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Energetics and Evolution: An Emerging Research Domain

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ABSTRACT The study of energetics is important to human biology because the availability and utilization of food energy influence health, survival, and reproduction. Over the last decade, human biologists, biological anthropologists, and other evolutionary scientists have increasingly come to recognize the importance of energy dynamics in shaping evolutionary processes. Thus far, different lines of energetics research have been conducted largely in isolation from one another. This thematic collection examines topics of evolutionary energetics from several different perspectives, drawing together research from human paleontology, comparative primate and mammalian biology, human population biology, and mathematical modeling. It represents a starting point for further integrative research on human evolutionary energetics. Am. J. Hum. Biol. 14: 547–550, 2002. © 2002 Wiley-Liss, Inc.

Energetics has long been a central focus of research in both ecology and human biology. Over the past decade, human biologists, biological anthropologists, and other evolutionary scientists have increasingly come to recognize the importance of energy dynamics in shaping evolutionary processes. Research into evolutionary aspects of energetics has included a wide variety of topics, ranging from population differences in daily energy expenditure (Ulijaszek, 1995; Panter-Brick, 1996) to the energetic consequences of brain evolution in early hominids (Leonard and Robertson, 1994; Aiello and Wheeler, 1995), and alternative perspectives on the energy costs of bipedal locomotion (Alexander, 1992; Minetti and Alexander, 1997; Taylor and Rowntree, 1973). To date, these different lines of energetics research have progressed largely in isolation from one another. This thematic collection of articles begins to integrate these disparate avenues of research into what is hoped will become a new domain of research within biological and evolutionary anthropology.

ENERGY AND EVOLUTION

The study of energetics is important to evolutionary research for several reasons. First, food and energy represent a key interface between organisms and their environments. The search for food energy, its consumption, and ultimately its allocation for biological processes are critical aspects of an organism's ecology. This energy dynamic between organisms and their environments —energy expenditure in relation to energy acquired—also has important adaptive consequences for survival and reproduction.

Indeed these two components of Darwinian fitness—survival and reproduction—are reflected in the way in which the total energy budgets of individual animals or populations are traditionally divided. As shown in Figure 1, maintenance (or respiratory) energy expenditure includes basal and activity costs; these are the components of the energy budget associated with keeping the organism alive on a day-to-day basis. Productive energy costs, on the other hand, are those associated with maturing and producing offspring for the next generation.

The type of environment in which an organism lives and its niche within this ecosystem will strongly shape the relative allocation of energy to these different components. The relative allocations also change over the lifespan. These issues represent important themes that integrate the articles in this thematic collection.

Ecological influences on energy demands

Several articles consider how environmental factors shape different components of energy expenditure. This includes the

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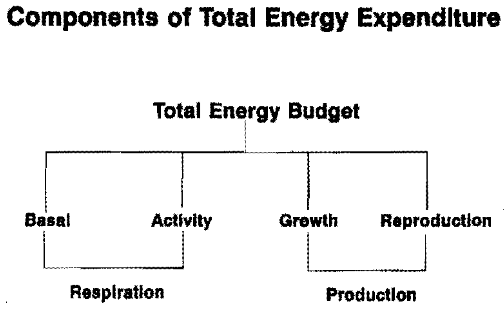

Fig. 1. Components of an animal's total energy budget. Respiratory (or maintenance) energy costs are those necessary for keeping the animal alive on a daily basis. Productive energy costs are those required for growth, development, and reproduction.

consideration of how ecological variation influences the energy costs associated with subsistence work, locomotion, and thermoregulation.

Variation in energy allocation to growth

Energy allocation to growth is a second important theme. It includes the consideration of both variation in allocation patterns among human population, as well as the differences between humans and other species.

Variation in energy allocation to reproduction

Similarly, the relative allocation of energy to reproduction is also considered using intra- and interspecific comparisons.

Life history theory: energetic trade-offs

Finally, several articles draw on life history theory to examine the trade-offs in the allocation of energy to survival, growth, and reproduction. As with the other themes, the life history approach is applied to intra- and interspecific comparisons.

ALTERNATIVE PERSPECTIVES ON HUMAN EVOLUTIONARY ENERGETICS

The articles in this collection also examine topics of evolutionary energetics from several different perspectives, drawing together research from human paleontology, comparative primate and mammalian biology, human population biology, and mathematical modeling. Each of these perspectives provides a different window into how energy dynamics shape evolutionary processes.

Human paleontology

The first two articles, by Aiello and Key and Steegmann et al., use energetic approaches to examine adaptive strategies among our hominid ancestors. Aiello and Key explore the energetic and life history consequences of the evolution of large body size in *Homo erectus* females. Paleontological evidence suggests that the emergence of *H. erectus* was associated with a dramatic increase in body size relative to earlier hominid ancestors, the australopithecines. Such changes likely had important consequences for energy needs associated with reproduction, development, and foraging behavior. Indeed, this study and other recent work (Gabunia et al., 2001; Leonard and Robertson, 1997) suggest the beginnings of a "human" subsistence and life history strategy are evident with *H. erectus*.

