Hay Aurignacian	2,950	60	5	?	34
MP Hay 200-349 bd	15 ^a	— ^b	— ^b	— ^b	— ^b
MP Hay 350-419 bd	437	89	5	<1	6
MP Hay 420-469 bd	2,625	95	<1	2	2
MP Hay 470-539 bd	2,371	97	<1	1	1

NOTE: Total counts are NISP. EP, Epi-Paleolithic; UP, Upper Paleolithic; MP, Middle Paleolithic. A time gap separates the Middle and Upper Paleolithic series in Hayonim Cave, and the data are separated accordingly. Snake remains, although common, have been excluded because their taphonomic origin is not yet clear. Tortoise/lizard category is dominated by tortoises (>95%). Small mammals are mostly brown hares, along with very low frequencies of Persian squirrel. Birds include a variety of species, mainly from the orders Galliformes and Columbiformes, but *Alectoris chukar* is dominant among the specimens identified to species.

^aVery small sample.

^bNo calculation feasible.

inution in the Upper through Epi-Paleolithic sequence of La Riera Cave in northern Spain.

The diminution trend for limpets in the Upper through Epi-Paleolithic sequence of Riparo Mochi is provocative, but larger samples and more cases from the Mediterranean Rim need to be examined. Size diminution in Paleolithic prey is not confined to shellfish, however. Diminution is evidenced much earlier in a different prey animal in northern Israel—the Mediterranean spur-thighed tortoise.

TORTOISE DIMINUTION IN THE NAHAL MEGED, ISRAEL

The Nahal Meged has a long history of human occupation, and tortoise remains (*Testudo graeca*) are preserved throughout the Middle and Upper Paleolithic sequence. Measurements of tortoise humeri (medio-lateral shaft diameter at its narrowest point) from Hayonim Cave and Meged Rockshelter reveal a clear size-reduction trend. The humeral diaphysis is especially suitable for comparison. As with other terrestrial vertebrates, loading sustained by the limbs translates in a predictable way to bone shaft diameter and cross-sectional area (Wainwright et al. 1976:7). Tortoises continue to grow for many years, and the dimensions of this weight-bearing member respond directly to increases in body mass (Castanet and Cheylan 1979, Walker 1973).

In evaluating tortoise size data, geographic locality must be held constant, because tortoises do not move easily from one valley to another and differences in energy flow (food supply and quality) among habitats can lead to significant differences in average adult sizes (Blasco, Crespillo, and Sanchez 1986–87, Lambert 1982). Energy flow can also change with climate, but this is a separate consideration. As with any analysis of dimi-

nution, time increments in a series must be kept as short and as equivalent as possible. The lengthy Middle Paleolithic portion of the Nahal Meged sequence is therefore subdivided according to sediment configuration and lithic industrial content to make the time increments roughly comparable to the short Upper Paleolithic and Epi-Paleolithic phases.

Figure 4 shows that the tortoises collected by Middle Paleolithic foragers in the Nahal Meged were large on average and considerably larger than those collected by later humans in the same valley. Rather than gradual diminution, the means in this series form two size-groups; an analysis of variance shows the size differences to be nonrandomly distributed in the time-ordered samples (F -ratio = 24.15, $p < .001$, d.f. = [8, 414]). The early Middle Paleolithic tortoise means vary, but none save that for the youngest assemblage approach the low values of the Upper Paleolithic phases. One possible explanation for the scale of variation found among the Middle Paleolithic samples is change in the quality and abundance of tortoises' food supply. However, climatic variation does not account for the major size decline in the late Middle Paleolithic. Nor does climate account for the fact that diminution is sustained through the Upper and Epi-Paleolithic, a time range characterized by radical shifts in world climate (also Bar-Yosef 1981, 1995, 1996; Tchernov 1992). The size trend in tortoises probably resulted from a combination of human-induced and climatic effects, but human involvement cannot be denied.

A hiatus in human occupations and sediment accumulation in Hayonim Cave separates the Mousterian (Middle Paleolithic) and the Aurignacian (Upper Paleolithic). Because the hiatus may have lasted some 40,000 years, the Nahal Meged series may not specify the exact timing of tortoise diminution. The late Middle Paleolithic and early Upper Paleolithic levels from Kebara

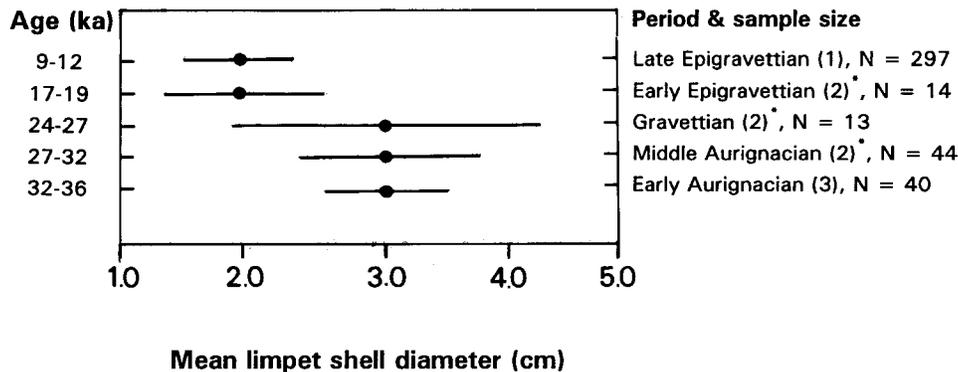


FIG. 3. Size reduction trend in limpets (predominantly *Patella caerulea* throughout) from time-ordered Upper Paleolithic layers of Riparo Mochi (Liguria, Italy), based on mean shell diameter (cm) and standard deviations. Numbers in parentheses are Shackleton and Opdyke's (1973) oxygen-isotope stages. *, generally colder/drier climate; ka, thousand years; N, number of whole shells measured. No substantial skewing (<10% difference between mean and median) occurs in the size distribution for each assemblage.

Cave (Bar-Yosef et al. 1992, 1996) help to fill this time gap. Kebara Cave is situated in a somewhat richer vegetation zone, where tortoises were always correspondingly larger. Nonetheless, a radical mean size decline in tortoises occurred between the late Middle Paleolithic, dated to 60,000–48,000 years ago (4.5 mm, $N = 169$, s.d. 0.6), and the earliest Upper Paleolithic (Ahmarian), dated to 44,000 years ago (4.0 mm, $N = 31$, s.d. 0.8). Thus, size suppression in tortoises in northern Israel began *at least* 44,000 years before present but probably earlier in light of the relatively small mean size for the youngest Middle Paleolithic sample in the Nahal Meged series.

Klein and Cruz-Urbe (1983; also Klein 1989:330–31) note size diminution in angulate tortoises (*Chersina angulata*) between the Middle and the Late Stone Age in South Africa, considerably later than in *Testudo graeca* in Israel. It seems that Paleolithic human population densities were increasing in different areas of the Old World at different times.

Implications of the Archaeofaunal Evidence: Critical Variables

The total contribution of small animals to Paleolithic diets shows no particular trend in either coastal Italy or the western hills of Israel, but the relative proportions of key prey types changed in significant ways. A sudden increase in the dietary importance of birds coincides with the early Upper Paleolithic in both regions. Lagomorphs became important rather late in both sequences. Some of the changes in small-game use over time are linked to size declines in the slow-maturing prey species, which are sustained across dramatic shifts in world climate. Marine limpets in Italy and spur-thighed tortoises in Israel underwent substantial size diminution during the later Paleolithic and likely became rarer because of

heavy harvesting. Limpet diminution in Italy (and Spain) is later than that for tortoises in Israel, however. The above observations do not present a simple story of subsistence change in the later Paleolithic, but together they testify to increasing predator pressure on prey. This implies that human population densities were rising, probably in several pulses. The archaeological findings and background information on the common prey types represented in the Mediterranean series suggest that two variables were of crucial importance: the ways prey elude predators and prey maturation rates.

PREDATOR-AVOIDANCE MECHANISMS

The means by which prey animals avoid predators greatly affect their relative rank in a foraging regimen. In the Mediterranean study areas we have two broad categories of small prey—those which are easily caught by hand and those which are not. These differences in “catchability” translate into distinct work-of-capture costs in the absence of special tools. A tortoise's defense against predators combines cryptic habits, slow movement, and a portable fortress. Safety in numbers replaces hiding in some mollusks. The attractions of these resources are of course their ease of capture and low processing costs. Humans should use these resources whenever they are encountered—the main challenge to human foragers posed by tortoises and most shellfish is finding them. Modern tortoises and shellfish can exist at very high densities in the absence of human disturbance on account of their low metabolic rates, high sub-adult/adult survival rates, and potentially long life spans (e.g., Hailey 1988, Shine and Iverson 1995). Mussel colonies and limpet patches are relatively easy to find along rocky shorelines. Terrestrial tortoises are less clustered in the environment because they lead solitary lives, but

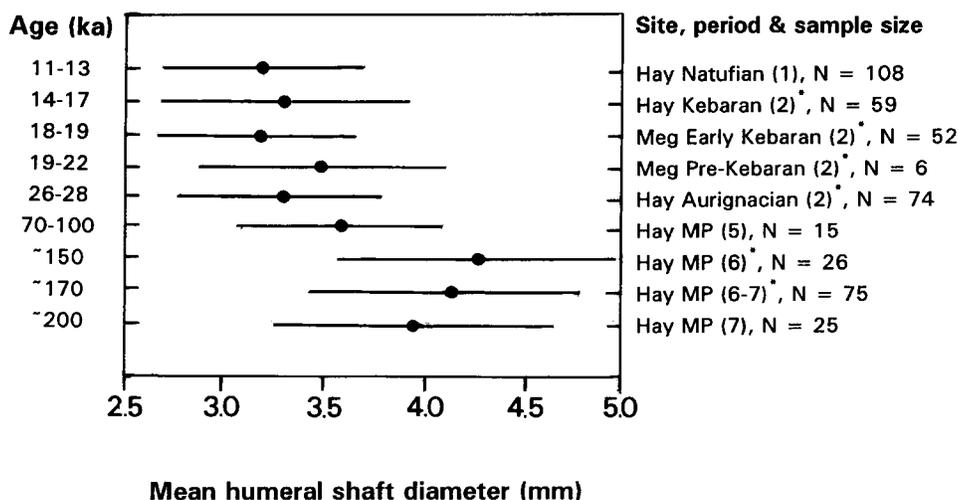


FIG. 4. Size reduction trend in Mediterranean spur-thighed tortoises (*Testudo graeca*) from the time-ordered Nahal Meged assemblages, based on mean values for the humeral diaphysis (mm) and standard deviations. The long Middle Paleolithic (MP) stratigraphic sequence is subdivided to render time spans similar to the Upper Paleolithic Aurignacian, Kebaran, and Natufian culture periods. N, number of humeri measured (right and left sides combined); other symbols as in figure 3. No substantial skewing (<10% difference between mean and median) occurs in the size distribution for each assemblage.

adults may be quite visible during the mating season and in less densely vegetated habitats.

All of the small species that were added in substantial numbers to later Paleolithic diets are quick-flight types. Hares, rabbits, and partridges (and other birds) are given to bolting from cover at high speed, and they generally are more difficult than tortoises or shellfish to catch without the benefit of nets, snares, or other traps. Because of the higher pursuit and handling costs, humans' incentives to switch to quick types would therefore have to have been strong. Prolonged scarcity of easily collected small prey would also have increased the selective advantage of any technology that reduced the cost of capturing agile animals.

