Chapter 6

MODELING PALEOLITHIC PREDATOR-PREY DYNAMICS AND THE EFFECTS OF HUNTING PRESSURE ON PREY 'CHOICE'

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Abstract: Working from archaeofaunal trends in the Mediterranean Basin and modern wildlife data, we present a demographic interpretation of Paleolithic prey "choice" with the aid of computer simulation modeling. Archaeological indications of expanding dietary breadth with the onset of the Upper Paleolithic period associate with increasing exploitation of highly productive small animals and smaller ungulate species, despite the higher procurement costs of some of these prey types. The study of small game exploitation capitalizes upon the extreme differences in behavioral and reproductive ecology of the prey species with similar body sizes. Predator-prey simulation modeling of large hoofed animals (artiodactyls) was also undertaken, since these animals constituted the bulk of meat acquired by Paleolithic foragers, but the simulation results for the ungulate taxa do not provide the same crispness in the test implications needed for addressing questions about demography, diet breadth, and possible predator pressure over the course of the Paleolithic. The sustainable yields for the small ungulates are not definitively higher than those for the large ungulates, and thus the shift down the ungulate body-size spectrum that we see in the Mediterranean data is not in itself solid evidence of human demographic growth. Given demographic growth as shown by other, better evidence (small game data), we nonetheless can attribute the shift to smaller ungulates as being the result of the population growth. Increasing dependence upon high producers, even if total volume of meat acquired remains the same, could have meant a significant reduction in the composite (cooperatively pooled) variance in foraging success, albeit at the price of greater hunting effort

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Zooarchaeological data from several world regions indicate that the collective human "footprint" on terrestrial ecosystems changed dramatically from the Late Pleistocene through Holocene periods, often in connection with increases in human population density. It is likely, as well, that directional shifts in human predator-prey relationships occurred and, further, that these changes played a significant role in the reorganization of subsistence labor in human societies. However, establishing connections between the archaeological patterns, demographic, and ecological processes is as challenging as it is interesting. Certain fundamental essays link changes in human trophic level, foraging efficiency, and demography, and these have been important for modeling predator-prey interactions that involve omnivorous foragers such as humans (e.g. Harpending and Bertram, 1975; Winterhalder and Goland, 1993). Other insights come from anomalies identified by zooarchaeological studies of Paleolithic human diet breadth.

Working from a base of archaeofaunal trends in the Mediterranean Basin (Figure 1) and modern wildlife data, we develop a demographic interpretation of prey "choice" with the aid of computer simulation modeling. This study began with a focus on small game exploitation that capitalized upon the extreme differences in behavioral and reproductive ecology of the prey species with similar body sizes. Differences in prey body size must also have been important from the predator's point of view, as body size affects food yield. The second phase of study therefore focused on predator-prey simulation modeling involving large hoofed animals (mainly artiodactyls). Large mammals do not provide the same crispness in the test implications needed for addressing questions about demography, diet breadth, and possible predator pressure, despite their obvious importance in Paleolithic economics. Complete presentations of modeling mechanics and archaeological correlates appear in Stiner (2005), Stiner et al. (2000), and Beaver (2007).

The presentation has three major parts. The first is an introduction to the archaeological patterns that precipitated our attempts to model the relations between predator prey relationships and dietary breadth. The second part presents key aspects and results of the small-game modeling project. The third part summarizes the more recent modeling work on large game animals (Beaver 2007). The presentation ends with a discussion of properties of the modeling studies and research design that we believe were critical for providing lasting insights on Paleolithic diet, demography, and human behavioral evolution.

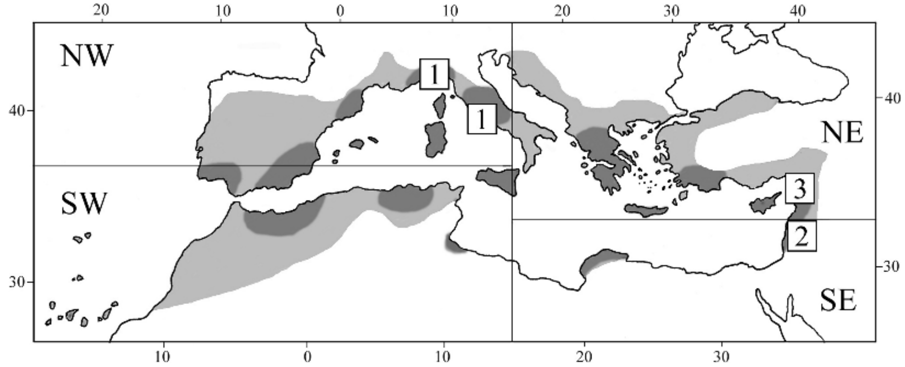

Figure 1: Geographical origins of the three Mediterranean faunal series: (1) western coast of Italy, with 16 assemblages; (2) Wadi Meged, inland Galilee of Israel, with 9 assemblages; and (3) Hatay coast of south-central Turkey, with 7 assemblages. Each faunal series originated in a distinct Mediterranean quadrant defined by somewhat distinct arrays of endemic species and environments. (Base map after Blondel and Aronson, 1999:8.) (Reproduced from Stiner, 2005.)

ARCHAEOLOGICAL BACKGROUND

Middle Paleolithic populations living between 250,000 and 35,000 years before present were quite carnivorous, more so perhaps than most human populations of later periods, and they relied most heavily on large hoofed game animals for meat. This fact placed these early foragers (including the Neandertals) at the top of the food chain. It therefore is not surprising that human populations of the period tended to be very small per unit land area (Stiner, 2005). It was only after the Last Glacial Maximum, and particularly after 13,000 years ago, that human hunting pressure on some ungulate populations led to unsustainable distortions in the structures of ungulate populations, as indicated by mortality patterns in archaeological sites and increasing reliance on high-turnover species. All of these shifts are in one way or another indicators of permanent expansions in human dietary breadth.

The breadth of forager diets can vary both within and between adaptations, depending upon the availability of high quality, high-yield foods (Pianka, 1978; Stephens and Krebs, 1986). Diet diversification is especially likely to occur when and where foragers put excessive pressure on preferred (a.k.a. highly ranked) resources, which in turn may force these resources into decline. A reduction in the predator population may occur as a result, or, rarely, changes in adaptation may occur instead.

The earliest indications of increasing dietary breadth in humans generally coincide with the transition from the Middle to Upper Paleolithic culture periods in the eastern Mediterranean Basin (Stiner 2001, 2003). Expansions in dietary breadth are most apparent from the relative emphasis Paleolithic people placed on a variety of quick versus slow-moving small animals, such as birds and lagomorphs as opposed to tortoises and shellfish. The most sensitive of the small prey populations in the Mediterranean Basin were tortoises (*Testudo* spp.) and certain marine shellfish such as limpets (*Patella* spp.). These prey animals can be abundant in some habitats yet represent the proverbial "canaries in the coal mine" for studying shifting human predator-prey interactions of the Pleistocene because of slow population growth rates (Stiner, 2001). No trend is apparent for the relative proportions (number of identified specimens, NISP) of ungulates and small game in most study areas (Figure 2). However, great changes took place in the *types* of small game emphasized by human foragers over 200,000 years, due mainly to the significant addition of birds and hares to Upper Paleolithic forager diets.

The classic models of prey choice and diet breadth assume that resources can be ranked in the energetic terms of the predator, according to the amount of nutritional return they yield relative to the cost of procuring them (Pianka, 1978; Stephens and Krebs, 1986). Broadly speaking, prey rank in the sense of relative nutritional payoff is directly related to some combination of body size and search and handling costs. Ethnographic and experimental evidence suggest that human hunting of large animals provides returns on effort that are several times those from smaller animals, and an order of magnitude larger than many vegetable foods (Kelly, 1995; Kuhn and Stiner, 2001). Holding body size constant, the most important key to Paleolithic rankings of prey in Mediterranean environments proves to be handling costs; quick running or flying animals, such as hares and partridges, have similar body weights to tortoises or several shellfish, but they are far more difficult to collect without the aid of tools and thus would be lower ranked in the absence of special capture devices. Simple differences in the ease of capture among the two broad groups of small animals in the Mediterranean Basin happens to correspond to great differences in prey population resilience, the latter governed mainly by the rates at which individual prey animals mature (Stiner et al., 2000). Tortoises and certain shellfish are especially susceptible to over-harvesting, because they require several years to reach reproductive age. In contrast, rabbits and some ground birds are notorious for their ability to reproduce rapidly and the resilience of their populations.

