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Human energetics in biological anthropology

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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

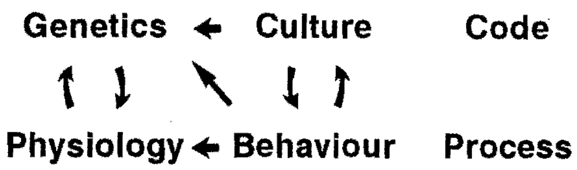

Figure. 1.1. Codes and processes in human adaptation.

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 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.

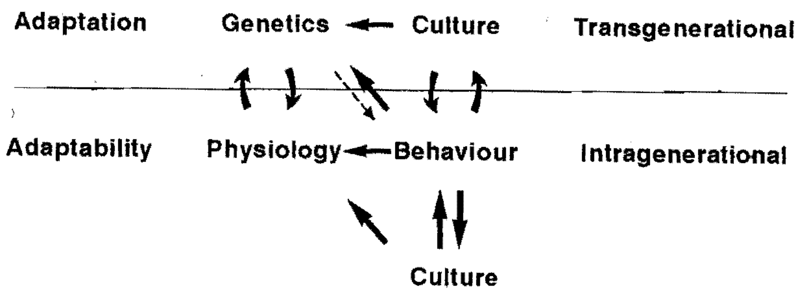

Figure 1.2. Relationships between human adaptation and adaptability.

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

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).

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

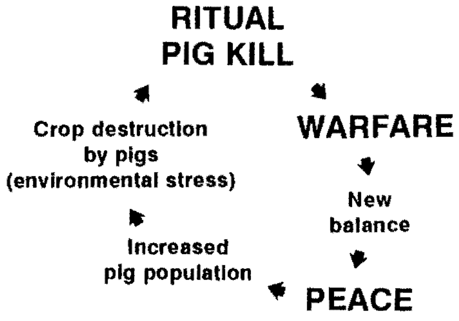

Figure 1.3. The Tsembaga Maring (Papua New Guinea) ritual cycle.

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 on a day-to-day basis, and Rappaport found some evidence of protein deficiency in the Tsembaga. He argued that the practice of killing and consuming pigs at times of misfortune and emergency provided 'physiological reinforcement' when it was needed to those that needed it, and was, thus, an effective way of using the limited amounts of animal protein available. Energy from the highly successful sweet potato staple was the key resource in fuelling the ritual cycle. Rappaport's use of energetics in analysis of Tsembaga subsistence has provided some understanding of the way in which the cultivation of a high-yielding, energy-rich staple crop, such as sweet potato, gives a high dietary energy return for the amount of human labour required to cultivate it and generates energy surpluses which can be used to generate energy-poor, but protein-rich resources, such as pigs (Table 1.2), which contributed only 8% of total energy intake, compared with 91% from root crops (Table 1.3).

Table 1.2. *The price of pigs in Papua New Guinea (time devoted to pig husbandry and root-crop cultivation by a group of 204 Tsembaga Maring)*

	Total work input	
	person hours[a]	(%)
Root cultivation		
For human consumption	33 920	54
For pig consumption	10 710	17
Herding pigs	17 000	27
Hunting and gathering	1340	2
Total	62 970	

Source: From Rappaport (1968).
[a] Total person hours measured across one year 1962–3.

A criticism of his original thesis, however, is that times of nutritional stress did not usually coincide with the cycle of ritual pig slaughters that were used to appease the ancestors. Therefore, it is difficult to claim that human population pressure was the signal for pigs to be killed and warfare resumed. This is supported by analyses from other investigators that the Tsembaga are rarely anywhere near their carrying capacity. Furthermore, although the intakes of protein in Papua New Guinea are the lowest in the world (Koishi, 1990), the energy subsidy used in pig raising does not appear

Table 1.3. *Daily energy intake of Tsembaga, by source*

	Daily energy intake (% of total daily intake)
Source	
Root crops	91
Pigs	8
Hunting and gathering	1
Total daily intake	
Adult males	10.77 MJ/day
Adult females	9.05 MJ/day

Source: From Rappaport (1968).

to provide a boost in protein intake at an appropriate time for the Tsembaga, as Rappaport claimed.