PREY MATURATION RATES

Predator-prey relationships are also mediated by the life-history characteristics of the prey species. Because slow-growing small taxa dominate the earlier portions of each Paleolithic sequence and fast-growing types become important later, the periodicity or intensity of predation relative to prey maturation rates must be important. While ground birds, lagomorphs, tortoises, and most shellfish may produce many young per year, tortoises require roughly a decade to mature and large-bodied shellfish up to half this time (minimally two to five years in the wild [e.g. Epifanio and Mootz 1976, Keck et al. 1973, Little and Kitching 1998]). In stark contrast, lagomorphs and game birds such as partridges reach reproductive age within a single year, which accounts in large part for the high turnover rates of these populations.

A harvesting bias favoring adults, females in particular, amplifies the sensitivity of slow-maturing species to predator pressure and accelerates diminution. In tortoises and edible mollusks, older females may produce more eggs on average because of their larger body size (e.g., Hailey and Loumbourdis 1988). Moreover, the sexes in tortoises are highly size-dimorphic, with females being significantly larger than males of equivalent age (e.g., Lambert 1982). Large body size also confers a reproductive advantage on females of many shellfish species (Levinton 1995:90-95). Selective removal of adults may erode the reproductive core of any sort of prey population, but its effect is especially strong among slow-maturing species because mature females lost to predation are only slowly replaced. Intense predation on reproductively active adults quickly outstrips the time required for prey population resurgence. The relationship between slow-maturing prey species and predatory humans is therefore particularly delicate, sustainable only if predator population density remains very low.

Simulations of Cyclical Predation on Slow- and Fast-growing Prey

Differences in small-prey productivity amount to differences in how animals occupy environments and stock them with progeny. Humans should be affected by the life-history characteristics of any prey animal that, for other reasons, is ranked highly in the foraging spectrum. Contrasting life-history strategies suggest that low-turnover and high-turnover prey species should respond quite

differently to human predation. What is poorly understood at present is the magnitude of difference in productivity among the subject prey animals. Our predator-prey simulations are designed around the life-history traits of three common small prey items—tortoises, hares, and partridges. The simulation models are constructed with two questions in mind: (1) What is the maximum annual “yield” that predators can take from a subject prey population without destroying it over the long term? (2) How much more resilient are hare and partridge populations than tortoises to the same increases in predator density?

As a stepping-stone to predator-prey model development, table 6 summarizes the main life-history and predator-avoidance characteristics of edible mollusks, tortoises, lagomorphs, and partridges. These generalizations liken tortoises to mollusks and lagomorphs to partridges and other common game birds, at least from the human perspective. It is clear that prey birthrates alone cannot explain the differences in prey population turnover rates in our study or the trends in small-game use of the later Paleolithic. The explanatory power of maturation-rate and predator-avoidance mechanisms are much more promising: work of capture influences prey rank, and birthrate and maturation rate should together determine a population’s potential resilience to heavy predation by humans.

The parameters for the simulations are taken from a variety of modern wildlife studies, preferably but not exclusively for the species identified in the Mediterranean archaeofaunas. Table 7 summarizes the life-history parameters for tortoises (*Testudo*), hares (*Lepus*), and partridges (*Alectoris* and *Perdix*). Not all wildlife studies are equally suitable sources of simulation parameters; while cases involving substantial habitat loss and/or catastrophic population decline are compelling ammunition for conservation issues, they are not necessarily appropriate standards for prehistoric prey population dynamics. Data from long-term studies of viable populations, with good control on birthrates, mortality rates, and their causes, are used preferentially for this modeling study.

To investigate the interplay of life-history traits in predator-prey systems, we model two extremes of population growth for each kind of small prey—a high-growth model (HGM) and a low-growth model (LGM). Truly average conditions are rare in the life of any individual, but most or all years in that individual’s life-

time will very likely fall between the curves defined by our models. Because prehistoric prey and predator densities cannot be known absolutely, our strategy is to compare the relative resiliences of tortoise, hare, and partridge populations under favorable and minimal conditions for prey reproduction and growth. The simulation was written by one of the authors (T.A.S.) as Visual Basic macros in Microsoft Excel 7.0. Populations are modeled as sets of actual individuals, each characterized by *age*, *sex*, and, in tortoises, *body mass*. Additionally, females are assigned *next age of reproduction* and *annual litter size* values. Individual age increases by a fixed value per unit time elapsed.

Population dynamics are governed largely by fertility and mortality rates. Fertility is controlled by three parameters in the model: *female minimum reproductive age* and the *minimum* and *maximum number of offspring per annum*. When a female is born, her next age of reproduction is set to the minimum age at which she can begin reproducing and to normal birth spacing thereafter. A predetermined number of offspring between the minimum and maximum values in table 7 is added to the population each year (except for tortoises [see below]). An even sex ratio at birth is maintained.

Mortality is controlled by four parameters in the model: *maximum potential life span*, *annual juvenile mortality*, *annual adult mortality*, and *age of onset of adult-level mortality*. Mortality effects are divided between only two age-groups, juveniles (including newborns) and adults, an approach justified by the available wildlife data. Adult mortality randomly removes a fixed percentage of adults from the population each year, in addition to removing any individuals lucky enough to have exceeded the maximum potential life span. Density-dependent mortality from nonhuman causes affects only juveniles, because young animals are most likely to suffer in high-density conditions. Thus, juvenile mortality is allowed to vary as a linear function of population density:

$$m_t = m_0 + [(pop_t / pop_k) (1 - m_0)],$$

where m_t is juvenile mortality at time t , m_0 is base-level juvenile mortality, and pop_t / pop_k is population density at time t . Therefore, $m_t = m_0$ when $pop_t = 0$ and $m_t = 1$ when the population is at environmental carrying capacity.

TABLE 6
Summary of Life-History and Predator-Avoidance Characteristics of the Common Small Prey in the Mediterranean Archaeofaunal Series

Prey	Offspring Production Rate	Maturation Rate	Predator-Defense Mechanisms
Shellfish	High	Slow	Safety in numbers, armor, some cryptic
Tortoises	Moderate	Slow	Freezing, hiding, armor
Lagomorphs	Moderate	Fast	Hiding, bolting, and rapid running
Game birds	Moderate	Fast	Hiding, bolting, and rapid flight

TABLE 7

Fertility and Mortality Parameter Values for Tortoises, Hares, and Partridges in the High-Growth (HGM) and Low-Growth (LGM) Models

Animal and Model	Fertility				Mortality			
	Female Age at First Reproduction (yrs.)	Birth Interval (days)	Offspring per Annum		Maximum Potential Life Span (yrs.)	Age of Adult-level Mortality Onset (yrs.)	Annual Adult Mortality Rate	Annual (Base-level) Juvenile Mortality
			Min.	Max.				
Tortoises								
HGM	8	365	7	14	60	1	0.053	0.70
LGM	12	730	7	14	60	1	0.093	0.85
Hares								
HGM	0.75	365	9	11	12	0.5	0.4	0.6
LGM	1.0	365	7	9	12	0.5	0.5	0.7
Partridges								
HGM	0.75	365	11	13	8	0.2	0.5	0.42
LGM	1.0	365	9	11	8	0.2	0.6	0.6

SOURCES: For tortoises, Blasco, Crespo, and Sanchez (1986), Castanet and Cheylan (1979), Hailey and Loumbourdis (1988), Lambert (1982, 1984), Meek (1989), Shine and Iverson (1995), Wilbur and Morin (1988), Willemsen and Hailey (1989). For partridges, Ali and Ripley (1969), Alkon (1983), Ash (1970), Bannerman and Bannerman (1971, cited in Alkon 1983), Blank and Ash (1962), Bohl (1957), Christensen (1954, 1970), Dement'ev and Gladkov (1967), Galbreath and Moreland (1953), Harper, Harry, and Bailey (1958), Jenkins (1961), Mackie and Buechner (1963), Middleton (1935), Potts (1986), Robbins (1984). For hares, Broekhuizen (1979), Bronson and Tie-meier (1958), Flux (1981), Frylestam (1979), Hansen (1992), James and Seabloom (1969), Keith (1981), Kovacs (1983), Lechleitner (1959), Petruszewicz (1970), Pielowski (1971, 1976, cited in Broekhuizen 1979), Raczynski (1964), Swihart (1983).

Hunting by humans is controlled by two constants in any given run—*minimum age (or size) to hunt* (a selectivity factor) and *annual kill percentage*. As long as individual prey above a given age or size threshold are available, it is assumed that humans will be attracted to them. If individuals above the threshold are no longer available, humans will target the oldest available individuals below that age threshold.

Parameter definitions and sources used in modeling the tortoise, partridge, and hare populations are provided separately below.

TORTOISES

Testudo, the common genus of tortoise in the archaeological series, provides an ideal standard for comparing uses of small game in the Mediterranean Paleolithic. Because little modeling work has been done on tortoises in general, it is necessary to begin from scratch (but see Doak, Kareiva, and Klepetka 1994). In so doing, we note several important insights from wildlife studies of modern *Testudo graeca* and *T. hermanni* in the Mediterranean Basin. First, the illegal pet trade, which favors large specimens for international markets, rapidly drove down mean individual size in affected tortoise populations in North Africa (Lambert 1982, Stubbs 1989) and Spain

(Blasco, Crespillo, and Sanchez 1986–87). Second, immature tortoises are much more difficult to find than adults in Mediterranean habitats (Lambert 1982). Third, adult female tortoises tend to be larger than males of the same age (Blasco, Crespillo, and Sanchez 1986–87, Lambert 1982), making the reproductive core of the population that much more vulnerable to size-dependent predation by humans. Our model takes into account the steeper growth curve of females relative to males (Blasco, Crespillo, and Sanchez 1986–87, Lambert 1982), because size-biased collecting should affect females and males differently. Tortoises over about 0.3 kg were considered adults on the basis of curve fitting, corresponding to 10 years of age for females and 12 years of age for males.

T. graeca and *T. hermanni* populations can be modeled as one taxon for our purposes, because they respond in nearly identical ways to variation in food supply and human-caused disturbances in areas where their distributions overlap and have similar reproductive rates as measured by annual egg mass production, clutch sizes, and laying frequencies (Blasco, Crespillo, and Sanchez 1986–87, Hailey and Loumbourdis 1988, Hailey, Wright, and Steer 1988, Stubbs 1989). *T. graeca* is the more widespread species (Ernst and Barbour 1989, Stubbs 1989), and a maximum adult weight of about 1–1.5 kg is typical today in our study area.

Information on the population dynamics of Mediterranean and other tortoises is scarce, and the available data on fertility and mortality are coarse-grained, making it necessary to broaden the taxonomic scope to estimate the ranges for certain parameters. Fortunately, tortoises differ little in terms of the variables employed here, especially if compared with most mammals and birds. Tortoise life histories are characterized by high hatchling mortality but very low subadult and adult mortality, long life spans, and delayed reproductive maturation (Hailey 1988, Shine and Iverson 1995, Wilbur and Morin 1988).

Adult mortality in *Testudo* varies among populations and across years, but composite study results show that survival tends to be continuously high after the first year of life (Hailey 1988, Lambert 1982, Meek 1989). Although tortoises are far from mature at this stage, the age of onset of adult-level mortality is set at one year in both models. We set hatchling mortality (i.e., for first year of life) at 70% in the high-growth model (females produce 2.1 to 4.2 yearlings per annum) and at 85% in the low-growth model (0.7 to 1.4 yearlings produced per annum), based partly on Doak, Kareiva, and Klepetka's (1994) estimates of hatchling survival in desert tortoises (*Gopherus*). High adult survivorship is essential to the health of tortoise populations, and hatchling survival rates can vary much more without detracting from the long-term fate of those populations (Doak, Kareiva, and Klepetka 1994, Heppel, Crowder, and Crouse 1996, Heppel et al. 1996); these observed characteristics are reflected in our models. Because egg production depends partly on female body size (Hailey and Loumbourdis 1988), the number of offspring (eggs) produced per annum is allowed to vary linearly with body mass within the specified range. Because wild individuals of the genus *Testudo* seldom live beyond 60 years (Lambert 1982), this value serves as the maximum potential life span. It allows 53.5 and 48.0 years of reproductive activity in the high-growth and the low-growth models respectively.

