A Paleoeconomic Theory of Co-Evolution and Extinction of Domesticable Animals

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Abstract

Of the many unsolved mysteries from Pleistocene times, people still ask why early North Americans eradicated their large, potentially domesticable animals (e.g., horses), whereas early Europeans did not. We explore this question by developing a paleoeconomic model that integrates into a co-evolutionary process human hunting investments and wildlife population responses. Our results suggest that investments in hunting ability could have mattered more than wildlife "naivety" in explaining the extinction of large animals. Human investments in hunting and the co-evolution with large animals could have both *caused* and *prevented* extinction. If human hunting investment depended on the relative scarcity of prey species, hunters could have prevented extinction in Eurasia by becoming more adept at hunting less-scarce species. While this acquired skill and co-evolution might have prolonged the existence of domesticable animals in North America, this would have occurred only if this skill applied *exactly* to the new species. Without co-evolution, North American hunters caused extinction because they had greater incentive to invest in hunting the large species.

Introduction

Archaeologists, paleontologists, paleobiologists, and anthropologists have identified several unsolved global puzzles including the origins of civilization, agriculture, modern humans, the colonization of early humans, and why human overkill might have caused a mass megafauna extinction (e.g., mammoths) at the end of the Pleistocene (see Gamble 1998; Brook and Bowman 2002; Roberts et al. 2001; Alroy 2001; Choquenot and Bowman 1998, Beck 1996, Smith 1975). And while many hypotheses have been put forth to address these puzzles, no story has been universally accepted. Researchers have responded to the challenge by turning to more formal analytical models to investigate various aspects of these mysteries (Dark 1995). A common feature of these models, however, is their tendency to abstract away from behavioral responses to economic stimuli. These models have largely focused on biological explanations (e.g., in the case of the Neanderthal extinction; see Flores 1998), or on results from mechanistic models of human-environment interactions that lack fundamental behavioral components (e.g., in the case of megafauna extinction; see Mosiman and Martin 1975, Alroy 2001).[1]

But these paleo-puzzles have a common thread—they all depend on human choices.[2] While primitive in terms of their technologies, early humans are believed to have had the same analytical capacities as modern humans (Tattersall and Schwartz 2000). One can envisage without apology that these early humans responded to economic stimuli with some degree of rationality (see Smith 1975, Nerlove 1991, 1993, Robson 2001; Mithen 1998). Since economic forces have played integral roles in shaping societies through recorded history, there is no reason

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[1] The exception is the case of the evolution of certain traits possessed by early humans, as developed in the economics literature.
[2] The possible exception is the case of hominid origins.

to discount the influence of economic incentives in the pre-historic dawning of humanity.[3]

And while some economists have recognized the potential contribution that economics might offer in addressing paleo-puzzles (Smith 1991), research into these behavioral underpinnings has been lacking.[4] In this paper we examine whether an explicit accounting of economics matters in addressing one important paleoeconomic puzzle—why did early North Americans eradicate their large, potentially domesticable animals such as horses and camels, whereas early humans preserved a similar group of animals in Europe? This question matters because its final outcome has had global implications. Biologist Jared Diamond (1992, 1997), for instance, argues that current patterns of power and control of natural resources can be traced back to the question of domestication of large animals. Domesticated animals facilitated agricultural production to feed a growing population (cattle, horses), enabled countries to create powerful armies (horses), and allowed people to develop resistance to germs and bugs that animals carry. These factors explain why people who first domesticated large mammals gained an advantage over the rest—particularly in the Americas where the horse went extinct along with the vast majority (70–80 percent or more) of the continents' large mammals (e.g., the mammoth, giant ground sloth, camel, and dozens of others) (Diamond 1992). Had Americans preserved these animals, today's world might look different.

Understanding the underlying behavioral forces that led to the extinction of domesticable

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[3] The interaction between economic and biological systems is now known to be critically important, as it must have been long ago when humans depended more on their environment for survival. See for example Shogren and Crocker's (1999) discussion on the lack of and need for better integration of economics into the biology of environmental risk assessment; and Crocker's (2001) critique on how economic circumstances affect biological definitions of resilience and biodiversity.

[4] Smith (1975) and Nerlove (1993), for instance, suggest economic models might help explain megafauna extinction. And in a related vein, Brander and Taylor (1998) develop an economic model to explain cultural decline on Easter Island. Another exception is the area of human evolution. Several studies explore how biological, economic, and environmental forces may have affected the natural selection of certain human traits such as preferences and associated economic behaviors (e.g., Robson 2001, Rogers 1994, Hansson and Stuart 1990, Bergstrom 1996) and inter-personal relationships (Bergstrom 1996).

animals in America becomes important. One behavioral hypothesis that has received attention is co-evolution. Co-evolution is a multi-directional process: economic systems influence the evolution of biological systems, and biological systems influence the evolution of economic systems, including technological and institutional innovations (Norgaard 1984). In the present context, the commonly-held co-evolution hypothesis is that prey species were 'experienced' (not naïve) in Europe because they had co-evolved with humans and earlier hominids such as Neanderthals, starting at a time when hominids' hunting skills were relatively undeveloped (Diamond 1997; Leaky and Lewin 1996; Brook and Bowman 2002). The interaction with Neanderthals and early modern humans resulted in evolution selecting traits that enabled these species to more effectively evade their human adversaries. Also, Neanderthals and early modern humans co-evolved with their prey. Over many millennia, they developed more advanced hunting strategies and technologies that enabled greater kill rates per hour of labor. In contrast, prey species were 'naïve' in America. Hominids did not arrive in America until humans crossed the Bering Strait about 12,000 years ago, and so evolutionary pressure in America until this time was not geared towards shyness or evasiveness. These naïve animals were unable to evade their new predator who arrived from Eurasia with well-developed hunting skills, and they were easily wiped out soon after humans entered the scene (Mosimann and Martin 1975, Diamond 1997, Leaky and Lewin 1996; Brook and Bowman 2002). Since some extinct megafauna would have been excellent candidates for future domestication, the prospects of this continent's inhabitants was changed forever, and the future of the world.

