

HUMAN ECOLOGY

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SUMMARY

1 Metabolic ecology provides a robust theoretical framework for understanding how individual metabolic processes constrain flows of energy and materials at all levels of biological organization as organisms interact with their environments. Here we use this framework to examine variation in human ecology across scales, from individual life histories to the ecology of populations, and from hunter-gatherer societies to modern nation-states.

2 Many aspects of human ecology, such as most life-history traits, are remarkably predictable for a mammal of our body size. Deviations from expectations occur primarily at the population level as human population energetics is not simply the linear sum of individual demands.

3 Humans and the complex social systems we create are clearly constrained by the energy fluxes at all scales of social organization. Moreover, the

same quantitative scaling relations indicative of economies of scale are found across the spectrum of human socio-economies. Specifically, as human systems grow in size they also increase in per-capita efficiency, due to the benefits of existing within complex social and infrastructure networks where resources, energy, and information can be shared widely and quickly across populations.

4 A metabolic approach to human ecology lends insight into those specific ways in which humans are a predictable mammal species, and the ways in which we differ. Consequently, human metabolic ecology provides anthropology with a theoretical framework to understand the energetic evolution of the human species, and why the human species became the most ecologically dominant species in Earth's history.

20.1 INTRODUCTION

Human ecology is the study of the interactions between humans and their environments. The human species is remarkable in many respects, but surprisingly similar to other species in other respects. The evolutionary history and biogeography of the human species is particularly noteworthy. Beginning around 50 000–

60 000 years ago, humans began their final major biogeographic expansion out of Africa and colonized all of Eurasia, Australia, and the Americas by the end of the Pleistocene some 12 000 years ago (Klein 2009). This expansion had major ecological impacts on Earth's terrestrial environments, including the replacement and/or assimilation of archaic hominid species throughout Eurasia (Klein 2009), and the global

extinction of Pleistocene megafauna (Lyons et al. 2004; Surovell et al. 2005). Beginning about 12 000 years ago, in many parts of the world human societies independently developed methods of cultivation (Bellwood 2004; Purugganan and Fuller 2009) and diets started to shift from a sole reliance on wild plants and animals to one that incorporated domesticates. As a consequence, human societies rapidly diversified along a new socio-economic spectrum of food production.

Today, the diversity of human societies ranges from populations that continue to rely on foraging economies, to large, complex industrial societies that rely on extracting energy sources of fossilized biomass from geologic deposits stored deep in the Earth's crust (Smil 2008). In the twenty-first century, our most developed societies rely on global communication networks that allow rapid transport of energy, materials, and information across vast distances. Currently, the majority of the world's human population, nearing 7 billion, lives in dense urban centers of millions of individuals, and performs specialized functions much removed from the actual task of food production. The human species is clearly the most ecologically dominant species in Earth's history, currently appropriating between 25% and 40% of potential global net primary production for human needs (Vitousek et al. 1997; Haberl et al. 2007). Much of this technological innovation has occurred relatively recently in human evolutionary history, within the last few centuries, and shows no sign of slowing. On the contrary, the pace of technological development is exponential (Arthur 2009), seemingly limited only by our ability to access increasing amounts of energy required to fuel its growth (Brown et al. 2011).

However, our internal biology is quite unremarkable. For example, we share about 99% of our DNA with our closest relative, the chimpanzee. Our bodies metabolize energy at a predictable rate for a mammal of our size (Ulijaszek 1995) and, like all other organisms, our diets must maintain a predictable balance of chemical elements in order to maintain our internal biochemistry (Williams and Frausto da Silva 2006). In comparison to other mammals, our life history is quite predictable for a primate species of our body size (see below), with some unique features, such as a particularly long lifespan, large encephalization, a significant post-reproductive lifespan in human females, and the requirement of large amounts of parental investment in our highly altricial, slow-growing offspring (see

Charnov and Berrigan 1993; Hawkes et al. 1998; Kaplan et al. 2000; Walker et al. 2006).

One of the most striking biological features of the human species is the large size of our brain, a powerful biophysical computer that allows us to absorb, process, interpret, and store large quantities of information about the external world (Eccles 1991; Schoenemann 2006, 2009). These abilities have led to a sophisticated understanding of basic chemical, physical, and biological principles, and have allowed us to use these principles to engineer solutions to many of the energetic and informational constraints faced by other biological species, beyond the genetic pathways shared with other organisms (Williams and Frausto da Silva 2006). The immense human cognitive capacity resulted in the evolution of a key secondary pathway of heritable information some time in our evolutionary past, which has ever since been fundamental to human biocultural evolution. In anthropology, this coevolutionary process is often referred to as dual inheritance theory (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985) and has been fundamental to the evolution of culture. Importantly, both biological and social information can now be shared through communication networks that span the entire planet.

