

tracted from bone, the occasional late dates reported for whole bone disappear, and dates based on extracted amino acids themselves⁸ cluster around 11,000 yr BP (ref. 9). This corresponds to the date of the first stone-tool horizon documented for the New World, the Clovis horizon. The same date is obtained for the extinction of the Shasta ground sloth based on carbon-14 analyses of its dried dung balls, whose provenance from the animal is unassailable. The last dung balls are dated around 11,000 yr BP, whether taken from caves in juniper-ash woodland at an elevation of 1,800 ft or from caves in spruce-oak woodland at 6,500 ft. If the Shasta ground sloth did succumb to climate changes simultaneously in two such different habitats just at the time that Clovis hunters arrived, this supposedly stupid animal deserves credit for hitherto unsuspected cunning in confusing later palaeontologists.

An extinction symposium held 10 years ago would have considered man as an architect but not a victim of extinctions. The formerly prevalent view was that there has been only a single hominid line, hence no extinctions of hominid species. There is now widespread agreement that two hominid lines co-existed in Africa until almost 1 Myr ago: the *Homo habilis*-*Homo erectus* line, that survived as *Homo sapiens*; and the *Australopithecus robustus* line, that became extinct (A. Walker, Johns Hopkins University). The latter line was a small-brained vegetarian with massive chewing muscles and teeth. (It is unclear whether other smaller hominid skulls represent female *H. erectus* or a third line that also became extinct.)

Walker saw the evolution of *Homo* and the extinction of *A. robustus* as related to changes in three African large-animal guilds between 2 and 1 Myr BP: the scavengers, stalking carnivores and running carnivores. During this period the carnivore guilds suffered the extinctions of the running hyena *Euryboas*, three sabretooth cats and a cheetah; *H. habilis* evolved to join and then leave the brown and spotted hyenas in the scavenger guild; *H. erectus* and the lion evolved to join the leopard in the stalking-carnivore guild; and the hunting dog evolved to join the cheetah in the running-carnivore guild¹⁰. By the time the dust from this evolutionary reshuffle had settled around 1 Myr BP, the three guilds had reached their modern composition, *H. erectus* had become the first hominid to expand beyond Africa (to Asia) and the prey species¹¹ *A. robustus* was gone.

It is possible, but disputed, that another hominid extinction occurred later: that of Neanderthal man. European Neanderthals either evolved very quickly into, or were replaced very quickly by, *H. sapiens*. Walker's analysis of skull shape shows that Neanderthals were much more similar in this respect to *H. erectus* than to *H. sapiens*. Does this suggest another

bifurcation and another extinction?

The constant background of extinctions, from which these occasional extinction catastrophes stand out, was reviewed by J. Diamond (University of California, Los Angeles) and illustrated for Rocky Mountain mammals by B. Patterson (Field Museum). Background extinctions reveal themselves on several time scales: over a decade or two, in the turnover of populations on islands¹²; over a century, in the extinctions of populations in patches of habitats fragmented by man^{13,14}; over the past ten millennia, in the extinctions of populations on land-bridge islands or habitats fragmented by late-Pleistocene changes in sea level and climate^{15,16}; and over geological time, in the extinctions implicit in patterns of endemism¹². Theoretical considerations suggest that the risk of extinction for isolated populations in a fluctuating environment should decrease with population density, island size, generation time, population stability, intrinsic rate of increase and the ratio of birth rates to death rates¹⁷. The latter two predictions remain untested, but the first four are confirmed by the studies at various time scales. The steep decrease in extinction rate with population density means that isolated populations of carnivores, large animals and habitat specialists are generally at greater risk than populations of herbivores, small animals and habitat generalists.

Finally, T. Lovejoy (World Wildlife Fund) described an experimental study that World Wildlife Fund is carrying out jointly with the Brazilian government to examine the effects of clearing Amazonian rain forest for agriculture¹⁸. The results of this study will be described in detail in a later article in *News and Views*. What World Wildlife Fund and the Brazilian government are doing as a small-scale controlled experiment in order to learn, man throughout the world is doing as a massive uncontrolled experiment in the name of development. Today's asteroid collision is of our own making. □

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Ecology

Cycling index

from John T. Finn

IN Robert May's *News and Views* article on energy cycling¹, an error has been occasioned by the use of different definitions of the cycling index in the earlier and later papers he discusses. In our early papers^{2,3} we defined the cycling index (as described by May) as 'the fraction of total flow through the system that derives from cycling, expressed as a ratio to the fraction of the total that derives from flow straight through the system'. This index can vary from zero to infinity. However, in my later papers^{4,5}, I redefined the cycling index as the fraction of total flow through the system that derives from cycling, expressed as a ratio to the total flow through the system. This index can vary from zero (no cycling) to one (complete cycling). In comparing nitrogen cycling of the Luquillo tropical rain forest in Puerto Rico and Hubbard Brook, May¹ used figures derived from the first definition for Luquillo (1.76) and figures derived from the second definition for Hubbard Brook (0.76), to conclude erroneously that Luquillo cycles more than Hubbard Brook. Using the second definition for comparison with Hubbard Brook, the proper value for Luquillo is 0.48, so according to these models, Hubbard Brook cycles more nitrogen (proportionately) than does the Luquillo rain forest.

At first, it seems that the models must be wrong. Indeed, some components of the gaseous flux of nitrogen at Hubbard Brook and at Luquillo have yet to be adequately measured, so the cycling indices may change. However, it is still instructive to wonder why a temperate forest should cycle more nitrogen than a tropical forest. First, the large forest floor of the temperate forest gives it an advantage in holding nutrients, especially for a forest like Hubbard Brook that is still accumulating both live and dead biomass. Second, higher temperatures at Luquillo speed up processes of nitrogen loss (decomposition and denitrification) as well as gain (fixation). Finally, greater rainfall subjects Luquillo to a higher potential loss of nutrients through leaching. The Puerto Rican rain forest may cycle nutrients faster by using primarily active biological mechanisms to prevent nitrogen from leaching away, but the proportion of nitrogen cycled compared with nitrogen flowing through the system could be less than at Hubbard Brook. □

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