In a critique of Rappaport's work, McArthur (1977) determined that over the 5 days of pork consumption during the ritual kill that he observed, 1 kg per day would be eaten, which would supply over 12 MJ of dietary energy and 109 g of protein. For an average 43 kg Tsembaga male (Rappaport, 1968), a safe level of protein intake would be about 32 g per day (FAO/WHO/UNU, 1985). Such high levels of pork consumption over a period of only a few days is an inefficient use of protein, since, taking the case of the adult male consuming 1 kg of meat per day, the body would use at the very most only a third of this protein in protein anabolic processes, while the rest would be deaminated and used as an expensive source of metabolisable energy. It is possible that such high intakes of pork over short periods of time may actually be harmful. High intakes of protein in subjects habitually consuming very small amounts of protein have been shown to be associated with the enteropathy pig-bel, or enteritis necroticans, which in its most severe manifestation leads to death (Lawrence, 1992).

Energetics and anthropology

Patterns of energy production and use in a community or population are a function of the type and extent of local energy acquisition, exchange relationships with other groups and other activities that are important for the maintenance of group function, including individual biological needs as well as group economic maintenance and reproduction (Nydon & Thomas, 1989). These are summarised in the flow diagram (Fig. 1.4).

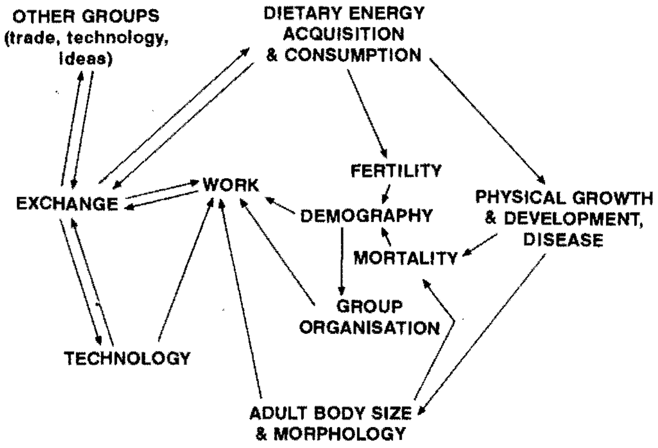

Figure 1.4. Human ecological relationships.

Dietary energy generated through various processes involving energy expenditure can be divided and consumed in a variety of ways, which, in turn, influences the pattern of energy expenditure, storage and mobilisation of bodily energy stores. The relationship between intake, expenditure and storage within group or community is usually complex but can be studied using appropriate energy balance (Ulijaszek, 1992a) and energy accounting methods. In the studies carried out by Lee (1969) and Rappaport (1968), energy was shown to be important in the regulation of human activity, although not as universally as the authors might have hoped. Studies carried out in the 1970s were more sophisticated in their methodology and cautious in their interpretations than those carried out by Lee and Rappaport, respectively. In particular, the relationships between physiological processes associated with energy expenditure and energy balance in the individual and energy transfer processes at community level have been examined.

Thomas (1973a, 1976) described the energetics of a high Andes Quechua community in the Nunoa District of Peru. He highlighted the importance of trade in animal products for the purchase of wheat flour and other imported foods, with groups living at lower altitudes, for the nutritional maintenance of their high population levels, relative to natural resources. In effect, the Quechua in Nunoa District have reached the carrying capacity of their land and rely on the husbanding and sale of the highly prized commodities, meat, fur and leather for their survival. In addition, he concluded that the Quechua could not sustain themselves without high levels of child labour in the herding of animals, freeing adults to carry out labour-intensive agricultural tasks. The mean completed fertility rate in the 1960s was 6.7 children (Hoff, 1968). With this high fertility rate providing a large child labour pool, demographic stability is maintained by migration, which can be seasonal or occur at times of scarcity or hardship and may be either temporary or permanent.

