

Examining the Extinction of the Pleistocene Megafauna



During the Pleistocene, the world saw a dramatic number of extinctions of very large terrestrial species. The losses of these megafauna have been attributed to either of two different hypotheses. One hypothesis states that global climate changes occurring during the Pleistocene caused environmental pressures that forced the extinction of several megafaunal species. The second hypothesis proposes that the global spread of Homo sapiens and hunter-gatherer subsistence practices were responsible for these deaths. Examining these two theories reveals that neither climate changes nor human overkill were likely to be individually responsible for the Pleistocene extinctions. Instead, a synthetic model that includes both hypotheses appears to be the most plausible explanation for the Pleistocene losses.

Robin Gibbons

There are two schools of thought regarding the underlying cause of the Pleistocene extinctions. Both attempt to explain the loss of nineteen genera and over fifty species in Australia and more than seventy genera in the Americas—almost all terrestrial animals, and virtually all large in size (Martin 1984). The North American fauna saw the extinction of “elephants, horses, camels, ground sloths, all but one pronghorn, several ovibovids, peccaries, and the giant beaver” (Guilday 1967:125). South America also lost elephants and sloths, in addition to horses, some camels, glyptodonts, and a rhinoceros-sized giant rodent species. Extinctions in Australia included all herbivorous marsupials larger than modern day kangaroos (Guilday 1967). The first theory states that global climatic changes at the end of the Pleistocene were responsible for the demise of so many large terrestrial animals. Conversely, the overkill hypothesis proposes that the extinction of large land animals was concordant with arrival of modern *Homo sapiens* in the New World and Australia and that man-the-hunter brought about these deaths. However, neither theory has managed to dominate the debate over the cause of the megafaunal extinctions. Instead, the

possibility exists that both explanations are simultaneously plausible. Therefore, it follows that studies should move beyond these individual arguments and start formulating multi-causal models that incorporate both climate and overkill into their reasoning.

Climate Changes

During the late Pleistocene, the retreat of the Wisconsin ice sheet caused global climate changes and changes in local environments. Temperatures became less homogenous, as winters became colder and summers became hotter. Essentially, seasonality increased. In addition, rainfall became more variable depending on the season, with distinctions between wet and dry seasons (Kiltie 1984). During the deglaciation, many streams in the glacial floodplains experienced net degradation and incision of their channels, and the water tables lowered, causing low order streams to become sporadic and transient and springs to dry up or significantly reduce discharge (Haynes 1984).

As a result of this climatic shift, several changes occurred. Some primary habitats were eliminated, while others that may have been only marginal during

the existence of the Wisconsin ice sheet expanded (Guilday 1967). Thus, some animals experienced range expansion while others saw their habitats shrink or disappear. In addition, new competition arose between formerly noncompetitive herbivores as a consequence of the changing environments (Guilday 1967). Selective evolution will favor one species in a direct competition and drive the other to extinction. Because of their large size, competition affected the megafauna more than the smaller existing species. Larger animals generally require a larger primary habitat, more forage, and more water to maintain themselves than a smaller species. Therefore, there are usually only a few of them in a given area. As Grayson says, “the inverse relationship between body size and population size plays a powerful role in increasing the risk of extinction faced by larger animals” (Grayson 1991: 214). Following Guilday’s logic, shrinking habitats forced large animals into cohabitating smaller areas, containing insufficient resources to support them all. The result was the elimination of some species due to competition.

There are several possible reasons underlying extinction in the face of environmental pressure brought about by

climate change. Overspecialization (inability to adjust to a new environment), competition with a superior species, inability to migrate to a more suitable habitat, and extremely rapid environmental change (impossibility of evolutionary adaptation) will all cause extinction of a species (Guilday 1967). These problems are magnified in shrinking habitats and will force the extinction of larger species first. This is not to say that smaller species are insensitive to climatic and environmental change. Rather, smaller specimens require smaller amounts of resources and can exist in smaller habitats. Therefore, they will not feel the effects of a shrinking habitat until well after the larger species have started to deal with the environmental pressures. The selective pressures brought about by environmental changes caused the extinction of several large species of land animals. Additionally, the minor halts and readvances of the Wisconsin ice sheet during this period of extinction (between 18,000 and 11,000 years ago), were insufficient to restore the previous environmental balance and merely temporarily slowed the inexorable extinction of several species under selective stress (Hester 1967).