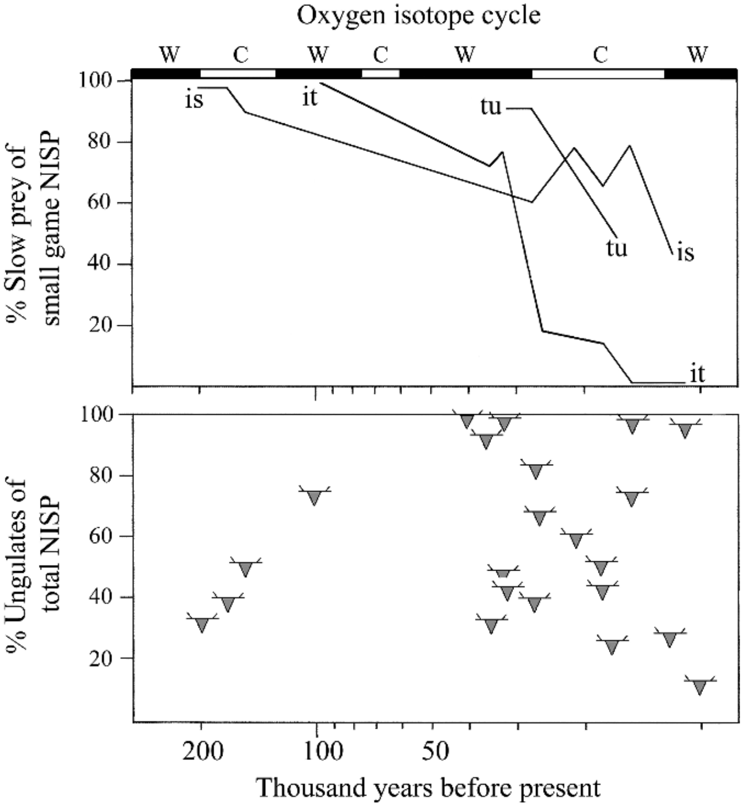

Figure 2: Trends in the percentages of slow small prey (lines) in the small game fraction of each assemblage from Israel (is), Italy (it), and Turkey (tu), together with ungulate remains (inverted triangles) in the total count of each assemblage. Time is expressed on a logged scale, as are oxygen isotope climate cycles (following Martinson et al., 1987; Shackleton and Opdyke, 1973). C denotes a cold stage, and W, a warm stage. (Reproduced from Stiner, 2001.)

It is significant that Middle Paleolithic foragers seldom pursued small prey except for those sessile or slow-moving animals (tortoises and shellfish) that could be collected with little effort. The situation changed around 45–50,000 years ago in the eastern end of the Mediterranean Basin, eventually spreading into adjacent regions of Eurasia. The proportional contribution in biomass of small game to Paleolithic diets is constant at about 3% until the late Epi-Paleolithic (after 15,000 years ago), when it rose to 17% or greater. The mix of small prey nonetheless was quite distinct from the early Upper Paleolithic onward (Munro, 2004; Stiner, 2001, 2005; Stiner and Munro, 2002). Given higher pursuit and handling costs of game birds and small mammal prey, Paleolithic humans' incentives to switch to quick-moving types would have to have been strong. Prolonged scarcity of easily collected small prey ultimately would also increase the selective advantage of any technology that reduced the cost of capturing quick, agile animals. Importantly, the changes in small game use occurred in the context of relatively stable biotic communities, especially during the Late Pleistocene, when the greatest changes occurred in Paleolithic diets (Stiner, 1994:68–77; Tchernov, 1981, 1992).

Of course the amount of food obtained from one or two individuals of a large species greatly outweighs the total food obtained from many individuals of a smaller species. Another means for comparing patterns of game use employs estimates of meat plus bone—biomass—yields by time period, or number of individual animals multiplied by the estimated average carcass weight for each taxon. Biomass variation in the prey spectrum of Paleolithic hunters (Figure 3) reveals a tendency towards a decline in the ungulate sizes most commonly hunted; this pattern precedes somewhat the rising dependence on small game biomass. Towards the end of the Upper Paleolithic, after the Last Glacial Maximum about 20,000 years ago, biomass of hoofed animals was obtained primarily from medium and small artiodactyl ungulates, and eventually from small ungulates alone.

Hunters' emphasis on faster-reproducing species rises with time, and this is apparent across the entire prey body size spectrum (gazelles and roe deer, game birds, lagomorphs). While the proportional contribution of small game animals to Paleolithic diets was constant at 3% until the Epi-Paleolithic, there was a continuous downward shift in prey size overall, and correspondingly greater hunting of the more biologically productive ungulate taxa (see Figure 3). Though the most obvious changes in subsistence ecology occurred after 15,000 years ago, the trend appears to begin in the early part of the Upper Paleolithic. Thus we must look to this time range if we are to understand the roots of fundamental changes in human predatory adaptations and socioeconomic patterns.

How do the data on small game exploitation stand up in a formal analysis of prey diversity and dietary breadth following the predictions of classic foraging theory? Evidence of increasing dietary breadth is expected to take the form of more species in the diet and/or greater proportional evenness between high-ranked and low-ranked prey items in response to the declining availability of preferred types. A predator can afford to ignore lower-quality prey at little cost if the chance of finding a superior type in the near future is high, fostering a narrower diet that emphasizes a favored type disproportionately to its availability in the environment (condition 1 in

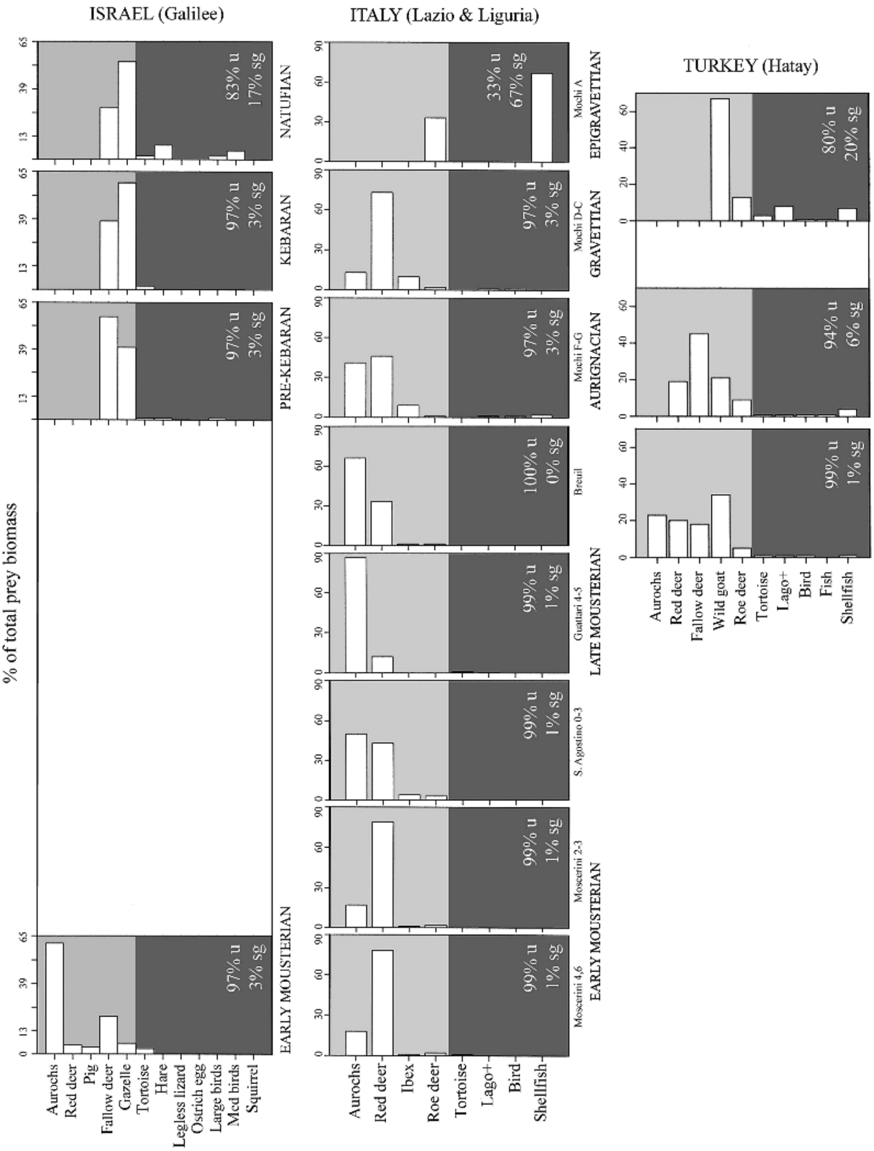

Figure 3: Percentages of total prey biomass obtained by Paleolithic hunters across periods for size-ordered prey species in three Mediterranean faunal series from Israel, Italy, and Turkey. Key: (u) total ungulate percentage; (sg) total small game percentage. Mochi A in the Italian series represents an extreme situation but is still fairly typical of coastal occupations for the period. (Reproduced from Stiner, 2005.)

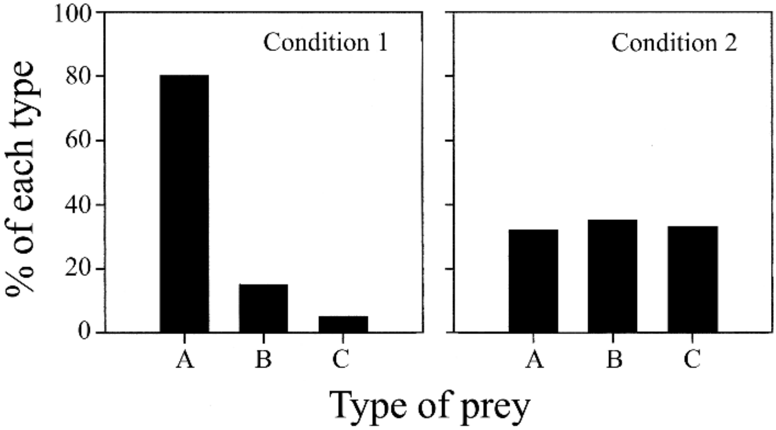

Figure 4: Predicted differences in evenness among three hypothetical types of prey taken by predators under distinct foraging conditions. Condition 1 is high availability of the highest-ranked prey types; condition 2 is declining availability of the highest-ranked types such that predator choice diversifies to include more of the lower-ranked types. (Reproduced from Stiner, 2005.)

Figure 4). As the supply of preferred prey dwindles, broadening the diet to include common but lower-yield prey types maximizes a predator's returns per unit of expenditure by reducing search time (Pianka, 1978). This second set of conditions therefore encourages a more diverse diet in the sense that the predator's emphasis is spread more evenly between two or more prey types that occur in the environment (condition 2).