Other studies have been carried out in semi-industrial systems, such as that of the people inhabiting the Polynesian atoll of Ontong Java (Bayliss-Smith, 1977), where energetics methods were used to examine the impact of industrial technology on a small-scale society. Bayliss-Smith showed that, despite increased inputs of energy from fossil fuels into subsistence work and greater productivity and export of surpluses, the overall efficiency of the system is no greater than it would be were there no subsidy from fossil fuels. Therefore, the increased export of products resulting from greater inputs largely benefits the world market, and not the producers. However, surplus income was available for the purchase of imported manufactured goods, something held as important by many modernising societies in the Pacific region and elsewhere.

Another semi-industrial system was studied in 1955 by Epstein (1962) in Tamil Nadu, South India. Observations repeated in 1975–6 (Rebello *et al.*, 1976) allowed a comparison of the energetics of rice farming over a period in which the impact of green revolution inputs on group labour activity and productivity could be assessed (Bayliss-Smith, 1982a,b). Overall, total food energy production increased by 57%, with 111% increase in energy inputs, mostly from fertiliser and fossil fuels. Thus, the aim of green revolution inputs, which were to increase yields per unit area of land, have succeeded in this region, but only at the cost of energy subsidies which exceed the increased energy output. The comparison showed that the efficiency of production had declined.

By the mid 1980s, a number of studies of systemic ecological energetics had been carried out in a wide variety of contexts. In addition, data collected as part of earlier studies, prior to the onset of the ecological energetics movement, had been reanalysed in energetics terms. Details of most of the studies carried out up to that time are given in Table 1.4. This body of data has allowed a comparison of the energetic efficiencies of different subsistence systems operating at different levels of technology.

A number of developments in the fields of human physiology and nutrition also began to be incorporated into anthropological inquiry in the 1980s. These included the changing understanding of the energetics of bodily maintenance, locomotion, work and physical work capacity, pregnancy, lactation and physical growth, and the methods for measuring it (Ulijaszek, 1992a). Therefore, it became possible to examine the energetics of an ecosystem in more detail by considering such things as the efficiency of work and the energy expended therein, the rationale of working in groups or bands as opposed to individually, and the impact of undernutrition on the ability to perform subsistence tasks.

Another development was the use of predictive models in examining variations on existing subsistence strategies, or the effects of change on different measures of ecological success. This was made possible by the availability of computing power which could perform the sometimes complex and usually tedious calculations involved in modelling. Notable among these were the analyses of !Kung female foraging strategies (Blurton Jones & Sibly, 1978), the impact of different types of change on highland Quechua populations (Thomas *et al.*, 1982) and the rationality of post-harvest gorging by Gambian agriculturalists (Dugdale & Payne, 1986). Modelling is useful in hypothesis generation and in understanding complex interactions. Drawbacks include a limited ability to predict outcomes in any realistic manner, and poor generalisability to groups other than those from which the data used in model building were obtained.

Improved field methods and modelling techniques have led to several theoretical advances, including: (1) theories of hunter–gatherer foraging strategies based on optimality modelling; (2) a changed understanding of reproductive ecology resulting from advances in the measurement of reproductive performance and the energetics of pregnancy; and (3) an improved understanding of the importance of work and work organisation, based on improved methods for the observation of physical activity and a changing knowledge of the energetics of human effort.

Energetics has entered the study of reproductive ecology (Rosetta, 1990, 1994; Ellison, 1991) since many of the biological stresses influencing reproductive function are energetic (Lunn, 1994). There have been reductions in total fertility rates in most parts of the developing world, but especially in countries experiencing some level of economic growth (United Nations Children's Fund, 1990). Smaller family size has implications for dietary energy requirements across the lifecycle of the family and for subsistence productivity. Total food requirements may be lower for a smaller family, but the potential family work-force is also smaller. The question of what constitutes reproductive success in humans becomes more complex and more difficult to answer as populations become more land-limited and integrated into the global cash economy. Generally, proxies such as nutritional or health status are taken as yardsticks of such success, but studies of energetics, ovulatory function, pregnancy, lactation and physical growth are beginning to create a new understanding of these

