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Evolutionary biology and health of hunter–gatherer populations

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Introduction

Hunter–gatherers display a wide variety of morphological and physiological characteristics, and should provide a good model for the evolution of human biological characters across a considerable range of environments in presumably isolated situations. This chapter examines both ecological and genetic aspects of the evolution of present-day hunter–gatherers and also comments on what the future will hold for those who now face or soon will face cultural and technological transition through contact with dominant groups. Hunter–gatherers are not recognisable by their biological characteristics – they are defined by their way of life, namely their relation to nature, which is a cultural, not a biological, definition (see Panter-Brick, Layton and Rowley-Conwy, this volume). However their close interaction with the physical and animal environment, their small and mobile groups, their dietary and work patterns, did create ecological and evolutionary characteristics which shaped biological outcomes. Existing variation in biological traits will be examined as evolutionary responses to climate, diet and disease.

Some partially unanswered questions related to evolution and transition can be listed. Concerning morphology, is small stature an adaptation to hunting and gathering? What is the genetic basis for anatomical characteristics and what room is there for modulation by nutritional and infectious variables? Is there a secular trend modifying these characters? Concerning physiology, is the diet of foragers (poor in fat, rich in protein and fibre) an evolutionary optimum? What was gained, or lost, with the adoption of agriculture and herding? Are there lessons, of health, well-being and wisdom, to be derived from knowledge of these societies? Above all, what is the future of marginal groups, who are not well equipped to survive an unprecedented social and ecological upheaval?

Adaptations to ecological constraints

Climate and adaptation

Climate modulates biodiversity and food availability. Thus, the variety of edible plants is wider in the rainforest than in savannah, and wider in savannah than in the cold desert. Most hunters now live in tropical areas but some who live in arctic conditions, like the Inuit and other populations from Siberia to Greenland, and Alacaluf and others in Tierra del Fuego, have no other choice than to rely mainly upon game and fish, in a near-absence of edible plants and carbohydrates. Despite their dark skin and low sunlight exposure, these populations avoid rickets by the intake of fresh fish liver. There are thermoregulatory adaptations to cold such as vascular shunts, which allow Inuit to keep their hands in cold water for longer than other peoples; the Australian Aborigines and the Alacaluf, who are able to sleep naked at a temperature of 0 °C, also display physiological adaptations to cold (Bittel 1992).

A correlation between climate and anatomy is difficult to assess. Pygmies who live in a very moist climate have as wide noses as do Australians and San[1], who live in dry environments. Newman

[1] San, who are hunter–gatherers, and Khoikhoi, who are herders, are usually united in a conglomerate of culturally different but linguistically related groups, called Khoisan or Koesaan. For political reasons, the picture of hunter–gatherers has been constantly manipulated, for worse, during colonial times, or for the better, since the emergence of ecological lobbying by ideologically inspired groups (churches, activists, etc.). Some ethnonyms widely used in the past like 'Bushman' (San), 'Pygmies', 'Eskimo', are offensive and it is certainly not by chance that most of these deprecatory terms have been used, by Europeans and also by sedentary neighbours, to qualify 'primitiveness' of hunters. The term 'Pygmies' confounds under the same label different populations (for instance the Baka, BaBongo, BaKola or Bagyeli, BaAka, BaSua, Efe, Asua, BaMbuti, BaBinga, Twa or BaTwa, Bedzan, and many other so-called Pygmies) with different histories and cultures. The term 'Pygmoid' is sometimes used for forager peoples living like the Pygmies, but whose stature is higher than the conventional threshold of 150 cm. Its use, as the use of terms like 'Negritos' or 'Aborigines', is only justified by convenience.

(1953) and Stinson (1990) reported some correlations between body size/shape and climatic variables in America, but conclusions are difficult to draw. In cold environments the stature of hunters is sometimes tall (males 176 ± 2 cm), as in the Aonikenk of Patagonia (Hernandez *et al.* 1998) and many North American hunters, and sometimes short (males 158 ± 2 cm) as in most Inuit or related arctic peoples (So 1980). Some authors (Holmes 1993) think that a reduction of body size is an adaptation to adverse ecological conditions, while for others (Spurr 1987), it is a pathologic impairment of development potential.

Small size is observed in all African hunter–gatherer populations (Twa Pygmies, San, Hadza) and in some other tropical groups like Andaman Islanders or Negritos (see Table 9.5 in Jenike, this volume). If nutritional deficiencies are excluded, several explanatory hypotheses have been advanced, all of which are disputed:

Thermoregulation needs (Ruff 1994). A smaller body in moist and warm areas like tropical rainforests is a well-known zoological law (Bergmann's rule, stated in 1847), but is also observed among Papua highlanders living in a fairly cold environment (Diamond 1991). By contrast, Australians living in a mainly dry environment have a very lean body with the most elongated lower limbs found in humankind (Norgan 1994), a morphology which fits with physiological adaptation to hot and dry savannah (Ruff 1994, Katzmarzyk and Leonard 1998). Conversely, San hunters are very short in a comparable climate. Comparing Bantu and Twa Pygmoids, Austin and Ghesquiere (1976) showed that larger bodied populations had a better heat tolerance, when exposed to a walk under the sun or to the immersion of an arm and a leg in warm water, than smaller-bodied populations. Thus no clear results support the thermoregulatory advantage of a smaller body.

