

Supporting Text

The Structure of Megafaunal Extinction Models. Overkill is a very specific and apparently tractable hypothesis, making it attractive to modeling. Models can be simplified greatly if it is assumed that hunters preferentially targeted individual prey species and that alternative animal and vegetable food sources were available to subsidize their hunting effort (1). This obviates the need to consider the added complexity of multiple prey species as was attempted by Alroy (2), although in the majority of his scenarios (79%) the simulated megafauna effectively functioned as a single “undifferentiated ecological unit.”

Fundamentally, all models of overkill depend on four terms: density of megafaunal prey populations (P), density of human populations (H), replacement rate of prey populations (r), and rate of off-take by human hunters (O). Extinction follows when the consumption of prey exceeds their replacement rate, that is,

$$OH > rP. \quad [1]$$

Although Eq. 1 is trivial, the estimation of its terms is not. Because of the impossibility of undertaking ecological studies of long-extinct animals and anthropological studies of Pleistocene human societies, overkill models are based on estimates derived from studies of contemporary hunter-gatherer and megafaunal populations (3). The timing and geographical pattern of human colonization is revealed by the archaeological record (4–6). Upper bounds of human population density and meat consumption are estimated from anthropological studies (1, 2). Prey replacement and density are usually modeled via a density-dependent relationship such as the logistic growth model, with the parameters inferred from body-mass allometry of extant species (1, 2). It is difficult to imagine how better estimates for these parameters can ever be obtained. Although it is routine for modeling exercises to undertake sensitivity analyses to determine the importance of uncertainty in input parameters, the results of such analyses are hostage also to a diverse array of explicit and implicit (often hidden) assumptions. For example, a rarely explicitly stated assumption is that predator efficiency is maximal (1). However, it is known that hunting success varies in response to the capacity of the prey to evade human hunting due to an ensemble of behavioral, genetic, and habitat-related factors. Incorporation of relative prey naivety in population-dynamics models is achieved by specifying a “functional response”; a concept fundamental to predator–prey theory (7, 8). In formal mathematical terms, the functional response can be described by the following equation (9).

$$\text{Predation rate} = \frac{FP^z}{G + P^z}, \quad [2]$$

where P is the density of prey populations, F is the maximal predation rate, G is a constant equal to the prey density at which predation is half-maximal, and z is a measure of the departure from maximal predation efficiency. Although the biological meaning of these terms is open to interpretation, clearly z would be strongly affected by relative naivety. In a “type II functional response” $z = 1$, and predation is modulated only by prey density and search efficiency. To date, all overkill models assume prey off-take is described by a type II functional response (e.g., refs. 1 and 2) or else take the extremely unrealistic view that off-take is entirely independent of prey density (e.g., ref. 10). If, however, prey are able to find safe refugia (e.g., ref. 11) or can adapt to new predators, they become harder to hunt at low densities, thereby stimulating predators to expand their dietary breadth to include other more abundant species that are easier to locate and/or catch. Such a predator–prey relationship can be described by the type III functional response where $z > 1$.

To explore the sensitivity of the generalized overkill model to the assumption of a type II functional response, we ran 10,000 parameter combinations for 20 different values of z ranging from 1 to 2 at increments of 0.05. The model was implemented by using the software @RISK 4.5 (Palisade Corporation, Newfield, NY) for Microsoft EXCEL. In our simulations, the values of megafaunal and human densities, prey-replacement rate and hunting off-take, were varied randomly according to uniform distributions between the minimum and maximum levels given by Alroy (2) and others (1, 10, 12, 13), where [min, max] were: r [0.01, 0.44], P [0.16, 17.2], O [0.14, 82.1], and H [0.02, 0.21].

Simulation to Determine Effect of Data Pruning of Megafaunal Remains. We used resampling simulations (see ref. 14) to determine how the lower 95% confidence bound for the sample age of the youngest articulated skeleton (46,000 yr old) changed as the number of samples (n) included in the analysis was increased consecutively. Starting with the three youngest sites, we successively introduced the next oldest site in each iterative step, thereby creating a total of 17 individual data sets (i.e., containing between 3 and 19 sites) where the upper age bound of each uniform distribution was set by the age of the oldest site included. For each of these 17 data sets, a uniform distribution was assumed as did Roberts *et al.* (15), and each distribution was sampled randomly 10,000 times by using @RISK 4.5.

When Did Humans First Arrive in Greater Australia? Resampling simulations also were carried out on three different data sets of archaeological data to determine the 95% confidence bound of the first arrival of human colonists in Greater Australia. The first data set was created by rejecting all dates derived from the application of new geochronological techniques (which are beyond the limits of established radiocarbon dating), yielding 26 dates of archaeological sites older than 34,000 yr (listed by ref. 4). Resampling of this data set, in the manner described above for the megafaunal remains, yielded an upper 95% confidence bound of 44,200 yr before present (B.P.). A second set of archaeological sites ($n = 7$) was created by including only radiocarbon-dated remains by using the most advanced sample-preparation techniques [e.g., acid/base/dichromate oxidation with stepped combustion (ABOX-SC) chemistry; see ref. 16]. Resampling this data set yielded a confidence bound of 56,000 yr B.P. Finally, a third data set was examined that included only the three

controversial older archaeological sites (with dates ranging from 53,000 to 61,000 yr B.P.) based on a range of new geochronological techniques [e.g., thermoluminescence/optically stimulated thermoluminescence (TL/OSL) and uranium-thorium series dating/electron spin resonance (U/Th/ESR); see refs. 4, 5, and 17]. Resampling this last data set yielded an upper 95% confidence interval of 71,500 yr B.P. (\pm laboratory measurement errors).

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