

Small game use and expanding diet breadth in the Eastern Mediterranean basin during the Palaeolithic

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Résumé

Les preuves archéozoologiques ayant trait à l'exploitation des petits gibiers sont résumées pour trois régions du Bassin méditerranéen, depuis le Paléolithique moyen jusqu'au Paléolithique supérieur. Les données indiquent que l'intérêt porté aux petites proies progresse à travers le temps, notamment s'agissant des espèces les plus productives. La modélisation des dynamiques proies-prédateurs et la diminution de l'exploitation des tortues dans les archéofaunes sont des indices de l'augmentation démographique humaine, et donc de la pression de la prédation. Ce processus commence dans la zone est du Bassin méditerranéen.

Abstract

This paper summarizes zooarchaeological evidence for fundamental changes in the ecology of early humans in three areas of the Mediterranean Basin from the Middle through Late Pleistocene, mainly from the viewpoint of small game exploitation. The data indicate greater use of smaller, more productive prey with time. Computer simulation modelling of predator-prey population dynamics and diminution in tortoises link the archaeofaunal trends to increasing human population densities and predator pressure, beginning in the eastern end of the Mediterranean Basin.

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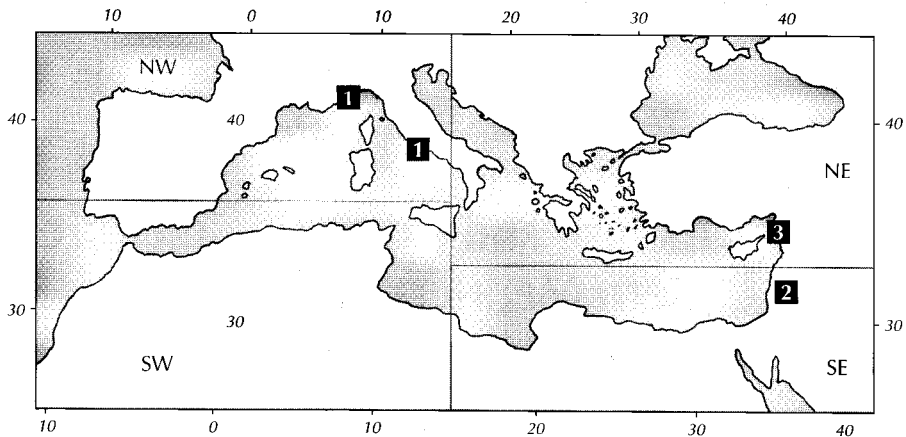


Fig. 1. Geographic origins of the three Mediterranean faunal series : 1, Italy in NW quadrant ; 2, Israel in SE ; 3, Turkey in NE (from Stiner, n. d.). Ecological quadrants are distinguished on the basis of endemic species distributions and dominant habitat structures (base map after Blondel, Aronson, 1999, p. 38).

Virtually everyone agrees that the shift to agricultural economies some $\leq 10\ 000$ years ago greatly increased humans' impact on ecosystems. Yet the earliest demonstrable human-induced effects on animal and plant communities are traceable to Palaeolithic hunter-gatherers ≥ 45 thousand years ago (ky) in the Mediterranean Basin (fig. 1).

Palaeolithic humans of the Mediterranean Basin obtained most of their meat from ungulates until very late in the Pleistocene, based on biomass-corrected data on prey species abundance (fig. 2). This fact has implications for human demography, since a heavy dependence on large game mammals generally cannot support high human population densities. Medium- to large-sized ungulates remained the preferred prey types in the Upper and Epi-Palaeolithic culture periods, but the biomass-corrected prey abundance data in figure 3 indicate greater use of lower ranked, faster-reproducing species, including smaller ungulates as well as lagomorphs and game birds. Exploitation of resources other than large game seems to have accelerated over time, rising to 17 % or greater by the late Epi-Palaeolithic.

These zooarchaeological data indicate significant, directional changes in dietary composition and specifically in dietary breadth. The greatest changes in Palaeolithic forager diets occurred with respect to small game use (Stiner, 2001 ; Stiner *et al.*, 2000). The conditional nature of small game use in the Palaeolithic, along with great differences in the reproductive ecology of the small species exploited, make these components of archaeofaunal records exceptionally informative about changes in Palaeolithic foraging ecology. The most sensitive prey populations – Mediterranean tortoises and certain marine shellfish – are the proverbial « canaries in the coal mine » for studying density-dependent shifts in human predator-prey interactions of the Pleistocene (Stiner, 2001).

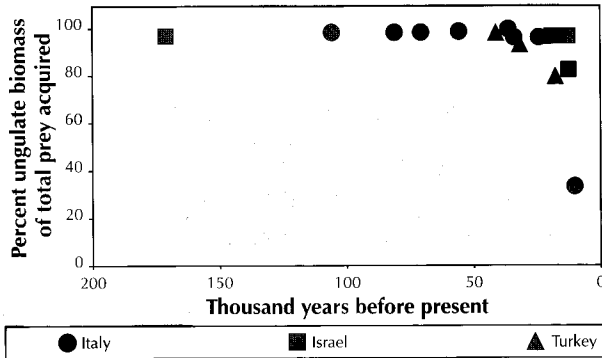


Fig. 2. Percentage of total ungulate biomass consumed over time in each of the three Mediterranean faunal series (biomass = bone-based MNI multiplied by average individual prey weight in kg).