While this story seems plausible, no formal models have been developed that capture evolution along both human and wildlife dimensions. Even analyses of the separate human and wildlife dimensions are lacking: no one has explicitly examined the human dimension, and little

has been done on the wildlife side. Brook and Bowman (2002) claim Alroy's (2001) extinction results could stem from unrealistic assumptions about wildlife naivety. They argue Alroy's overkill results stem from his assumption that North American wildlife maintained a constant level of naivety even though these wildlife populations dwindled due to human hunting pressures – wildlife populations never became more evasive but rather were always easy to kill. There was no natural selection process to reduce naivety and make the wildlife harder to kill. By exogenously reducing the level of naivety (e.g., consistent with but not in direct response to human hunting pressure), Brook and Bowman find overkill may no longer hold; at least in a single species model in which wildlife and human population growth are independent, and there are no human investments in response to increased scarcity. Brook and Bowman also cite a sizable literature that finds wildlife naivety drops quickly in response to hunting by humans or other completely novel predators. But Brook and Bowman do not model wildlife responses explicitly, nor do they model human responses to increased scarcity.

Herein we develop an analytical framework to capture the idea of endogenous human investments in hunting ability, and wildlife population responses to human hunting pressure. We find investments in hunting ability may be more important than wildlife naivety in explaining the extinction of large, domesticable animals. Plus our results add a twist to the story. We find human investments in hunting ability might have *prevented* the extermination of large, domesticable animals in both Eurasia and North America. Human dimensions within the co-evolutionary process could have saved Eurasian domesticable animals. The reason is that humans make investments in response to the relative scarcity of prey species—over time hunters become more adept at hunting the less-scarce species. We also find that conditions exist under which the co-evolutionary development of hunting skills in Eurasia could have prolonged the

existence of domesticable animals in North America.   But if the acquired Eurasian skills did not

apply in exactly the same way to the new mix of species in North America, the incentives facing

North American hunters may have biased additional investments towards hunting domesticable

species, resulting in their demise.

2. A Model of Hunting with Technological Investments

Imagine a group of primitive hunters, consisting of N identical households. They sustain

themselves by consuming meat, m, from two species: megafauna, which includes large,

domesticable animals (horses, camels, cattle) and minifauna (deer, hare).[5] For simplicity and

because they are believed to have minimal impact on the likelihood of extinction (Bulte et al.,

2003), we do not address nutritional impacts of agriculture or gathering.[6] Utility, U, is a function

of meat consumption and other goods like clothes, tools, and shelter, denoted v. Utility is

defined as:

(1) $U = m^{\beta} v^{1-\beta}$.

Households maximize (1) subject to a time constraint:

(2) $l = e + s + y,$

where l is the total labor endowment, e is hunting effort, s is effort devoted to investing in new

hunting technologies, and y measures effort to produce other goods. Assume primitive hunters

solve a series of static labor allocation problems, rather than a single dynamic optimization

problem, which is consistent with observations by Mithen (1990, p.224): "hunter-gatherers do

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[5] We use the commonly made distinction between 'megafauna' (animals heavier than 450 pounds) and 'minifauna' (other prey) to characterize the potential prey species that humans can harvest.
[6] Bulte et al. (2003) examine possible causes for the megafauna extinction in the Pleistocene. They develop a model in which primitive man allocates his labor between hunting two wildlife species (megafauna and minifauna), agricultural production, and the production of non-food goods. While agriculture is a substitute activity for hunting, they find the presence of agriculture has little bearing on whether megafauna go extinct. The presence of a substitute prey is the most important factor. Agriculture would have been viable in parts of Eurasia during the time frame being considered, while gathering would be the only relevant alternative in North America (Smith 1975).

not appear to plan subsistence activities over time scales longer than one year." This restriction is also consistent with more contemporary instances of open access resource exploitation (see Conrad 1995; Bulte and Horan 2003). We abstract away from institutional change that might occur in response to changes in resource scarcity (see Ostrom 1990, Erickson and Gowdy 2000, Pezzey and Anderies 2003, Baker 2003).

Assuming constant returns to scale to produce other goods, we choose units such that $v = y$. Production of meat is given by the traditional Schaefer production function (Clark 1990). Assume humans do not discriminate hunting effort between and among different types of animals; they decide about the optimal level of aggregate effort.[7] This presumption is consistent with observations by Mithen (1999), who argues the predominant mode of hunting was on an *encounter basis*. But although hunters non-selectively kill the species they come across, they do selectively invest in hunting technologies/knowledge to increase the catchability of those species they are more likely to encounter (Gamble 1999), thus improving their overall returns per unit effort. We use the terms technology and knowledge interchangeably in what follows. Following Mosimann and Martin, Smith (1975), Brander and Taylor and others who have looked at resource extraction in a "simple economy," we combine all megafauna into a single aggregate variable, x, focusing on large, domesticable animals like horses, cattle, and camels rather than, say mammoths. We introduce heterogeneity into the megafauna population to examine the role of natural selection.[8]

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[7] This assumption is not required for our results, but it is realistic and it simplifies the exposition relative to a model with selective harvests. See Bulte et al. (2003) for a discussion of selective harvesting and bonus killings.