Easier mobility, at least in rainforest (Hiernaux 1974). Holliday and Falsetti (1995), in a sample of 19 recent hunter–gatherer groups, failed to demonstrate any relation between relative lower-limb length and spatial mobility. Diamond (1991) notes that the short-statured San of the Kalahari live in an open landscape, where the argument of mobility according to density of trees is not relevant. So, unless the San first adapted to a forest ecosystem and kept a related morphology despite a drastic change in their environment, the hypothesis is not valid.

Economy of energetic requirements. A smaller body permits survival with less food: basal metabolism is 5.0 MJ (1200 kcal) for a Pygmy of 37 kg and 142 cm, as compared to 6.9 MJoules (1647 kcal) for a US citizen of 65 kg and 172 cm (Mann *et al.* 1962). In a context of limited resources, this reduction may allow more individuals to survive.

An optimal adequacy between body shape and weapon (Brues 1959), or a more efficient behaviour. Lee (1979) showed a better yield of hunting among short than tall !Kung men, a difference very apparent after the age of 35. In the same group, Winkler and Kirchengast (1994) found that slender men had a lower social position, fewer children with a higher offspring mortality and a higher ratio of daughters, than robust men. If shorter men can feed more children, a spread of genes conferring short stature can be expected.

Diet and adaptation

Many traditional societies which use a combination of swidden horticulture, hunting, fishing and foraging cannot be easily classified as hunters or agriculturists. For example, the Ok people of Papua New Guinea rely on game for 64% to 75% of their animal protein supply (Hyndman *et al.* 1989). Conversely, groups considered as 'pristine' hunter–gatherers, like Pygmies or San, who had long decided to live without agriculture – despite a close symbiosis, common language and long proximity to agriculturists – have now turned to some food production. Cassava, a crop introduced by colonisation from America, allows absence from the fields for several months, which fits in well with the seasonal movements of semi-nomadic 'Pygmy' communities; in drier environments, maize,

another American crop, has been grown by the Hadza hunters of Tanzania since the mid-1960s (Bennett *et al.* 1970: 858). Symmetrically, the Hukwe ('black Boschimans') are a group of former herders said to have taken up hunting and gathering (Nurse *et al.* 1985: 67, see Layton this volume.).

The diet of hunter–gatherers used to be much more varied, and richer in animal protein, than the diet available to farmers. However, the small proportion of foods actually used from the edible wild species available argues for a recent change of the diet in favour of the security and ease of cultivated products, away from the uncertainty and difficulties involved in obtaining wild products. The dependency of hunters-gatherers *vis-à-vis* cultivated starchy food (cassava, plantain banana, or domesticated cereals) is a political issue, discussed by Bahuchet *et al.* (1991) in the case of Pygmies. Due to demographic increase, Pygmies will either be dominated by Bantu societies, through food dependency, or will have to abandon their way of life and become farmers. Cavalli-Sforza (1986: 424) noted that the Aka Pygmies of Central African Republic in the 1970s obtained 50% (in fresh weight) of their food from working 20% of their time in Bantu plantations, a good strategy. Cultivated food sources contribute around 20% of the diet among the Bakola of Cameroon (Koppert *et al.* 1993) and 65% among the Mbuti Efe of the Ituri forest (Bailey and Peacock 1988).

Nutritional issues are extensively developed by Jenike (this volume), and only some aspects relevant to human biology will be discussed here. Acute protein-energy malnutrition and anaemias have been reported in many foraging groups (Kent and Dunn 1996), mainly among sedentarised populations who are easier to monitor; reliable statistics on mobile bands are rare. It is also difficult to compare growth status in populations where children's age cannot be determined accurately. In Bakola Pygmies from Cameroon, the current nutritional status of men is reasonably good, but less satisfactory among women, who are very physically active, and have an adiposity of only 19% in contrast to 25% among Bantu women. This makes the Bakola women's health a little precarious, especially during pregnancy and breastfeeding (Froment *et al.* 1993). In the Ituri forest (Dietz *et al.* 1989), Pygmies' skinfolds, fat mass and lean mass are also significantly smaller, in both sexes, relative to Bantu neighbours. However, muscular development and fitness, determined by physical tests, are good in both men (Ghesquiere and Karvonen 1981, Ferretti *et al.* 1993) and women (Pagezy 1978).

Most hunters, in either cold or tropical areas, have a deficiency of intestinal lactase, which makes them unable to digest milk; the persistence of the enzyme in adults is found among herders and their modern descendants. The domestication of animals and dairying practices appeared only a few millennia ago, and favoured a genetic ability to use milk as an important source of energy and nutrients (Simoons 1978).

Taste thresholds, probably under genetic control, vary according to populations, and food environment may have played a significant selective role in that differentiation (Hladik and Simmen 1996). In arctic environments, Inuit have a remarkable sensitivity to salt, which is traditionally considered to be dangerous. Living on a very rich protein diet, they have to drink large amounts of water to prevent urea excess, and the use of small melted icebergs as drinking water could dangerously increase their salt intake. All rainforest populations, including Bakola and Twa Pygmoids, have a low sensitivity for salt and for glucose, which may be related to an abundance of sweet fruits in forests, as compared to savannahs. Despite a close resemblance in diet, prevalence of endemic goitre in Efe foragers is far less than observed among their Lese farmer neighbours (9% versus 43%), even for Efe people living in Lese villages; a genetic mechanism has been suspected, as an intermediate frequency of 29% has been reported in a small sample of 14 subjects of mixed Lese–Efe descent (Dormitzer *et al.* 1989).