Dietary breadth and palaeodemography

The breadth of forager diets can vary a great deal, depending on the availability of high quality, high-yield foods (Pianka, 1978 ; Stephens, Krebs, 1986). Narrow diets, in which low quality or low-yield prey may go ignored, are sustainable only if the chances of finding superior types remain high. If the encounter rates with preferred prey types decline, predators must broaden their diets by taking more of the lower yield types. Situations expected to lead to subsistence diversification include those in which foragers put excessive pressure on preferred resources, forcing them into decline, or in which forager populations increase to a point that they can no longer be sustained by preferred, high-yield resources alone.

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 (Stephens, Krebs, 1986). Broadly speaking, prey rank (relative payoff) is directly related to body size and escape strategy. Ethnographic and experimental evidence suggest that hunting large animals provides returns on effort several times those for smaller animals, and an order of magnitude greater than many vegetable foods (*e.g.* Kelly, 1995 ; Kuhn, Stiner, 2001). Holding body size constant, another means for ranking prey is in terms of handling costs. Among the range of small animals taken by Middle and Upper Palaeolithic foragers, tortoises and rock-dwelling marine shellfish can be placed into a single category here termed « sessile » game, because they are sluggish or immobile and easily gathered. Quick running or flying animals, such as hares and partridges, have similar body weights to tortoises or armfuls of shellfish, but they are far more difficult to catch by hand and thus would be lower ranked in the absence of special harvesting equipment.

Prehistoric expansions in dietary breadth are most apparent within the small game fraction of the Mediterranean archaeofaunal assemblages considered here (Stiner, 2001). Specifically, the relative emphasis that humans placed on slow-moving or sessile types declined, and fast-running hares and rabbits,

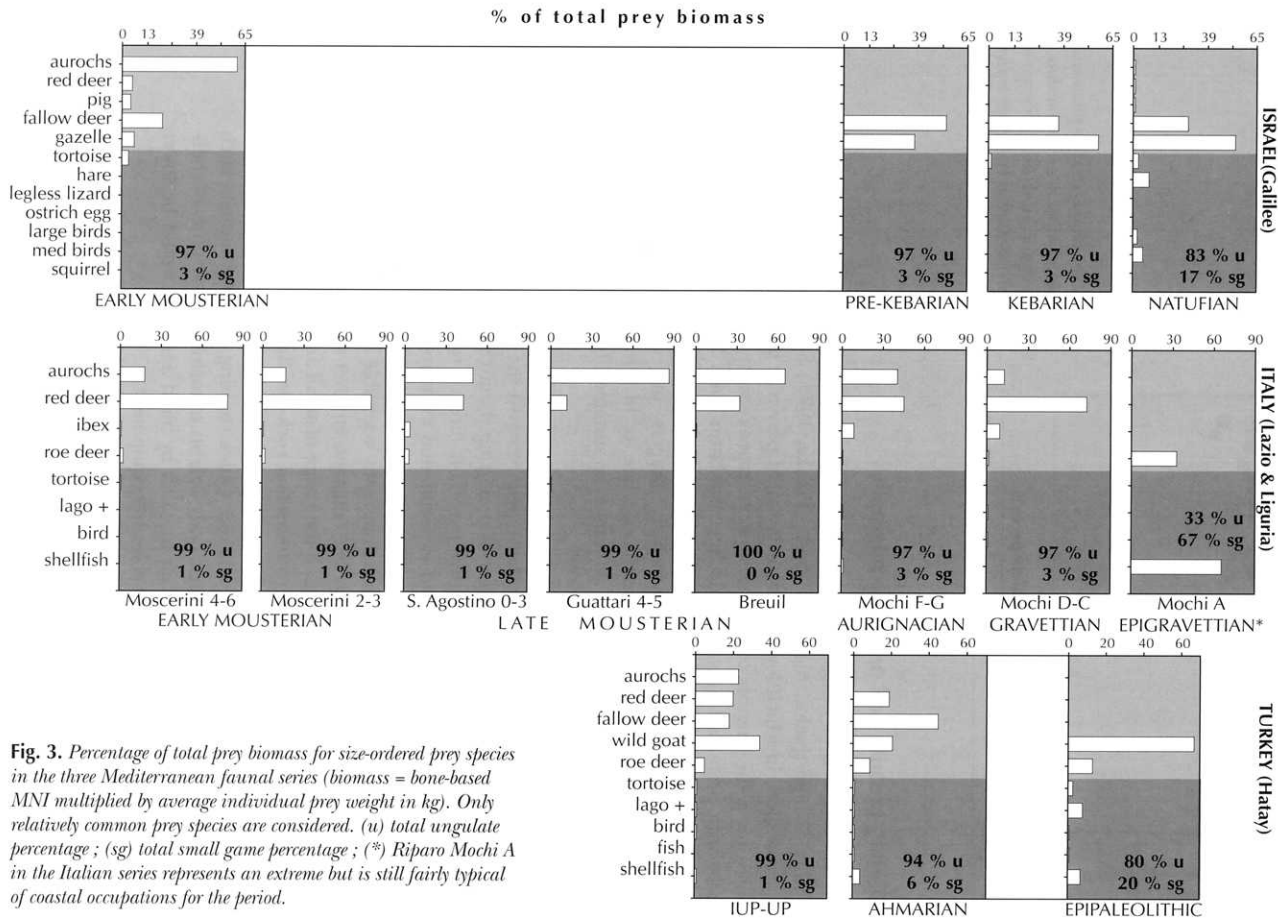


Fig. 3. Percentage of total prey biomass for size-ordered prey species in the three Mediterranean faunal series (biomass = bone-based MNI multiplied by average individual prey weight in kg). Only relatively common prey species are considered. (u) total ungulate percentage; (sg) total small game percentage; (*) Riparo Mochi A in the Italian series represents an extreme but is still fairly typical of coastal occupations for the period.

