1 *Introduction*

The use of energetics in biological anthropology began with the ecosystemic approach but has been used in less holistic ways to examine processes of human adaptation and adaptability. Ecosystematics attracted anthropologists, largely because it allowed holistic studies of humans in their environment (Moran, 1990) and suggested the possibility of common principles in biology and anthropology (Winterhalder, 1984). Ambitious in scope, many studies employing such techniques failed to match the claims made for them (Burnham, 1982). In particular, although biological anthropology seeks to elucidate the causes of variation within- and between-human populations, systems ecology has rarely ventured into causal explanations. At best, the ecosystem concept offers a macro-scale descriptive frame for the study of human ecology (Smith, 1984). However, such descriptions have helped to improve the understanding of subsistence-related processes in human population biology. More limited use of energetics within the human adaptability framework has provided insights into some of the processes that lead to human population variation (e.g. James, 1988; Waterlow, 1990a; Ellison, 1991; Bailey *et al.*, 1993; Ulijaszek, 1993).

In this volume, energetics approaches and the issues that can be addressed with them are examined, acknowledging that the adaptability approach is nested in the ecosystemic one. The adaptability approach has ceased to be practised to any significant degree, but it is argued that data collected in the past can continue to inform the understanding of human adaptive processes, especially when used in conjunction with newer information. In this chapter, the studies of ecosystematics, human adaptation and adaptability are outlined and related to energetics. An historical background is given, with examples of the type of work carried out, where appropriate.

Ecological energetics

Although the German biologist Ernst Haeckel is credited with being the first to use the term ecology (Haeckel, 1868), the science of ecology did not get underway until the turn of the twentieth century. Ecology has been defined as the study of the interrelationships between living organisms and their environment (Lincoln, Boxshall & Clark, 1982). Despite the obvious implications of ecology for understanding human biology and behaviour, anthropologists were attracted to this approach only in the 1920s, when the term 'human ecology' was first used by the geographer H. H. Barrows (1922). In this and subsequent formulations (Adams, 1935; Park, 1936; Hawley, 1950) there was little attention paid to the causes and consequences of energy use, while adaptation was expressed in terms of social competition rather than biological function and Darwinian fitness.

The term 'ecosystem' was formally proposed by Tansley as a general term for the total complex of interacting organisms and their habitat. Through their interactions, the entire system is maintained (Tansley, 1946). These interactions involve a relatively stable set of relationships in which material, information and energy are in continuous circulation. The American biologist Lindeman (1942) focussed on the fixation of energy in ecosystems and the quantitative relations that must exist between different users of energy as it is spread around various populations of organisms within an ecosystem. This work helped to consolidate ecology as a discipline and was a major influence on anthropologists interested in understanding the relationships between human groups and their environments (Ellen, 1982).

Subsequently, the American anthropologist Julian Steward developed a theoretical framework, which he called cultural ecology (Steward, 1955), the first appropriation of ecological principles in anthropology. Stewart was convinced that the natural environment, through its effects on human subsistence behaviour, had a strong effect on the types of social and political structure which developed in societies that used comparable natural habitats. He was concerned with the relationships between environment and productive technology, the patterns of behaviour involved in resource acquisition through specific technologies in particular areas and the extent to which behaviour patterns involved in such acquisition influence other aspects of human behaviour. However, the quantification of these relationships was not a major concern.

Human ecologists have used a variety of approaches in their attempts to understand human group function and reproductive success. These have included: (1) demography; (2) the importance of culture and ritual in subsistence-related decision making; (3) economic and exchange relationships; and (4) energetics.

Demographic measures include vital statistics such as births and deaths at various stages of life, as well as fertility levels and in- and out-migration. If the aim is to measure fitness, then demography must be considered in the context of other factors, including food-getting ability, social stratification and economics, and knowledge and power. Anthropologists have examined the human ecology of ritual (Rappaport, 1968), warfare (Rappaport, 1968; Ferguson, 1989), trade (Thomas, 1976), foraging strategies (Hill *et al.*, 1984; 1985), and technological change (Bayliss-Smith, 1977).

Although the exchange value of materials and the relationships that ensue from exchange and distribution have long been the concern of economic anthropology (Seymour-Smith, 1986), they can, at best, only give a partial understanding of human ecosystemic relationships. Similarly, the study of information control, exchange and use in relation to subsistence strategies can lead only to partial knowledge of ecosystemic regulation (Moran, 1982). One way in which the biological factors involved in ecosystemic regulation can be understood is in terms of energy exchanged, used, created and stored in various forms. Ecological energetics could not develop until practical problems of the measurement of energy, in its many forms, were resolved.