Variation within the small game fraction of each Mediterranean faunal series tends toward more even dependence on high-ranked and low-ranked small prey overall (Figure 5), confirmation of expanding dietary breadth during the later part of the Mediterranean Paleolithic based on a significant correlation between time and the Inverse of Simpson's index ($n = 18$, $r = 0.606$, $p = .01$). Much of the dietary expansion took place during a cold climate stage (OIS 2). This is the opposite of what is usually expected to result from climate-driven changes in animal community composition, because the number of small animal species tends to be higher in warmer environments (Blondel and Aronson, 1999; Pianka, 1978). The evidence indicates a categorical, or stepwise, change in the way humans interacted with small animal populations as early as 40–50,000 years ago in some areas.

Differences in the relative productivity of prey species are a key to understanding the implications of the economic trends for Paleolithic demography, and rising human population densities in particular. An important

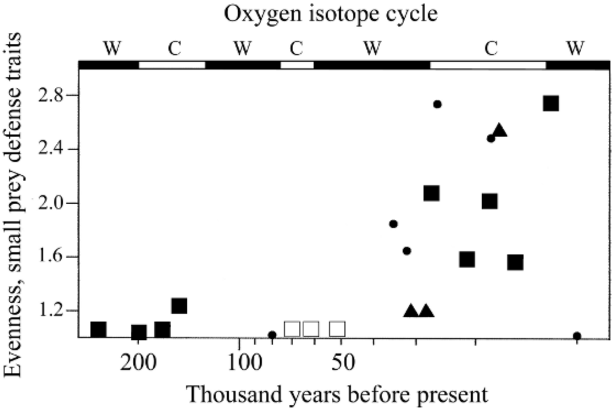

Figure 5: Evenness among three prey categories within the small game fraction only, based on prey defense mechanisms—slow game, quick-running terrestrial mammals, and quick-flying birds—using the Reciprocal of Simpson's Index (3 = most even). Filled circles represent cases from coastal Italy; filled triangles represent cases from coastal Turkey (Hatay region); filled squares represent assemblages from the Wadi Meged faunal sequence (Hayonim Cave and Meged Rockshelter); open squares are estimates for the late Mousterian of Kebara Cave (Speth and Tchernov 2002); other symbols as in Figure 2. (Reproduced from Stiner, 2001.)

quality of small prey animals that reproduce quickly is their greater potential reliability as a food source. Large mammals are less productive than many small species as a rule, but some productivity gradient must exist within the large species as well, since they vary in body weight. One goal of the large mammal prey simulation study is to understand better the potentially variable yields and the possible signatures of diet breadth expansion. The second goal is to integrate the findings on large and small game exploitation.

SIMULATIONS OF PREDATOR EFFECTS ON SMALL PREY

Differences in prey population resilience and the work of capture should have constrained Paleolithic people's uses of small game in predictable ways. *Resilience* here refers to a prey population's ability to withstand heavy, cyclical predation. It is linked most directly to individual maturation rate. Slow-growing small taxa dominate the earlier portions of each Paleolithic sequence and fast-growing types become important later, thus the periodicity or intensity of predation relative to prey maturation rates must have been

Table 1: Summary of life history and predator defense characteristics of the common small prey types in the Mediterranean Paleolithic faunas

Prey	Offspring production rate	Maturation rate	Predator defense mechanisms
Shellfish	high	slow-moderate	safety in numbers, armor, cryptic
Tortoises	moderate	slow	freezing, hiding, armor
Lagomorphs	moderate	fast	hiding, bolting & rapid running
game birds	moderate	fast	hiding, bolting & rapid flight

important. Ground birds, lagomorphs, tortoises, and most shellfish may produce many young per year (Table 1). However, Mediterranean tortoises require roughly a decade to mature (Hailey, 1988). Lagomorphs and game birds such as partridges reach reproductive age within a single year and their populations turn over rapidly. It is clear that prey birth rates alone cannot explain the differences in prey population turnover rates or the trends in small game use of the later Paleolithic.

Work of capture is determined by a prey animal's defense and escape mechanisms and therefore also influences prey rank. Work of capture in this sense may represent the cost of searching for prey, investment in technological aids, or the energetics of a true chase. It may also include processing costs, although in the study areas under consideration people used fire to do much of the processing work for them. In the Mediterranean Basin, we have two broad categories of small prey—those that are easily caught by hand and those that are not. Even with the aid of harvesting tools, the work-of-capture costs may be significantly higher for quick animals. The attractiveness of tortoises to humans is their ease of collection in combination with (in many cases) relatively low processing costs. Also significant is the fact that modern tortoises (and shellfish) can exist at very high densities in the absence of human disturbance, because of their low metabolic rates, high sub-adult and adult survival rates, and potentially long life spans (e.g. Hailey, 1988; Shine and Iverson, 1995).

The contrasting life history strategies of tortoises, lagomorphs, and game birds suggest that low-turnover prey species should respond quite differently to human predation than high-turnover species. Of great interest to us is the magnitude of difference in productivity among the subject prey animals. We assume that hunting intensity increases with the population density of predators on a landscape. The Monte Carlo simulation models were designed to address two questions: First, what is the maximum annual "yield" that predators can take from a subject prey population without surpassing the threshold for a stable (sustainable) predator-prey relationship? Second, how much more resilient are hare and partridge populations than tortoises to similar increases in predator density?

Model design: High and low growth conditions

The parameters for the simulations were taken from a variety of modern wildlife studies, preferably but not exclusively for the species identified in the Mediterranean archaeofaunas. Table 2 summarizes model structure and Table 3 the life history parameters used for tortoises (*Testudo*), hares (*Lepus*), and partridges (*Alectoris* and *Perdix*); the sources of data in Table 3 are many and will not be repeated here (see instead Stiner et al., 2000). Data from long-term studies of viable populations, with good control over birth rates, mortality rates, and their causes, were favored for modeling purposes.

To investigate the interplay of life history traits in predator-prey systems, we modeled two extremes of population growth for each kind of small prey animal—a high growth model (HGM) and a low growth model (LGM).

Table 2: Predator-prey simulation model structure and variables (from Stiner et al., 2000)

- Individual variables by sex:
  - MALE
    - Age
    - Mass (tortoises only)
  - FEMALE
    - Age
    - Mass (tortoises only)
    - Next age of reproduction
    - Litter size
- Fertility parameters:
  - Female minimum age of reproduction
  - Birth interval (spacing)
  - Minimum number of offspring
  - Maximum number of offspring
- Natural (non-human) mortality parameters:
  - Maximum potential life span
  - Age of onset of adult mortality rate
  - Annual adult mortality rate
  - Juvenile mortality rate
- Hunting parameters:
  - Minimum age/size to hunt
  - Annual kill percentage

Because prehistoric prey and predator densities cannot be known absolutely, our strategy was to compare the relative resiliencies of tortoise, hare, and partridge populations under favorable and lean conditions for prey reproduction and growth. Truly average conditions are rare in the life of any individual, and most or all years in that individual's lifetime will likely fall between the curves defined by our high and low growth models. The simulations were written by T. A. Surovell as Visual Basic macros in Microsoft Excel 7.0 (Figure 6). Populations were modeled as sets of actual individuals, each characterized by age, sex, and, in tortoises, body mass. Additionally, females were assigned values for next age of reproduction and annual litter size. Individual age increased by a fixed value per unit of time elapsed.

Fertility was controlled by three parameters in the model: female minimum reproductive age and the minimum and maximum number of offspring per annum. When a female was born, her next age of reproduction was set to the minimum age at which she could begin reproducing and to normal birth spacing thereafter. A predetermined number of offspring, between the minimum and maximum values in Table 3, was added to the population each year (except for LGM tortoises, as we discuss shortly). An even sex ratio at birth was maintained on the basis of empirical evidence.

Table 3: Assigned fertility and mortality parameter values for tortoises, hares, and partridges in the High Growth (HGM) and Low Growth Models (LGM) (from Stiner et al., 2000).

Parameter type	Tortoises		Hares		Partridges	
	HGM	LGM	HGM	LGM	HGM	LGM
Fertility:						
female age at first reproduction years)	8	12	0.75	1.0	0.75	1.0
birth interval (days)	365	730	365	365	365	365
maximum number of offspring per annum	14	14	11	9	13	11
Mortality:						
maximum potential lifespan (years)	60	60	12	12	8	8
age of adult-level mortality onset (years)	1	1	0.5	0.5	0.2	0.2
annual adult-level mortality rate	0.053	0.093	0.4	0.5	0.5	0.6
annual (base-level) juvenile mortality	0.70	0.85	0.6	0.7	0.42	0.6

