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Item Type	Report
Authors	Formicolal, V;Holt, Brigitte M.
Download date	2025-05-17 18:43:59
Link to Item	https://hdl.handle.net/20.500.14394/2220

Resource availability and stature decrease in Upper Palaeolithic Europe

Vincenzo Formicola¹ & Brigitte M. Holt²

1) Department of Biology, University of Pisa, via A. Volta 6, 56126 Pisa, Italy
e-mail: vformicola@biologia.unipi.it

2) Department of Anthropology, University of Massachusetts, Amherst, MA 01003, USA

Summary - The stature of the first anatomically modern Europeans decreases dramatically following the Last Glacial Maximum (LGM), the culminating point, around 20.000 BP, of a period of climatic deterioration that had profound effects on demographic, biological and economic aspects of Upper Palaeolithic populations. Declines in nutritional and life conditions are commonly assumed to play a major role in stature reduction. The aim of this paper is to test this hypothesis using skeletal indicators of biological and functional stress in samples from the early and late phases of Upper Paleolithic (respectively EUP and LUP), and integrating the results with the relevant archeological and paleoecological information. Analysis of biological stress markers indicates that after the LGM only a minor decline occurred in health conditions. This and the absence of marked or frequent growth disruptions suggests that nutritional deficiencies alone do not explain the observed trend. Biomechanical data, however, show an increase in upper limb robusticity, indicating that LUP populations were devoting more effort to subsistence activities. Those results dovetail with archaeological information pointing to increased competition for access to resources by growing populations living in a less productive environment. Based on that, we suggest that a microevolutionary adaptive process, involving reduction in body size to reduce energy requirements and hence nutritional demands, took place in the moderately adverse conditions following the LGM.

Keywords - Stature, Microevolution, Bioarcheology, Upper Paleolithic, Europe.

Introductory remarks

Body size in humans, like in other mammals, is modeled by environmental and life conditions (Eveleth & Tanner, 1990; Ruff, 1994) and provides a useful tool for analysing adaptive processes in modern and past populations. Unfortunately, as one goes back in time, the fossil record becomes increasingly scanty, preventing a study of stature and body size at the population level. However, the number of Upper Palaeolithic skeletal remains and their state of preservation makes such an approach possible. A recent study of stature variation among Upper Palaeolithic samples (Formicola & Giannecchini,

1999) indicates that the Last Glacial Maximum (LGM) (approximately 20.000 BP) represents a watershed in body size of these populations. In particular, samples dating before the LGM differ significantly from their Late Upper Palaeolithic successors (EUP and LUP respectively). In particular, EUP show a high stature (mean = 176.2 cm in males and 162.9 cm in females), markedly exceeding that of LUP (mean = 165.6 cm in males and 153.5 cm in females)(Fig.1).

Population here is meant in a broad sense, i.e. as individuals that lived in Europe during the same cultural period, under the same climatic conditions and had the same lifestyle (Brennan, 1991). Archaeological and biological

evidence (Fruyer, 1981, 1984; Gamble, 1986; Djindjian *et al.*, 1999) suggests that those groups were lineally related. Thus, change in body size probably reflects the effects of selective forces operating through time. Identifying factors involved in this process and evaluating their relative importance are the goals of this paper.

Interpreting the negative trend

The Last Glacial Maximum represents a period of climatic deterioration peaking around 20,000 BP during which mean temperatures dramatically dropped, making distribution of human groups more patchy and restricted to areas of central and southern Europe (Soffer & Gamble, 1990). Environmental changes, new organizational systems and technological innovations following the LGM had important effects on nutritional conditions, lifestyle, gene flow and bio-cultural and climatic adaptations of LUP populations (Gamble, 1986; Holliday, 1997; Churchill *et al.*, 2000; Holt *et al.*, 2000).

Body size and proportions among living populations largely reflect long term climatic adaptations. Populations living in tropical areas tend to have longer limbs and a more elongated physique than those from temperate regions

(Ruff, 1993). Differences in body size and in body proportions result in differences in the surface area/body mass ratio that increases in populations from tropical areas and reduces in those living under cold climatic conditions. EUP groups possess “tropical” body proportions and long lower limbs, indicative of their African origin (Holliday, 1997). Thus, while the tall stature of early anatomically modern Europeans likely reflect ancestry, the climatic deterioration that occurred between 22,000 and 18,000 BP may have caused a shift towards a more cold adapted, less elongated body shape. However, theoretical models (see Ruff’s 1991, cylindrical model) and observations in fossil and modern populations (Ruff, 1993) suggest that body breadth, rather than body height, is the critical factor in changing surface area/body mass ratio. Thus, climate likely played only a minor role in determining the dramatic stature change occurring after the LGM.

