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Of mice, mastodons and men: human-mediated extinctions on four continents

S. Kathleen Lyons,* Felisa A. Smith and James H. Brown

Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA

ABSTRACT

Numerous anthropological and ecological hypotheses have been proposed to explain the extinction of many large-bodied mammals at the terminal Pleistocene. We find that body size distributions of all mammals in North America, South America, Africa and Australia before and after the late Pleistocene show a similar large-size selectivity of extinctions across continents, despite differences in timing. All extinctions coincide with the colonization of the continent by aboriginal man, but only two coincide with periods of climate change. Further, historical (within the last 300 years) extinctions in Australia demonstrate a higher susceptibility of small and medium-sized mammals. On all four continents, large-bodied Recent mammals are threatened by human hunting practices, whereas small-bodied species are not. We conclude that the late Pleistocene extinctions were caused primarily by anthropogenic factors such as human hunting, whereas historical extinctions were due mostly to habitat alteration and exotic species introductions.

Keywords: body size distributions, climate change, human hunting, late Pleistocene, megafaunal extinction, size-biased extinction.

INTRODUCTION

During the late Pleistocene, many species of large-bodied mammals became extinct over much of the globe (Martin, 1967, 1984; Murray, 1991; Lessa and Farina, 1996; Flannery and Roberts, 1999; Martin and Steadman, 1999; Stuart, 1999). Before this time, mastodons, giant ground sloths, giant beaver, saber tooth cats and other megafauna were widespread and abundant in North and South America; giant kangaroos, marsupial lions, diprotodons and other marsupial giants inhabited Australia. Despite a long and fractious debate dating from the early 1800s, the cause of these extinctions remains controversial. Numerous theories have been proposed and can be classified into two main types. Anthropogenic models assume that man is the underlying cause of the extinctions, although the mechanism can be either direct or indirect. The most prominent of these is the 'overkill' hypothesis, which attributes the extinction of the Pleistocene megafauna to hunting by newly colonizing

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* Address all correspondence to S. Kathleen Lyons, National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, CA 93101, USA. e-mail: lyons@nceas.ucsb.edu

aboriginal humans (Martin, 1984). Conversely, ecological models assume that climate or vegetation change was the underlying cause of the extinctions (Alroy, 1999). The most prominent of these hypotheses is the 'environmental change hypothesis', which attributes the extinctions to rapid changes in climate and vegetation at the Pleistocene–Holocene transition (Guilday, 1967; Lundelius, 1967; Graham and Lundelius, 1984; Owen-Smith, 1988; Graham and Grimm, 1990; Guthrie, 1990). Mixed-model hypotheses assume that both climate and man had an effect on the extinctions, but generally assume that climate change was the main driving force (Barnosky, 1989). Moreover, mixed-model hypotheses often assume that anthropogenic roles are indirect rather than direct. For example, the disease hypothesis attributes the extinctions to the diseases that humans brought when they immigrated to new lands (MacPhee and Marx, 1997).

Each hypothesis has both its critics and supporters. Until recently, there was some debate as to the timing of the co-occurrence of man and the extinctions, especially for Australia (Roberts *et al.*, 2001). In addition, some authors have questioned whether aboriginal hunting could exert sufficient pressure to drive species to extinction (Graham and Lundelius, 1984; Stuart, 1999). Moreover, many carnivorous species that went extinct were unlikely targets of human hunting (Grayson, 1984). However, a recent simulation model that coupled human population dynamics and hunting practices with the population dynamics of large mammals concluded that humans could have caused the extinctions observed in North America (Alroy, 2001). The extirpation of large carnivores and scavengers would then result from the loss of their large-bodied prey base (Martin, 1984). The removal of megaherbivores may also have resulted in substantial habitat changes that led to further extinctions. Modern elephants and rhinos are known to reduce the densities of trees and shrubs and create savannahs and other patchy habitats through foraging behaviours (Grayson, 1984; Owen-Smith, 1988).

Critics of the environmental change hypothesis question why extinctions occurred only during the last glaciation cycle. Of the approximately 20 glacial–interglacial cycles during the Pleistocene, only the last resulted in widespread extinction of mammals. Moreover, there was no corresponding extinction in the marine realm (Martin, 1984) despite the fluctuating sea levels associated with glaciation cycles. Additionally, climate change alone should not selectively eliminate large vertebrates (Alroy, 1999). A modification of the theory ('co-evolutionary disequilibrium') was proposed for North America and invokes wholesale community reorganization to explain why climate change would selectively eliminate large vertebrates (Graham and Lundelius, 1984). It posits that changes in vegetation composition resulted in communities that no longer met the nutritional requirements of large herbivores. It is still not clear, however, why such changes would have occurred *only* during the last glacial–interglacial transition, and whether a similar scenario could explain extinctions in Australia, which occurred at a different time. Furthermore, recent work examining species associations within biomes (Alroy, 1999) and turnover in local species composition (Lyons, 1998) indicates that the magnitude of community reorganization has most likely been overestimated.

Proponents of the disease hypothesis accept the co-occurrence of man and the extinctions and the coincidence of the spread of man and the extinctions (i.e. 'wavelike' pattern of the extinctions; Martin, 1984). Nonetheless, the disease hypothesis attributes the extinction to the indirect effects of man (MacPhee and Marx, 1997) because of the purported inability of aboriginal man to hunt species to extinction and the lack of extinctions into the Holocene. However, the disease hypothesis has been criticized on many levels. Recent epidemic diseases that affect mammals are typically restricted to a single order or, if they do attack multiple orders, they have low transmission and mortality rates (Alroy, 1999). Furthermore, as with the climate change hypothesis, the disease hypothesis does not easily explain the size selectivity of the extinction. Certainly, we know of no mechanism that would cause a disease to attack only large-bodied mammals. Although large mammals have many life-history traits that might make them more vulnerable to extinction (e.g. low population densities, low reproduction, low basal metabolic rates), so too do many small mammals. Many have small geographic ranges, low population densities, low dispersal rates or low reproduction (Alroy, 1999).