A corollary argument to the climate hypothesis concerns gestation length. Slaughter (1967) proposes that the inability of certain species to adjust their mating habits to the changing climates of the late Pleistocene brought about their extinctions. These species tended to be larger, with longer gestation periods. Different species mate at different times of the year depending on either direct cues or correlated cues (Kiltie 1984). Those species that possess a gestation period shorter than the favorable season for producing offspring determine when to reproduce using direct cues—conditions that make birth favorable, such as temperature and food availability. Conversely, those species with gestation periods longer than the favorable season for producing offspring initiate mating using correlated cues. Correlated cues do not affect reproductive success, but

rather, correlate with conditions that directly influence the survival of the mother and her offspring, such as temperature, rainfall, or photoperiod (Kiltie 1984). Larger species generally use correlated cues because their increased size lends itself to increased gestation periods. Correlated cues influence the time of mating such that the offspring will arrive during the favorable season, given that the seasonality does not change.

However, during the late Pleistocene, seasonality increased. Unpredictable environment skews the correlated cues such that the reproductive rates of larger species decreases. Therefore, the increasing seasonality of the late Pleistocene would increase the risk of extinction of these larger species due to their decreased birth rates. Kiltie (1984) also states that uncertainty in the length of gestation period and timing of birth with respect to season can reduce fitness. This uncertainty reduces the reproductive success in seasonal environments because the favorable season is more limited and survival of the offspring is directly related to whether or not birth occurred during the favorable season. Larger species are more affected by uncertainty because of their increased gestational period and decreased favorable season (offspring need sufficient time to reach a favorable size for upcoming harsh weather). Additionally, Kiltie (1984) says that reproductive rates decreased during the increasing seasonality of the late Pleistocene because time was lost synchronizing reproductive cycles to the changing environmental cycles. The “lost” time should have been used to produce offspring, but was instead wasted waiting for favorable breeding cues. This problem is magnified in large species with long gestation periods because more time is lost. Reduced reproductive success in these large species precipitated their extinction because their intrinsically smaller populations are much more sensitive to decreasing numbers of offspring. If insufficient offspring are produced to carry a population, it will disappear.

Another climate-related argument was made by Gingerich (1984). He states that the late Pleistocene extinctions are merely a response to a high rate of species origination in the early Pleistocene because “origination and extinction are in dynamic equilibrium constrained by environmental diversity” (Gingerich 1984:216). During the early Pleistocene, originations far outnumbered extinctions, thus suggesting a high level of environmental diversity. The glacial period exhibited high environmental heterogeneity, and therefore, supported diverse fauna (Gingerich 1984). However, during the retreat of the Wisconsin ice sheet and the deglaciation of the landscape, environmental heterogeneity decreased, rendering a high level of faunal diversity unsupportable. Thus, Gingerich (1984) makes the argument that the high rate of extinction during the late Pleistocene was a natural equilibration response to the previous high rate of origination during the early Pleistocene.

Human Overkill

In addition to the climatic changes occurring in the late Pleistocene, modern *Homo sapiens* hunter-gatherers were migrating across the Beringia land bridge into North and South America. The dates of the extinctions of the megafauna coincide with the Clovis culture in the Americas. Thus, the argument has been made that human hunting caused the Pleistocene extinctions.

According to Martin (1967), the extinctions of the megafauna are not consistent with climatic change because the majority of losses were in North and South America and Australia. In addition, the extinctions were largely terrestrial animals with very few marine or plant extinctions. Martin (1967) also points out that the previous glaciation cycles were roughly equivalent in magnitude to that of the Wisconsin ice sheet in terms of environmental stress, but did not experience nearly the same scale of extinctions. Many of the spe-

cies that became extinct during the late Pleistocene survived the previous glacial cycles, necessitating another explanation. The only unique thing about the Wisconsin glacial cycle is the global spread of *Homo sapiens*.