Levels of gene flow represent an additional factor to take into account. Archaeological and biomechanical data (Gamble, 1999; Roebroeks *et al.*, 2000; Holt, 2003) indicate that EUP populations were highly mobile and dispersed from Mediterranean Europe to the Russian plains. Similarities in technological, symbolic and stylistic components of their culture suggest that these hunter-gatherers were able to maintain

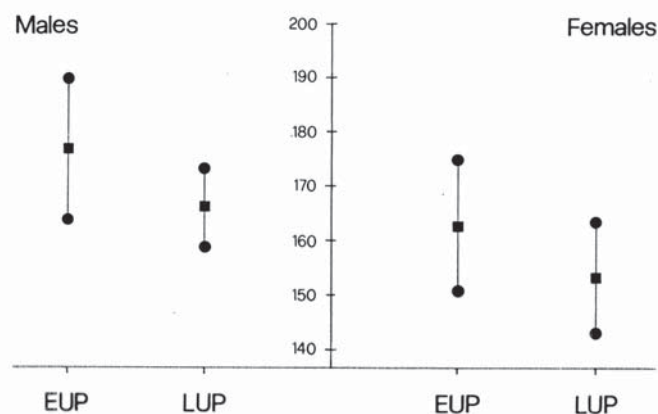


Fig. 1 – Temporal change in stature ($M \pm 2\sigma$) between early Upper Palaeolithic (EUP) and late Upper Palaeolithic (LUP) .

intergroup contacts and biological continuity over vast territories (Gamble, 1999; Mussi *et al.*, 2000). This points to the establishment of expanded mating networks and high level of gene flow among distant populations. The worsening of climatic conditions at the LGM brought an end to those “open systems” (Gamble, 1986), pushing populations towards more protected areas (glacial refugia), breaking intergroups contacts and their cultural homogeneity (Jochim, 1987; Soffer & Gamble, 1990). Territorialism dictated by the climatic constraints of the LGM persisted throughout the LUP, as suggested by increased regional cultural diversification (Rozoy, 1989; Bosinsky, 1990), while the number and broader distribution of the sites point to a significant population increase (Mellars, 1985; Bocquet-Appel & Demars, 2000). This, and increased morphological variability among regions (Fruyer, 1987, 1988), suggest restriction of mating networks (Wobst, 1976; Chapman, 1989) and decreased gene flow. Relationships between gene flow and stature were shown by Little and Malina (1986), and exogamy has been included among the possible factors responsible for the recent positive secular trend (Wolansky, 1974; Malina, 1979). However, socio-economic factors that drove the breakdown of isolates also resulted in significant improvements in life conditions (Susanne, 1985). This renders difficult the evaluation of the relative importance of genetic versus environmental components.

Among environmental factors affecting stature, the importance of nutrition has been repeatedly pointed out (Malina, 1987; Eveleth & Tanner, 1990; Steckel, 1995) and Eaton & Konner (1985) stress that the stature of modern Europeans returned to the level of their Palaeolithic forebears when nutritional conditions returned to high standards. The generally open-steppe EUP environment with large herds of herbivores such as mammoth, bison, horse and rhino provided remarkable opportunities for large mammal-hunter specialists (Guthrie & van Kolfshoten 2000). It is therefore likely that EUP nutritional conditions were particularly good and diet rich in components of basic importance

to the growth process. Dietary information provided by stable isotope analyses supports this point of view (Richards *et al.*, 2001). After the LGM, reduction in grassy areas resulted in the gradual substitution of the gregarious megafauna by small, low ranked preys, leaving a void in the protein supply. At the same time, the reduction in nomadic fauna limited hunting mobility, leading to increased exploitation of all available resources (Clark & Straus, 1986; Montet-White, 1994; Straus, 1995; Stiner *et al.*, 1999; Richards *et al.*, 2005). This and demographic expansion (Bocquet-Appel & Demars, 2000) likely affected the positive relationship that earlier populations enjoyed with the available biomass, increasing competition for resources. Thus, archaeological and paleoecological data suggest a decline in LUP nutritional and life conditions that might represent a crucial factor in the negative trend affecting stature of Upper Palaeolithic populations after the LGM. We examine health and stress indicators in skeletal samples from the two time periods to test this hypothesis.