[8] In our model, evolution of the species (i.e., gradually shedding its naivety) is captured by natural selection resulting in an increased share of hard-to-catch animals in the population. This approach is convenient but effectively puts a lower bound on naivety—if all individuals are hard-to-catch further evolution is not feasible. In reality, naivety could fall over the very long term, enabling an ongoing "arms race" between predator and prey, in which both players continuously improve their type. Nevertheless, because of tractability we chose to consider changes in relative abundance of experienced and naive animals within the population. This allows us to show all mechanisms clearly; similar patterns could emerge when using alternative models of (co)evolution.

The megafauna population consists of two sub-populations. Define x_h to be the hard-to-catch megafauna (*H-Mega*) sub-population, having a relatively small *catchability coefficient, q_{xh}*. Define x_e to be the easy-to-catch megafauna (*E-Mega*) species, having a relatively large catchability coefficient q_{xe}, i.e., $q_{xe} > q_{xh}$. Harvests of sub-population j ($j=h, e$) are represented by $m_{xj} = q_{xj}(\theta_x e)x_j$, where $\theta_x e$ represents "effective hunting effort" in hunting megafauna, in which θ_x is an index of hunting technology or knowledge that improves the productivity of labor in hunting this species, i.e., a Hicks-neutral technology that augments catchability.

Minifauna are also combined into an aggregate variable, z, in which we again have a hard-to-catch minifauna (*H-Mini*) sub-population, z_h, and an easy-to-catch minifauna (*E-Mini*) sub-population, z_e. We define the harvests of these sub-populations by substituting z for x. Total household meat consumption is

(3) $\qquad m = e\theta_x[q_{xh}x_h + q_{xe}x_e] + e\theta_z[q_{zh}z_h + q_{ze}z_e] = e\theta_x\sigma_x x + e\theta_z\sigma_z z$

where $\sigma_j = [q_{jh}\rho_j + q_{xe}(1-\rho_j)]j$ represents average catchability and $\rho_j = j_h/j$ ($j=x,z$) represents the proportion of species j that is hard-to-catch.

Investments of labor (e.g., spending time developing innovations) can affect the technological parameter θ_j ($j=x,z$). Assume the relation is

(4) $\qquad \theta_j = \int_0^t [\mu_j s_j]dt$, $\quad \theta_j(t=0)=1 \qquad$ ($j=x,z$)

where μ_j is a parameter. Expression (4) says that the technological component of catchability depends on cumulative investments. For now we do not address depreciation; we do examine its impacts when we consider how knowledge is transferred from Eurasia to North America. For notational ease, define θ'_j as cumulative past investments such that $\theta_j = \theta'_j + \mu_j s_j$.

Although investment has cumulative effects, the primitive subsistence hunters do not plan

on this due to their limited foresight. Substituting expressions (3) and (4) into the static

optimization problem defined by (1) and (2), the optimal levels of effort and investment are[9]

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(5) \qquad s_j^* =
\begin{cases}
Max\{\dfrac{1}{1+\beta}(\beta l - \dfrac{\theta_j'}{\mu_j} - \dfrac{\theta_v'}{\mu_v}\dfrac{\sigma_v v}{\sigma_j j}),0\} & \\
& \text{if} \quad \mu_j \sigma_j j \quad \begin{matrix} > \\ \\ < \end{matrix} \quad \mu_v \sigma_v v \quad j,v=x,z \\
0 &
\end{cases}
$$

$$
(6) \qquad e^* = \beta(l - s_x - s_z)
$$

Expression (5) illustrates that investments in technological innovations depend on the relative

scarcity of the species. More investments are spent on species *v* when *v* is abundant relative to *j*.

Aggregate investments also depend on past investment levels, and investments are bounded from

above because the marginal product of effort in hunting is always greater than the marginal

product of labor in knowledge generation when cumulative investment is sufficiently large.

Accordingly, relative scarcity during the innovation process drives the ultimate mix of

innovations – i.e., innovations are scarcity-dependent and path-dependent. This implies the

initial immigrants to North America would have arrived with an irreversible initial set of relative

skills that (i) would probably not have been developed in North America, and (ii) may not be the

most compatible with the relative wildlife scarcities that existed in North America at that time.

Consequently, outcomes in North America would be both scarcity-dependent and path-

dependent, driven in part by the co-evolution that occurred on Eurasian hunting grounds.

Human and wildlife dynamics

We now turn to human and wildlife dynamics, which are based on a modified form of a

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[9] Equation (4) exhibits constant returns to scale in labor, which makes the objective function linear in the amount of labor allocated to investments. The result is that investments are reallocated quickly as relative scarcity changes. If

conventional predator-prey model (e.g., Freedman 1980). Such models have been used to examine human-wildlife interactions in other contexts (e.g., Brander and Taylor 1998). We extend this earlier work by distinguishing between multiple wildlife sub-populations so we can consider natural selection in a co-evolutionary context.

Human population growth (fertility) depends on the available food supply, particularly for people living close to subsistence (see Dasgupta 1995; Frisch 1978; Nerlove 1991, 1993). Let the dynamics of the human population be

(7) $\dot{N} = rN(1 - S/m)$,

where r is the intrinsic growth rate of the population and S is a subsistence rate representing the minimum quantity of food that humans need to support themselves. From expression (7), if $S/m > 1$, the population growth rate is negative and the population diminishes. If $S/m = 1$, the population does not change. The population grows when $S/m < 1$. The population growth function in (7) rests on the assumption that food intake single-handedly determines fertility.