The extinctions of the late Pleistocene occurred relatively rapidly, within a few thousand years. Additionally, there are very few kill or processing sites in the archaeological record connecting *Homo sapiens* to the lost fauna. Grayson (1984) says that this lack of associations between extinct Pleistocene mammals and humans in North America refutes the overkill hypothesis, but Martin (1984) states that this paucity supports a blitzkrieg model. Blitzkrieg is a “special case of faunal overkill that maximizes speed and intensity of human impact and minimizes time of overlap between the first human invader and the disappearance of native fauna” (Martin 1984: 396). The blitzkrieg model explains the lack of kill sites by reasoning that the extinction of these animals occurred too rapidly to have left much, if any, evidence. Therefore, the uniqueness of *Homo sapiens* in the New World and Australia, coupled with the lack of kill sites in the archaeological record, can be taken as evidence of blitzkrieg human overkill causing the late Pleistocene extinctions.

During the deglaciation process, the general ambient temperature increased along with the net usable moisture over the land. Equability of temperatures and seasonality most likely decreased in the northern and central portions of North America, but remained stable in the coastal areas, southern North America, and the North American peninsula (McDonald 1984). Essentially, areas existed where temperatures and seasonality remained stable. Therefore, animals unable to cope with the climate changes in their habitats might have migrated. In addition, deglaciation caused an increase in continental land area due to the retreat of the ice sheet. Land area positively correlates with species diversity, thus the increased land area could have supported

a greater number of species (McDonald 1984). Overall, the climate change was favorable to terrestrial animals due to increased primary productivity of the land and cannot account for extinction. Following this argument, *Homo sapiens* were the only disruptive element in the existing environment of the late Pleistocene. The disruption caused by this new, highly successful predator was enough to exterminate several species of large land animals due to lowered population sizes (McDonald 1984). Given the low reproductive rate of large animals, a diminished population size can lead to inadequate fitness to sustain the population as a whole.

During migration across the Beringian land bridge, *Homo sapiens* brought with them a meat-based diet and new bacteria and parasites. A meat-based subsistence pattern evolved during the Upper Paleolithic in Europe as a response to the frigid environment (Jelinek 1967). This same adaptation allowed *Homo sapiens* to survive during migration across the tundra environment of Asia and Berengia. This predilection for animal protein as the mainstay of diet combined with the inexperience of local prey (large animals in the Americas) with *Homo sapiens* hunting practices led to profligate extermination of these species (Jelinek 1967). Since the indigenous species of the New World had not evolved in the presence of *Homo sapiens*, they also had not developed the natural wariness exhibited by similarly large species in the Old World. Thus, the megafaunal species were easy hunting targets. In addition, *Homo sapiens* served as a transport method for foreign bacteria and parasites during migration across Berengia. The diffusion of new diseases into a population of herbivores unadapted to exposure decimated the indigenous large animal species (Edwards 1967). While disease alone is probably not sufficient to cause extinction alone, the resultant reduction in population size combined with *Homo sapiens* hunting practices and low reproductive rates common to megafauna most certainly

caused some populations to shrink to numbers impossible to maintain.

Modeling studies done by Whittington and Dyke (1984) and, more recently, Alroy (2001) lend further credence to the human overkill hypothesis. Whittington and Dyke (1984) utilized the Mosimann and Martin model positing that megafaunal extinction in North America could be caused by a small number of *Homo sapiens* migrating in a “front” across the landscape, leaving little archaeological evidence behind. A “front” occurred when the hunting of the human population caused the extinction of megafaunal species in the inhabited area. The model was run using baseline parameters including initial prey biomass, prey carrying capacity, prey biomass growth rate, initial human population size, human population growth rate, human carrying capacity, and minimal kill, defined as the minimum value of prey destruction rate required to cause simulated megafaunal extinctions (Whittington and Dyke 1984). By assigning values to these parameters based on empirical archaeological evidence, Whittington and Dyke (1984) found that overkill is a plausible explanation for the late Pleistocene extinctions. Alroy (2001) used a computer simulation to model *Homo sapiens* and large herbivore population dynamics in the North American end-Pleistocene. He assumed slow *Homo sapiens* population growth, random hunting that was nonselective and limited, and low maximum hunting efforts combined with parameters culled from published values. Simulations found that *Homo sapiens* growth rate and hunting ability almost always led to mass extinctions, with hunting ability being the most important of all parameters (Alroy 2001). Alroy (2001) concluded that the overkill hypothesis was not only credible, but “an anthropogenic extinction was unavoidable given the facts of ecology and the fossil record—even assuming that human predation was limited and nonselective” (Alroy 2001: 1896).

