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# Pleistocene Extinctions – Counterintuitive Results of Combining Hypotheses (Overkill, Second Order Predation, and Environmental Degradation)

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### Abstract

There are two popular hypotheses to explain extinctions at the end of the last ice age, Climate Change and Overkill (humans hunting herbivores to extinction); each has significant problems. Some have suggested that the two hypotheses in combination would yield a stronger explanation. The Pleistocene Extinction Model (PEM)(Whitney-Smith, 1991, 2003) was originally developed to test a third hypothesis, Second Order Predation (2OP)– humans reducing carnivore populations – and test it against Overkill. Now, PEM has been expanded to include a simplified Climate Change factor. Its results show that, in combination, Climate Change counteracts the effect of Overkill, reducing not increasing extinctions, while exacerbating the impact of 2OP, hastening extinctions. Archaeologists have only used quantitative models as descriptions to clarify the assumptions underlying a single hypothesis. The continuing development of PEM shows the value of a model that can be used to test multiple hypotheses, alone or in combination, using consistent assumptions.

### Introduction

Archaeologists studying the last ice age have only used quantitative models as descriptions to clarify the assumptions underlying one or another hypothesis. The Pleistocene Extinction Model (PEM) has begun the task of creating a modeling environment in which various hypotheses can be simulated using the same assumptions and values.

### Background

### Pleistocene extinctions and environmental change

Imagine what we would see if we could go back to the last ice age – the Pleistocene. Eighteen thousand years ago, at the height of the Pleistocene in North America, the land not covered by ice looks like a park with mixed trees and grass.

Massive lions and sabertooth cats are killing and eating mammoths. Bison are almost as big as elephants. Beavers are as big as bears. The short faced bear stands more than 5 feet at the shoulder, almost twice the size of today's grizzly bear. These big animals merit their name: mega-fauna.

Ten thousand years ago the ice caps are wasting away. *Homo sapiens* uses beautiful fluted points to hunt the bison, the mastodons, and other mega-fauna in parklands of North and South America. If they are like modern hunter/gatherers, they work little – about 10 hours per week – and live well (Gowdy, 1998; Lee & Devore, 1968; Lee, 1969). Game and vegetation is available for the taking. Theirs is a world of plenty – an Eden. Archaeologists identify these people by their technology as Clovis.

Just a thousand years later – at the beginning of the Holocene – the current geological era, the huge ice caps, horses, sloths, other giant animals, and the carnivores that ate them, all are gone.

The few humans we find are living in small, isolated bands. Their stone technology is far less developed than that of their predecessors. Who are these people? What happened to the people who produced the Clovis technology?

Climate is like it is today – it is more continental – hotter summers and colder winters. The parklands are gone. There are belts of closed canopy forest on the coasts and a vast grassland in the center of the North American continent.

Why did the pattern of vegetation change? Why are bison and beavers so small? Where are the mastodon, the mammoth, the horse and the big cats that hunted them?

Further the extinctions have biases there are few large herbivores the biggest are gone completely and though bison, moose, and elk are all big animals they are smaller than they were in the Pleistocene. Mid size animals like the beaver are much smaller and there are local extinctions – for example, foxes that thrive in patchy ecological systems are confined to the forest fringe. Finally, there are far more ruminants than non-ruminants extant.

These are the mysteries of the extinctions at the end of the last Ice Age – the Pleistocene Holocene transition.

In the archaeological community, the Overkill hypothesis and the Climate Change hypothesis are the most popular explanations of extinction. Both of these hypotheses pose problems for the community.

### **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 (Fig. 1).



Figure 1 – Increase in H. sapiens decreases herbivores

This is consistent with the observation that extinctions across the continents follow the "march of man" – the least severe extinctions occurring in Africa, where people have lived the longest (Martin, 1967) and the most severe in the New World, where they came to most recently. And it is only in the New World that the extinctions are associated with Climate Change. Quantitative simulation models support the Overkill hypothesis. These have been used to clarify relationships and specify the size of human population and the hunting effort per human required to achieve extinction through Overkill (Mossiman and Martin, 1984, Whittington and Dyke, 1989, Alroy, 2001).