Steegmann et al. consider a later stage in human evolutionary history, examining the Neandertals of the last Ice Ages of Europe. These authors draw on comparative data from human circumpolar populations and other mammalian species to evaluate how adaptation to a glacial environment likely shaped both the morphology and physiology of Western European Neandertals. Daily energy demands for Neandertals appear to have been extremely high, reflecting the combined influence of metabolic adaptation to cold stress and very high activity levels (see also Sorensen and Leonard, 2001). Additionally, the authors suggest specific physiological and genetic avenues that Neandertals may have used to adjust to their extreme environment.

Comparative primate and mammalian biology

Dufour and Sauther draw on data from nonhuman primates to provide a comparative and evolutionary context for exploring the energetics of human growth and reproduction. They consider the high energetic costs of pregnancy and lactation in humans and nonhuman primates, and adaptations that have evolved to accommodate those costs. Humans and other primates have longer periods of gestation and lactation than other mammals of comparable size. The prolonged gestation and lactation lengths contribute to slower rates of pre- and postnatal growth of primates, while reducing the daily energy costs of reproduction to the mother.

Ulijaszek examines the energy costs of fetal growth in humans and nonhuman primates. He finds that the energy demands of fetal growth are relatively lower in human and apes compared to other primates. This suggests that human prenatal development is more resistant to energy stresses on the mother than is the case for other primate species. These energetic differences have implications for better understanding the mechanisms responsible for promoting brain evolution in apes and humans.

Human population biology

Leonard et al., Tracer, and Panter-Brick draw on comparative data from human populations to examine evolutionary aspects of energy dynamics. Leonard et al. examine evidence for elevations in basal metabolic rate (BMR) among indigenous circumpolar populations, and consider potential mechanisms and selective agents underlying this variation. Regardless of which reference values are used, indigenous human populations of the arctic and subarctic show significant elevations in basal energy expenditure. The pattern of variation in BMRs suggests that the elevations are attributable to both functional and genetic factors.

Tracer discusses how variation in energy availability in different environments influences the allocation of energy to growth, survival, and reproduction. The energetic trade-offs between somatic "maintenance" and reproductive function in human populations are considered, drawing largely on work with the Au of Papua New Guinea. Tracer demonstrates that among Au women, pregnancy and lactation contribute to sharp declines in body fat reserves over the course of women's reproductive careers. The findings have important public health implications because they suggest that greater attention should be given to aspects of maternal health when formulating recommendations on infant feeding.

Panter-Brick examines how sexual division of labor varies in human societies with different subsistence regimes to evaluate alternative scenarios for changes in the sexual division of labor over the course of human evolution. Historically, hunting and gathering has been viewed as a key feature that distinguished members of the genus *Homo* from earlier hominids (Lancaster and Lancaster, 1983). Thus, models of human behavioral evolution have generally regarded early human hunter–gatherers as having a marked sexual division of labor and high levels of sexual dimorphism in body size and skeletal robusticty. These high levels of sexual dimorphism are generally thought to decline with the advent of agriculture, because of reductions in male/female differences in labor and work requirements (Frayer, 1980; Larsen, 1995). By looking at energy expenditure and activity data from living subsistence-level populations, Panter-Brick effectively shows that male/female differences in workload do not markedly differ between foraging and agricultural societies. The findings suggest current models of human behavioral evolution need to be reconsidered with greater attention to the diversity observed in contemporary populations.

Modeling

The volume concludes with R. McNeill Alexander's Pearl Memorial Lecture, "Energetics and optimization of human walking and running." Professor Alexander is the world's leading expert on the mechanics and energetics of human and animal locomotion. He uses a computer modeling approach to investigate optimal bipedal gaits under different environmental conditions. The model predicts that with increasing speed of movement, aspects of gait (e.g., stride length) are adjusted to minimize the energy costs of locomotion. Furthermore, Alexander finds that when walking in environments where the costs of movement are elevated (e.g., steep hills, soft, marshy terrain), it is often most economical to walk in a diverted path, rather than in a straight line. Models such as this one are critically important for gaining insight into early hominid locomotion and ranging behavior, particularly as information about the environments in which our ancestors evolved continues to improve.

FUTURE DIRECTIONS

This thematic collection represents a starting point for the development of further integrative research on "Human Evolutionary Energetics." The development of such a research domain has great importance to human biology. It will further promote the framing of human biology research in a comparative and evolutionary perspective, and it will also promote the broader use of human biological data for developing models to understand major patterns and trends in human evolution.

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