Clovis and Extinctions – Overkill, Second Order Predation, Environmental Degradation in a Non-equilibrium Ecosystem

Elin Whitney-Smith, Ph.D.
Geobiology, Netalyst Inc.
508 2nd Street SE,
Washington, DC 20003
elin@quaternary.net

Abstract

It is recognized that both popular hypotheses to explain extinctions at the end of the last ice age, Climate Change and Overkill, (i.e. people hunted herbivores to extinction) have significant problems. Some have suggested that the two hypotheses in combination yield a stronger explanation, essentially 1+1=2. The Pleistocene Extinction Model (Whitney-Smith, 1991, 2004) has been expanded to test this combination. The Pleistocene Extinction Model (PEM) was originally developed to test the Second Order Predation Hypothesis, (i.e. humans reduced carnivore populations leading to herbivore boom then bust) against Overkill. The expanded PEM includes a simplified Climate Change factor. In these PEM simulations, Climate Change counteracts the effect of Overkill, reducing not increasing extinctions, essentially 1+1=0. In contrast, Climate Change exacerbates the impact of Second Order Predation, hastening extinctions. This suggests that carnivore reduction may have been a successful strategy for pre-Clovis people, – killing the carnivore competition indeed increased game – prior to climate change. However, with climate change, Second Order Predation may have become a losing strategy resulting in environmental collapse and extinction.

Introduction

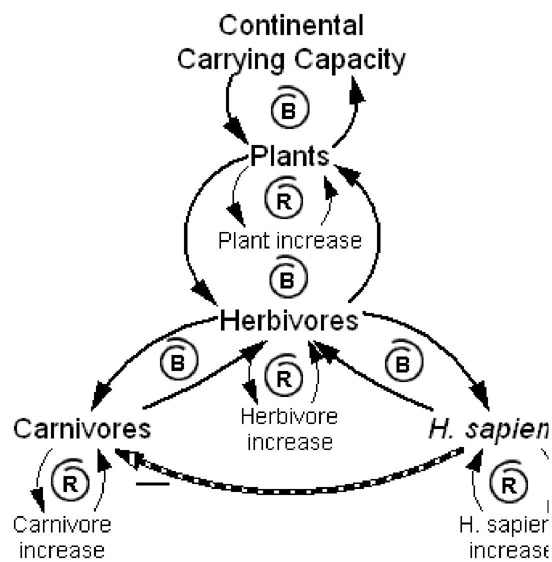
Clovis strikes the imagination. In 1974 I turned over a fluted point on a survey of Abbott Farm in New Jersey. The thought that I was the first person to hold it in thousands of years gave me a rush and I was hooked. Clovis, the people who came out of nowhere, spread through out the western hemisphere and disappeared seemingly without a trace leaving their beautiful points and a host of questions behind. Were they a broad network of people who shared knowledge? Were they all of one stock whose population expanded to fill two continents? Were they a thinly spread people? Or were they a few small groups widely ranging over the landscape following the animals they hunted? Did they hunt the megaherbivores to extinction or were they and the megaherbivores overtaken by climate change that drove the animals they hunted and them to extinction? We may never know the answers to these questions but we may be able to glean more knowledge about their world by thinking carefully about the ecological context of their time.

Scientists have proposed various hypotheses to account for the extinctions. Though each is based on sound observations and good reasoning, together they are like an Escher drawing where each individual piece is correct and detailed but the overall picture doesn't hang together well.

I have proposed a new theory of extinction – Second Order Predation (2OP) – and to get the overall perspective created a modeling environment, Pleistocene Extinction Model, (PEM) that compares 2OP to Overkill (Alroy, 2001, Mosimann, & Martin, 1975). PEM showed that using the same structure, assumptions and values 2OP produces extinction and Overkill does not. This chapter will review that work and then will expand upon it to include an examination of Combination Hypotheses: Overkill plus Climate Change and 2OP plus Climate Change.

Figure 1 shows a causal loop representation of PEM (for a detailed discussion see Whitney-Smith, 2004).

Figure 1 – Pleistocene Extinction Model (PEM)
The top three trophic levels are divided:
Continental Carrying Capacity is divided into: Carrying capacity for trees and Carrying capacity for grass
Plants are divided into:
Large and small trees, High and low quality grass
Herbivores are divided into:
Browsers, Mixed Feeders, Ruminant grazers and Non-ruminant grazers
Key:
B in a spiral means that the loop is balanced. R in a spiral means that the loop is reinforcing. The minus sign on the bottom arrow signifies that the relationship varies inversely – as H. sapiens *increases Carnivores decrease. The dashed line arrow at the bottom signifies that there are two theories tested with this model – Overkill(OK) without H. sapiens reducing carnivore populations (without the link) and –Second Order Predation (2OP) H. sapiens reducing carnivore populations (with the link)*



Overkill and its problems

The Overkill hypothesis, proposed by Paul Martin (1975), holds that *H. sapiens* entered the New World and swept through the continent killing herbivores until they were extinct. Mossiman and Martin (1984) and Whittington and Dyke, (1989) created computer models that suggest that it is possible for *H. sapiens* to over hunt herbivores if they kill more herbivores each year than are replaced through natural population increase. They concentrate on the relationship between *H. sapiens* and herbivores. Alroy (2001) concentrates on the same relationship though his herbivore sector is considerably more complex.

The Overkill hypothesis would be modeled as figure 2a

The problems with the Overkill hypothesis are:

1. In general, it is difficult for predators to over-hunt their prey since it is their food supply and it does not recognize any role for either plants or carnivores.
2. The time period from the first appearance of *H. sapiens* in the New World to the extinctions seems too short.
3. Animals not hunted by humans, such as the giant ground sloth, also went extinct.

Climate change and its problems

Vastly simplified, the Climate Change hypothesis suggests that as the ice age waned, climate changed so drastically that animals were not able to adapt. There have been a number of variations on this theme (Axelrod, 1967; and Slaughter, 1967; Kilti, 1989; Hoppe, 1978; Guthrie, 1980, 1989; Guilday, 1989; Graham & Lundelius 1989).

One of the major pieces of evidence is based on Hansen's (1978, Phillips, 1988) study of Ground Sloth dung from Rampart cave. It shows that over time the sloth ate less and less of its' preferred food and more and more of the food that other herbivores couldn't digest.