However, there are problems with the Overkill hypothesis. In general, it is difficult for predators to overhunt their prey since it is their food supply (Fig. 2) and it does not recognize any role for either plants or carnivores. More specifically, the time period from the first appearance of *H. sapiens* in the New World to the extinctions seems too short. Also, and perhaps most curiously, animals not hunted by humans, such as the giant ground sloth, also went extinct.



Fig. 2 – Increase in Herbivores leads to an increase in H. sapiens – balancing loop

#### 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).

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.
- 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. Thus the Climate Change hypothesis can be modeled as shown in figure 3. There is an exogenous reduction in the capacity of the land to produce plants which reduces plants and therefore reduces herbivores.



Figure3 – Exogenous Reduced Carrying Capacity reduces plants, which in turn 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 that became extinct 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).

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.

### **Combination of Climate Change and Overkill**

Since both the Overkill and the Climate Change hypotheses are unsatisfactory, most scientists believe that the extinctions are due to some combination of Overkill and Climate Change. This seems to be the most intuitive explanation. However they do not propose a mechanism of how that combination would have worked. (Fig. 4)



Figure 4 – Combination of hypotheses

### Problems with Climate Change, Overkill and Combination Hypotheses

None of the hypotheses attempt to explain the pattern of extinctions – the loss of most 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.

In addition, none of the proposed hypotheses Climate Change, Overkill, or the Combination Hypothesis recognizes of the role of carnivores in maintaining the balance on an ecosystem.

Therefore, before any hypotheses could be tested it was necessary to create an equilibrium ecosystem. All hypotheses in this work are based on a three level ecosystem (Fig 5).



#### Figure 5 – Three Trophic Level ecosystem

To account for the pattern of extinctions it was necessary to disaggregate the system into browsers, mixed feeders, ruminant and non-ruminant grazers and their respective plant foods – trees and grass

Figure 6 shows the same Three Trophic Level ecosystem disaggregated into 2 kinds of plants (trees and grass) and 4 kinds of Herbivores (Browsers, Mixed Feeders, Ruminant and Non-ruminant Grazers). This is a balanced ecosystem. All self-reinforcing loops are balanced by balancing loops that serve as limits. Minor perturbations, including the introduction of *H. sapiens* create a situation where either the old equilibrium – in the case of slight perturbations or a new equilibrium – in the case of the introduction of a new predator, *H. sapiens* – is restored.



Figure 6 – Three Trophic Level with Herbivores disaggregated into Browsers, Mixed Feeders, Ruminant and Nonruminant Grazers; Plants disaggregated into Trees and Grass. It is a balanced ecosystem

### **Second Order Predation hypothesis**

In prior work, I have proposed an alternative hypothesis of anthropogenic extinction: Second Order Predation (Whitney-Smith, 2003).

According to this hypothesis *H. sapiens* entered the New World, and not only killed herbivores for food but reduced carnivore populations such 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 overshoots the limit set on herbivores by plants – bust. (Fig. 7)



*Figure 7 – H. sapiens reduces carnivore populations. The self-reinforcing loop, Herbivores produce Herbivores, dominates the system.* 

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

To specify and test the Second Order Predation hypothesis, I built a modeling environment – the Pleistocene Extinction Model (PEM) – with four plant stocks (high and low quality grass, big and small trees), four herbivore stocks (browsers, mixed-feeders and ruminant and non-ruminant grazers), carnivores, and *H. sapiens*. I used PEM to test Second Order Predation against Overkill using the same values for initial stocks and relationships, except for *H. sapiens* reducing carnivore populations.