Now consider the ecological side of the model, starting with the growth of megafauna. The megafauna population consists of two heterogeneous sub-populations, in which growth of one sub-population depends on the other. H-Mega animals bear either H-Mega or E-Mega offspring; likewise, E-Mega animals bear either E-Mega or H-Mega offspring. Let η_{xh} denote the proportion of H-Mega offspring that are H-Mega; η_{xe} is the proportion of E-Mega offspring that are E-Mega. Since heredity is likely to bias the distribution of offspring's evasive skills along the lines of parentage, assume $\eta_{xh} > 0.5$, $\eta_{xe} > 0.5$. The H-Mega sub-population grows according to

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there were decreasing returns to investment, then reallocations would occur more slowly. This could be detrimental to scarce species that are slow-growing and easy-to-catch.

(8) $\dot{x}_h = -d_x x_h + \eta_{xh} b_x x_h + (1 - \eta_{xe}) b_x x_e - \alpha_x x_h (x_h + x_e) / k_x - N q_{xh} \theta_x e x_h$

where d_x is the natural mortality rate, $b_x x_h$ is the birth rate, α_x is the intrinsic growth rate ($\alpha_x = b_x - d_x$), and k_x is the carrying capacity which introduces compensated, density-dependent growth into the model (accounting for other limiting factors such as habitat and food availability, other predators, etc.).   The stock grows due to births within both the H-Mega and E-Mega sub-populations; it is reduced by natural mortality, competition among population members living in a fixed habitat, and human harvests. Growth of the E-Mega stock is given by switching the h and e subscripts in equation (8). Growth of the aggregate megafauna stock, x, is

(9) $\dot{x} = \alpha_x x (1 - x / k_x) - N e \theta_x \sigma_x x$.

       We obtain the expressions for the growth of the aggregate minifauna population and sub-populations by substituting z for x in the analogous expressions for megafauna. The parameters and variables can be interpreted analogously to the megafauna. Aggregate growth of the minifauna stock is

(10) $\dot{z} = \alpha_z z (1 - z / k_z) - N \sigma_z \theta e z$.

Natural selection and co-evolution in Eurasia

Natural selection affects the average catchability for each species. We define natural selection as changes in the proportion of species j that are hard-to-catch, ρ_j ($j=z,x$). Natural selection rewards traits that increase an individual's chances of survival or fertility or both. Acting as a "filter" through which genes are passed from one generation to the next, natural selection ultimately changes the population's composition of E-Mega and H-Mega animals. We define the *rate of natural selection* of H-Mega animals within the megafauna species by $\dot{\rho}_x / \rho_x = (1 - \rho_x)(\dot{x}_h / x_h - \dot{x}_e / x_e)$. Natural selection favors H-Mega animals when $\dot{\rho}_x / \rho_x > 0$;

it favors E-Mega animals when $\dot{\rho}_x / \rho_x < 0$. The selection rate is defined analogously for minifauna: selection favors H-Mini or E-Mini animals when $\dot{\rho}_z / \rho_z > 0$ or $\dot{\rho}_z / \rho_z < 0$.

Several factors determine the rate of natural selection within a species. Consider the rate of selection of H-Mega animals within the domesticable species (the rate for minifauna is analogous)

$$(11) \quad \frac{\dot{\rho}_x}{\rho_x} = (1-\rho_x)[b\eta_h - b\eta_e + b(1-\eta_e)(\frac{1-\rho_x}{\rho_x}) - b(1-\eta_h)(\frac{\rho_x}{1-\rho_x}) + (q_{xe} - q_{xh})\theta_x Ne]$$

The relevant tradeoffs occur within the bracketed ([ ]) term on the right hand side of expression (11). The terms $b\eta_j$ ($j=h,e$) represent a sub-population's *own-fertility effects* - the direct fertility effects a sub-population has on its own sub-population. The terms $b(1-\eta_e)(1-\rho_x)/\rho_x$ and $b(1-\eta_h)\rho_x/(1-\rho_x)$ represent the sub-populations' *cross-fertility* effects - the direct fertility effects that a sub-population has on the other sub-population. Greater own-fertility by one sub-population has a positive impact on the rate of natural selection for that sub-population. The more one sub-population supplements its own kind, the greater its relative growth. In contrast, greater cross-fertility by one sub-population has a negative impact on the rate of natural selection for that sub-population.

In the absence of hunting, the fertility effects are the only factors influencing natural selection. Here the steady state value of ρ_x is unique and stable (see Appendix A). With hunting, however, an additional term arises: $(q_{xe} - q_{xh})\theta_x Ne$. This term shows that greater differences in catchability, as augmented by θ_x, favor selection of the H-Mega animals, as does greater aggregate hunting effort. Technological change could also indirectly impact selection to the extent that increases in θ_x impact meat consumption, resource scarcity, and therefore the

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human population N. Because changes in ρ_x and θ_x affect changes in N, the uniqueness of a steady state value of ρ_x is now uncertain, as is the monotonicity of the path $\dot{\rho}_x / \rho_x$.

Extinction of domesticable species in Eurasia

Minifauna and megafauna have several differences. Assume minifauna (e.g., deer and hare) replenish faster than megafauna (e.g., horses and cattle), i.e., $\alpha_z \geq \alpha_x$, and are more difficult to catch, i.e., $q_{ze} \leq q_{xh}$. Megafauna tend to congregate in herds, for instance, which makes them relatively simple to detect and harvest.[10] Assume $\alpha_x / \sigma_x < \alpha_z / \sigma_z$, where the ratio of a species' intrinsic growth rate to its average catchability coefficient measures a species' average *biotechnical productivity* (see Clark 1990, p.315).