Evaluation of each hypothesis has been hampered by a lack of quantitative data and further by the tendency to examine each continent in isolation. For example, extinct mammals were previously characterized as 'small' (< 1 kg), 'medium' (1–44 kg) or 'large' (> 45 kg), and most authors have ignored species that did not go extinct (Graham and Lundelius, 1984; Grayson, 1984; Martin, 1984; Graham and Grimm, 1990; Murray, 1991; Lessa and Farina, 1996; Flannery and Roberts, 1999; Martin and Steadman, 1999; Stuart, 1999). Also, most studies have focused on a single continent, although a more general picture would emerge from intercontinental comparisons (Kurtén and Anderson, 1980; Graham and Lundelius, 1984; Martin, 1984; Graham and Grimm, 1990; Murray, 1991; Lessa and Farina, 1996; Alroy, 1999, 2001; Martin and Steadman, 1999; Stuart, 1999). Here, we have assembled a database containing the complete late Pleistocene mammalian faunas of Africa, Australia, North and South America (Smith *et al.*, 2003). By characterizing body size for *all* mammals on each continent, we were able to conduct the first quantitative comparisons of the body size distributions before and after human colonization. Furthermore, by comparing similarities in the timing and selectivity of the events across the different continents, we were able to evaluate the generality of the patterns. Because some authors have argued that any apparent size selectivity was due to shared ecological characteristics common to a taxonomic group, we also examined extinction patterns across the entire taxonomic hierarchy on each continent and across the different continents. Over the past 300 years, coincident with European colonization, Australia suffered many well-documented extinctions (Flannery and Schouten, 2001). We compare the size selectivity of the terminal Pleistocene extinctions on Australia with these historical extinctions to determine if the causal mechanisms were similar. Finally, for all continents, we compare the distributions of Recent species that have been identified by the IUCN as 'threatened' or 'endangered' with those that are not. Our emphasis is on how the causal mechanisms underlying the threat categories impact the body size distribution. Note that despite considerable discussion and speculation, quantitative analyses of mammalian body size distributions over the late Pleistocene have not been conducted previously. Thus, our analyses represent the first rigorous examination of late Pleistocene extinction patterns that span multiple continents and taxonomic scales.

METHODS

We obtained species lists for the late Pleistocene terrestrial faunas of the four continents from a variety of sources (see Appendix in on-line version). Underlying our analysis is the assumption that species currently extant were also present during the late Pleistocene. Note, however, that the median duration for Eocene–Pleistocene mammals is estimated as

2.6 million years (ma). Thus, any species extant today was likely extant during the late Pleistocene (Alroy, 2000). We define 'late Pleistocene' as 12–15 thousand years ago (ka) for Africa, North and South America, and 50 ka for Australia. This older time frame was chosen for Australia because recent studies indicate that megafaunal extinctions occurred approximately 46 ka (Roberts *et al.*, 2001).

Estimates of body mass for extinct and extant mammals (bats and marine mammals were excluded) were derived from a variety of literature, museum and web sources, and log-transformed before analysis. Masses for extant species were extracted from a database compiled by the Body-Size working group at the National Center for Ecological Analysis and Synthesis (www.ucsb.nceas.edu; Smith *et al.*, 2003). Those for extinct mammals were gathered from the primary literature, other scientists, estimated from regressions of teeth measurements or obtained from web sources (see Appendix in on-line version). Using these methods, we were able to obtain estimates for all but 12 South American species. For eight of these relatively rare species, a generic average was used. In four cases, a crude estimate was made using verbal descriptions of the species. For example, *Agalmaceros* spp. was estimated to be approximately 60 kg because it was described as being 'slightly larger' than a modern deer (50 kg). For modern species, the IUCN threat level of each species was noted along with the basis for the determination (www.redlist.net). All redlisted mammals were assigned to one of three factors for the threatened status. Species were identified as threatened by intrinsic factors and not by habitat or hunting ('Restricted range'); threatened by habitat loss, but not hunting ('Habitat loss'); and threatened by hunting ('Hunting').

We constructed body size distributions for each continent both before and after human colonization. These distributions were compared using Kolmogorov-Smirnov two-sample tests, which are sensitive to differences in skew and kurtosis as well as to location. Therefore, Mann-Whitney *U*-tests, which are sensitive only to location, were also performed (Sokal and Rohlf, 1981).

Comparisons of body size distributions for species that went extinct in historical times (i.e. after the arrival of Europeans) on Australia were compared with the body size distributions of the species that went extinct ~46 kya. On all four continents, the body size distributions of species threatened by hunting were compared with the body distributions of species that were threatened by a variety of other factors, including habitat loss and restricted range. Again, we used both Mann-Whitney *U*-tests and Kolmorgorov-Smirnov tests to examine distributional differences.

RESULTS

Continental distributions

The frequency distributions of body sizes for the terrestrial mammals of Africa, North and South America were qualitatively similar before the late Pleistocene extinctions (Fig. 1). Although it has been reported that modern continental distributions for the three major continents are quantitatively dissimilar (Smith *et al.*, in press), the addition of the extinct species results in North and South America being statistically indistinguishable from Africa (Table 1, Mann-Whitney *U* two-sample tests, $P > 0.05$). Kolmogorov-Smirnov two-sample tests yielded identical results. Moreover, with the exception of Australia, each continent contained animals occupying the same body mass range (~6.5 log units; Table 2), and