Adaptation and adaptability

Adaptation and adaptability are central concepts in biological anthropology because they are the processes whereby beneficial relationships between humans and their environment are established and maintained. They are also the processes that allow change or accommodation to new conditions or circumstances. Adaptation has been considered from four perspectives: genetic, physiological, behavioural and cultural (Ellen, 1982; Harrison, 1993).

Genetic adaptation takes place through selection of the genotype, the genetic structure of the population being shaped by differential fertility and mortality. Physiological adaptation involves the shorter-term changes which individuals show in response to any of a variety of environmental stressors, among them low food availability. Behavioural adaptation includes types of behaviour that can confer some advantage, ultimately reproductive. Such behaviours may include proximate determinants of reproductive success, including patterns of resource acquisition, especially food and energy. Cultural adaptation involves the transmission of a body of knowledge and ideas, objects and actions being the products of those ideas. Although cultural structures can evolve as adaptive systems in response to environmental factors, not all aspects of culture can be assigned adaptive significance (Morphy, 1993).

The four types of adaptation do not exist in isolation from each other. Rather, they are linked across time and feed back on each other (Fig. 1.1). Genetic adaptation takes place across generations, as do many aspects of cultural adaptation. In this sense, genetic and cross-generational cultural

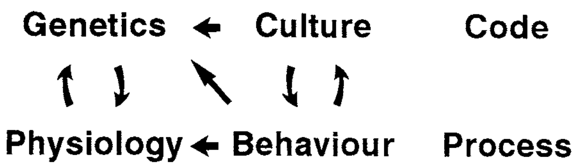

Figure. 1.1. Codes and processes in human adaptation.

adaptation can be regarded as codes. Adaptation as process arises out of adaptation as code and includes physiological and behavioural adaptation. The physiological processes have a basis in genetics, while the processes that have a basis in culture are the behaviours that operate within the lifespan of the individual. They range from the extremely short-term behaviours, such as instantaneous decisions, to longer-term behaviours, such as the choice of marriage partner. If either physiological or behavioural processes serve to enhance reproductive success, either directly or indirectly, then they can become fixed in the genetic and cultural codes, respectively.

Thus there is feedback between processes and codes: physiological processes operating within the lifespan feed back on genetic code, influencing genetic adaptation, while behavioural processes, also taking place within the lifespan, feed back on cultural code. Behaviour and culture also influence genetic adaptation through, for example, kinship patterns and marriage laws which may affect differential reproductive success and biologial population structure through assortative mating. Furthermore, behaviours may influence physiological processes, while the diffusion of culture that has not evolved cross-generationally but has been adopted from another group or population is of increasing importance in a world in which the transmission of information across traditional barriers is ever increasing.

Although there is considerable overlap between definitions of human adaptation and adaptability (Ulijaszek, 1995), adaptability does not overlap with genetic adaptation. Furthermore, adaptability is also the ability to adapt. However, to be of some analytical value, it is important to define the limits of this ability, whether it be physiological, behavioural or cultural adaptation. From Fig. 1.1, it is clear that there are adaptive processes that take place across generations, and processes that occur within the lifespan but have influence on, or drive, cross-generational processes. The term adaptability has from the outset been reserved for the kind of responses that individuals make to changes in their environment that facilitate their survival and reproduction and is thought of as a

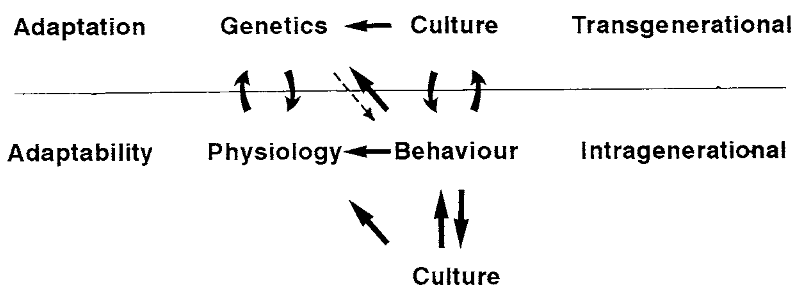

Figure 1.2. Relationships between human adaptation and adaptability.

property of an extant group (Harrison, 1993). Figure 1.1. can be redrawn to include human adaptability as a within-generational process (Fig. 1.2) and adaptation as a cross-generational process. Thus, human adaptability includes physiological and behavioural processes, as well as the adoption of cultural factors that may be of adaptive significance from other populations. There may also be behavioural adaptability in the choice of what cultural factors are adopted.

