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LETTERS SCIENCE & SOCIETY POLICY FORUM BOOKS *ET AL.* PERSPECTIVES REVIEWS

A Family Tree for Heavyweights

A CLOSE KINSHIP OF WHALES TO HOOFED mammals, and to hippopotamuses in particular, is discussed in two articles in the issue of 21 Sept., "The ancestry of whales," a Perspective by K. D. Rose (p. 2216), and a Report, "Origin of whales from early artiodactyls: hands and feet of Eocene Protocetidae from Pakistan" by P. D. Gingerich, M. ul Haq, I. S. Zalmout, I. Hussain Khan, and M. Sadiq Malkani (p. 2239). This is not a new idea. Rather, it is a vindication of the earliest explicitly phylogenetic classification of mammals. In 1866, the pioneering evolutionary biologist Ernst Haeckel classified the order Cetacea (in which he also included the sirenians) and the order Ungulata (with Artiodactyla and Perissodactyla as suborders) together under his legion Pycnoderma (*1*). In his formal classification, the hippos were placed as family Obesa, which, along with the pigs, anthracotheres, and their close allies, comprised section Choeromorpha under the suborder Artiodactyla. However, in his phylogenetic tree of the Mammalia (Plate VIII), he depicts the Cetacea and the Obesa as sister taxa; this whale-hippo clade was, in turn, the sister taxon to the clade containing the pigs and anthracotheres.

Later, Haeckel abandoned this phylogeny and considered the origin of whales questionable (*2*). Most subsequent cetologists dismissed or ignored the possibility of a relationship between whales and ungulates until the idea was revived by molecular biologists in the late 20th century.

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Ernst Haeckel and friend Allens (Italy, 1862).

Letters to the Editor

Letters (~300 words) discuss material published in *Science* in the previous 6 months or issues of general interest. They can be submitted by e-mail (science_letters@aaas.org), the Web (www.letter2science.org), or regular mail (1200 New York Ave., NW, Washington, DC 20005, USA). Letters are not acknowledged upon receipt, nor are authors generally consulted before publication. Whether published in full or in part, letters are subject to editing for clarity and space.

Did Human Hunting Cause Mass Extinction?

JOHN ALROY'S SIMULATION OF NORTH American terminal Pleistocene mammalian extinctions (Reports, "A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction," 8 June, p. 1893) leads him to conclude that people caused the loss of 41 species of mammals. However, the overkill argument is confronted by overwhelming empirical problems, two of which I mention here.

In Alroy's model, the median age of the extinction event falls 1229 years after the initial human invasion. Using a date of 13,400 yr B.P. for the appearance of Clovis and 12,260 yr B.P. for the youngest extinctions, he obtains a close match between his prediction and the empirical data he uses. However, of the 35 genera of mammals that were lost toward the end of the Pleistocene in North America, only 15 can be shown to have survived into Clovis times (*1*). One can assume that the remaining 20 genera must also have been lost during those times, but assuming that all the extinctions occurred specifically during Clovis times, and then using Clovis to explain them, is problematic.

Alroy correctly observes that "humans are known to have hunted extinct megafauna" in North America, but mammoth is the only extinct mammal to have been found in secure kill association in North America. This is unlikely to be the result of sampling error, since mammoth account for only about 20% of the known late Pleistocene occurrences of extinct noncarnivores in the comprehensive FAUNMAP database (*2*).

Overkill is confronted by other significant problems (*1*, *3*), but these suffice to make the point. There is little in the empirical record to support the argument that the initial human colonization of North America led inexorably and rapidly to massive extinction.

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Response

GRAYSON OVERLOOKS THE MODEL'S KEY predictions concerning overall extinction rates, extinction outcomes, human population densities, and human diet, and just as importantly, its robust logic and parameterization. The model correctly predicts that terminal megafaunal dates should be no younger than Clovis interval, but Grayson demands that no apparent terminal dates should be older than Clovis. The data are sufficient to test the former prediction but not the latter: radiocarbon dates are scarce for all but six megafaunal genera—and these genera did overlap with Clovis (*1*). Regardless, speculating that some megafaunal species went extinct earlier accomplishes nothing, because all reasonable models predict rapid extinctions. Indeed, Grayson himself offers no possible explanation for staggered extinctions.

As for Grayson's second point, there are kill sites not just for mammoths (*2*), but also probably for mastodons (*3*) and even giant tortoises (*4*); thus, humans clearly were capable of hunting all terrestrial species. Kill sites for smaller species are not expected because small bones are fragile, and so skeletons of smaller taxa are preserved only rarely outside of kill-free natural trap environments. Furthermore, the distribution of radioisotopic dates (*1, 5*) shows that proboscideans attract disproportionate study. More importantly, of 61 confirmed latest Pleistocene *M. columbi* fossil sites (*6*), some 9 sites, or 15%, include kills (*2*), but the simulation model conservatively predicts that just 9% of Clovis-era *M. columbi* deaths were caused by human hunting. Thus, the kill site data do confirm overkill.

In addition, overkill accounts for a string of dramatic and otherwise inexplicable patterns. Why else would an extinction pulse (i) range from Alaska to Patagonia, but have no contemporary effect on islands and Old World continents (although extinctions did invariably follow the invasion of these places by humans at earlier and later times); (ii) focus on geographically widespread, environmentally unspecialized species, but spare virtually all mammals less than 10 kg or plants of any kind (*7*); (iii) have no clear impact on surviving mammal communities; (iv) occur during a deglaciation that doubled the habitable area of the continent; (v) fail to occur during any of a half-dozen comparable, earlier deglaciation events; and (vi) find itself unmatched in selectivity and severity by any extinction during the preceding 65 million years (*8*), during which time climate change showed no correlation with extinction (*9*)?