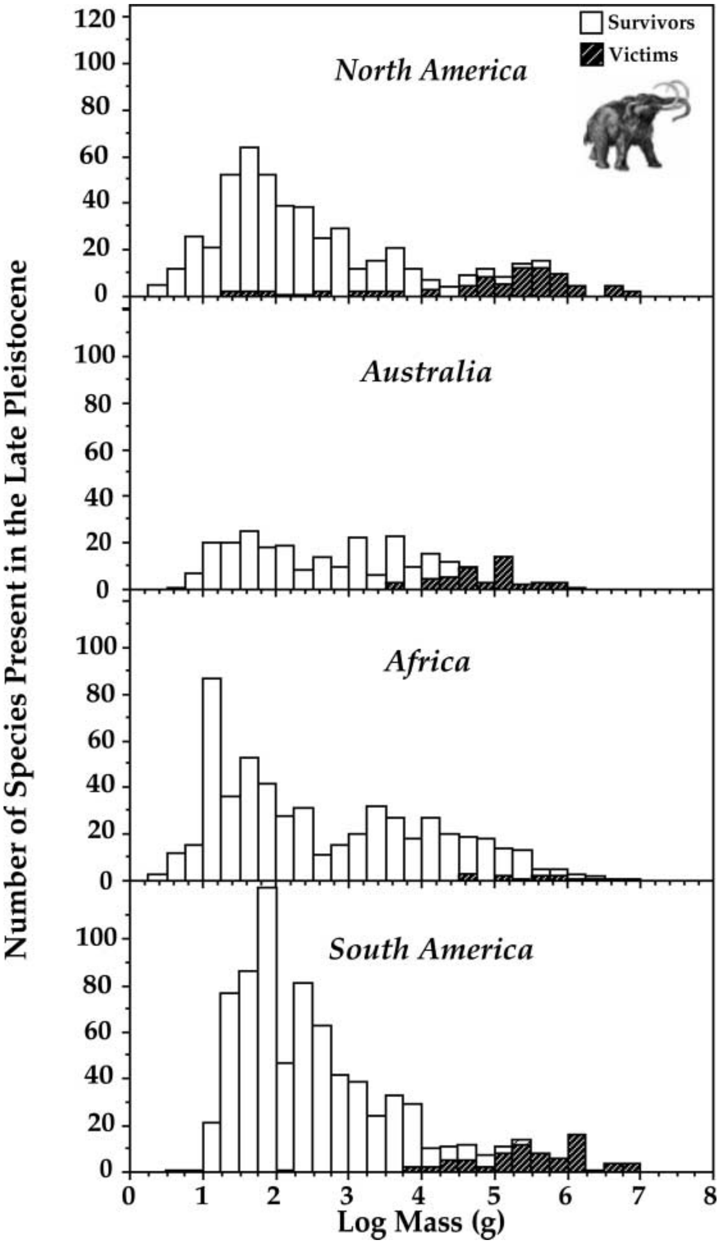

Fig. 1. Late Pleistocene faunas for four continents. Body size frequency distributions of the late Pleistocene faunas of Africa (12–15 ka), Australia (~50 ka), North America (12–15 ka) and South America (12–15 ka). Kolmogorov-Smirnov two-sample tests indicate that extant species (white bars) have a significantly different body size distribution (Africa: $\chi^2 = 39.232$, $P < 0.0001$; Australia: $\chi^2 = 111.675$, $P < 0.0001$; North America: $\chi^2 = 145.324$, $P < 0.0001$; South America: $\chi^2 = 232.823$, $P < 0.0001$) than species that went extinct in the late Pleistocene (black bars with hatching).

Table 1. All pairwise comparisons of continental body size distributions of late Pleistocene mammals

Continent	Africa	North America	South America	Australia
Africa	—	−0.491	−1.606	**−4.010**
North America	0.624	—	**−2.667**	**−4.604**
South America	0.108	**0.008**	—	**−3.802**
Australia	**<0.001**	**<0.001**	**<0.001**	—

Note: The triangle on the lower left contains *P*-values from Mann-Whitney *U*-tests. The upper right triangle contains *Z*-values from Mann-Whitney *U*-tests. Values in **bold** indicate significance.

Table 2. Descriptive statistics for the body size frequency distributions for the late Pleistocene of each continent

	All species	Africa	North America	South America	Australia
Area of continent (km^2)		30,065,000	24,256,000	17,819,000	7,687,000
Number of species	2130	558	512	770	286
Mean body mass	2.711	2.676	2.599	2.675	3.052
Median	2.320	2.260	2.155	2.365	2.995
Mode	1.170	1.170	1.600	2.450	5.180
Standard deviation	1.403	1.458	1.477	1.270	1.455
Variance	1.969	2.126	2.181	1.612	2.117
Standard error	0.030	0.062	0.065	0.046	0.086
Coefficient of variation	0.518	0.545	0.568	0.475	0.477
Minimum	0.260	0.260	0.380	0.670	0.630
Maximum	7.000	6.810	7.000	6.880	6.200
Range	6.740	6.550	6.620	6.210	5.570
Skewness	0.808	0.555	0.966	1.240	0.274
Kurtosis	−0.212	−0.799	0.043	0.970	−1.119

Note: Continental areas were taken from worldatlas.com.

maximum size on each was approximately 7 log units (10,000 kg; Table 2). The distributions were bimodal in shape with the greatest species diversity in the 10–100 g category (Fig. 1). These similarities in the moments of the distributions are striking given the substantial differences in species diversity and composition owing to the differences in history, climate and land area (Table 2). Australia was significantly different from the three major continents in all aspects of the distribution, presumably because of the much reduced land area (Fig. 1, Tables 1 and 2). Australia did not support as many species or such large-bodied mammals as other continents (Fig. 1, Table 2).

On each of the four continents, the late Pleistocene extinctions were significantly size selective (Fig. 1). Mammals that survived into the Holocene were significantly smaller than those that went extinct (Kolmogorov-Smirnov two-sample tests, $P \ll 0.05$). This resulted in the extirpation of all mammals over ~600 kg in North and South America, and all mammals greater than 50 kg in Australia. The loss of the second mode in the distributions of North and South America is the likely reason for the significant difference between the modern distributions (Smith *et al.*, in press).

Ordinal patterns

Seven orders had sufficient numbers of extinct and extant species that further analyses were possible. Of those orders, four were significantly size selective on one or more continents (Table 3; $P \leqslant 0.05$). For example, large numbers of carnivores and xenarthrans went extinct in the late Pleistocene of North and South America. These extinctions were significantly skewed towards larger body size ($P \leqslant 0.01$ for all comparisons; Fig. 2). Rodent extinctions were not significantly size selective on any continent (Kolmogorov-Smirnov two-sample test, $P > 0.05$). However, even within rodents, the largest species on each continent went extinct (e.g. *Casteroides ohioensis*, *Neochoerus* spp.; see Appendix in on-line version). Results for lagomorphs and perissodactyls should be interpreted with caution because sample sizes were relatively small. For example, on North America only one perissodactyl survived of 18 species, whereas on South America only three survived of 11 species.