A key goal of anthropological science is to develop a core body of theory that can be used to understand human ecology, evolution and diversity in all its dimensions. This theory must be general and consistent with the evolution of all other forms of biological life, and it must follow from the universal laws of physics and chemistry that govern all exchanges of energy, matter, and information in the universe. Such theory is crucial, not only for the basic scientific understanding of human ecological and evolutionary history, but also for the applied aspects of environmental and sustainability science (Brown et al. 2011). Our approach here is to examine how we can quantify energy flows in human systems, across different biological and cultural scales, and from there begin to develop a predictive theory of human energetics, based on first principles of physics, chemistry, and biology.

In this chapter we explore several ways in which metabolic theory (Brown et al. 2004) can be used to model human ecology: (1) in comparison to other mammalian species; (2) across scales of biological organization, from individuals to populations; and (3) across the spectrum of human socio-economic development, from hunter-gatherer societies, to twenty-first-century nation-states.

20.2 COMPARATIVE HUMAN LIFE HISTORY

In Figure 20.1, we compare various human life-history variables with chimpanzees, other primates, and mammals. We exclude bats and non-placental mammals from the analysis because they are known to have unusual life histories (Hamilton et al. 2011). Metabolic theory predicts that across species, life-history parameters scale as power functions of the form $Y = Y_0 M^\alpha$ (see Sibly, Chapter 5), where Y is the life-history parameter of interest, Y_0 is a normalization constant, M is body size, and α is a scaling parameter, predicted to be $-1/4$ for biological rates, and $+1/4$ for biological times and sizes (Brown et al. 2004). The scalings in Figure 20.1 are close to these predicted values, and provide a useful benchmark for comparing different aspects of human life history.

Figure 20.1A,B shows that newborn mass and weaning mass are tightly correlated with adult mass across placental mammals, and while primates in general seem to have slightly higher newborn and weaning masses, human developmental masses are predictable given our adult body mass. In terms of the timing of life-history events, shown in Figure 20.1C–G, primates generally have slow life histories throughout life relative to other mammals (Charnov and Berrigan 1993). While humans have among the slowest life histories of all mammals by most measures, their rates are not exceptional for primates (with the possible exception of maximum lifespan) and, again, seem to follow primarily from the fact that we are large-bodied primates.

Reproductive output can be measured in several ways. Humans normally give birth to a single offspring at a time, as do many other mammals (Fig. 20.1H) and have particularly low litter frequencies (Fig. 20.1I), resulting in low annual fertility rates for a mammal of our size (Fig. 20.1J). Combining some of the above life-history measures to calculate mass-specific production = (weaning mass)/(adult mass) \times (litter size) \times (litter frequency) (Sibly and Brown 2007), a useful estimate of the overall speed of the life history shows that, again, humans have slow life histories, though not exceptionally slow for a primate of our body size (Fig. 20.1K). Indeed, human hunter-gatherer lifetime reproductive effort is much as predicted (Burger et al. 2010).

This kind of comparative scaling approach to human life history allows us to consider humans in a

wider ecological and evolutionary context than is often considered in anthropology. For example, human life histories are often compared to chimpanzee life histories, our closest living genetic relatives, in order to gauge the evolutionary divergence of hominins with reference to our most recent common ancestor (e.g., Kaplan et al. 2000; Kaplan and Robson 2002; Walker et al. 2006). Given the consistent (and thus predictive) scaling relations between body size and life-history components across species shown above, MTE predicts that the slower speed of life history in humans compared to chimpanzees is partially explained by the fact that humans are larger-bodied animals than chimpanzees.

20.3 COMPARATIVE HUMAN POPULATION ECOLOGY

We can use a similar scaling approach to compare human ecology to mammalian ecology at a population level. A key macroecological measure of an animal's spatial energetics is the home range, the area it requires to fuel its metabolic demand (Peters 1983). Across species the size of the home range, H , increases proportionally with adult body size, M , and so scales as $H \propto M^1$. Figure 20.2A demonstrates that hunter-gatherers have the largest home ranges for their body size, and among the largest home ranges of all mammals, irrespective of body size. The one mammal with a larger home range in Figure 20.2A is the orca, a marine species. The large size of hunter-gatherer home ranges is a result of large social group sizes (see below). Sharing a home range with group members allows individuals access to larger areas than most solitary mammals. Chimpanzee home ranges are also larger than the average for a mammal of their body size, but much as predicted for primates.

