

MACROECOLOGICAL ANALYSES SUPPORT AN OVERKILL SCENARIO FOR LATE PLEISTOCENE EXTINCTIONS

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(With 2 figures)

ABSTRACT

The extinction of megafauna at the end of Pleistocene has been traditionally explained by environmental changes or overexploitation by human hunting (overkill). Despite difficulties in choosing between these alternative (and not mutually exclusive) scenarios, the plausibility of the overkill hypothesis can be established by ecological models of predator-prey interactions. In this paper, I have developed a macroecological model for the overkill hypothesis, in which prey population dynamic parameters, including abundance, geographic extent, and food supply for hunters, were derived from empirical allometric relationships with body mass. The last output correctly predicts the final destiny (survival or extinction) for 73% of the species considered, a value only slightly smaller than those obtained by more complex models based on detailed archaeological and ecological data for each species. This illustrates the high selectivity of Pleistocene extinction in relation to body mass and confers more plausibility on the overkill scenario.

Key words: overkill, macroecology, Pleistocene, extinction, hunter-gatherers.

RESUMO

Análises macroecológicas apoiam o cenário de sobreexploração para as extinções do final do Pleistoceno

A extinção da megafauna no final do Pleistoceno tem sido tradicionalmente explicada por grandes mudanças climáticas ou pelo efeito de “sobreexploração” por parte dos primeiros caçadores (*overkill*). Apesar das dificuldades e controvérsias na distinção desses dois cenários não mutuamente exclusivos, a plausibilidade do cenário de sobreexploração pode ser avaliada por modelos de interação predador-presa. Neste estudo, demonstrou-se como um modelo macroecológico determinístico (isto é, utilizando parâmetros derivados de relações alométricas para diferentes espécies pode ser utilizado para avaliar a dinâmica das presas potenciais dos primeiros caçadores na América. Esse modelo previu corretamente o destino de 73% das espécies, valor apenas pouco inferior ao obtido por outros modelos mais complexos para o cenário. Isso ilustra a elevada seletividade do cenário de sobreexploração em relação ao tamanho do corpo e sua plausibilidade como explicação para as extinções da megafauna no final do Pleistoceno.

Palavras-chave: “sobreexploração”, macroecologia, Pleistoceno, extinções, colonização da América.

INTRODUCTION

The extinction of megafauna at the end of Pleistocene has received special attention since the

end of 60s when Paul Martin developed the overkill hypothesis, according to which waves of hunters caused the extinction of most megafauna species in North America. The coincidence between extinction

of large animals and the first arrival of human populations was also noticed for many other parts of the world and at different times (Marshall, 1988; Stuart, 1991; Miller *et al.*, 1999; Holdanay & Jacomb, 2000; Schuster & Schule, 2000; Roberts *et al.*, 2001; Haynes, 2002; Bowler *et al.*, 2003). However, the detailed scenario, called “blitzkrieg”, proposed for overkill in North America was not fully accepted and many researchers attributed these extinctions to global climatic changes that occurred at this period (see Ward, 1997, for a recent review of the controversy). The debate continues until the present, especially because of the uncertainties involving the archaeological record and the interaction between the two most probable causes (i.e., human impact and climatic changes) (Beissinger, 2000; Grayson, 2001; Powell, 2002; Bowler *et al.*, 2003).

Ecological models and computer simulation started to play an important role in the overkill debate in the 1980s, but with ambiguous results depending on the assumptions underlying the models (Beck, 1996; Choquenot & Bowman, 1998). More recently, Alroy (2001) developed a detailed simulation model to test the overkill hypothesis using a spatial diffusion model to verify, based on realistic demographic and distributional parameters, whether low-density hunter-gatherer populations could cause the extinction of large preys in North America. These parameters include human nutritional needs, human and prey demography (including respective population growth and competition among them), and the spatial distribution of prey species and the expansion of humans in North America, inferred from archaeological and paleoclimatic data. Alroy (2001) concluded that, even using conservative parameters, expanding populations of hunter-gatherers could cause the extinctions observed in a period ranging from 1,000-2,000 years, similar to real time estimates according to the archaeological record.