Historical patterns

On Australia, there was a difference in the body size selectivity of the late Pleistocene and historical extinction events. Although the late Pleistocene extinction was size selective, eliminating all species over 50 kg, historical extinctions spanned the entire size spectrum (Kolmogorov-Smirnov two-sample test; $P \leqslant 0.01$; Fig. 3). Both Kolmogorov-Smirnov and Mann-Whitney U two-sample tests indicate that historical extinctions are randomly distributed across the Recent body size range ($P > 0.05$).

Modern patterns

There were differences in the body size distributions of species in our three categories (i.e. Hunting, Habitat loss, Restricted range). On all four continents, Recent species that are threatened or endangered due to pressures from human hunting are significantly larger than species that are not affected by human hunting, but are under threat by other factors such as habitat loss or intrinsic factors (Figs. 4–7). For Africa and South America, more than 50% of species larger than ~10 kg are threatened by human hunting (Figs. 5 and 6). In contrast to those threatened by hunting, species threatened by habitat loss are spread throughout the body size spectrum.

DISCUSSION

Three major conclusions can be drawn from our analyses. First, mammal extinctions on all continents demonstrated a strikingly similar pattern of size selectivity (Fig. 1). Not only were they highly skewed towards the large-bodied species, but the very largest mammals on each continent were completely eliminated (> 580 kg in North America, > 300 kg in South America, > 50 kg in Australia). Such size-biased extinctions are absent elsewhere in the mammalian fossil record (Alroy, 1999), and their consistency across geographic space argues for a common causal mechanism. The environmental change hypothesis predicts

Table 3. Comparisons of the body size distributions of extinct and extant late Pleistocene species within each order

Continent	Rodentia	Carnivora	Artiodactyla	Perissodactyla	Lagomorpha	Primates
Africa	No Extinctions	No Extinctions	**0.009**	0.732	No Extinctions	No Extinctions
Australia	No Extinctions	No Extinctions	—	—	No Extinctions	None
North America	0.164	**0.0083**	**0.077**	**0.041**	0.574	No Extinctions
South America	0.138	**0.0001**	**0.003**	0.387	No Extinctions	—

Continent	Proboscidea	Xenarthra	Diprodontia	Monotremata	Peramelemorphia
Africa	—	None	None	None	None
Australia	None	None	**0.0001**	—	—
North America	All Extinct	**0.0043**	None	None	None
South America	All Extinct	**0.0001**	None	None	None

Note: Different continents are evaluated separately. Distributions were compared using Kolmogorov-Smirnov two-sample tests and values in the table are *P*-values. Values in **bold** indicate significant differences. — insufficient sample size; No Extinctions = only extant species; All Extinct = only extinct species; None = no species of that order occurs on that continent.

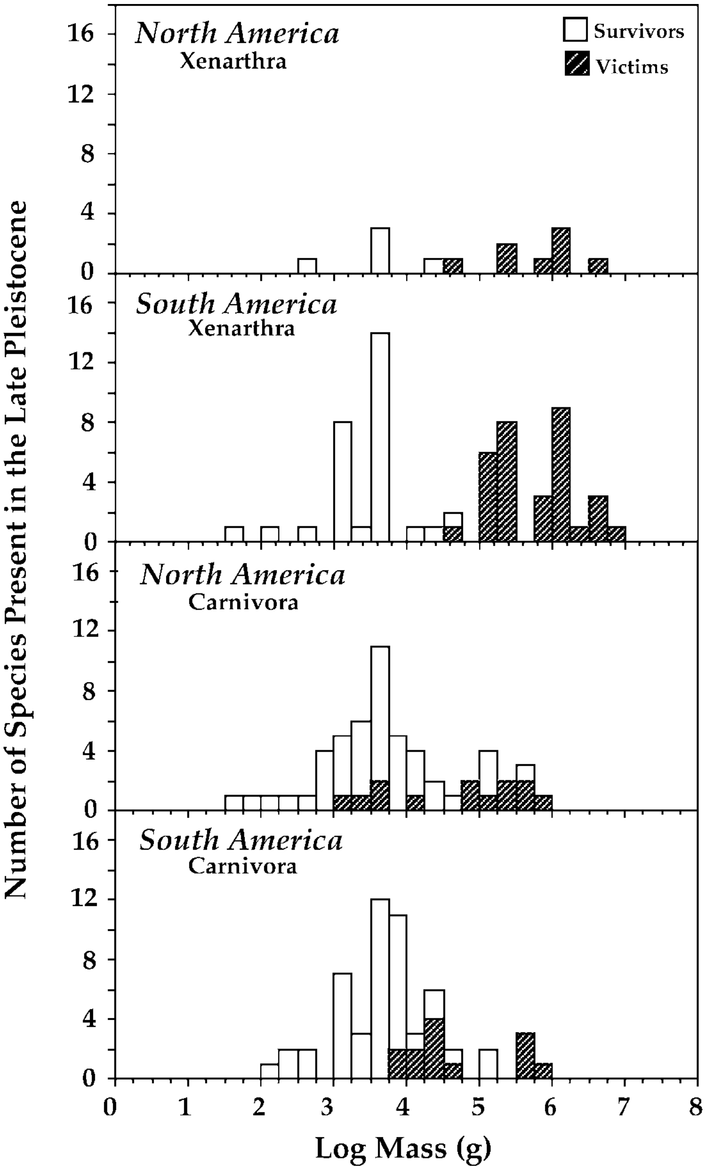

Fig. 2. Body size frequency distributions for the Xenarthra and Carnivora of the late Pleistocene of North America and South America. Kolmogorov-Smirnov two-sample tests indicate that extant species (white bars) have a significantly different body size distribution (North American Xenarthra: $\chi^2 = 12.308$, $P = 0.0043$; South American Xenarthra: $\chi^2 = 60.852$, $P < 0.0001$; North American Carnivora: $\chi^2 = 10.972$, $P = 0.0083$; South American Carnivora: $\chi^2 = 21.312$, $P < 0.0001$) than species that went extinct in the late Pleistocene (black bars with hatching).