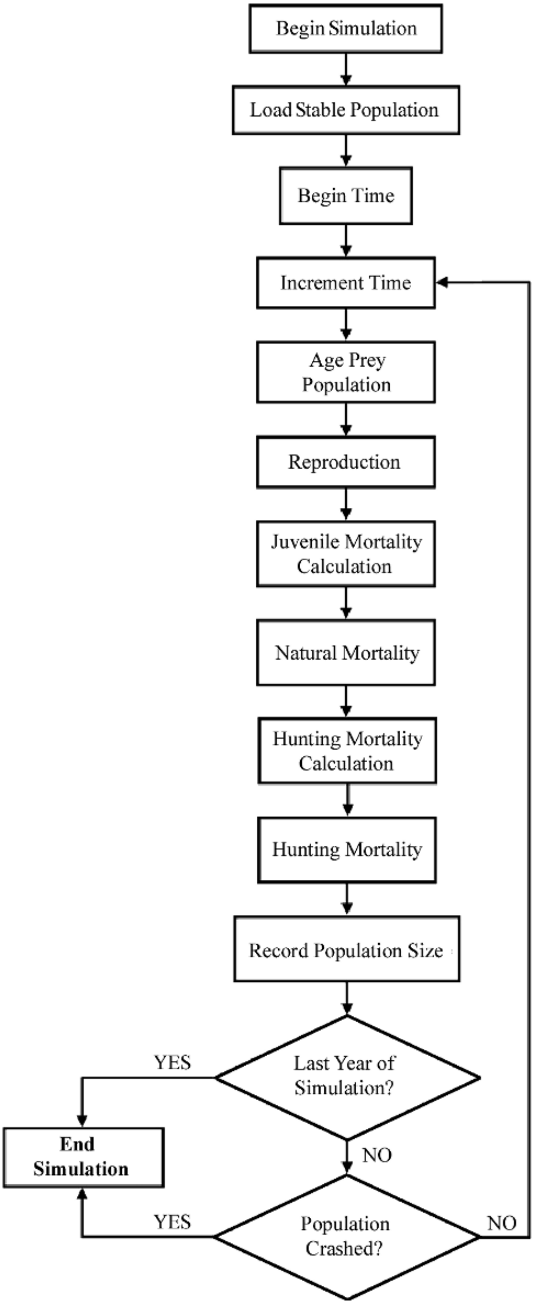

Figure 6: Model structure for simulations of predator-prey dynamics involving humans and small prey animals

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

$$\mathrm{m}_{jt} = \mathrm{m}_{jb} + [(\mathrm{pop}_t/\mathrm{pop}_k)(1 - \mathrm{m}_{jb})]$$

where m_{jt} is juvenile mortality at time t; m_{jb} is base-level juvenile mortality; and $\mathrm{pop}_t/\mathrm{pop}_k$ is population density at time t. Therefore, $\mathrm{m}_{jt} = \mathrm{m}_{jb}$ when $\mathrm{pop}_t = 0$, and $\mathrm{m}_{jt} = 1$ when the population is at environmental carrying capacity.

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

Parameter development—the example of tortoises

The process of parameter research was quite involved and is described elsewhere for each type of prey (Stiner et al., 2000). It is useful, however, to provide one example in order to illuminate important decisions in parameter development from empirical data. *Testudo,* the common genus of tortoise in the archaeofaunal series, provides an ideal standard for comparing small game use in the Mediterranean Paleolithic. Apart from a study by Doak et al. (1994), little modeling work has been done on tortoises, making it necessary to begin from scratch. In doing so, 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, has rapidly driven down mean individual size in affected tortoise populations in North Africa (Lambert, 1982; Stubbs, 1989) and Spain (Blasco et al., 1986–1987). Second, immature tortoises generally are much more difficult to find than are adults in Mediterranean habitats (Lambert, 1982). Third, adult female tortoises tend to be larger than males of the same age (Blasco et al., 1986–1987; 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, because size-biased collecting should affect females and males somewhat 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.

Testudo graeca and *T. hermanni* populations can be modeled as one taxon for our purposes. Information on the population dynamics of Mediterranean and other tortoises is scarce. 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, in addition to 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 was set at one year in both models. We set hatchling mortality (i.e. for the first year of life) at 70% in the HGM (females produce 2.1 to 4.2 yearlings per annum) and at 85% in the LGM (0.7 to 1.4 yearlings produced per annum), partly on the basis of estimates by Doak et al. (1994) for hatchling survival in desert tortoises (*Gopherus*). High adult survivorship is essential to the health of tortoise populations, whereas hatchling survival rates can vary much more without detracting from the long-term fate of those populations (Doak et al., 1994; Heppel et al., 1996a; Heppel et al., 1996b); 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 was 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 served as the maximum potential lifespan. It allowed 53.5 and 48.0 years of reproductive activity in the HGM and LGM, respectively.

A strong negative correlation exists between age at sexual maturity and the adult mortality rate in turtles and tortoises and in reptiles in general (Shine and Iverson, 1995). We used the regression line associated with this correlation to control the covariance of these parameters. To account for published variation in age at first reproduction (cf. Blasco et al., 1986–1987; Castanet and Cheylan, 1979; Hailey, 1990), values for *T. graeca* and *T. hermanni* were set at 12 years in the HGM and at 8 years in the LGM. These correspond to adult mortality values of 5.3% and 9.3%, respectively, well within the range documented for 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 was set to 365 days in the HGM but at 730 days in the LGM, on grounds that as few as half the adult females in a tortoise population might reproduce in a given year (Wilbur and Morin, 1988).

Simulation results for tortoises, partridges and hares

Figure 7 presents the simulated outcomes of incremental increases in predation on tortoises and on partridges over 200 years under high growth (HGM) and low growth (LGM) conditions. Adult tortoises were assumed to be preferred wherever available to the predators. It is clear from this exercise that tortoise populations cannot tolerate annual losses of more than 4 to 7% (LGM and HGM respectively) of reproductively mature individuals without crashing. In comparison with hares and birds, tortoise populations are exceptionally sensitive to predation and are easily destroyed. Sustainable harvesting is possible only below these thresholds. The same may have been true for certain shellfish (e.g. limpets, *Thais*) that Paleolithic humans in the Mediterranean area depended upon for food, although they are not modeled in this study.

The partridge simulations are based on wildlife data on chukars (*Alectoris chukar*) and gray partridges (*Perdix perdix*), species that are widely distributed in the Mediterranean area. The simulated outcomes of incremental increases in predation on partridge populations over 200 years under high growth (HGM) and low growth (LGM) conditions show that partridges are very resilient to sustained heavy predation. Their populations are difficult to destroy, even where off-take is consistently high. The simulated partridge populations can tolerate up to about 65% annual losses of adults in the HGM, and about 22% in the LGM. Similar results were obtained for Old and New World hare and rabbit species.

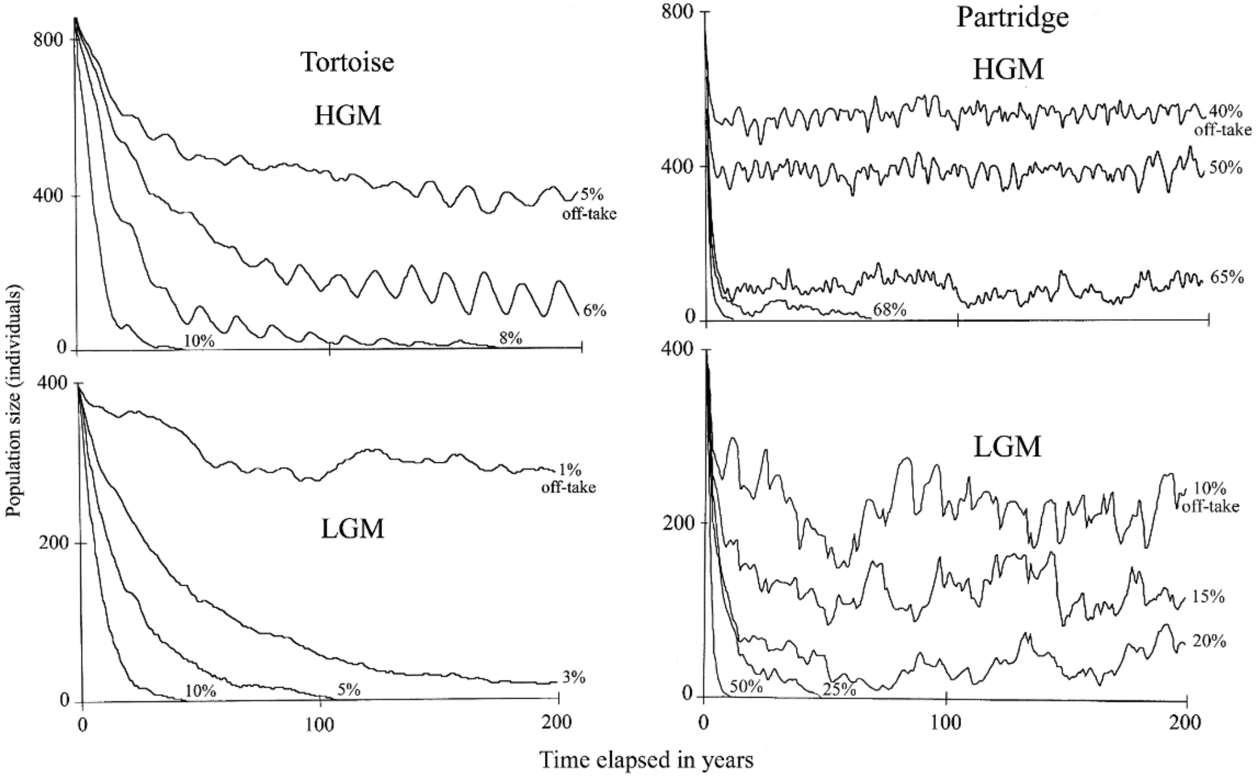

Figure 7: Simulated predation on tortoise populations (Testudo) and on partridge populations (Alectoris, Perdix) under high growth (HGM) and low growth (LGM) conditions. Percentages refer to annual off-take (mortality) from the total population, with adults weighing more than 0.3 kg taken preferentially. The undulations (chattering) in some of the HGM curves are due to alternating focuses on male and female prey, a product of model design. (Reproduced from Stiner et al., 2000.)