From expressions (9) and (10), an interior steady state solution ($\dot{x} = \dot{z} = 0$, with $x > 0$ and $z > 0$) only exists for points (x,z) on the line segment:

(12) $\qquad \dfrac{\alpha_x}{\theta_x \sigma_x}(1 - \dfrac{x}{k_x}) = \dfrac{\alpha_z}{\theta_z \sigma_z}(1 - \dfrac{z}{k_z}),$

where $0 < x \leq k_x$, and $0 < z \leq k_z$. Rewrite condition (12) as:

(13) $\qquad z = k_z(1 - \dfrac{\alpha_x \theta_z \sigma_z}{\alpha_z \theta_x \sigma_x}) + \dfrac{\alpha_x \theta_z \sigma_z k_z}{\alpha_z \theta_x \sigma_x k_x} x.$

The first term on the right-hand-side (RHS) of expression (13) is positive, as is the coefficient of x. Thus, z is positive for very small values of x, and is increasing in x.

For an interior equilibrium solution, the human population should also be constant ($\dot{N} = 0$ and $N > 0$); $m = S$ from equation (7), which implies

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[10] This presumption applies to domesticable megafauna such as horse, cattle, sheep etc. One of the conditions for easy domestication, as discussed by Diamond (1992, 1997) is that animals accept leadership from another animal in the group, which in this context is a human.

$$(14) \quad z = \frac{S}{\sigma_z \theta_z e} - \frac{\theta_x \sigma_x}{\theta_z \sigma_z} x .$$

While not illustrated here, the equilibrium conditions (13) and (14) could easily be plotted in a z-x phase plane. Drawing minifauna z on the vertical axis and megafauna x on the horizontal axis, condition (13) is an upward sloping line segment and condition (14) is a downward sloping line segment, both with positive intercepts.

Now define the condition to determine megafauna species survival or extinction given minifauna. An interior equilibrium exists for domesticable species survival if and only if the two line segments cross, and this only happens if the intercept in equation (14) is greater than the intercept in equation (13):

$$(15) \quad \phi = [\frac{S}{\sigma_z \theta_z e}] - [k_z (1 - \frac{\alpha_x \theta_z \sigma_z}{\alpha_z \theta_x \sigma_x})] > 0 .$$

If (15) holds ($\phi > 0$), a unique interior solution exists and may be found by solving expressions (7), (9) and (10). If the reverse inequality holds ($\phi < 0$), an interior solution does not exist and megafauna—with low average biotechnical productivity—are driven to extinction by the expanding human population, feeding mainly on minifauna.

From (15) we ascertain the impacts of evolution and technological investment on the likelihood of species survival. Consider first the impact of evolution. From condition (11), the initial impact of harvesting is to increase the natural selection of hard-to-catch members of both species, decreasing both σ_z and σ_x. But the rate of natural selection is not monotonic since increased wildlife scarcity creates fluctuations in e and N, which occurs in such predator-prey models (e.g., Brander and Taylor 1998). In either case, however, the natural selection of harder-to-catch animals within a population decreases both σ_z and σ_z. The first RHS term in (15) is increased, decreasing the likelihood of extinction. This occurs because the human population

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depends more on megafauna for food whenever minifauna catchability is decreased, other things being equal. The second RHS term in (15) depends on how changes in average catchability affect the ratio σ_z / σ_z. An increase in the ratio (i.e., minifauna become easier to catch relative to megafauna) reduces the probability of extinction; a decrease in the ratio increases the likelihood. It is unclear *a priori* whether natural selection will increase or decrease the ratio; both are possibilities. If the ratio is increased, it is unclear whether the net effect of natural selection is to increase or decrease the likelihood of extinction (i.e., whether the effect on the first or second RHS terms dominates). If minifauna experience proportionately greater natural selection than megafauna in response to increased hunting pressure, natural selection could cause a greater chance of extinction than if selection did not occur within either population.

Technological advances trigger the opposite results relative to decreased average catchability. The first RHS term in (15) decreases for increases in θ_z, which ups the likelihood of extinction. The second RHS term in (15) depends on the ratio θ_z / θ_x. An increase in this ratio decreases the likelihood of extinction because minifauna become easier to catch relative to megafauna. We expect the ratio to increase because, as megafauna become scarce due to their initial low relative average biotechnical productivity rate, hunters have incentives to invest in technologies to capture the more abundant species. The result is that the *effective* average biotechnical productivity rate of minifauna is reduced relative to that of megafauna, making extinction less likely. The ability of hunters to invest selectively in harvesting technologies could help to conserve the more vulnerable species.

Coming to North America

When humans immigrated into North America, they came with an advanced set of

hunting knowledge and technologies.[11] They again faced groups of minifauna and megafauna in the new world, and the general species classes had both familiar and new species. Habitat conditions were likely somewhat different and so was animal behavior. Their accumulated specialized knowledge could not have been transferred to this new set of species/conditions on a perfect one-to-one basis. Some strategies/technologies found effective for catching megafauna in Eurasia could have been (i) fully applicable new world megafauna, (ii) partially applicable to new world megafauna, depreciated somewhat as hunters would have to learn new strategies to deal with their new prey, (iii) applicable to both new world megafauna and minifauna (generalized skill), or (iv) not applicable to new world megafauna but instead applicable to new world minifauna (skill transfer). The same story applies to minifauna.