Theoretical background

Modern bio-archaeological research has developed the concept of “skeleton as a biological archive” (Goodman *et al.*, 1984; Borgognini & Pacciani, 1993), meaning that bones and teeth register events that interfered with their development (biological stress) in an interpretable way. Nutritional deficiencies are a major source of stress because they deprive the organism from elements that are important for its regular development and metabolism. Those deficiencies affect health conditions and render an individual more susceptible to diseases (Goodman *et al.*, 1984; Saunders & Hoppa, 1993; Larsen, 1997 for more information). Thus, paleopathological data and frequency and severity of biological stress shown by EUP and LUP groups can provide insights on their nutritional status.

Activity, meant as amount of work required for food procurement, is a further source of stress (mechanical stress) that needs to be evaluated for

inferences on life conditions. Mechanical stress results in degenerative changes at articular level and affects robusticity of long bones. Robusticity was analysed using a biomechanical approach, i.e. analysing cross-sectional properties of the main long bones (Churchill *et al.*, 2000; Holt *et al.*, 2000) This approach takes into account both amount and distribution of cortical bone and thus reflects robusticity and activity levels better than traditional methods based on external measurements only (Ruff, 1989; Larsen, 1997).

Analysis of biological and mechanical stress

The issue of health and life conditions of the last European hunter gatherers has been addressed in various papers (Meiklejohn *et al.*, 1984; Brennan, 1991; Trinkaus *et al.*, 2005). The pattern emerging from those studies suggests that those populations enjoyed good health conditions and that severe nutritional and health problems arose only later in time with intensification of agriculture. Preliminary analysis of data drawn from our own observations, from information provided by colleagues and from the literature

confirms those results, but also suggest differences through time (Holt & Formicola, n.d.).

EUP – The sample shows a well developed skeletal structure, fairly robust and scarcely affected by pathological processes. Those results are in agreement with archaeological information indicating a rich environment populated by small groups of well equipped hunter-gatherers (Fig. 2). In particular, frequency of Harris lines is low and enamel hypoplasias, if present, are generally very light and not recurrent. Oral health conditions are excellent considering the rarity of caries and of abscesses and the slight degree of periodontal affections. Evidence of infectious diseases are very rare and include a diffuse periostitis of uncertain origin affecting Brno 2 (Oliva, 2000) and the possible signs of actinomycosis shown by Cro-Magnon 1 (Dastugue, 1967). The latter diagnosis is, however, contested by Thillaud (1981-1982) who attributes the bone changes exhibited by this specimen to a systemic disorder (histiocytosis X). EUP pathological conditions also include a rare congenital disease (chondrodysplasia calcificans punctata) (Formicola *et al.*, 2001) and a case of localised ossification defects (congenital bowing of long bones), possibly resulting from a diabetic



Fig. 2 – Arene Candide 1 (Il Principe) is an example of the high stature and good health and nutritional conditions enjoyed by EUP people.

maternal condition (Formicola & Buzhilova, 2004). The identification of those anomalies provides important information on the history of congenital disorders and on paleoethnological aspects but is irrelevant for inferences on levels of environmental stress that are the main issue here.

LUP – Samples from this time period show an increase in frequency but not in severity of enamel hypoplasia and of Harris lines. This indicates that disruptions to the growth process, while more frequent, were still of minor intensity. Cases of periostitis are infrequent and mostly localised to the main long bone diaphyses, as a likely effect of minor traumatic injuries. In comparison to EUP, caries become less sporadic, indicating a possible shift in dietary habits with an increase in consumption of vegetal food rich in carbohydrates. Robusticity of long bones, expressed by external measurements, is high and is paralleled by cases of degenerative joint disease affecting the humerus, clearly resulting from intense work activity. Biomechanical indicators support this point showing an increase in male upper limb robusticity of LUP compared to their EUP forebears. Upper limb lateralization, however, does not change (Fig 3). The marked asymmetry in humeral torsional strength in both

UP samples probably reflects the use of throwing-based hunting weapons. As with EUP, the LUP sample includes cases of inherited diseases such as acromesomelic dwarfism (Frayer *et al.*, 1987) and of X-linked hypophosphatemic rickets (Formicola, 1995) and a possible hydrocephalic child (Vallois, 1971; but see Tillier *et al.*, 2001). As previously pointed out, those abnormalities provide mostly biological information concerning the history of the diseases.

