of climatically caused megafaunal extinction. They must now posit a climatic phenomenon that could have devastated megafauna before the glacial maximum as well as just after it. They must also explain how climatic change could have extirpated the large, emulike *Genyornis* in Australia 50,000 years ago but left New Zealand's 11 species of Moa, living just across the Tasman Sea, entirely unaffected until just 800 years ago.

A new school of thought has recently established itself in the extinction debate. It advocates the idea that a combination of human impact and climate change was responsible for the extinction of the world's megafauna. The new *Genyornis* data (*2*) also weaken that argument, for the following reason. Fifty thousand years ago, Australia was experiencing mild cooling; 11,000 to 12,000 years ago, the Americas were experiencing rapid warming. These disparate climatic conditions, all coincident with megafaunal extinction, suggest that whatever was happening with climate, it was bad for the big animals. Under these conditions, the hybrid model becomes indistinguishable from the human-caused extinction model, for the influence of climate becomes extremely weak, and only the arrival of humans is important in predicting extinction.

References

1. A. R. Wallace, *The Geographical Distribution of Animals, with a Study of the Relations of Living and Extinct Faunas as Elucidating Past Changes of the Earth's Surface* (Harper, New York, 1876).
2. G. H. Miller *et al.*, *Science* **283**, 205 (1999).
3. R. G. Roberts *et al.*, *Quat. Sci. Rev.* **13**, 575 (1994).
4. R. L. K. Fullagar, D. M. Price, L. M. Head, *Antiquity* **70**, 51 (1996).
5. R. G. Roberts, *Radiat. Measur.* **27**, 819 (1998).

PERSPECTIVES: CLIMATE CHANGE

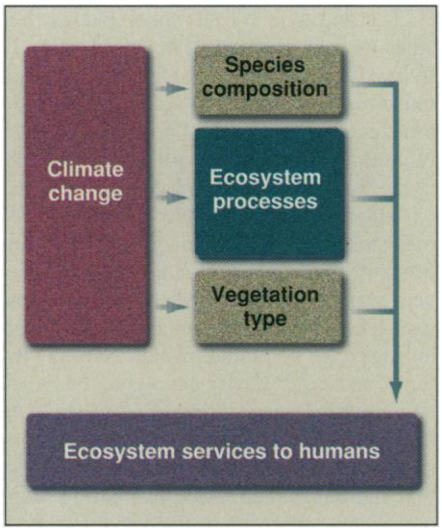
Warm, Warm on the Range

Jerry M. Melillo

The climate of Earth is changing. Climatologists are confident that over the past century, the global average surface temperature has increased by about half a degree Celsius (*1*). This warming is thought to be at least partly the result of human activities, such as the burning of fossil fuels and the clearing of forests for agriculture. As the global population grows and national economies expand, the global average temperature is expected to continue increasing by an additional 1.0 to 3.5°C by the year 2100 (*1*).

Climate change is one of the most important environmental issues facing humankind. Understanding the potential impacts of climate change for natural ecosystems is essential if we are going to manage our environment to minimize the negative consequences of climate change and maximize the opportunities that it may offer. Because natural ecosystems are complex, nonlinear systems, it follows that their responses to climate change are likely to be complex. Climate change may affect natural ecosystems in a variety of ways (see figure). In the short term, climate change can alter the mix of plant species in land ecosystems such as grasslands. In the long term, climate change has the potential to dramatically alter the geographic distribution of major vegetation types—savannas, forests, and tundra. Climate change can also potentially alter global ecosystem processes, including the cycling of carbon, nitrogen, phosphorus, and sulfur. Moreover, changes in these ecosystem processes can affect and be affected by changes in the plant species of the ecosystem and vegetation type. All of the climate change–induced alterations of natural ecosystems affect the services that these ecosystems provide to humans.

The global average surface temperature increase of half a degree Celsius observed over the past century has been in part due to differential changes in daily maximum and minimum temperatures, resulting in a narrowing of the diurnal temperature range. Decreases in the diurnal temperature range were first identified in the United States, where large-area trends showed that maximum temperatures have remained constant or increased only slightly, whereas minimum temperatures (T_{MIN}) have increased at a faster rate (*2*). On page 229 of this issue, Alward *et al.* (*3*) report on the different sensitivities of rangeland plants to T_{MIN} increases.