and quick-flying game birds, increased dramatically with time. A simple measure of evenness (the Inverse of Simpson's Index, see Simpson 1949 ; Levins 1968) in the prey types eaten reveals significant expansion – or evening-out in the use of high- and low-yield small prey types – in human diets (fig. 4), beginning around 40-50 000 years ago in the eastern end of the Mediterranean Basin. Before this time, Middle Palaeolithic foragers (250 ky to 40-50 ky) seldom bothered with small prey except for those sessile types that could be collected with little effort.

The indications of increasing dietary breadth occur roughly around the time of the Middle and Upper Palaeolithic transition in at least three areas of the Mediterranean Basin. However, this cultural transition dates to before 45 ky in the eastern end of the basin and progressively later in a westward direction (Stiner, 2002, 2003 ; Stiner *et al.*, 2000). Most of the changes in forager diets took place during a phase of climate cooling, namely oxygen isotope stage (OIS) 2 (following Martinson *et al.*, 1987). Had diet expansion occurred only in conjunction with global warming, climate-driven shifts in animal community diversity and structure would represent the most parsimonious explanation. Instead, the evidence from the Mediterranean faunal series indicates a categorical change in how humans interacted with small animal populations. The burgeoning importance of lagomorphs and other fast moving, fast-reproducing small game in human diets became remarkably widespread, extending from the northern interior of Europe to arid lands to the south (reviewed in Stiner, 2002). Environmental changes brought on by global warming (*e.g.* Madeyska, 1999) may have expanded the habitats favoured by lagomorphs and thus their numbers in Eurasia. However, as palaeontological evidence indicates that lagomorphs existed in most or all of these regions in earlier times, they were largely ignored by humans (Stiner, 1994 ; Tchernov, 1994).

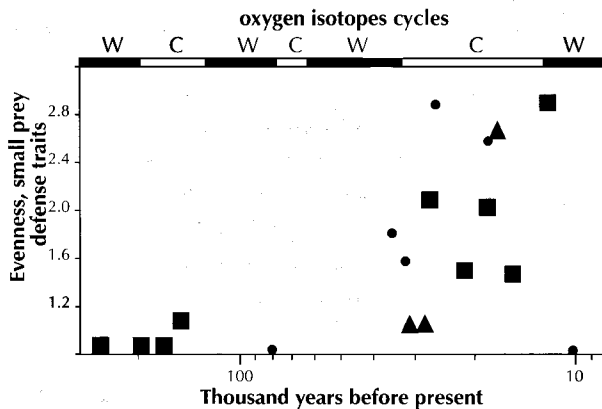


Fig. 4. Evenness among three small game categories in Paleolithic faunas, based on prey defense mechanisms (slow game, quick running terrestrial mammals and quick-flying birds) (3 = most even, 1 = least even). Symbols are for Italy (circle), Israel (square), and Turkey (triangle). Oxygen isotope climate cycles : (c) cold stage, (w) warm stage (from Stiner, 2001).

Evidence for harvesting pressure in Middle Eastern tortoises

In the Mediterranean Basin, a simple distinction in the « catchability » of various small animals happens to correspond to a great difference in prey population resilience (Stiner *et al.*, 2000). Population resilience is governed foremost by the rate at which individual prey animals mature. Slow-moving tortoises and certain shellfish are especially susceptible to over-harvesting, because it takes them several years to reach reproductive age. In contrast, rabbits and some ground birds are notorious for their rapid reproduction, quick development rates, and resilience in the face of heavy predation. Predator-prey computer simulations (Stiner *et al.*, 2000) indicated that hare and partridge populations may have supported seven to ten times the annual off-take compared to tortoise populations. Differential productivity of prey populations is essential to understanding the implications of trends in small game exploitation for hominid demography. Additionally, an important quality of small prey populations that reproduce quickly is their greater potential reliability as a food source if capture costs can be kept low.

It is striking that Middle Palaeolithic foragers focused on slow-growing prey types so consistently, to the extent that they bothered with small animals at all. While tortoises (mainly *Testudo graeca*) were a regular part of the Middle Palaeolithic diet in the eastern Mediterranean Basin, there is no evidence of over-harvesting of the tortoises – in the form of body size diminution – until the very end of the Middle Palaeolithic in Israel (Stiner, n. d. ; Stiner *et al.*, 2000) ; the size reduction trend is based on measurements of the narrowest breadth of the humeral shaft and length versus breadth of the nuchal plate of the carapace. Heavy use of slow-growing tortoises during the Middle Palaeolithic, yet no reduction in mean tortoise size during most or all of the Mousterian, implies that these hominid populations were very small and dispersed, and that they remained so for more than 100 000 years. Tortoise size reduction is evidenced only towards the end of the Middle Palaeolithic or the earliest phases of the Upper Palaeolithic in the Middle East. Rather than a gradual pattern of diminution, the mean sizes in the time series from Hayonim Cave and Meged Rockshelter in the Wadi Meged form two groups. An analysis of variance shows the size differences at the shift-point to be nonrandomly distributed in the time-ordered samples (F-ratio = 24,15 ; $p < 0,001$; $df = [8414]$).