A strong negative correlation exists between age at sexual maturity and the adult mortality rate in turtles, tortoises, and many other reptiles (Shine and Iverson 1995). We use the regression line associated with this correlation to control the covariance of these parameters. To account for published variation in age at first reproduction (compare Blasco, Crespillo, and Sanchez 1986–87, Castanet and Cheylan 1979, Hailey 1990), values for *T. graeca* and *T. hermanni* are set at 12 years in the high-growth model and at 8 years in the low-growth model. These correspond to adult mortality values of 5.3% and 9.3%, respectively, well within the range documented in modern wild populations (Hailey 1988, 1990; Lambert 1982; Meek 1989).

Annual egg production for *T. graeca* varies between 7 and 14 according to Hailey and Loumbourdis (1988). Birth spacing is set to 365 days in the high-growth model but at 730 days in the low-growth model because as few as half of the adult females in a tortoise population may reproduce in a given year (Wilbur and Morin 1988).

Figure 5 presents the simulated outcomes of incremental increases in predation on tortoises over 200 years

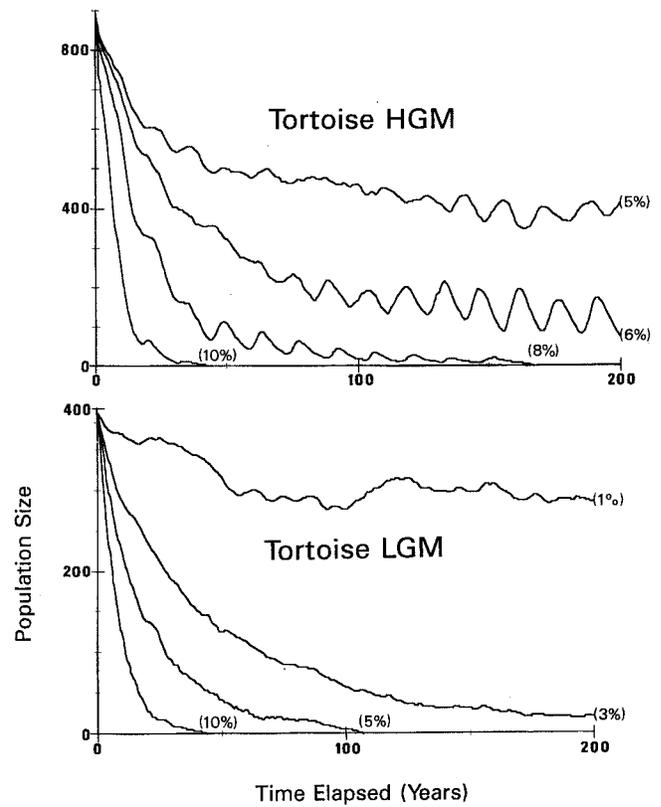


FIG. 5. Simulated predation on tortoise (*Testudo*) populations under high-growth (HGM) and low-growth (LGM) conditions. Percentages refer to annual off-take (mortality) from the total population, with adults (≥ 0.3 kg) taken preferentially. The undulations (chattering) in some of the HGM curves are due to alternating foci on male and female prey; this is largely a product of model design.

under high-growth and low-growth conditions. Adults were taken preferentially by the predators. It is clear from this exercise that tortoise populations cannot tolerate more than 4–7% annual losses of reproductively mature individuals without crashing. In comparison with hares and birds (below), tortoise populations are exceptionally sensitive to predation and are easily destroyed.

PARTRIDGES

Our partridge is a somewhat idealized animal, since the faunal series from Israel and Italy include three species—chukar (*Alectoris chukar*), gray partridge (*Perdix perdix*), and quail (*Coturnix coturnix*). Of these, our simulations emphasize the parameters available for chukar and gray partridge, which are widely distributed in the Mediterranean area and have recently been introduced into numerous habitats worldwide (Alkon 1983, Potts 1986). The gray partridge is better adapted to cold winters, the chukar to arid conditions, but otherwise these

species have similar needs and population characteristics.

Normally gregarious, partridges and chukars disperse into breeding pairs in spring, and most hens lay one clutch of eggs per year (Alkon 1983, Bohl 1957, Christensen 1970, Mackie and Buechner 1963). The onset of egg laying and hatching is not fully synchronized among reproducing females, however, particularly in milder climates. The average number of hatchlings per female chukar per year is 11 with a standard deviation of 2 (Ali and Ripley 1969; Alkon 1983; Bannerman and Bannerman 1971, cited in Alkon 1983; Bohl 1957; Christensen 1954, 1970; Dement'ev and Gladkov 1967; Galbreath and Moreland 1953; Harper, Harry, and Bailey 1958). Gray partridges' reproductive output is similar. One standard deviation is therefore added and subtracted from mean annual production and the result rounded to the nearest whole number to produce the high-growth and low-growth birthrates.

Juvenile mortality in partridges is greatest during the first and second week after hatching and declines rapidly as the chick approaches adult size (Blank and Ash 1962, Potts 1986). Winter mortality for chukars and gray partridges is comparable where their ranges overlap in southern Europe. Adult mortality from predation is especially high for hens during the spring laying periods (Potts 1986) and can be as much as ten times the normal level for adults at large. Our adult average mortality rate value of 55%, plus or minus one standard deviation, relies heavily on Potts's (1986) long-term study of gray partridges and his summaries of over 50 other sources on partridges in England, mainland Europe, and the United States (e.g., Ash 1970, Blank and Ash 1962, Jenkins 1961, Middleton 1935). This average incorporates the risks unique to nesting hens. The onset of the adult mortality rate is set at two months of age for both models following Jenkins's (1961) and Potts's (1986) assessments. Both juvenile and adult mortality rates significantly influence the growth and maintenance of partridge populations (see also Caughley 1977 on birds). Robbins (1984) reports that female partridges are capable of breeding through four to seven reproductive seasons. Eight years thus serves as the maximum potential life span for both models, with a maximum of one year devoted to individual development.

Figure 6 presents the simulated outcomes of incremental increases in predation on partridge populations over 200 years under high-growth and low-growth conditions. Individuals aged two months and older were taken preferentially. Partridges are very resilient to sustained heavy predation, and their populations are difficult to destroy, even where off-take is consistently high. Partridge populations can tolerate up to about 65% annual losses of adults in the high-growth and about 22% in the low-growth model. Certain other game birds, such as common doves, probably also fit this pattern.

HARES

The brown or cape hare (*Lepus capensis*) is the most common lagomorph in our Paleolithic samples, but little

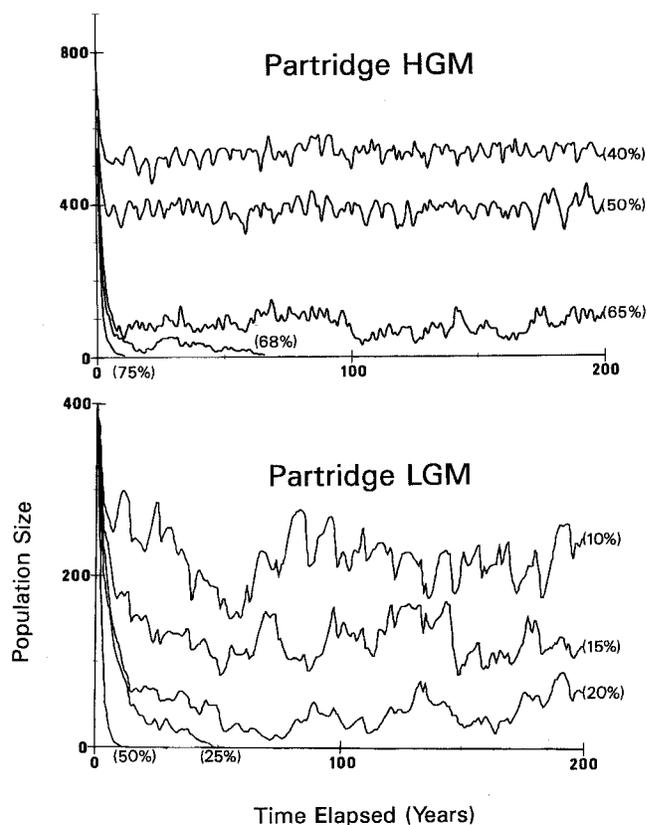


FIG. 6. Simulated predation on partridges (*Alectoris* and *Perdix*) populations under high-growth (HGM) and low-growth (LGM) conditions. Percentages refer to annual hunting off-take (mortality) from the total population, with adults (≥ 2 months of age) taken preferentially.

reliable information could be found for this animal in modern western Asia. The closely related European hare (*L. europaeus*) is widespread and well studied in Europe, however, including the northern Mediterranean Rim. Some biologists argue that it is the same species as the brown hare; all others agree that they are closely related. Because adult mortality for modern European hares varies greatly among studies, largely because of their popularity among sport hunters, we distinguished hunted from nonhunted populations in our use of mortality parameters. The North American jackrabbit literature (*L. californicus* of grassland/desert scrub habitats and *L. alleni* and *L. townsendi* of grassland habitats) was also consulted.

In warm environments hares have reproductive seasons lasting eight to nine months each year. The age at first reproduction normally varies between nine months (the value for our high-growth model) and one year (the low-growth value), although females are physically capable of reproducing at six months of age. Our use of reported birthrates is conservative and relies mainly on

observed rather than estimated values, as many biologists' techniques for estimating birthrate assume extraordinary rather than normal reproductive conditions (cf. Gross, Stoddart, and Wagner 1974, Hansen 1992, Lechleitner 1959, Bronson and Tiemeier 1958). A doe's annual production of young (leverets) in each of the two models (table 7) is based on standard deviations around an average from nine studies, six on the brown hare and three on North American jackrabbits (Bronson and Tiemeier 1958, Flux 1981, Hansen 1992, James and Seabloom 1969, Keith 1981, Petrušewicz 1970, Pielowski 1976, cited in Broekhuizen 1979, Raczynski 1964). As with partridges, one standard deviation is added and subtracted from the mean annual production value for hares and then rounded to the nearest whole number to produce the high-growth and low-growth birthrates respectively.

The maximum potential life span is set at ten years for both models, a compromise based on studies by Pielowski (1976), Abildgård, Anderson, and Barndorf-Nielsen (1972), and Broekhuizen (1979). Three studies conducted in areas minimally impacted by humans suggest that adult mortality rates should apply to all individuals past the minimum reproductive age (six months) in both models (Abildgård, Anderson, and Barndorf-Nielsen 1972, Marboutin and Peroux 1995, Pielowski 1976, cited in Broekhuizen 1979). Mortality in recreationally hunted hare populations is consistently higher (cf. Broekhuizen 1979, Frylestam 1979, Kovacs 1983, Lechleitner 1959, Marboutin and Peroux 1995, Pépin 1987, Petrušewicz 1970) and cannot be taken to represent the human-independent dynamics of hare populations.

Juvenile mortality rates in hares are high, ranging between 60% and 89% per annum (Frylestam 1979, Gross, Stoddart, and Wagner 1974, Hansen 1992, Petrušewicz 1970). However, these figures represent stable hare populations existing at high densities; juvenile mortality naturally increases as a population approaches equilibrium. In our model the effects of population density on juvenile mortality rate are such that the hare population reestablishes equilibrium at a reduced population density with an associated reduction in juvenile mortality. The variation produced by our simulations matches well the variation observed by Gross, Stoddart, and Wagner (1974) for a real hare population that adjusted between high- and low-density conditions over several years.

Figure 7 illustrates the simulated outcomes of incremental increases in predation on hares over 200 years under high-growth and low-growth conditions. Clearly, hare populations are very resilient in the face of heavy predation and difficult to destroy. They rebound easily after heavy harvesting, providing that no more than about 53% (high-growth) to 18% (low-growth) of mature or nearly mature individuals are removed from the population in a given year. These are conservative estimates—real populations are likely to be considerably more resilient than our model suggests.