Interrelations of global climate change and Earth's ecosystems.

On the basis of a decade of measurements at the National Science Foundation's (NSF) Long-Term Ecological Research site in the short-grass steppe in northeastern Colorado, Alward *et al.* concluded that increased spring T_{MIN} was correlated with a reduction in the abundance of buffalo grass, *Bouteloua gracilis*, and an increase in native and exotic forbs. This alteration in species composition of the rangeland affects its ability to provide an ecosystem service that ranchers have come to rely on—the availability of a productive, palatable, drought-resistant grass, buffalo grass, which is important to livestock production in the region.

From their work at the Toolik Lake site in the Alaskan arctic (another NSF Long-Term Ecological Research site), Chapin *et al.* have also reported that climate change can alter plant species composition (*4*). Over a 9-year period, they increased the mean daily air temperature above the vegetation by 3.5°C at a tussock tundra site by placing clear plastic tents over the vegetation. One of the major effects of the warming was to increase the availability of nitrogen to plants by speeding up its release from decaying organic matter. The enhanced nitrogen availability increased the dominance of the four plant species that were initially most abundant and decreased abundance of (or eliminated) plants that were initially least abundant, including forbs and lichens. Forbs in the tundra are nutritionally important and selectively grazed by caribou during lactation, whereas lichens are critical to the over-winter nutrition of caribou. The loss of forbs and lichens from the tundra as a result of climate change could lead to reductions in the caribou herds that are important to the lives of Alaska's native peoples.

Over decades to centuries, climate change may cause large-scale alterations in the distribution of major vegetation types such as grasslands and forests. Global-scale simulations (the new dynamic global vegetation models, for example)

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predict how changes in climate parameters such as maximum and minimum temperatures and the spatial and temporal patterns of precipitation affect the distribution of major vegetation types across the globe (*5*). Using these models with scenarios of future climate change, researchers have identified many potential consequences of large-scale vegetation shifts. The composition of one-third of Earth's forest could change markedly as a result of climate changes associated with a doubling of atmospheric CO_2. Over the next 100 years, the ideal range for some North American forest species could shift as much as 300 miles to the north. Economically and aesthetically important species, such as the sugar maple, could be lost from New England by the end of the next century (*6*).

One of the most robust predictions of the new dynamic global vegetation models is that by 2100, boreal forest will occupy a substantial portion of the land that is now covered by tundra vegetation. Because boreal forests absorb much more solar radiation than tundra does, poleward shifts in the location of the forest-tundra boundary during a period of warming can amplify climate changes by as much as 50% (*7*).

Researchers are using three main approaches for investigating the consequences of climate change on natural ecosystems. Through long-term observations, including those taken from the paleorecord, scientists have begun to detect some of the effects of warming on the structure and function of natural ecosystems. Through experimental manipulations of the environment and the use of ecological simulation models, scientists are gaining insights into possible future consequences of warming and other aspects of climate change for our life support system, the biosphere. These three approaches—observation, experimental manipulation, and simulation modeling—are complimentary and are all needed to improve our understanding of the consequences of climate change for Earth's life support system, the biosphere.

References

1. Intergovernmental Panel on Climate Change (IPCC), *Climate Change 1995: The Science of Climate Change*, J. T. Houghton *et al.*, Eds. (Cambridge Univ. Press, Cambridge, 1995).
2. D. R. Easterling *et al.*, *Science* **277**, 364 (1997).
3. R. D. Alward, J. K. Detling, D. G. Milchunas, *ibid.* **283**, 229 (1999).
4. F. S. Chapin III *et al.*, *Ecology* **76**, 694 (1996).
5. International Geosphere-Biosphere Programme (IGBP), *IGBP Science, No. 1: A Synthesis of GCTE and Related Research*, B. Walker and W. Steffen, Eds. (IGBP, Stockholm, Sweden, 1997).
6. Intergovernmental Panel on Climate Change (IPCC), *Climate Change 1995: Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses*, R. T. Watson *et al.*, Eds. (Cambridge Univ. Press, Cambridge, 1995).
7. J. A. Foley *et al.*, *Nature* **371**, 52 (1994).