The very developed adipose buttocks (steatopygia) displayed in San women, but also in Khoi herders, could be a genetic adaptation to food shortage, though there is no convincing demonstration of this hypothesis. If nutritional conditions were poor, a secular trend on stature would then be predicted with better access to food or Westernisation of diet. This trend has not been observed among aboriginal South Australians (Pretty *et al.* 1998) nor in Bakola Pygmies (Pasquet *et al.* 1995), but changes of 1 cm per decade have been noticed in Canadian Inuit (Rode and Shephard 1994).

Genetic issues

Hunter–gatherers genetics and plasticity

Some anatomical evolution has occurred, towards gracilisation (a structural reduction of the skeleton or of skull robustness), since modern human appeared: Henneberg (1988) notes that there is a general decrease of skull size and robustness since the Mesolithic. Have changes in food consistency between the Palaeolithic and the Neolithic induced this lighter skull morphology? In fact San, and even Pygmies, have a light, paedomorphic skull, while Australians, Inuit and Fuegians have a very robust one, with no dietary correlations. San gracile morphology is not explained by sex hormones levels, though there is a deficit in testosterone when compared to their Bantu neighbours and Efe Pygmies (Christiansen 1991); no elevation of estrogen hormones could be found in males, when compared to European and South African Bantu (Van Der Walt *et al.* 1978). Bribiescas (1996) proposed that a low testosterone level, also observed among Aché hunters of Paraguay, may be advantageous under conditions of chronic energy shortage.

Present-day hunter–gatherers reproduce some of the genetic characteristics of human ancestors such as endogamy (spouse choice within the group), with consequent genetic diversity lowered within groups and enhanced between groups. Australian Aborigines arrived some 40 000 to 60 000 years ago, probably through several waves of migration. Since then they have remained virtually isolated, scattered in a very wide territory where genetic clines can be observed (Birdsell 1993). They therefore provide a good model for the study of genetic evolution of small communities since the Palaeolithic. A difficulty in the study of the genetic structure of hunter–gatherers groups is related to their usually very small size, which causes strong genetic drift with important and recurrent founder effects (i.e. the small number of founders of a new group can lead to a large drift). There is debate regarding the smallest size of a group required for its survival, and bottlenecks experienced by humankind in the past are closely related to the group size of reproductive foragers (Hassan 1975). Cavalli-Sforza and Bodmer

(1971: 431), discussing the demographic data relevant to the analysis of such drift, mention densities of 0.2 humans per km^2 for the Pygmies, 0.6 per km^2 for Aleuts, 0.03 per km^2 for Australians, 0.04 per km^2 for Caribou Inuit and 0.06 h per km^2 for Greenland Inuit.

The wide range of environmental adaptations, dating from earliest anatomically modern humans, has generated wide genetic diversity. No common genetic characters are to be expected for this large group of foraging populations occupying the most extreme terrestrial ecosystems. Far more realistic is the study of genetic affinities between present-day hunter–gatherers and their sedentary neighbours. Gene flow between the two communities is subjected to strong social barriers related to the prejudices that most nomadic societies suffer from villagers. Such prejudices favour endogamy and genetic drift. In rainforest Bantu villages, Pygmies are often considered as half-apes, both feared and despised (Kazadi 1981, Vansina 1990: 57). In the Democratic Republic of Congo, Oto villagers despise the Twa but describe in a myth a common kinship which justifies a strong prohibition of intermarriage. The genetic exchanges between San and their Kavango (Bantu) neighbours are also very limited (Nurse *et al.* 1985). Thus selective pressures are associated with both environmental and social constraints.

The short stature of African Pygmies, evident early in life, has been attributed to a genetic mutation on the receptor to growth hormone. Insulin-like growth factor I (IGF-I), present at low concentrations in the blood level of African Pygmies, is normal in a short statured population of Papua New Guinea (adult male stature 151 ± 3 cm, weight 50 ± 3 kg), while the level of growth hormone transport protein is diminished (Baumann *et al.* 1991). Baka Pygmies of Cameroon do not differ from Europeans or Bantus in average serum IGF-I concentrations, nor in the relationship between serum IGF-I and its major binding protein (IGFBP-3), which Dulloo *et al.* (1996) attributed the low levels observed in some individuals to infections rather than to any inherited defect in the growth-hormone–IGF-I axis. However, Cortez *et al.* (1996) showed that cells from Mbuti cultivated *in vitro* have a genuine and unique resistance to IGF-I. The hormonal status of Pygmoid groups of intermediate stature, and the genetic mechanism involved (its penetrance and expressivity), are still unclear.

With a short stature (155 ± 6 cm), an elongated skull and marked prognathism, wide flat nose, dark skin and woolly hair, some Kainantu horticulturists groups of eastern Papua New Guinea (Littlewood 1972) look very similar to African Pygmies (more than Philippine Negrito hunters do). One can wonder if some adaptive convergence, arising from an uneven chain of mutations, is the only explanation for such a resemblance. Blood groups are too different to suggest any common recent origin between African and Asiatic short-statured peoples, but one cannot exclude the resurgence of a very old tropical morphotype interpreted, in the absence of fossil evidence, as a plesiomorphic heritage, i.e. the conservation of an ancestral pattern.