For example, physiological responses to low dietary energy availability include weight loss and body composition changes, as well as possible down-regulation of basal metabolism. Once body size matches energy resources, homeostasis is regained at a lower level of intake. However, a behavioural response might be to reduce physical activity. These are not mutually exclusive, and the mix of physiological and behavioural adaptability is constrained by cultural and genetic codes and states nested in both higher and lower levels of organisation than that of the individual.

At a lower level, the physiological state of different organs and tissues will determine the ability of the individual to undergo weight loss without functional impairment. In the maintenance of individual physiological homeostasis, there are circumstances in which a reduction in physical activity may be preferable to weight loss. This may, however, be in conflict with strategies suggested at higher levels of organisation, such as the group or community. For example, the need to perform arduous time-limited seasonal tasks such as planting or harvesting of crops to ensure food supplies for the coming year may rule out the possibility of reduced activity in the face of low food availability.

Energetics

Many aspects of human activity involve energy transfer of one sort or another (Harrison, 1982), and since the early 1960s there has been considerable attention paid by anthropologists to the energetics of human ecology Lee, 1965; Rappaport, 1968; Montgomery & Johnson, 1977; Little & Morren, 1977; Morren, 1977; Ellen, 1982; Ohtsuka, 1983). In particular, estimates of energy intakes, total expenditures, costs of activity and balances and flows have been used in attempts to understand human subsistence within the adaptation and adaptability framework (Bayliss-Smith & Feachem, 1977; Pimentel & Pimentel, 1979; Bayliss-Smith, 1982a,b; Thomas, Gage & Little, 1989; Ulijaszek & Strickland, 1993a). Concern is often with how the need for dietary energy and the ways in which it is obtained affect different aspects of human population biology or ecology (Haas & Pelletier, 1989; Thomas, McRae & Baker, 1982; Thomas *et al.*, 1989; Weitz *et al.*, 1989), or the implications of different subsistence and foraging strategies for fertility and biological fitness (Smith, 1979; Bertes, 1988; Hill & Kaplan, 1988a,b).

More recently, this has been extended to consider human responses and adaptations to seasonal energetic stresses (Dugdale & Payne, 1986; Brenton, 1988; de Garine & Harrison, 1988; Hitchcock, 1988; Huss-Ashmore & Goodman, 1988; Huss-Ashmore & Thomas, 1988; Little, Galvin & Leslie, 1988; Messer, 1988, 1989; Nyerges, 1988; Wheeler & Abdullah, 1988; Abdullah, 1989; Lawrence *et al.*, 1989; Payne, 1989; Ferro-Luzzi, 1990b; Ferro-Luzzi *et al.*, 1990; Thomas & Leatherman, 1990), and the role that energetics plays in reproductive ecology (Rosetta, 1990, 1994; Ellison, 1991; Bailey *et al.*, 1992).

Energy is an interconvertable currency that can be used in quantitative analysis of activities of human groups that are minimally or only partially involved in the cash economy. Thus, although the approach may not lead to a comprehensive understanding of human adaptation (Smith, 1979; Burnham, 1982), it can give an extensive account of that aspect of human functioning related to resource acquisition, subsistence and ecological and reproductive success (Ellen, 1982; Thomas *et al.*, 1982).

It is generally assumed that energy is the limiting factor in meeting the subsistence needs of most human populations, and if energy needs are met, the need for all other nutrients will also be met. This is not necessarily true, particularly in relation to iron and vitamin A intake. Furthermore, protein adequacy may be low when the staple food is low in protein. In practice, very few of the world's staple foods are low enough in protein to suggest likely deficiency in adults, even at low activity levels (Table 1.1). The safe level of protein intake, as defined by FAO/WHO/UNU (1985), is 0.75 g/kg of body weight. For adult males weighing 55 kg, the safe level of protein intake is 41 g. Of the 15 staple foods shown in Table 1.1, ten would supply this level of protein intake at all levels of physical activity (and therefore of

Table 1.1. *Protein content of staple foods and protein intakes of an hypothetical adult male, weighing 55 kg, at 1.4, 1.8 and 2.2 times basal metabolic rate (representing an inactive, moderately active, and very active person)*