PERSPECTIVES: HUMAN PHYSIOLOGY

Beyond Sloth—Physical Activity and Weight Gain

Eric Ravussin and Elliot Danforth Jr.

Obesity is not sought. It appears uninvited and is epidemic in modernized societies in which overconsumption of food is promoted and physical activity discouraged (*1*). Gluttony and sloth are frequently blamed, but in fact it is not clear why some of us in this environment become obese (despite considerable effort not to) while others, without such effort, do not. It has been difficult to accurately solve the energy balance equation in people to determine whether differences in energy expenditure explain these differences in obesity. Now Levine *et al.* (*2*) on page 212 of this issue offer evidence that the best predictor of interindividual differences in fat gain during overeating is the amount of certain physical activity triggered by the excess food. More specifically, this physical activity consists of movements during daily living, termed nonexercise activity thermogenesis, or NEAT.

The acronym NEAT encompasses, besides the energy costs of activities of daily living, the energy costs of all nonvolitional muscle activity such as fidgeting, muscle tone, and maintenance of posture when not lying down—essentially all physical activity not picked up by a pedometer.

Although humans have evolved thrifty mechanisms to defend energy stores during times of privation, they cannot easily prevent storage of energy when food is abundant. The survival mechanisms that evolved during times of famine, which Neel (*3*) referred to as the "thrifty genotype," becomes a liability for some during times of feast. At the turn of the century Neumann (*4*) from studies on himself, was the first to suggest that the consequences of overeating were not always reflected in the weight gained, referring to it as "luxuskonsumption." "Easy" and "hard gainers" (of weight) were uncovered in response to purposeful overfeeding by Sims *et al.* (*5*), and resistance to change in body energy stores was recently documented by Leibel *et al.* (*6*). Bouchard *et al.* (*7*), in studies of identical twins, established that the ease of weight gain is influenced by genes. The responsible mechanisms, however, have remained elusive.

Selective breeding of rodents, cattle, pigs, and chickens have uncovered breeds with variable energy efficiencies during growth, and variable energy requirements for maintenance of adult weight (*8*). Overfeeding activates the sympathetic nervous system, resulting in increased thermogenesis in brown fat through uncoupling of oxidative phosphorylation. Such a mechanism wastes energy as heat and is similar to what is observed during exposure to cold in small animals and human infants (*9*). Whether some humans may be hard gainers because of their greater retention from birth of active brown fat remains to be established.

The energy expenditure upon overfeeding can be divided into several components (see the figure). After overfeeding, the resting metabolic rate—popularized by Boothby for the diagnosis of thyroid disorders (*10*)—increased modestly, accounting on average for 8% of the excess calories consumed. The increase in the thermic effect of food (the cost of absorbing and storing the ingested calories) was only proportional to the increase in the ingested calories, accounting for 14% of the daily excess. Similarly to resting metabolic rate, the increase in the thermic effect of food could not account for the differences between individuals. So what did account for the interindividual variability in gain in body fat? The authors concluded that it must be the remaining way that energy is expended—in physical activities, volitional or otherwise.

As pointed out by the authors and suggested years ago by Widdowson (*11*), the fidgetiness of an individual likely plays a more important role in daily energy expenditure than previously thought. Within the confines of a respiratory chamber spontaneous physical activity (fidgeting) accounted for an average of 348 kcal/day (*12*). More important, it is a major cause of individual differences in 24-hour energy expenditure (100 to 700 kcal/day) and is a predictor of gain in weight (*13*).

In the present study, the energy cost of physical activity was carefully apportioned between voluntary exercise (such as walking and running) and nonvoluntary exercise (NEAT). Accomplishing this is a "tour de force" in the use of state-of-the-art modern techniques for assessing energy metabolism and body composition in humans. The key was the use of the dou-

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