Hunter-gatherer population densities are low for a mammal of our body size (Fig. 20.2B), likely reflecting the greater need for space with increasingly carnivorous diets across species (Haskell et al. 2002). In comparison, chimpanzee population densities fall on the mammalian scaling slope, suggesting that human population densities exceed those of chimpanzees in part because of the more carnivorous human diet. Figure 20.2B also includes the population density of the current human global population for comparison, showing an increase of about three orders of magnitude in density from that of hunter-gatherers, thus

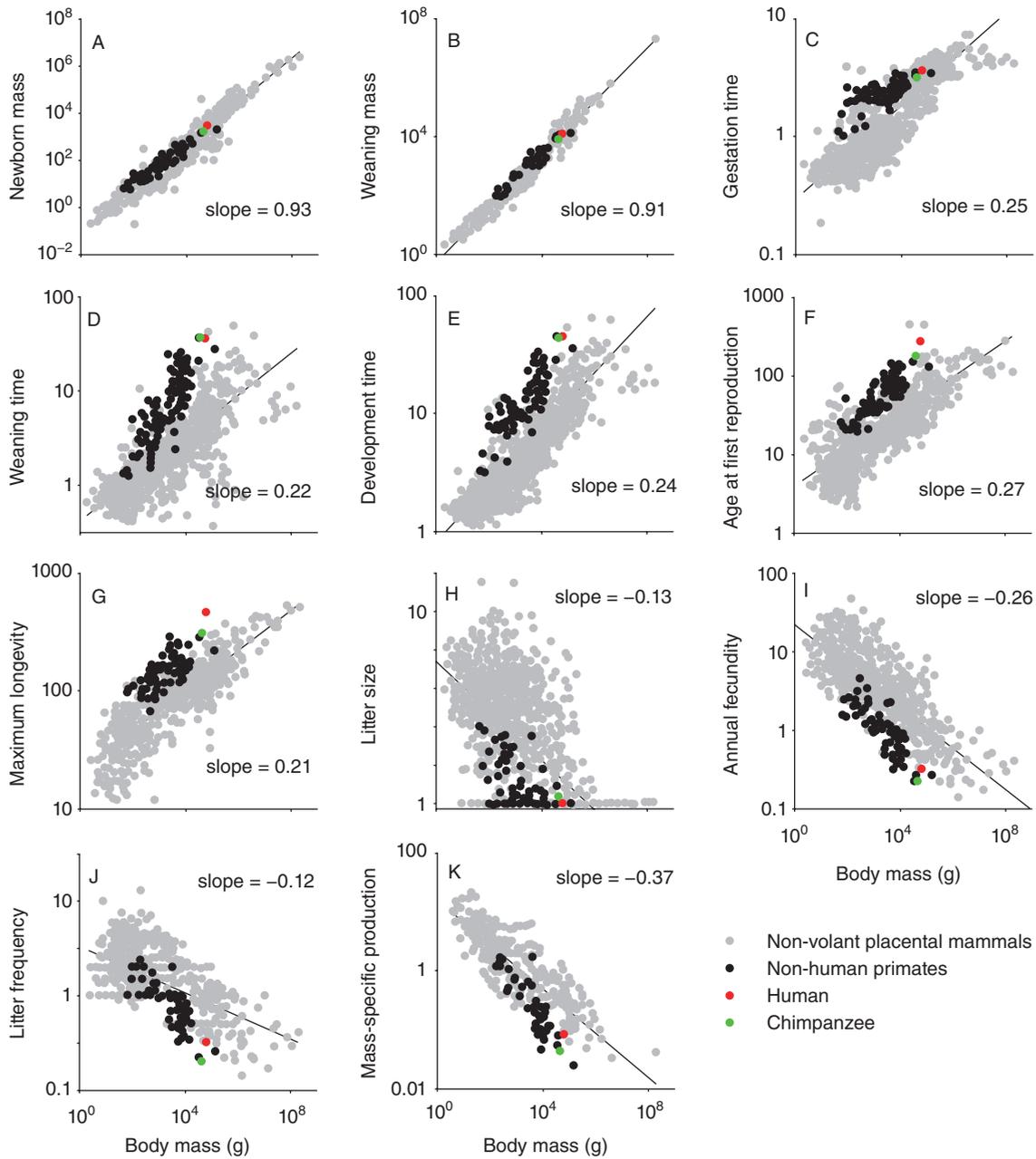


Figure 20.1 Comparative life-history scalings across ~4000 mammal species, organized into life-history sizes (A,B), life-history timings (C-G), and components of reproduction (H-K). Overall, the human life history falls within the range of variation of all other mammals, particularly primates. However, panels D-G show that humans have delayed life-history events after birth, and we have a particularly long maximum lifespan for a mammal of our size. Similarly, panels I-K show that while humans have slow rates of reproduction, they are not exceptionally slow for a large primate and are relatively fast for an ape of our size.