Staple food	Energy (kJ/100 g)	Protein (g/100 g)	Protein intake (g) at		
			1.4 × BMR	1.8 × BMR	2.2 × BMR
Rye (*Secale* sp.)	1397	12.8	81.6	104.9	128.2
Oats (*Avena* sp.)	1565	13.1	74.6	95.9	117.2
Wheat (*Triticum* sp.)	1389	11.6	74.4	95.7	116.9
Millet (*Pennesetum* sp.)	1402	11.4	72.5	93.2	113.9
Barley (*Hordeum* sp.)	1368	10.5	68.3	87.8	107.3
Sorghum (*Sorghum* sp.)	1431	10.0	62.3	80.1	97.9
Maize (*Zea* sp.)	1460	9.1	55.5	71.4	87.2
Potato (*Solanum* sp.)	343	2.0	51.9	66.7	81.6
Taro (*Colocasia* sp.)	393	2.2	49.8	64.0	78.3
Rice (*Oryza* sp.)	1481	7.6	45.7	58.8	71.8
Yam (*Dioscorea* sp.)	427	1.5	31.3	40.2	49.2
Sweet potato (*Ipomoea* sp.)	452	1.0	19.7	25.3	31.0
Plantain (*Musa* sp.)	469	0.9	17.1	22.0	26.9
Cassava (*Manihot* sp.)	565	1.0	15.8	20.3	24.8
Sagopalm (*Metroxylon* sp.)	1494	1.4	8.4	10.8	13.2

Source: Basal metabolic rate from the Schofield (1985) prediction equation using body weight. Food composition values from the Food Composition Table for use in East Asia (United States Department of Health, Education and Welfare, 1972).

intake), while five would not. Those five are yam, sweet potato, plantain, cassava and sagopalm.

The situation is not quite the same with children, however. Protein requirements are highest in early life when growth is rapid, and the weaning diet of some groups is likely to give an inadequate intake of protein to young children. Shortages of other nutrients are also possible. In addition to protein, it has been suggested that zinc (Golden, 1988; Ann Prentice & Bates, 1994), calcium (Fraser, 1988) and possibly other deficiencies may contribute to the growth faltering experienced by children in the developing world.

Therefore, in studies of human adaptation and adaptability, it cannot always be assumed that energy is the primary nutritional stressor, although this is likely to be the case in most situations. As with any research tool, therefore, its usefulness needs to be evaluated and not assumed. Consideration of some early studies of ecological anthropology using energy as an analytical tool may be instructive in this regard.

Early studies incorporating measures of energy

The first anthropologist to consider energy was White, in his examination of the capacity of different human groups to harness increasing amounts of energy (White, 1949, 1959). This was followed by a number of studies in the 1960s using energy as the core currency in ecological exchange. From the perspective of the 1990s, these were rather crude and often flawed, but they generated a body of data and an understanding of traditional subsistence systems which are debated to this day. Notable studies were those of Lee (1965) of the subsistence ecology of the !Kung bushmen, and Rappaport's (1968) study of the Maring ritual cycle, as it related to sweet potato cultivation and pig husbandry.

The work of Richard Lee

Lee had three aims in his examination of the ecological basis of an African hunting and gathering economy. These were (1) to outline the subsistence strategy which allowed the !Kung bushmen to live well in a harsh environment with only rudimentary technology; (2) to show that the !Kung had an elementary form of economic life; and (3) to trace, from a primate baseline, the origin and evolution of human energy relations. In carrying out his study, Lee was careful to exclude all !Kung who were reliant, to any extent, on neighbouring Bantu cattle herders for work and food.

In summary, Lee (1968) demonstrated that the !Kung in the Dobe area where he worked could derive an adequate living from only a modest expenditure of time and effort, challenging the conventional wisdom of the time that hunter–gatherer subsistence was conditioned by scarcity and that life was a constant struggle. That the !Kung had an elementary economy was illustrated by Lee in his descriptions of generalised reciprocity, in which sharing of resources was universal, and the accumulation of surplus non-existent. Lee's study was important, therefore, because it shed new light on hunter–gatherer subsistence.

Problems arose, however, when Lee's conclusions were taken to represent all hunter–gatherer groups. The !Kung are not 'typical' hunter–gatherers. Indeed, no such thing exists, as is amply demonstrated in the benchmark volume on hunter–gatherers edited by Lee and de Vore (1968). It is, therefore, impossible to generalise from one group to all others, past and present. Lee's work has been criticised for a lack of representativeness in a number of areas. Although true hunter–gatherers, the groups he chose were not typical of all contemporary !Kung. However, Lee made this clear when reporting his observations. Furthermore, the study period did not take into account seasonality of food availability (Wilmsen, 1978), and his results are unlikely to generalise across the entire year for the !Kung alone.