Differentiation and affinities

The quest for the primordial modern humans is a major agenda in palaeontology. According to an hypothetical 'African Eve', Khoisan and some Pygmy groups would have diverged from the root of anatomically modern humans' root earlier than other Africans (Maddison *et al.* 1992, Ruvolo *et al.* 1993) and would even represent the very stem of humankind. Genetic comparisons with other primates, such as the haplotype XIII of the Y-chromosome (Lucotte 1990), lead to the very suspect conclusion that some human groups could be a little more 'ape-like' and 'primitive' than others. In fact, Pygmies display genetic configurations which are closer to West Africans for Gm (specific antigens), to Bantus for HLA (human leukocyte antigens) and to Nilotes for Rhesus blood sub-groups (Excoffier *et al.* 1987) as if they belonged to an earlier, undifferentiated African group. They are African, and even 'hyper-Africans' for some traits; they also share (especially Mbuti, who are the most peculiar, with respect to both morphology and genetics) some traits with the San (erythrocyte acid phosphatase and phosphoglucomutase in particular). On this basis, Cavalli-Sforza (1986: 409) postulated a 'proto-African' stock (including San) diverging from non-

Pygmies at around 15 000 BP. Hiernaux (1974) thought that populations ancestral to present Pygmies and Pygmoids might have significantly differed in the past and converged later, due to adaptation to a similar environment and to gene flow. Genetic relations between San and Tanzanian (Sandawe and Hadza) click-speaking hunters are not established.

In many cases, forager groups have been geographically isolated (e.g. Inuit, Australians), receiving no gene flow. Elsewhere, cultural contacts existed, but there is no close parallel between language shift and gene admixture. Measuring hybridisation between hunting and farming populations presupposes the preexistence of two clear-cut separate gene pools; this assumption is probably untrue, as in many cases the groups under consideration share a common descent. From the few genetic surveys available (Cavalli-Sforza 1986: 404–17), it appears that, as in most small foraging bands, Pygmies display important genetic inter-group heterogeneity; for instance Aka (Babinga) from Central African Republic are much closer to their farmer neighbours than to Ituri Mbuti, which are classically considered 'true' Pygmies. They also have a few genetic peculiarities concerning some rare markers, which correspond to mutations which occurred, at very low frequencies, after their differentiation from other populations. One of the aims of the Human Genome Project (Cavalli-Sforza *et al.* 1991) is to explore the specificities of such small groups, before they disappear or become admixed.

In order to test the physical resemblances between different groups of hunter–gatherers, from North America, the Arctic, Asia, Australia and Africa, six of their cephalic measurements were compared to those of African farmers, in a multivariate analysis (Figure 9.1). The populations differ mainly by their nose breadth (horizontal axis) – narrow in North America, intermediate in Asian Negritos, large in Africa, very large in Australia – and also by head shape (vertical axis) – rounder head for Pygmies, and a broader face for native Americans and Australians. These differences in head and face morphology are observed on a world-wide basis within the human species (Froment 1992), and probably have a strong genetic basis. Within Africa, the clusters of 'true' Pygmies and Khoisan do

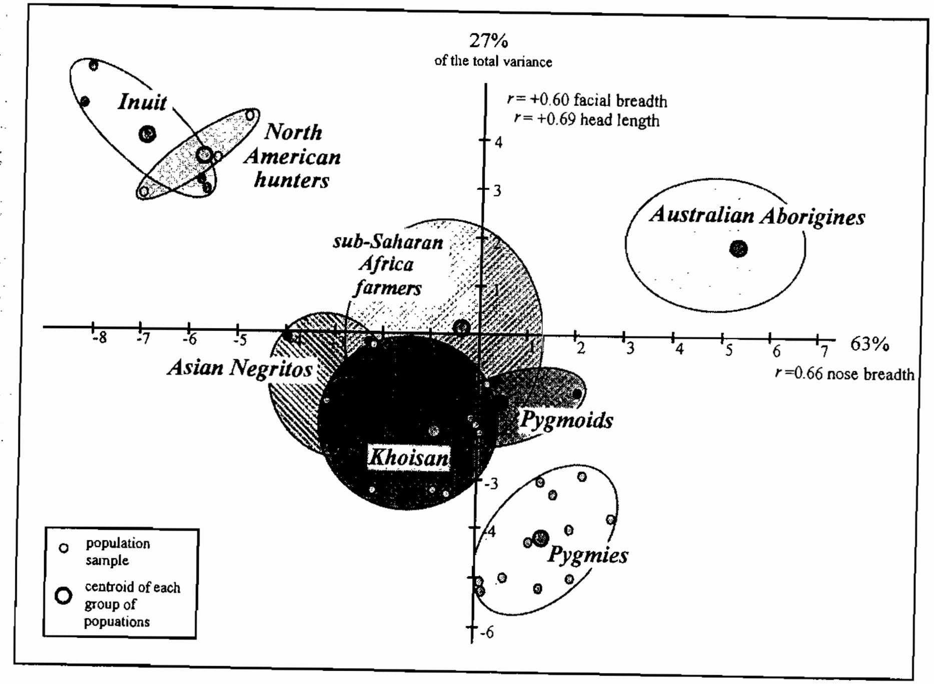

Figure 9.1. Multivariate discriminant analysis of head morphology for hunter-gatherers from North America, the Arctic, Asia (Negritos), Australia and Africa (San, Pygmies and Pygmoids), compared to the variation for farmers of sub-Saharan Africa. The six variables used are head length, head breadth, total face height, facial breadth (bizygomatic), nose breadth and nose height, for 215 populations (adult males only; the same pattern is obtained for females for a smaller sample). The two axes express 90% of the total variance; 83% of the populations are correctly classified in their group of origin by the analysis.

not overlap, while Khoisan and Pygmoids are closer to the observed biological variation of sub-Saharan farmer populations than are Pygmies. This could be attributed to a genetic heterogeneity between Pygmies and Pygmoids, possibly due, as Hiernaux (1974) proposed, to different histories of adaptation to the rainforest.