Denote the level of technology/knowledge when hunters left Eurasia to be θ_x^{EA} and θ_z^{EA}, so that the *accumulated* technology in Eurasia is $\theta_x^{EA} - 1$ and $\theta_z^{EA} - 1$ (recall $\theta_j(t=0)=1$, $j=x,z$). We capture the notions of *cross-species skill transfer* and *depreciation* of specialized hunting abilities according to:

$$(16) \quad \theta_j^{NA} = 1 + (\theta_j^{EA} - 1)(1 - \varepsilon_j)(1 - \delta_j) + (\theta_v^{EA} - 1)(\varepsilon_v + \varsigma_v), \qquad j=x,z$$

where θ_j^{NA} represents the efficiency index for hunting species j in North America, $\varepsilon_j \in (0,1)$ represents the proportion of skills relevant for hunting species j in Eurasia and are more relevant to species v in North America, ς_j is the proportion of accumulated knowledge for hunting

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[11] The earliest North Americans, who migrated from Eurasia across the Bering Strait, are now known as the Clovis people, named after the first important site examined near Clovis, New Mexico in 1932 (Diamond 1992). Clovis people used stone tools, and are renowned for their fluted projectile points, although some groups apparently favored fish-tailed projectiles and others bifacially trimmed points. From excavations we now know that they used fluted projectiles ranging from 1.5 to 5 inches, but also tools like bone tools, hammer stones, scrapers, and various woodworking and butchering artifacts. The diversity in tools and hunting weapons illustrates the various 'investment decisions' made by these people.

species j in Eurasia that becomes generalized in North America, and δ_j represents depreciation of remaining skills due to differences in North American and Eurasian species/habitats.

Recall that specialization in Eurasia ensured that effective catch per unit effort ($\theta_j^{EA}\sigma_j j$, for $j=x,z$) favored minifauna since it was the faster growing species, and it was this specialization that could have helped both species groups to survive in Eurasia. The key implication of equation (16) is that this minifauna bias may have been diminished upon arrival in North America, due to the depreciation/redistribution of skills (because humans would be hunting a different mix of species in different habitats in North America) or the initial relative abundance of megafauna or both.[12] If these effects resulted in effective catch per unit effort favoring megafauna in America, then humans would have had incentives to invest in megafauna technologies in those early years on the new continent. This could have led to greater cumulative megafauna investments in North America than in Eurasia, increasing the risk of American megafauna extinction. We now turn to a numerical analysis to explore the implications.

Numerical Analysis

For our numerical analysis, suppose hunting begins in a pristine ecosystem with humans possessing no specialized hunting technologies or knowledge (i.e., $\theta_x = \theta_z = 1$), like that which might have occurred in Eurasia when hominids first arrived. Co-evolution of species and investments occurs over the next several millennia until an equilibrium is reached, although reaching an equilibrium in Eurasia is not required. Next, the advanced hunters move to another pristine ecosystem, North America. Appendix B provides the model calibration details.

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[12] Humans had depleted megafauna to low levels of abundance in Eurasia. In contrast, megafauna were somewhat abundant in North America when humans first arrived (Diamond 1992).

Table 1 reports the simulation results for eight scenarios. Scenario 1 assumes there is no evolution among hunters or their wildlife prey: neither in Eurasia nor in America. Wildlife natural selection does not occur. In a pristine setting, 50 percent of each species would be hard-to-catch and 50 percent would be easy-to-catch. This ratio is maintained throughout this scenario, in effect turning off the natural selection process. Human hunting technologies do not evolve while humans are in Eurasia because there is no investment. Accordingly, hunters entering North America are identical to those that initially entered Eurasia, and the species being hunted are identical on each continent. The results for Eurasian and North American species are identical: extinction of megafauna within 447 years.

Natural selection (but not investments) is allowed in Scenario 2. Again, an identical group of hunters enters both Eurasia and later North America, with wildlife on each continent initially being hunted in an identical, pristine state. Comparing scenarios 1 and 2 highlights the effects of natural selection—when selection is possible, extinction takes another century on both continents. This result occurs because natural selection decreases average catchability of megafauna by more than minifauna: 76 percent of megafauna are hard-to-catch compared while only 67 percent of minifauna fit this category, as compared to an even split in scenario 1. But by itself, natural selection does not prevent extinction of megafauna, either in Eurasia or in North America. That species quickly adapt and lose their naivety is consistent with evidence that wildlife quickly adapts to new predators (see Brook and Bowman 2002). Our extinction result can be interpreted to contradict Brook and Bowman's (2002) single species model results.[13] The results differ across models because we account for the availability of a substitute resource (minifauna) that can sustain a growing population as the minifauna are hunted to extinction, and

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[13] Considering megafauna extinction in Australia, Brook and Bowman find a positive probability of extinction over a range of prey naivety indices, although the overall probability declines as prey grow less naïve. It is unclear how

it is the *relative* impact of natural selection on the naivety of the two species that matters. We find natural selection does not sufficiently reduce megafauna naivety relative to minifauna; both species become less naïve, but the average biotechnical productivity of minifauna is still sufficiently greater than that of megafauna.

The next scenarios (3-8) illustrate the case of co-evolution, in which humans respond to the relative scarcity of wildlife by investing in hunting technologies/knowledge. Here we find that megafauna always survive in Eurasia—human investments made in response to the relative species scarcity prevent megafauna extinction. Before the final Eurasian horse or cow has been killed, humans have switched their focus to an alternative prey base. For North America, however, the result critically depends on how the investments in technology/knowledge transfer to the North American ecosystem.