The !Kung have been shown to exhibit signs of energy nutritional stress (Truswell & Hansen, 1976) and have a high infant-mortality rate, which increases across the parity of the mother (Pennington & Harpending, 1988). This would suggest that they are not living in a state of 'primitive affluence'; rather, their population is regulated by a number of constraints. It has been suggested that their fertility may be regulated by energetic stress of one sort or another (Bentley, 1985) and that their low work output, in terms of the proportion of the population engaged in hunting or gathering at any time, may be a way of regulating the use of resources in relation to their population size (Ulijaszek, 1993a). That is, the !Kung population may be close to carrying capacity.

The challenging view that Lee (1969) put forward has been resisted on the grounds of poor generalisability. Furthermore, his conclusions have been questioned after more detailed investigation and analysis of different aspects of the energetics of !Kung life, notably energy nutritional status, energy balance in pregnant and lactating women and the seasonality of available sources of dietary energy.

The work of Roy Rappaport

Rappaport carried out fieldwork among the Tsembaga Maring, a group of swidden cultivators in Papua New Guinea (PNG) in 1962 and 1963. He applied ecosystemic methodology in attempting to understand how ritual acts as a mechanism that regulates some of the relationships of the Tsembaga with components of their environment. The Tsembaga Maring are sweet-potato cultivators who practise pig husbandry. They engage in cycles of warfare and pig raising which are punctuated by ritual pig-kills involving large numbers of animals and exchange within and between warring groups. Rappaport used an ecological energetics approach to explore the rationality of the Tsembaga system.

In particular, he examined the part that the pig-killing ritual, which was carried out to appease the ancestors, played in the following: (1) the relationships between people, pigs and gardens, and competition of different human groups for limited land resources; (2) the regulation of the slaughter, distribution and consumption of pigs and its relationship to dietary protein requirements; (3) the regulation of the consumption of non-domesticated animals; (4) the redistribution of the population over time across available land, and between territorial groups; and (5) the regulation of the frequency of warfare and the severity of intergroup fighting. A summary of the ritual cycle is given in Fig. 1.3.

The length of the ritual cycle is largely regulated by the demographic fortunes of the pig population. Rappaport (1968) calculated that on

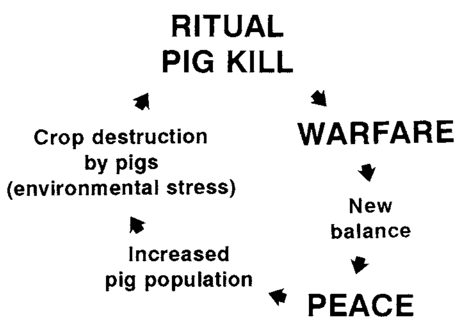

Figure 1.3. The Tsembaga Maring (Papua New Guinea) ritual cycle.

average a cycle lasts between 12 and 15 years. The ritual signals the time to resume hostilities with a neighbouring group; this is the time when territorial boundaries are removed. Warfare proceeds for a number of years and ceases when a new balance between the population of one group and the neighbours is established. Then follows a period of peace, when the pig population, which is fed cultivated yams and sweet potatoes, increases. The time taken to grow enough pigs to appease the ancestors varies according to how 'good' or productive the land is, but it is at least 6 years. Eventually, the pig population is unmanageable; the pigs do not get enough food from cultivated sources, so they take to foraging and begin to destroy gardens and consume tubers planted for human consumption. At this point, a festival is held in which the vast majority of pigs are slaughtered, reducing the amount of land needed to sustain the combined populations of pigs and human beings. Hostilities are resumed with neighbouring groups, the environmental stress of maintaining the pigs signalling the time for a sacrifice, and the sacrifice signalling the time to attempt to obtain more resources by extending the land boundaries through warfare.

Whether or not warfare resulted in increased land availability then depended upon the numerical strength of the neighbours who were being opposed at that time, and the new boundaries, Rappaport claimed, represented the new balance in land according to population size. In this way, there was an ecological regulation of the human population to land availability, mediated by the pig population growth and slaughter.

Rappaport claimed that pigs, ceremony and nutritional stress all played their part in ecosystemic regulation for the Tsembaga. The gardening of sweet potatoes generated surpluses of dietary energy which was used to feed domesticated pigs, who were a poor source of energy but a good source of protein. Pigs and wild animals provided only small amounts of protein