Clearly, the North American climate changed at the end of the Pleistocene:

- At the beginning of the Holocene (the age following the Pleistocene), the mixed parklands and woodlands throughout the continent were transformed into the great (and treeless) prairie, and the mixed parkland/woodland on the coasts has become closed-canopy forest. What Guthrie has called a shift from plaid to striped (1980, 1989)
- There was an increase in continentality (hotter summers and colder winters);
- There was less rainfall, and it was more variable;

Though there are some implications about weather (animals being born into snowstorms instead of a warm spring), the major impact on the animals is that they are unable to get enough plants or enough of the right kind of plants at the right time to eat. Thus they were unable to reproduce, survive pregnancy, or nurse, or the young were unable to find sufficient food to eat. The Climate Change hypothesis can be modeled as shown in figure 2b. There is an exogenous reduction in the capacity of the land to produce plants, which reduces plants and therefore reduces herbivores.

These hypotheses have been challenged by the observation that increased continentality resulted in an increased prevalence of grasses. McDonald (1981, 1989) suggests the horses, which became extinct, on this continent, actually should have prospered during the shift from mixed woodland-parkland to prairie, because their primary food source, grass, was increasing rather than decreasing (Birks & West, 1973; McDonald 1981, 1989) and horses successfully live and reproduce in those same places today

Further, the increase in continentality was not greater than the continentality of Siberia during the Pleistocene, where these same animals prospered. Indeed, climate change is associated with extinctions only in the Americas, and not in Africa, Asia, Europe, or Australia.

Finally Mammoths, sloths, mastodons and other animals that went extinct had survived similarly warm periods during previous inter-glacials and New World horses, which went extinct at the end of the Ice Age, are thriving in that same climate today.

Clue: Shift from plaid to striped environments, the lack of preferred food for the ground sloth, and horses living and reproducing on those same foods today.

Combination of Climate Change and Overkill

Most scientists find both the Overkill and the Climate Change hypotheses unsatisfactory; they believe that the extinctions are due to some combination of Overkill and Climate Change.

Gary Haynes (1991) supports a combination hypothesis. His observations suggest that mammoths were suffering from environmental stress. He compares their condition to that of African elephants that experience die offs. But observes that elephant populations recover from environmental die offs but they are less likely to survive modern hunting. He says:

> While climatic changes were driving proboscideans to die off, the added stress of Clovis hunting drove them to die out. In the absence of Clovis hunters, mammoths and mastodonts (and other megafauna) should have been able to survive the changing conditions of terminal Pleistocene environments (p.317).

He reasons that people opportunistically hunted mammoths as they became more and more stressed and hence more vulnerable to predation. He argues that the long, marrow containing bones are not broken indicating that the animals had little fat on them and that this indicates environmental stress. He also argues that most carcasses do not show signs of full utilization by either people or carnivores.

However though he has a developed theory of proboscidean extinction he invokes another reason for the extinction of the American camel (mixed feeders) and horses (non-ruminant grazers) – increased snow cover (Haynes, 1991) – thus requiring two theories instead of one making his theories less parsimonious than 2OP. He notes that proboscidean populations increase after the decline in camels and horses.

Though the combination hypothesis seems to be the most intuitive explanation, there aren't proposals of how that combination would have worked. The basic concept is shown in figure 2c.

Clues: The proboscideans were suffering from environmental stress, the non-synchronous decline of species.

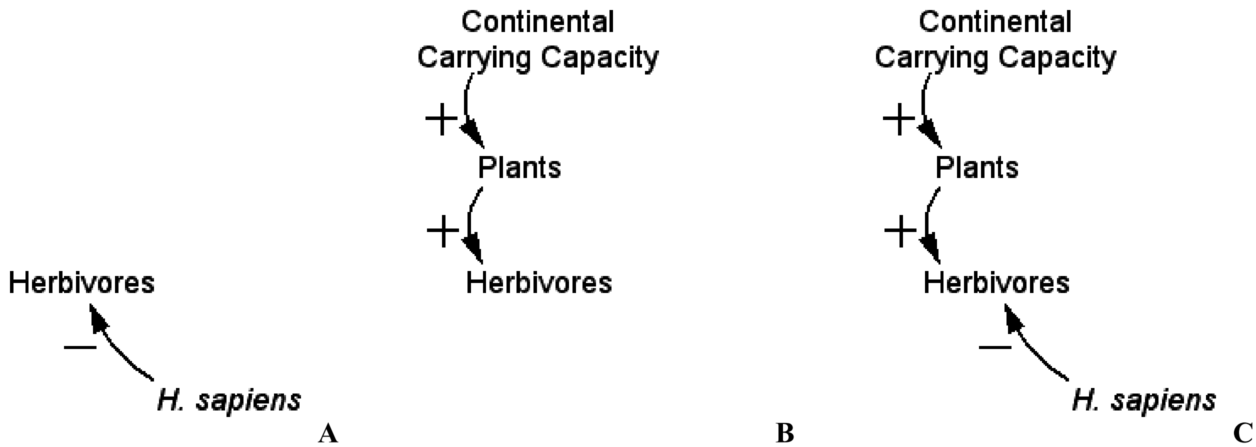


Figure 2 Theories of Pleistocene Extinctions
A – Overkill H. sapiens kills herbivores,
B – Climate change, exogenous reduced carrying capacity reduces plants, which in turn reduces Herbivores,
C – Combination Hypothesis both arrows into herbivores reduce their population size.
Key Plus at the end of an arrow indicates co-variance (As plants decrease, herbivores decrease) Minus at the end of an arrow indicates varying inversely (As *H. sapiens* increases herbivores decrease)

Problems with Climate Change, Overkill and Combination Hypotheses

The hypotheses do not attempt to explain the pattern of extinctions – the loss of many browsers, and mixed feeders and the favoring of ruminant over non-ruminant grazers and the general dwarfing of many species including bison, beavers, elk and moose (Guthrie, 1989).

None of the competitors for 2OP – Climate Change, Overkill, and some Combination of Climate Change and Overkill, recognize of the role of carnivores in maintaining the balance on an ecosystem.

In addition, none of the hypotheses recognize that all of these relationships are balanced relationships. There are feedbacks between the population of herbivores and plants, between the populations of herbivores and carnivores and between the populations of *H. sapiens* and herbivores. Each of the three trophic levels depends upon the upper level for food and the lower level for controlling population. Before any hypotheses could be tested it was necessary to create an equilibrium ecosystem. Any balanced ecosystem model used to represent a combination hypothesis needs loops representing the fact that population levels of a time period determine the upper levels of population of the time period following – plants beget plants, herbivores beget herbivores, carnivores beget carnivores and humans beget humans as shown in figure 1 above.