Utilizing newer dating methods, Roberts (2001) looked at extinctions in Australia in attempt to determine if *Homo sapiens* or climate changes were the underlying cause. He rejected dates calculated by radiocarbon (^{14}C) as unreliable. Using optical dating, which measures the time elapsed since sediments were last exposed to light (luminescence method), and $^{230}\text{Th}/^{234}\text{U}$ dating, which measures crystallization age of flowstone, he determined the burial ages of 28 sites. From these measurements, he found that extinctions occurred around 46,400 years ago across Australia, thus ruling out any climatic impacts from the late Pleistocene as the underlying cause (Roberts 2001). Since *Homo sapiens* arrived in Australia at least 40,000 years ago (Horton 1984), Roberts' (2001) data concurs with the human overkill hypothesis of extinction.

While hunting large game seems to counter expectations generated by optimal-foraging and diet-breadth models, Hildebrandt and McGuire (2002) see it as an important social aspect in hunter-gatherer society apart from group provisioning. Large-game hunting served as an activity that had the added bonus of increased fitness due to increased mating opportunities and favorable treatment for offspring, in addition to greater access to social networks, political alliances, and political authority (Hildebrandt and McGuire 2002). This view is corroborated by Kaplan and Hill (1985), who contend that sharing behaviors had their origins in increased fitness benefits accrued from certain activities. Given that large game is most conducive to sharing outside the immediate family, it stands that *Homo sapiens* would pursue these animals, even after their numbers had dwindled, because of the perceived benefits. This is an example of "show off" behavior. These aspects of late Pleistocene *Homo sapiens* hunter-gatherer societies would be evident in the archaeological record in the form as specialized tools for hunting big game. An example of these tools includes the fluted points found in Clovis sites in

North America. Hildebrandt and McGuire (2002) confirm that the relationship between hunter and hunting weaponry is fundamental to the high-risk, yet high-reward, behavior of hunting large animals. Thus, it is possible to argue that human overkill of megafauna was motivated by the pursuit of fitness benefits associated with hunting large game animals and resulted in extinction.

Discussion

In looking at these arguments, it becomes apparent that they are not mutually exclusive. It is quite possible that climate worked cooperatively with *Homo sapiens* to produce the extinction effect that claimed so many terrestrial animals in the New World and Australia. The changing climate, complete with rising temperatures, desiccation of the environment, and retreat of the Wisconsin ice sheet could have pushed large terrestrial animal populations into dangerously low numbers due to the environmental pressures. Then, the hunting practices of *Homo sapiens* groups, unaware of the imminent dangers of small population sizes for megafauna, could have pushed these animals over the brink, onto the inexorable path towards extinction. In this model of megafaunal extinction, both arguments play a role, yet neither is dominant enough to assume sole responsibility for the late-Pleistocene extinctions. If *Homo sapiens* groups were not present, population numbers might have recovered after an unstable period of adjusting to the new climate and habitat. Conversely, if climate had not already reduced the population sizes of large animals, the relatively small number of migrating *Homo sapiens* arriving in the New World and Australia may not have been sufficient to decimate entire species of megafauna.

The models proposed by Whittington and Dyke (1984) and Alroy (2001) are used to further the hypothesis that human overkill caused the late-Pleistocene extinctions; however, there are some aspects that they do not address.