A 70 000-year hiatus in human occupation and sediment accumulation separates the Mousterian and the Aurignacian in the Wadi Meged faunal series of northern Israel. The late Middle Palaeolithic and early Upper Palaeolithic levels from Kebara Cave on the western face of Mount Carmel help to fill this gap. Kebara Cave today is situated in a somewhat richer vegetation zone, where tortoises may have been larger as a rule. Nonetheless, a significant decline in mean size of tortoises occurred between the late Middle Palaeolithic, dated from 70 ky to 55 ky (4,5 cm ; $N = 169$; $sd 0,6$) and the earliest Upper Palaeolithic (Ahmarian, Bar-Yosef *et al.*, 1996), dated to 44 ky (4,0 cm ; $N = 31$; $sd 0,8$), a

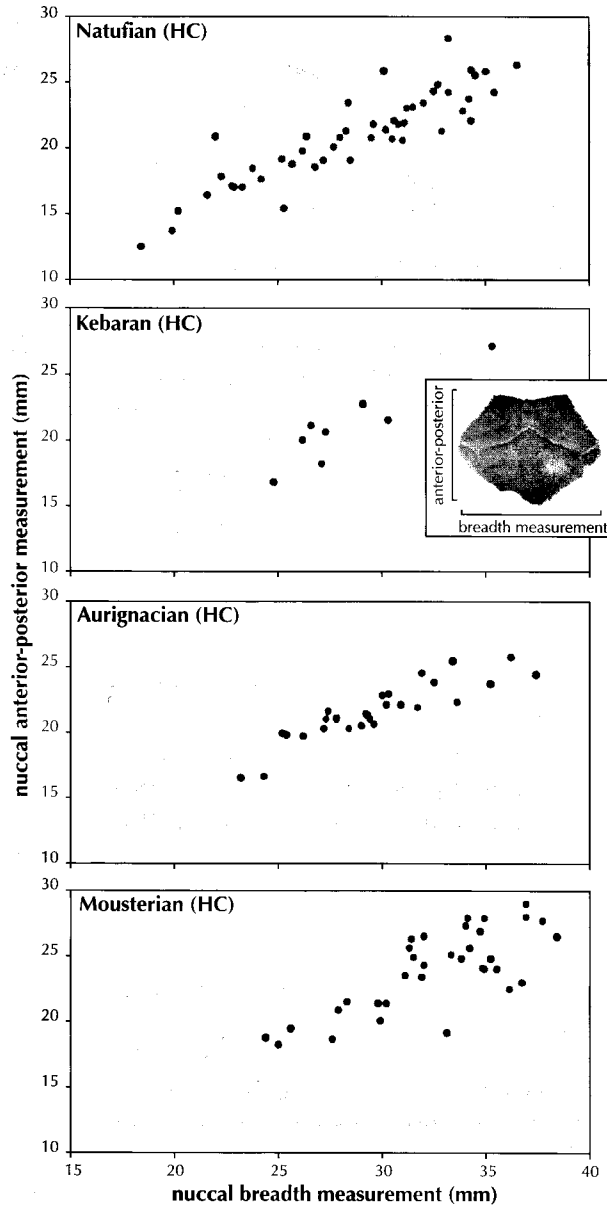


Fig. 5. Size distributions of tortoise nuchal plates in four cultural layers of Hayonim Cave (Wadi Meged, Galilee), based on anterior-posterior length and maximum breadth (mm).

result recently confirmed with larger samples by Speth and Tchernov (2002). Size reduction in tortoises therefore began at least 44 000 years before present, possibly earlier in light of the relatively small mean size for the youngest Middle Palaeolithic sample in the Wadi Meged series.

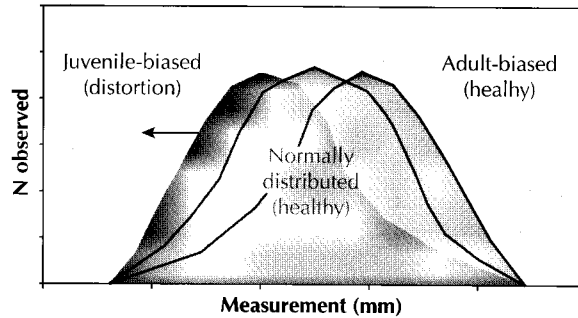


Fig. 6. Modeled patterns of size (= age) skewing in relation to population state, based on a morphometric trait. Normally distributed size/age patterns and those biased toward older adults are typical healthy population structures (black curves), because adult mortality rates are very low in natural settings and juvenile mortality is high. A bias toward juveniles (skewing to the left of the normal distribution, gray curve) reflects abnormal distortion of the size/age structure, due to unusually high adult mortality, and is known to result from heavy exploitation of adult animals by humans.