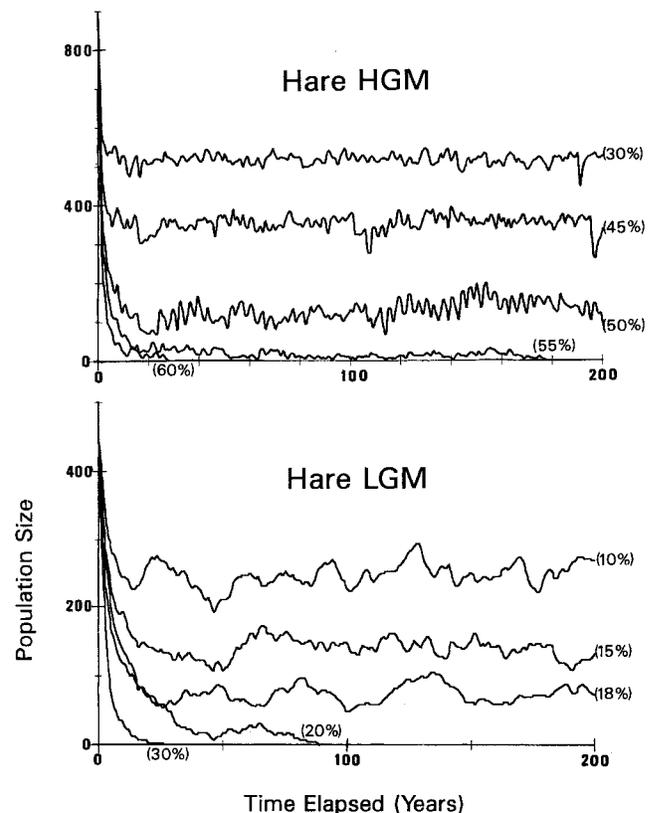


FIG. 7. Simulated predation on hare (*Lepus*) populations under high-growth (HGM) and low-growth (LGM) conditions. Percentages refer to annual hunting off-take (mortality) from the total population, with adults (≥ 6 months of age) taken preferentially.

SUMMARY OF THE SIMULATION RESULTS

Folk wisdom tells us that lagomorphs are exceptionally productive. What it does not tell us is how game birds and tortoises compare with them. Figure 8 compares the areas between the high- and low-growth curves for tortoises and hares. The area enclosed by the two curves for tortoises does not overlap at all with that for hares during population growth, despite our rather puritanical limits on hare productivity. Hare populations reached equilibrium between about 7 and 25 years, whereas tortoise populations reached equilibrium between about 50 and 125 years. Partridge populations may be even more resilient than hares, reaching equilibrium by about 5 years in the high-growth and 10 years in the low-growth model (not shown). Apart from this qualification, the areas enclosed by the curves for partridges and hares overlap almost completely and may be considered to be about the same.

Figure 9 further summarizes the resilience ranges of the three types of small prey animals common to the Paleolithic series. The simulations confirm major differences in the scale at which humans could hope to

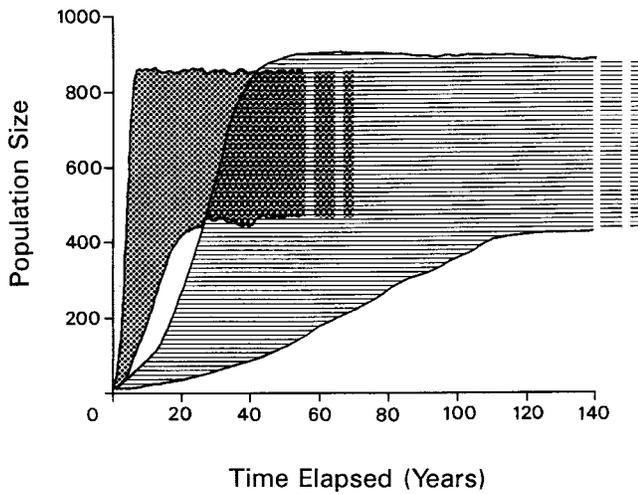


FIG. 8. High- and low-growth curves for tortoises (linear shading) and hares (stippled shading). The upper line represents the high-growth model and the lower line the low-growth model for each kind of prey. Initial population size is 10 individuals for each; carrying capacity is set at 1,000 for tortoises and at 1,250 for hares to render population sizes comparable in this graph.

depend on tortoises, hares, and partridge-like birds for meat. The same may have been true for the shellfish that Paleolithic humans in the Mediterranean area depended on for food, although we have not modeled them here. Inherent differences in prey population resilience would have been especially important if human populations were experiencing stress from territorial circumscription and rising densities. Other things being equal, hare populations can support proportionally seven times and partridges ten times greater off-take by predators than tortoises. This means that humans' reliance on tortoises is sustainable only if human population densities are very low but reliance on partridges and hares is sustainable in both low- and high-density conditions. Relative differences in small-animal productivity make considerable economic sense of Upper and Epi-Paleolithic humans' increasing interest in birds and hares when suitably large tortoises were in short supply. One can also argue that partridges and hares represented more stable or reliable sources of small meat packages as human population densities increased. However, the high-turnover prey species in the two Mediterranean study areas are also quick and thus more difficult to catch by hand. It is for this reason that they may have been ranked lower in early Paleolithic foraging systems, qualities which humans could overcome only with the help of technology.

Discussion

Paleolithic foragers responded very differently to slow and quick small prey. As it happens, prey catchability

correlates closely with differences in prey population resilience, at least among the species that were important to Paleolithic foragers in the Mediterranean Basin. Tortoises and most shellfish require years to mature, their populations are relatively unresilient, and they can seldom elude humans once discovered. Their high rank in humans' eyes relates only to the latter characteristic, however. By contrast, partridges, rabbits, and hares mature in well under one year, and populations of these animals rebound rapidly in the face of harvesting pressure. But partridges and lagomorphs would have been less attractive to early foragers because they are quick and difficult to catch. By the Upper Paleolithic, people had no choice but to pursue more quick prey to meet their need for dietary protein. Some of the radiations in Upper and Epi-Paleolithic foraging technology may have evolved on the heels of demographic increase as ways to reduce the cost of acquiring agile prey.

Small-animal species vary far more with respect to predator-defense mechanisms and population resilience than the ungulate species that were commonly hunted by prehistoric humans. It is for this reason that data on small-game exploitation can reflect subtle changes in Paleolithic demography. Adult tortoises and shellfish ideally must contribute young to their population for many years if they are to enjoy any measure of reproductive success. Heavy harvesting reduces prey population viability and, soon, the frequency with which human foragers can find suitably large individuals of the affected species (Botkin 1980, Christenson 1980, Earle 1980, Mithen 1993, Pianka 1978). It is therefore remarkable that up to 52% of the identifiable animal remains in

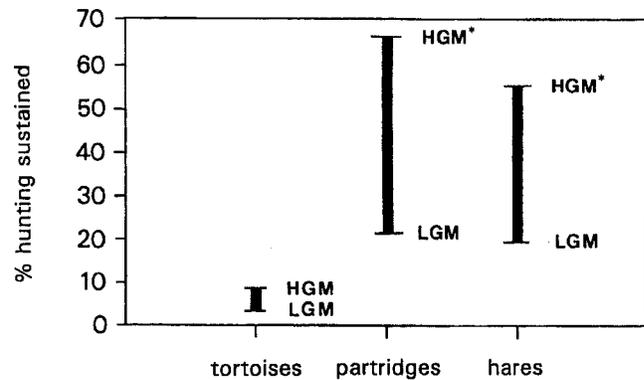


FIG. 9. Hunting tolerance thresholds for tortoise (4–7%), partridge (22–66%), and hare (18–53%) populations in high-growth (HGM) and low-growth (LGM) conditions. The upper horizontal bars represent crash thresholds, above which predators' dependence on the designated prey type is no longer sustainable; vertical bars represent natural variation in population resilience as defined by the LGM and HGM. *, HGM threshold is conservative and could be higher in reality.

some early Middle Paleolithic assemblages are species known to be sensitive to heavy predation. What is more, the sizes of the individual prey taken were large on average. High archaeological frequencies of nonresilient species, along with large individual body sizes, imply that early human populations were exceptionally small and highly dispersed. Middle Paleolithic populations simply may not have experienced the sorts of stresses that would make agile, fast-growing small animals attractive—at least not until quite late in this period. Low human population densities during most of the Middle Paleolithic also imply small social groups, certainly limiting the numeric scope of individual interactions. Under these conditions the possibilities for evolution of complex sharing and exchange behavior as a way to counter the effects of unpredictable resource supplies would also have been quite limited.

Increasing reliance on birds and lagomorphs during the Upper and Epi-Paleolithic was almost certainly a response to the declining availability of higher-ranked prey types relative to the number of consumers. While one would expect the natural abundances of shellfish, tortoises, game birds, and lagomorphs to have shifted somewhat with global climate, the trends in small-prey emphasis bear a strong human signature and indicate that human population density was increasing. Heightened rates of social contact could themselves have provided stimulus for change. This is not to say that climatic shifts of short periodicity, such as the Younger Dryas, had no effect on human life and evolution. They almost certainly altered effective latitude, precipitation, resource patchiness, and available life space for humans (Keeley 1995; see also Bar-Yosef 1995, 1996; Binford 1968; Flannery 1969). They were not, however, the main determinants of change in small-game use by Paleolithic foragers.

Our data identify more than one pulse of growth in human population density during the later Paleolithic in the Mediterranean Basin. Tortoise diminution in Israel is evidenced by at least 44,000 years ago, probably earlier, whereas mollusk diminution in Italy first occurred about 23,000 years ago. The link between patterns of small-game use and Paleolithic demography is encouraging, because the rapid increases in Pleistocene human populations suggested by studies of modern genetic variation (Long 1993, Reich and Goldstein 1998, Sherry et al. 1994) are notoriously difficult to date. There appears to be little hope for developing a mutation clock as accurate as radiometric dating techniques (personal communications, P. Taberlet, 1997, and H. Harpending, 1998). Information on small-game use by Paleolithic humans thus provides an independent, fine-scale means for examining the demographic environment of modern human origins, pinpointing population growth pulses in time and space, as well as the circumstances immediately preceding the rise of food-producing economies.

Our results also indicate a notable increase in dietary breadth during the later Paleolithic, following the predictions of classic foraging theory. This is apparent from variation within the small-game fraction of the archaeo-

faunas. As the availability of easily hand-caught small prey declined because of rising human numbers and shorter exploitation intervals, more difficult-to-capture small prey became an added staple. Our results thus concur with the basic premise of Flannery's (1969) broad-spectrum-revolution hypothesis but not with the units commonly used to measure it. One will find greater statistical evenness in the proportions of small-prey types with time *only* if prey are subdivided according to the characteristics that control their accessibility to humans. By this criterion, Upper and Epi-Paleolithic patterns of exploitation involved more even use of slow and quick small-prey types. Changes in numbers of species taken by Paleolithic foragers, the more common measure used in zooarchaeological studies of the broad-spectrum revolution, are minimal in the faunal series we examined. Taxonomic-diversity approaches have been valuable for isolating the economic transition from foragers to food producers but apparently not for investigating the evolution of the foraging economies prior to this dramatic transition. However fine a device the Linnaean taxonomy is for measuring species diversity, it was not designed for assessing the kinds of variation among organisms that most affect their economic utility to foragers. The unimpressive results of taxonomic-diversity approaches to the broad-spectrum-revolution question (compare Edwards 1989, Neeley and Clark 1993, Bar-Oz, Dayan, and Kaufman 1999, Stiner 1992) may be explained in part by the great time spans represented by Paleolithic faunal series: the more time it takes for an assemblage to form, the higher the probability that unusual events will enrich its species profile (e.g., Stiner 1992). Middle Paleolithic layers invariably took longer to accumulate and thus were subject to greater time-averaging effects than the Upper and Epi-Paleolithic layers. It is also possible that some aspects of taxonomic diversification are invisible because the added species were mainly plants.