Neither model takes climate change into account, which is negligent considering the widespread acknowledgement that climate was changing during this time period. Given ethnographic data collected from modern hunter-gatherer groups, hunting behavior varies depending on environment. The Whittington and Dyke (1984) model assumed a rapid rate of migration as a "front" that left extinction in its wake. It ascribes the lack of archaeological data for this front to the rapidity with which *Homo sapiens* migrated across the continent, following Martin's (1984) blitzkrieg model. Attributing the lack of associated sites to being caused by a short time frame of extinction and migration is somewhat questionable. Sites might be sparse and lack high densities of accumulated material because of the short time frame, but that is not to say they do not exist. Simply, these sites have yet to be uncovered. If they were uncovered, this would not refute the blitzkrieg model unless they showed evidence of long inhabitation periods (i.e.: high densities of accumulated debris). In addition, Alroy's model (2001) sets the minimum number of people entering a given region at 100. Modern hunter-gatherer group size tends to hover around 25 individuals, especially if they exhibit high mobility like the overkill hypothesis assumes. It is unknown from Alroy's (2001) data what effect reducing group size to 25 individuals would have on the outcome of his model.

It is possible to combine the arguments presented by some of these studies, such that they would support a multifaceted model of extinction. For example, Guilday (1967) proposes that the changing climate in the late Pleistocene caused many habitats to shrink. This reduction in suitable habitat size forced a higher number of large terrestrial animals to inhabit a given area than normally would. While Guilday (1967) argues that the concentration of megafauna in these habitats caused competition such that several species became extinct, this accumulation also served

to concentrate prey for hunter-gatherer groups. A high number of prey in a small area increases the chance for successful hunting. Hildebrandt and McGuire (2002) argue that hunter-gatherer groups pursue large game for the perceived fitness benefits gained by successful hunters. Thus, it makes sense that a higher hunting success rate in a given area due to concentration of large game animals into climate-shrunk habitats would encourage increased hunting. Combined with competition between species, this increase in hunting activities could very well push a species to extinction. This blending of arguments, originally sup-

porting opposing hypotheses, works very well to support combining the effects of *Homo sapiens* with global climate change to explain megafaunal extinction in a multifaceted model.

Whereas a resolution to the debate between the climate and overkill hypotheses may not be possible to reach, a compromise might serve as a better conclusion. The opposing arguments agree on the fact that the late-Pleistocene climate changes occurred at approximately the same time as the arrival of *Homo sapiens* in the New World. There is simply no separating the two events. Since there is no differentiating between the time

frames of these two events, it follows that the effects of climate and *Homo sapiens* on the megafaunal populations should not be differentiated either. Both hypotheses seem to have holes that are most logically filled with data from the opposing argument. Therefore, a multifaceted model, incorporating arguments and data from both sides of the debate, makes the most sense in explaining the late-Pleistocene megafaunal extinctions.