Could the pattern of diminution represent one tortoise population's response to an external pressure, or was there a complete replacement of that population by another whose inherent maximum body size potential was less than the first (Speth, Tchernov, 2002)? The second condition should be evidenced by substantial reduction in the sizes of the largest individuals in each assemblage, in addition to a reduction in mean size. The data from northern Israel contradict the second hypothesis, because the *maximum sizes* reached by adult tortoises in the Wadi Meged were about the same in the Middle Palaeolithic, Upper Palaeolithic, and Epi-Palaeolithic (and today) based on nuchal plate dimensions (fig. 5), even though mean sizes declined.

There is evidence also of distortion in the size (age) structures of the tortoises during the later Palaeolithic. The significance of this pattern is rooted in the life history strategy of tortoises: infant mortality is very high, adult mortality very low (Hailey, 1988; Shine, Iverson, 1995; Wilbur, Morin, 1988), and healthy tortoise populations tend to pack habitats with long-lived adults as a rule. The high densities typical of healthy, unmolested tortoise populations are potentially a mine-able resource for predators, but tortoise populations possess limited ability for resurgence if exploited heavily. While spur-thighed tortoises do well in a variety of Mediterranean regions, Hailey *et al.* (1988) and Lambert (1982, 1984) found that the opening-up of habitats by human disturbance of any sort (*e.g.* from overgrazing, extensive ploughing, or increased incidence of range-burning) reduced hatchling survival and intensified interference competition from adult tortoises. This situation seems to produce an age bias in favour of adults (Hailey *et al.*, 1988; Lambert, 1984), skewing the size structure toward the older end of the size continuum. Otherwise, populations display a normally distributed, bell-shaped pattern (fig. 6).

If the tortoise size distribution were to be measured in terms of « skewness », negative values and those close to zero would reflect natural tortoise populations free from human depredation, even if human-induced environmental disturbance occurs. Strongly positive values of skewness instead indicate an unstable structure or distortion of the tortoise population due to heavy predation in particular – either from hunting or, in recent decades, capturing individuals for sale as pets (reviewed in Stiner *et al.*, 2000). Healthy tortoise size/age structures are apparent during much of the Mousterian. In the later periods (fig. 7), distortion or « destabilization » of tortoise populations indicates over-exploitation by humans. This result refutes the hypothesis that size changes in the Wadi Meged tortoises are the result of phenotypic differences in the potential for maximum growth (population replacement), or simply from increasing aridity or opening-up of plant cover.

In fact, the Wadi Meged assemblages span several oxygen isotope stages (OIS 7 through 1) : the early Kebaran of Meged Rockshelter dates to the Last Glacial Maximum (Kuhn *et al.*, 2004), the later Kebaran to early phases of global warming, and the Natufian near the Pleistocene/Holocene transition when the pace of global warming accelerated (Bar-Matthews *et al.*, 1999 ; Martinson *et al.*, 1987 ; see also Munro, 2001 on Natufian faunas). Mean tortoise size shifted suddenly downward in the middle of OIS 3, and mean tortoise sizes remained low for the rest of the Pleistocene sequence. Thus, climatic variation and species/population replacement do not seem to account for the size decline after the late Middle Palaeolithic in the Wadi Meged archaeofaunal series, nor for the fact that diminution is sustained through the Upper and Epi-Palaeolithic periods. Finally, species or subspecies replacement is not apparent from bony carapace and plastron morphology based specifically on anal (pygal) plate morphology or the degree of flaring of the posterior margin of the carapace. Therefore a chance biogeographic shift unrelated to climate change is also rejected by these observations.

At the very least, the size trend in tortoises is the result of a combination of human-induced and climatic effects, and human involvement cannot be denied. Between 50 000 and 40 000 years ago, at the threshold of the Middle-Upper Palaeolithic cultural transition, the sudden addition of many fast-reproducing but difficult to capture small animals to the diet also indicates that human populations had begun to exceed the potential of higher-ranked, high-return resources (large game and tortoises) to support them. The zooarchaeological evidence from three distinct Mediterranean localities testifies to additional human demographic growth over the course of the Late Pleistocene, accelerating especially after *c.*15 ky.

Discussion

The archaeofaunal data suggest that the « inflexibility » we see in Middle Palaeolithic culture was a product of the success and stability of the adaptation (Kuhn, Stiner, 2001 ; Stiner *et al.*, 2000), not a question of lower intelligence