Discussion and conclusions

Evidence provided by health indicators suggests that, after the LGM, only a minor decline occurred in life conditions enjoyed by EUP. In particular, LUP samples do not show marked or frequent growth disruptions that could indicate significant impoverishment of the diet. Thus, severe nutritional deficiencies are not a likely explanation for the observed negative trend. These results, however, do not invalidate the “nutritional” hypothesis but allow, instead, to define it more precisely and coherently with data from biomechanical analyses and with archaeological and palaeoenvironmental evidence.

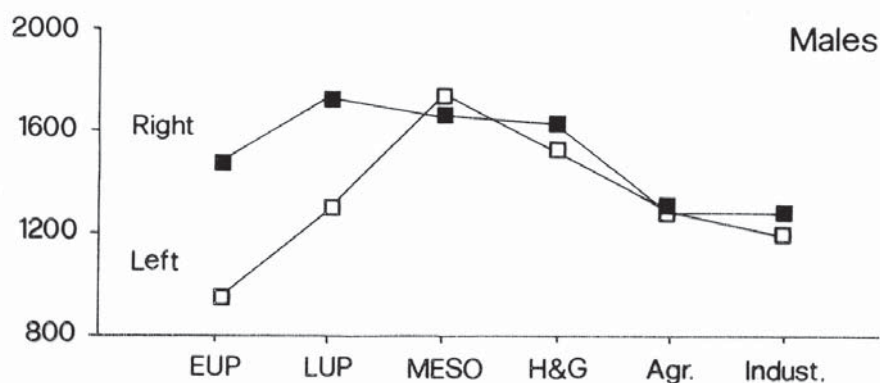


Fig. 3 – Size standardized humeral strength ($J = \text{polar moment of inertia}$) in early Upper Palaeolithic (EUP, $n = 9$), late Upper Palaeolithic (LUP, $n = 10$) and Mesolithic (MESO, $n = 8$), and in samples of recent foragers (H&G, $n = 30$), agriculturalists (Agr., $n = 27$) and industrialized (Indust., $n = 31$) groups. Due to small sample sizes, only males are represented.

Faunal and artifactual records following the LGM reflect an economic shift characterised by expansion of diet breadth, accelerated development of foraging technology and an increase reliance on labor intensive, low ranked resources (Clark & Straus, 1986; Stiner *et al.*, 1999). It seems very likely that the increase in robusticity after the LGM shown by cross sectional properties of upper limb bones results from changes in foraging behaviour and that LUP people were devoting more effort to subsistence activities (Churchill *et al.*, 2000; Holt *et al.*, 2000).

Thus, after the LGM, the gradual increase in population density (Bocquet-Appel & Demars, 2000) along with declining productivity of the environment further increased competition for resources and for maintaining adequate caloric intake. In that scenario, the maintenance of large body size would have resulted in high energetic costs for LUP people. This suggests that in those populations struggling to overcome increased environmental stress, selection may have operated towards a reduction in body size to reduce metabolic needs and hence nutritional demands (Frayer, 1981). The hypothesis of an adaptive significance of stunted growth, first suggested by Stini (1971, 1975) and Frisancho and co-workers (1973), has been re-emphasised by Seckler's (1982) "small but healthy" paradigm. According to this view, small body size represents a physiological adjustment (Scrimshaw & Joung, 1989) to moderately adverse conditions by reducing the body's energetic requirements. Based on that, the microevolutionary model for the negative trend affecting stature of Upper Palaeolithic populations is taken here as an adaptive process activated after the LGM in a context characterised by increased competition for resources by human groups coping with a changing, less productive environment.

Acknowledgements

Grant sponsors: MIUR (Cofn. 01) and University of Pisa (V.F.); L.S.B. Leakey Foundation and NSF (SBR 9530828) (B.M.H.). We are grateful to E. Bernardini and O. Levati for the permission to publish figure 2.

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Associate Editor, Rita Vargiu