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) contrast the Overkill hypothesis (Fig. 5 above) with the Second Order Predation Hypothesis (Fig 6 above). (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 (near yellow line at -10750).
- 3. A period of equilibrium.
- 4. An increase in plants followed by another crash in all other populations (orange line at -9750).
- 5. A final equilibrium with plants very high and all other populations reduced significantly.



Graph 1 – Overkill (A) vs. Second Order Predation (B) (H. sapiens kills 0.25lbs of carnivore per year) using the same assumptions

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.

The Plant (Graph 1D) 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



Graph 1C&D – Behind the Scenes of Second Order Predation – Herbivores (C) and Plants (D)

Looking at the disaggregated causal loops associated with the "Behind the Scenes" graphs will help explain what is happening.

In the first phase causal loop Figure 7 below we see that 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:

 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.



Figure 8 – Phase 1 causal loops – The link between H. sapiens and Carnivores renders the balancing loops between Carnivores and the various Herbivore stocks ineffective – Browser and Grazer stocks are dominated by the reinforcing recruitment loops driving Mixed Feeders out of the system – Trees are not able to recruit fast enough to compensate for the boom in Browser; With the loss of trees Browsers go extinct – Grass takes over area previously used by Trees.

In second phase causal loop Figure 8 below we see the ecosystem without Browsers or Mixed Feeders. This necessitates disaggregating Grazers into Ruminants and Non-ruminants.

In this phase, following the extinction of Mixed Feeders and Browsers,

1. Grass, with it's 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.

- 2. 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)
- 4. Trees begin to re-establish themselves retaking land previously occupied by grass
- 5. 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



Figure 9 – Phase 2 – Grass is higher than it was in the beginning of the simulation and is able to support both Ruminant and Non-ruminant Grazers There is now less constraint on trees and they eventually achieve much higher levels – Re-population of trees leaves less grass for the grazer populations. Non-ruminant Grazers go extinct.

The final phase (Figure 10 below) shows the loops remaining 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



Figure 10 – Phase 3 The final phase has only one kind of Grazer – Ruminants

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.

The Second Order Predation boom bust scenario gives us a way to think about the change in the 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.

### Goals for this work

#### **Expand PEM to include Exogenous Climate Change**

The challenge for this presentation 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 (Carrying Capacity Fig 5 & 6). 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 initial 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)



Graph 2A – 13% Exogenous Decline – Climate Change

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. Both Grazer stocks increase then Nonruminants 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 2B & C – 13% Exogenous Decline – Climate Change – Herbivores (B) Plants (C)

## Results: 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).



Graph 3A – Overkill combined with 13% Exogenous Decline

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 B & C – Overkill combined with 13% Exogenous Decline – Herbivores (B) Plants (C)

### Second Order Predation with extreme Climate Change

Reviewing Figure 6 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 to this both the increase in Herbivores and the exogenous deterioration in climate reduce plants, which further exacerbates the ultimate collapse in climate.

Graph 4A-C show 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 1B-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 (Climate change) combined with Second Order Predation

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.



*Graph 4 B &C 13% Exogenous Decline (Climate change) combined with Second Order Predation – Herbivores (B) and Plants (C)* 

### Discussion

### **Exogenous Decline (Climate Change) and Overkill**

Overkill reduces herbivore stocks, albeit slightly, and 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. Counterintuitively, the combination has a smaller impact than Climate Change alone.

We can make sense of this by considering the role of the plant stocks as mediating variables. In the Overkill scenario, plant stocks increase slightly: 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. Both herbivore and plant stocks have time to equilibrate to the new circumstances. Thus, Overkill counteracts this level of Climate Change impact on plant stock, thus reducing the impact on the herbivore stock.

### **Exogenous Decline (Climate Change) and Second Order Predation**

By adding Second Order Predation (humans both hunting herbivores and reducing carnivore populations) to environmental decline, extinctions happen more quickly than with either Second Order Predation or Environmental Decline 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 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 have caused extinction the impact of Climate Change would have had to have been 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.

### **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 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

### 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. What 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

Not only policies have counterintuitive results. 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.

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