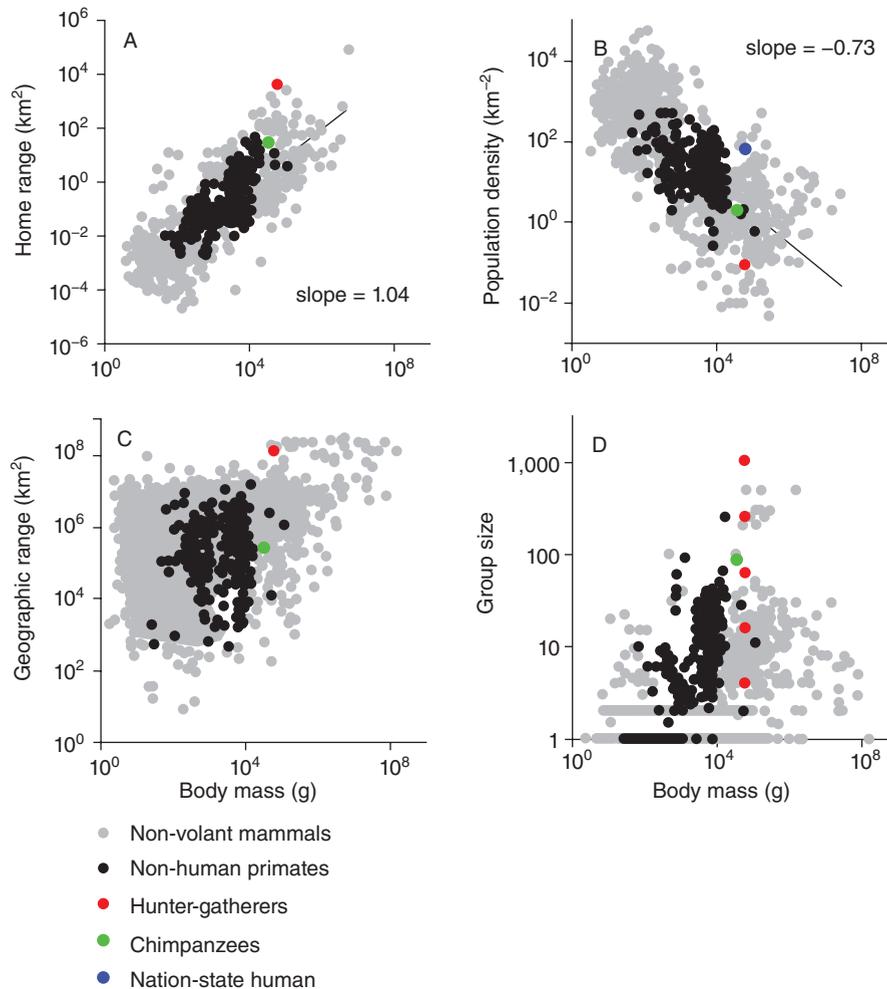


Figure 20.2 Bivariate plots of comparative population ecology across mammal species and human socio-economic conditions. Similar to Figure 20.1, most measures of human ecology fall within the overall range of other mammals, but vary in interesting ways. Hunter-gatherer home ranges are particularly large for our body size (A), but this is primarily due to large hunter-gatherer group sizes (D). Hunter-gatherer population densities are particularly low for a mammal of our body size (B), but densities in modern nation-states have increased from hunter-gatherers by about three orders of magnitude, pushing the upper mammalian bound. We humans have a particularly large species geographic range (C) for terrestrial mammals of our size. Hunter-gatherer group sizes vary throughout the year due to their fission-fusion structure, but interestingly, the average size of total populations is about 1000 individuals, close to the apex of a triangular-shaped distribution of variation of group sizes across mammals (D), suggesting that the large size of human social groups is facilitated by our body mass.

approaching the upper bound for mammals in general, but again, within the overall range of variation for a mammal of our size.