Second Order Predation hypothesis

The Second Order Predation hypothesis posits that *H. sapiens* entered the New World, and not only killed herbivores for food but reduced carnivore populations to the extent that they were unable to control herbivore populations. The model does not address either why or how humans reduced carnivore populations. Killing carnivores may have been for fur, a strategy to reduce competition, a response to carnivore predation on humans, or the result of an introduced carnivore disease. We know that when wolves enter a new territory they kill existing predators – fox, coyote (Carbyn et al 1995) – humans have the added advantage of planning, policy and rational thought and communication. We also know from work done in the Serengeti (Sinclair, 1979) that when herbivore populations are reduced through the introduction of a new predator existing predators will turn to killing *H. sapiens* , giving *H. sapiens* a reason for killing carnivores. Soffer (1985) has documented carnivore killing in Siberia during the same time period and suggests it was for fur. And since, *H. sapiens* does not use carnivores for food there is no natural feedback loop as there is with herbivores.

Regardless of the reason, reduction in carnivore populations allows the reinforcing loop, (herbivores increases herbivores) to dominate the system – boom. The herbivore boom kills off most of the vegetation – bust (Fig. 3).

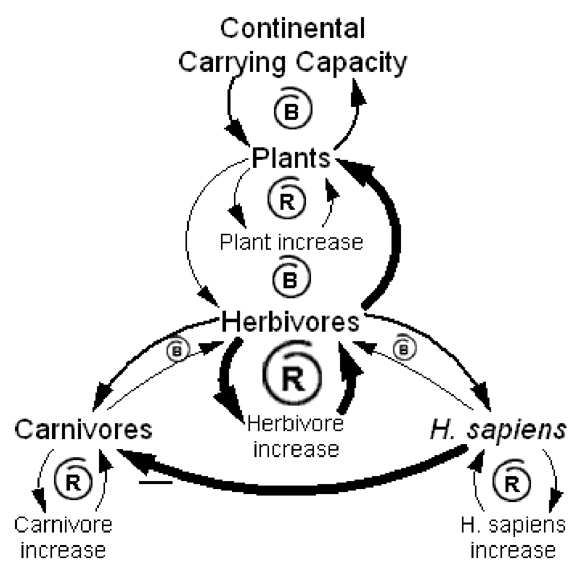


Figure 3 –H. sapiens reduces carnivore populations. The self-reinforcing loop, Herbivores produce Herbivores, dominates the system.
The heavy arrow from Herbivores to Plants indicates heavy usage of plants. Then as plants are reduced the plant increase is reduced. The balancing loop between plants and Herbivores means that herbivores begin to starve as plants disappear.
The balancing loops between Carnivores and Herbivores and between H. sapiens and Herbivores are ineffective and almost disappear.
Key:
B in a spiral means that the loop is balanced. R in a spiral means that the loop is reinforcing. The minus sign on the bottom arrow signifies that the relationship varies inversely – as H. sapiens increases Carnivores decrease. The dashed line arrow at the bottom signifies that there are two theories tested with this model – Overkill(OK) without H. sapiens reducing carnivore populations (without the link) and Second Order Predation (2OP) H. sapiens reducing carnivore populations (with the link)

Pleistocene Extinction Model (PEM): Second Order Predation vs. Overkill

To go from a theory to a model that will account for the pattern of extinction it is necessary to expand and disaggregate. Expand to recognize that there is an upper limit to the ability of the land to produce plants. And disaggregate plants into 2 kinds of plants (trees and grass) and 4 kinds of Herbivores (Browsers, Mixed Feeders, Ruminant and Non-ruminant Grazers). The two top-level predators remain the same Carnivores and *H. sapiens* .

The model runs in two modes one where *H. sapiens* hunts Herbivores but doesn't reduce carnivore populations to represent the Overkill hypothesis and one where *H. sapiens* does reduce carnivore populations to represent the Second Order Predation hypothesis

Values used were based on Mossiman and Martin (1975) and Whittington and Dyke (1989). Carnivore values were based on the needs of modern carnivores – 20 lbs of food per pound of carnivore per year (Carbyn et al 1995; Cat House, 1996). *H. sapiens* hunting values were based on food need of 10 lbs of meat per pound of *H. sapiens* per year or half the food necessary to support an obligate carnivore. In other ways Carnivores and *H. sapiens* are modeled similarly. This is probably fairly high since modern hunter/gatherers generally have a diet of only 20% meat. This would favor Overkill rather than Second Order Predation. Both Carnivores and *H. sapiens* hunt herbivores based on their density.

Results showed that Second Order Predation leads to herbivore extinction, and Overkill does not.

The graphs below (Graph 1 A&B) contrast the Overkill hypothesis (A) with the Second Order Predation Hypothesis (B). (The origin of all curves is at equilibrium and all variables have been normalized for comparability)