Scenario 3 represents a baseline case in which investments in technology/knowledge occur in combination with natural selection of the species, and skills transfer from Eurasia to North America on a one-to-one basis. We find extinction does not occur on either continent: species-scarcity-induced investments transfer hunting pressure from megafauna to minifauna. Natural selection within the megafauna population is reduced, but is increased among minifauna. A key result is the outcomes in Eurasia and North America are identical even though humans arrived in North America with an advanced set of hunting skills and tools. Eurasian co-evolution saves the new world megafauna, even though the technology evolved separately from the North American species. This contrasts with the hypothesis that co-evolution in Eurasia is responsible for North American extinctions. Rather, co-evolution in Eurasia enables humans to conserve the North American megafauna when it reaches low levels of abundance - even with no additional

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naïve the prey in our model are relative to their index, so their model might also predict extinction. But we contend that relative naivety, not absolute naivety, matters. Their focus on a single prey represents an important restriction.

investment in North America. The key to this result, as we show next, is that all of the technological/knowledge developments are *perfectly* transferable to North America.

Scenario 4 illustrates the effects when minifauna-specific technology/knowledge depreciates across continents. All the accumulated knowledge for hunting minifauna is useless (i.e., fully depreciated) on arrival in North America, whereas all the accumulated knowledge for hunting megafauna remains intact. While this should bias hunting pressure towards megafauna, particularly since they are initially plentiful in North America, it does not take long before investments in minifauna technologies become profitable. These investments ease the pressure on megafauna, and survival of both species is the result. Depreciation of knowledge/technology has little effect.

The final four scenarios (5-8) illustrate how megafauna can go extinct in North America with some cross-species knowledge transfers or when some knowledge generalizes for both species. Under Scenario 5, 30 percent of the knowledge gained in hunting one species in Europe applies to hunting the other species in North America. Now North American megafauna go extinct. A smaller cross-species knowledge transfer also results in extinction, although the time interval is large (e.g., > 3,000 years when ε=0.1). The cross-species knowledge transfer in this case goes in both directions: 30 percent of the accumulated knowledge for hunting European minifauna (megafauna) is more applicable to North American megafauna (minifauna). While unreported in Table 1, we find extinction occurs in less than half the time (1098 years) if the knowledge transfer only goes in one direction, reducing hunting efficiency for megafauna and increasing minifauna hunting efficiency.

Scenario 6 shows that when 25 percent of the knowledge acquired in Eurasia generalizes to North America, megafauna again go extinct. Less generalizable knowledge also results in

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extinction, although it takes longer; the extinction interval would be shorter if megafauna knowledge was more generalizable in the new world than was minifauna knowledge.

Finally, scenarios 7 and 8 illustrate that the extinction time intervals are much shorter when knowledge is both transferable and generalizable. Comparing scenarios 7 & 8 with 5 & 6 shows that generalizable knowledge matters more to megafauna extinction than transferability—changes in generalizable knowledge have a greater marginal impact on extinction intervals. We also ran simulations with various levels of depreciation and found no effect.

Conclusion and Discussion

Some theories suggest the European conquest of America and its ensuing consequences can be traced back to humble beginnings—Eurasians were the first to domesticate megafauna and this event eventually translated into the world order we now know. This begs the question why domestication started there and not elsewhere. It has been postulated that Eurasians had a larger set of animal to choose from as suitable megafauna candidates on other continents as America and Australia suffered from major collapse shortly after the first humans entered the local scene. This collapse, supposedly, did not happen in Europe because the 'prey base' was not naive and unsuspecting. Instead, it was trained by many thousands of years of predation by Neanderthals and early modern humans.

In a recent paper, Brook and Bowman challenge this view. They argue that megafauna extinction in the Americas and Australia may not have been the inevitable outcome of an encounter between smart hunters and naive prey. Evidence exists to suggest that prey species are able to learn and adapt quickly, casting doubts on the overkill hypothesis. But the capacity of prey to adapt is only half the story. We explore herein the story's logical complement—hunter's behavior. Now what matters is explaining the interaction between evasive animals and humans

investing in ever-superior hunting techniques.

One can view our numerical results in two ways. One take is that extinction occurs because Eurasian co-evolution was not completely compatible with the North American ecosystem. Another view is that neither the Eurasian nor the North American ecosystems would have survived in tact if it were not for co-evolution. Co-evolution saved Eurasian species from certain extinction. In North America, co-evolution prolongs extinction relative to the case in which co-evolution does not occur (scenarios 1 and 2). But regardless of your perspective, it is apparent that human investments may have mattered as much as, if not more, than selection and evolution on the prey side.[14] Economics matters, both in Eurasia and the new world, and the interaction with the ecological system may trigger unexpected outcomes.

We appreciate that mathematical models might never tell us the answer to the question of why domesticable wildlife went extinct in the Americas but not in Eurasia. These events happened long ago and no current method exists to validate these sorts of models (Brook and Bowman 2002). But these models can provide insight into what may have happened, and hopefully they can spur further research, both theoretical and applied, into the issues that seem to matter. If researchers can at least identify what may matter, science has more direction to look for the clues that could eventually help to validate or reject alterative theories.

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[14] One could contend that natural selection in our model is limited by our specification and parameter choices, and that cross-continental natural selection differences over the course of hundreds of thousands of years prior to human arrival in North America would have resulted in much larger catchability coefficients for all North American species. We could exogenously increase all North America catchability coefficients to account for larger-scale differences between North American and Eurasian catchability. The result, however, depends on how *relative* catchability is changed. For instance, in our baseline scenario 3 with perfect knowledge transfer, all North American catchability coefficients could be uniformly increased by up to 75 percent and the results would be unchanged: megafauna extinction would still result.