Humans achieved the majority of their current geographic range by the late Pleistocene. Subsequently,

while human population densities have increased by about 1000-fold over the last 13 000 years or so, the extent of our geographic range has not changed significantly. The human species has an extremely large geographic range for our body size, effectively occur-

ring on all available landmasses, excluding Antarctica, and among the largest for any terrestrial mammal. Those with larger ranges in Figure 20.2C are all marine mammals.

Group size in humans is particularly interesting. While the definition of group size is often somewhat ambiguous because there are many reasons why social species form groups (e.g., defense, foraging, cooperative breeding, and so on), humans have an adult body size that falls at the apex of the triangular distribution of group sizes across mammals (Fig. 20.2D). The determinants of group size are poorly understood, but clearly the upper constraints to how large social groups can be must be related to the opposing forces of the benefits of cooperation, and the density-dependence of available resources. Some combination of these forces seems to change abruptly at ~60 kg. Below this size, maximum group sizes increase approximately linearly with body size, and above this size, decrease linearly. Multiple group sizes are shown for hunter-gatherers because hunter-gatherer populations consist of a nested hierarchy of social groups that fission and fuse throughout the year as ecological and social conditions vary (Hamilton et al. 2007b). These groups include nuclear families, seasonally varying sizes of foraging groups, local populations, and regional ethnolinguistic populations (Binford 2001). Consequently, hunter-gatherer societies cannot be meaningfully characterized by a single group size estimate. However, the average size of a hunter-gatherer ethnolinguistic population (the largest social group) is about 1000 individuals (Binford 2001; Hamilton et al. 2007b), a value that falls at the apex of the distribution in Figure 20.2D. So, Figure 20.2D suggests that at a mass of ~60 kg, the size of a human, the balance between access to energy and the cost/benefit of cooperation leads to the largest social group sizes in mammals.

Available data suggests that contemporary human populations form a similar nested hierarchy of groups (Arenas et al. 2001, 2004), but it is often difficult to quantify what those group sizes are. If we take the population sizes of current nation-states, the number of speakers of a language, or adherents of a religion, as measures of the largest, most broadly defined social networks, then these values extend into the millions, even billions. Intriguingly, Figure 20.2D suggests that mammals the size of humans would be predicted to have the largest group size, and so perhaps are subject to the weakest constraints on maximum social group size.

20.4 HUMAN ECOLOGICAL AND EVOLUTIONARY ENERGETICS

We now consider the comparative energetics of human populations by reference to the metabolic theory of ecology (MTE), according to which

$$B = B_0 M^\alpha e^{-E/kT} \quad (20.1)$$

where B is mass-specific metabolic rate, B_0 is a normalization constant, independent of body size and temperature, M^α is the power-law scaling with body mass, M , with α an allometric scaling exponent, and $e^{-E/kT}$ is the exponential Arrhenius function, where E is an “activation energy,” k is Boltzmann’s constant ($8.62 \times 10^{-5} \text{ eV K}^{-1}$), and T is temperature in kelvin (Brown and Sibly, Chapter 2). A central insight of MTE is that the mass-dependence results from the geometry of the vascular networks that supply nutrients to plants and animals (West et al. 1997, 1999a; Brown et al. 2004; Banavar et al. 2010). In most organisms these networks are hierarchically self-similar, fractal-like structures, an especially efficient design for a distribution network to maximize delivery of nutrients to all points within a three-dimensional organism (West et al. 1997, 1999a). Thus, the metabolic rate of an organism is largely a function of the engineering of its underlying distribution network, and the sublinearity of the mass-dependence captures the fact that, as organisms change in size, the overall rate at which they operate, their metabolism, changes nonlinearly, rather than simply proportionally. Equation 20.1 also shows how mass-specific metabolic rate is affected by the operating temperature of an organism.

While this model for the effects of size and temperature on metabolic demand is constructed at the individual level, it has important implications for understanding the structure and dynamics of ecological systems at all levels of biological organization. Moreover, the model’s implications can be generalized straightforwardly to any biophysical system that metabolizes energy in order to maintain structure: the amount of energy a system requires is a function of its size and structure, and the availability of energy is a function of the temperature of the larger system within which that system operates.