Table 1.4. *Populations in which studies of ecological energetics have been carried out*

Group or location	Country	Subsistence pattern	Study period	Reference
Jiaxing	China	Rice cultivation	1765	Chen Hengli, 1958 Calcualtions: Dazhong & Pimentel, 1986
Wiltshire	United Kingdom	Wheat and barley cultivation, sheep farming	1820s	Cobbett, 1830 Calculations: Bayliss-Smith, 1982a,b
Iban	Sarawak, East Malaysia	Rice cultivation	1949–51	Freeman, 1970 Calculations: Harris, 1971
Genieri	Gambia	Cereal and peanut cultivation	1947–9	Haswell, 1953 Calculations: Harris, 1971
Karnataka	India	Rice cultivation	1955	Epstein, 1962 Calculations: Bayliss-Smith, 1982a,b
Hanunoo	Philippines	Rice cultivation	1957	Conklin, 1957 Calculations: Weiner, 1972
Tepozoztlan	Mexico	Maize cultivation		Lewis, 1963 Calculations: Pimentel & Pimentel, 1979; Harris, 1971
Hadza	Tanzania	Gathering, hunting	1958–60	Woodburn. 1972
Lamotrek Atoll	Micronesia	Root cultivation, fishing	1962–3	Alkire, 1965 Calculations: Odum, 1971
Tsembaga Maring	PNG	Root cultivation, pig husbandry	1963	Rappaport. 1968
!Kung San	Namibia	Gathering, hunting	1963–5	Lee, 1965
Bomagai Angoiong Maring	PNG	Root cultivation, pig husbandry, hunting	1964–5	Clark, 1971
Moscow Oblast	Russia	Collective farm: wheat, potatoes or fodder crops, barley or oats, and grass with clover, in rotation	1966 (statistical average)	Moscovskaia Oblast, 1967 Calculations: Bayliss-Smith, 1982a,b
Raiapu Enga	PNG	Root cultivation, pig husbandry	1966–7	Waddell, 1972 Calculations: Morren, 1977; Bayliss-Smith, 1977
Quechua, Nunoa	Peru	Herding, root cultivation	1967	Thomas, 1973b
Eskimo	Baffin Island, Canada	Hunting, fishing	1967–8	Kemp, 1971
Tasbapauni Miskito	Nicaragua	Root and rice cultivation, fishing, hunting	1968–9	Nietschmann, 1973
Miyanmin	PNG	Root cultivation, pig husbandry, hunting	1969	Morren, 1977; Little & Morren, 1977
Ruhua Nuaulu	Seram, Indonesia	Root cultivation, gathering, hunting	1969–71	Ellen, 1978
Ontong Java	Solomon Islands	Root and coconut cultivation, fishing	1970–71	Bayliss-Smith, 1977
Wiltshire	United Kingdom	Large farm: barley and wheat cultivation, sheep and cattle husbandry	1971 (statistical average)	Ministry of Agriculture, 1973; Leach, 1976 Calculations: Bayliss-Smith, 1982a,b
Wonie	PNG	Sago horticulture, hunting, fishing	1971–2	Ohtsuka, 1983
Nacamaki	Koro, Fiji	Root and coconut cultivation, fishing	1973–4	Bayliss-Smith, 1977
Nasaqalau	Lakeba, Fiji	Root and coconut cultivation, fishing	1974	Bayliss-Smith, 1977
Alyawara	Australia	Hunting and gathering	1974–5	O'Connell & Hawkes, 1981
Karnataka	India	Green revolution, rice cultivation	1975	Rebello *et al.*, 1976 Calculations: Bayliss-Smith, 1982a,b
Wopkaimin	PNG	Taro horticulture, hunting	1975	Hyndman, 1979
Etolo	PNG	Hunting and horticulture, sago	1979–80	Dwyer, 1983
Arnhemland	Australia	Hunting and gathering	1979–80	Altman, 1984
Ache	Paraguay	Hunting and gathering	1981–2	Hawkes *et al.*, 1982
Maharashtra	India	Rice and sorghum cultivation	1983	Edmundson & Edmundson, 1989

ecological relationships. However, there are a number of methodological problems that have yet to be resolved including: (1) the use of data collected using a variety of techniques, including biological and social variables, without undue loss of accuracy and precision; (2) the development of modelling and statistical techniques that will allow complex relationships to be understood; and (3) the development of longitudinal data collection and modelling techniques that allow the effects of change to be observed and analysed.