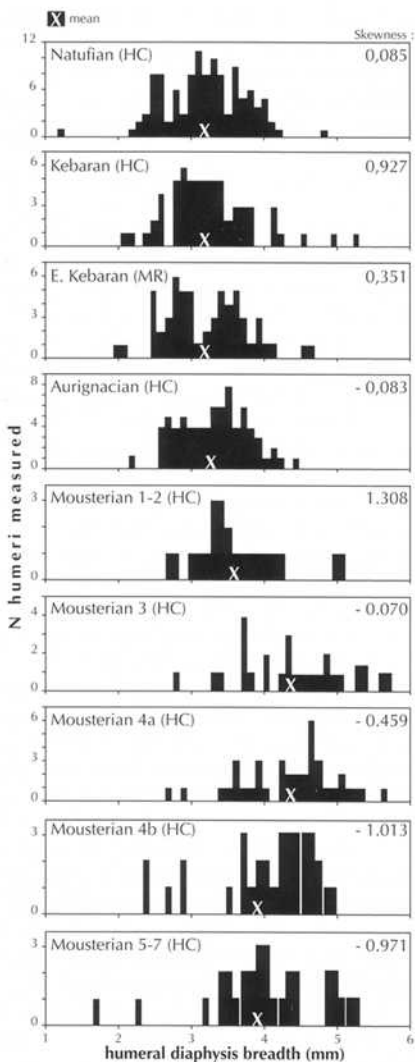


Fig. 7. Size skewing in tortoise humeral diaphysis mean breadth for the Wadi Meged series, from the early Mousterian through Natufian periods in the Galilee of Israel. (HC) Hayonim Cave; (MR) Meged Rockshelter. Negative and near-zero values indicate normal population structures; positive values indicate significant distortion from heavy predation on adults.

(Klein, 1989). There seems to have been a lack of pressure or economic incentive for these mobile hunters to squeeze more out of traditional food supplies, and little if any selection for greater foraging efficiency. Indeed the biogeography and demography of Middle Palaeolithic foragers is consistent with the large carnivores (Stiner, 1994). More difficult to explain than Middle Palaeolithic conservatism is the downward shift in trophic level that is so characteristic of later humans. This shift associates quite early in the Upper Palaeolithic culture sequence with subsistence diversification via the inclusion of lower-ranked foodstuffs that had greater collecting and/or processing costs, and it is symptomatic of increases in human population densities.

Why did demographic increase become a permanent condition for humans in the late Pleistocene? Greater dependence on more biologically « productive » or resilient prey populations may or may not have allowed people to obtain more meat volume per unit habitat area. On the other hand, prey population resilience can substantially affect the reliability and the diversity of meat sources to which a population has access. A more consistent supply of animal protein and fats may also significantly improve child survivorship, thereby swelling the ranks of a human population by reducing variance in the access to key foodstuffs.

Many technological innovations of the Upper Palaeolithic appear to relate to the exploitation of small prey, particularly aquatic, burrowing and flying types (reviewed in Kuhn, Stiner, 2001). While some of these prey populations can rebound quickly from heavy hunting, they are reliable resources to humans only if the work of capture can be reduced with new technology, such as tended and/or untended traps (*sensu* Oswalt, 1976). Although the material evidence is fragmentary, there is good reason to think that trapping and net technologies developed rapidly during the later Upper and Epi-Palaeolithic or Mesolithic periods (*e.g.* Adovasio *et al.*, 1996; Gamble, 1986; Jochim, 1998; Nadel *et al.*, 1994). The tools for overcoming the quick-flight strategies of birds and small mammals no doubt also permanently altered foragers' systems for ranking prey. The pressure to do so began, however, with predator-prey relationships already gone sour.

A distinct but related side of the technological record concerns carcass-processing innovations, which grew much more complex in the late Upper Palaeolithic and especially the Epi-Palaeolithic. Major shifts in processing efficiency include grease rendering via stone boiling, evidenced by the thick litter of fire-cracked stones in some later Upper Palaeolithic sites (Audouze, 1987; Stiner, 2003; Svoboda, 1990; Weniger, 1987). Such heat-in-liquid techniques are labour-intensive but raise the protein and fat yields per carcass well beyond what is possible from cold-extraction techniques (Binford, 1978; Brink, 1997; Lupo, Schmitt, 1997). Only cold-extraction techniques focusing on the concentrated marrow reserves in large medullary cavities were employed during the Middle Palaeolithic and earlier periods. Interestingly, the evidence for concerted harvesting of quick small animals antedates or accompanies the changes in marrow processing of large mammals in Mediterranean Palaeolithic sequences.

These behaviours are merely different forms of resource intensification and all may represent responses to the declining availability of high-ranked resources.

As one of the very few sources of complete protein in nature, animal tissue represents something more than a source of food energy to humans (Speth, Spielmann, 1983). The rarity and value of meat introduces scheduling and spatial discontinuities in availability, sharpening humans' interest in obtaining it in large packages. Any foraging behaviours that enhance the predictability of critical nutrients can improve childhood survivorship, and some of the most consistent sources of protein, and in some cases fat, for hunter-gatherer children are the small animals that children procure for themselves or are provided by kin. The opportunities to obtain small animals (two kilogrammes or less) are also considerably more diverse and widespread than are the opportunities to obtain large game. Access to large game tissues is particularly constrained if the natural supply is chronically low or unreliable, and even under conditions of abundance large game animals are available to hunters much more sporadically. Thus, the trends in small game use along the Mediterranean Rim, which included increasing focus on more productive animal resources, may inadvertently have stabilized humans' access to protein as the absolute or relative abundance of highly-ranked but relatively unproductive prey declined.

The small-large dichotomy in prey body size and the slow-quick dichotomy in small prey correspond to some extent with the division of labour among recent hunter-gatherers. Fresh meat from large game animals generally must be obtained by hunting, most typically a male activity, and access to large meat packages by non-hunting members of the social group is limited mainly by propinquity. Quick small animals present other challenges, as they are most efficiently caught with special tools and, in some cases, substantial vigilance, or through large-scale cooperation in the case of net hunting. Access to small quick game is limited by technical skill, but this skill usually is learned in late childhood among recent hunter-gatherers. The activities of large game hunting, birding, snaring or fishing therefore can involve different personnel and distinct patterns of movement and time allocation. The novel resources of the Upper Palaeolithic may also have allowed different members of a human group to become productive foragers (see also discussions by Binford, 1968; Lupo, Schmitt, 2002). 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 Palaeolithic records.