In this note, I show that a much simpler deterministic model, using macroecological allometric relationships (Brown, 1995; Gaston & Blackburn, 2001; see also Moses & Brown, 2003), based mainly on body mass variation among prey species, can accurately predict megafaunal extinctions, furnishing a close match to more complex simulation models of spatial predator-prey dynamics recently developed by Alroy (2001) and lending more plausibility to the overkill hypothesis.

METHODS

I obtained a species list and average estimated body mass from supplemental material supplied by Alroy (2001) (see www.sciencemag.org). With this basic dataset and using the strategy that follows, I developed a simple model showing species interaction with hunter-gatherers.

Based on Alroy (2001), I defined human individual nutritional needs as 2200 kcal/day. Since meat furnishes 3 kcal/g, each human individual must consume 733.3 g/day obtained from big game (Campbell, 1998; Alroy, 2001). Therefore, consumption of meat (C) by a human population with H individuals is given by

$$C = [(2200/3) * E] * H * 365$$

where E is the proportion of meat in the diet. Using this C -value, it is possible to infer the number of individuals removed from a prey population (N_R), based on two other values: the body mass (M) of the species and the proportion of the prey used as food by the hunter-gatherers (A), so that

$$N_R = (C * A)/M$$

With these basic parameters, both prey and hunter-gatherer population dynamics can be modeled using a discrete-time logistic equation, whose basic form is

$$N_{t+1} = N_t + rN_t(1 - N_t/K),$$

where N_{t+1} is the population size at time $t + 1$, N_t is the population in time t , K is the carrying capacity, and r is the intrinsic growth rate (see Gotteli, 1999; Alroy, 2001). For extinct preys, the population growth rates can only be estimated by the relationship with body mass, thus (also obtained from Alroy, (2001):

$$r = \text{EXP}(1.4967 - 0.37(\ln(M)))$$

In this way, prey-population dynamics can be modeled as

$$N_{t+1} = [N_t + rN_t(1 - N_t/K)] - N_R$$

In the simulations, I conservatively assumed that prey populations were at optimal equilibrium values (K) when humans arrived. Notice that hunting could be introduced directly into standard logistic models by reducing growth rate r , but I separated “natural” mortality, implicit in the growth parameter,

from “hunt mortality”. I did this because the last parameter can be adjusted to human population growth. Also, the N_R value, rather than as a rate, can be given based on human nutritional needs and established in terms of number of individuals removed. Of course, the initial values ($N_0 = K$) must also be known in absolute terms (i.e., number of individuals). I then assumed, following Brown (1995, p. 133), that the relationship between population density and body mass, for mammals, takes the form of a constraint triangular envelope, for which the maximum density (D), in individuals/km² for a species with a given body mass, is given as

$$\ln(D) = 13,816 - 1.000 (\ln(M))$$

After estimating population density, I assumed an area of 2,000,000 km² for the great plains in North America south of the Laurentia icesheet at the end of the Pleistocene (12,500 years ago), and then obtained the absolute number of preys N_t by simply multiplying this area by density D (see Ward, 1997).

However, it bears consideration that a reduction in hunting rates would occur if a prey had become rare, so that N_R in fact represents a maximum theoretical value defined by human needs that would be satisfied with this specific prey. Thus, I included another parameter in the prey dynamics by multiplying N_R by (N_t/K) , the ratio between actual population size and its theoretical maximum (K). In this way, the actual number of preys removed from the population deviates from the maximum predicted by human needs when prey population size decreases and is no longer represented by its initial value. Thus, the final model for prey population dynamics is given by:

$$N_{t+1} = [N_t + rN_t(1 - N_t/K)] - [N_R(N_t/K)]$$

The N_R values must be recalculated for each generation of the simulation, because human population is simultaneously growing under a logistic model, thus forming a Lotka-Volterra-like system. The main difference in relation to the classical predator-prey system is that, due to high adaptability and opportunistic behavior characterizing human survival strategies (Charles, 1997; Miotti & Salemm, 1999; Kusimba, 1999), the model does not include a parameter generating increased human mortality as prey becomes rare (because hunters can simply target another prey, e.g., a small-bodied one, or increase vegetal food ingestion).