Medical constraints

Medical surveys are difficult to conduct in remote groups, as people are often reluctant to accept investigations, especially the sampling of urine, stools and blood. X-rays or refined biochemical investigations are technically complicated, and autopsy records are virtually unknown. With rapid acculturation, it will soon be too late to have a precise idea of the health of genuine foragers. Hence, the interesting question of knowing whether past populations had a better life than nowadays could remain partially unanswered: Webb (1995) was unable to conclude whether Australians had fewer diseases in pre-colonial times despite studying extensive skeletal material. The biology of living groups may not reflect the health status of past populations, and palaeopathological data must be handled with caution, because of many biases; for instance, one may hypothesise that the increase of visible diseases could be balanced by a decrease of diseases which do not leave lesions on bones. However, with methods in palaeopathology still limited to anatomical examinations, future improvements in DNA amplification may reveal evidence of microbial past infections.

Epidemiological transitions

Barrett *et al.* (1998) distinguished three major 'epidemiological transitions' with neolithisation, industrialisation and disease re-emergence. Transition to agriculture – associated with food crises, increase of workload, contact with cattle and bush clearing favouring the extension of transmissible diseases like malaria – was accompanied with an apparent deterioration of health and nutri-

tional status (Larsen 1995), but also with extraordinary biological success exemplified by a demographic explosion.

The traditional way of life of foraging bands modulates exposure to diseases as follows. A very low density (less than one human per km^2) is under the critical threshold necessary for the transmission of some acute and destructive infections like smallpox, influenza, poliomyelitis or measles (Black 1975), a set of epidemics which probably did not affect early human evolution. Low density is also protective, by host 'dilution' in the environment, from vector-borne parasites (*Plasmodium* of malaria, *Onchocerca* of river blindness, *Trypanosoma* of sleeping sickness in Africa and of Chagas' disease in South America). Limited contacts with other nomadic groups, and remote situations, keep people away from sedentary habitats where the usual epidemics, including sexually transmissible diseases, circulate. Also, nomadic life prevents the accumulation of refuse and faecal pollution around the habitat. Fungal dermatoses, ectoparasites like lice and scabies and cutaneous fly larvae are dependent on limited hygiene and washing facilities. People in hot climates were less exposed when nearly naked, before missionaries urged them to wear clothes, which are often very dirty in places where water or soap are rare.

As well as such advantages, foraging societies experience specific epidemiological risks. A closer contact with wild animals exposes them to rare or new viruses (including emerging HIVs, HTLVs and filoviruses), and to more violent deaths from snake bites, hunting accidents or others hazards (not eliminated by technological progress, as in the case of snow motorbike accidents among Inuit). The overall result is, at least nowadays, a shorter life expectancy compared to other types of societies (see Pennington, this volume), usually in the context of great economic poverty. Even in countries where the standard of life is better than in Third World tropical areas, differences in life span are very marked; for instance, national Canadian statistics give a life expectancy of 59 years and 63 years for male and female Inuit versus 70.3 and 77.8, respectively, in the rest of the population.

The ecology of infectious diseases

Infections have been a major cause of mortality in the past. This strong pressure, however, did not select many genetic adaptations to viruses or bacteria, and these pathogens are still very harmful in poorly medicalised societies. Despite the variety of ailments affecting different hunter–gatherer populations in such diverse environments, some problems are common to many groups (Polunin 1979).

Epidemiological studies show that while the forest diet is rich and varied, people have a low life expectancy; the hot and humid environment is favourable to the transmission of numerous pathogens, notably infectious diarrhoeas and intestinal parasites (Froment *et al.* 1993). Hence malnutrition is no less frequent there than in the savannah where food availability is more precarious but the environment healthier (Nurse and Jenkins 1977). Dunn (1977) developed an opposition between complex (tropical rainforest) and simple (tundra, desert bush, thorn woodland) ecosystems; the main difference is climatic and modulates biodiversity. Consequently, the number of human parasitic diseases can range from 1 (central Australian desert) or 3 (San of Africa) to 20 (African Pygmies) or 22 (Semang of Malaya). In the wooded savannah of Mato Grosso, Brazil, Neel *et al.* (1968) conducted extensive biological studies among the Xavante Indians, and found them to have low rates of malaria, a disease of African origin, and virtually no sign of treponemal infections, but a high exposure to *Toxoplasma* and to many viruses (poliomyelitis, measles, arboviruses), indicating a wide variety of pathogenic contacts. Many foraging peoples, as do the Xavante, look very healthy but they experience very high childhood mortality.

Table 9.1 shows some key health indicators among Cameroon Pygmoids compared to their agriculturist neighbours, in two different ecosystems, in order to examine differences between foraging and farming ways of life. Haemoglobin levels indicate anaemia, gamma-globulin levels reflect antigenic contacts, malaria and blood filariae are linked to exposure to biting insects, and intestinal worms are indicators of faecal contamination. The Bedzan Pygmoids in the forest–savannah contact area are less healthy than the forest Bakola

Pygmoids, and less so than Tikar (Bantoid) farmers. Bakola score better than Mvae (Bantu) farmers for malaria and ascaris, but have higher immunoglobulin levels indicating cumulated infections, related to a lifestyle close to nature. The very significant difference between Pygmoids and farmers, especially marked in children, is confirmed by Dulloo *et al.* (1996), Constans (cited by Heymer 1992: 187) and Pagezy (personal communication). High exposure to infections is also noticed in drier areas, like the Kalahari (Brontë-Stewart *et al.* 1960), where !Kung had higher rates of gamma-globulins (27.4 g/l) than Okavango Bantus (23.4 g/l), and Cape Town Bantus (17.2 g/l). However, no such high levels are seen among Hadza (Bennett *et al.* 1970); it is interesting that, as noted by Pennington (this volume), survival in Hadza is better than in others foragers, probably because of a safer environment.