In sum, the massive « ecological footprint » of humans today is a recent development. For a very long time, hominids were energetically of little significance in the ecosystems in which they lived. Distinct human impact on animal community structure and the composition of prey populations first became detectible at roughly 50 000 to 40 000 years ago, with the onset of the earliest Upper Palaeolithic, taking the form of imbalances between humans and their preferred prey. What is so remarkable is that these imbalances became widespread toward the close of the Late Pleistocene. In contrast to earlier humans, Upper

Palaeolithic foragers more often responded through social and technological adjustments rather than simple demographic decline to resource scarcity, thereby intensifying their impact on the world around them. Zooarchaeological data on small game use suggest that the ecological and demographic crises that seem so unique to the modern world have deeper roots in human evolutionary history. In western Asia, human demographic pressure preceded rather than followed the earliest technologic innovations of the Upper and Epi-Palaeolithic periods, even if its effects are most obvious by the Epi-Palaeolithic period (compare Binford, 1968 ; Flannery, 1969 ; Stiner, 2001).

Bibliography

- ADOVASIO J. M., SOFFER O., KLIMA B., 1996.– Paleolithic fiber technology : Data from Pavlov I, ca. 26,000 BP, *Antiquity*, 70, p. 526-534.
- AUDOUZE F., 1987.– The Paris Basin in Magdalenian times, in : O. Soffer (ed.), *The Pleistocene Old World : Regional Perspectives*, New York, Plenum, p. 183-200.
- BAR-MATTHEWS M., AYALON A., KAUFMAN A., WASSERBURG G. J., 1999.– The Eastern Mediterranean paleoclimate as a reflection of regional events : Soreq Cave, Israel., *Earth and Planetary Science Letters*, 166, p. 85-95.
- BAR-YOSEF O., ARNOLD M., BELFER-COHEN A., GOLDBERG P., HOUSELEY R., LAVILLE H., MEIGNEN L., MERCIER N., VOGEL J. C., VANDERMEERSCH B., 1996.– The dating of the Upper Paleolithic layers in Kebara Cave, Mt. Carmel, *Journal of Archaeological Science*, 23, p. 297-307.
- BINFORD L. R., 1968.– Post-Pleistocene adaptations, in : S. R. Binford, L. R. Binford (eds), *New Perspectives in Archaeology*, Chicago, Aldine, p. 313-341.
- BINFORD L. R., 1978.– *Nunamiut Ethnoarchaeology*, New York, Academic Press, 509 p.
- BLONDEL J., ARONSON J., 1999.– *Biology and Wildlife of the Mediterranean Region*, Oxford University Press, 328 p.
- BRINK J. W., 1997.– Fat content in leg bones of Bison bison, and applications to archaeology, *Journal of Archaeological Science*, 24, p. 259-274.
- FLANNERY K. V., 1969.– Origins and ecological effects of early domestication in Iran and the Near East, in : P. J. Ucko, G. W. Dimbleby (eds), *The Domestication and Exploitation of Plants and Animals*, Chicago, Aldine, p. 73-100.
- GAMBLE C., 1986.– *The Palaeolithic Settlement of Europe*, Cambridge, Cambridge University Press, 471 p.
- GAMBLE C., 1999.– *Paleolithic Societies of Europe*, Cambridge, Cambridge University Press, 505 p.
- HAILEY A., 1988.– Population ecology and conservation of tortoises : the estimation of density, and dynamics of a small population, *Herpetological Journal*, 1, p. 263-271.
- HAILEY A., WRIGHT J., STEER E., 1988.– Population ecology and conservation of tortoises : the effects of disturbance, *Herpetological Journal*, 1, p. 294-301.
- JOCHIM M. 1998. *A Hunter-gatherer Landscape : Southwest Germany in the Late Paleolithic and Mesolithic*, New York, Plenum Press, 247 p.