that the end-Pleistocene extinction should be no more or less size selective than other extinction events. Although several previous analyses supported this prediction (Webb, 1984; Barnosky, 1989), they did not account for sampling. Recent work has shown that

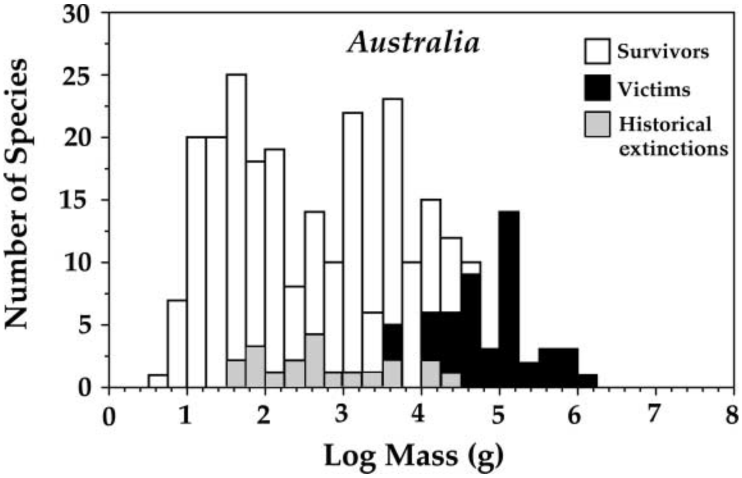

Fig. 3. Body size frequency distribution for the late Pleistocene (~50 ka) of Australia. A Kolmogorov-Smirnov two-sample test indicates that historical extinctions (black bars) have a significantly different body size distribution ($\chi^2 = 39.940$, $P < 0.0001$) than species that went extinct in the late Pleistocene (grey bars). Extant species are represented by white bars.

speciation and extinction rates are strongly affected by sampling biases (Foote, 1997, 2000). A more recent analysis of the mammalian fossil record using techniques that account for sampling indicated strongly that the end-Pleistocene event was unique (Alroy, 1999). Moreover, the evolutionary dynamics of mammals did not correlate well with other climate changes over the Cenozoic (Alroy *et al.*, 2000). Modifications such as the co-evolutionary disequilibrium hypothesis (Graham and Lundelius, 1984) explained size selectivity by arguing that large herbivores were unable to cope with the wholesale reorganization of vegetative communities as the glaciers receded. However, there is little evidence for the wholesale reorganization of vegetation or mammalian communities; most did not disappear altogether, but simply shifted location (Webb, 1981, 1992; Overpeck *et al.*, 1992; Alroy, 1999; Edwards *et al.*, 2000; Elenga *et al.*, 2000; Prentice and Jolly, 2000; Takahara *et al.*, 2000; Tarasov *et al.*, 2000; Thompson and Anderson, 2000; Williams *et al.*, 2000; Yu *et al.*, 2000; Lyons, 2001, 2003). Large herbivorous mammals should have been able to track changing vegetation. It is the smaller mammals, with their more limited vagility, that ought to have suffered extinctions. Yet, our results clearly indicate a significant extinction bias against large, not small, animals (Fig. 1).

Not only were mammal extinctions strikingly size selective on each of the continents, but within most orders the larger species were differentially targeted (Fig. 2; Table 3). This common pattern suggests that size selectivity was not due to shared ecological traits. Both environmental change hypotheses and the disease hypothesis explicitly assume that certain life-history characteristics (e.g. low reproductive rates and low population densities) determine extinction risk. Yet, within orders where species typically share these life-history characteristics, only the smallest species survived (Table 3).

Second, there were significant differences between the patterns of late Pleistocene extinctions and Recent extinct or threatened species (Figs. 3–7). Extinctions in the late Pleistocene (~46 ka) of Australia followed colonization by aboriginal humans, whereas

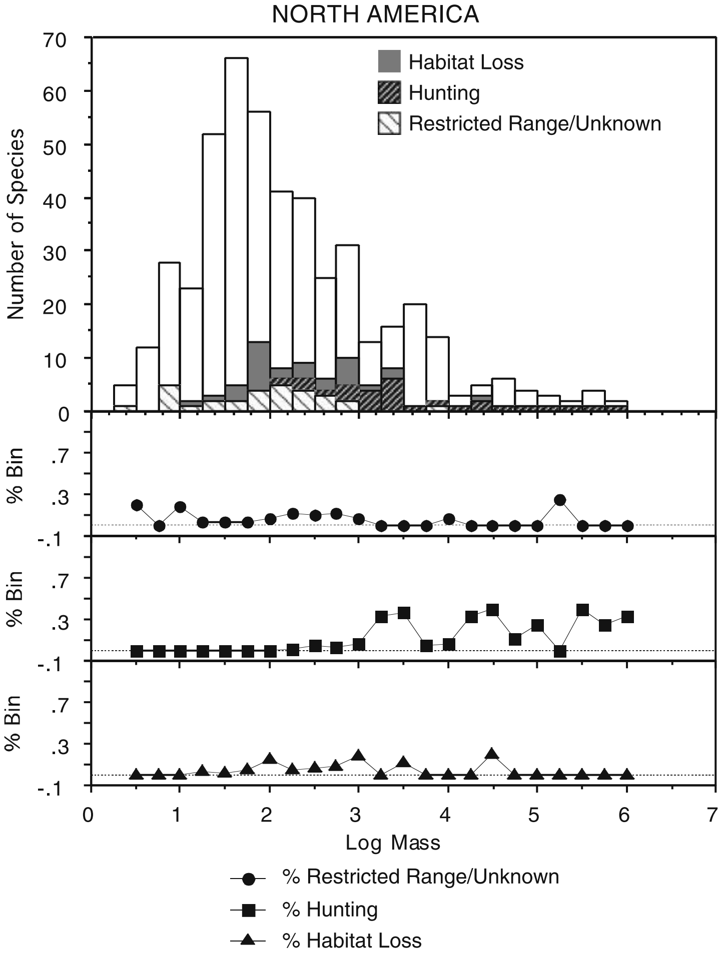

Fig. 4. (Top panel) Body size frequency distribution for Recent mammals in North America. A Mann-Whitney *U*-test indicates that species that are threatened by hunting (black hatching) have a significantly different body size distribution ($Z = -6.418$, $P < 0.001$) than species that are threatened by habitat loss (grey shading) and other factors (white hatching). (Bottom panel) Percentage of species in each body size bin that is threatened by hunting (squares), habitat loss (triangles) and other factors (circles).