For simulations, I followed Alroy (2001) and evaluated the dynamics of 41 prey species (Table 1), hunted by a small initial population of 100 humans that had arrived in North America and started to grow at the relatively small rate of 2% a year ($r = 0.02$). The 41 prey species contributed equally to 1% of the diet, totaling 41% of meat obtained from big game, a value only slightly larger than the maximum (36%) used by Alroy (2001) but still within the range obtained for recent human populations living in high latitudes (Campbell, 1998). Moreover, I assumed that 75% of the prey mass was used as a food source, a conservative value following recent observations on human populations living in cold regions (Frisson, 1998; Campbell, 1998). Since a non-preferential use of these preys occurs, the extinction of one of them does not affect human population dynamics since other can replace it.

All computations above were performed using the software OVERKILL, written in QB-Basic and available from the author upon request.

RESULTS

Using the equations described above, I derived carrying capacities (initial population sizes N_t) and growth rates (r) for the 41 preys, based on their body mass, and generated independently of their population dynamics. For example, for a 500 kg prey such as *Cervus elaphus*, the initial abundance would be slightly higher than 4,000,000 individuals and the intrinsic growth rate (r) would be equal to 3.5% per year but, even so, this prey would become extinct in 1,463 years (Fig. 1). At the same time, the human population was growing almost exponentially, under a logistic model with a very high carrying capacity of almost 28,000,000 individuals (suggested by the same macroecological model, assuming a 70 kg average for human body size).

For a multi-prey system, out of the 41 prey species 14 survived using the parameters described above. For the 27 species that did not, the average time for extinction to occur was equal to 1,544.3 years, and all of them had body masses exceeding 150 kg. The number of surviving species is, therefore, only slightly larger than that of the actual number (14 against 11 species) and the simple macroecological model used here correctly predicts the fate of 73% of the species (Table 1). Also, the

real and predicted statuses of the species are significantly associated according to a χ^2 test using Yates correction ($\chi^2 = 4.16$; $p = 0.041$). In other

words, the species that survive and those that became extinct tend to be associated in real data and in the model.

TABLE 1

Macroecological data for 41 species of Pleistocene megafauna analyzed in this paper (as defined by Alroy, 2001), including their body mass (BM, in kg), real present status (1 – alive; 0 – extinct), status predicted by the model (PS), growth rate (r , expressed in year⁻¹), initial abundance (= carrying capacity K) and time to extinction (TE) in years.