This metabolic perspective and the physical and biological principles on which it is based explain much of the observed variation in hunter-gatherer land use (Fig. 20.3). Hunter-gatherer societies are complex adaptive systems that access energy from surrounding

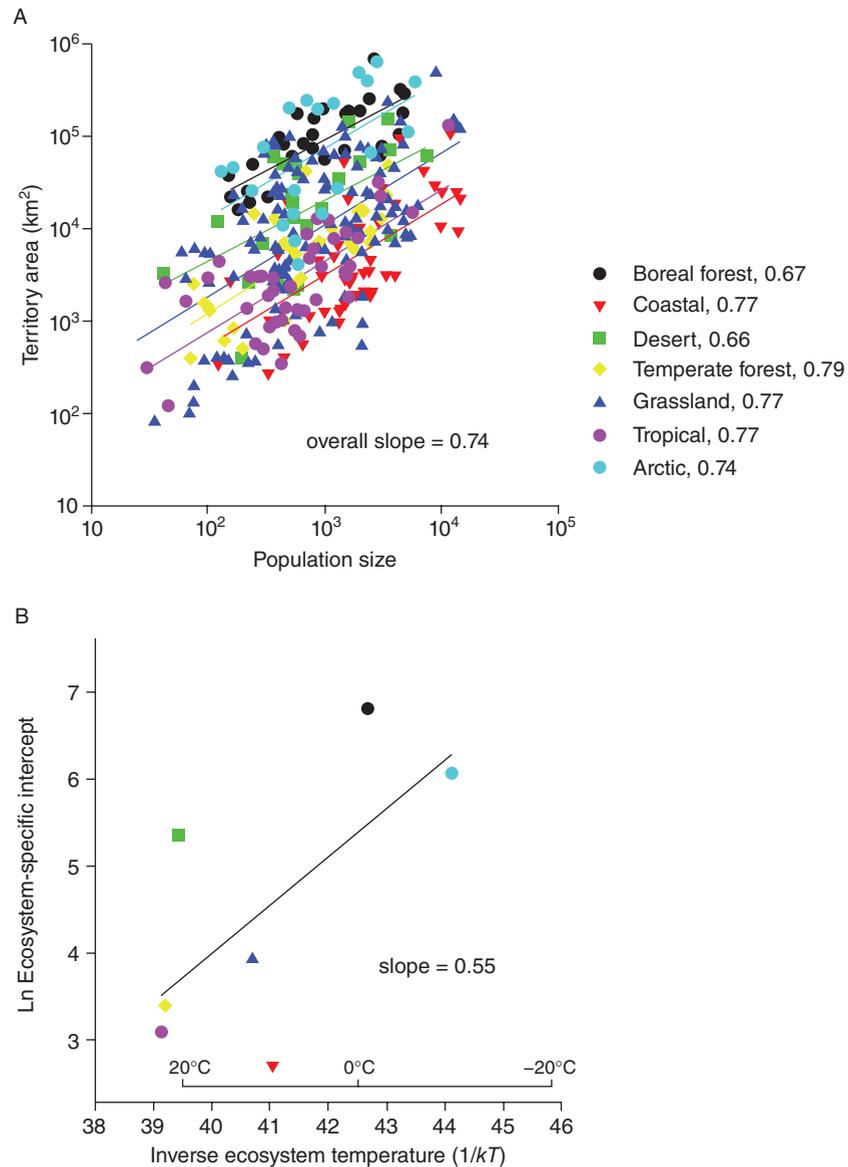


Figure 20.3 Scaling plots of hunter-gatherer territory size by population size for 339 societies, broken into seven primary ecosystem types. (A) shows that populations in all ecosystem types display economies of scale (slopes < 1), with slopes ranging between 0.66 and 0.79, with a consensus GLM slope of 0.74. Generally, intercepts decrease at a consistent rate as ecosystem productivity increases, from Arctic societies, with the highest per-capita space requirements (i.e., highest intercepts) to coastal foragers, reliant primarily on abundant and predictable marine resources, with the lowest per-capita space requirements. (B) plots the intercepts of (A) (i.e., per-capita space requirements) as a function of the average temperature of each ecosystem type. Results demonstrate that much of the change in value of the intercept is explained by ecosystem temperature, a general measure of ecological turnover.