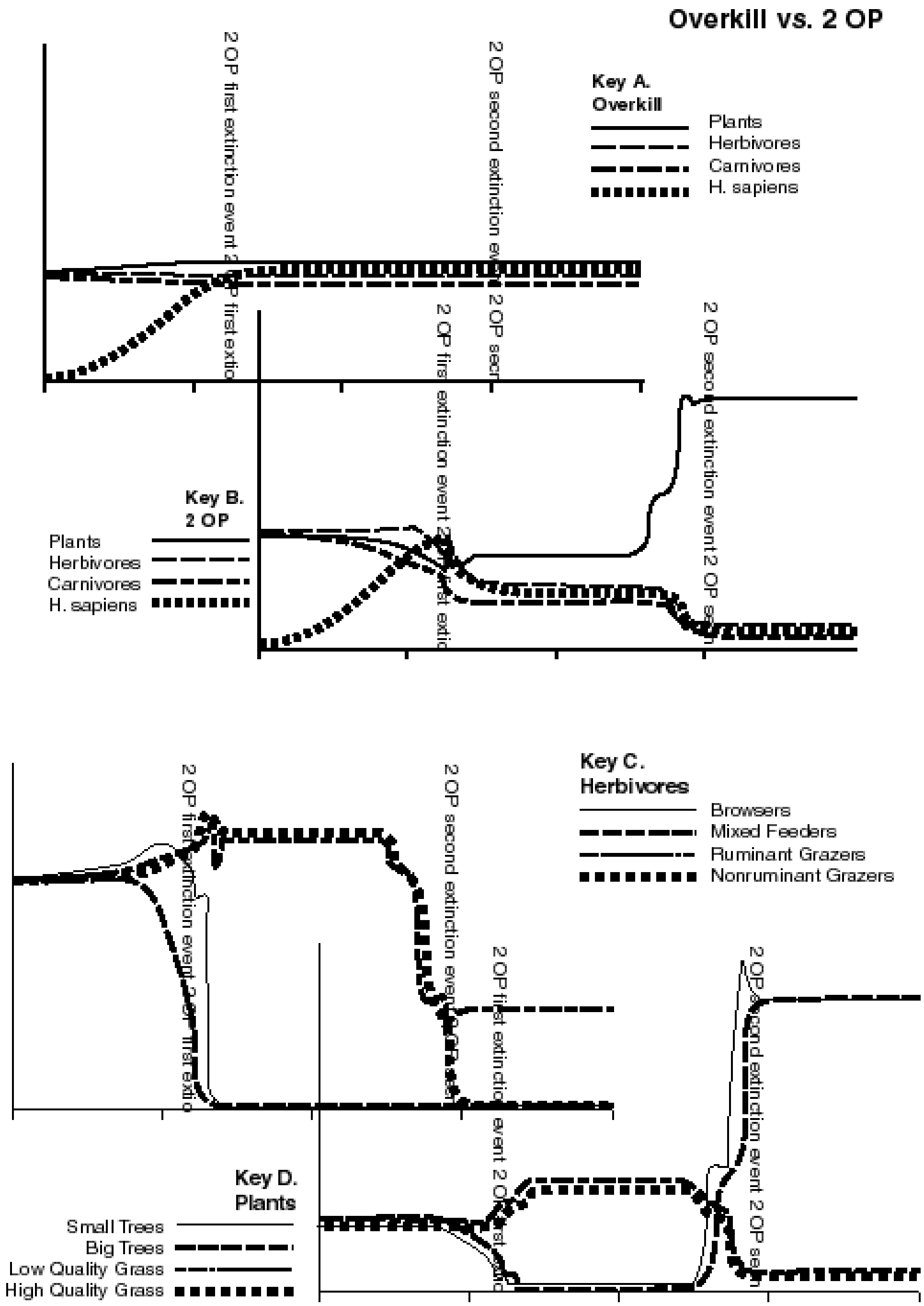
In the Overkill scenario (Graph 1A) as *H. sapiens* increase there is a slight increase in trees, a decrease in carnivores and herbivores but no extinction.

In the Second Order Predation scenario (Graph 1B) as *H. sapiens* increase, and reduce carnivore populations as well as herbivores, the decrease in carnivore populations leads to

1. An initial increase in all herbivore populations and a decrease in plants
2. A major crash of all populations (first extinction -10735).
3. A period of equilibrium.
4. An increase in plants followed by another crash in all other populations (second extinction -9750).
5. A final equilibrium with plants very high and all other populations reduced significantly.

Behind the scenes in Graph 1 C&D there is more detail. In the herbivore graph (Graph 1C) the initial equilibrium is followed by:

1. Browsers, Ruminant and Non-ruminant grazers increase Mixed Feeders decline
2. Mixed Feeders followed by Browsers go extinct
3. Ruminant and Non-ruminant grazers are at equilibrium
4. Ruminant and Non-ruminant grazers decline and Non-ruminants go extinct
5. Ruminants establish a new equilibrium at a lower level.



Graph 1 – Overkill vs. 2OP

A – Overkill B – 2OP (H. sapiens kills 0.25lbs of carnivore per year) using the same assumptions

C – 2OP Herbivores D – Plants

For all graphs time is 1.5K years and curves are normalized at their equilibrium level.

The Plant (Graph 1 D) shows

1. Tree stocks decline and grass stocks increase
2. Trees reach almost to zero

3. There is a period of high grass at equilibrium
4. Then trees begin to repopulate
5. Grass and trees establish a new equilibrium with many more trees and much less grass

If we break down the results into phases we can understand what is happening.

In the first phase (between 11117 and 10735 BP) as carnivore stocks are reduced the link between carnivores and the various herbivore stocks are weakened so the balance of the carnivore-herbivore loops is lost. This allows the reinforcing loops of herbivores increase herbivores to dominate the system. This accounts for the increase in Browsers, and both Grazer stocks. The high gain in the recruitment loop for Browsers has two impacts:

1. Browsers drive Mixed Feeders to extinction (Browsers only eat Trees Grazers only eat Grass Mixed Feeders need both Trees and Grass and yet are less efficient at obtaining either – under equilibrium conditions they buffer the system from shocks since they are able to substitute grass for trees in small amounts. Under more extreme conditions they are not able to get enough trees and decline.)
2. The low recruitment rate for trees results in browsers overshooting the limit of tree stocks so they follow Mixed Feeders to extinction.

In second phase (between 10735 and 9780 BP) following the extinction of Mixed Feeders and Browsers,

Grass, with its high recruitment rate is able to takes over the area Trees formerly occupied, but because grass does not create as much standing crop the overall level of plants remains lower than at the simulation start.

Non-Ruminant Grazers lead slightly in recruiting because the gain on their reinforcing recruitment loop is slightly higher

Ruminant and Non-Ruminant Grazers recruit until them reach the new grass limit and establish an equilibrium, with higher population levels then they had at the beginning of the simulation (Ruminants are more efficient at processing grass but Non-ruminants have a faster reaction time to changes in resources).

Trees begin to re-establish themselves retaking land previously occupied by grass

As grass gives way to trees ruminant grazers, having a more efficient biology are able to withstand the reduction in grass better than non-ruminant grazers

The final phase (after 9780 BP) after the extinction of Non-ruminant Grazers:

1. Trees reach their limit and grass is greatly reduced
2. The only herbivores left are Ruminant Grazers that establish equilibrium with the lower grass limit.
3. *H. sapiens* and Carnivores are also held to a lower limit
4. The entire system finds a new equilibrium

As herbivores boom, they denude the parkland of trees leaving trees only in mountain refugia on the coasts. Once browsers become extinct, trees repopulate from the refugia until they reach the plains. On the border between the encroaching trees and the prairie, ruminant grazers maintain the grassland by eating the new shoots and by trampling the ground. Thus, the vegetation pattern observed by supporters of the Climate Change hypothesis is endogenous to the Second Order Predation scenario. There is no second theory needed.

The Second Order Predation boom bust scenario gives us a way to think about the change in vegetation pattern suggested by the supporters of the Climate Change hypothesis. Mixed parklands and woodlands throughout the continent transformed into the great (and treeless) prairie, and the mixed parkland/woodland on the coasts has become closed-canopy forest is implied by this scenario. As *H. sapiens* reduced Carnivore stock herbivore stocks would overgraze and browse thus denuding the mixed parkland. Proboscideans (Mammoth and Mastodon) would have knocked over large trees to get at the tender shoots. Once browsers and mixed feeders were extinct trees could reinvade from mountain refugia along the coasts. In addition the loss of Proboscideans meant that they were no longer breaking up permafrost in the arctic. Thus permafrost would have claimed more and more area creating cold, poorly drained soils rather than the well-drained Mammoth Steppe (Guthrie, 1980) of the Pleistocene.