It is interesting as well that prey body-size ratios did not elucidate trends in the Paleolithic series we examined. The great differences in work of capture among the small-prey types discussed above may have canceled out the more obvious difference between small-animal and ungulate body "package" sizes. Ungulate remains are generally more abundant than those of small game in Paleolithic faunas and may have exerted greater pull on human foraging decisions. There is, however, little evidence for "choosiness" in humans' use of ungulate species in Italy or Israel (Stiner 1992, 1994; Stiner and Tchernov 1998), apart from the elevations to which hunters were willing to travel to find them (Stiner 1990–91; see also Gamble 1986). A possible explanation for the apparent lack of relation between ungulate exploitation and the trends in small-game use is that more than one resource-ranking system existed in early human foraging systems—such as between the search requirements of large-game hunting versus generalized gathering. In any case, there may have been considerably more room for adjustment in meat acquisition in the arena of small-game exploitation, short of the evolution of animal and

plant husbandry. More outstanding than any change in the taxonomic diversity or size ratios of animal prey in Paleolithic diets was the greater range of foraging substrates used by humans over time, with the heightened reliance on birds and, elsewhere, on fish (e.g., Binford 1968, Flannery 1969, Mellars 1985).

POPULATION GROWTH, NUTRITION, AND CHILD SURVIVORSHIP

For the bulk of human prehistory, mobility was the favored solution to local resource scarcity. Some of this flexibility was lost during the later Paleolithic with local demographic packing, which may also have raised the level of intraspecific competition (*sensu* Bar-Yosef 1981; Binford 1968; Cohen 1977, 1985; Flannery 1969). Our data expose the likely impact of increasing predator density in the evolutionary process but not necessarily its cause. Why did higher human population densities become a permanent condition? It is possible to draw some speculative conclusions.

Hominids' tendencies to manipulate and restructure their environment were long in the making. This behavior is manifest in food transport, for example, quite early in the evolution of humankind. Other, more sophisticated tactics for insulating human groups from the unpredictable nature of their food supplies appeared considerably later in foraging cultures. Among these, small-scale storage of consolidated animal tissues and/or seeds and nuts may have been pivotal. Storage buffers human groups against lows in annual resource abundance, especially in situations where residential mobility, exchange, or sharing cannot solve the problem. The human body cannot store undedicated protein as it does the nutrients that yield food energy, nor can it assimilate protein effectively in the absence of energy supplements (Speth and Spielmann 1983). While daily requirements for complete dietary protein are quite modest, they are fairly constant, especially for children and the women who produce them. Children are at particular risk in lean times, and it may be of direct reproductive advantage in some circumstances to lessen the impact of seasonal and annual oscillations in the availability of critical nutrients (protein and fats). The trends in small-game use along the Mediterranean Rim, which increasingly included very productive small animals, may inadvertently have stabilized humans' access to meat as the abundance of highly ranked but relatively unproductive small prey declined (for a related argument, see Winterhalder and Goland 1993).

Any behavior that enhances the predictability of critical nutrients can improve childhood survivorship and thereby swell a population without a prerequisite change in birthrate. Recent research by Hawkes, O'Connell, and Blurton Jones (1997) suggests that the most consistent sources of protein and in some cases fat for hunter-gatherer children in arid environments are the small animals and certain nuts and roots that children procure for themselves or are provided by female kin. If this is so, then small-game use is relevant to human population

growth in prehistoric foraging societies, as is the intensive exploitation of plant mast. The opportunities to obtain small animals are considerably more diverse and widespread than are the opportunities to obtain large game: because of the physical and reproductive demands of human existence, not everyone can hunt large mammals, nor can everyone be first in line for a big piece of meat. Access to large-game tissues thus is particularly constrained if the supply is chronically low or unreliable. The small packages of food that small animals provide may arrive at modern hunter-gatherer camps in dribs and drabs (e.g., Yellen 1991a, b). But protein from small animals is widely accessible in small doses, consistent with the pace of human dietary need, and thus may have contributed to improved survivorship and population growth.

With the development of capture devices such as snares, deadfalls, and nets (*sensu* Oswalt 1976) may have come more reliable access to small protein packages from formerly elusive small animals. There is a clear association in time between increases in human diet breadth and some magnificent radiations in Paleolithic technology. While it is doubtful that all evolution in tool design can be explained by superior mechanical performance and efficiency (Kuhn and Stiner 1998b), some of it may have been spurred by dwindling supplies of certain traditional resources. In western Asia human demographic pressure preceded rather than followed the earliest technological innovations of the Upper and Epi-Paleolithic periods, since tortoise diminution appears to have begun in the late Middle Paleolithic. Some Upper and Epi-Paleolithic tools were directed to nut and seed processing, others to hunting large game (e.g., Knecht 1997), and perhaps others to trapping small animals in quantity. Common game birds were the first agile, high-turnover small prey types to gain importance in Paleolithic diets in the Mediterranean area, probably because they are sufficiently gregarious to be netted or group-snared in quantity (see Oswalt 1976, Winterhalder 1981). We do not know who in Paleolithic societies did the inventing, but innovations in trap, snare, and net technology for hunting small prey could have been the province of women, children, and the elderly (see also Binford 1968). Unfortunately, most elements of trap technology do not preserve well because they are made from sinew, cordage, wood, and other biodegradable materials. We see only rare hints of these complex tools in the form of possible bone triggers, cord imprints in mud, and art, a topic that merits more study.

TO THE FUTURE

The insights we offer on Paleolithic subsistence evolution are made possible by theoretical integration of archaeofaunal and wildlife data. The conclusion that human population densities were rising during the late Paleolithic will not surprise many archaeologists, but they may not have appreciated the unique potential of small-game data for examining when and where demographic increases took place. Twelve years of research

have allowed us to assemble faunal series for only two regions of the Mediterranean Basin. A closer look at the Middle Paleolithic record relative to later periods revealed an appropriate way to test the hypothesis of increasing diet breadth in response to human population pressure. The kinds of phenomena we report in Italy and Israel probably occurred elsewhere too, although the details and timing of subsistence change certainly will differ. Much work remains to be done on Paleolithic small-game exploitation, and in this work it will be critical to hold geography and environment constant as much as possible while assembling local faunal series. Of course not all of the small-animal remains found in archaeological sites are attributable to humans. Those that are linked to Paleolithic human activities have the unique power to clarify the timing and geographic centers of rapid population growth suggested by research on human molecular phylogenetics, as well as to clarify factors contributing to the earliest forager-producer transitions.

Comments

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Stiner, Munro, and Surovell present a new and exciting approach to the understanding of changes in dietary choice and in body sizes of animals of indeterminate growth. Indeed, they are also the first to point clearly to a temporal pattern of change in the use of small-game species. We can see, in hindsight, that small game has not received the attention that it merits. Scientists will now atone for this neglect; in the coming years we will all be searching for changing patterns of human exploitation of swift and slow small game.

Much the same as any other exciting step forward in scientific research, the proposed model opens up many new questions. Stiner et al. have defined a new research agenda with many possibilities. Future research will also enable us to fine-tune some points. We focus on the Israeli faunal sequence, with which we are better acquainted, and mention a few.

What is the time scale of these developments? Stiner et al. suggest that size suppression in tortoises occurred at least 44,000 years before present (and fig. 4 suggests that an earlier date is indeed appropriate). The increase in occurrence of bird remains (especially chukar partridges) follows only after a significant time lag (26,000–28,000 years ago), and hares increase in occurrence even later, mostly during the Natufian (11,000–13,000 years ago). The time lag may well be accounted for by the hiatus in Hayonim Cave reported by Stiner et al. The basic premise of this study is that increasing reliance on birds and lagomorphs was almost certainly a response to the declining availability of higher-ranked prey types relative to the number of con-

sumers. Therefore, it would be very exciting if a cause-and-effect relationship could indeed be established at a much finer temporal resolution.

How general is this phenomenon? Stiner et al. make the strong argument that since the series they analyze originate in two distinct ecogeographic zones, the trends cannot be dismissed as local phenomena. Now, however, we would like to know if this pattern is indeed representative of either region. Hayonim Cave and Meged Rockshelter may represent a local phenomenon within Israel. Does this shift occur in other sites? We know of some exceptions (Neve David [Bar-Oz, Dayan, and Kaufman 1999], Hefzibah [unpublished data]), and a rule remains to be established. Such a rule, if found, may be key to understanding the exceptions. Are these sites of different character or different duration? Or do they represent a different region where food stress was not an issue? Clearly, we should strive for finer geographical resolution now.

Can this model be extended to other animal taxa or age-groups? The young of some taxa may be significantly more easily caught and consumed than adults (e.g., Yellen 1991a). The young of the very common and commonly hunted mountain gazelle (*Gazella gazella*) lie alone hidden in vegetation for the first few weeks of their lives and do not escape from predators when found (Mendelssohn and Yom-Tov 1987). Because of the extended period of reproduction of gazelles, their young may well have been easily collected prey for early humans and prey that required different food procurement strategies than those for adults. The same is true for some other ungulate species. Moreover, other mammal species such as hedgehogs (*Erinaceus europaeus*) and even porcupines (*Hystrix indica*) can be easily "collected" and require no pursuit or sophisticated hunting strategies. How do they fit into this proposed framework?

Why did bird trapping increase millennia prior to lagomorph trapping? Stiner et al. suggest that perhaps the more gregarious habits of these game birds account for this trend. Chukar partridges spend most of the year in groups of 10–20 individuals of both sexes and of varied ages (Paz 1986). Finding a pattern congruent with a mixed age and sex group would certainly lend support to Stiner et al.'s hypothesis.

Stiner et al. view this exciting development as an expansion in dietary breadth during the later Paleolithic. Thus they feel that the results concur with the basic premise of Flannery's (1969) broad-spectrum-revolution hypothesis but not with the taxonomic units commonly used to measure it. In our view it serves no purpose to confound these two issues. We view their results not as vindicating the broad-spectrum model, evidence for which has been controversial (Edwards 1989, Neeley and Clark 1993, Bar-Oz, Dayan, and Kaufman 1999), but rather as suggesting that for many years our view of changing economies has been overly simplistic. If there is a lesson to be learned after years of analyses of large data sets, it is that there is no substitute for meticulous analysis of details.

While these and other questions remain to be ad-

dressed, Stiner et al. have made a very significant contribution towards our understanding of possible density-dependent processes in the evolution of human economies and have identified a new research agenda for the future.

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Stiner, Munro, and Surovell's paper focuses on a very important issue for understanding Paleolithic economy and subsistence. While the importance of small game in prehistoric diets has been demonstrated during the past decade (Hockett 1991, Straus and Clark 1986, Villaverde and Martínez Valle 1995, Zilhão 1995), it is only within the past two years that these data have become the center of attention for Paleolithic archaeologists. Stiner et al.'s paper is very comprehensive in presenting both data and a set of definitions and simulations that help the reader to follow their rationale. I would like to emphasize the importance of rate of species growth, predator avoidance mechanisms, and prey maturation rates to the study of prehistoric subsistence patterns.

This study shows that in certain areas of the Mediterranean the contribution to diets of small game and the diversity of species during the Paleolithic was of very little importance; instead, the key data are the types of small game and shifts in their use. These shifts depended on prey population resilience and the work of capture, showing clear directional diachronic changes in small-game assemblages without any significant diachronic variation in the ratio of small to large fauna. As a general trend, the use of small game started in the Middle Paleolithic with slow-moving prey such as tortoise and shellfish. By the early Upper Paleolithic birds were included in the diets, while lagomorphs became an important element in the Tardiglacial. The most important aspect of these data is an increase through time in the use of species that are less easily caught by hand. Simultaneously, there was a decrease in size of the slow-moving species, pointing to a decline in prey abundance and an increase in predator density.