Folk wisdom tells us that lagomorphs are exceptionally productive. What it does not tell us is how game birds and tortoises compare with them. Figures 8 and 9 compare the areas and ranges of the high and low growth curves for tortoises and hares in our simulations of population growth. The area enclosed by the HGM and LGM curves for tortoises does not overlap at all with that for hares (or partridges) during the years of population growth, despite our rather puritanical limits on hare productivity. In our simulations, hare populations reached equilibrium between about 7 (HGM) and 25 (LGM) years, whereas tortoise populations reached equilibrium between about 50 (HGM) and 125 (LGM) years.

The simulations confirm the existence of major differences in the scale at which humans could possibly hope to depend on tortoises, hares, and partridge-like birds for meat. Other things being equal, hare populations can support proportionally 7 times greater off-take by predators than tortoises can support, and partridges can support 10 times greater off-take than tortoises. This means that humans' reliance on tortoises is sustainable only if human population densities are very low. Humans' reliance on partridges and hares is sustainable in both low- and high-density conditions.

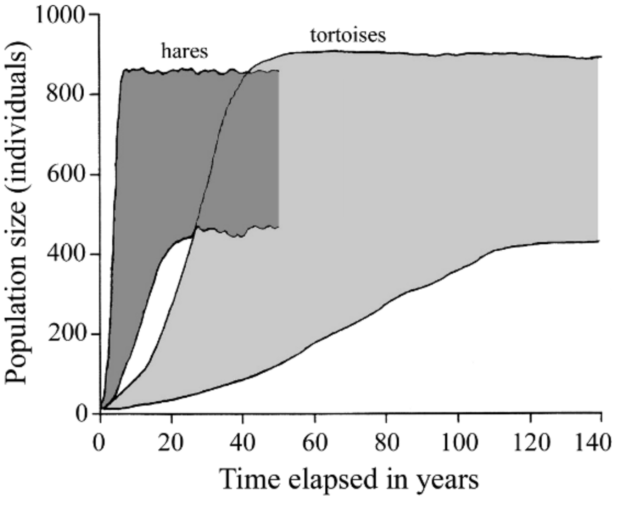

Figure 8: Comparison of areas between the high and low growth curves for simulated tortoise and hare populations. The upper line represents the high growth model (HGM) and the lower line the low growth model (LGM) for each kind of prey. Initial population size was 10 individuals. Carrying capacity was set at 1,000 for tortoises and 1,250 for hares in order to render population sizes comparable in the graph. (Reproduced from Stiner et al., 2000.)

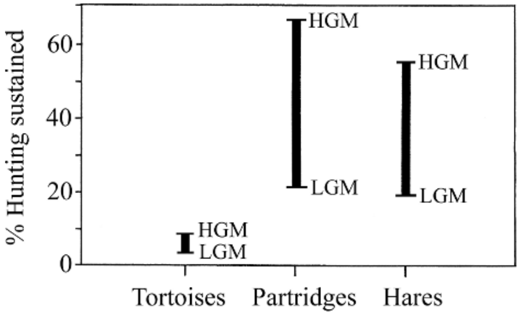

Figure 9: Comparison of hunting tolerance thresholds for tortoise (4–7%), partridge (22–66%), and hare (18–53%) populations under high (HGM) and low (LGM) growth conditions. Upper horizontal bars represent thresholds above which predators' dependence on the designated prey type is no longer sustainable. Vertical bars represent natural variation in population resilience as defined by the LGM and HGM. (Reproduced from Stiner et al., 2000.)

Differences in small animal productivity make greater economic sense of Upper Paleolithic and Epipaleolithic humans' increasing use of birds and hares when 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 Middle Paleolithic foraging systems, and humans overcame the disadvantages of these prey items only with greater technological investment in the Upper Paleolithic.

Links between predator pressure and population density

Small animal species vary tremendously in predator defense mechanisms and population resilience, in contrast to the ungulates that were commonly hunted by prehistoric humans. In addition, small animal species vary less in body weight relative to humans than do large game animals. It is for these reasons that data on small game exploitation can reflect subtle changes in Paleolithic demography. Heavy harvesting of tortoises or any other sensitive prey species reduces the viability of that population and, soon, the frequency with which foragers can find suitably large individuals of the affected species (Botkin, 1980; Broughton, 1997; Christenson, 1980; Earle, 1980; Mithen, 1993; Pianka, 1978).

It therefore is remarkable that up to about half of all identifiable animal remains (NISP) in some early Middle Paleolithic assemblages of Hayonim

Cave are from a reptile that is exceptionally sensitive to predation. What is more, the sizes of the individual tortoises taken during the Mousterian were larger on average than those of the later Paleolithic periods (Stiner, 2005; Stiner et al., 2000). High archaeological frequencies of a low-resilience prey species, along with large individual body sizes, imply that the early human populations that depended upon the species were small and highly dispersed. Middle Paleolithic populations may simply not have experienced the sorts of stresses that would have made agile, fast-growing small animals attractive.

Predator-prey simulation of small animals modeling illustrates how rising human population density and associated predator pressure may alter prey abundances and thereby select for changes in the prey types that were emphasized by foragers. More surprising is the evidence that resource intensification began so early in the story of subsistence revolution in Eurasia. The results suggest a notable expansion in dietary breadth with the onset of the early Upper Paleolithic and an even greater expansion during the later Upper Paleolithic and Epipaleolithic.

SIMULATIONS OF PREDATOR EFFECTS ON ARTIODACTYL UNGULATES

The small game simulation study is advantaged by the extreme differences in the reproductive ecology and predator avoidance behaviors of birds, small mammals and reptiles, all of which are similar in body size (at least relative to the body sizes of humans). However it was the large mammals that formed the bulk of animal biomass consumed by foragers prior to the end of the Paleolithic in the Mediterranean Basin (Figure 10), and in many other world regions as well. Similation modeling of predator-prey interactions involving large mammals would therefore seem necessary. This endeavor involves some distinct challenges, because ungulate species are much more similar to one another with respect to reproductive rates and predator avoidance characteristics. Unlike the situation with small game animals, ungulates also differ also greatly in body weight.

The archaeological observations nonetheless indicate that the earlier faunas contained more large ungulates and the later faunas more small ungulates. The potential explanations for the decline in mean ungulate body sizes acquired by hunters include hunting pressure and climate-induced changes in natural community structure; in the Mediterranean case, however, these changes co-occur in time with the small game trends, which are

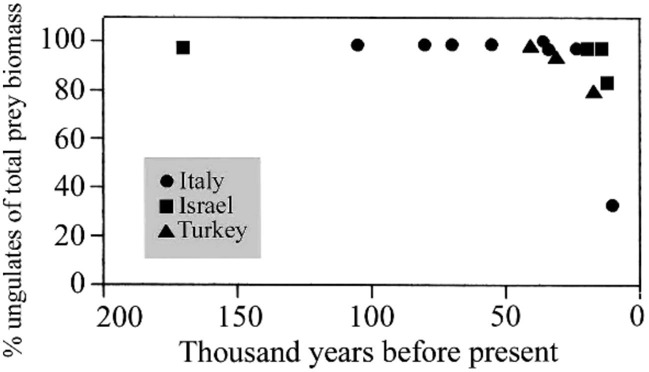

Figure 10: Percentages of total ungulate biomass obtained by Paleolithic hunters across periods in each of the three Mediterranean faunal series from Israel, Italy, and Turkey. (Reproduced from Stiner, 2005.)

attributable in large part to human effects (Stiner, 2005). Body size in ungulates generally correlates inversely with the rate of reproductive output and population turnover rate, and presumably prey population resilience. Small ungulate species, such as gazelles and roe deer, mature in a much shorter time than do larger deer (about 2 yrs for fallow deer, 2–3 yrs for red deer), and all of these species mature faster than do large ungulates such as aurochs (Table 4). In addition, larger ungulates occur in fewer numbers on a given landscape overall, and encounters with them may more sporadic and less predictable.

One goal of the large mammal prey simulation study is to understand the potentially variable yields among large mammals and to look for reliable signatures of diet breadth expansion. The second goal is to integrate the findings on large game exploitation to those for small game animals. The simulation model attempts to capture the essential population dynamics of each species, while remaining simple enough to avoid model-specific behaviors.