Species	BM	Status	PS	r	K	TE
<i>Alces alces</i>	457	1	0	0.036	4378510	1490
<i>Antilocapra americana</i>	68	1	1	0.073	29426200	–
<i>Bison bison</i>	422	1	0	0.037	4741657	1545
<i>Cervus elaphus</i>	500	1	0	0.035	4001958	1436
<i>Odocoileus hemionus</i>	118	1	1	0.059	16957500	–
<i>Odocoileus virginianus</i>	107	1	1	0.062	18700700	–
<i>Oreamnos americanus</i>	91	1	1	0.065	21988800	–
<i>Ovibos moschatus</i>	286	1	0	0.043	6996431	2011
<i>Ovis canadensis</i>	91	1	1	0.065	21988800	–
<i>Pecari tajacu</i>	30	1	1	0.099	66699300	–
<i>Rangifer tarandus</i>	61	1	1	0.076	32802900	–
<i>Bison priscus</i>	523	0	0	0.034	3825964	1412
<i>Cervalces scotti</i>	486	0	0	0.035	4117241	1452
<i>Bootherium bombifrons</i>	753	0	0	0.030	2657343	1265
<i>Camelops hesternus</i>	995	0	0	0.027	2011034	1189
<i>Capromeryx minor</i>	21	0	1	0.112	95284700	–
<i>Equus complicatus</i>	439	0	0	0.037	4558039	1517
<i>Equus conversidens</i>	306	0	0	0.042	6539147	1893
<i>Equus francisi</i>	368	0	0	0.039	5437443	1663
<i>Equus niobrarenensis</i>	533	0	0	0.034	3754182	1402
<i>Equus occidentalis</i>	574	0	0	0.033	3486026	1367
<i>Equus scotti</i>	555	0	0	0.033	3605368	1382
<i>Euceraterium collinum</i>	499	0	0	0.035	4009978	1437
<i>Glyptoterium floridanum</i>	666	0	0	0.031	3004473	1306
<i>Hemiauchenia macrocephala</i>	238	0	0	0.046	8407475	2511
<i>Holmesina septentrionalis</i>	312	0	0	0.041	6413395	1864
<i>Mammot americanum</i>	3298	0	0	0.017	606725	1013
<i>Mammuthus columbi</i>	5827	0	0	0.014	343398	966
<i>Mammuthus primigenius</i>	3174	0	0	0.018	630428	1016
<i>Megalonyx jeffersonii</i>	1320	0	0	0.024	1515893	1131
<i>Mylohyus fossilis</i>	74	0	1	0.071	27224200	–
<i>Navahoceros fricki</i>	223	0	0	0.047	8973001	2805
<i>Nothrotheriops shastensis</i>	614	0	0	0.032	3258924	1338
<i>Oreamnus harrington</i>	45	0	1	0.085	44466200	–
<i>Palaeolama mirifica</i>	245	0	0	0.045	8167262	2406
<i>Paramylodon harlani</i>	1990	0	0	0.021	1005517	1069
<i>Platygonus compressus</i>	53	0	1	0.080	38113900	–
<i>Stockoceros conklingi</i>	53	0	1	0.080	38113900	–
<i>Stockoceros onusrosagris</i>	54	0	1	0.079	37055200	–
<i>Tapirus veroensis</i>	324	0	0	0.041	6175861	1810
<i>Tetrameryx shuleri</i>	61	0	1	0.076	32802900	–