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Appendix A

This Appendix shows the existence of a unique and stable value of ρ_x in the absence of hunting. An analogous discussion holds for ρ_z. From (11), an equilibrium (steady state) for ρ_x occurs when either $\rho_x = 1$ or when the following condition holds

(A1) $b[\eta_h - \eta_e] - b[(1-\eta_h)(\frac{\rho_x}{1-\rho_x}) - (1-\eta_e)(\frac{1-\rho_x}{\rho_x})] = 0$

Since $\rho_x = 1$ is impossible when $\eta_{xj} < 1$ (*j=h,e*), an equilibrium can only occur when condition (A1) is satisfied. Denote the first term on the left-hand-side (LHS) of (A1) by χ. Denote the second term by $\xi(\rho_x)$, which is strictly increasing in ρ_x. Note that $\xi(1) > \chi$, and $\xi(0) < \chi$. By the intermediate value theorem, there exists a unique value $\rho_x^* \in (0,1)$ such that $\xi(\rho_x^*) = \chi$: a unique steady state exists. The sign of $\dot{\rho}_x / \rho_x$ depends on the sign of the LHS of (A1). Because $\xi(\rho_x)$ is monotonically increasing in ρ_x, we have $\dot{\rho}_x / \rho_x > 0$ when $\rho_x < \rho_x^*$, and $\dot{\rho}_x / \rho_x < 0$ when $\rho_N > \rho_N^*$: the unique equilibrium is stable. Finally, $\rho_x^* = 0.5$ when $\eta_h = \eta_e$.

Appendix B – Parameters for the simulation models.

We selected parameter values to be realistic, but obviously we are limited by the fact that no good data exists from 12,000 years ago to calibrate a model. We calibrate our model keeping one stylized fact in mind: megafauna went extinct in North America, but did not in Eurasia.

Modeling wildlife: According to Pratt and Gwynne (1977) and Prins et al. (2000), a reasonable assumption for the carrying capacity for herbivores is approximately 4 ha/AU, or 64 AU per square mile (1 AU [animal unit] measures 1,000 pounds of living animal). Assume early human hunters consider 30 percent of biomass as "prey", and half of this biomass is megafauna (e.g., horses and cows) and the other half is minifauna (e.g., deer). Given the available range in the late Pleistocene, this translates into k_j=30 AU (*i=x,z*). Mosimann and Martin assume the available range for herbivores in North America in the late Pleistocene was 3 million square miles; the rest of the land surface was unsuitable, possibly covered with ice sheets. Although

Eurasia is bigger, we assume k_j=30 AU in Eurasia; numerical simulations indicate this choice has a small impact on the results. Assume the intrinsic growth rate of megafauna is 25% (Mosimann and Martin), with $d_x = 0.05$. Finally, assume $\eta_{jv} = 0.8$ ($j=x,z, v=e,h$).

Modeling human population and behavior: Assume an initial population of 100 households. Following Whittington and Dyke (1984, p.454) who present "parameters based upon empirical evidence generally acceptable to archeologists and human ecologists," we assume $r = 0.0443$. Assume a prehistoric working day for the representative household (man, woman and two kids) has about 20 hours per day (7300 hours per year), and that meat is the predominant source of food so that β=0.8. Finally, Dasgupta (1993) estimates that active humans should consume 2000 calories (0.73 AU) per day to sustain themselves, and for a household of four we compute that S=2.9 AU per year.

Modeling harvesting of megafauna and investments: Bulte et al. (2003) adopt a value of $q = 8.3\times10^{-11}$ for minifauna and megafauna harvesting, which assumes each species is of uniform naivety. For non-uniform naivety, we assume $q_{zh} = 8.3\times10^{-11}$, and that more naïve minifauna are 60 percent easier to catch $q_{zh} = 0.6q_{ze}$. The analogous catchability coefficients for megaufauna are 20 percent larger—$q_{xh} = 1.2q_{zh}$ and $q_{xe} = 1.2q_{ze}$. Finally, the investment parameter is set at $\mu_z = \mu_x = 4.57\times10^{-4}$, which is equal to 2/β$l$.

Table 1.

Scenario	Eurasia Simulation			North America Simulation				
	Time (in years) to extinction of domesticable species (if extinction occurs)	ρ_x in equilibrium (prior to extinction)	ρ_z in equilibrium	Time (in years) to extinction of domesticable species (if extinction occurs)	Initial level of technology θ_x	Initial level of technology θ_z	ρ_x in equilibrium (prior to extinction)	ρ_z in equilibrium
1. No natural selection, no investment	447	0.5	0.5	447	0	0	1	1
2. Natural selection, no investment	588	0.76	0.67	588	0	0	1	1
3.-8. Natural selection and investment								
3. δ=0, ε=0, ς = 0	----	0.73	0.71	----	1.17	1.70	0.73	0.71
4. δ_z=1, ε=0, ς=0	----	0.73	0.71	----	1.17	1.0	0.73	0.71
5. δ=0, ε=0.3, ς=0	----	0.73	0.71	2349	1.33	1.54	0.74	0.71
6. δ=0, ε=0, ς =0.25	----	0.73	0.71	1706	1.34	1.74	0.74	0.71
7. δ=0, ε=0.3, ς=0.1	----	0.73	0.71	935	1.4	1.56	0.74	0.71
8. δ=0, ε=0.1, ς=0.25	----	0.73	0.71	946	1.39	1.69	0.74	0.71

Note: Parameters without subscripts means that the same value is applied to both species.