Common viruses and bacteria

The presence of viral infections, like smallpox, influenza, HIV or measles, which represent an enormous burden for humankind, is closely related to population size and density. Diarrhoeal diseases, the highest cause of childhood morbidity and mortality in developing countries, also show a relationship with the mode of settlement; in an Australian Aboriginal community, with an average of less than one episode per child per year, diarrhoea was less frequent in families living the traditional way than among those living in houses (Ratnaike and Ratnaike 1989). Hepatites follow the same rule and are common in any society where hygiene is deficient and promiscuity frequent, as in foraging bands; chronic infection by hepatitis B and hepatitis C leads to high incidence of liver cancer, long noticed among native Alaskans (Alberts *et al.* 1991) and in the tropics. HIV is rare among hunters-gatherers, because they have few sexual contacts with outside populations. Other retroviruses like HTLV-I (Yanagihara *et al.* 1995) and HTLV-II (Black 1997), transmitted from generation to generation through breast-feeding, and found at endemic level in Pygmies, hunters from Amazonia, Ne-

Table 9.1. Comparisons between semi-sedentarised Pygmoid foragers and neighbouring farmers in two ecological areas of Cameroon

Health indicators[a]	Rainforest (2°30' N, 10° E)				Forest–savannah transition (5°30' N, 11°30' E)				Comparisons[b]		
	A. Kola Pygmoids foragers		B. Mvae Bantu farmers		C. Bedzan Pygmoids foragers		D. Tikar Bantoid farmers		A vs. B	C vs. D	A vs. C
Haematology											
Haemoglobin g/100 ml	76	11.8 ± 1.8	173	11.4 ± 1.6	174	10.7 ± 1.5	409	10.9 ± 1.8	ns	ns	**
Gamma-globulins g/l	76	33.7 ± 9.2	173	24.2 ± 11.0	174	—	409	—	**	—	—
Blood parasites											
Malaria	84	2%	193	8%	153	45%	359	39%	*	ns	**
Filariae	84	8%	193	13%	153	7%	359	16%	ns	*	ns
Stool parasites											
Ascaris	68	51%	213	69%	108	90%	227	63%	*	**	**
Trichuris	68	85%	213	89%	108	83%	227	68%	ns	**	ns

[a] Results (n, mean ± standard deviation, or frequency) are for adults and children, male and female, pooled.
[b] The statistical tests have been paired by column: Kola vs. Mvae (A vs. B), Bedzan vs. Tikar (C vs. D) and the two pygmoid groups (A vs. C). ns: not significant, *: significant, **: highly significant.
Source: Surveys by Froment, Cameroon 1984–94.

gritos and Australian Aborigines, prove to be potential markers of past world-wide human migrations.

Yaws, the endemic (not venereal) form of syphilis, transmitted from person to person or by flies, can be used as a marker of poverty. In Africa, its incidence is more common among Pygmies than villagers: 55% among Bakola (and even 72 to 85% among East Cameroon and Ituri Pygmies (Cavalli-Sforza 1986: 160) versus 37% among Bantus in south-atlantic Cameroon (Froment *et al.* 1993). This difference has two main causes: lower corporeal hygiene, and the fact that Pygmies had more limited access to the campaigns of penicillin injections which attempted to eradicate yaws in central Africa in the 1960s. In the savannah where yaws is replaced by a less visible infection called bejel, only 6% of Hadza had a positive treponema serology (Bennett *et al.* 1973).

Lung diseases such as bronchitis are widespread in either cold or tropical climates, because hearth fires generate heavy pollution in small huts. Tuberculosis is now spreading among foragers, but most of cases observed would have come from their contacts with settled populations. Probably due to the severity of climate, otitis media, which impairs hearing, is remarkably frequent among Inuit (Reed *et al.* 1967). Eye diseases, which follow accidents or infections like trachoma, and which severely limit hunting abilities, often lead to blindness: among the Hadza, 29% of 484 people examined suffered from an eye disease, while two were blind (Bennett *et al.* 1973: 255).

Parasites

Blood parasites

Malaria, caused by an African parasite (*Plasmodium falciparum*) imported to Asia, America and the Pacific, is one of the highest causes of mortality in tropical countries. The percentage of children with enlarged spleens, an indirect symptom of chronic malaria, is two or three times higher among present-day Bakola foragers than among the rainforest villagers; conversely the frequency of sickle-cell anaemia, conferring genetic protection against malaria, is two times lower, a characteristic shared by all the Pygmy populations (Cavalli-

Sforza 1986). Coursey and Alexander (1968) described the relationships between agricultural systems, malaria and sickle-cell anaemia: deforestation during the Neolithic created the habitats for the malarial vector in agricultural areas. The Pygmy populations, formerly little exposed, would not have had time to develop the high frequency of protection provided by sickle-cell anaemia. Out of 256 Mbuti of all ages (Mann *et al.* 1962), 48% had an enlarged spleen and as many as 20% (51% between age 5 and 9 years) had blood smears positive for malaria. Moreover, between 55% and 100% of the sample were positive for *Dipetalonema perstans*, and more than 60% of adults suffered from onchocerciasis, two insect-borne filariae.