Model structure

The model for the ungulate predator-prey simulations is descended from that employed in the small game study, but with two modifications (Beaver 2007). First, both "natural" (non-anthropogenic) and human-caused mortality occur multiple times per year, rather than once a year. The similarities in the reproductive characteristics of ungulate species in comparison with tortoises, partridge, and hares makes a more fine-grained

Table 4: Simulation model parameters for ungulate species, based on wildlife data sources (Beaver 2007)

Species	Model	Pregnancy Rate	Mean Number of Offspring	Female Age of First Reproduction	Age of Onset of Adult Mortality	Maximum Age	Base Rate of Natural Juvenile Mortality		Adult Natural Mortality Rate	
							Female	Male	Female	Male
Aurochs	LGM	0.3	1.0	4	3	16	0.11	0.13	0.05	0.08
	HGM	0.5	1.0	4	3	18	0.1	0.1	0.04	0.06
Fallow Deer	LGM	0.8	1.0	2	2	12	0.21	0.21	0.11	0.12
	HGM	0.9	1.0	2	2	14	0.15	0.15	0.07	0.08
Gazelle	LGM	0.9	1.0	1	1	12	0.4	0.4	0.2	0.2
	HGM	1.0	1.2	1	1	12	0.25	0.25	0.15	0.15
Goat	LGM	0.6	1.5	2	1	12	0.25	0.25	0.15	0.15
	HGM	0.7	1.7	2	1	12	0.15	0.15	0.1	0.1
Ibex	LGM	0.7	1.0	2	2	12	0.2	0.2	0.12	0.12
	HGM	0.8	1.1	2	2	12	0.12	0.12	0.08	0.08
Red Deer	LGM	0.5	1.0	3	2	14	0.15	0.19	0.06	0.11
	HGM	0.7	1.0	3	2	14	0.12	0.15	0.04	0.07
Roe Deer	LGM	0.8	1.8	2	1	10	0.3	0.3	0.15	0.15
	HGM	0.9	2.0	2	1	12	0.2	0.2	0.1	0.1

model desirable, and spreading the two sources of mortality through the model year significantly reduces the effect of scheduling decisions on which type of mortality should occur first. Second, hunting levels are determined in the model relative to the initial, stable population size, rather than in terms of each year's population size. This approach holds the food yield constant as the prey population is exploited. Yield is of greater importance in examining ungulate species exploitation if human population sizes are also an issue. This is because the different types of small game populations vary so much in inherent resilience yet are more similar than ungulates are in body size, whereas ungulate population resilience increases as body size decreases. An approach that can be used to compare sustainable yields among species is thus more important with large game (Figure 11).

Ungulate model results

Ungulate population responses to human predation are modeled for seven Artiodactyl species that occurred in and around the Mediterranean Basin during the Paleolithic: aurochs (*Bos primigenius*), fallow deer (*Dama dama/mesopotamica*), gazelle (*Gazella gazella*), ibex (*Capra ibex*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and wild goat (*Capra aegagrus*). High (HGM) and Low Growth Model (LGM) sets of population parameters were derived for each species from the ecological and wildlife management literature (Table 4), using substitute species where necessary (e.g. *Bison bison*, *B. bonasus*, and *Syncerus caffer* for the extinct aurochs). The maximum sustainable hunting rates for the modeled species range from 0.26% (aurochs, LGM) to 11.3% (roe deer, HGM) of the initial population, with the LGM-HGM range for each species overlapping with that for at least one other species. The maximum sustainable hunting rate is the most important difference in ungulate population responses to continuous human predation; hunting rates considered as a fraction of the species model's maximum sustainable rate have essentially indistinguishable effects, regardless of species (Figure 12, Table 5). For example, a hunting rate half of the maximum sustainable rate depresses any ungulate population by about 14%, and a hunting rate that is 90% of the maximum sustainable rate depresses the population by approximately 30%.

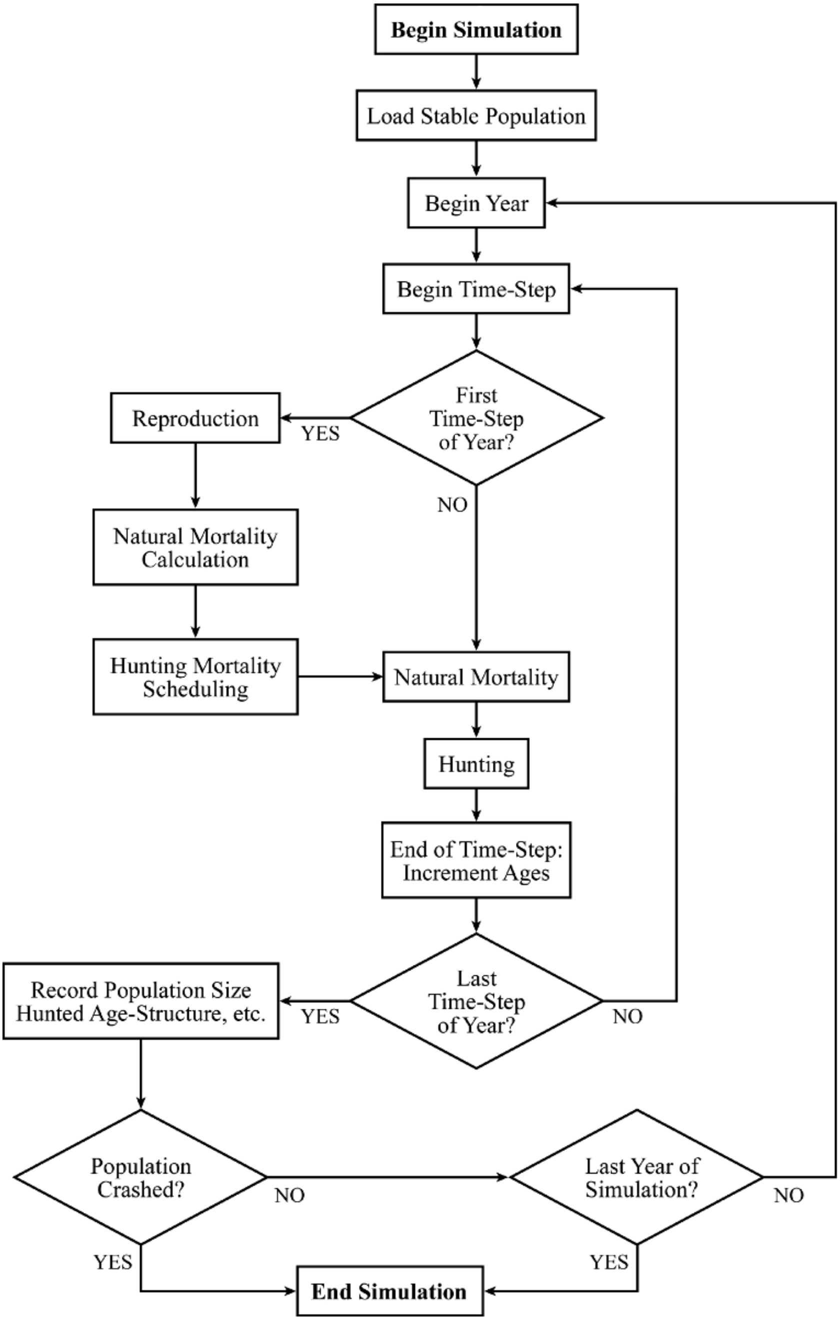

Figure 11: Model structure for simulations of predator-prey dynamics involving humans and ungulates (from Beaver 2007)

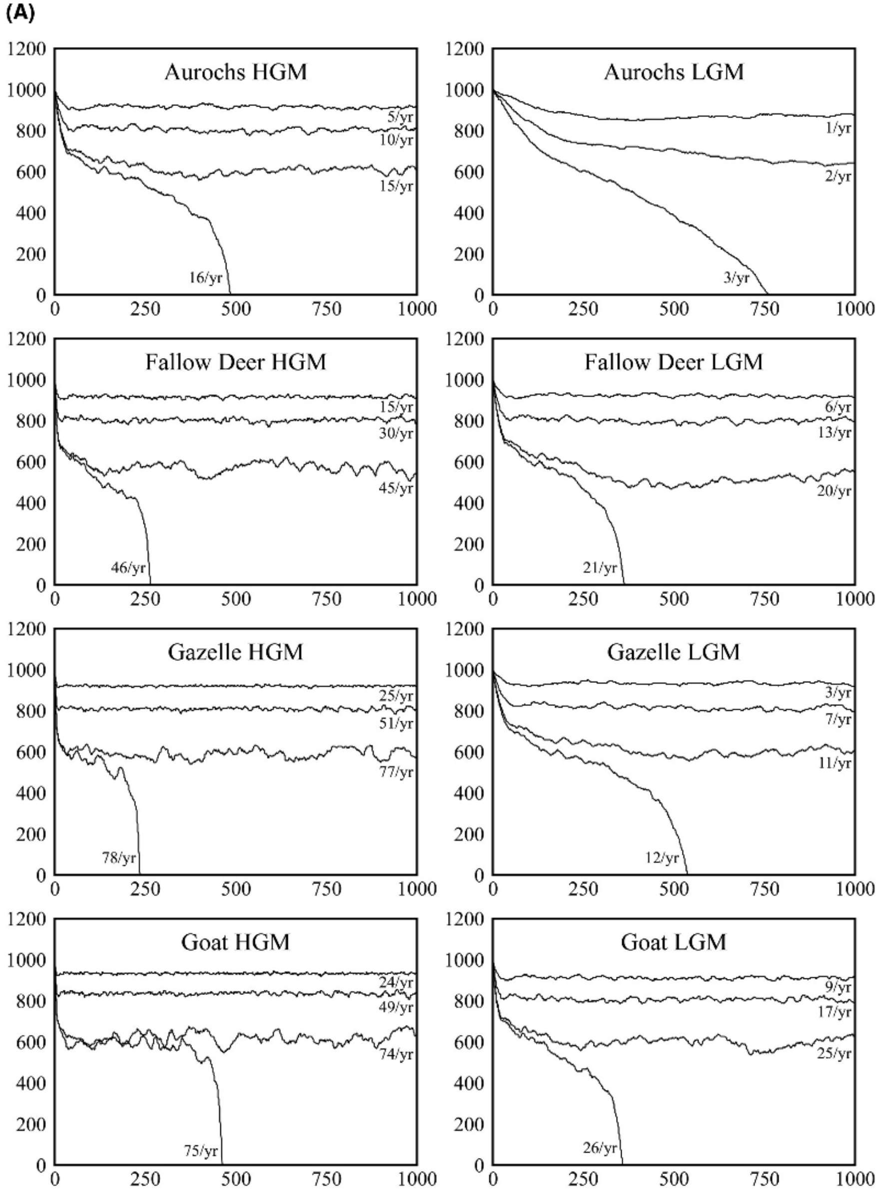

Figure 12: Ungulate population responses by species to human hunting of the indicated number of individual animals per year. The x-axis represents time in years; the y-axis represents prey population size