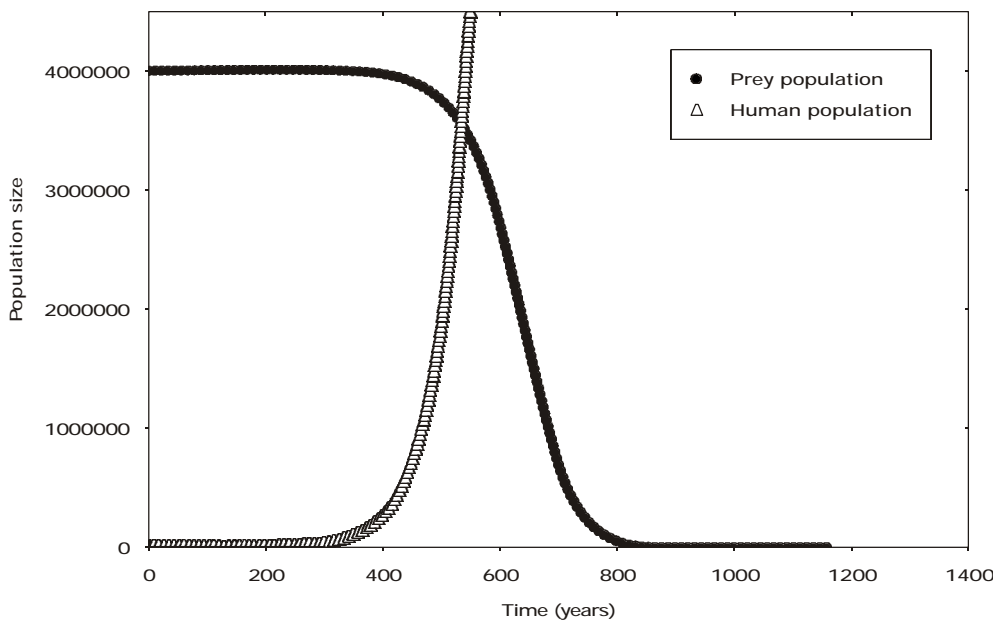


Fig. 1 — Temporal dynamics of human and prey population for a species with 500 kg under the macroecological model presented in this paper. Both intrinsic growth rate and carrying capacity (initial density) of prey population were determined by allometric relationships (see Table 1). For human population, initial population was set to 100 individuals growing at $r = 2\%$ up to around 28,000,000 (the K also suggested by allometric relationship). Only 1% of the human diet was based on this specific prey population, and 75% of the prey biomass was converted into food.

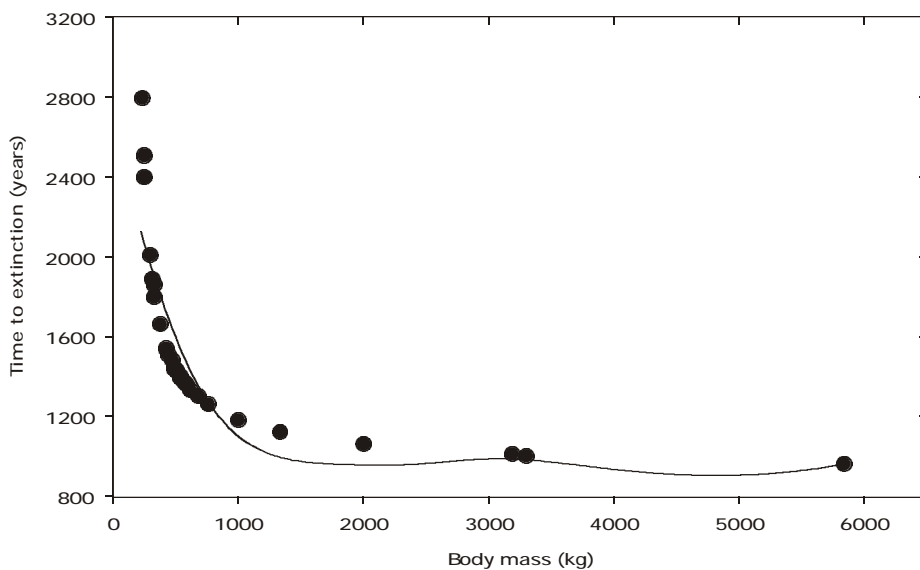


Fig. 2 — Relationship between time to extinction and prey body size for 27 species that went extinct in the macroecological model presented here (see Table 1 for parameters). The non-linear fit was defined using a distance weight least-squares (DWLS) algorithm.

Because the parameters of the simple macroecological model presented here are almost entirely based on body masses, it is not surprising that extinction times are associated with body mass, although this relationship is not well described by simple mathematical functions such as power and exponentials (Fig. 2). The relationship seems to be better explained by a threshold, above which extinction becomes highly probable.

DISCUSSION

The simple macroecological model presented here correctly predicts the fate of 73% of the large preys available to human hunters at the end of Pleistocene. Despite its simplicity, this model is only slightly inferior to the complex model developed by Alroy (2001) that correctly predicts 78% of the destiny of species; otherwise the two models match in many respects. For example, the four species that survived the extinction events at the end of the Pleistocene but vanished in the macroecological model presented here, also did so in Alroy's (2001) model. The current explanation is that these species expanded their distribution in the direction of the Laurentia ice sheet up to Canada, escaping overkill.