In savannah areas, malaria has an epidemic pattern with a peak during the rainy season. Among 885 !Kung examined (Brontë-Stewart *et al.* 1960), 52% had splenomegaly, attributed to malaria contamination around the Okavango River area, and also to some urinary bilharziasis. Bennett *et al.* (1970) found a rate varying from 10% (dry season) to 26% (wet season) of blood smears positive with malaria in the Hadza; the corresponding figures for enlarged spleens were 22% and 32%; no differences occurred between nomadic camps and settlements, and all the 132 sera tested were positive for *Plasmodium* malaria antibodies.

Intestinal parasites

Helminth transmission is related to the faecal pollution of the surrounding environment. The relatively high mobility of hunters used to protect them from high rates of infection, but most of the groups are now semi-sedentarised. Among Ituri Mbuti (Mann *et al.* 1962), as much as 85% of the population had hookworms (*Necator americanus* or *Ancylostoma duodenale*), 70% had *Trichuris* and 57% had *Ascaris*; 7% had intestinal bilharziasis, and 36% had pathogen amoebas (*Entamoeba histolytica*), while 13% of children under age 15 had *Giardia lamblia* infection, a cause of severe diarrhoea. Surveys in Australia showed high rates of infection with hookworm in the tropical northwest (Holt *et al.* 1980) or protozoa (*Giardia*, *Entamoeba*) in the Kimberley (Meloni *et al.* 1993); near-total absence of infection with *Ascaris*, *Trichuris* and *Entamoeba* species (all frequent in eastern

Australian Aboriginal communities) is noted in this western area (Jones 1980), probably for ecological reasons. Among the San of Namibia (Evans *et al.* 1990), stools examination revealed that out of 31 inhabitants of a camp, 63% had hookworms and 35% *Trichuris*; among 105 children 6–17 years of age attending schools in Bushmanland, 85% had hookworms, and 25% *Strongyloides*, one of the highest prevalences in South Africa. In Hadza figures are low (Bennett *et al.* 1970): only 14% of nomads had *Trichuris* and 4% *Ascaris*, and in settled villages, maybe due to medical treatments (Bennett *et al.* 1973: 249), prevalences were even lower or nill; serological tests for amoebiasis proved, however, that nomads had the lowest incidence.

In circumpolar areas, people in contact with wild animals (mammals and fish) are exposed to parasites via direct contamination (*Echinococcus*, *Taenia*, *Diphyllobothrium*, *Trichinella*) and human-to-human transmission (*Ascaris*, *Enterobius*, *Trichuris*, amoebas), but not to parasites which have an external cycle of maturation (*Ancylostoma*, *Necator*, *Strongyloides*) in the ground – a cycle unlikely to suceed when soils are frozen. In a comprehensive synthesis of Amerindians' epidemiology, Salzano and Callegari-Jacques (1988: 87–113) reported heavy rates (40% to 99%) of *Ascaris*, *Trichuris* or hookworms in most groups, but it was unclear whether foragers got these helminths from recent contacts with farmers or had been infected prior to contacts. More generally, as for HTLV viruses, molecular genetics of parasites found in remote living populations could provide some clues to human migrations.

Chronic diseases

Neel's fruitful hypothesis of a 'thrifty genotype' (Neel 1962) proposes that useful genes in adverse environments become harmful in a context of affluence, with the observed consequences on obesity and diabetes observed in American Indians (Barsh 1999) or Aboriginal Australians (O'Dea 1991). In South Cameroon, Pygmies are noticeably affected by arterial hypertension (15% of adults in the author's survey of Bakola); the explanation lies in high salt consumption, alcohol and tobacco, and perhaps stress, as their life is not one of leisure and affluence as famously claimed by some anthropologists such as Turnbull (1961) or Sahlins (see Winterhalder, and Rowley-Conwy, this volume). In Mbuti (Mann *et al.* 1962), only 5% of adults had excessive blood pressure, while Kesteloot *et al.* (1996) found no blood pressure difference between Bantus and Baka Pygmies, and observed a tendency for blood pressure to increase with age, a trend absent among the !Kung (Truswell 1979). Hunters are said to have remarkable powers of endurance in following game; however not many cardiac tests have been performed to check this claim, and the epidemiology of heart diseases is not well known; the same is true for cancers, but this type of affliction is dependent on life span, and cannot appear if people die early from other, mainly infectious, causes.

Beside heart pathology, other non-communicable diseases are to be considered. Osteoporosis is not only a disease of modernity and inactivity, as decalcification has been observed in Inuit (even in the pre-contact era) with ageing (Harper *et al.* 1984); arthritic inflammation is also common in most traditional societies. Tooth health is often poor and most hunter–gatherers show a high level of dental attrition, abrasion, tartar deposit and gingivitis (Kent 1991); however cavities are usually rare, in both present-day and Palaeolithic samples. Another category of diseases, psychiatric disorders, is not absent in non-acculturated foraging societies, but is very difficult to study (among Pygmies or San for example; Doob 1965). Adaptability to a changing world is strongly dependent on mental equilibrium, a crucial issue that foraging societies have now to face.