Discussion of Second Order Predation

Let us revisit the clues and see how Second Order Predation fits them.

Extinctions followed the introduction of humans becoming more severe as they invaded continent after continent (Africa least severe – New World most severe).

This makes sense as Second Order Predation, like Overkill is anthropogenic.

Shift from plaid to striped vegetative environments. AND Proboscideans were suffering from environmental stress.

As vegetation became scarce, proboscideans knock over the trees in the mixed parkland/woodland in order to get at the leaves at the tops. Grass, with its' short recruitment time took over and the only trees left were in inaccessible places at the tops of mountains. Trees reinvaded from the mountaintops once herbivores populations stabilized and the "bottleneck" was over. Prairie continued to be maintained by obligate grazing bison.

Species declined non-synchronously (bison up mammoths down and vice versa).

In the graphs presented above we see that initially browser populations increase the most as mixed feeders crash, and that the grazer populations increase more slowly.

Horses are able to survive and reproduce on Holocene vegetation.

The scenario presented here suggests a bottleneck when food for herbivores was very scarce. This favored smaller animals and animals who could extract the maximum nourishment from each blade of grass. Horses, being non-ruminants would have been at a selective disadvantage during the bottleneck but once the ecosystem stabilized horses could once again survive.

Animals not hunted by humans went extinct. AND Ground sloth cannot find its' preferred food.

Again the notion of a bottleneck of scarcity suggests first, animals not hunted by man would starve and second, animals would eat less favored food when their favored food was unavailable.

Goals for this work

Expand PEM to include Exogenous Climate Change

The challenge for this work is to begin to address the intuitive hypothesis – a combination of Overkill and Climate Change. To do this it is necessary to propose a simplified version of Climate Change and then to test it with Overkill and Second Order Predation. The proximate cause of extinction for most of the Climate Change scenarios is related to changes in the floral environment, i.e., a reduction in plant stocks. Therefore, I have chosen to use a reduction in the ability of the land to produce plants as a first pass proxy for Climate Change.

Climate change is modeled as an exogenous impact: a smooth 500-year decrease in the capacity of the land to produce plants. For instance, in a 10% climate change scenario, a land area that, at t=0, was able to produce 100 plant units annually would, at t=500, only be able to produce 90 plant units annually. (This model of Climate Change does not take into account the addition of more land as the ice sheets retreated.)

Modeling Climate Change

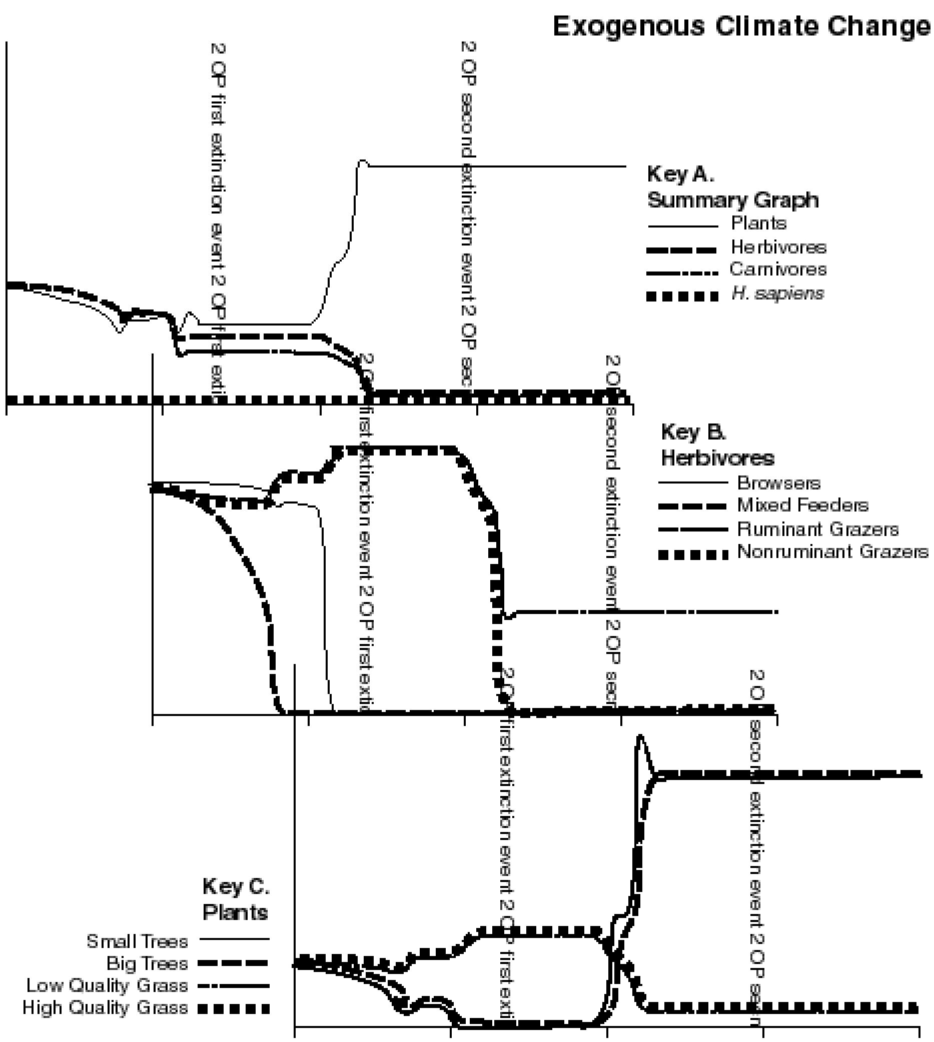
Make it extreme 13% (vs. 5%)

What level of Climate Change to use? I wanted Climate Change to have at least as severe an impact as the leading contender – Second Order Predation. In addition, to make the Overkill plus Climate Change scenario as strong a contender as possible, I sought a value that maximized the joint impact. I found this to be 13%, a value much larger than anyone would think actually occurred. To ensure that there were no further counterintuitive effects or non-linearities, I also tested lesser values of Climate Change, all the way down to 5%. In every case, a smaller value of Climate Change impact led to less impact on herbivore populations, both with Climate Change in isolation, and with that Climate Change in combination with Overkill.