- KELLY R., 1995.– *The Foraging Spectrum : Diversity in Hunter-Gatherer Lifeways*, Washington, D. C., Smithsonian Institution Press, 446 p.
- KLEIN R. G., 1989.– *The Human Career : Human Biological and Cultural Origins*, First Edition. University of Chicago Press, Chicago.
- KUHN S. L., BELFER-COHEN A., BAR-YOSEF O., VANDERMEERSCH B., ARENSBURG B., STINER M. C., 2004.– The Last Glacial Maximum at Meged Rockshelter, Upper Galilee, Israel, *Journal of the Israel Prehistory Society* (in press).
- KUHN S. L., STINER M. C., 2001.– The antiquity of hunter-gatherers, in : C. Panter-Brick, R. H. Layton, P. A. Rowley-Conwy (eds), *Hunter-gatherers : Interdisciplinary Perspectives*, Cambridge, Cambridge University Press, p. 99-142.
- LAMBERT M. R. K., 1982.– Studies on the growth, structure and abundance of the Mediterranean spur-thighed tortoise, *Testudo graeca* in field populations, *Journal of Zoology*, London, 196, p. 165-189.
- LAMBERT M. R. K., 1984.– Threats to Mediterranean (West Palaearctic) tortoises and their effects on wild populations : an overview, *Amphibia-Reptilia*, 5, p. 5-15.
- LEVINS R., 1968.– *Evolution in Changing Environments : Some Theoretical Explorations*, Princeton, Princeton University Press, 120 p.
- LUPO K. D., SCHMITT D. N., 1997.– Experiments in bone boiling : Nutritional returns and archaeological reflections, *Anthropozoologica*, 25-26, p. 137-144.
- LUPO K. D., SCHMITT D. N., 2002.– Upper Paleolithic net-hunting, small prey exploitation, and women's work effort : a view from the ethnographic and ethnoarchaeological record of the Congo Basin, *Journal of Archaeological Method and Theory*, 9 (2), p. 147-179.
- MADEYSKA T., 1999.– Palaeogeography of European lowland during the late Vistulian, in : M. Kobusiewicz, J. K. Kozłowski (eds), *Post-pleniglacial Re-colonization of the Great European Lowland*, Kraków, Folia Quaternaria 70, Polska Akademia Umiejętności, Komisja Paleogeografii Czwartorzędu, p. 7-30.
- MARTINSON D. G., PISIAS N. G., HAYS J. D., IMBRIE J., MOORE T. C., SHACKLETON N. J., 1987.– Age dating and the orbital theory of the ice ages : development of a high-resolution 0 to 300,000-year chronostratigraphy, *Quaternary Research*, 27, p. 1-29.
- MUNRO N. D., 2001.– *A Prelude to Agriculture : Game Use and Occupation Intensity during the Natufian Period in the Southern Levant*, Ph. D. Dissertation, Department of Anthropology, University of Arizona, Tucson, Arizona, 387 p.
- NADEL D., DANIN A., WERKER E., SCHICK T., KISLEV M. E., STEWART K., 1994.– 19,000-year-old twisted fibers from Ohalo I, *Current Anthropology*, 35 (4), p. 451-458.
- OSWALT W. H., 1976.– *An Anthropological Analysis of Food-Getting Technology*, New York, John Wiley and Sons, 310 p.
- PIANKA E. R., 1978.– *Evolutionary Ecology* (Second Edition), New York, Harper and Row, 397 p.
- SHINE R., IVERSON J. B., 1995.– Patterns of survival, growth and maturation in turtles, *Oikos*, 72, p. 343-348.
- SIMPSON E. H., 1949.– Measurement of diversity, *Nature*, 163, p. 688.

- SPETH J. D., SPIELMANN K. A., 1983.– Energy source, protein metabolism, and hunter-gatherer subsistence strategies, *Journal of Anthropological Archaeology*, 2, p. 1-31.
- SPETH J. D., TCHERNOV E., 2002.– Middle Paleolithic tortoise use at Kebara Cave (Israel), *Journal of Archaeological Science*, 29 (5), p. 471-483.
- STEPHENS D. W., KREBS J. R., 1986.– *Foraging Theory*, Princeton, Princeton University Press, 247 p.
- STINER M. C., 1994.– *Honor Among Thieves : A Zooarchaeological Study of Neandertal Ecology*, Princeton, Princeton University Press, 447 p.
- STINER M. C., 2001.– Thirty years on the « Broad Spectrum Revolution » and Paleolithic demography, *Proceedings of the National Academy of Sciences*, 98 (13), p. 6993-6996.
- STINER M. C., 2002.– Carnivory, coevolution, and the geographic spread of the genus *Homo*, *Journal of Archaeological Research*, 10 (1), p. 1-63.
- STINER M. C., 2003.– Zooarchaeological evidence for resource intensification in Algarve, southern Portugal, *Promontoria*, 1 (1), p. 27-61.
- STINER M. C., n. d.– *The Faunas of Hayonim Cave (Israel) : A 200,000-Year Record of Paleolithic Diet, Demography & Society*, Cambridge, Peabody Museum Press, Harvard University (in press, 262 manuscript p.).
- STINER M. C., MUNRO N. D., SUROVELL T. A., 2000.– The tortoise and the hare : Small game use, the Broad Spectrum Revolution, and Paleolithic demography, *Current Anthropology*, 41 (1), p. 39-73.
- SVOBODA J., 1990.– Moravia during the Upper Pleniglacial, in : C. Gamble, O. Soffer (eds), *The World at 18,000 BP, vol. 2 : Low Latitudes*, New York, Plenum, p. 193-203.
- TCHERNOV E., 1994.– New comments on the biostratigraphy of the Middle and Upper Pleistocene of the southern Levant, in : O. Bar-Yosef, R. S. Kra (eds), *Late Quaternary Chronology and Paleoclimates of the Eastern Mediterranean*, Tucson, Radiocarbon, University of Arizona, p. 333-350.
- WENIGER G. C., 1987.– Magdalenian settlement pattern and subsistence in Central Europe : The southwestern and central German cases, in : O. Soffer (ed.), *The Pleistocene Old World : Regional Perspectives*, New York, Plenum, p. 201-215.
- WILBUR H. M., MORIN P. J., 1988.– Life history evolution in turtles, in : C. Gans, R. B. Huey (eds), *Biology of the Reptilia*, vol. 16, *Defense and Life History*, New York, Alan R. Liss, p. 387-439.