historical extinctions (~300 years ago) followed settlement by European immigrants. Note that *neither* of these occurred during a time of significant climate change (Kershaw, 1974, 1978, 1994; Kershaw and Nix, 1988; D'Costa *et al.*, 1989; Kershaw and Nanson, 1993; D'Costa and Kershaw, 1995; Roberts *et al.*, 2001). The differences in the size selectivity between the two episodes of extinctions in Australia suggest different underlying causal mechanisms (Fig. 3). The late Pleistocene event selectively eliminated large mammals, including seven species much larger than any found today (Fig. 1). The more recent historical extinctions, however, were primarily of small to medium-sized mammals (Fig. 3; Flannery and Schouten, 2001). Although causes of the late Pleistocene extinctions are still hotly debated, those underlying historical extinctions are fairly well characterized. Factors

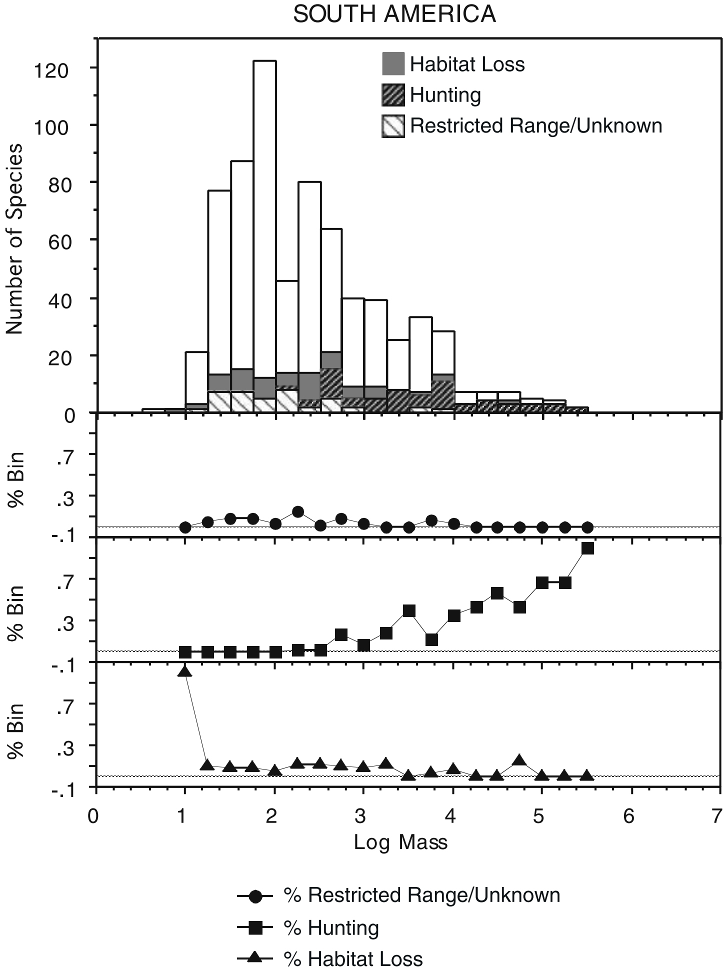

Fig. 5. (Top panel) Body size frequency distribution for Recent mammals in South America. A Mann-Whitney *U*-test indicates that species that are threatened by hunting (black hatching) have a significantly different body size distribution ($Z = -8.659$, $P < 0.001$) than species that are threatened by habitat loss (grey shading) and other factors (white hatching). (Bottom panel) Percentage of species in each body size bin that is threatened by hunting (squares), habitat loss (triangles) and other factors (circles).

such as the introduction of exotic predators and competitors, land-use practices such as tillage agriculture, grazing by domestic livestock, and fragmentation of native habitats have all been implicated (Flannery and Schouten, 2001). These habitat alterations differentially extirpated mammals that occupy particular habitats or have specialized niches (Flannery and Schouten, 2001) and are randomly spread across the body size spectrum (Fig. 3). Such changes might also be expected if significant climate change were the proximate causal mechanism underlying the late Pleistocene extinctions. Yet, not only is the pattern of extinctions significantly different (Fig. 3), but there is no evidence of substantial vegetative turnover at this time (Kershaw, 1974, 1978, 1994; Kershaw and Nix, 1988; D'Costa *et al.*, 1989;