Conclusion: future changes

For most indigenous minorities, the transition to modernisation is synonym of impoverishment, racism, violence, alcoholism, drug addiction, suicide and social disintegration. In fact, the tendency to consume toxic substances can be symptomatic of an unconscious desire of self-destruction, and a mute protest against the collapse of the old values. For Pygmy, San, Negrito, Inuit and other economically marginal groups, ways of life have already changed or will soon do so, with modifications of the environment, such as game depletion and competition from other types of economies.

Coping with hazards and a heavy burden of diseases, hunter–gatherers do not live – and have never lived – in the Garden of Eden; they are not affluent, but poor, with limited needs and limited satisfaction, and little access to any facility. We cannot be sure, however, that more-or-less acculturated present-day hunter–gatherer populations are a true reflection of their past – perhaps this poverty is a consequence of contacts (yet in Africa, both Pygmies and Khoisan have been in contact with Bantus for thousands of years). The human species may well be more adapted to a hunter–gatherer diet, usually poor in fat and sugar and rich in fibres, than to what is ours today, and the price to pay will be the so-called 'diseases of civilisation' (Eaton and Eaton 1999), but the multiple infections, the uncertainty of survival and the demographic limitations imposed by a hunting way of life cast serious doubts on any nostalgia of a lost Paradise. Of course, as Eaton and Eaton argue, past foragers had a healthy way of life, a good diet and physical exercise, virtually no salt, alcohol or tobacco, no pollution, fewer cancers, and a life span and child mortality not so different of what was observed in Europe a few centuries ago. But this condition of isolated bands has vanished, and the present context is radically different.

The challenge, for present-day hunter–gatherers groups, is to adapt quickly to radical changes in lifestyle, a problem they already faced, to lesser extent, in the past, since they are not immobile cultures fossilised since the Palaeolithic. Among expected changes, some are positive, others negative or neutral. The quantifiable changes may include demographic expansion, due to improved sanitation and medical care, and to increased fertility. With the modification of ecosystems and game depletion, the growing importance of agriculture will modify, and probably mitigate, the exposure to transmissible diseases. However, nutritional disorders, like anaemias and other deficiencies, obesity, hypertension and diabetes, will appear because of dietary imbalance and alcoholism (O'Keefe and Lavender 1989), especially where people are regrouped in artificial villages or reserves. This new crowding favours the spread of acute and chronic diseases. In these mostly egalitarian communities, old social structures will vanish and the emergence of a hierarchical order can be predicted; possible psychiatric troubles, sometimes leading to homicidal tendencies (Headland 1989), are seen as the symptoms of refusal to change. The loss of knowledge of resources for food or medicine from the environment will be replaced, not necessarily for worse, by another – more scientific – corpus. An enhanced admixture will lead to a breakdown of genetic isolation, and plausibly to the appearance of secular trends such as increase in stature.

Hunter–gatherers have poorer access to schools and to medical assistance than sedentary populations, and the transition to modernity raises specific problems. Some hopes relate to a better access to land, a difficult matter for people believed to be nomadic, but this increased food security, together with a better access to schools and health services, will also precipitate the disappearance of their traditional life style. And despite such a cultural disappearance, physical differences based on different phenotypes will persists. Due to a persistent social segregation, the former hunter–gatherer, when becoming a farmer, an industry worker or a civil servant, will still be viewed as a 'Pygmy', a Negrito, a Bushman, an Aborigine, for as long as distinctive physical features are present.

Though hunting and gathering is a legacy for humankind, it is disappearing everywhere without much hope of revival. Considering the difficulties that the last hunter–gatherer societies are facing, especially in maintaining food resources and coping with diseases, we may wonder whether hunter–gatherers should themselves keep that way of life. The romantic myth of a Golden Age, revitalised by some ecological activists or by the paternalism of some religious institutions, is far from actual reality. In the end, the biological consequences of modernity for hunter–gatherer groups will be dictated by the evolution of social prejudice against them, their access to school, affluence and health facilities, the acknowledgement of traditional rights to land, as well as their own choices in the matter of development.

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10

Hunting for images, gathering up meanings: art for life in hunting–gathering societies

MARGARET W. CONKEY

Introduction

In 1879, the now-famous Ice Age cave paintings on the ceiling of the cave of Altamira in Cantabrian Spain were 'discovered'. As the story goes, it was the little daughter of the landowner who noticed them. The landowner, Sautuola, was already doing some archaeology in the cave, but, at that time, it was still not widely accepted or understood that humans had an ancestry earlier than 4004 BC, the date for Creation established by the Church. Excavations in archaeological sites in Europe had, however, already recovered pieces of bone and antler, often shaped into implements, with engraved animals and geometric shapes on them, and these could be attributed to very ancient cultures because they were found in stratigraphic layers. Engraved bones were considered to be more 'craft' products and tools, whereas the polychrome animals on the Altamira ceiling (mostly bison, already long extinct in the region, but also deer and horse) were not accepted, even by the leading thinkers in prehistory, as having been the work, the 'art', of ancient peoples.

The ancient peoples in question had left the traces of their lifestyle, especially their hunting activities, and the notions of the day held that those who lived by hunting and gathering were primitive indeed, and they certainly could not have been responsible for, or capable of, the creation of the lively, dynamic, even aesthetically powerful images of curled, perhaps charging or dying bison in browns, reds, and blacks painted upon and using the natural shapes

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In : Panter-Brick C. (ed.), Layton R.H. (ed.), Rowley-Conwy P. (ed.) Hunter-gatherers : an interdisciplinary perspective. Cambridge : Cambridge University Press, (13), 239-266.

(Biosocial Society Symposium Series ; 13). ISBN 0-521-77672-4