References

- Alroy, John. (2001). "A Multispecies Overkill Simulation of the End-Pleistocene Megafaunal Mass Extinction." *Science* 292:1893-1896.
- Edwards, William Ellis. (1967). "The Late-Pleistocene Extinction and Diminution in Size of Many Mammalian Species." In *Pleistocene Extinctions: The Search for a Cause*. Paul S. Martin and H.E. Wright, Jr., eds. Pp. 141-154. New Haven: Yale University Press.
- Gingerich, Philip G. (1984). "Pleistocene Extinctions in the Context of Origination-Extinction Equilibria in Cenozoic Mammals." In *Quaternary Extinctions: A Prehistoric Revolution*. Paul S. Martin and Richard G. Klein, eds. Pp. 211-222. Tucson: University of Arizona Press.
- Grayson, Donald K. (1984). "Archaeological Associations with Extinct Pleistocene Mammals in North America." *Journal of Archaeological Science* 11(3):213-221.
- Grayson, Donald K. (1991). "Late Pleistocene Mammalian Extinctions in North America: Taxonomy, Chronology, and Explanations." *Journal of World Prehistory* 5(3):193-231.
- Guilday, John E. (1967). "Differential Extinction During Late-Pleistocene and Recent Times." In *Pleistocene Extinctions: The Search for a Cause*. Paul S. Martin and H.E. Wright, Jr., eds. Pp. 121-140. New Haven: Yale University Press.
- Haynes, C. Vance. (1984). "Stratigraphy and Late Pleistocene Extinction in the United States." In *Quaternary Extinctions: A Prehistoric Revolution*. Paul S. Martin and Richard G. Klein, eds. Pp. 345-353. Tucson: University of Arizona Press.
- Hester, James J. (1967). "The Agency of Man in Animal Extinctions." In *Pleistocene Extinctions: The Search for a Cause*. Paul S. Martin and H.E. Wright, Jr., eds. Pp. 169-192. New Haven: Yale University Press.
- Hildebrandt, William R. and Kelly R. McGuire. (2002). "The Ascendance of Hunting During the California Middle Archaic: An Evolutionary Perspective." *American Antiquity* 67(2):231-257.
- Horton, David R. (1984). "Red Kangaroos: Last of the Australian Megafauna." In *Quaternary Extinctions: A Prehistoric Revolution*. Paul S. Martin and Richard G. Klein, eds. Pp. 639-680. Tucson: University of Arizona Press.
- Jelinek, Arthur J. (1967). "Man's Role in the Extinction of Pleistocene Faunas." In *Pleistocene Extinctions: The Search for a Cause*. Paul S. Martin and H.E. Wright, Jr., eds. Pp. 193-200. New Haven: Yale University Press.
- Kaplan, H. and K. Hill. (1985). "Food Sharing Among Ache Foragers: Tests of Explanatory Hypotheses." *Current Anthropology* 26: 223-245.
- Kiltie, Richard A. (1984). "Seasonality, Gestation Time, and Large Mammal Extinctions." In *Quaternary Extinctions: A Prehistoric Revolution*. Paul S. Martin and Richard G. Klein, eds. Pp. 299-314. Tucson: University of Arizona Press.
- Martin, Paul S. (1967). "Prehistoric Overkill." In *Pleistocene Extinctions: The Search for a Cause*. Paul S. Martin and H.E. Wright, Jr., eds. Pp. 75-120. New Haven: Yale University Press.
- Martin, Paul S. (1984). "Prehistoric Overkill: The Global Model." In *Quaternary Extinctions: A Prehistoric Revolution*. Paul S. Martin and Richard G. Klein, eds. Pp. 354-403. Tucson: University of Arizona Press.
- McDonald, Jerry N. (1984). "The Reordered North American Selection Regime and Late Quaternary Megafaunal Extinctions." In *Quaternary Extinctions: A Prehistoric Revolution*. Paul S. Martin and Richard G. Klein, eds. Pp. 404-439. Tucson: University of Arizona Press.
- Roberts, Richard G. et al. (2001). "New Ages for the Last Australian Megafauna: Continent-Wide Extinction About 46,000 Years Ago." *Science* 292:1888-1892.

- Slaughter, Bob H. (1967). "Animal Ranges as a Clue to Late-Pleistocene Extinction." In *Pleistocene Extinctions: The Search for a Cause*. Paul S. Martin and H.E. Wright, Jr., eds. Pp. 155-168. New Haven: Yale University Press.
- Whittington, Stephen L. and Bennett Dyke. (1984). "Simulating Overkill: Experiments with the Mosimann and Martin Model." In *Quaternary Extinctions: A Prehistoric Revolution*. Paul S. Martin and Richard G. Klein, eds. Pp. 451-465. Tucson: University of Arizona Press.
-

Robin Gibbons



Robin Gibbons is a senior majoring in Human Biology with an area of concentration in Evolutionary Studies. At Stanford, she has been a member of the Leland Stanford Junior University Marching Band and has served as a College Assistant at Freshman-Sophomore College. This is her first submission to a Stanford publication. After graduating in 2004, she hopes to attend medical school. She would like to thank Dr. Teresa Steele for all of her insightful comments and helpful suggestions in the writing of this paper.