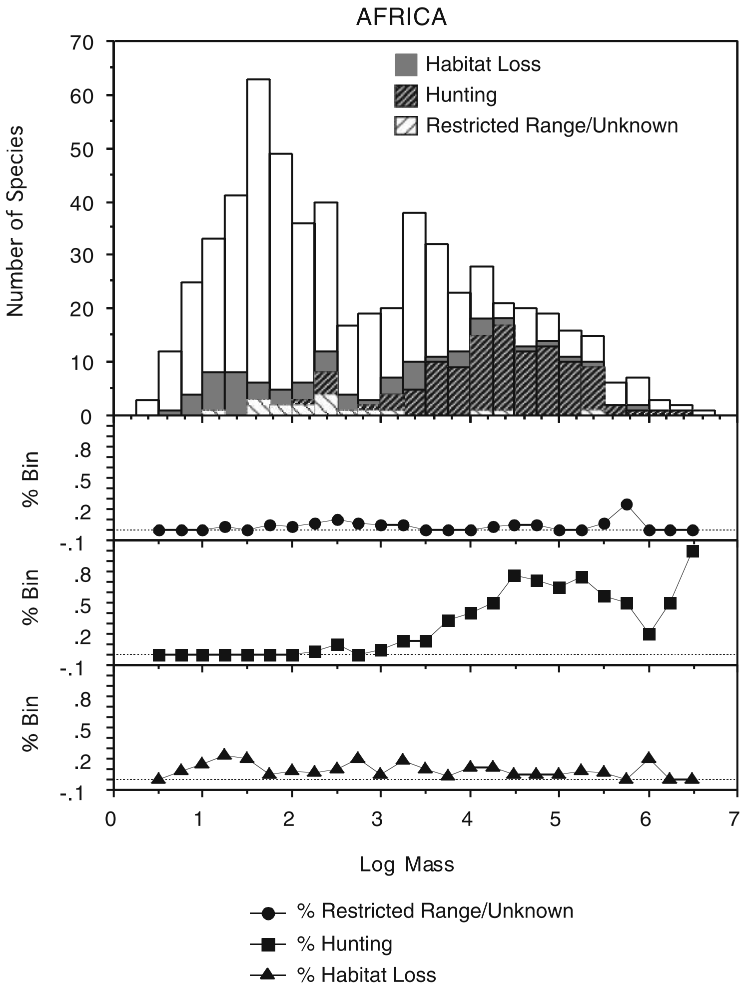

Fig. 6. (Top panel) Body size frequency distribution for Recent mammals in Africa. A Mann-Whitney *U*-test indicates that species that are threatened by hunting (black hatching) have a significantly different body size distribution ($Z = -8.743$, $P < 0.001$) than species that are threatened by habitat loss (grey shading) and other factors (white hatching). (Bottom panel) Percentage of species in each body size bin that is threatened by hunting (squares), habitat loss (triangles) and other factors (circles).

Edney *et al.*, 1990; Kershaw and Nanson, 1993; D'Costa and Kershaw, 1995). The importation of diseases should have accompanied both immigrations of humans into Australia; thus if exposure to novel disease posed a significant extinction threat to the native fauna, it should have operated on historical scales as well as during the late Pleistocene. Although aboriginal Australians were certainly affected by diseases brought by European settlers, there is no evidence that disease played a significant role in the extinction of any mammal (Flannery and Schouten, 2001).

Our analysis of the causal mechanisms for the IUCN list of threatened and endangered mammals clearly indicated that there were significant differences with respect to body size. Those mammals threatened by human hunting were significantly larger than those subject to different extinction pressures (Figs. 4–7). Although human hunting significantly targets

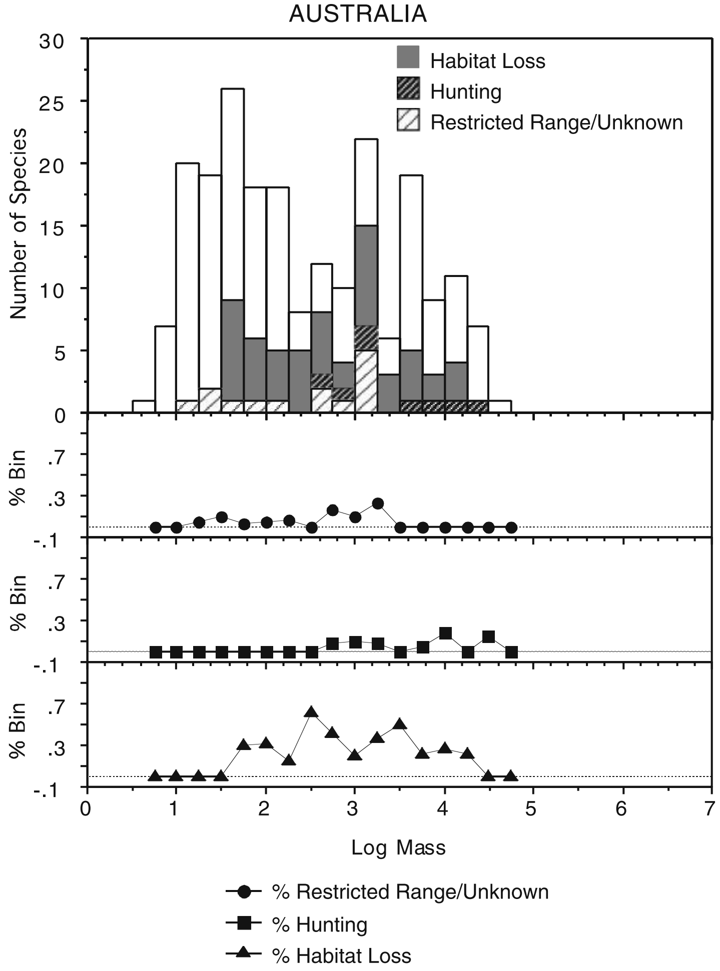

Fig. 7. (Top panel) Body size frequency distribution for Recent mammals in Australia. A Mann-Whitney *U*-test indicates that species that are threatened by hunting (black hatching) have a significantly different body size distribution ($Z = -2.601$, $P = 0.009$) than species that are threatened by habitat loss (grey shading) and other factors (white hatching). (Bottom panel) Percentage of species in each body size bin that is threatened by hunting (squares), habitat loss (triangles) and other factors (circles).

the larger-bodied mammals on each continent, habitat alterations and other factors affect mammals throughout the body size distribution. Thus the prediction that early human hunters preferentially targeted large mammals is substantiated by modern hunting practices. Some authors have questioned why aboriginal humans would hunt species to extinction (Graham and Lundelius, 1984; Stuart, 1999). Adaptive foraging models predict that predators will often selectively kill the largest prey because of higher food returns per unit effort (Davies, 1977; Elner and Hughes, 1978). In fact, the high value of a mastodon-sized prey to a group of hunter-gatherers make it plausible to see why humans would be motivated to kill every last individual, whereas specialized hunting for smaller prey would become uneconomical well before populations were driven to extinction. The humans that entered the New World were already skilled hunters with sophisticated weaponry.