Though I agree with most of the authors' conclusions, I also see two problems. The first is that the main conclusion, the identification through the use of small-game data of human demographic pulses, is a circular argument. Though I believe that their conclusion is correct, the authors do not show, using independent data, that there were increases in human population and, more important, that they occurred in pulses. The second problem relates to the applicability of this model to other areas of the Mediterranean. Stiner et al. imply that this model can probably be extended to the rest of the basin, though not at the same time or involving the same species. In Portugal, small fauna has been identified only in a few sites, and therefore data are still scarce. Trends point, however, to different patterns from those seen in

Israel and Italy. During the Portuguese Paleolithic small game is composed of European rabbit and shellfish and to a lesser degree marine fish and birds (Antunes 1992; Bicho 1997, 1998; Bicho et al. n.d.; Hockett and Bicho 1999; Zilhão 1995). Here, in contrast to the two areas studied by the authors, small fauna is extremely rare before the Upper Paleolithic. Only one cave site, Figueira Brava, has evidence of shellfish during the Late Middle Paleolithic, and it may be a natural occurrence (Bicho 1994a). The use of shellfish becomes common only after ca. 10,500 B.P. (Bicho 1994b), with a clear intensification after 8,000 B.P. Rabbits seem to have been used extensively after 13,000 B.P. (Bicho 1998). Fish become common after 12,000 B.P., while birds were never a major component of subsistence.

In summary, in Portugal, the slow-moving species (shellfish) were used only after the quick species and clearly during or after the increase in human population that occurred after 10,500 B.P. (Bicho 1994b). Rabbits and fish were the key elements in the subsistence change that occurred during the Tardiglacial. Both are likely to have been exploited through the use of nets and/or traps; thus the work of capture decreased markedly, except with regard to the maintenance of the technological aids. In contrast to the situation in Italy and Israel, pulses in human population occurred after the changes in technology and subsistence. Small-game use, however, seems to be as important as Stiner et al. document in the identification of human demographic pulses. In the case of Portugal, the shifts in subsistence seem to have been simultaneous with technological changes and to have preceded increases in human population. In Portugal it is the diversity and intensification in the use of all small-game species that are the key elements as indicators for increase in population and not the shift from slow- to fast-moving species.

In conclusion, I believe that Stiner et al. are correct in their approach and in their conclusions about the data and the importance of small-game use for demographic studies. I think, however, that the model presented here is not yet comprehensive enough to account for the wide diversity of data that can be found around the Mediterranean basin and in the Paleolithic. Thus, the work will have to continue; Stiner and her colleagues have only raised the curtain on this issue.

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This paper has the interesting feature that the emphasis is on small game (hares, birds, tortoises, etc.) and shellfish instead of, as is customary, on large mammals and their protein and energy content.

The exploitation of small game (even micromammals), fish, birds, and shellfish as a substitute for the large game that disappeared with climatic change (at the Bølling oscillation of stage 2, about 13,000 B.P. in conventional

radiocarbon dates) was pointed out many years ago in Italy by A. M. Radmilli (1960) as the beginning of the Mesolithic, with a substantial reduction of food resources. The model presented in this paper by Stiner et al. points instead to a demographic expansion *directly linked* to small-game and shellfish exploitation and due not only to the possible scarcity of large game but to better-organized and more skillful use of new hunting capacities and greater knowledge of the reproductive potential of the species exploited.

According to the authors, this model is in agreement with Flannery's (1969) broad-spectrum-revolution hypothesis, but in my opinion that hypothesis was essentially based on data collected in the Middle East, where we have clearly a *primary* process of agriculture and animal husbandry. Stiner et al. admit, of course, that the broad-spectrum argument, based only on the small-game finds in archaeological sites, presents major difficulties. Several years ago (Bietti 1981) I proposed, following Taschini (1968), that the Mesolithic in Italy was characterized by an *expansion* of activities on an Upper Paleolithic foundation; such expansion may in my opinion be considered as a particular case of the broad-spectrum phenomenon in the case of pure hunter-gatherers without any necessary demographic expansion.

The basis of Stiner et al.'s model is a series of layers of two sites in Israel, Hayonim and Meged, and, in Italy, several layers of Riparo Mochi in Liguria and the sites of Palidoro and Grotta Polesini in Latium. The sample chosen is rather heterogeneous, and in fact, the climatic situation in the two regions is completely different, even as regards isotopic stages (the indications of cold and warm oscillations of stage 2 may vary considerably). Furthermore, tortoises are very common in the Israeli sites and shellfish not, and the opposite is true for the Italian sites. I think that, already at this stage, the model should be proposed separately in the two regions.

Because I am not very well versed in the Upper Paleolithic of the Middle East, I will restrict my attention in what follows to the Italian sites. First of all, I do not clearly understand why Grotta dei Moscerini, in the early Mousterian of Latium, is cited while all the later Mousterian sites of the same region, clearly indicating a development towards more efficient hunting practices (Stiner 1994), are ignored. As regards shellfish collection, Moscerini seems to be a case of opportunistic activity, mainly connected with the proximity of the seashore at that time (at the end of stage 5).

Even in the Upper Paleolithic, I think that shellfish collection was a specialized seasonal activity not present in all the sites listed in table 2 for the simple reason that most of them are in the interior (by the way, in fig. 2 Mochi A, Palidoro, and Polesini are considered to be coeval, but the first site is undated, the second is dated to about 15,000 B.P. on average, and Polesini has an absolute date of about 10,3000 B.P. [see the references in Bietti 1990]) while Riparo Mochi was on the coast. The authors think that Mochi A was a specialized site for shellfish collection, but the industrial assemblage, at least according to the preliminary data presented by G. Laplace

(1966), consists of typical hunting and maintenance items such as backed tools, geometrics, and endscrapers. In contrast, a very interesting special-purpose site for shellfish collection is the Boreal site (about 8,600 B.P.) of Riparo Blanc, on Monte Circeo (Taschini 1964), where the faunal remains are overwhelmingly limpets of various types and *Monodonta*. The lithic assemblage in this site is composed mainly of notched and denticulated flakes, which were probably used for detaching limpets from rocks. Another interesting case, not yet published, is layer I of Grotta della Madonna at Praia in Calabria, dated to approximately the same period as Riparo Blanc but with a mixed economy: abundant shellfish but also consistent remains of large mammals, together with mixed tools, hunting items, and notches and denticulates like the ones found at Riparo Blanc (Cardini 1970, Bietti 1981).

From table 2 it is clear that the small-game/ungulate index is appreciable only at Riparo Mochi (but one must bear in mind that the data are based on NISP counts!), where as in Latium, even in the Mousterian site of Grotta Breuil (a more "advanced" late Neandertal site, also according to the authors), this index is negligible. A similar situation occurs also for other Epigravettian sites in Latium, such as, for instance, Riparo Salvini, dated between the Bølling and the Dryas II, which is not considered in this analysis. It may well be that other Epigravettian sites, on the Adriatic coast or in northern Italy, show a situation similar to that of Latium or perhaps intermediate between it and the Mochi case.

Another important point to be stressed is the *nature and function* of the site, a factor that seems to be mostly ignored in Stiner et al.'s model. As regards the Fucino basin in Abruzzi, for instance, the importance of small mammals, fish, and birds over the macrofauna at Grotta Ortucchio, dated to the Bølling, was one of the key arguments for Radmilli's (1960) hypothesis for the beginning of the Mesolithic economy, whereas a recent analysis (Alhaique and Recchi n.d.) shows clearly that Ortucchio was a site of short-term occupations by the Upper Paleolithic human groups and thus cannot be considered on the same level with other sites.

In conclusion, the model presented in this paper is quite interesting but probably needs further investigations in the regions in question and, in particular, a closer analysis of the function and the nature of the sites considered. It may well be that in Italy, for instance, the application of the model to various regional entities would not necessarily produce the same results everywhere. Demographic expansion (in the simple terms of number of sites) seems to start from about 16,000 B.P. and remain stable at least up to the end of the Boreal, and we do not have, at least in Italy, any proof that it is *everywhere* due to a shift towards small-game or shellfish procurement. It is certainly very impressive to propose global perspectives of change, but we should always remember that even while "thinking globally," to show actual global results one must first work very hard "acting locally."

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For the past few decades, archeological thought has supported the emergence of diversified resource procurement at the beginning of the Upper Palaeolithic, with special emphasis on a relative hunting specialization in ungulates and small-game use. This expansion of human diet breadth, involving the exploitation of various biotopes, would reflect profound changes in the organization of human foragers accompanying major technological innovations (especially projectiles and raw materials) and social and symbolic networks (exchange). This general framework, at least in Western Europe, is correct on the whole, although detailed studies taking into account the nature and rate of socioeconomic change are needed, especially at the regional scale. A focus on small-game exploitation through time remains relatively poorly documented in the contrasting regions of the Holarctic. In southern Europe, however, a heavier reliance on small animals occurred in the latest as contrasted with the earliest Upper Palaeolithic, for instance, on fish and birds during the Magdalenian in southwestern France and on lagomorphs and birds in Mediterranean Spain (see, e.g., Le Gall 1992; Vilette 1983; Villaverde and Martínez 1992, 1995), with an increase in sites/levels for the same period interpreted as a positive human demographic pulse. The faunal diversity appears linked with geographically diversified hunting practices from specialized sites in close relationships with available seasonal resources in their ecosystems.

In a series of recent papers, Stiner and colleagues have assessed some important issues regarding subsistence shifts over a long period (200,000 years), covering a great part of the Middle to Upper and Epi-Palaeolithic in two distinct areas of the Mediterranean biome. Their diachronic approach and the demoecological model proposed here help to highlight several methodological and theoretical questions, not all of which can be covered here.

It is assumed that the relation between demographic conditions for Palaeolithic foragers and expansion of species harvesting could result in important sociocultural changes. Studies based on taxonomic diversity in the archaeozoological record seem inappropriate for evaluating the variation in prey important in the human diet, whereas the proportions in the small-game spectra would provide more information. In my opinion we cannot totally dissociate large (herbivores and carnivores) from small animals in research on the interplay between Palaeolithic subsistence and paleoenvironments. The richness and diversity indices (Legendre and Legendre 1984), used in combination, provide reliable analytic tools for examining the structure of animal communities with possible comparisons between different biocenoses (see Bridault 1997 for macrofauna). The disappearance of large nonhuman predators at the end of the Pleistocene in Europe and a probable increase in medium-sized car-

nivores (canids, felids, mustelids)—major predators on small game (leporids, birds, etc.)—would have modified predator-prey relationships; human foragers are not the only active predators. Similarly, how are we to interpret the data of the sequence (MST-KEB-NAT) from Hayonim, showing an increase in small (*Gazella*) versus medium-sized (*Cervus*, *Dama*) ungulates concomitant with an increase in hare and bird exploitation (Stiner and Tchernov 1998:fig. 5)—climatic or human (biomass/package size)-induced changes? And what about the frequent presence of porcupine in the Palaeolithic levels of Western Asia?