ecosystems that vary widely in temperature, and therefore in the availability of energy. Figure 20.3A shows the territory size of a population plotted as a function of the population size. Territory size estimates the population's total catchment area. While there is considerable variation, the overall scaling relation between territory size, A , and population size, N , is well-described by a power function $A = A_0 N^\beta$, where β is significantly less than 1, and near 3/4 (Hamilton et al. 2007a). Therefore, larger hunter-gatherer populations require proportionally less area to support their energy demands, resulting in an economy of scale in space use where the system increases in efficiency with size. Figure 20.3A shows that when these groups are classified by primary ecosystem type, the same scaling holds within each ecosystem type, and it is only the intercept, A_0 , the height of the scaling function, that changes. The slopes vary between 0.66 and 0.79, and have a consensus slope of 0.74 using generalized linear model (GLM) regression methods. This result demonstrates that hunter-gatherer populations exhibit economies of scale independently of ecosystem type, but the absolute amount of area they require to meet their energy demands varies predictably with ecosystem type. This

result accords with intuition that suggests a society foraging in the Arctic requires more space to harvest resources than one in the tropics. However, it is remarkable that the variation in the intercepts in Figure 20.3A that quantify the amount of space needed in each ecosystem seems to be driven by ecosystem temperature, reflecting the effect of metabolic rate on primary production. As such, this leads to the prediction that the ecosystem-specific per-capita space requirements (the intercepts of the scaling relations in Fig. 20.3A) should increase with decreasing environmental temperature with a slope E of between 0.2 and 1.2, the approximate range of activation energies in terrestrial ecosystems. The Arrhenius plot, Figure 20.3B, shows that the slope of this relation is 0.55, which supports the MTE prediction that variation in space use across hunter-gatherers is driven by the effects of temperature on the rate at which energy fluxes through ecosystems.

Do we see similar macroecological scaling relations in other types of human socio-economies? In particular, are similar economies of scale found in societies that process energy more intensively?

In Figure 20.4 we plot territory size as a function of population size for 1030 subsistence-level societies

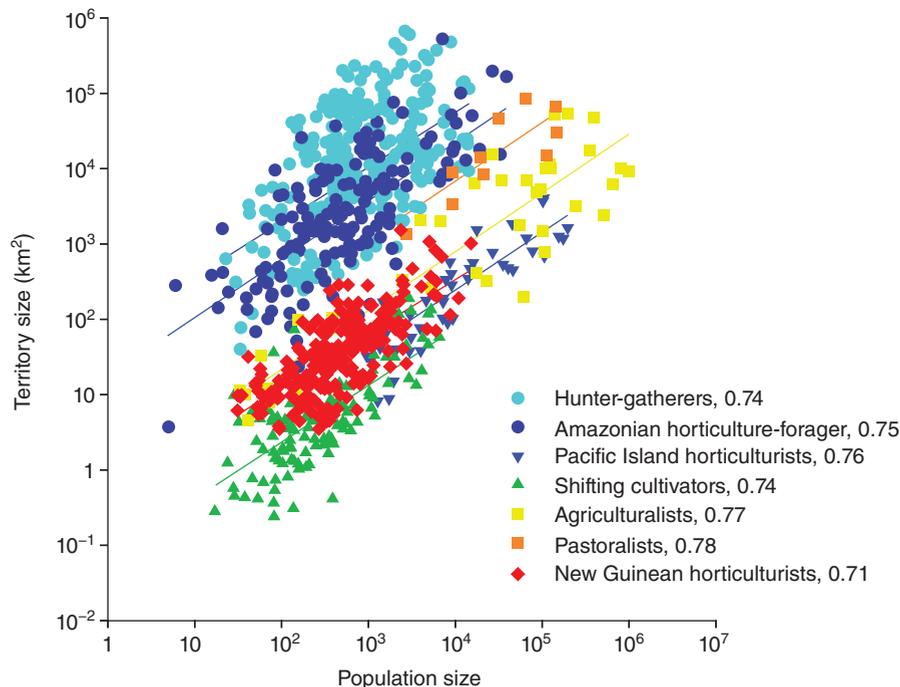


Figure 20.4 Bivariate log-log plot of territory size vs. population size for subsistence-level societies. Sample size is 1030 societies, including ~9 million individuals, covering a total of ~17 million km², ~13% of the planet's land surface.

gathered from the literature, including the 339 hunter-gatherer societies described above, as well as various types of horticulturists, pastoralists, and agriculturists. The slopes range between 0.71 and 0.78, similar to hunter-gatherer societies (Fig. 20.3A), and again, the only quantitative difference between the scaling relations is the change in the intercept, which seems to follow the increasing intensity of land use. The intercepts decrease about three orders of magnitude from hunter-gatherers with the greatest spatial requirements, about 10 km^2 per person on average, and the least intensive energy extraction methods, to shifting cultivators, with the least spatial requirements, about 0.1 km^2 per person on average, and particularly intensive, non-sustainable slash-and-burn agriculture. Thus, empirical data suggests that subsistence-level human societies developed simple yet fundamental economies of scale and maintained them with remarkable consistency. As societies diversified and developed new methods of agriculture that increased the intensity of land use, the energetic outcome was reduced per-capita space requirements. In some cases these methods of resource intensification (i.e., agriculturists, island horticulturists, and pastoralists) increased the total size of populations, from a maximum of a few thousand in hunter-gatherer societies, to hundreds of thousands in the largest agriculturalist societies.