Results of Extreme Climate Change

Graph 2A shows the result of the 13% Climate Change simulation. It is very similar to the graph of Second Order Predation (Graph 1B) except that things seem to be somewhat more compressed and *H. sapiens* is not included in this simulation, and thus remains at zero (0)

Looking behind the scenes is again similar to Second Order Predation (Graph 2B contrasted with Graph 1C) Again Mixed Feeders go extinct first followed by browsers. First both grazer stocks increase, then Non-ruminants go extinct, and only Ruminants survive. In the Plant graph too there is an overall similarity to the Second Order Predation Graph (Graph 2C contrasted with Graph 1D) there is a decrease in plants followed by extinction of browsers and mixed feeders, a decrease in carnivores, and an increase in plants. As in the Second Order Predation scenario, as trees begin to repopulate, non-ruminant and ruminant grazers are in competition with one another for the remaining grass. Ruminant grazers win this competition and the ecosystem reaches a new stability.

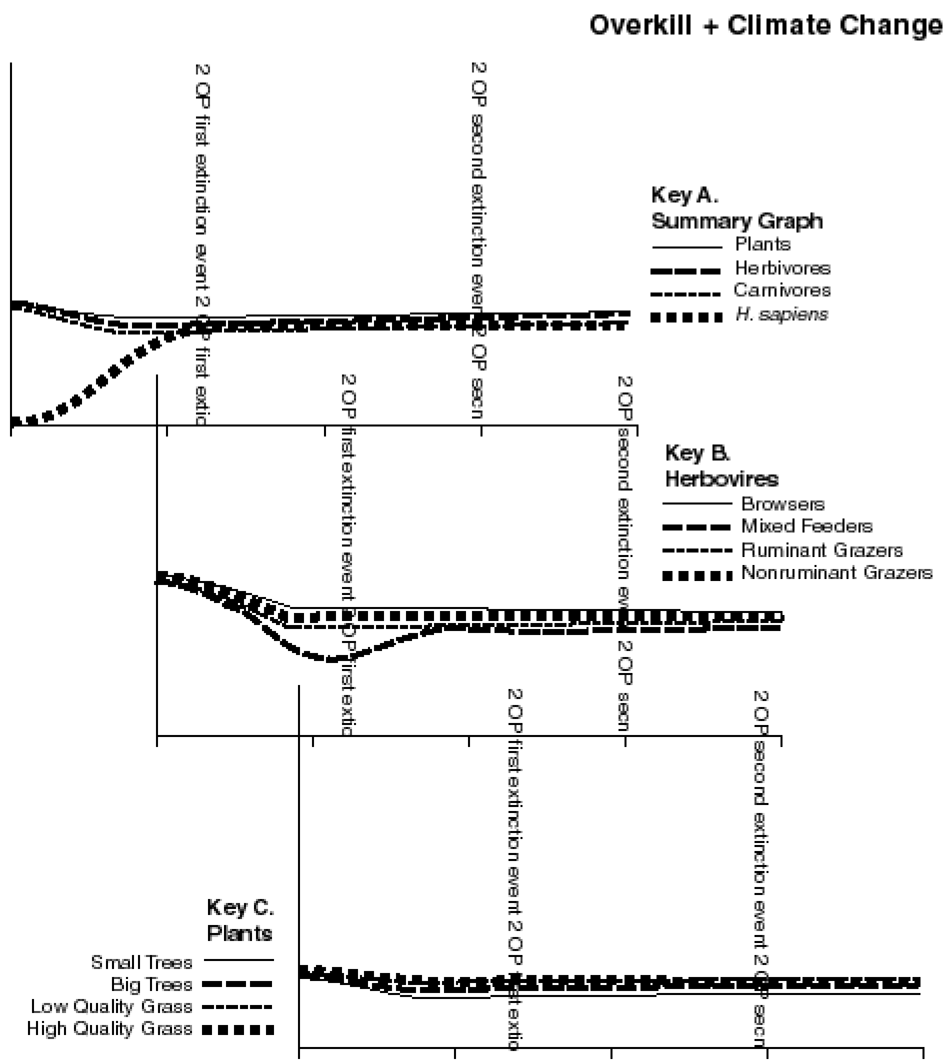


Graph 2 – 13% Exogenous Decline: Climate Change A – Summary, B – Herbivores, C – Plants
For all graphs time is 1.5K years and curves are normalized at their equilibrium level.

Results: Extreme Climate Change combined with Overkill and Second Order Predation

Overkill combined with Extreme Climate Change

If one then adds Overkill to this simulation —*H. sapiens* migrating into the continent killing herbivores combined with a 13% Exogenous Decline in Carrying Capacity (Graph 3A) – there is an initial decline in all sectors but then all sectors recover. The recovery is not as good as in Overkill alone Graph 1A but compared with Climate Change alone it is obvious that Overkill counteracts this degree of decline in Carrying Capacity (Graph 1A-C). Behind the scenes Graph 3B&C shows the increase in *H. sapiens* moderates the decline of Mixed Feeders and so the model regains its stability



Graph 3 – 13% Exogenous Decline combined with Overkill A – Summary Graph, B – Herbivores C – Plants
For all graphs time is 1.5K years and curves are normalized at their equilibrium level.

Second Order Predation with Extreme Climate Change

Reviewing Figure 3 above shows the loops for combining Extreme Climate Change with Second Order Predation. There is a positive feed back loop from *H. sapiens* reducing Carnivores, which increases Herbivores, which in turn increases *H. sapiens* . In addition, both the increase in Herbivores and the exogenous deterioration in climate reduce plants, this further exacerbates the ultimate collapse in climate.

Graph 4A-C shows the results of combining exogenous decline (Climate Change) with Second Order Predation. The combined scenario produces extinction more quickly than Second Order Predation alone (Graph 4B-D). In the Second Order Predation scenario, there is an initial increase in herbivore populations because carnivores are not able to control them.