Stiner et al. compare archaeofaunas from two ecogeographic zones: ten sites/levels from combined Italian samples (only eight in table 3/fig. 2, and just two are coeval), mostly from oxygen-isotope stages 3 to 1, and nine sites/levels from Israel, mainly from stage 2, then 6–7. The Upper Palaeolithic levels span 1,000 to 5,000 years and the Middle Palaeolithic layers several millennia (10,000 to 50,000 years); they represent a long and uneven period in the late Pleistocene in which numerous climatic shifts of short and abrupt periodicity (e.g., "Dansgaard-Oeschger" events, almost 20 successive century-to-millennium-scale cooling events for the last glacial period) favour relatively unstable biotic communities. These sample effects raise various problems, among them the demonstrated body-size reduction. In fact, it has been recognized that climatic factors affect biotopes (or their productivities) and the biological features of species (distribution, number, and body size [see Delpech 1983 for reindeer, Davis 1981]). Furthermore, one of the striking variables of the Mediterranean in the late Pleistocene was the pronounced paleosea-surface temperature gradient, which along with sea-level variations could influence the size of coastal mollusks. In the Near East, two tortoise size-groups are depicted, one showing a gradual increase for the Middle Palaeolithic (prior to 70,000 to 100,000 years ago) and the other showing size fluctuations; the time increments in this example are quite variable. Stiner et al. relate the size diminution to heavy human predation pressure over time (by the way, what are the dimensions of limpets or tortoise during Roman or recent times?), and that constitutes a point in the demonstration. Nevertheless, as is noted by Stiner et al., it is difficult to draw this conclusion, especially since the length of human occupation of a site is associated with the intensity of local predation. A link between body-size variability and human predation pressure would imply continuity over time in the peopling of the areas in question—continuity through successive prehistoric human societies.

The trends in small-game use show a clear distinction first of all between sessile and faster prey (translated as indicating gathering and hunting/trapping activities) and between the Middle Palaeolithic and the Upper Palaeolithic and Epi-Palaeolithic, revealing a transitional story with occasional versus complementary resources. The nature and timing of the human demographic pulse at the end of the Pleistocene are topics which have to be considered in a complex multifactor integration at a re-

gional scale. According to ungulate species and vegetal biocenose variations in Western Europe, a sharp negative pulse may have occurred just after 13,000 years ago (Delpech n.d.).

In the composite Italian sequence, birds are dominant in inland sites and mollusks in coastal sites; lagomorphs are more variable, and there is a significant frequency of other small animals in the Upper Palaeolithic of Riparo Mochi. Small-game categories are delineated differently according to the region and the ecosystem: indeed, small vertebrates represent broad classes divided into micro- (insectivores, rodents, amphibians) and meso-faunas (rodents, lagomorphs, small carnivores, fish, birds, tortoises). All are low in food weight, and some may have been targeted as raw materials (bone, fur, feathers, claws, etc.). Other small game includes insects, arthropods, and sea and land mollusks. Their contributions to total game assemblages generally remain small, although they may be a dominant component in some types of sites or in particular areas (i.e., 80–95% of rabbits in some Upper Palaeolithic sites from Iberia). The differences here suggest differences in structure between habitats (biocenoses) and differences in socioeconomic strategies (mobility and site function): geotopographic and seasonality factors and cultural parameters are among the determinants constrained by human densities. Indeed, small game species were probably a dietary staple in the Upper Palaeolithic, especially during times of shortage; special harvesting tools (projectiles, nets, snares) and special processing for storage or for immediate or deferred consumption are the signatures of foraging adaptations which can be employed with both small and large game. Inferences of a causal framework and about divisions of labour or society are, however, speculative (see Charles 1997 for discussion).

The evolutionary perspective of this paper, based on interesting simulated ecomodels, greatly contributes to a better understanding of the expansion of the subsistence base during Palaeolithic times. It confirms the importance of small-game use for the discussion of socioeconomic change between different cultures and human types. And, although Aesop's (or La Fontaine's) "The Hare and the Tortoise" sounds a note of caution, this field of research offers new and promising possibilities.

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This article presents a dialectical combination of three elements of considerable interest. The first of these is the use of the broad-spectrum-revolution hypothesis, based on the work of Binford (1968), Flannery (1969), and Odum (1971), as a theoretical and methodological approach to both explaining the problem and proposing an explanatory hypothesis for demographic changes in the Upper Pleistocene. The second is the application of this hypothesis to a specific subject—small-animal remains,

including terrestrial, marine, and avian species. The third is an empirical test of the hypothesis, contrasting the Upper Pleistocene sequences from Italy (110,000–9,000 years ago) with those from the final Middle Pleistocene and the Upper Pleistocene in Israel (200,000–11,000 years ago).

Their proposition is based on the detailed analysis of hunting techniques from the perspective of their role in the trophic chain. The dialectic relationship between predator and prey is clearly illustrated with the case of humans and small-game animals. Stiner and colleagues draw an important distinction between fast- and slow-moving animals as well as between slowly and quickly reproducing animals. The size of the predator population is also considered important here. In other words, the reproductive strategies of a prey species are as important as its numbers or adaptation to the environment.

The role humans play as hunters and gatherers and regulators of animal populations can be quite significant when they use the full array of their technical skills. A population of hominids with sophisticated hunting techniques can selectively target certain animals, as seems to have occurred in Italy around 23,000 years ago with mollusks and in Israel around 44,000 years ago with tortoises. In both cases these organisms are either stationary or slow-moving and are easily caught. The development of new hunting techniques could have had a significant influence on the taking of small-game animals, especially fast-moving ones, but the scant archaeological evidence makes this hypothesis difficult to test.

The hunting of small game animals is certainly an ancient practice among hominids. At the Acheulean site of Aridos in the Spanish Meseta, elephant hunters and scavengers also seem to have consumed small game, according to the work of López (1980). However, at the Middle Pleistocene sites of Atapuerca, also in the Spanish Meseta, we have not been able to establish the hunting and consumption of small game animals.

Throughout the Pleistocene, occupations occur which reflect either specialized hunting or broad-spectrum hunting. This dynamic is basic to the social organization of these hominids, who strategically adapt to exploit their territory. It is clear that knowledge of the territory and an effective decline in large-mammal populations due to hunting pressure or climatic change stimulates a widening of the spectrum of animal resources exploited by hominids. The random hunting of prey species without respect to their ecology and biology or the selective hunting of slow-reproducing animals of a certain age because of their body size would clearly endanger species survival.

Pressure of this sort will, however, be difficult to identify and compare on a temporal scale. The data from Israel at the end of oxygen-isotope stage 3 and from Italy during stage 2 are very important, but it will be necessary to compare them with data from other sites as well as from other species of small game animals, since they could be due to either constant pressure (i.e., sedentism) or seasonal pressure (i.e., nomadism). At the same time,

an increase in the number of predators could be responsible for the documented change.

The relationship suggested by the authors between broad-spectrum hunting and gathering, an increase or decrease in the presence of some small game animals in fossil assemblages, and hominid demographic factors is intriguing, and I agree with their interpretations. Further, I feel that consideration of the catchability of certain species is also a critical contribution to the study of Paleolithic subsistence patterns. Nevertheless, it is possible that the suggested relationship between hominid population increase and broad-spectrum hunting and scavenging characterized only certain regions.

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Donald O. Henry (1989:14) once began a book section with the heading "Broad-Spectrum Subsistence: Fact or Fiction?" Stiner et al. not only show that broad-spectrum subsistence is fact but also present us with more sophisticated tools for measuring it than I could have foreseen in 1969.

At first I was puzzled by Henry's confusion. He admitted that Natufian sites yielded "the remains of numerous species of lizards, snakes, tortoises, amphibians, birds, small mammals, and even fishes" and said that "traditionally" this would be interpreted as denoting "a broad-spectrum dietary pattern" (Henry 1989:214). Indeed it would! Then, inexplicably, he concluded that it could not be a broad-spectrum diet because the Natufians "obtained most of their meat from one animal: the gazelle." But that was irrelevant; I never suggested that Near Eastern hunters had abandoned ungulates, merely that they had begun to eat species they had previously ignored. I later decided that Henry's misunderstanding resulted from confusing my paper (Flannery 1969) with one by Hayden (1981), who characterized broad-spectrum subsistence as greater use of *r*-selected species. Neither Hayden nor I, however, implied that this meant reducing the use of *K*-selected species. As I recently put it, the ultimate significance of a broad-spectrum diet "lay not in small game and molluscs. When such previously ignored species are considered worth harvesting, it increases the chance that even grass seeds will be considered worth harvesting" (Flannery 1998:xvii). And that, of course, set the stage for cereal agriculture.

Now we can all go back to our data and apply the distinction of "slow" and "quick" small prey proposed by Stiner et al. However, in the Mediterranean and the Near East there is an additional complication: the broad-spectrum revolution had not one but two axes. One axis was time-related: diet breadth increased as the Paleolithic gave way to the Epipaleolithic and then to the prepottery Neolithic. The other axis was geographic: the dietary shift apparently began in the western Mediterranean and moved slowly east to the Zagros Mountains.

One of the earliest sites showing broad-spectrum sub-

sistence is a Mousterian rock shelter at Devil's Tower, Gibraltar (Garrod et al. 1928). The Mousterian levels there produced 33 species of birds including partridges, doves, cormorants, shearwaters, and birds of prey. Land tortoises and fish were also present. Five of the upper strata contained "numerous shells of molluscs, obviously kitchen-refuse" (Fischer 1928:111). The most common were limpets (*Patella* spp.), mussels (*Mytilus edulis*), and land snails (*Helix* spp.).

It took longer for such diet breadth to travel east to the Levant. In much of that region, according to Gilead (1998:127), small mammals, reptiles, fish, and snails were still "absent or marginal" in bone assemblages as late as the Upper Paleolithic. One rock shelter where we can monitor the increasing use of molluscs is Ksâr 'Akil in Lebanon. Van Regteren Altena (1962), who studied the invertebrates from the excavations of 1937-48, found only two oysters in late Mousterian strata (Levels XXVIII-XXVIa). Near the transition from Middle to Upper Paleolithic (Levels XXV-XIX) the bivalve *Glycymeris* first appears in quantity, and by the Levantine Aurignacian (Levels XVIII-X) it is present by the hundreds, along with the cockle *Cardium*. Limpets (*Gibbula* and *Patella*) increase steadily through the Late Paleolithic or Kebaran (Levels V-I). By then the diet had expanded to include land snails, of which the genus *Helix* alone was represented by over 100 specimens.

Just as the Levant lagged behind Gibraltar, the Zagros Mountains lagged behind the Levant. For example, land snails such as *Helix salomonica* were "not common in archaeological sites [of the Zagros] prior to the late cave-living period of the uppermost Pleistocene (i.e., the Zarzian, ca. 15,000-12,000 years ago)" (Reed 1962:4). Once the use of molluscs began, however, it exploded all over the Zagros during Epipaleolithic and prepottery Neolithic times. *Helix* was abundant in Zarzian levels at Palegawra (Iraq) and Warwasi (Iran). At Asiab, an Epipaleolithic site in Iran's Kermanshah Valley (Braidwood, Howe, and Reed 1961), freshwater clams of the genus *Unio* were so abundant that excavator Bruce Howe stopped counting individual shells and began recording them by standardized bucketloads.

The Italian sites reported by Stiner et al. lie midway between Gibraltar and the Levant and seem generally to fit the west-to-east trend. Use of molluscs at the Italian sites is earlier than in the Levant, yet their overall use of birds and lagomorphs does not show a jump until after the Aurignacian. Why did the trend toward greater diet breadth seem to move west-to-east? Did the postulated demographic pulses begin earlier in the western Mediterranean than in the Zagros? Or were there also some environmental trends we need to understand?

Finally, we should remember that the broad-spectrum revolution was essentially a change in ethnoscientific classification by hunters and gatherers. All foragers have "first-," "second-," and "third-choice" foods. !Kung hunters of the Kalahari provide an ethnographic example: they can name 223 species of animals but classify only 54 species as "edible" and hunt only 17 of those on a regular basis (Lee 1968:35). Late Pleistocene and early

Holocene foragers of the Mediterranean and Near East clearly put ungulates in their “first-choice” category. To create a broad-spectrum diet, they had to move some “third-choice” foods to their “second-choice” category and some “second-choice” foods to “first-choice.” When they finally moved wild cereal grasses to “first-choice” they had paved the way for a truly profound change.