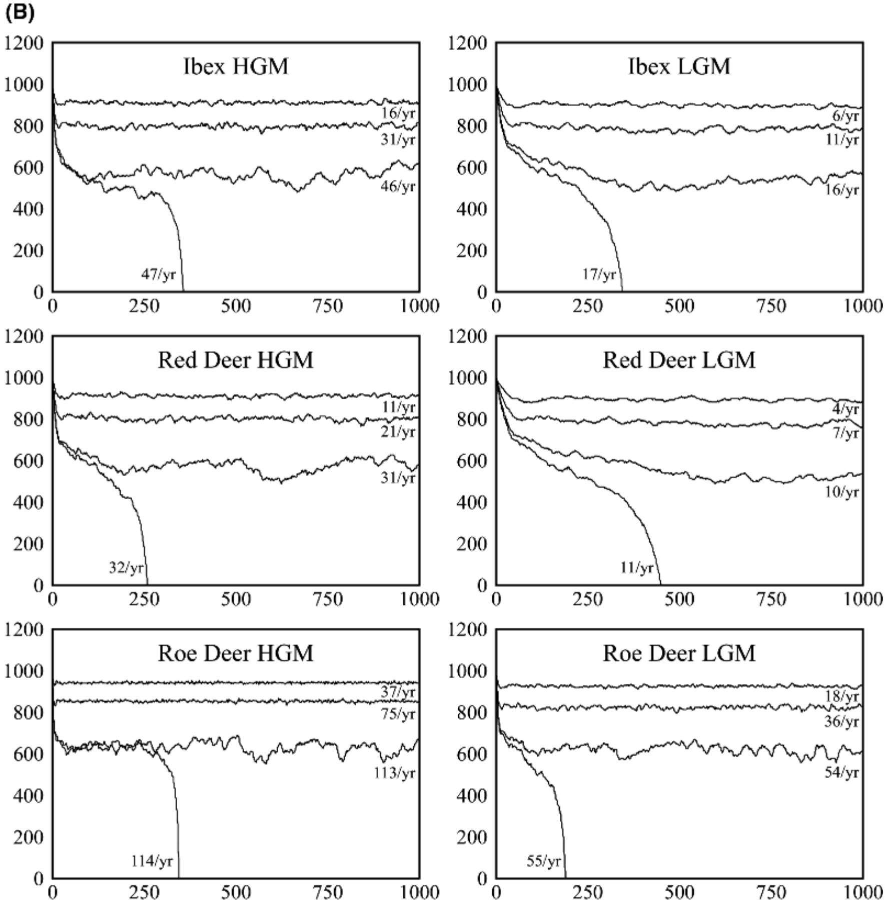

Figure 12: (*Continued*)

Ungulate results compared to those for small game

There are several factors that make ungulate exploitation a less profitable analytical focus than small game for paleodemographic research. Stiner et al.'s (2000) discussion of small game emphasized the importance of the differences in hunting technology and human behaviors required to hunt different types of small game. In that case, substantially greater technological and/or energetic investment is required to exploit substantially more resilient, but also very similarly sized, animals. In the case of ungulates, very similar technological/energetic investment may allow the exploitation of

Table 5: Mean maximum hunting rates that can be sustained by the modeled populations under low growth (LGM) and high growth (HGM) conditions (Beaver 2007)

Species	Sustainable Percentage	
	LGM	HGM
Aurochs (*Bos taurus*)	0.260	1.513
Fallow Deer (*Dama dama*)	1.989	4.529
Gazelle (*Gazella gazella*)	1.102	7.727
Goat (*Capra aegagrus*)	2.524	7.393
Ibex (*Capra Ibex*)	1.598	4.584
Red Deer (*Cervus elaphus*)	0.999	3.102
Roe Deer (*Capreolus capreolus*)	5.397	11.277

similarly resilient but very differently sized ungulates. It is the convergence of all three factors—exploitation cost differentials, population resiliency differentials, and body size similarities—that favors demographic interpretations of trends in small game use.

Even the total potential yield of different ungulate species is difficult to apply to problems of human demography. The maximum sustainable hunting rates obtained for ungulate species models correlate strongly and negatively with body size, following a power-law relationship; $h = .307m^{-526}$, where h is the mean of the maximum hunting rates sustainable by the high and low growth models for each species and m is the estimated mean adult body mass for that species; $r^2 = .886$, $p = .002$. A human population can hunt many more roe deer than red deer without crashing the population, but humans *must* do so in order to acquire the same amount of food, making the relative population densities of the different ungulate species an important consideration. This situation contrasts strongly with that for the three types of small game modeled by Stiner et al. (2000), whose maximum sustainable hunting rates are not closely related to body size.

Because prey population density is negatively correlated with body size, the population densities of smaller animals are higher than those of larger animals, and especially within closely related groups of species (e.g. among the Artiodactlya). This relationship is on average one where population density increases more slowly than body size decreases (e.g. Damuth, 1981, 1987; Peters and Wassenberg, 1983). Thus the sustainable yields for the smaller ungulates are not definitively higher than those for the larger ungulates (compare Figures 13–15).

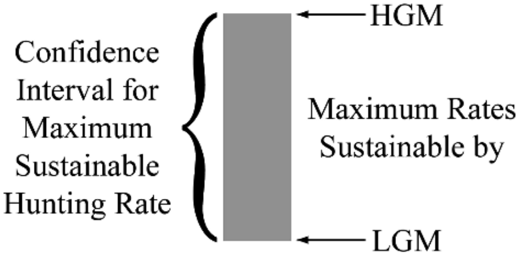

Figure 13: Definition confidence interval based on the HGM and LGM maximum sustainable hunting rates

The picture is complicated further by the question of just what was happening with the human population increases in the Paleolithic. It is clear that human populations in the Middle Paleolithic were small and spread sparsely around the Old World. When these populations increased, did group sizes (and thus local exploitation levels) increase while groups remained equally scattered and equally mobile? Or did more or larger groups form, filling up more territory but with similar local exploitation levels? In the latter case, were areas exploited more often or for longer periods? It seems likely that all of these conditions occurred at various times and places. Sustainable hunting rates and food yields were also examined under different durations of exploitation (from one-year to century-long episodes) and different rates of reoccupation (leaving the prey populations unexploited from 50% to 95% of the time). These simulations indicate that, while the smallest ungulate species can sustain higher yields under some patterns of local occupation or reoccupation, under other patterns it is the largest species that can do so. Under yet other conditions, the species of intermediate size are most capable of supporting the highest yield! A careful consideration of ungulate species exploitation alongside other data may eventually allow us to better understand how human population growth in the Paleolithic manifested, but such data are difficult to use to identify faunal changes caused by demographic increases.

DISCUSSION

The archaeological record of small game hunting during the Mediterranean Middle Paleolithic indicates nearly exclusive use of sessile or slow-moving prey. This is followed in the early Upper Paleolithic by major proportional increases in quick-flying common game birds and, by the

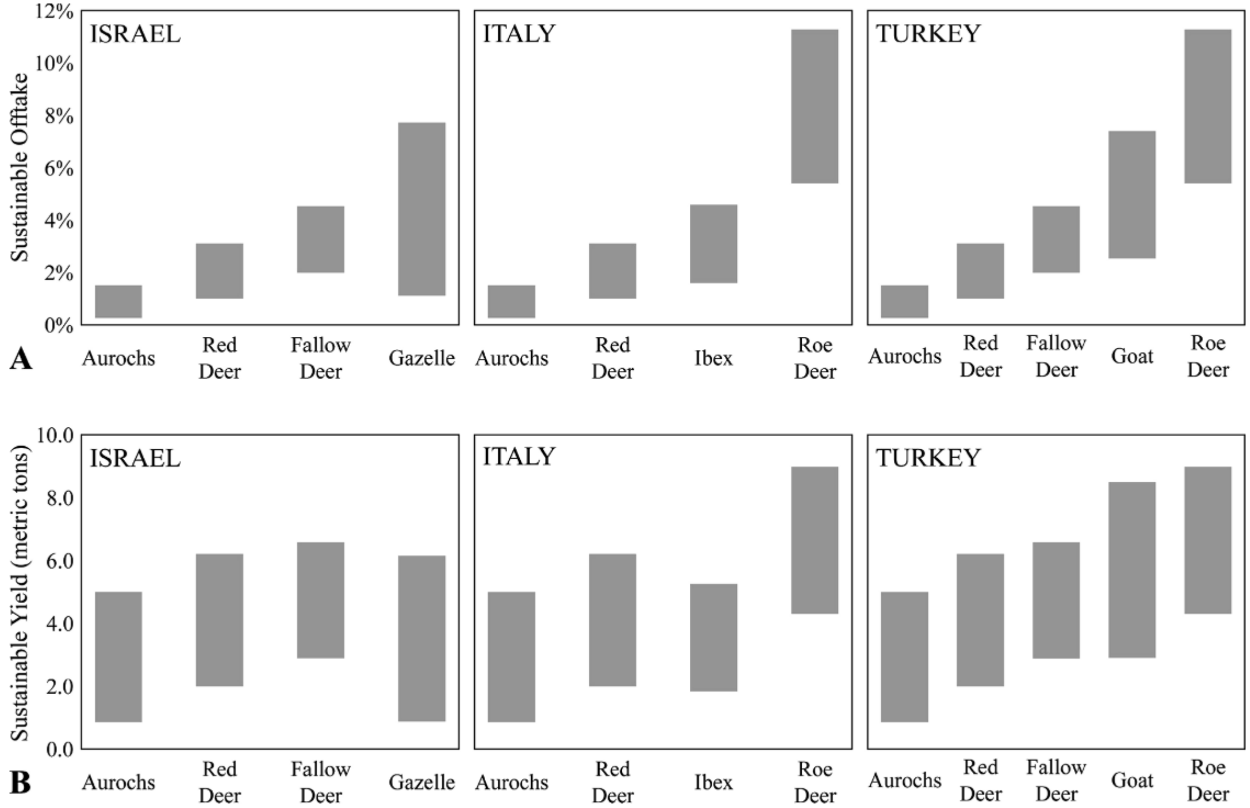

Figure 14: Comparisons of sustainable annual off-take rates for ungulate species in each Mediterranean data set (A) as percentages of the initial unhunted population and (B) as biomass yields from populations ‘ecologically equivalent’ to a population of 1000 red deer. Bars represent confidence range for maximum sustainable off-take rates from low growth to high growth model values.