From several points of view, the model developed here is simpler than the one developed by Alroy (2001). First of all, the present model is deterministic and does not include stochastic variations (see Gotteli, 1999). Also, in my model, initial prey densities are derived from a maximum theoretical value predicted by the macroecological relationship with body mass, and no spatial diffusion component for human populations or spatial distribution of preys was included. Thus, collapse of prey populations is modeled here as a regional broad-scale effect caused by a global hunt, and I had to assume that both humans and preys were randomly distributed in the Great Plains 12,500 years ago. On the other hand, in Alroy's (2001) simulations, there is a diffusion process in which advancing waves of humans affect local prey populations and the recurrence of these local effects tends to produce regional extinction processes.

Despite random distribution of humans and preys in space and time being obviously unrealistic, the convergence between the results of the two models suggests that spatial components (original spatial distribution of preys and diffusion of human populations) are not critical in corroborating the overkill

hypothesis. Probably, the accumulation of local extinction events matches a regional extinction event, in terms of overall population dynamics. For example, in my model human population attained a very large size in carrying capacity (around 28,000,000 people), which could be 4 or 5 times larger than the estimated population in pre-historic America (see McEvedy & Jones, 1978) and, thus, is an unrealistic value. Consequently, hunting pressures are unrealistically high here because of the very large human population size. In the original overkill scenario, small nomadic human populations advanced as a colonization wave, never in excess of 1,000,000 people. However, two points are important and ensure the validity of the model presented here: 1) although human densities suggested by the upper limit of the macroecological relationship between density and body mass are certainly overestimated, it is important to remember that prey populations may also be overestimated for the same reasons (see below); 2) the small human populations at the wave front will also hunt relatively small preys in local populations, so that, in any case, impact is high at a local spatial scale. This may be equivalent to a large human population hunting a large prey population. In fact, Alroy (2001) included a similar scenario with no human diffusion, and obtained similar results in terms of predicting the fate of the species.

Despite these many differences, I believe that the most important feature of my model is that it is quite conservative. Firstly, prey populations are assumed to be in equilibrium (K) and, even so, for all species they are at the maximum possible K predicted by macroecological models based on body mass (see Brown, 1995). Cardillo & Lister (2002) recently showed that life-history parameters, although clearly more difficult to estimate, are even better predictors of extinction risks in the overkill scenario. Anyway, it is quite possible that prey densities would be lower than assumed here, increasing their probability of extinction. This is especially likely if there had been simultaneous environmental stress, generated by the strong climatic changes directly affecting prey densities or causing changes in plant communities, as argued by some researchers (Zimov *et al.*, 1996; Grayson, 2001; see also Ward, 1997). In that case, preys would have become extinct faster than indicated here. Also, I assumed that a total of only 41% of human needs was met by big game, a value that would be higher were hunters to have come from the cold northern regions, in which meat was almost the food source (Campbell, 1998). Equally, a high estimate

for conversion of prey mass into food (75%) was used, and smaller values would also reduce time until extinction (see Diniz-Filho, 2002, for a more detailed analysis of the sensibility of the model to variations in parameter space).

In addition and of great significance is that there have been many indications that human occupation in America occurred long before the hunter-gatherers of Clovis culture (see Meltzer, 1995; Bonato & Salzano, 1997). Thus, the model presented here is also quite conservative with respect to time of human colonization, because increasing hunting time means that even lower hunting pressures and human growth rates would be sufficient to cause regional extinctions.

Although computer simulation and ecological models, such as the one developed here and the much more complex model presented by Alroy (2001), cannot provide direct evidence for or against the overkill scenario, they are quite useful in the sense that even using conservative parameters, prey extinctions could indeed have occurred in a relatively short time after human colonization. These findings reinforce the plausibility of the overkill scenario for late Pleistocene megafaunal extinction and, more important, illustrate how macroecological models can be useful in understanding complex processes at broad scales of space and time.

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