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On the whole this is a very useful and stimulating paper. The ideas put forward have the potential to raise the profile of small-game use in prehistoric foraging groups beyond the simple “supplementary” role usually ascribed to them, and the authors are to be thanked for their contribution. They suggest that “small-package” food—even if it arrives in dribs and drabs—plays an important role in long-term survivorship by keeping food supply relatively constant, in accordance with realistic human dietary needs, in contrast to occasional gluts of ungulate meat. The detailed ecological and animal-behaviour information used in the analysis also makes this article a useful update to Flannery’s “broad-spectrum-revolution” ideas. Consideration of body size (and hence meat potential) alone never appeared adequate in the traditional models, and here we have been given a useful alternative—or additional—approach. The fact that the range of small animals studied is broad, encompassing mammals, reptiles, and birds, makes it a doubly useful reference point for further work on subsistence choices in other regions. The revelation that partridges are even more resilient under predation than lagomorphs—legendary for their reproductive output—is also a useful point to keep in mind. It is encouraging, too, that the needs and abilities of different age-groups within forager societies are taken into consideration, albeit not in any detailed way in this particular paper.

Nevertheless, there are some minor criticisms that may be levelled at this article. First, dismissing “human dietary preferences” as a factor seems presumptuous, given how difficult cultural preferences are to trace reliably in early prehistoric low-resolution studies. The importance of a human behaviour does not rest solely upon our ability to analyse it. Furthermore, it is surprising that the motive—even if secondary—of gathering small resources for use as raw materials is largely ignored, especially as the authors’ consideration of technology makes it clear that they believe food is not the only important factor in demographic growth. For example, one major impetus behind the rabbit drives of the American Southwest was use of numerous rabbit skins for blankets and clothing (Shaffer and Gardner 1995). There is also a suggestion that birds may have been exploited in the Magdalenian of the Pyrenees as much for their feathers, to be used as arrow flights, as for their meat (Bahn 1983). The degree to which human groups

may have recognised prey depletion and reacted to it intelligently, other than simply killing fewer of a particular species, is not really covered either. Granted, this is difficult to assess archaeologically, but I do feel that the possibility merits consideration. If a summary can do it justice, the scenario of the authors seems to be *increased human population*→*need for more food*→*“better” technology*→*increased exploitation of birds and lagomorphs* rather than the alternative and also potentially feasible sequence *increased human intelligence/experience*→*“better” technology*→*increased exploitation of birds and lagomorphs*→*increased human population*. Nowhere in the paper is the possibility that the Middle Palaeolithic people were Neanderthals rather than fully modern *Homo sapiens* considered explicitly. Even if there is no species difference, we must surely allow for augmented experience and familiarity with a particular environment over time, which will influence decision making.

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Stiner, Munro, and Surovell offer a compelling program for capturing one of the most critical and elusive of archaeological signatures—that of shifts in Paleolithic demography. Demographic packing is a notion upon which models explaining everything from the origins of art, language, and other symbolic behaviors to the origins of agriculture have been built. The idea that small game provide the zooarchaeologist with a barometer of fluctuations in human exploitation pressure is not new (e.g., Parmalee and Klippel 1974; Casteel 1976; Bailey 1983*b*; Cohen 1997; Klein and Cruz-Urbe 1983; Klein 1994, 1998). However, a sound means of separating out human demographic pulses from other variables is a new contribution.

For the extension of Stiner et al.’s methods to more seasonal environments such as more temperate and northern regions of Eurasia or African zones of wet and dry seasonality, it will be necessary to attend to the additional variables of seasonality and settlement patterns when modeling. As the authors suggest, pressure on the exploiting population (e.g., population size exceeding carrying capacity of the home range) must be distinguished from pressure on the exploited population, which in the case of many small-game taxa may result from just about any climatic, physiogeographical, or anthropogenic factor one can think of. One critical variable for foragers and collectors is the seasonal availability and accessibility of resources. For example, many game birds migrate, and turtles hibernate. In Winters’s (1969) classic study of the Riverton culture (Midcontinent Archaic), these were two of several important categories of small game whose dietary importance varied according to site location and season of occupation. Also, evidence of heavier predation pressure, such as a size decrease in

molluscs, may reflect a shift in settlement pattern whereby the regional group repeatedly spent a particular time of year along the coastline. "It is not unequivocal evidence that people were engaged in mitigating the effects of stress caused by a previous imbalance between their population numbers and their existing food supply" (Bailey 1983c:129). Moreover, when taking Paleolithic settlement pattern shifts into consideration it is important to remember the potential bias inherent in our often unavoidable reliance on evidence from caves or rock shelters.

In addition to offering methods and theory for the simulation and detection of demographic pulses, the authors contribute by refocusing our attention on the importance of the more quotidian elements of the Middle and Upper Paleolithic record. The importance of the small, gathered resources reminds us of the interplay of procurement and processing technology as well as culinary practices. This in turn nudges us a step closer to contextualizing Paleolithic social life by getting closer to another intuitively recognized but eminently elusive variable—that of the division of labor according to the health, gender, reproductive state, age, and skill of individuals. In sum, further applications and refinement of Stiner et al.'s empirical modeling promises important insights into Paleolithic demography and lifeways.

Reply

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We are grateful to the commentators for their insights and in most cases enthusiasm about the results of this study. Perhaps most rewarding is Bar-Oz and Dayan's response, which turns a deep understanding of the subject into testable predictions for one region of the world.

Flannery correctly notes that there are two axes of variation implied by our research—time and geography. Neither axis can be understood without controlling for the influence of the other. It is for this reason that we have focused on two areas and a limited range of sites for which consistent, reliable information is available on taphonomic history, chronology, skeletal recovery practices, and faunal counting units. It is unlikely that the faunal accounts published between 1928 and 1962, while fine studies for their time, can live up to these criteria. Robust contradictions to the southeast-west demographic gradient suggested by our results require control of all of the conditions named above, including the taphonomic question of whether the small-animal remains were collected by humans at all. Unfortunately, assessments of diet breadth are also limited by what have proved to be incomplete accounts of the range of prey eaten by prehistoric humans, a shortcoming that is only beginning to be redressed in many regions. We also note

that, while we obviously came to a different conclusion about human diet breadth than did Henry, our study benefits nonetheless from Henry's observations about subsistence specialization trends during the Epi-Paleolithic.

Brugal raises numerous issues not unfamiliar to us, but his use of them does not resolve to addressable points. We certainly agree that life is complicated, now as in the past. What we apparently don't agree about is whether scientific investigations can answer specific questions by holding other key variables constant. Bietti's questions about our choice of cases in Italy are addressed in the main text, and the information he provides does not indicate to us that we should have chosen differently. We do not understand, moreover, why the presence of certain formal tools in a cultural layer should better define a site's economic function (as least as concerns hunting) than the prey species profile of the associated faunal assemblage. If the Late Epigravettian occupants of Riparo Mochi came there principally to hunt large terrestrial game, they suffered repeated disappointment and learned nothing from the experience. Nowhere in this paper do we argue that human population growth was the result of eating tortoises and shellfish.

Bietti's concerns about assigning ages to assemblages obviously follow a different logic from ours. We know that Palidoro and Polesini are not the same age in radiocarbon years (see table 1), but their ages are much closer to each other than either is to the other Paleolithic phases considered by this study. We think that the standard deviation that normally accompanies all radiocarbon dates is not the only source of ambiguity when the technique is applied to archaeological problems. We use generous time ranges in recognition of composite error arising from, among other sources, (1) error inherent to radiocarbon technique, (2) its application to only one or a few items selected from large assemblages of objects, and (3) the total time scale defined by our study. Few dates are available for Grotta Polesini, for example, and more than 1,000 individual ungulates (not to mention small prey) are represented from the units sampled during a salvage excavation (Stiner 1994). Can a few direct dates for a very rich site provide superior time estimates to those obtained indirectly on the basis of similar tool industries dated at other sites in the same region? While the radiocarbon method has revolutionized archaeologists' access to information about time, its results generally do not guarantee high resolution in most archaeological applications. Fortunately, the problems in evolutionary ecology to which we are attracted are not about fine-grained time intervals.

With this in mind, we turn to the potential impact of seasonal occupations and patterns of land use on variation in faunal series. Seasonal responses to foraging opportunities continue to be an important area of archaeological research, one to which Pike-Tay has contributed a great deal. We are not convinced, however, that this scale of perception relates well to the large-scale patterns we treat. First, while it is true that changes in land-use patterns can alter humans' potential for overexploiting certain taxa and foragers may adopt different strategies

and schedules of exploitation in the same kind of environment, what are the forces selecting for variation? Variation in human foraging schedules does not necessarily alter the natural productivity of wild populations and may in fact represent ways of working around local or periodic declines in the availability of a high-ranked resource. Second, data on the ecology of modern animals indicate that, while birth and death pulses are often seasonal, they are best examined as annual differences if the question is population dynamics. Species-specific patterns of recruitment may be more of an issue for relatively immobile types such as tortoises, much less for large mammals and marine shellfish. Third, the sheer volume of material in the sites we have studied cancels the likelihood that any of the assemblages represent single, short episodes of accumulation. We consider this to be one of the strengths of our sample. Finally, predator-prey models played against archaeofaunal data on length of seasonal occupation during the Epi-Paleolithic and Natufian in Israel (Munro 1999, Surovell 1999) reveal only subtle variation in the ratio of slow to quick small game. While these results are important in their own right, the seasonal and spatial effects of extended stays on small-game use in the Natufian (Munro 1999) fall well short of the magnitude of variation for the total time spans we consider.

Bicho suggests that there could be a better case in Portugal for technological change's preceding subsistence change rather than the other way around. This may or may not prove correct as more studies are conducted in the region. In any case, the available evidence suggests to us that the two developments occurred around the same time—and quite late in comparison with those in regions to the east. What makes increased lagomorph exploitation in Portugal so interesting is what lies beyond its borders. The relatively later emphasis on lagomorphs (mainly after the Last Glacial Maximum) is geographically widespread, certainly including areas of the northern interior of Europe and arid lands to the south (Kuhn and Stiner n.d.) and easily transcending the cave/open-site distinction raised by Pike-Tay. Hares were important prey at some Solutrean or (more commonly) Magdalenian sites in southern Europe (Clark 1987, Davidson 1983, Hockett and Bicho 1999, Stiner et al. 1999, Straus 1990, Zilhão 1990), western Europe (Albrecht and Berke 1982–83, Berke 1984), Moravia (Svoboda 1990), the Dnestr region (Kosoutsky Layer 4 [Borziyak 1993]), and even Novgorod-Severskii on the Central Russian Plain (Soffer 1990). The surge in lagomorph exploitation occurs by roughly the same time in western Asia (Byrd and Garrard 1990, Munro 1999) but apparently a good deal later in North Africa (Smith 1998). Environmental changes brought on by global warming may have expanded the habitats favored by lagomorphs and thus their numbers in Eurasia. However, paleontological evidence shows that lagomorphs existed in most or all of these regions in earlier times but were largely ignored by humans.

We do not understand why Bicho finds our argument circular. The interpretations of the impact of humans on prey populations derive from real, independently con-

ducted studies of diverse modern species. These modern referents are critical and cannot be obtained from archaeological sources. We agree with Bicho that more work in more regions is needed, ideally with better information than was available previously. Because our interpretations are developed in the same areas as the initial research was conducted, further tests of the timing and geography of Paleolithic demographic pulses must be carried out using new sets of appropriately controlled cases. This is not circular reasoning but rather an essential first step in original, disciplined research on the nature of extinct systems.

In closing we emphasize that some natural phenomena and the patterns that allow us to recognize them can only be appreciated close-up. Others are visible only from afar, regardless of whether the axis of variation is time or conventional distance. As for Newton's views on the central importance of human intentions in evolutionary time, we can only urge her to test these ideas.

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