Third, we note the striking similarities in the body size distributions of mammalian faunas on different continents before and after the Pleistocene extinctions (Fig. 1, Table 1). This is even more remarkable because of the large difference in faunal composition; no extant species is common to Africa and the New World (Smith *et al.*, in press) and only two were shared in the late Pleistocene. The modern size distributions of both South and North America are similar to that of Africa, except that the New World continents are missing the largest mammals that are still found in Africa (Smith *et al.*, in press). The lack of extinctions in Africa (Fig. 1) is especially notable given the long history of humans on this continent. The co-evolution of man with the African megafauna may have resulted in the evolution of effective anti-predator behaviours (Diamond, 1984; Martin, 1984). It is also likely, however, that the entire Pleistocene fossil record for Africa would show corresponding 'pulses' of human-caused extinctions of large mammals as human culture and hunting technology developed. The diversity of very large mammals in Africa has declined. For example, during the early Pleistocene at approximately the time when humans began developing more complex culture and societies (i.e. the time of *Homo erectus*), 12 species of elephant-like proboscids were extant in Africa (Coppens *et al.*, 1978). By the Middle Pleistocene, only two remained (Coppens *et al.*, 1978).

Our results support the idea that the terminal Pleistocene extinctions were anthropogenic in nature. Although the timing of extinctions in North and South America coincided with the climate changes at the glacial–interglacial transition, there were few extinctions in Africa, and those on Australia occurred well *before* the Pleistocene–Holocene transition. Neither the increased aridity at the last glacial maximum about 20 ka, nor the rising sea level and climate and vegetation change about 10 ka, caused substantial extinctions in Australia (Horton, 1984). There is *no* evidence of dramatic climate change at ~46 ka when the megafaunal extinctions occurred (Kershaw, 1974, 1978, 1986, 1994; Kershaw and Nix, 1988; D'Costa *et al.*, 1989; Edney *et al.*, 1990; Kershaw and Nanson, 1993; D'Costa and Kershaw, 1995). Indeed, climate and vegetation turnover is mild during the time bounding the extinction event compared with changes that occur during the height of the glacial maximum. Thus, only two of the four continents demonstrate patterns consistent with the environmental change hypothesis.

We note that implicit in the characterization of the environmental change hypothesis is the idea that climate and vegetation changes made the environment unsuitable for megafauna. The establishment of vigorous, naturalized, self-maintaining populations of exotic megaherbivores on North America, South America and Australia clearly demonstrates that these kinds of mammals can flourish in contemporary climatic regimes and ecological communities. Examples include horse (*Equus caballas*), donkey (*Equus asinus*) and Oryx (*Oryx gazella*) in North America, and camel (*Camelus dromiedarius*), water buffalo (*Bubalus bubalis*) and horse in Australia. In the absence of population control by human hunting, these species increase to become pests and create serious ecological damage. Interestingly, attempts to model the niche space of extinct Pleistocene species from North America using genetic algorithms and various Pleistocene climate models indicate that they should have expanded their range as the glaciers receded and not gone extinct (E. Martinez-Meyer, A.T. Peterson and W.W. Hargrove, unpublished). Indeed, habitat reconstructions indicate that North America improved as large mammal habitat between 18,000 and 7000 years B.P. (MacDonald, 1984).

Mixed-model hypotheses that count climate as the driving factor behind the extinctions even if they allow that human hunting may have played a role suffer from some of the same criticisms as the environmental change hypothesis. Such models would argue that human hunting may have provided the extra impetus needed to push the system over the edge and cause extinction (e.g. Guilday, 1967; Barnosky, 1989). Although these models could explain the extinctions in North and South America and relative lack of extinctions in Africa and Eurasia, they cannot explain the timing of the extinctions in Australia because of the lack of evidence for climate change (Kershaw, 1974, 1978, 1986, 1994; Kershaw and Nix, 1988; D'Costa *et al.*, 1989; Edney *et al.*, 1990; Kershaw and Nanson, 1993; D'Costa and Kershaw, 1995).

On each continent, the megafaunal extinctions *did* occur shortly after colonization by aboriginal humans (Martin, 1967, 1984; Roberts *et al.*, 2001). Extinction dates correspond well with the accumulating evidence of the timing and pattern of human immigration (Roberts *et al.*, 1990, 1994; Whitley and Dorn, 1993; Fiedel, 1999; Thorne *et al.*, 1999). The extinctions occurred much earlier (40–50 ka) in Australia than in either North or South America (10–12 ka), and may have occurred over a longer span of time. Note, the colonization of Australia predated the development of the atlatl and other sophisticated hunting technologies. In contrast, humans who immigrated into the New World possessed weapons that facilitated long-range killing and entailed less physical risk. They were undoubtedly more efficient hunters. Thus, the selective pressures on megafauna may have intensified as human tool-making technologies and hunting strategies became more sophisticated. Moreover, episodes of extinctions on islands, such as Madagascar, New Zealand, the Caribbean, and the Hawaiian and other Polynesian archipelagos, also coincided with arrival of humans, but not with the Pleistocene–Holocene transition (Olson and James, 1982; Alcover *et al.*, 1999; Burney, 1999; Martin and Steadman, 1999). Certainly, isolated populations of a species (e.g. Irish elk) may have gone extinct on islands before the arrival of man (Barnosky, 1986; but see Gonzalez *et al.*, 2000, for new dates). However, the extinction of a remnant island population that was once widespread on the mainland is very different from the near simultaneous extinction of large-bodied endemic fauna. Thus, the patterns on *all* continents are consistent with human-mediated extinctions.

We do not intend to suggest that changes in climate and vegetation at the end of the Pleistocene did not play some role in the extinction of the megafauna in North America, South America and perhaps other landmasses. We do suggest that any such effect was minor and secondary compared with anthropogenic factors such as the selective hunting of large mammals by recently arrived humans. There were more than 20 glacial–interglacial cycles during the ~1.6 million years of the Pleistocene, but *only* in the last one, and only in North and South America, were these climatic changes associated with wholesale extinctions of large mammals. In contrast, on every continent and island examined to date, the colonization by humans has been followed by highly size-selective extinctions (Coppens *et al.*, 1978; Olson and James, 1982; Martin, 1984; Farina, 1995; Farina and Vizcaino, 1997; Alcover *et al.*, 1999; Burney, 1999; Roberts *et al.*, 2001).

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