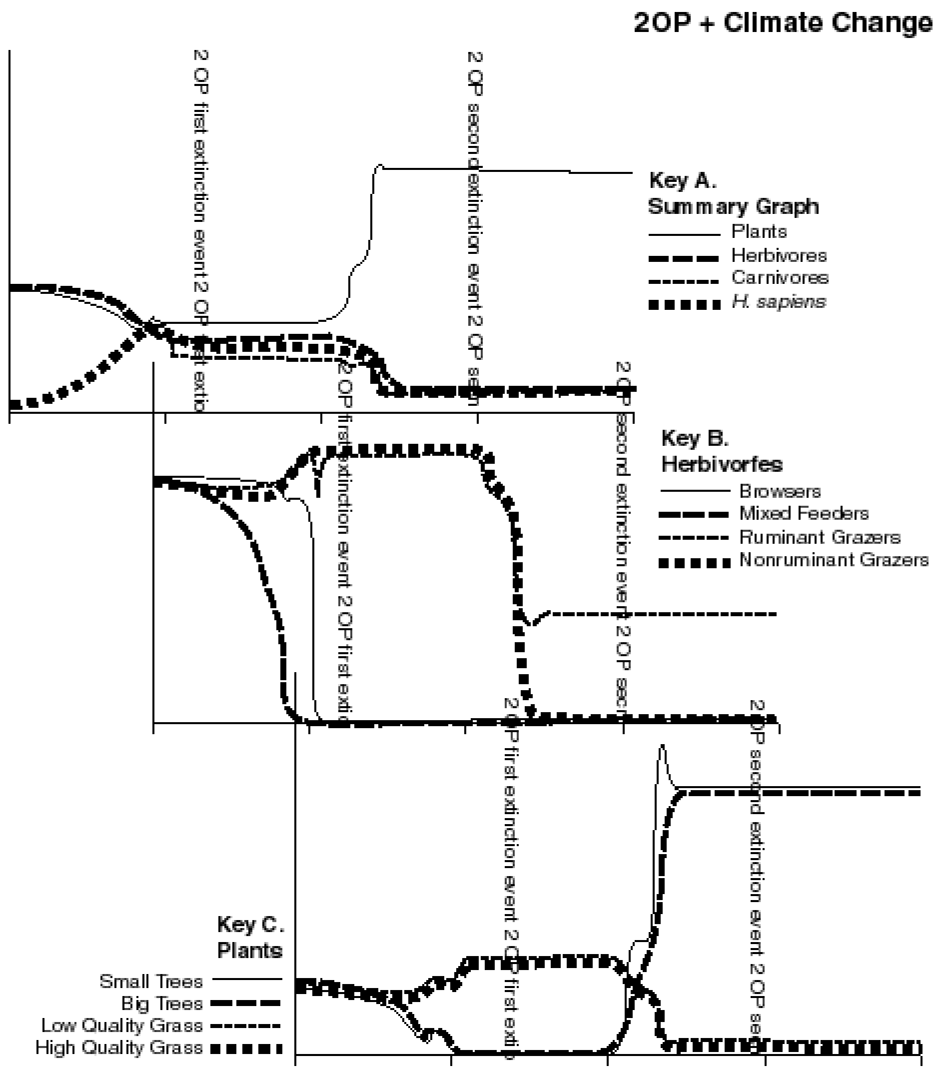


Figure 4 – 13% Exogenous Decline combined with Second Order Predation A – Summary Graph, B – Herbivores C – Plants For all graphs time is 1.5K years and curves are normalized at their equilibrium level.

Behind the scenes in the combined Climate Change with Second Order Predation scenario, the initial boom is limited to Browsers. Mixed Feeders still go extinct first followed by Browsers and as trees reinvade (in the absence of browsers) Non-ruminant Grazers are not able to successfully compete with Ruminant Grazers.

Discussion

Exogenous Decline (Climate Change) and Overkill

Overkill reduces herbivore stocks, albeit slightly, and Extreme Climate Change also reduces herbivore stocks, much more significantly. Therefore, we might expect both factors, in combination, to have an even greater impact on the herbivore stock. Counter-intuitively, the combination has a smaller impact than Climate Change alone.

We can make sense of this by considering the scenario from the point of view of plants. The role of the plant stocks as mediating variables. Herbivores eat plants by reducing herbivore populations in the Overkill scenario, plant stocks increase slightly. In other words: hunting reduces the herbivore stock directly, which in turn increases the plant stock. Climate Change (as a 13% reduction in Carrying Capacity) directly reduces the plant stock and herbivore populations suffer because there are fewer plants. Reducing herbivore populations while plant stocks decline lets the plant stocks reduces the pressure on plants so they have time to equilibrate to the new circumstances. Thus, Overkill counteracts this level of Climate Change impact on plant stock reducing the impact on the herbivore stock.

Exogenous Decline (Extreme Climate Change) and Second Order Predation

By adding Second Order Predation (humans both hunting herbivores and reducing carnivore populations) to Extreme Climate Change, extinctions happen more quickly than with either Second Order Predation or Extreme Climate Change alone. Since Second Order Predation allows herbivore stocks to boom, plant stocks are stressed, and under Exogenous Decline (as a 13% reduction in Carrying Capacity) plant stocks are stressed as well. The relationship between the impact of exogenous Extreme Climate Change and Second Order Predation is additive.

Conclusion and implications

This modeling effort has significant implications for those Climate Change hypotheses that can be modeled as a smooth reduction in the ability of the land to produce vegetation.

Overkill reduces the impact of Climate Change on herbivore populations. Therefore, Climate Change in combination with Overkill is less consistent with extinction than is Second Order Predation (by itself or in combination with Climate Change). Or in other words, for a combination of Overkill and Climate Change to cause extinction, the impact of Climate Change would have had to be far *more* severe than it would have to be for

Climate Change alone. This would undoubtedly have left evidence in the climate and fossil record. Since herbivores did not go extinct in previous interglacial periods and since there is no evidence that Climate Change was more severe at the boundary of this interglacial, it is even more unlikely that a combination of Overkill and Climate Change caused the extinctions.

The combination of Climate Change and Second Order Predation suggests that herbivores would have been stressed. They would have been easy to hunt and to scavenge making large kills more likely so there would have been little need to fully utilize each carcass and there would have been little fat on each making breaking long bones uneconomic.

The combination of Climate Change and Second Order Predation explains why camels (mixed feeder) and horses (non-ruminant grazer) went extinct before Proboscideans. Mixed feeders go extinct in the modeling environments first because they are in competition with both grazers and browsers. If the climate stress was drought then proboscideans could have dominated access to water excluding horses.

The implication for modern ecology

This work underlines the importance of threshold and combination effects that interact in counterintuitive ways. Though this is a model of an archaic ecosystem, the same principles apply in the present day. Something that seems like a good policy, killing off the competition – carnivores – may have disastrous long-range results and, as in modern ecosystems, the most likely path of anthropogenic extinction is through habitat destruction.

Implications for system dynamics and science

Explanatory factors, hypotheses and policies may have counterintuitive results. System dynamics models can help scientists to:

Test theories that are not testable in the field,
Make counterintuitive results and theories more understandable,
Test a variety of hypotheses against each other using the same assumptions, and
Test a variety of hypotheses in combination.