In modern industrialized nation-states, where most individuals are not directly involved in food production, and even fewer exist at a purely subsistence level, there is a fundamentally different relation between population size and area. Clearly, the spatial size of a nation is not determined directly by the subsistence needs of its population, but is determined by a combination of geographic, historical, economic, cultural, and political factors. As such, populations of industrialized nations with complex infrastructure and communication networks have a different set of constraints on how individuals aggregate and fill space than members of subsistence economies. However, this does not mean that the internal structures of industrial societies are not subject to the same overarching energetic constraints that operate on subsistence-scale societies. For instance, Figure 20.5 shows that the total energy consumption of a nation-state scales sub-linearly with population size with a slope of about $3/4$, similar to the scaling in Figures 20.3 and 20.4. This scaling suggests that individuals within more populous nations benefit energetically from existing within

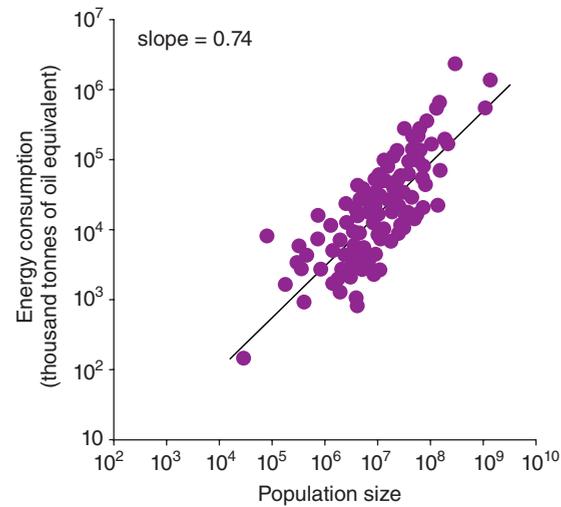


Figure 20.5 Total energy consumption scaling as a function of population size in modern nation-states (data from the World Resources Institute, 2005; <http://www.wri.org/>). The sublinear scaling between the total energy consumption and population size of a nation of ~ 0.75 is similar to the economies of scale exhibited by subsistence-level populations in Figures 21.3 and 21.4.

increasingly developed distribution networks, resulting in economies of scale in national-level energy use.

More generally, these results show that the same economies of scale can be traced from hunter-gatherers across the socio-economic spectrum of subsistence societies to industrialized nation-states, suggesting some degree of universality in the energetics of human populations. Moreover, these economies of scale are quantitatively similar to the scaling of individual metabolic rates in mammals, where larger-bodied mammals are more energetically efficient per unit mass than smaller mammals. This consistent scaling suggests that economies of scale can occur in populations just as they do within individual organisms, and for similar reasons. It is interesting to note that similar $3/4$ -power scaling has recently been reported in studies of the metabolism of social insect colonies (Hou et al. 2010; Waters et al. 2010) (Hayward, Gillooly, and Kodric-Brown, Chapter 6, Fig. 6.6, and Waters and Harrison, Chapter 16, Fig. 16.6), as well as in the energetics of human economies (Brown et al. 2011), suggesting that these scaling relations may be common to social species in general, and quantify the energetic benefits of cooperation.

20.5 CONCLUSIONS

In this chapter we have shown that fundamental components of human ecology, including the speed of life history, rates of reproduction, the energetics of space use, and socio-economic development across populations, are constrained by the same metabolic processes as other mammals, at rates well-predicted by MTE. We have also started to outline a general approach to understanding the ecological and evolutionary energetics of human societies.

MTE provides anthropology with a quantitative body of theory based on the first principles of physics, chem-

istry, and biology. Because the human species is just another mammalian species, this theoretical perspective has much to offer in the study of humans. Importantly, metabolic theory provides a robust theoretical framework which can be used to both predict relationships, and to understand deviations from those predictions, thus gaining a novel perspective into those biological properties the human species shares with all other mammals, and the ways in which the human species is unique in Earth's history.