The well-being of the mother and the children she bears are closely related. Dugdale (1986) has suggested that the mother and nursing infant should be considered as a unit, or dyad. The size of the infant is related to the maternal size and the environment which she experiences, the breastmilk she produces in response to the child's demands and other feeding behaviours which she introduces to the child. New methods of, and increased accuracy in, energy-balance measurement have led to greater understanding of the energetics of child-bearing. In most traditional societies, the pattern of human growth is different from that of populations in industrialised nations, resulting in smaller adult body size. The suggestion that smaller body size of adults carries no cost to biological function (Seckler, 1982) has been convincingly discredited (Satyanarayana *et al.*, 1977; Spurr, Maksud & Barac-Nieto, 1977; Brooks, Latham & Crompton, 1979; Immink & Viteri, 1981; Immink *et al.*, 1984; Spurr, 1988a; Ferro-Luzzi *et al.*, 1992; Strickland & Ulijaszek, 1993), while the process of becoming small, or growth-retarded relative to western growth references, is associated with greater risk of death in most populations (Pelletier, 1991).

The energetics of work must be considered in relation to subsistence practices and behaviour. The organisation of work by individuals and groups varies with the types of subsistence practice adopted. The formation of communities, villages or settlements, although fundamentally social, has consequences for energy balance. For example, social relations may involve reciprocity in food distribution and communality in work-group formation. Both acts can serve to reduce the level of energetic stress experienced by individuals within the groups. Ecological anthropologists are often concerned with the energetic rationale of different types of subsistence strategy, either in the context of other activities or when attempting to plot the evolution of such strategies in relation to land availability and demographic pressure.

In seasonal environments, the requirement for hard work varies across the year, as does the availability of food, often resulting in fluctuating energy balance across the year (Ferro-Luzzi & Branca, 1993). It is possible that food sharing and work-group formation may not successfully buffer all individuals under such conditions. The identification of individuals or groups at risk of energy stress is useful in attempting to understand the process of adaptation in any population or community, as well as being of potential public health significance.

Finally, a new approach in evolutionary ecology has involved energetics modelling. Data on the energetics of locomotion and of growth and development in contemporary human and non-human primate populations has been used in association with body size estimates for extinct hominids to examine the energy cost of encephalisation (Foley & Lee, 1991; Leonard & Robertson, 1992, 1994), increased body size (Leonard & Robertson, 1994) and bipedalism (Leonard & Robertson, 1992).

Summary

In this chapter, the use of ecological energetics and energetics in human adaptability is described. The history of ecological energetics is a brief one, beginning in the 1960s. Early studies were crude but provided a new quantitative approach to the study of traditional subsistence economies, using systems theory. Since then, estimates of energy intake, expenditure, cost of activity, balance and flow have been used in attempts to understand human subsistence within the adaptation and adaptability framework. Research has focussed on: (1) how the need for dietary energy and the ways in which it is obtained affect different aspects of human population biology or ecology; (2) the implications of different subsistence and foraging strategies for fertility and biological fitness; and (3) human responses and adaptations to seasonal energetic stresses. Modelling procedures have allowed energetics data to be used predictively and in hypothesis generation, in these areas and in some aspects of evolutionary ecology.

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, it can give an extensive account of that aspect of human functioning related to resource acquisition, subsistence and ecological and reproductive success. Furthermore, improved methodology and precision of measurement of different components of individual energy expenditure have allowed anthropologists to address such issues as: (1) the energetics of different physiological states, including undernutrition, obesity, pregnancy and lactation; (2) the ecological correlates and functional consequences of small body size; (3) the influence of energetic stress on ovulatory function; and (4) the levels of work effort and output in different types of subsistence system.