Implications for archaeologists

The obvious issue for archaeologists is to find direct evidence of *H. sapiens* killing carnivores and evidence of a reduction in the ability of the land to produce plants at the same level as during the Pleistocene – e.g. drought or overall reduction in the quality of the soil.

The Second Order Predation with Exogenous Climate Decline results may explain the differential extinction patterns seen across the continents. In the Old World *H. sapiens* may have reduced carnivore populations, but that reduction did not coincide with Climate Change

Implications for Clovis

Second Order Predation accounts for the change in the pattern of vegetation as during the boom phase animals kill off the vegetation and when it recovers it does so in a different pattern, trees migrate from mountain refugia until the migration front meets the prairie, which is maintained by ruminant grazers (bison). Second Order Predation also accounts for an increase in continentality and the change in rainfall amount and variability since there is a reduction in transpired moisture with the loss of trees.

The dynamics described above suggest that Clovis may be a response to the boom phase of the boom bust scenario. A widespread boom in herbivore populations exacerbated by a reduction in plants, due to climate change, would force people to adopt a hunting strategy or to die. Populations of people who did not adopt a hunting style of life would soon disappear as food became scarce. In addition as herbivores become stressed by the lack of food it would have been easier for hunters/scavengers to kill the stressed animals.

If we think slowly about possible scenario we may be able to come to new implications. I propose that the earliest immigrants to the New World followed a policy of reducing carnivore populations in order to increase herbivore stocks. This policy, in moderation, allows human population to increase, as populations of herbivores increase and decreases plant populations slightly.

Two things may have been new in the New World that had not been true in the Old World:

> First that the carnivores, like the herbivores may have been naive so the rate of carnivore killing may have exceeded that of Old World. This would have pushed herbivores closer to their ecological limit.
>
> Second, climate change, as we see from the simulation, would have exacerbated the impact of Second Order Predation on the environment so that herbivore populations exceeded the ability of the land to support them. Before people could monitor the impact of their policy they would be in the herbivore boom and regardless of how quickly they killed animals the bust was the inevitable outcome.

References

Alroy, J.

2001.A multispecies overkill simulation of the End-Pleistocene megafaunal mass extinction. *Science* 292:1893-1896

Axelrod, D. I.

1967. *Quaternary extinctions of large mammals*. University of California Publications in Geological Sciences 74:1-42

Carbyn, L.N.; Fritts, S.H.; Seip, D.R.

1995. *Ecology and conservation of wolves in a changing world*. Edmonton: Canadian Circumpolar Institute, Univ. of Alberta.

Cat House

1996. Personal communication in response to an e-mail request. World Wide Web publication site *http://www.cathouse-fcc.org/*

Graham, R.W. & Lundelius, E.L.

1989. Coevolutionary disequilibrium and Pleistocene extinctions. In *Quaternary extinctions: A prehistoric revolution*, ed. P.S. Martin and R.G. Klein, 223-250. Tucson: Univ. Arizona Press.

Gowdy, J

1998. *Limited Wants, Unlimited Means: A reader on Hunter-Gatherer economics and the environment*. Island Press.

Guilday, J. E.

1989. Pleistocene extinction and environmental change: case study of the Appalachians. In *Quaternary extinctions: A prehistoric revolution*, ed. P.S. Martin and R.G. Klein, 250-259. Tucson: Univ. Arizona Press.

Guthrie, R. D.

1968. Paleoecology of the large mammal community in interior Alaska during the late Pleistocene. *Am. Mdl. Nat*. 79:346-363.

1989. Mosaics, allochemics, and nutrients: an ecological theory of Late Pleistocene megafaunal extinctions. In *Quaternary extinctions: A prehistoric revolution*, ed. P.S. Martin and R.G. Klein, 259-299. Tucson: Univ. Arizona Press.

Hansen, R. M.

1978. Shasta ground sloth food habits, Rampart Cave, Arizona. *Paleobiology* 4:302-319

Haynes, G

1995. *Mammoths, mastodonts, and elephants: Biology, behavior, and the fossil record.* Cambridge Univ. Press.

Hoppe, P. P

1978. *Rumen fermentation in African ruminants*. Proceedings of the 13th Annual Congress of Game Biologists. Atlanta.

Kilti, R. A.

1989. Seasonality, gestation time, and large mammal extinctions. In *Quaternary extinctions: A prehistoric revolution*, ed. P.S. Martin and R.G. Klein, 299-315. Tucson: Univ. Arizona Press.

Martin P. S.

1967. Prehistoric overkill. In *Pleistocene extinctions: The search for a cause*, ed. P.S. Martin and H.E. Wright. New Haven: Yale Univ. Press.

1988. Prehistoric overkill: A global model. In *Quaternary extinctions: A prehistoric revolution*, ed. P.S. Martin and R.G. Klein, 354-404. Tucson: Univ. Arizona Press.

McDonald, J.

1981. *North American bison: Their classification and evolution*. Berkeley: Univ. Calif. Press.

1989. The reordered North American selection regime and late Quaternary megafaunal extinctions. In *Quaternary extinctions: A prehistoric revolution*, ed. P.S. Martin and R.G. Klein, 404-440. Tucson: Univ. Arizona Press.

Mosimann, J. E. & Martin, P. S.

1975. Simulating overkill by Paleoindians. *American Scientist* 63:304-313.

Phillips, A.M.

1988. Shasta ground sloth extinction: Fossil packrat midden evidence from the Western Grand Canyon. In, Martin, P.S. & Klein, R.G. (eds) *Quaternary extinctions: A prehistoric revolution.* Univ. Arizona Press, Tucson

Sinclair, A.R.E.

1979. Dynamics of the Serengetti ecosystem: pattern & process. In *Serengetti: Dynamics of an ecosystem*, ed. A.R.E. Sinclair and M. Norton-Griffiths, 1-31. Chicago: Univ. Chicago Press.

Soffer, O.

1985. *The Upper Paleolithic of the Central Russian Plain.* Orlando, Florida. Academic Press.

Whitney-Smith, E.

2004. Late Pleistocene extinctions through second-order predation. In *Settlement of the American Continents: A multidisciplinary approach to human biogeography*, ed. C. M. Barton, G. A. Clark, D. R. Yesner. 177-189. Tucson: Univ. Arizona Press.

Whittington, S. L. & Dyke, B.

1984. Simulating overkill: experiment with the Mossiman and Martin model. In *Quaternary extinctions: A prehistoric revolution*, ed. P.S. Martin and R.G. Klein, 451-466. Tucson: Univ. Arizona Press.