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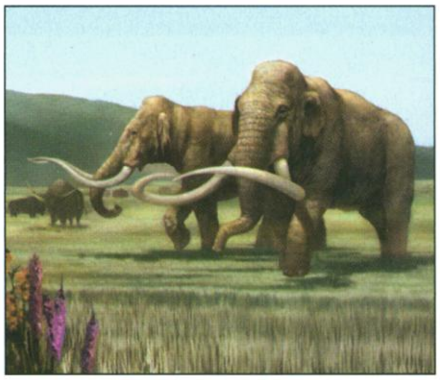

Was the extinction of mammoths and other megafauna of the Americas at the end of the Pleistocene due to human hunting?

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Alroy's claim that hunting by humans could explain the end-Pleistocene mass extinction of large herbivorous mammals in North America (8 June, p. 1893) was based on simulations that were computed with a mathematical model. However, in his model

Alroy used unrealistically low "r_m" values—species-specific growth constants that describe the maximum or intrinsic rates at which populations can increase—for the prey species, and thereby overestimated the ability of humans to hunt these mammals to extinction. Because any species whose population is killed off faster than it can increase is obviously doomed to extinction, the ability of a prey species to survive human predation is critically dependent on r_m.

Because there is a roughly inverse relationship between r_m and body mass (*1–3*), r_m values can be approximated using body mass estimates. The equation Alroy uses to generate r_m values for the large herbivores in his model is

$$r_m = \exp(1.4967 - 0.37\ln[\text{body mass, g}])$$

which simplifies to

$$r_m = 4.4669 \times [\text{body mass, g}] - 0.37.$$

Although cited as the source of this equation, Hennemann (*1*) actually gives

$$r_m = 4.9 \times [\text{body mass, g}] - 0.2622$$

For any given species, Alroy's equation yields an r_m that is much lower than those generated by other equations (*1–4*). In addition, Alroy's r_m values for extant species are substantially less than those based on field observations (e.g., *5–7*). For example, using Alroy's figure of 106.85 kg for the average adult mass of a white-tailed deer, Hennemann's equation gives an r_m of 0.24. Observed values for this notoriously prolific species range up to 0.57 (*6*). Alroy's equation, on the other hand, generates an r_m of 0.06, which is lower than that observed for the African elephant (*8, 9*).

In Alroy's best-fit simulation, no species with an $r_m \geq 0.08$ goes extinct. However, if Hennemann's equation is substituted, every species has an $r_m \geq 0.08$. Based on this, we suspect that if Alroy's model were run with reasonable estimates of r_m, fewer extinctions would occur, and that considerably more humans would be needed to achieve these extinctions. Because the smallest mammals would experience the largest gains in r_m, we also anticipate that Alroy's model would be even less accurate at predicting the true fates of extinct species with body masses below 250 kg. As it stands, 6 of the 10 extinct species weighing less than 250 kg survive in the best-fit simulation. In a more ecologically realistic version of Alroy's model, human predation could not account for the full spectrum of megafaunal extinction.

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Response

I THANK SLAUGHTER AND SKULAN FOR pointing out a minor programming error, which lowered both intrinsic rates of population growth r_m (as they noted) and equilibrial prey population densities.

These errors have no substantial qualitative impact on the results. Correcting coefficients for the original trial 8 actually increases the predicted number of extinctions from 27 to 29 and leaves most other parameters largely unchanged: the maximal human population growth rate (1.90%), the relative amount of primary production consumed by herbivores (0.554), and the median time to extinction (895 years). So, contrary to Slaughter and Skulan's speculation, the model still leads to multiple extinctions of deer-sized species, with victims having r_m values as high as 0.28 (e.g., *Stockoceros conklingi*).

The reason for the almost unchanged results is feedback: Larger and more rapidly growing prey populations merely make life easier for hunters, thereby fueling the strong, indirect interspecific competition that generates most extinctions. High game abundance increases both the equilibrial proportion of calories obtained by hunting (0.294) and final human population density (28.31 people/100 km^2). However, both figures are still easily within the known ranges for hunter-gatherers in a variety of habitats (*1, 2*).

Despite the increase in the predicted human population density, variations of the model still show that even marginal populations could generate a mass extinction. Lowering the hunting ability coefficient to 0.30 drops the population density by almost half to 15.23 people/100 km^2, and yet 24 species still go extinct. Decreasing the caloric subsidy from plants and small game by one-quarter cuts the density to 15.91 people/100 km^2, but still leads to 25 extinctions. A decrease of one-half drops the density to just 5.75 people/100 km^2, but still leaves 14 species extinct and six others doomed.

In sum, the model's results are, if anything, improved by these minor corrections. Indeed, a simulated extinction of herbivores ranging in size from mammoths to four-horned antelopes is inevitable in the simulation regardless of how one fixes all sorts of parameter values: the relative degree of human hunting ability; the initial geographic point of invasion; prey dispersal rates; and direct competition for food among prey species (*3*). Likewise, exactly the same 29 extinctions result—albeit at slightly different times—if one changes either the 3% maximum population growth rate or the 40% upper limit to killing rates when prey are superabundant. Ultimately, the only important factors in this model are the undeniable ones: substantial variation among prey species in reproductive rates, strong dependence of human population growth on prey availability, and the broad, unspecialized predatory habits of humans.

Standard ecological theory (*4*) shows that these factors lead inexorably to strong apparent competition, and therefore to mass extinction.

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Unpublished Record of a Career in Meteoritics

IN HIS NEWS FOCUS ARTICLE ABOUT METEoriticist John Wood and his views on the state of meteoritic science, Richard A. Kerr says, "The editor of the field's lead-