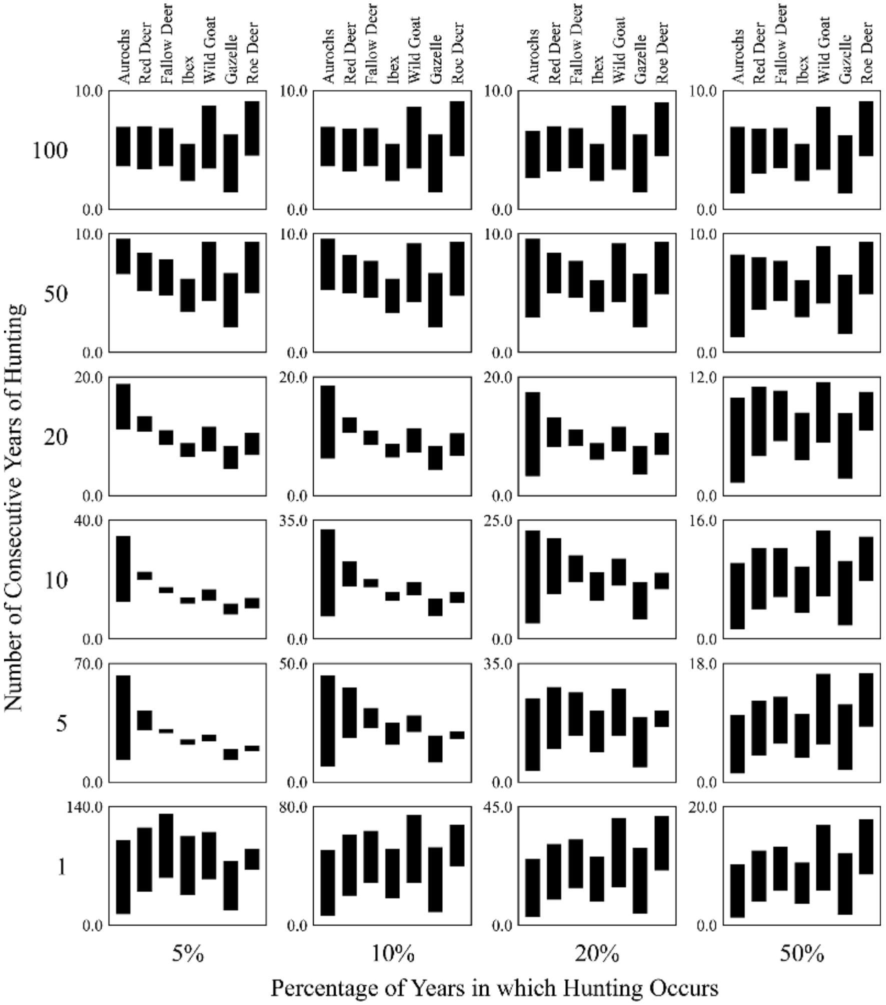

Figure 15: Comparison of biomass yields sustainable by modeled ungulate populations at varying durations and intervals of exploitation. Y-axes of graphs are biomass yield in metric tons per year during periods of exploitation. Bars represent confidence range for maximum sustainable yield from low growth to high growth model values

Epi-paleolithic, in fast-running lagomorphs as well. Highly ranked prey animals, as defined by Middle Paleolithic exploitation, were the slow-moving tortoises and shellfish. Use of these animals continued through the Upper Paleolithic and Epipaleolithic, but agile types supplemented the diet in greater proportions, despite their lower ranking on grounds that their capture costs were higher. More significant than any expansion of the taxonomic spectrum in Paleolithic human diets was a rising emphasis on a few highly productive taxa that were less easily caught by hand. We also see an increase in small, fast-reproducing ungulate species in Paleolithic diets with time. However, the sustainable yields for the smaller ungulates are not definitively higher than those for the larger ungulates. The shift down the body-size spectrum that we see in your Mediterranean data through the Upper Paleolithic is not in itself solid evidence of demographic growth. However, given demographic growth as shown by other, better evidence (like the small game), we can attribute the shift to smaller ungulates as being the result of the population growth. Put another way, smaller ungulate prey are not sufficient for a conclusion of predator population growth, but significant predator population growth is sufficient (in the absence of a good environmental cause) for a focus on smaller ungulate prey. We suggest that an increasing dependence upon high producers, even if total volume of meat acquired remains the same, could mean a reduction in the composite (cooperatively pooled) variance in foraging success, albeit at the price of greater hunting effort.

For the bulk of prehistory, mobility has been humans' primary solution to local resource scarcity. With increasing population, humans in some regions seem to have had fewer options for solving problems of resource availability through mobility, beginning sometime in the Upper Paleolithic, and the situation deteriorated further in the Epipaleolithic (*sensu* Bar-Yosef, 1981; Binford, 1968, 1999; Cohen, 1977, 1985; Flannery, 1969; Tchernov, 1993, 1998). Increasing dependence on a variety of more biologically "productive" or resilient prey populations over time might have allowed people to obtain a greater volume of meat per unit of habitat area. Perhaps more important is that prey population resilience could have substantially increased the reliability (i.e. reduced the variance) and diversity of meat sources to which a population had access, especially as the costs of acquisition or processing were controlled through technology. A more reliable supply of animal protein and fats has significant implications for child survivorship.

Middle Paleolithic humans in the Mediterranean region maintained remarkably narrow diets across a wide range of latitudes. The evidence indicates that human populations were exceptionally small throughout the Mediterranean Middle Paleolithic. A categorical shift in human predator-prey dynamics accompanied by demographic expansion seems to demarcate the Middle to Upper Paleolithic cultural boundary. There seems to have been a lack of pressure or economic incentive for these clever, mobile hunters to squeeze more out of their traditional food supplies—that is, there was little selection, if any, for greater foraging efficiency. More difficult to explain are the downward shifts in trophic level so characteristic of later humans. These shifts took the form of subsistence diversification via the inclusion of lower-ranked foodstuffs associated with greater processing costs, and they coincided more than once with increases in human population densities. Low human population densities during the early Middle Paleolithic also imply small social groups and networks, 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 limited. Larger social networks for spreading risk might also have appeared in conjunction with expanding diets, possibly setting some Upper Paleolithic populations at an advantage.

Subsistence behaviors that enhance the predictability of supplies of critical nutrients can improve childhood survivorship and thereby help a population grow without a change in birthrate. Changes in the character and regularity of meat acquisition also hold social implications: the small-large dichotomy in prey body size and the slow-quick dichotomy in small prey may correspond to the emergence of significant divisions within labor networks among modern hunter-gatherer cultures. Immobile or sluggish small animals are essentially gatherable resources and thus directly accessible to both sexes and all age groups in human societies. Fresh meat from large game animals generally must be obtained by hunting—normally the job of grown men. Quick small animals present other challenges: they are most efficiently caught with special tools and, in some cases, a substantial measure of vigilance. Although access to small quick game is limited by technical skills, these often are learned in late childhood. The price of these activities was higher labor investment in tool preparation and maintenance or direct inputs of cooperative labor to capture small animals in quantity. In western Asia, demographic pressure preceded rather than followed the earliest technological innovations of the Upper Paleolithic and Epipaleolithic periods.

To date, most information on human population history has been obtained from studies of modern human genetic diversity, which on the whole suggest several demographic pulses originating from western Asia, Africa, or both that ultimately affected peripheral populations of Europe and elsewhere (e.g. Ammerman and Cavalli-Sforza, 1984; Barbujani and Bertorelle, 2001; Hewitt, 2000; Reich and Goldstein, 1998; Relethford, 1998, among others). Time is the most difficult variable to control for in these studies: biological clocks inferred from gene mutation rates are notoriously inaccurate, and so there is dismaying variety in their interpretation. In contrast to the situation for the genetic data, demographic pulses evidenced by the archaeological record of human subsistence and human cemetery data (Bocquet-Appel, 2002) can be dated by radiometric techniques over geographical gradients, permitting independent tests of prehistoric human population dynamics and population history. In our zooarchaeological case, a close look at the Middle Paleolithic record relative to the records of later periods revealed an appropriate way to test the hypothesis of expanding dietary breadth in response to human population pressure. The Mediterranean spur-thighed tortoise, a species long ignored in zooarchaeological research in the Levant, provided new insights into the nature of Mousterian subsistence and demography. The small animal remains found in archaeological sites are attributable to Paleolithic human activities hold 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 some of the factors that contributed to the earliest forager-producer transition.

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